EFFECTS OF CHRONIC GAMMA IRRADIATION ON PLANT COMMUNITIES

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ABSTRACT

Three plant communities or assemblages of plants—the vascular plants of an oak-pine forest, the lichens of that forest, and herbs of an old field—have been studied after being exposed experimentally to chronic gamma irradiation. Several kinds of changes in the communities have resulted, including: (1) in all three communities irradiation reduced community structure toward the lowest strata or growth-forms of the community; (2) dominant species replaced one another along the gradient of radiation intensity producing population curves similar to those found along natural environmental gradients; (3) significant changes in productivity occurred; (4) species-diversity decreased with increased exposure to radiation; (5) in respect to various tests used in the study, increasing community sensitivity to irradiation was in the sequence: forest lichens, old-field herbs, forest vascular plants. Radiation effects on communities relate to evolutionary and ecological phenomena of broad interest, including nuclear volume effects on radiation sensitivity, stature and evolutionary level of plants, population processes determining community composition, and relations of communities to succession and natural environmental gradients.

INTRODUCTION

EXPOSURE to ionizing radiation at intensities much above the background from natural radioactive decay and cosmic rays is a new problem in biology. It has arisen because of the use of atomic energy in both war and peace, a use that has been accelerating for the past quarter century and holds almost incomprehensible potential for both benevolence and destruction. The need to know the consequences of exposure to ionizing radiation is real; no less real is the interest inherent in understanding the effects of a factor which, while "unnatural" at intensities far above background, has been present throughout the evolution of life and has fundamental effects on heredity. The effects occur, of course, at all levels of integration in living systems, ranging from the molecular through ecological levels.

The effects of ionizing radiation on plants have been studied extensively (Sparrow, Binnington and Pond, 1958; Sparrow, 1960, 1961; Gunckle and Sparrow, 1961; Schultz and Clement, 1965; Sparrow, Sparrow, Thompson, and Schairer, 1965; Hungate, 1966). Some of the generalized conclusions are: (1) that damage from irradiation involves production of mutations (Muller, 1927), using "mutations" in its broadest context to include gross and subtle changes in chromosomes; (2) that the most sensitive tissues are meristematic (Bergonie and Tribondeau, 1906); (3) that there is great variation among species in sensitivity to radiation (Odum, 1959; Sparrow and Woodwell, 1962); and (4) that sensitivity is related to characteristics of the nucleus, especially to the average volume of chromosomes (Epstein, 1953; Terzi, 1961, 1965; Sparrow, Underbrink and Sparrow, 1967).

Information specific to community-level effects is beginning to accumulate from studies at bomb test sites (Fosberg, 1950a, 1959b; Palumbo, 1962; Beatley, 1965a, 1965b, 1966;
Shields and Wells, 1962, 1963; Martin, 1963), around reactors (Platt, 1963, 1965; Witherspoon, 1965; Witkamp, 1961), gamma sources (McCormick, 1963), and from more recent experiments at Oak Ridge National Laboratory (Taylor, 1966), Savannah River (Monk, 1966; McCormick and Golley, 1966), Puerto Rico (Odum, 1965), Brookhaven National Laboratory (Woodwell, 1962, 1967; Woodwell and Sparrow, 1965; Woodwell and Rebuck, 1967), and elsewhere. The studies reveal that impact of radiation effects on communities goes far beyond simple observation of damage and that effects are related to various other basic ecological phenomena. This summary is offered to focus attention on some of the broader biological questions raised by work to date on the ecological effects of ionizing radiation.

COMMUNITIES STUDIED

Responses to irradiation have been studied at Brookhaven National Laboratory in four types of plant communities: a forest, an abandoned field, and in the shrub and lichen communities of the forest. The forest is an oak-pine stand such as described by Conrad (1955), and is dominated by white oak (Quercus alba), scarlet oak (Q. coccinea) and pitch pine (Pinus rigida). [Nomenclature of higher plants follows Fernald, 1950.] There is a high coverage of vaccinioseous shrubs (Gaylussacia baccata, Vaccinium vacillans and V. angustifolium), and a sparse herb stratum (about 1 per cent cover) with Carex pensylvanica, Gaultheria procumbens, Pteridium aquilinum and other species (Woodwell and Rebuck, 1967). In the abandoned field the response of communities of herbaceous plants to irradiation was observed. These communities had developed through one and two years following abandonment from agriculture. The shrub and lichen subcommunities, or synusiae, of the oak-pine forest merit separate treatment because of the difference in their responses from those of the trees (Reiners, 1965; Brayton and Woodwell, 1966; Woodwell and Gannutz, 1967). All these communities occur on the sandy, glacial outwash soils of nearly level terrain in central Long Island. Forests of this area have been subject to fire; the experimental forest was burned, probably about 1918. Although not a climax community, the forest is late successional or near-climax on these soils (Whittaker and Woodwell, 1967); “climax” is used, not in the sense of a single, climatically determined end-point of successions, but rather, in the sense of a community in steady-state in relation to its own environment (Whittaker, 1953). Study of both forest and field allows comparison of responses to irradiation in the unstable, pioneer assemblages of herbs and the more stable, late-successional forest.

