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Radiation and the Patterns of Nature

Sensitivity of natural plant populations to ionizing radiation seems to follow known ecological patterns.

George M. Woodwell

The partial answers we have to the question of what radiation does *in* and *to* nature are revealing not only of the effects of radiation on living systems, but also of the architecture of the systems themselves. My object is to show the patterns of the effects of radiation on natural communities, and how the patterns parallel and help to explain the normal patterns of structure, function, and development of these communities. It is important in this discussion to remember that most life as we know it has evolved in environments in which total exposures to ionizing radiation have amounted to less than a few tenths of 1 roentgen per annum, and that ionizing radiation is generally thought to have played a very minor role among the selective processes of evolution. It is somewhat surprising therefore that the effects of radiation on natural communities follow predictable patterns apparently related to the evolution of life.

The significance of natural communities to biology and to man is not immediately apparent. For my purposes it is important to recognize that all organisms have evolved as functional units in communities of organisms, and that the structure and function of these communities have determined in some measure the structure and function of the organisms themselves. So we can think of Darwin's struggle for existence as operative in the evolution of not only species but also groups of species and whole communities. This is not a new concept; it was set down by Darwin in his *Origin of Species*, published in 1859.

The evolutionary implications of Darwin's struggle for existence at the community level are shown most clearly by a simple example, which is based rather freely on Darwin's own studies in the Galápagos Islands. Let us assume a small group of islands in the tropics, volcanic, and therefore young in a geologic sense, but supporting the limited flora and fauna that have arrived from the mainland some 1000 kilometers away. The climate is diversified, ranging from desert to moist forest. The islands have trees, grasses, and shrubs, but no mammals and few birds.

Over the years, probably hundreds of years, chance, possibly in the form of westering storms, brought small flocks of birds. From among these flocks at various times some finches survived and found a favorable habitat, rich in a diversity of foods and free of both mammalian and avian predators; reproducing rapidly, each new immigrant population became a plague, much as the Japanese beetle, the sparrow, the starling, the gypsy moth, and a host of other introductions have become plagues in our own experience. Food, although at first abundant, quickly became limiting, and the struggle for existence intensified. Competition for food was fierce and a premium attached to any ability to exploit new food supplies—foods different from those exploited by competitors. Small differences in behavior or in size or shape of beak resulted in small differences in survival and in ability to rear young. These differences, when hereditary and useful, were passed on and amplified in the population, and on each island there developed a population of finches peculiarly adapted to that environment and different from populations on other islands.

There was one additional complication. Exchanges of individuals or small groups of individuals occurred occasionally among the islands, continually testing the degree of genetic isolation achieved by the evolution of different races. Frequently these transported populations failed on the new island or were absorbed into the now-indigenous population; occasionally, however, a small one found itself partially isolated ecologically, by behavior, food supply, or local preference of habitat, from the indigenous population and survived as a distinct population, competition and evolution tending to accentuate the isolating mechanisms. Thus the islands gradually acquired a diverse bird fauna consisting largely of races of finches: ground finches, tree finches, a warbler finch, a woodpecker finch—each race using a set of resources used elsewhere in the world by a totally different species. Ecologists call the resources used by any one species a niche; where niches overlap and resources are shared, they say that competition occurs.

We see from this example, which is a grossly simplified version of *Darwin's Finches* (*1*), that the evolution of life proceeds toward reduction of competition, toward utilization of space and other resources, toward diversity in form and function, toward the filling of niches. We see, moreover, that the evolution of a race is affected not only by its physical environment, but also by the evolution of other races whose evolutions are in turn affected. Thus the chain of cause and effect here becomes entangled in bewildering ways. The product is a complex and, in

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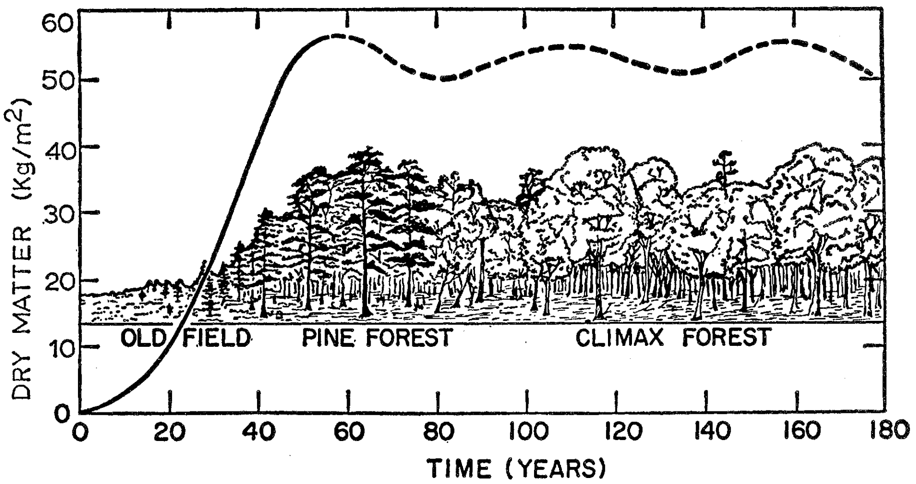


Fig. 1. Field-to-forest succession in the eastern United States. The oscillations of climax are assumed.

some degree, mutable array of plants and animals which, itself, has clear and predictable patterns of structure, function, and development; these are "natural communities." Thus physical environments that are similar tend to support organisms that are similar in form and function, if not in species. So certain climates support forests the world over; others, grasslands; others, desert; and these words—forest, grassland, desert, and tundra—have meaning for us in terms of climate and flora and fauna.

Thus, where environments are similar, we find organisms that may have little or no common genetic past performing parallel functions. In Australia the marsupials, for instance, fill the grazing niches filled by placental mammals elsewhere; and the genus *Eucalyptus* has filled the tree niches occupied elsewhere by a score of other genera. The communities in which these organisms participate are one answer, tested through millions of years of evolution, to the very fundamental question: How can the resources of environment be used to perpetuate life? This is, of course, a fundamental objective of man: the use of environment to best advantage.

The evolutionary answer is a magnificently durable one and, in terrestrial communities, usually a surprisingly stable one, free of plagues or rapid changes in sizes of population. By this I mean that controls of population size have evolved, building stability into these complex biological systems—putting the "balance" into nature.

Now let us consider for a moment certain other characteristics of natural communities. It is clear that the communities have developed over long periods and are very much a product of the evolution of life; and that they vary in a spatial sense with geography, climate, topography, and a host of other environmental factors. They also vary with time.

To show the variation with time, let us assume for a moment that after we harvest our corn crop in the eastern United States we simply abandon the land. The weeds of the garden take over; crabgrass, at first; later, grasses; then, pine forest; and finally, after 100 years or so, an oak forest. The general pattern is familiar; environmental circumstance may modify details. The change from herbaceous weed field to forest involves not only changes in the species forming the communities, but also changes in the total weight of living matter on a unit of land, in the total amount of essential nutrients available, in the total amount of water used, in the total number of niches available, and probably in the rates of biologic evolution itself. This process—succession—becomes one of the great central principles of biology.

