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EFFECTS OF CHRONIC GAMMA RADIATION ON THE STRUCTURE AND DIVERSITY OF AN OAK-PINE FOREST[1]

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INTRODUCTION

The higher plants and the communities they form on land have evolved under radiation exposures rarely exceeding ½ Roentgen/yr. In contrast to these low exposures, use of atomic energy introduces the possibility of contamination through war or accidents, raising exposure levels for relatively brief periods to hundreds or even thousands of R/day and to lower levels for much longer periods. Such exposures are clearly beyond the evolutionary experience of higher plants and raise the practical question of what high radiation exposures would do to the natural communities of forest and field which form the living matrix of civilization. In addition, ionizing radiation, because it has far-reaching and fundamental effects on living systems and can be controlled easily, offers new opportunities for the study of life itself.

Studies of the ecological effects of ionizing radiation seem particularly pertinent and fundamental because the principal effects of such radiation appear to be on the hereditary material, the chromosomes. Some of the most convincing evidence for this relationship is the correlation shown by Sparrow and his colleagues between the sensitivity of plants to radiation and volume of the cell nucleus (Sparrow & Evans 1961), total DNA per nucleus (Sparrow & Miksche 1961) and interphase chromosome volume (Sparrow, Schairer & Sparrow 1963). The correlation is especially significant because there is within the plant kingdom an enormous range of radiosensitivities among taxa, microorganisms being in general resistant and higher plants, especially the woody plants (Sparrow & Sparrow 1965), generally sensitive. The range spans several hundredfold among the higher plants and more than a thousandfold if mosses, lichens and microorganisms be included. The correlation between chromosome volume and radiosensitivity has been useful in predicting radiation damage to plants and even to vegetations (Sparrow & Woodwell 1962; Woodwell & Sparrow 1965), although it is clear that many additional factors are involved in the ecological effects of radiation (Woodwell 1962; Sparrow & Woodwell 1963 and others).

With the dual purpose of providing for basic studies of a natural community and of resolving some of the ecological questions associated with radiation exposures, a natural forest stand on Long Island is being irradiated chronically with gamma radiation from 9500 curies of Cesium^{137} (Woodwell 1963a). Irradiation over three years has produced striking changes in the structure of this forest, some of which have been reported elsewhere (Woodwell 1962, 1963a,b, 1965; Rebuck 1964; Brower 1965; Brayton & Woodwell 1965). The purpose of this paper is a detailed analysis of the changes in structure and diversity of the plant community during the first 3 yr following commencement of the irradiation.

Few quantitative studies are available on the effects of ionizing radiation on plant populations in nature. Bomb test sites have been restricted generally to deserts and tropical atolls with limited floras. Dosimetry has been necessarily poor at test sites and the effects on plants of radiation exposures have usually been difficult to distinguish from effects of heat, blast (Shields & Wells 1962; Fosberg 1959; Blumberg & Conard 1960; Palumbo 1961) and dust deposits (Beatley 1965). At the Lockheed reactor in northern Georgia, R. B. Platt and his students have made a series of detailed studies of the effects of intermittent mixed gamma-neutron radiation from a partially shielded reactor on both forest (Platt 1965; McGinnis 1963; Pedigo 1963) and old-field communities nearby (Daniel 1963). Here, pines (*Pinus taeda* and *P. echinata*[*]) were killed by total

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[1] Research carried out at Brookhaven National Laboratory under the auspices of the U. S. Atomic Energy Commission.

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[*] Nomenclature follows Fernald 1950.

exposures of about 7500 rads while certain dominant oaks (*Quercus alba, Q. stellata, Q. velutina, Q. falcata,* and *Q. coccinea*) survived total exposures exceeding 10,000 rads. Herbaceous old-field communities were substantially more resistant (Daniel 1963). The reactor was operated intermittently and dosimetry was difficult because of shielding from the terrain and from stems of large trees and because the ratio of neutron to gamma radiation shifts with distance from a reactor (Cowan & Platt 1963). Nevertheless, these studies have shown that exposures of 10,000 rads administered in any period of less than a few days cause widespread mortality among plant populations of both coniferous and deciduous forests. The studies have, moreover, raised the possibility of using ionizing radiation for experimental studies of the structure and function of natural vegetations.