The communities were exposed to chronic irradiation by gamma sources that produced approximately equivalent radiation fields. Irradiation of the forest was started in November, 1961; the herbaceous communities were allowed to develop during 1961–63 in sectors of the Gamma Radiation Field established a decade earlier at Brookhaven. Irradiation of the forest was with 9500 Ci of $^{137}$Cs; that of the field with 3000–4000 Ci $^{60}$Co. Both sources were shielded four hours daily to permit access to the vegetation. Details of the techniques and equipment of the experiments have been given by Woodwell (1963), Sparrow (1966), and Woodwell and Oosting (1965). The field has been observed through two years and the forest through five years of exposure to radiation, which was continuous except for the daily periods when the sources were shielded.

Intensity of radiation decreases with the square of distance from such sources, with minor exceptions because of absorption and backscatter (Cowan and Meinhold, 1962; Cowan and Platt, 1963). Trunks of trees produce significant shielding, revealed in the forest by green “shadows” of living Carex in a zone where most other vascular plants were killed. The reduction in exposure is roughly 5 per cent per cm of woody tissue. Thus a 10 cm tree would make a “shadow” where the minimum exposure was one-half that in front of the tree (Woodwell, 1963; Woodwell and Rebuck, 1967). Because of this variation in the radiation field, detailed biological studies have been based on the average exposures at any distance, derived from a study of the frequency distribution of exposures in the forest (Woodwell and Rebuck, 1967). The research was designed as an experiment comparing responses of communities along the gradient of intensity of radiation from
background (in control areas remote from the source) to the very high, commonly lethal levels within a few meters of the source. The approach is thus gradient analysis — the study of relationships of gradients of species populations and the characteristics of natural communities on the one hand to environmental gradients on the other (Whittaker, 1967) — applied to the "unnatural" environmental gradient of radiation intensity. Responses of communities to this gradient will be discussed as five types of effects: effects on physiognomy, on populations of species of plants, on production, on diversity, and on community composition measured as "relative similarity."

THE ECOLOGICAL EFFECTS OF RADIATION

Effects on Physiognomy

Effects of irradiation on the physiognomy (or structure) of communities are best generalized in a transect diagram of a forest (Fig. 1, cf. Woodwell, 1967, Fig. 12). Zones of disturbance have been classified as follows (Woodwell and Rebuck, 1967): (1) Devastated Zone, the inner zone receiving more than 200 R/day, where all woody and most herbaceous plants were killed during the first year of the experiment; (2) Carex Zone, where all woody plants were killed and the sedge Carex pensylvanica expanded its populations in two years to cover as much as 50 per cent of the ground surface in certain areas (the expansion occurred in areas receiving average exposures of between 200 and 150 R/day in 1962, although the limits of all such zones must be drawn somewhat arbitrarily); (3) Shrub Zone (40–150 R/day in 1962), a "heath" where the tree canopy had been reduced to 50 per cent or less of its normal canopy cover, and where the vaccinaceous shrubs were the dominant plants; (4) Oak Forest (16–40 R/day in 1962), in which pitch pine had been killed leaving an oak canopy and undisturbed undergrowth (although the oaks were living, bud and twig development, and amount and timing of leaf fall were affected (Woodwell and Rebuck, 1967; cf. McGinnis, 1963); (5) Oakpine Forest, at exposures less than 12 R/day in 1962 (7 R/day in 1963, 4.2 R/day in 1964), where no mortality of plants was observed, although there was appreciable reduction of shoot growth at exposures as low as 1 R/day (Woodwell and Sparrow, 1963).