We can examine one succession, from abandoned field to forest, most easily by considering stored energy in plants over time. By plotting such data (my own, and those produced by workers elsewhere in eastern North America) we obtain an S-shaped curve similar to the growth curve of a single organism (Fig. 1). It rises slowly during the early herbaceous stages, rises much more rapidly during the pine-forest stage, and levels during the deciduous-forest stage as the degree of stability increases. Along this curve several very fundamental changes occur in community structure and function. There is, of course, a shift in species from herbaceous plants to trees. But there is also thought to be increase in diversity—total numbers of species present—from the few of the abandoned field to the many of the ultimate forest. There is change in degree of stability from the field, with its patches of ragweed and crabgrass which may be rapidly replaced by any of several species, to the forest with its spatial uniformity and slow replacement. There is increase in the total pool of minerals within the system: small amounts held within the herbaceous communities, large amounts in the forest. Total respiration and total photosynthesis increase, but at different rates, producing a regular change with time in the ratio of photosynthesis to respiration during the course of succession. We assume in addition that

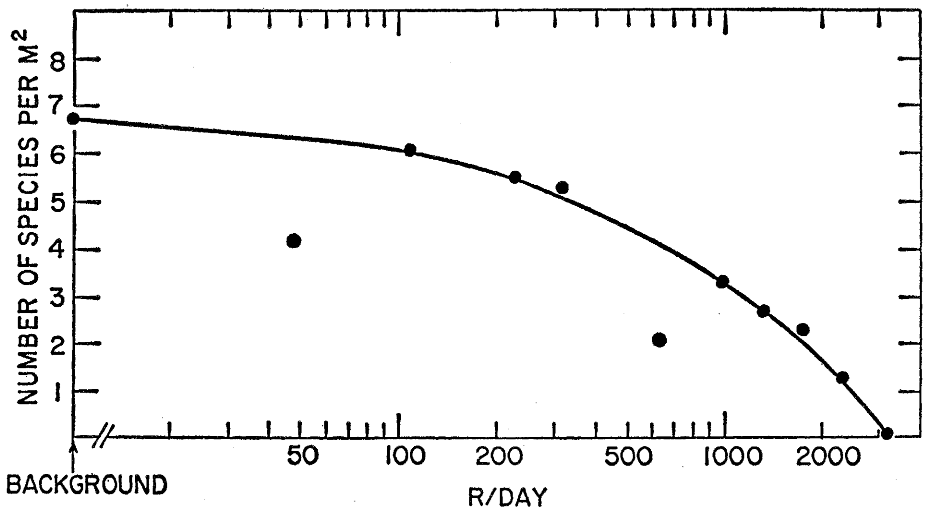


Fig. 2. Diversity in the 1st-year-old field.

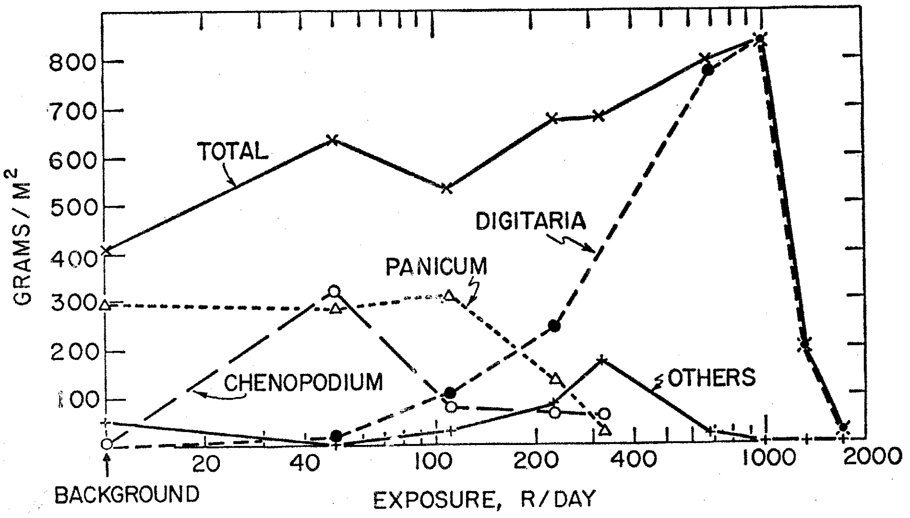


Fig. 3. Total dry weight of plants, by species, in the irradiated old field. Dry weights were measured at the end of the season and do not represent total production.

the total amount of water used increases along this succession (*2*).

If, in the course of such a succession, one or more factors essential to the system become exhausted or available only in short supply, the rate of succession is slowed and the climax is diverted, possibly by as much as from forest to grassland. Thus, in areas of low rainfall, succession ends in a stable grassland or woodland; where little mineral nutrient is available, whatever the reason, the succession is slowed and the S-shaped curve levels.

If, on the other hand, the environment is changed drastically by erosion or by sudden change in climate, or catastrophically by fire or windstorm or even by fallout from a bomb, then the changes that occur in these arrays tend to be just the reverse of those occurring during a normal succession: the communities are simplified, niches are opened, the nutrient inventory accumulated during succession is lost at least partially, the community becomes less stable, and a new succession begins, possibly marked by large fluctuations in populations that reproduce rapidly (such as insects) and can exploit the open niches.

Succession, then, is such a fundamental part of biology that it forms the logical core for appraisal of the effects of any change in environment, most especially a change that has such far-reaching and basic implications for life as ionizing radiation.

At first glance the problems in appraisal of the effects of ionizing radiation on the communities along a successional gradient seem so complex as to be impossible. But we can borrow a trick from the mathematicians and examine the effects on the extremes: we can use a gradient of exposures from very high to very low and examine the early stages of succession, which, in eastern North America, are abandoned fields, and the later stages, which are forests. The question we ask is, in each of these stages: What are the effects of irradiation on the community? In the forest, for instance, we need to know what exposure to radiation changes the composition of the plant community. When the composition does change, how does it change? Do species behave individually, or are there groups of species having similar characteristics? After what exposures do we expect insect populations to change? Do we affect metabolism, use of water? How do we affect them? Are there any patterns of radiosensitivity that may be useful for prediction of effects of radiation or for interpretation of the structure and function of unirradiated communities? The overriding question is: What are the patterns of radiation effects on the structure, function, and development of natural communities? This was the question posed in 1961 when the work at Brookhaven, which I shall discuss, was started.

We had then considerable information on radiation effects on many species of plants (*3*). It was known that the amount of damage caused by any exposure was related to the size and number of chromosomes in the cell nucleus (*4*). Sparrow had observed that certain species of pine trees are killed by exposures in the same general range as those killing man. Other data had shown a very great range, more than 1000-fold, in the sensitivity of plants to damage by radiation (*5*). The sensitivity of pines had been confirmed (*6*), and it had been shown that forests are generally more sensitive than had been known (*7*). Field observations, how-