The high sensitivity of pitch pine trees to damage from ionizing radiation was noticed in an oak-pine stand at the edge of the gamma radiation field at Brookhaven, an observation which brought widespread interest in the potential ecological effects of radiation (BNL 1959). The progressive mortality of *Pinus rigida* in this forest since 1958 has been described by Sparrow *et al.* (1965), with emphasis on the changing relationship between exposure rate, total exposure and mortality. With increasing time and increasing total exposure, the rate of mortality dropped as some equilibrium between damage and repair approached.

A complementary series of studies has been reported by Woodwell & Oosting (1965) for herbaceous plant communities of old fields on Long Island. The principal effect of irradiation here was simplification in species composition, a 50% reduction in diversity occurring at approximately 1000 R/day. Total organic production increased in the first-year community to about 800 g/m^2 at 1000 R/day and declined abruptly at higher exposures. Diversity and other indices of community structure related to species presence were approximately linearly related to the logarithm of exposure rate. Measures of dominance showed no simple relationship to radiation exposures, an observation suggesting that dominance is determined principally by competitive factors, not by the intensity of disturbance. In general, these communities were resistant to radiation damage in comparison with forests, the differences being as much as ten times (Woodwell 1965a).

One of the most revealing experimental studies of the effects of ionizing radiation on a plant community is that reported by McCormick & Platt (1963). In this study herbaceous communities characteristic of the rock outcrops of upland Georgia were transported to a gamma radiation field on the Emory University campus and radiation-induced changes in these communities were observed over a 3-yr period. The herbaceous communities here again were substantially more resistant than the forests. At 8,000 R total exposure, density of the most sensitive species was reduced, with a concomitant increase in density of more resistant species. At exposures in excess of 40,000 R, the community was drastically simplified by the selective elimination of sensitive species. An unusual type of "stimulation" of a population was observed. In the year following irradiation Arenaria, an annual, increased in abundance and vigor in the irradiated communities at the expense of Diamorpha, another annual. The cause of this shift is unknown.

Most other work on radiation effects on plants has dealt with individual plants or plant populations under cultivation. This work has been extensive (Sparrow, Binnington & Pond 1958) and has been reviewed elsewhere (Sparrow 1962; Read 1959; Gunckel & Sparrow 1961).

OBJECTIVES

The Irradiated Forest Experiment was established specifically to provide a research facility for quantitative study of the effects of chronic gamma radiation on plant and animal populations in nature. The work reported in this paper was restricted to the plant populations and had two central objectives: first, measurement of the relationship between radiation exposure and damage to plants in nature; and, second, but of no less importance, determination of the patterns of change caused in the community by irradiation.

METHODS

Design of the experiment. Design of the Irradiated Forest Experiment has been described in detail by Woodwell (1963a). The source of radiation is 9500 curies of Cesium^{137}, centrally located in an oak-pine stand on the Brookhaven National Laboratory site. The source was installed on November 22, 1961. It can be lowered into a lead container by operation of a winch in a remote station allowing safe entry to the forest. Radiation exposures range from several thousand R/day within a few meters of the source through about 1.5 R/day at 125 m and to background levels at greater distances. The source normally irradiates the forest for 20 hr daily and is shielded during 4 hr.

Two restrictions on the selection of the forest were imposed by the need for information about the effects of ionizing radiation of different intensities on this vegetation. The forest had to be relatively homogeneous throughout the area in which effects would occur. This requirement allowed replication of plots for at least the most abundant species. The requirement of homogeneity and practical limitations imposed on the size of the source by the interests of human safety meant that the ecosystem had to be relatively simple as well. The Long Island oak-pine forest contains few species and is relatively homogeneous. Furthermore, it occurs on deep, sandy soils which are comparatively uniform over large areas and on level or nearly level land (Conard 1935). In these respects both vegetation and site appeared particularly well suited to this study.

Size and arrangement of the permanent plots. Permanent plots were placed after professional surveyors had marked sixteen radii around the source, each bisecting a 22.5° sector.

Plot size and orientation were dictated by the dosimetry. The difficulty of using curved lines in the field precluded plots with curved sides. Small square plots were arbitrarily chosen as the best ultimate units. Plots were arranged in concentric ring zones (Woodwell & Hammond 1962; Woodwell & Bourdeau 1962; Woodwell 1963a). The basic plot size was established as 2 x 2 m, but within 10 m of the source, where the exposure gradient with distance was steep, plots ½ x ½ m were used and, between 10 and 30 m, plots were 1 x 1 m. The 2 x 2 m plots were used at all greater distances. Areas studied in each of the 4 yr appear in Fig. 1.