This sequence of life-forms — lichens and mosses, herbs, shrubs, trees — is familiar, for it appears in many successions. It appears also, with perhaps more striking parallelism to the effects of irradiation, in the gradient of vegetation on mountains from the lichen and moss communities of highest altitudes, through sedge meadow and ericaceous shrub communities, to forests at lower elevations (Woodwell, 1967). The latter gradient is an example of the well-known generalization that stature of dominant plants, community coverage, and differentiation into strata tend to increase with progression toward more favorable environments, and to decrease toward more severe environments (Dansereau, 1951; Whittaker, 1954, and others). The response of the forest to irradiation conforms to this generalization, with reduction of stature of dominants, total coverage, and stratal complexity toward more severe exposure to irradiation.

The pattern appears not only for the forest as a whole, but within its shrub community. Among the shrub species, Gaylussacia baccata is more sensitive than Vaccinium vacillans, which in turn is more sensitive than V. angustifolium and the sedge Carex pensylvanica (Brayton and Woodwell, 1966). The sequence
is one of decreasing stature from Gaylussacia (about 0.5 m mean height) through the two Vaccinium species (0.25 m and 0.10 m) to Carex (less than 0.1 m). Other unexpected physiognomic trends in response to irradiation appear in the old-field and lichen communities. The first-year old-field communities consist of herbs of which, in the control samples, 85 per cent of the species are erect and 15 per cent prostrate (including decumbent or geniculate according to Fernald, 1950). The proportion of prostrate species rises to 50 per cent at about 100 R/day, and to 100 per cent at about 2000 R/day (Woodwell, 1967). In the lichen synusia the numbers of both fruticose and foliose species decline until, at about 2000 R/day, only the crustose species remain (Woodwell and Gannutz, 1967).

Patterns of survival in all four communities or subcommunities thus show increasing disadvantage of erect stature with increasing exposure to radiation. Since the sources of irradiation were above ground, the effect is not one of ground-surface shielding. Effects on dose from shielding by tree trunks and from backscatter are largely averaged out by considering populations at different distances from the source, rather than by considering individual plants. At a given distance from the source mean radiation exposure should be nearly equal for tissues of Quercus, Vaccinium and Carex, and for tissues of foliose and crustose lichens. Despite differences in radiation sensitivity of species of a given growth-form, there appears to be significant correlation of radiation sensitivity with growth-form. It is this correlation that underlies the physiognomic responses of communities to ionizing radiation.

Effects on Populations of Species

Changing balances among species populations, including replacement of dominant species, have been observed in natural communities exposed to different intensities of irradiation (Auerbach, 1958; Woodwell, 1962, 1967; McCormick, 1963; Daniel, 1963). In the Brookhaven experiments irradiation both reduced populations of some species, and permitted compensatory expansion in the populations of other ones. The most conspicuous changes in abundance in the forest involved inverse relationships between coverage of trees and shrubs and of the sedge, Carex pensylvanica (Fig. 1). As cover of trees and shrubs declined the cover of Carex increased from less than 1 per cent in the undisturbed forest to more than 50 per cent in certain areas at high radiation exposures. A similar but less striking replacement of dominance occurred in the shrub community when density (as distinguished from the somewhat less sensitive index, coverage) was considered. As the tree canopy was reduced at increasing radiation exposures there was an increase in the density of Gaylussacia. An inverse relation of Gaylussacia to tree cover was observed also in unirradiated forests by Reiners (1967). At higher radiation exposures, Gaylussacia densities declined while Vaccinium vacillans increased slightly; at still higher exposures, V. vacillans declined while V. angustifolium increased. As all of the shrubs were excluded by still higher exposures, the Carex replaced them as the dominant plant and was itself replaced close to the source by Cladonia cristatella and other lichens (Woodwell and Rebuck, 1967; Brayton and Woodwell, 1966; Woodwell and Gannutz, 1967).

Harvest of the standing crop of first-year old-field herbs along the gradient of radiation also showed shifts in the abundance of species (Woodwell and Oosting, 1965; Woodwell, 1967). The most important changes were: (1) replacement of the dominance of Chenopodium album and Erigeron canadensis by Digitaria species. (2) Standing crops of populations along this gradient and the gradient of radiation in the forest showed peaked curves (Woodwell, 1967, Fig. 3; cf. McCormick, 1968) resembling binomial distributions, the form suggested for populations along natural environmental gradients (Gause, 1930; Whittaker, 1951, 1952; Brown and Curtis, 1962). (3) These distributions are symmetrical only in relation to the logarithm of radiation intensity; they are strongly skewed along a linear gradient of radiation intensity. The relation to the logarithmic gradient suggests that (in analogy with the Weber-Fechner law) the effect of increase in radiation exposure is proportional to ΔR/R, the increase in relation to the radiation intensity beyond which the increase occurs. Similar responses of populations in relation to
a logarithmic gradient of salinity in inland lakes were observed by Whittaker and Fairbanks (1958). (4) Although “zones” characterized by physiognomy or dominant species are convenient for description, the change in the importance of species and in community composition along the radiation gradient is continuous. In general, the manner in which importance values and community composition relate to the radiation gradient are consistent with those observed in continua of natural communities in relation to natural environmental gradients studied by Whittaker (1951, 1956, 1967), Curtis and McIntosh (1951) and others.