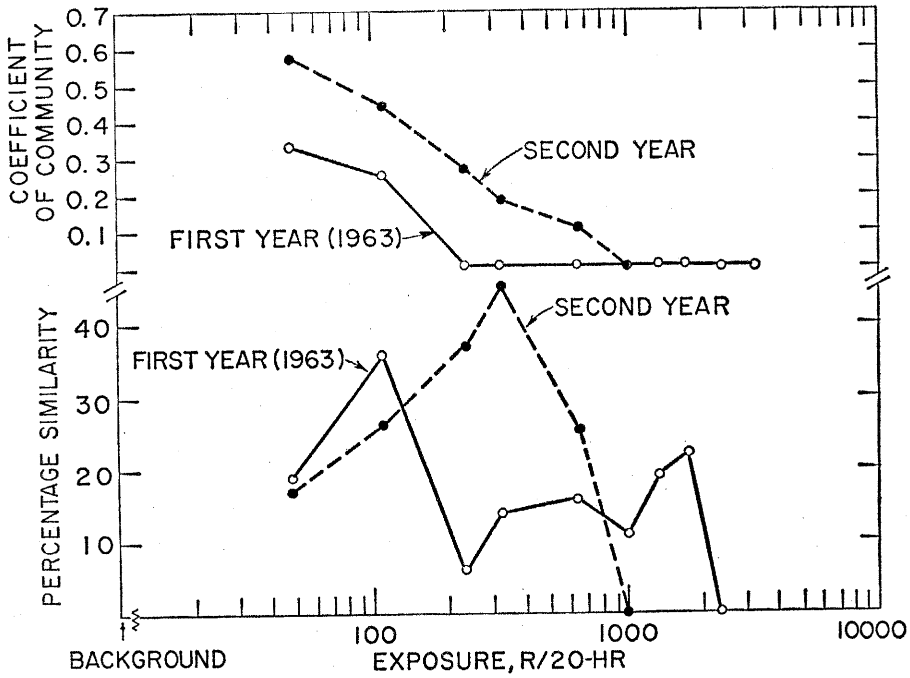
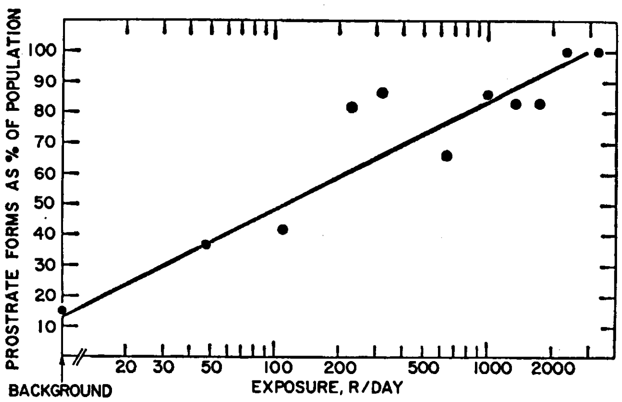


Fig. 4. Coefficient of community, and percentage similarity for irradiated communities compared with the control community (2 kilometers distant). The linear relation between coefficient of community and the logarithm of exposure rate shows that species composition, alone, independent of density, is a useful criterion of the severity of disturbance by radiation.



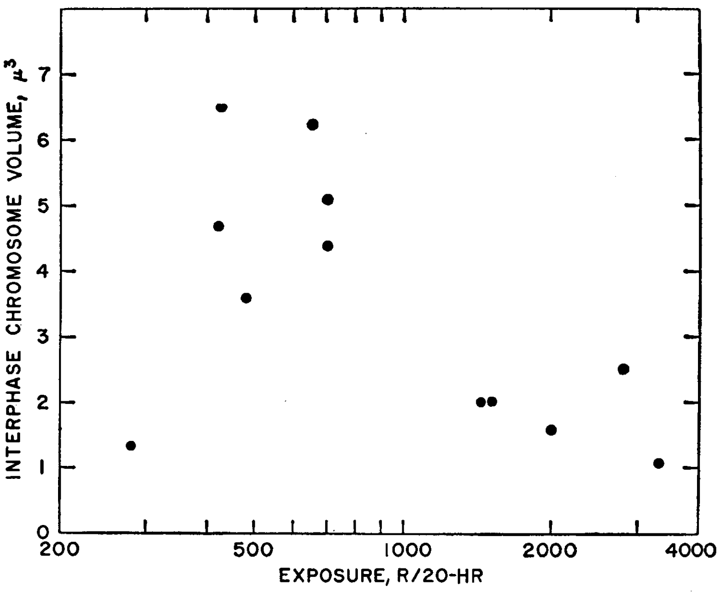


Fig. 5 (above). Life-forms in an irradiated field (1963, 1st year); "prostrate" forms include forms labeled normally prostrate, decumbent, or geniculate by Fernald (*13*). Fig. 6 (right). Average interphase chromosome volumes of 12 species of plants, showing maximum exposure at which any individual lived [from Wagner (*25*)].

ever, were most limited, and there was good reason to explore the problem experimentally and in detail.

Our approach entailed the establishment of two experiments, in each of which we used a single large source of γ-radiation (equivalent to about 9500 curies of Cs^{137}), arranged in such a way that it could be lowered into a shield (for safe approach) or suspended several meters above ground to provide radiation over a large area. The sources were large enough to administer several thousand roentgens per day within a few meters, the dose approaching background levels beyond 300 meters. The two experiments were conducted in an irradiated old field in the now-well-known γ-radiation field established in 1949 (*8*), and in an irradiated forest —a completely new installation (*9, 10*); thus they gave us a sample from each end of the successional curve that I have discussed.

A section of the γ-radiation field was abandoned in the fall, after harvest, and the herbaceous communities common to abandoned gardens were allowed to develop. On Long Island about 40 herbaceous species participate in colonizing land prepared in this way; one of the most conspicuous is pigweed (*Chenopodium album*) because of its height (up to 1 meter) and abundance. During the 2nd year, horseweed (*Erigeron canadensis*) is the most conspicuous and one of the most abundant. In subsequent years, grasses such as broom sedge (*Andropogon* spp.) and asters (*Aster ericoides*) become dominants, to be followed by pine, and oak-hickory forest (*11, 12*).

Irradiation produced striking changes in the communities of the early stages of the succession. Although we have studied several of these communities over five summers at Brookhaven, I shall discuss here only the 1st-year communities. The most conspicuous change was drastic simplification at high exposures. We can measure simplification as a reduction in numbers of species per unit area, or in "diversity." Figure 2 is a plot of diversity along the radiation gradient. Irradiation at 1000 roentgens per day reduced diversity to about 50 percent of that of the unirradiated community, another field 2 kilometers distant. This decrease was continuous along the radiation gradient and was not marked by any abrupt decline indicating exclusion of several species in a narrow range of rates of exposure. Certain species survived daily exposures that exceeded 2000 roentgens.

The pattern of distribution of standing crop, or total weight of plants, at the end of the growing season,