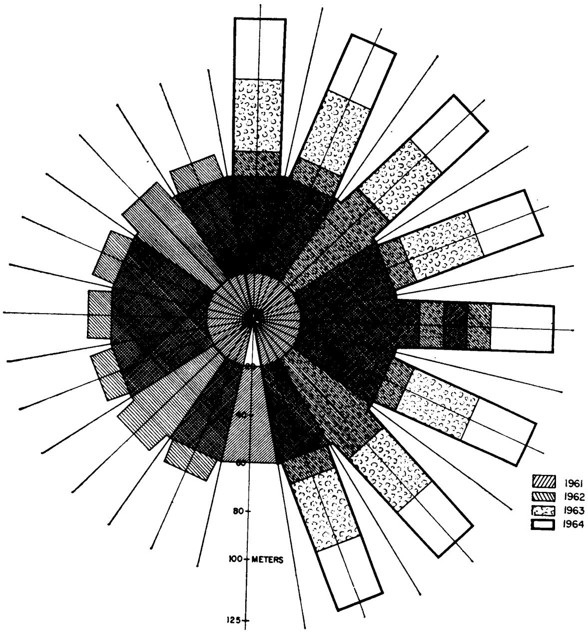

FIG. 1. Areas of the Irradiated Forest in which the vegetation was inventoried. The inventory was applied annually to all woody plants 1 m and taller; other vegetation was sampled. The methods of inventory are described in Woodwell & Hammond (1962).

The use of small plots provided detailed information about the location of any unit of vegetation with respect to the source and, within limits of the size of the plot, established the basis for the dosimetry for that plot.

Dosimetry. The distribution of radiation exposures in this forest has been measured in a variety of ways and described in detail (Woodwell 1963a). The principal variability other than distance was introduced by shielding from the stems of trees, which reduced exposures by as much as 50%. A rule of thumb useful in such work is that there is a 5% reduction in dose for each centimeter of tissue intervening in a direct line to the source. The net effect of this shielding was to allow survival of shielded plants or portions of plants at distances where the average exposures were in fact lethal for those species. Radiation exposures reported in this work are average exposures at the middle of each ring zone, measured along the central line of each sector 1 m above the ground. Original dosimetry was with film badges (Woodwell 1963a). Thus the exposure for ring zone 31, between 20 and 22 m from the source, was measured at 21 m in the center of each sector. This radiation exposure was subject to two sources of variation: first, variation contributed by shielding from the stems of trees; and second, variation across the span of each ring zone. Shielding from trees produced the frequency distribution of exposure shown in Fig. 2. In general, average exposures rose slightly at heights above 1 m as the density of vegetation decreased, and dropped substantially at the soil surface where shielding was much greater. Average energy of the radiation had parallel variation, declining near the ground and increasing with height as the mass of vegetation declined.

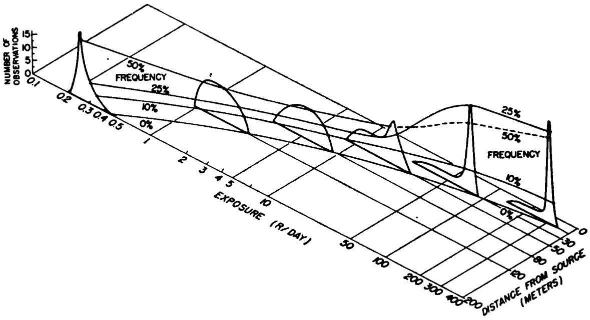

FIG. 2. Radiation exposures at 1 m above ground in the Irradiated Forest. Shielding by the vegetation produced this pattern of radiation exposures. Curves were based on about 600 measurements. The distribution of mass in the vegetation was such that the span from maximum to minimum exposure at any distance was less than that indicated at heights above 1 m and more than indicated at heights less than 1 m.

Vegetation survey. The survey of vegetation was designed to provide detailed information about species composition, physiognomy, and vigor of the vegetation and to provide as well a measure of the height and vigor of all plants 1 m tall and taller. The survey was therefore a total inventory of these plants; plants of lesser height were sampled (Rebuck 1964).

A coding system was used for recording data so they could be punched conveniently onto cards and tabulated by machine (Woodwell & Hammond 1962).