A further relation to disturbance and successional gradients may be illustrated for the principal species of shrubs in the forest. The species Gaylussacia baccata, Vaccinium vacillans, V. angustifolium and Carex pensylvanica form, as indicated, a sequence of dominance replacement with increasing exposure to radiation and also a sequence of decreasing plant height. The response of these species to frequency of fires (Buell and Cantlon, 1953) is generally parallel to their response to irradiation (Brayton and Woodwell, 1966). Full parallelism of species responses to radiation and fire exposure should not be expected. These parallels suggest, however, along with the physiognomic observations, that there is correlation of the tolerance of irradiation with tolerance of other environmental stresses, especially physical stresses, among different plant species and growth-forms (Woodwell, 1967).

Effects on Productivity

One usual effect of irradiation has been decreased net production, but this has not always been true. In the first-year old field, the end-of-season harvest (including roots) increased from 400 g/m²/yr in the control community to 800 g/m²/yr at 1000 R/day; beyond 1000 R/day production decreased to near zero at 2000 R/day (Woodwell and Oosting, 1965; Woodwell, 1967). The meaning of the increase in harvest up to 1000 R/day is uncertain but the contrast between the sets of samples seems statistically significant. The results suggest that the prostrate Digitaria, which has trivial production in communities in which it is shaded by erect herbs, is able, when released from shading, to use resources for short-range production more effectively than the erect herbs. In this case, irradiation results in replacement of an open herb community of moderate production by a mat of Digitaria, which has high production for a dry grassland. It seems clear that in this old-field community effects of radiation are expressed in changing composition without reduction in total productivity, up to levels of radiation (approaching 2000 R/day) which exclude even the most resistant of the community’s species.

Above-ground net annual production of forest outside the irradiated area is estimated from unpublished data to be 846 g (dry weight) per m² (802 g/m² for trees, 42 g/m² for shrubs, and 2 g/m² for herbs); total above- and below-ground net annual production is estimated at 1124 g/m². The production is near, but lower than, the range of 1200–1400 g/m²/yr observed for climax forests of more favorable environments (Whittaker, 1966). Exposure to more than 300 R/day for six months reduced production of the forest to very close to zero. Here virtually all of the indigenous higher plants were excluded. Production of trees was zero at exposures in excess of 150 R/day and was reduced substantially at exposures of 40 R/day. Within the five years of this study there was a modest increase in production of the more resistant undergrowth plants, which compensated only in part for the reduction of the tree production. In the zone exposed to 17–18 R/day (50–52 m), where the tree canopy had been reduced substantially after five years exposure, there was a 20 per cent increase in net production of the low-shrub stratum to 50 g/m²/yr, above-ground. This was the maximum production of low shrubs along the gradient. The production of Carex pensylvanica, however, increased from about 2 g/m²/yr to 100–200 g/m²/yr in this zone and in areas receiving exposures up to 160 R/day. At higher exposures it dropped abruptly to zero. Although a few scattered herbs occurred at higher exposures (Wagner, 1966), combined production of these was less than 1 g/m². The contrast between the forest and old-field in productivity under irradiation is striking. In the more stable and highly organized forest,
exposure over 6 months to 40 R/day destroyed the dominant species within one year and reduced production to less than one-half of that of the control. In the unstable and loosely organized old field increasing exposure up to 1000 R/day changed its composition without reducing production.