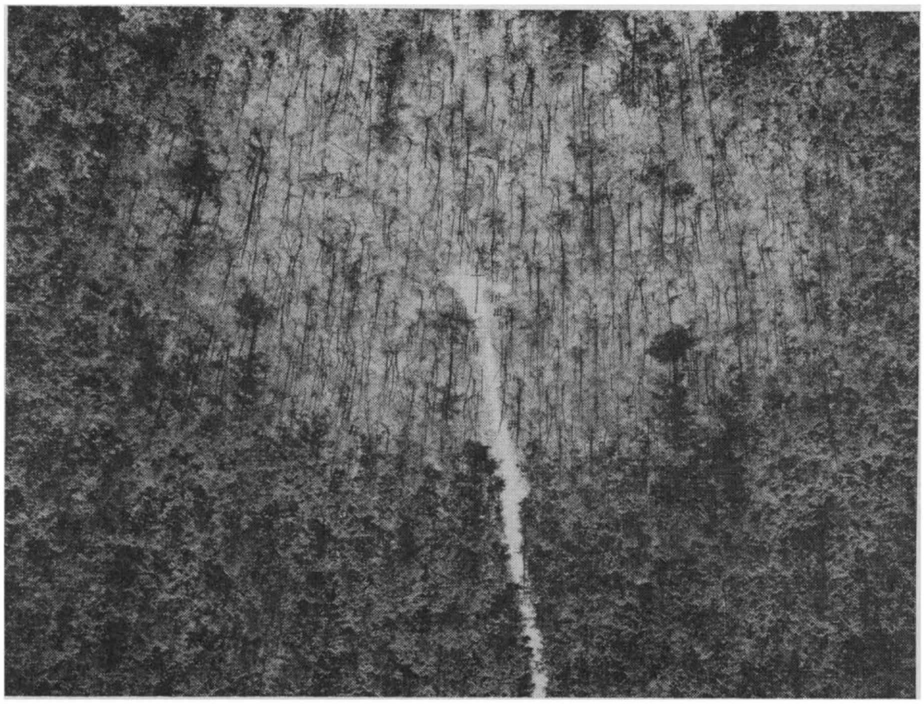
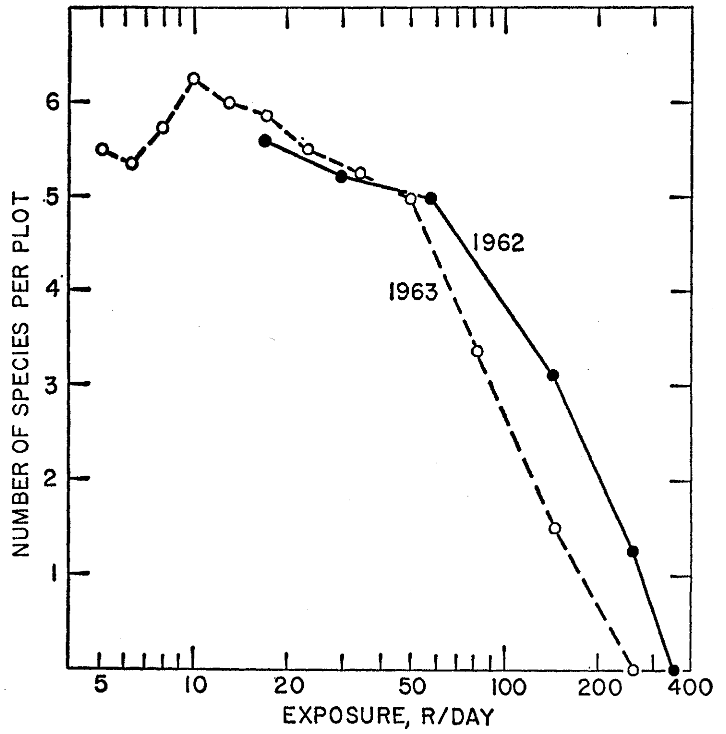


Fig. 7. Effects of 6-month exposure to gamma radiation ranging in intensity from several thousand roentgens per day near the center of the circle to about 60 roentgens at the perimeter of the defoliated area. The experiment is part of a study at Brookhaven National Laboratory of the effects of chronic exposure to ionizing radiation.



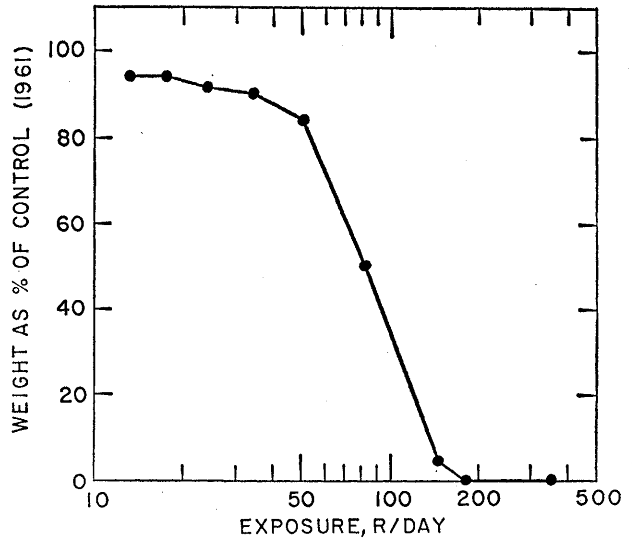


Fig. 8 (left). Species diversity along the radiation gradient in the irradiated forest in 1962 and 1963. Measurement of diversity in a forest requires differently sized samples for differently sized plants; thus the unit of diversity here is "species per plot" [from Woodwell and Rebuck (*15*)]. Fig. 9 (above). Total weight of above-ground shoots in irradiated forest in 1962.

was strikingly different (Fig. 3). Total standing crop along the radiation gradient ranged between about 400 grams per square meter in the control community and 800 grams at 1000 roentgens per day, with a consistent increase with increase in exposure between these extremes. While the significance of this increase is not entirely clear, it is plain that, at exposures exceeding 1000 roentgens per day, total standing crop dropped abruptly to a few grams per square meter and, although some species survived even higher exposures, production of plant mass was very low indeed. There is clear evidence that at intermediate exposures exclusion of one species freed resources for others, crabgrass being by far the most benefited; at exposures exceeding 200 roentgens per day it was the major contributor to the total standing crop. Thus these old-field communities appear to be plastic, maintaining and possibly even increasing the total amount of energy fixed, despite a reduction in diversity of up to 50 percent. It also appears that diversity of species is more sensitive to radiation effects than is organic production. This relation is borne out by a brief consideration of coefficient of community, and percentage similarity.

The coefficient of community is simply the total number of species common to two communities, expressed as a percentage of the total number of species in both communities; Fig. 4 shows an approximately linear relation between the coefficients of community along the radiation gradient, calculated for the control community, and the logarithm of radiation-exposure rate (*11*). There appears to be no threshold for effects on composition by species at exposures as low as 50 roentgens per day. If we weight the coefficient of community with a measure of abundance of each species, we can calculate what is called percentage similarity, and Fig. 4 shows that there is no simple relation between these figures and radiation exposure, an observation that seems to confirm the earlier observation that the relative abundance of any species, however measured, is primarily controlled by competition with other species. Thus diversity and coefficient of community (and probably any other index of species diversity) emerge as relatively sensitive measures of radiation damage—and probably of any type of environmental change; abundance, density, and standing crop are insensitive.

Let us examine somewhat more closely the characteristics of plants that survive high rates of exposure. Two characteristics seem particularly signifi-

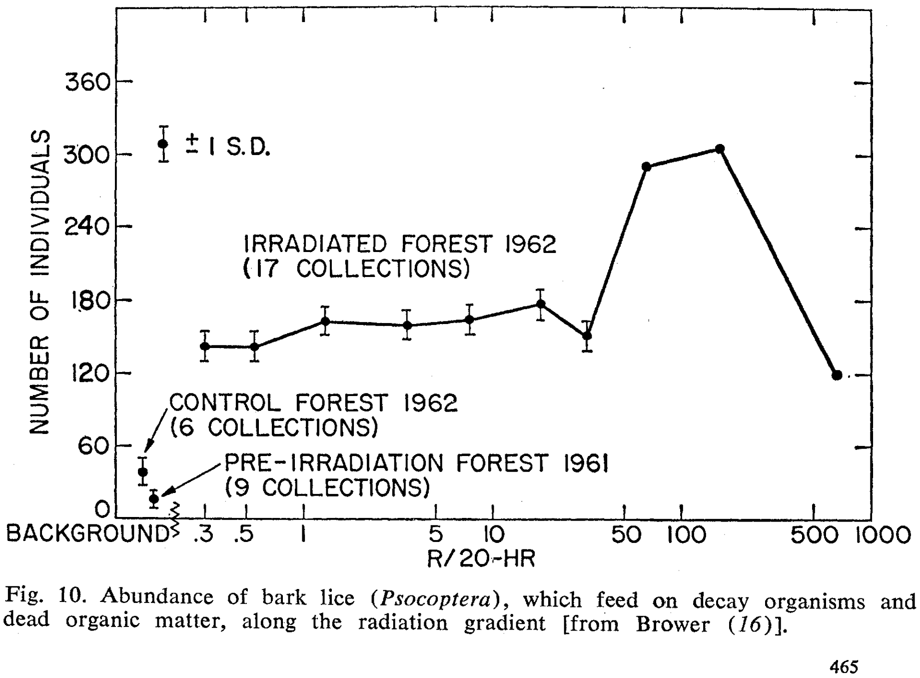


Fig. 10. Abundance of bark lice (*Psocoptera*), which feed on decay organisms and dead organic matter, along the radiation gradient [from Brower (*16*)].

cant: first, at high exposures the incidence of species that normally grow close to the ground [prostrate, decumbent, or depressed (*13*)] is substantially higher than in unirradiated communities (Fig. 5); second, there appears to be sorting on the basis of chromosome size, plants with large chromosomes being excluded from the areas receiving high exposures (Fig. 6). While it is difficult to venture a reason for apparent correlation between small size of chromosomes and a prostrate or decumbent growth habit among plants of old-field communities, these observations suggest that such a pattern may exist.