The vigor or condition of individual trees was appraised by a series of condition classes that were designed as appropriate for the species of this experiment and for the types of changes anticipated. Condition classes in angiosperms were estimates of the fraction of twigs in the living crown which bore leaves and were also an indication of the proportion of buds which survived. Length of the living crown and the presence and abundance of stem and basal sprouting were also measured. A tree which bore no leaves, either in the crown or as sprouts, was considered "dead." This meant that mortality was arbitrarily based on the absence of green foliage (for details see Woodwell & Hammond 1962).

These criteria, applied to angiosperms, could not be applied conveniently to the pines, which may retain their needles under irradiation for as much as two years. Instead, needle color and extent of shoot elongation were the basis for the condition code used in 1963, 1964 and 1965 (Rebuck 1964).

The condition of vegetation less than 1 m in height was appraised by condition classes applied to the entire population of each species in each plot. All condition data were expressed as living buds as a percentage of total buds.

In 1961 and 1962, sampling of the low shrub and sedge layers was by plots, randomly placed in rings at 10 m intervals, in which stems were counted by species and cover of any species in excess of 50% was noted. Dry weights were obtained by species from two ½ x ½ m clipped subplots. Because the method was time consuming and provided an inadequate sample it was replaced in 1963 with estimates of cover in per cent. Fifteen plots were chosen randomly from every third ring zone and cover was estimated on each of four ½ x ½ m subplots in each main plot, making a total of 60 estimates of cover in each ring zone. The sample plots were resampled in subsequent years.

RESULTS

Structures of the Oak-Pine Forest

The Long Island oak-pine forest contains four layers (synusiae, *sensu* Daubenmire 1952; Reiners 1964), their distinctiveness being largely the result of dominance by one or a few species in each layer. The tree layer includes all trees over 3 m tall. The high shrub layer consists of shrubs and trees 1-3 m tall; the low shrub layer, shrubs 0.3-1 m tall. The ground-cover layer includes all the herbaceous species and woody plants less than 0.3 m tall.

In the tree layer the most abundant species are white oak (*Quercus alba*), with 50% of the total tree density (Table 1), scarlet oak (*Q. coccinea*), pitch pine (*Pinus rigida*) and black oak (*Q. velutina*). Species present at very low densities are red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and sassafras (*Sassafras albidum*). While the density of tree stems is relatively high (2203 stems per hectare), low stature and poor crown development, of white oak in particular, give the forest an open appearance. The open aspect may be due in part to its relative youth. Age determinations of more than 100 trees showed most oaks to be 40-45 yr and none over 64 yr of age, while some of the large pines were as much as 100 yr old. These older pines survived one or more fires between 1910 and 1920, and considerable disturbance from military activity during the First World War.

TABLE. 1. Density and conditions of plants in the Brookhaven oak-pine forest in 1961 prior to irradiation. X indicates less than .001 stems/m².

Species	Height Class				Total	Avg. crown condition
	< 0.3 m	0.3–1 m	1–3 m	3 m and taller		
	Stems/m²					% live twigs
Quercus alba	.046	.150	.056	.126	.378	62
Quercus coccinea	.039	.106	.057	.049	.251	68
Pinus rigida	.035	.018	.017	.034	.104	75
Quercus velutina	.005	.029	.011	.011	.056	60
Quercus ilicifolia	.029	.029	.097	.001	.156	62
Prunus serotina		.001	x	x	.001	—
Acer rubrum	.001	.001	.001		.003	—
Quercus prinoides	.006	.005			.011	—
Sassafras albidum	.001	.001			.002	—
Vaccinium vacillans		4.53			4.53	
Gaylussacia baccata		1.45			1.45	
Myrica pensylvanica		0.71			0.71	
Lyonia mariana		0.31			0.31	
Amelanchier stolonifera		0.01			0.01	
Carex pensylvanica	1.75				1.75	
Vaccinium angustifolium	1.51				1.51	

The high shrub layer is dominated by bear oak (*Quercus ilicifolia*), the only important species with a high shrub life-form. *Lyonia mariana, Clethra alnifolia* and *Vaccinium corymbosum,* characteristics of wetter sites, and *Quercus prinoides,* more abundant in open spaces, are all infrequent here. Bear oak occurs somewhat irregularly and the high shrub layer is discontinuous.

The dense low shrub layer consists primarily of black huckleberry (*Gaylussacia baccata*) and low blueberry (*Vaccinium vacillans*). Also present are bayberry (*Myrica pensylvanica*), lambkill (*Kalmia angustifolia*) and shadbush (*Amelanchier stolonifera*).