Part of the meaning of exposure to ionizing radiation for forest production involved effects on photosynthesis and respiration. Irradiation of pine trees during the winter reduced net photosynthesis, probably due in part to an increase in rate of respiration and in part to a depression in the efficiency of photosynthesis (Bourdeau and Woodwell, 1964). Field and greenhouse studies of the effects of irradiation on photosynthesis and respiration show that there is a consistent general depression in the rate of net photosynthesis under chronic and acute irradiation (Hadley and Woodwell, 1965; Woodwell, unpublished). Dark respiration of leaves and respiration of stems follow less clearly defined patterns. Under chronic irradiation dark respiration of pine branches was stimulated, especially as the tree approached death under high chronic exposure (Bourdeau and Woodwell, 1964). After acute irradiation no change in the rates of dark respiration of branches could be detected in pine seedlings, although there was an immediate increase in the rate of respiration of the stem followed by a persistent depression (Hadley and Woodwell, 1965). Rates of decay of organic matter in soil and of litter were enhanced by irradiation at about 600 R/day, further supporting the conclusion that respiration rates are often enhanced by irradiation (Woodwell and Marples, 1967; Romani and Bowers, 1963; Kaman, Aharoni, and Lattar, 1965), although certainly not universally so (Woodstock and Justice, 1967; Bourdeau and Woodwell, 1964). The depression of photosynthesis and enhancement of respiration implies a decrease in net production due to direct effects of irradiation on metabolism. The mechanisms of these shifts in metabolism under irradiation have not been clearly defined.

These effects, however, are compounded under chronic irradiation, which partially defoliates the trees, reducing photosynthetic area without proportional reduction in the total amount of tissue respiring. The shift is most important in large perennial plants which have a larger investment in living support tissue in proportion to their photosynthetic tissue than smaller plants. Physiological and morphological effects of irradiation converge in these plants to make the balance of photosynthesis and respiration unfavorable. More broadly, the physiognomic trend of decreasing stature and stratal diversity of communities toward more severe environments may be based in part upon shifting balances between the advantage of plant height for light interception in favorable environments, and the disadvantage of erect woody structure and its respiratory requirements in less favorable environments that limit the amount of photosynthesis.

Effects on Diversity

The diversity of species of the oak-pine forest of Long Island averages 4.8 tree, 7.6 shrub, and 5.6 herb species per tenth-hectare plot; the total of 18 vascular plant species per plot is in a lower middle species-diversity range for a forest, and in the range of many mountain forests of high elevations (Whittaker, 1965; Whittaker and Niering, 1965). Plots smaller than 0.1 ha are needed to measure diversity along the radiation gradient; numbers of species in plots of different sizes appropriate to strata have been combined in a forest diversity index (Woodwell and Re buck, 1967; Woodwell, 1967). Diversity thus expressed averaged 5.5 to 6.0 species in the unirradiated forest. Exposures of about 20 R/day (affecting P. rigida) caused a slight reduction in diversity in the first year of the experiment. At exposures above about 50 R/day diversity declined with a slope that was nearly linear in relation to the logarithm of radiation exposures. Diversity was reduced to one-half of the control at about 150 R/day in the 1962 samples, and to zero at 350 R/day (Fig. 2). There was a depression of the 50 per cent diversity point in the two subsequent years to about 90-95 R/day. Diversity of species in the old field showed no marked decrease at exposures up to 100 R/day or more; beyond these levels diversity decreased to zero at 8200 R/day. Diversity was reduced to 50 per cent
of the control at about 1000 R/day in the first-year old field.

Data on the diversity of the lichen populations in the first year of the experiment are incomplete. The threshold for reduction of diversity in the lichen community in the first year is believed, however, to have been 200-300 R/day, and reduction to 50 per cent diversity occurred at 2700 R/day (Woodwell and Gannutz, 1967). Some lichen species are highly resistant. Eleven species survived on trees at exposures of 2250 R/day after 32 months. A point of zero diversity could not be obtained, but the slope of the diversity curve suggests that this point should lie above 5000 R/day, possibly substantially higher.

Points of threshold reduction of diversity, of 50 per cent reduction, and of reduction to zero for the three communities are thus all in the sequence — forest vascular plants, old-field herbs, and forest lichens. There are also differences in the relationship between diversity and production, and in the response to irradiation of the forest and old-field communities. Stratification, species-diversity, and production are poorly correlated with one another in general (Whittaker, 1965) and in detail along these gradients of radiation. Along the gradient in the forest, however, there was approximately parallel reduction of these three community characteristics with increasing exposure. The response of the community is in this case, within the period of observation, one of reduction and simplification without appearance of new species not present in the control forest. In the old field, in contrast, the response to irradiation involved (1) non-

parallelism of the effects on production and diversity, (2) maintenance of full (or increased) production by communities of lower diversity with increased exposure up to 1000 R/day, a relationship similar to that along the salinity gradient in inland water bodies (Whittaker and Fairbanks, 1958), (3) addition to the flora at middle and higher radiation levels of species not present (or at least very rare) in the un-irradiated old field.