Thus the first year of succession is characterized by a loose array of herbaceous plants, most of them annuals or biennials, of varying life-forms and physiologies. Diversity in form and function allows rapid colonization of a wide variety of disturbed areas, and contributes toward making the community as a whole resilient in the face of disaster—such as a gardener's hoe or a gradient of ionizing radiation. The primary effect of stresses, including irradiation, is reduction of diversity. In the case of radiation, the reduction is continuous along the radiation gradient and not characterized by simultaneous exclusion of two or more closely associated species, an observation testifying to the looseness of the community organization. Although it is true that the plasticity of the community as a whole makes it resistant to radiation damage, it is certainly not true that all species in the community are equally resistant. Daily irradiation at 50 or more roentgens produced continuous sorting of species according to life-form and according to the average volumes of their chromosomes.

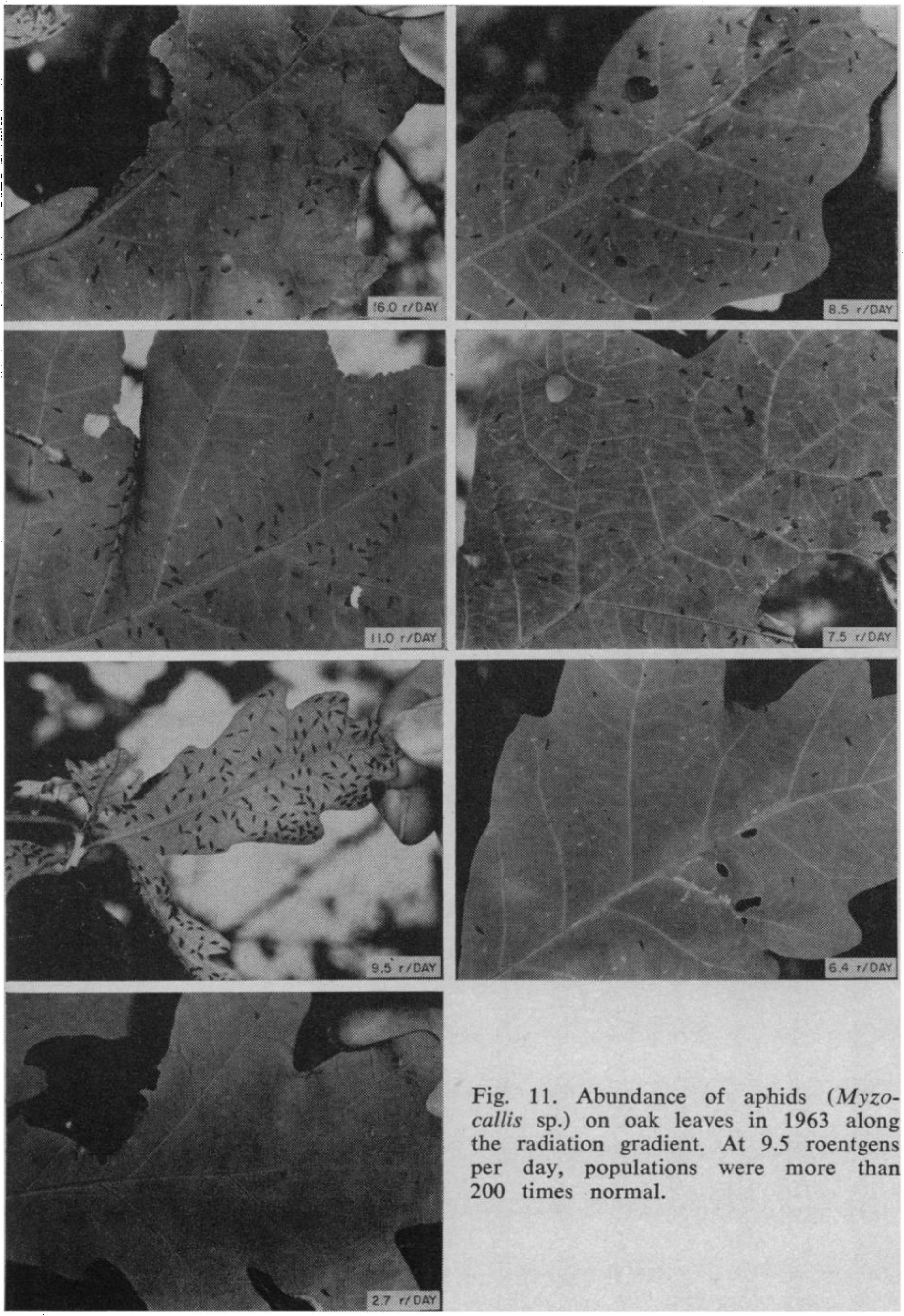


Fig. 11. Abundance of aphids (*Myzocallis* sp.) on oak leaves in 1963 along the radiation gradient. At 9.5 roentgens per day, populations were more than 200 times normal.

Irradiation of the forest commenced in November 1961 after a detailed series of preirradiation studies. The approach was to make a case-history study of one relatively complex ecological system by examining as many aspects as possible of its structure and function, both normal and pathological (*10*). Six months after installation of the source the forest appeared as in Fig. 7; my data, with few exceptions, apply to the forest as it was in the summer of 1962, after approximately the same period of exposure as the old field.

Five zones were apparent along the radiation gradient: a central zone in which no higher plants survived; a sedge zone containing *Carex pensylvanica* and a few sprouts of the heath-shrub layer; a shrub zone where the two blueberries and huckleberry survived; an oak-forest zone at daily exposures less than about 40 roentgens; and the oak-pine forest in which radiation effects on growth were apparent, without change in species composition (*14*).

The zoning of vegetation reflected the decline in diversity along the gradient (Fig. 8). If the normal "plot" in this forest be accepted as having 5.5 species, then 50-percent diversity occurred at 160 roentgens per day, or less than one-fifth the exposure to reduce diversity by 50 percent in the herbaceous community. Shielding by the stems of large trees in the forest allowed survival by species at average exposures substantially greater than the normally lethal exposures. Therefore the differential is probably even greater, and the forest may have its diversity depressed by 50 percent at exposures as low as one-tenth of those required in the herb field (*15*).