Extensive colonies of low sweet blueberry (*Vaccinium angustifolium*) form the ground-cover layer, along with a few herbaceous species. The density of *Carex pensylvanica,* counting single clumps as "stems," approximates the density of *V. angustifolium* stems. Other species are infrequent and were not recorded from the sample plots in 1961. They include in approximate order of frequency: *Helianthemum canadense, Melampyrum lineare, Solidago odora, Aralia nudicaulis, Pteridium aquilinum, Panicum* sp., *Baptisia tinctoria, Chrysopsis mariana, Deschampsia flexuosa, Cypripedium acaule* and *Apocynum androsaemifolium.*

Zonation of Vegetation After Irradiation

Radiation effects were conspicuous in the spring of 1962, approximately 6 months after installation of the source. In general, the pattern of effects was closely related to the stratification of the vegetation, with the tree stratum the most sensitive and the ground cover layer the most resistant. Five concentric rings were apparent: a Devastated Zone where all perennials were killed and only a few herbaceous plants, lichens, and mosses occurred during the entire year; a Carex Zone in which the sedge, *Carex pensylvanica,* was the principal vascular plant; a Shrub Zone in which both Carex and the ericaceous shrubs survived; an Oak Forest Zone in which oak and the more resistant plants survived but not pine; and an Oak-Pine Zone in which the forest was intact (Woodwell 1962). During the following years these zones became appreciably wider (Fig. 3).

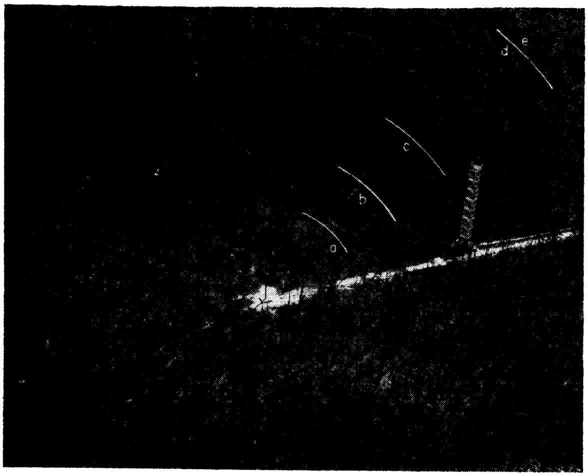

FIG. 3. Irradiated Forest, 1964. Five zones of vegetation persisted throughout 4 yr of irradiation: a, Devastated Zone; b, Carex Zone; c, Shrub Zone; d, Oak Forest; and e, Oak-Pine Forest. Zones became somewhat wider with time but changed little in terms of diversity of species.

Devastated Zone. All woody plants and most herbaceous plants were killed in the first year in the central area where average exposures were more than 200 R/day. Mortality was apparent first in the pines near the source which turned brown during the winter. By spring the mortality of deciduous plants and the sedge was conspicuous within 18 m of the course (203 R/day). A few new green leaves were borne on shielded buds of the more resistant species but most of these survived only a few weeks. By midsummer the principal species of higher plant surviving within 18 m of the source was *Carex pensylvanica,* which persisted in the zone receiving 200-300 R/day (average exposure) as small tufts in well shielded spots through 4 yr irradiation.

No adventives were observed in the Devastated Zone in the first year of irradiation (1962). Herbaceous plants indigenous to the forest did survive here, usually as isolated individuals. These included *Baptisia tinctoria, Apocynum androsaemifolium, Solidago* spp. and *Melampyrum lineare.* In subsequent years adventives have survived including principally *Erigeron canadensis* and *Erechtites hieracifolia* but their success has been limited and no clear successional pattern has been established in four summers. There is, however, a striking increase in the amount of Cladonia on the soil surface. The succession of herbaceous plants has been described in detail by Wagner (1965).

Carex Zone. *Carex pensylvanica* is one of the most radiation resistant of the higher plants of this forest. It has an irregular distribution in the normal forest, occurring as dense patches where the canopy is open and as scattered individuals or small tufts in the closed canopy stands (Rebuck 1964). In the irradiated forest it survived in zones where average exposures were less than 300 R/day but its vigor and density were reduced substantially at these high exposures (Figs. 3 and 4). Where competition by other species, especially the trees, was removed by irradiation, it expanded its populations in 2 yr to cover as much as 20% of the total ground surface and as much as 37% in 3 yr (1965). Locally, in areas of 10 m x 10 m, it covered as much as 90% of the ground, but its distribution tended to be irregular. Increases in its abundance were apparent within an exposure range of 17-160 R/day beginning in 1962 (Fig. 4).