Responses of the composition of communities to irradiation may also be expressed by such comparative indices as “coefficient of community” and “percentage similarity.” Coefficient of community (Jaccard, 1902, 1912) is calculated as $CC = c / (a + b - c)$, in which $c$ is the number of species shared by two community samples or floras, one of which includes a total number of species $a$ and the other a total number of species $b$. Percentage similarity is calculated as $PS = 1 - \frac{5}{a} \Sigma / a - b / = \Sigma \min (a, b)$, in which $a$ is the percentage which one species comprises among the total number of individuals (or other relative measure of importance) in the first sample and $b$ is the percentage which the same species comprises of the total in the second sample (Whittaker, 1952; Odum, 1950). Percentage similarity is usually computed by summing for all species the smaller of the two values of percentage representation for each species. A number of related measurements have been used by other authors (Dagnelie, 1960; Bray and Curtis, 1957; Greig-Smith, 1964; Whittaker, 1967). Coefficient of community expresses the relative similarities of two samples in terms of floristic composition; percentage similarity expresses relative similarity in terms of quantitative composition, with strong influence by the proportions of dominant species in the samples. Since they are different expressions of community response to environment, there is often advantage in using both, especially for a study of communities from contrasting environments (Whittaker and Fairbanks, 1958; Whittaker, 1960; Woodwell and Oosting, 1965).

The responses of the three communities —
forest, old field and the lichens of the forest — were similar in that a logarithmic increase in intensity of exposure produced an approximately linear reduction in coefficient of community (of samples from irradiated communities compared with controls). The similarity of the coefficient of community curve to the diversity curve was conspicuous in the forest, where there was little invasion of species not originally present in the undisturbed stand. Percentage similarity proved less useful for comparisons of communities along the radiation gradient, especially in the herbaceous field where changes in densities of species occurred irregularly, apparently in response to shifts in competitive relations (Woodwell, 1967).

Zero values for community similarity occurred at about 350 R/day in the forest vascular plants (for the first year of exposure), 1100 R/day in the second-year old field, and (by extrapolation) possibly 9000–10,000 R/day in the lichen community. When resistant species not present in the control are present at the higher radiation intensities, these values differ from values for zero species-diversity. Zero similarity is consequently more nearly an expression of the radiation sensitivity of the original community, as represented in the control sample, than is zero diversity. Both these zero values may be strongly influenced by a single, most resistant species. A 50 per cent reduction in community similarity provides a measurement more nearly expressing the sensitivity of the whole community to radiation. It should also be observed, however, that two replicate samples from the control community will give similarity values (“internal association” — Whittaker, 1952; cf. Bray and Curtis, 1957) of less than 100 per cent, and often they will be in the range of 60 to 80 per cent. The appropriate expression of community response is consequently reduction of similarity value to 50 per cent of that for replicated control samples; the measurement is one of a “half-change” in community composition (Whittaker, 1960; Whittaker and Niering, 1965) as a unit of ecological distance.

Radiation intensities to produce half-change in coefficient of community were 120 R/day for the forest vascular plants in 1962 (after 6 months’ exposure), about 200 R/day for the second-year old field, and 1500 R/day for the forest lichens. These measurements, and reduction to 50 per cent of species-diversity of the control, are both possible expressions of community radiation sensitivity analogous to the LD_{50} as an expression of radiation sensitivity of populations. The two community measurements are necessarily correlated but, because of differences in species responses, they are loosely correlated. Fifty per cent diversity, like zero diversity, may be influenced by occurrence of species not present in the control samples; the half-changes in community similarity are more directly expressive of the sensitivity of the control community. Of the two half-change measurements (using coefficient of community or percentage similarity), coefficient of community is the more stable and less affected by population irregularity. CC_{50}, reduction of coefficient of community to half that of replicated unirradiated samples, consequently represents the authors’ preference as an expression of relative sensitivity of communities to irradiation.