Unlike the old field, standing crop in the forest declined at approximately the same rate as diversity (Fig. 9). This relation between diversity and abundance measured by standing crop is, of course, to be expected, since there is no possibility of a population of oak trees, 9 meters in height, expanding within a year to fill a niche vacated by pine. Nor was there invasion

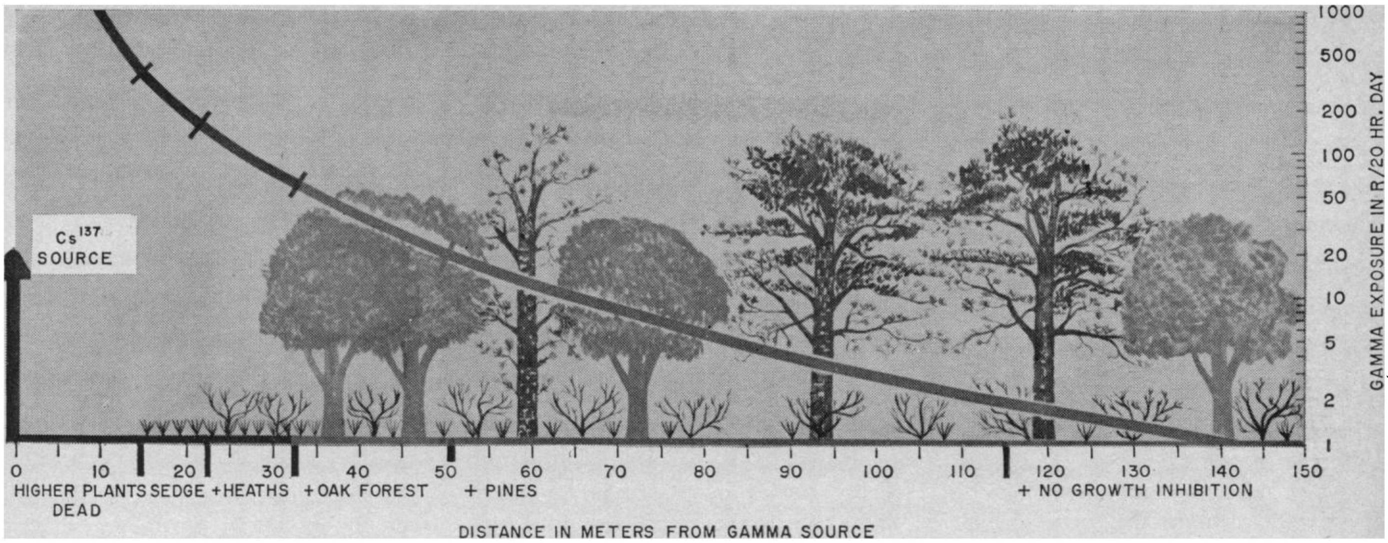


Fig. 12. Pattern of radiation damage to oak-pine forest in 1962 after about 6 months' exposure.

by any of the herbaceous species more resistant to radiation. There was, however, expansion of the population of *Carex*, a plant that normally occurs as an ubiquitous but very sparse herb, to cover as much as 20 percent of the total ground surface. This expansion was in response to the demise of the tree and shrub cover; it points to the potential importance of rare, or at least inconspicuous, species, capable of rapid regeneration, in maintaining certain aspects of function in disturbed communities.

Other examples of rapid response to the changed resources in the damaged community abound, especially among insect populations. In general these populations have followed quite closely change in food supply (*16*). Populations that utilize dead organic matter and decay organisms increased in the central zone of high mortality to the vegetation; bark lice are a good example (Fig. 10). While this type of change seems quite straightforward and predictable, all changes in insect populations were not: during the 2nd year of the experiment, for instance, there was an unexpected and still-unexplained population explosion of aphids on white oaks exposed to 5 to 10 roentgens per day (Fig. 11). Aphids share with certain fungi, such as wheat rust, ability to reproduce asexually very rapidly to exploit any available resource. Although mobile, they are not strong fliers and do not migrate far; it is unlikely that the high populations resulted from migration from neighboring forests. It seems much more probable that leaves of trees exposed to 5 to 10 roentgens per day differed qualitatively from leaves of unirradiated trees sufficiently to support large populations of aphids; the difference appears to be not in either total sugars or total proteins, but in some more subtle factor detectable by aphids but not yet by man (*17*).

The effects of irradiation on the forest are best summarized by the profile (Fig. 12) showing the five vegetation zones and their approximate distribution along the radiation gradient in 1962. The most striking observation is the relative sensitivity of all the higher plants. No higher plant indigenous to the forest survived the 1st year of exposures exceeding 350 roentgens per day; in the old field, certain species survived more than 3000 roentgens per day. The 50-percent diversity point occurred in the forest at less than 160 roentgens per day; in the field, at 1000 roentgens per day. It seems abundantly clear that the forest as a unit is substantially more sensitive than the herb field. A second important relation is that there is sorting by size along the radiation gradient, smaller forms of life being generally more resistant than trees; this relation also extends to mosses and lichens.

This sorting by size, which now seems to be a well-established characteristic of radiation damage, has interesting parallels elsewhere in nature. It occurs along gradients of increasing climatic severity, such as the transition from forest to tundra in the north, and on mountain slopes. At such transitions, forest is replaced by low-growing shrubs, frequently blueberries and other members of the heath-plant family. In more extreme environments the heath shrubs are replaced by a sedge mat formed by a species of *Carex*; in the most extreme, the *Carex* is restricted to protected spots, and mosses and lichens are the only vegetation. The parallel with the irradiated forest is quite remarkable, holding even to genera and species, in certain instances. The conclusion to be drawn from this relation is merely that characteristics that confer resistance to certain types of environmental extremes also, curiously enough, confer resistance to damage by radiation.

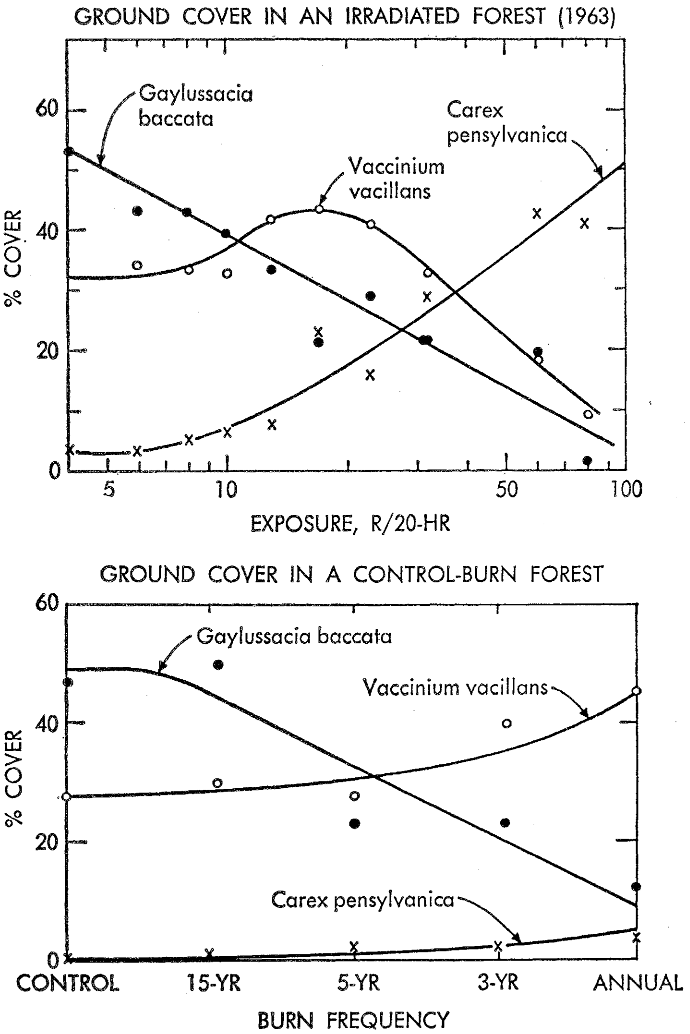
We can test the hypothesis a little more rigorously by examining in detail the shrub layer of the forest, which is itself a small community containing two species of blueberries, the huckleberry, and the sedge. Changes in this community after burning have been studied intensively (*18*); their general pattern appears in Fig. 13: with increased frequency of fire, the huckleberry populations decline, the blueberries increase, and the sedge increases. Under irradiation the pattern is strikingly similar until the point at which radiation kills the blueberry. The parallelism between the effects of fire and of radiation should not be expected to be universal, for many factors are implicated. Nonetheless there seems to be a strong parallel between the effects of radiation and the effects of another extreme; and in both instances, as well as in the herb field, the correlation between durability and small stature applies (*19*).