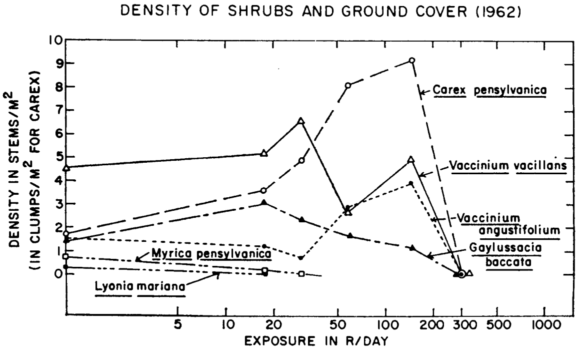

FIG. 4. Density of shrubs and ground cover in Irradiated Forest (1962). The expansion of Carex and Vaccinium populations continued in subsequent years, with the peaks of density shifting toward slightly lower exposures.

Within this zone flowering and seed set were common.

Other higher plants occurring in this zone as scattered individuals over the 3 yr of irradiation have included those listed for the devastated zone above. Of these Baptisia, Solidago, Melampyrum and probably Apocynum were present in 1962.

Shrub zone. While the responses of the several shrub species were far from uniform, the general ranges of radiosensitivities coincided sufficiently to produce a zone in which the shrubs and Carex both survived, the shrubs forming a conspicuous if discontinuous layer. The boundary of any such zone must be somewhat arbitrarily drawn. In 1962 few shrubs reached their normal stature at exposures above 150 R/day and the shrub zone was defined as extending from areas exposed to 150 R/day to areas receiving 40 R/day, where the tree canopy was about 50% normal. The shrubs survived at lower exposures in the intact forest, of course. Within the shrub zone there were individual differences in the

TABLE 2. Abundance of low shrubs and ground cover in 1963, 1964 and 1965, approximately 18, 30 and 42 months after commencement of irradiation. Abundance measured as per cent cover averaged over 60½ m x ½ m plots. Dash indicates no sample taken. Blank indicates absence of species from sample.

		Mean exposure in R/day												
	Year	3.45	4.15	5.1	6.3	7.8	10.1	13.1	17.3	23.7	34	50	81	145
								Shrubs						
Gaylussacia baccata	63	—	—	23	22	20	21	11	6.6	7.8	4.8	4.0	0.2	
	64	18	16	16	19	12	20	15	9.0	10.6	5.8	4.0	0.7	0.2
	65	22	19	19	18	19	14	12	14	11.5	6.9	3.1	0.6	
Vaccinium vacillans	63	—	—	14	18	16	18	10	14	12	7.2	3.8	1.4	1.1
	64	12	17	15	10	12	12	9.2	17	12	12	7.1	2.3	1.7
	65	11	16	9	11	9.6	12	13	13	12	13	5.1	1.9	1.3
Myrica pensylvanica	63	—	—		1.2		0.2	2.3	3.0	0.5	0.2	0.3	0.3	
	64	0.2	1.0	1.0	2.0			2.0	1.3	2.2	0.2	1.3	0.3	
	65		0.5	1.0	1.0	1.7		0.7	1.0	2.2	0.3		0.3	
Kalmia angustifolia	63	—	—					2.5						
	64				1.0			1.0					0.2	
	65					1.0							0.2	
Amelanchier stolonifera	63	—	—	0.2										
	64			0.2										
	65		0.2				0.2							
Clethra alnifolia	63	—	—											
	64													
	65													
Lyonia mariana	63	—	—					1.0	0.3	0.5				
	64													
	65		0.2	0.2	0.2		0.3	1.0	0.3			0.2		
								Ground Cover						
Carex pensylvanica	63	—	—	2.1	2.3	2.5	3.5	2.6	7.4	4.7	7.1	8.6	6.4	4.2
	64	2.5	2.7	1.7	3.8	3.5	5.0	4.4	14.2	18.1	20.5	21.9	13.5	6.7
	65	3.0	3.7	2.3	3.0	4.3	4.6	7.6	20.0	27.4	29.0	36.6	20.3	5.2
Vaccinium angustifolium	63	—	—	4.3	8.6	8.6	9.3	3.0	1.1	3.3	3.3	3.3	1.3	0.2
	64	5.8	6.1	3.2	6.6	6.9	1.7	0.6	2.5	3.1	1.5	2.6	0.2	0.2
	65	6.1	8.9	8.5	7.2	9.8	6.2	5.0	1.3	3.9	2.5	0.3	0.5	
Helianthemum canadense	63	—	—		0.2	0.3			0.2	0.3		0.3		0.2
	64					0.2				0.3		1.3		
	65	0.2			0.2	0.2		0.2		0.3		0.3		
Melampyrum lineare	63	—	—	0.5		0.2		0.2	0.5					
	64					1.0								
	65													
Solidago odora	63	—	—			0.2			0.3		0.2			
	64								0.2					
	65				0.2	0.3				0.2				0.2
Panicum sp.	63	—	—					0.2	0.2	0.2				
	64								0.2					
	65										0.2			
Aralia nudicaulis	63	—	—	0.2		0.2								
	64													
	65													
Pteridium aquilinum	63	—	—		0.2									
	64													
	65		0.2											
Lysimachia sp.	63	—	—						0.2					
	64													
	65													
Gramineae	63	—	—		0.2				0.2					
	64													
	65													
Baptisia tinctoria	63	—	—											
	64													
	65				0.2									
Rumex acetosella	63	—	—											
	64													
	65				0.2									
Apocynum androsaemifolium	63	—	—								0.2			
	64										0.2			
	65				0.2									
Euphorbia Ipecacuanhae	63	—	—							0.2				
	64													
	65													
Erechtites hieracifolia	63	—	—											
	64										0.2			
	65						0.2					0.3	0.2	