**Relationship to Cellular Characteristics of Species**

Damage from ionizing radiation is widely recognized to have its basis in phenomena on the cellular level, and much effort has been devoted to discovery of the principal site of damage (Lea, 1962; Bond, Fiedlner, and Archambeau, 1965; Bacq and Alexander, 1961). There is wide agreement that the chromosomes are the primary targets and that the larger this target the more energy is absorbed from a given flux of radiation (Terzi, 1961, 1965; Sparrow, Sparrow, Thompson, and Schairer, 1965). This means that the sensitivity to radiation is correlated with volume of the chromosomes, a relationship which has been examined in detail for plants by A. H. Sparrow and his colleagues at Brookhaven National Laboratory and by others (Bowen, 1962; Evans and Sparrow, 1961; Miller and Sparrow, 1964; Sparrow, 1961, 1962, 1965; Sparrow and Miksch, 1961; Sparrow, Schairer, and Sparrow, 1963; Sparrow, et al., 1965; Sparrow, Underbrink, and Sparrow 1967; Yamakawa and Sparrow, 1965, 1966). The correlation has important implica-
tions at cellular and molecular levels; but, more important for us, it has been used successfully to predict radiosensitivity of organisms under experimental conditions from chromosome volume alone (Sparrow and Evans, 1961). With somewhat less accuracy it can be applied in attempts to predict ecological effects of radiation in the field.

Volume of the nucleus of meristematic cells as described by Sparrow and Miksche (1961) was used to predict effects of the first year's exposure of the Brookhaven Forest (Sparrow and Woodwell, 1962). All species involved in the prediction had chromosome numbers of \(2n = 24\) (Woodwell and Sparrow, 1963), eliminating chromosome number as a variable. The prediction was largely correct in implying that trees would be the most sensitive species of the forest, and pitch pine (\(P. \text{rigida}\)) the most sensitive tree species. The high sensitivity of pitch pine at Brookhaven is consistent with that of loblolly pine (\(P. \text{taeda}\)) and other pine species, compared with deciduous trees in Georgia (Platt, 1963; Pedigo, 1963). All tree species at Brookhaven were, however, more sensitive than anticipated; and the relative sensitivities of different species varied from the prediction. Scarlet oak (\(Q. \text{coccinea}\)), expected to be the most resistant of the trees, was more sensitive to the first year's exposure than white oak (\(Q. \text{alba}\)). In later years under chronic exposure relative sensitivities shifted with the scarlet oak becoming more resistant than the white in accordance with the prediction (Woodwell and Rebuck, 1967; Woodwell and Marples, 1967). The pattern was complicated by sudden mortality in the scarlet oaks in these latter years, apparently from unexplained secondary effects of irradiation.

The shrubs of the forest were also more sensitive than anticipated and, as with the trees, relative sensitivities of different species varied from the predicted pattern. Growth of shrubs was inhibited by approximately 1/10 the exposure predicted and mortality occurred at about 1/5 the exposure predicted. The huckleberry (\(Gaylussacia \text{baccata}\)) was predicted to be the most resistant of the shrubs; it proved instead to be the most sensitive (Woodwell and Sparrow, 1963; Brayton and Woodwell, 1966).

Nevertheless, the significance of the average volume of the chromosomes in determining the ecological effects of radiation becomes apparent when the exposures to inhibit growth by 90 per cent are plotted against the average volume of the chromosomes at interphase, using logarithmic scales (Fig. 3). A similar relationship applies in the old field in that species with larger interphase chromosome volume (4-7 \(\mu^3\)) occurred only at the lower exposure rates (<1000 R/day). While these correlations are conspicuous and emphasize the importance of the chromosomes as the site of damage, the variation in the relationship, the shifts from year-to-year in relative sensitivities, the anomalous radiation-linked mortalities as in scarlet oak, the variation introduced by annual as opposed to perennial growth, and other factors, all emphasize that cellular characteristics alone cannot be expected to explain all aspects of radiosensitivity or to provide a sufficient basis for predicting ecological effects. It is, nevertheless, striking that nuclear characteristics do fix the general range of sensitivity and that partial correlations relate plant size and community stature, sensitivity to irradiation and to other stresses, and chromosome volume to one another.

![Fig. 3. Correlation Between Average Volume of the Chromosomes and Damage from Irradiation in the Irradiated Forest, Brookhaven National Laboratory](From Woodwell, 1967)
DISCUSSION

Some broader features of radiation sensitivity of communities converge with those of radiation sensitivity of organisms:

1) In both cases sensitivity has a complex meaning in relation to varied organic processes, parts of the system, and time in life cycles. For the organism, L50 is not a measurement based on a unitary process comparable to radioactive half-life, but an index of gross response based on integration of effects on different parts and processes of the organism for a particular kind, rate, and life-cycle-timing of dose. For the community, C50 is an index of gross response, integrating effects on different processes and populations and probably also influenced by seasonal timing, exposure rate, and other factors.