While there is no completely satisfactory explanation of the parallels, one important contributory factor may be simply the size of the plant. Perennialism, height and complexity of structure all represent investments of energy in nonphotosynthesizing tissue, tissue that requires energy for maintenance. We might think of this tissue as a mortgage that must be paid off with income from photosynthesis. As the size of a plant increases, both mortgage and total income increase, but at different rates. In Fig. 14 are plotted the total weights of trees against $h \times d^2$, a measure of size (*20*). Since total weight of the tree is not a proper measure of total living tissue (there being considerable nonliving tissue in a tree), we have also plotted an estimate of the weight of tissue that may normally be considered living. It seems clear that in small trees leaves represent a substantially larger fraction of the total weight of live tissue than in large trees. An increase in size thus puts greater demands on the photosynthetic mechanism simply for maintenance, leaving less for growth and repair.

A similar relation applies along the successional gradient that we have discussed (Fig. 15). In the early stages of succession most of the tissue produced is green, and the mortgage payments to support respiration are small. As succession progresses, the complexity of structure increases, but total living tissue increases more rapidly than the weight of leaves, which supply the energy for respiration; the mortgage increases, but income does not increase proportionally. It is true that the existence of the structure allows greater use of space, greater total photosynthesis up to a point, and greater diversity of species. But it is also true that the maintenance of the structure and diversity hinges on the annual interest paid from photosynthesis into the structural mortgage, and, if for any reason the interest is not paid, the structure begins to decay.

And here lies the crux of the matter: the mechanisms related to energy fixation—bud set, bud burst, leaf production, photosynthesis—are at much greater hazard than mechanisms related to energy use. Almost any disturbance of a forest may reduce its capacity for fixing energy; it either increases respiration or reduces it relatively slightly. If the disturbance is chronic, the vegetation comes to a new equilibrium, supporting a less complex structure. For this reason we might expect a forest to be more sensitive to disturbance than is an herb field because the forest is less plastic in species composition and because its capacity for fixing energy must remain substantially intact or it will burn up more than it fixes and deteriorate. And that is exactly what happens, but it is far from the whole explanation.

We have shown for the herbaceous field that there was sorting along the radiation gradient, dependent on chromosome volume: plants with large average chromosome volumes are sensitive; those with small volumes, resistant. The pattern in the forest was similar. If we plot the average chromosome volumes (*8, 21*) against the daily exposure required to inhibit growth to 10 percent of growth of unirradiated plants (Fig. 16), it is abundantly clear that radiosensitivity correlates with size of



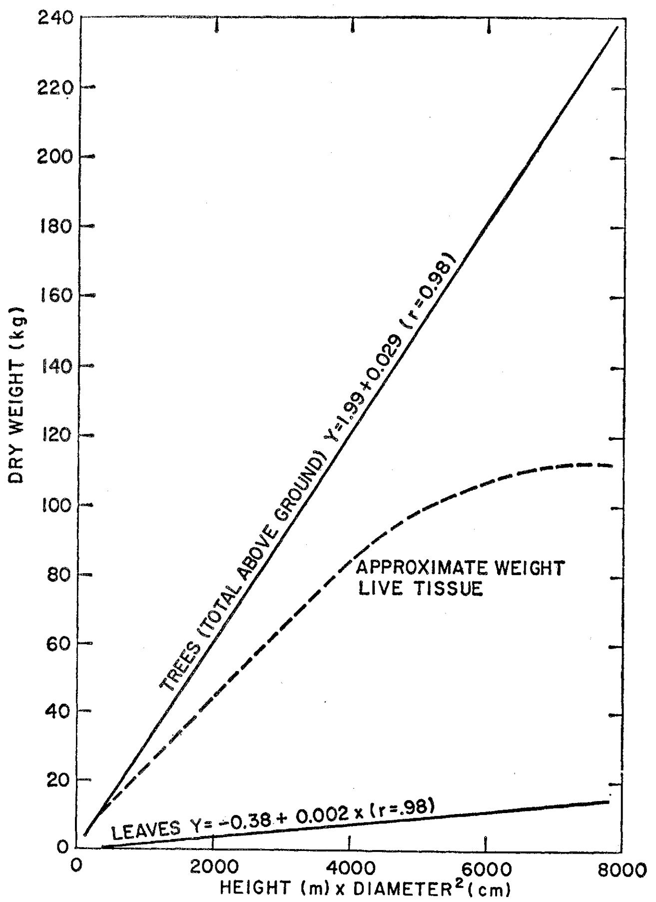
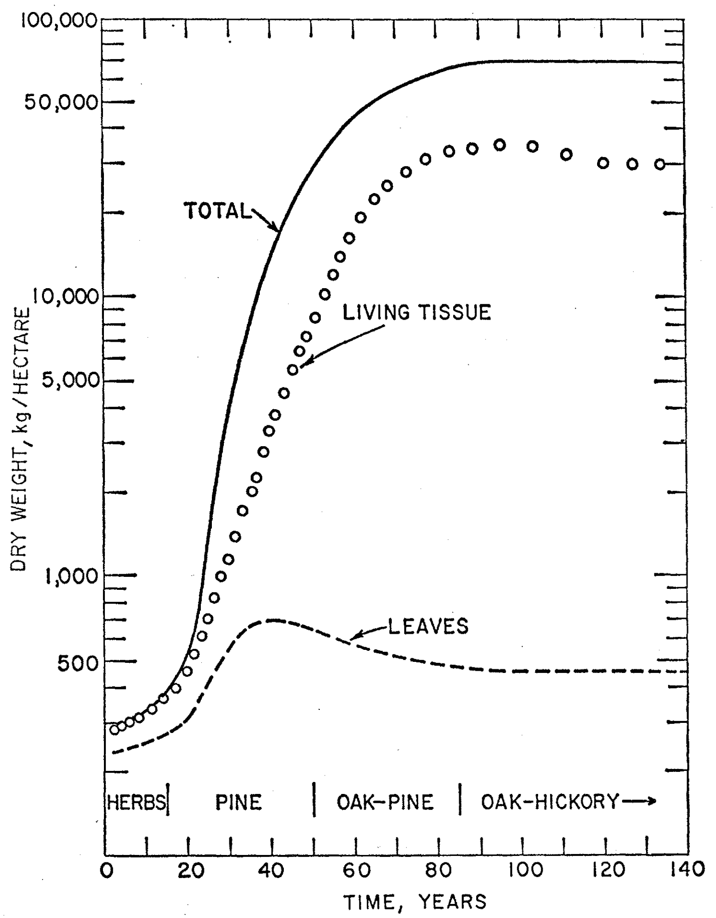


Fig. 13 (left). Comparison of effects of ionizing radiation and different frequencies of burning on the shrub-and-sedge community [from Brayton and Woodwell (*19*)]. Fig. 14 (above). Relation between weights of leaves, weights of trees, and tree sizes for an oak-pine forest on Long Island.