TABLE 2. Continued

		Mean exposure in R/day												
	Year	3.45	4.15	5.1	6.3	7.8	10.1	13.1	17.3	23.7	34	50	81	145
Rubus sp.	63	—	—									0.2	0.2	
	64											0.3	0.3	
	65											0.5	2.0	
Polygonum sp.	63	—	—										0.2	
	64													
	65													
Comptonia peregrina	63	—	—										0.2	
	64												0.2	0.2
	65												3.5	0.3
Erigeron canadensis	63	—	—											0.2
	64													0.2
	65													0.2

responses of the various species. In general the Vacciniums were more resistant than the Gaylussacia (Fig. 4). For example, the density of *Vaccinium vacillans* at 150 R/day was approximately the same as in the nonirradiated zone, while the Gaylussacia populations declined continuously at exposures above 17.5 R/day.

By summer of 1963 the tree canopy had been reduced to about 50% of normal under chronic exposures as low as 8 R/day, changing the environmental conditions for shrubs and ground cover greatly. These changes included gradual further shifts in the abundance of the indigenous species and invasion by a limited number of adventives. The distribution of species for 1963 to 1965 is shown in Table 2. There was a regular decline in the average cover of Gaylussacia all along the radiation gradient. *Vaccinium vacillans* populations increased slightly as the Gaylussacia declined while the Carex increased greatly. The parallel between this pattern of radiation-induced damage in the shrubs and the ground cover and that induced by fires has been discussed in detail by Brayton & Woodwell (1965).

Several species occurred only in the area where the forest had been disturbed (Table 2). These were species characteristic of early stages of succession, such as *Erechtites hieracifolia, Polygonum* sp., *Comptonia peregrina, Erigeron canadensis* and *Rubus* sp. While the presence of these species is an indication of succession in this devastated central area, it is clear that the establishment of successional species has been slow, despite the influx of an abundance of seeds (Wagner 1965).

Oak forest. The pine, *Pinus rigida,* was the most sensitive plant and was selectively killed over the largest area. Its removal left a ring of oak forest containing standing dead pines and an intact ground cover. The radiation exposures at the boundaries of the oak forest can be defined only relatively arbitrarily since shielding and possible differences in radio-sensitivity within and among species produced a transition zone spanning a considerable range of exposures. Using 50% cover as a criterion, the boundary of the forest in 1962 occurred at 40 R/day. Rapid changes were occurring in the pine populations at this time. By October 1962, 50% of the pines were dead at 16 R/day, leaving the oak forest showing varying degrees of radiation damage at exposures between 16 and 40 R/day. In 1963 by the same criteria the oak forest zone spanned an exposure range between 15 and 24 R/day and in 1964 between 7.4 and 12 R/day.

Oak-pine forest. At exposures less than 12 R/day in 1962, approximately 7 R/day in 1963 and 4.2 R/day in 1964 there was no mortality of pines or other species in the forest and composition of the plant community was unchanged. In this zone, however, and extending to areas receiving as little as 1 R/day, there was measurable reduction in the height growth of stems of trees, including both pines and oaks (Woodwell & Sparrow 1963). Radiation will probably affect succession in the forest at these low exposures in time.