2) Radiation effects have biological meaning and relevance beyond simple destruction of cells, tissues or organisms. Radiation effects on individual organisms have meaning in relation to such general phenomena as mutation rate, evolutionary level, and the aging process (Woodwell and Reubuck, 1967; Sparrow, Underbrink, and Sparrow, 1967; Johnson, 1963; Curtis, 1966). Radiation effects on communities involve not simply destruction, but effects on balances between respiration and photosynthesis, balances of production by different community strata and components, and balances between populations.

3) At both organismic and community levels a wide range in relative sensitivity to radiation exists. Sensitivity of individual organisms, from bacteria to man, ranges over several orders of magnitude. Sensitivity of communities ranges through at least two orders of magnitude, as represented in the lichens and forest vascular plants of this study.

As a basis for the correlation of radiation sensitivity with evolutionary level, it is tempting to assume that the more complex the organism, the greater the variety, interdependence, and probable range of sensitivities of its essential functions and the more sensitive it may be to irradiation. Thus, lichens, mosses, and certain algae appear relatively resistant; higher plants appear to be sensitive; and mammals appear to be still more sensitive. Additional support for this seems to come from recognition that in mammals several different radiation-damage syndromes are dependent on dose-rate and total exposure (Bond, Fiedlner, and Archambeau, 1965) and are traceable to the sensitivity of various tissues or tissue systems. No parallels are known among higher plants, although they may exist (Woodwell and Reubuck, 1967). In analogy at the community level the forest has greater complexity (diversity of species, growth-forms, and functional relations) than the lichen and old-field communities and is more sensitive to irradiation. The forest has also greater stability; it shows evidence of community-level homeostasis in the relative constancy of its populations and maintenance of an internal soil and microclimatic environment favorable for the persistence of those populations; this is lacking in the old field. As on the level of the organism, there is a paradoxically greater vulnerability to one kind of environmental variation (irradiation) resulting from the higher organization which confers stability in the face of other environmental variations (in relation to which species adaptions have evolved).

The basis for the forest’s sensitivity to irradiation appears to lie, however, not simply in complexity of the forest but in the greater sensitivity of woody plants (Sparrow and Sparrow, 1965). Dominance by sensitive woody species implies: (1) destruction of the dominant species themselves by lower radiation exposure than is the case in the old field, (2) more profound change in environmental factors affecting other species, resulting from changed soil and microclimatic conditions following death of the dominants, (3) more evident loss of the characteristics of the mature community than in the old field, in which other herb species replace the sensitive dominants without marked loss of community production or structure, and (4) more lasting, less easily reversible effects on the forest community, with destruction of its long-lived dominant plants.

In general, through the course of succession in terrestrial communities, there is progressive increase in community complexity and diversity, stature or massiveness, and in productivity, maturity of soil, and relative stability of populations (Whittaker, 1953). Most of these trends in succession are subject to reversals in some
circumstances, especially from the later successional stages to climax. It appears, however, that succession progresses toward communities of greater sensitivity to radiation and that relatively high sensitivity should be expected of many climax communities, especially those dominated by woody plants. It is furthermore evident that the kinds of changes in communities that occur with increased exposure to ionizing radiation—reduction of complexity, diversity, productivity, stature and massiveness, and stability—are similar in character to the retrogressive succession that may be produced by other chronic disturbances such as overgrazing. Radiation effects are thus consistent with most general observations on the behavior of communities in relation to other environmental factors—processes of succession and retrogression, responses of community production and structure to environmental severity, and relations of species populations and community composition to natural environmental gradients.

The general lack of success in discovering simple, consistently unifying correlations between gross aspects of nuclear or chromosome morphology and ecological or evolutionary patterns in the major plant and animal groups (Stebbins, 1966), emphasizes the hazards of asaying ecological patterns from cytological data alone. The relationships observed between radiation sensitivity, kinds of plants, and nuclear characteristics thus become part of a whole complex of correlations, some simple and some complex, some strong and some weak, some probably causal and others coincidental, among chromosome volume, evolutionary level, plant stature, length of life cycle, radiation sensitivity on a genetic basis in the laboratory, radiation sensitivity of populations in the field, vulnerability as affected by ratio of photosynthetic to nonphotosynthetic tissue, and ecological relations of plant populations in relation to succession and environmental severity. It would be gratifying if an effective sorting and evaluation of these relationships as they bear on community sensitivity could be stated. It may be more appropriate to say that, apart from the relation of sensitivity to chromosomal volume, they have not received the study they deserve in view of the broad interest of the evolutionary and ecological problems involved.

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