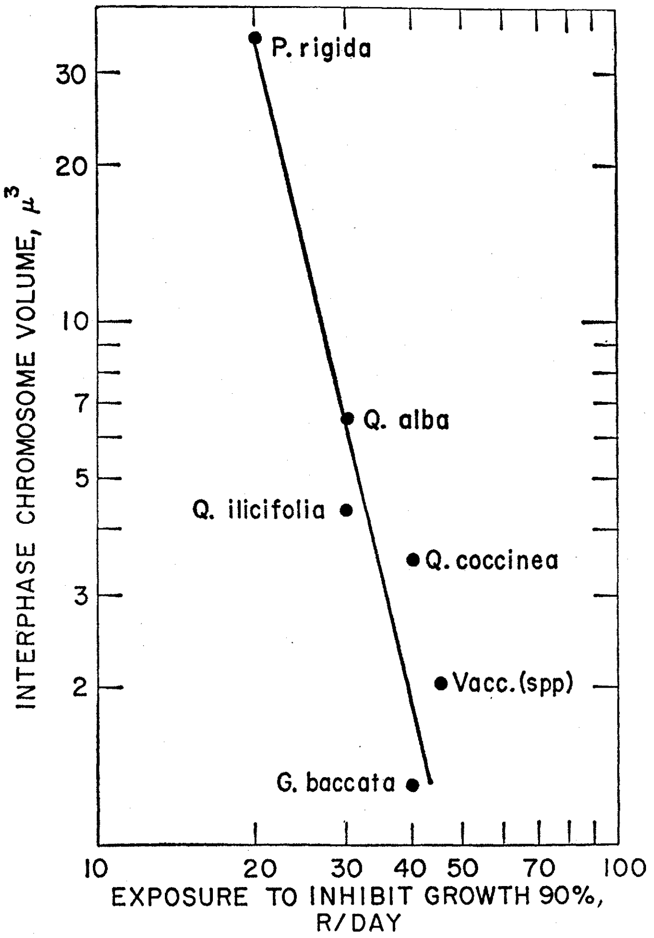


Fig. 15 (left). Approximate relations between total above-ground standing crop of plants, weight of living tissue, and weight of leaves in a normal field-forest succession of eastern North America. Fig. 16 (right). Relation between radiosensitivity, measured as inhibition of growth (90 percent), and interphase chromosome volume in irradiated forest (*21*).

the chromosomes, and that this correlation applies to populations in nature as well as to cultivated populations. Also, the larger plants tend to have larger chromosome volumes; the smaller plants, smaller. Clearly, chromosome volume has played a role in the persistence of plants along the radiation gradient in the forest as well as in the field.

Now let me recapitulate briefly: the successional gradient we have used to explore effects of radiation on natural communities is characterized in the early stages by a loosely structured community or series of communities shifting in species composition, diversity, dominance, density, total mass of living matter, and probably in every other measurable parameter, within relatively broad limits, in response to disturbance. It is also true that the species of the early successional communities, including mosses and lichens, tend generally to be resistant to radiation. The forest does not share the plasticity of communities having simpler structure; in this respect the forest is more sensitive to any disturbance. In plants, large size alone, because of its effects on the ratio of photosynthesis to respiration, contributes to this type of sensitivity; but, more importantly, plants of the forest are inherently sensitive to radiation damage because they have large chromosomes and because woody species in general are more sensitive than herbaceous plants having the same-sized chromosomes (*22*).

Thus there seems to be a shift toward greater sensitivity to radiation as succession progresses. The shift is due to at least three factors: (i) what I term the relative plasticity of the communities; (ii) increase in the amount of structure in the communities, with its implications for the photosynthesis:respiration ratio; and (iii) changes in the intrinsic characteristics of the plants participating in these communities, including changes in size of chromosomes. All these factors work in the same direction, contributing toward greater sensitivity to radiation and probably to other types of disturbance later in succession.

What do the patterns of radiosensitivity mean? Could they be sheer coincidence, on the one hand, or a useful new clue to the mechanisms of evolution on the other?

It is difficult to discard them as mere coincidence: true, they are imperfect: there are radiation-resistant plants in the forest and radiosensitive plants in the field; furthermore, the pines, the most sensitive of all, are a minor part of the mature forest, and the pattern of increasing radiosensitivity along succession is imperfect in detail. Yet the difference in sensitivity between field and forest spans a factor of nearly 10; if we include lichen communities, which sometimes precede herbaceous communities in succession, there is a factor of 10 of additional resistance beyond that of the herbs (*23*). And the correlations between life-form and size and radiosensitivity, and the parallels between radiation effects and known effects of environmental gradients are too strong to be set aside lightly. There is no evidence at all that the enormous range of radiosensitivities among higher plants correlates in any way with the distribution of radioactivity in nature; nor is there reason to believe that radiation levels have changed appreciably during the quarter-billion years or so of existence of the higher plants. Rather, it seems that we must look further for other environmental factors or combinations of factors that have affected the evolution of that constellation of characteristics we measure when we measure radiosensitivity, including especially chromosome size.

It is an intriguing if somewhat oversimplified hypothesis that sensitivity to radiation damage is a measure of sensitivity to environmentally induced mutation (mutation is used in its broadest sense). It seems reasonable to accept the concept that rates of mutation tend toward some optimum, which is under hereditary control (*24*). If the rate were too high, there would be reduction in reproductive success; if too low, there would be insufficient variability to meet the evolutionary demands of constantly changing environments.

Certainly it is conceivable that environments vary in capacity to produce mutations. If, on the basis of current evidence about mutations, one were to seek a mutagenic natural environment (independent of radiation intensity), he would probably seek one characterized by extremes: extremes of temperature, moisture availability, and solar radiation. One thinks immediately of surfaces exposed to the sun: soil, rock, bark. The evidence that I report suggests strongly that plants that normally inhabit such surfaces—algae, lichens, mosses, and prostrate-growing vascular plants—are more resistant to ionizing radiation (and doubtless to many other stresses) than plants of more ameliorated environments such as forests.

Whether this suggestion will prove to be true when examined in a larger context than has yet been possible remains to be seen. Nonetheless, we now infer that ability to survive such rigorous environmental conditions also confers in some degree, at least, resistance to ionizing radiation. The factors that confer resistance involve growth form, length of life cycle, regenerative capacity, and cytological characteristics, especially average interphase chromosome volume. Experimental examination of this question is a current challenge to radiation research. Only by willingness to look at such really tough questions will we gain further insight into both radiation and the patterns of nature.

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Atom Reactions in Flow Tubes

Reactions of atoms and free radicals from electric discharges can be studied in fast flow systems.

B. A. Thrush

Free atoms, such as oxygen and hydrogen, and free radicals (for example, OH) play vital roles in combustion reactions, in the chemistry of the upper atmosphere, and in radiation chemistry. With these systems, it is difficult to isolate an elementary step, but reliable experimental data on such steps are important in the development of theoretical chemical kinetics, as well as for establishing overall reaction mechanisms. The production of free atoms and radicals in electric discharges has been known for many years, but the sudden growth in the use of this method in the last decade has been greatly stimulated by the development of specific methods for determining concentrations of atoms or free radicals.

The long-lived yellow afterglow of "active nitrogen" produced by a discharge through nitrogen gas was discovered nearly a hundred years ago. Over the period 1910–1940, Strutt (Lord Rayleigh) (*1*) showed that this afterglow was associated with the recombination of ground-state nitrogen atoms formed in the discharge. The use of this afterglow, or of related afterglows, to measure the concentrations of free atoms came later, when a variety of experimental techniques showed that the main reactive products of electric discharges through gases at low pressures were free atoms in their electronic ground states. The

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