SPECIES DIVERSITY

The zonation of vegetation around the source reflected a systematic decline in the numbers of species of higher plants at higher radiation exposures. The shift in numbers of species is best indicated in terms of species per unit land area. In a forest measurement of diversity on a unit land area is difficult because of the very great differences in sizes of plants. For that reason plots of different sizes were used for the several strata: plots of 1 m^2 were used for the herbs, shrubs and transgressives up to 1 m tall, and plots 2 x 2 m for larger plants. Fifteen randomly selected plots were used at each exposure level. The curve of diversity for 1962 (Fig. 5) shows an abrupt decline from about 5.5 species per plot at exposures less than 17 R/day to zero at exposures above 300 R/day. The curves of later years paralleled this at slightly lower exposures. The 50% diversity point occurred in 1962 at 160 R/day; in 1963 at about 95 R/day and 1964 at about 90 R/day. Zero diversity by this sampling technique occurred in all 3 yr at 300 R/day. The few herbaceous invaders occurring at higher exposures did not occur in the samples taken for diversity.

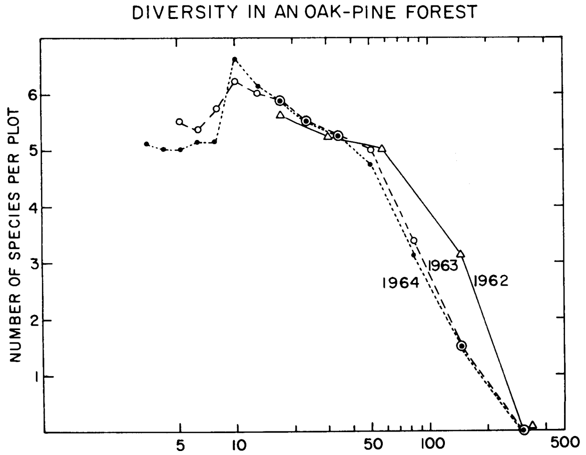

Fig. 5. Diversity of species along the radiation gradient. Diversity of plants 1 m tall and taller was measured on plots 2 m x 2 m; diversity of smaller plants was measured on plots 1 m^2. Fifteen such plots were measured at each radiation exposure in each year. Invasion had virtually no effect on these curves through 1964.

Mortality of Trees

Tree survival and radiation exposures. Pine trees near the source were the first of the plants in the forest to show conspicuous signs of damage from irradiation. During the winter and spring of 1962 needles of damaged trees became progressively mottled and brown. Browning was particularly rapid during warm periods in February and March and was followed by dehiscence. Damage to deciduous trees and shrubs was apparent only as buds failed to expand normally during the spring. Those leaves which appeared, persisted throughout the growing season until dehiscence in the fall. In pines the progression of damage was apparent throughout the year, although increments were most conspicuous during periods of hot, dry weather.

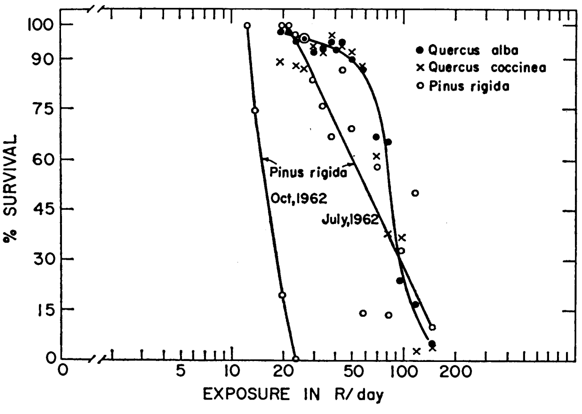

Fig. 6. Survival of trees in the Irradiated Forest in summer 1962, about 8 months after commencement of irradiation. Many pines exposed to between 20 and 100 R/day died during the summer. The rate of mortality of pines dropped markedly in the fall when the pattern of survival was that shown by the October curve. There was very little additional mortality of oaks during the summer, the next increment of damage appearing at the time of bud break in the spring of 1963.

Mortality of the three dominant tree species as measured in July and August of 1962, appears in Fig. 6. In compiling these curves, any tree bearing a green leaf was "alive" and any tree with no green leaves was "dead." Because sprouting from shielded buds at the base of the stem was common, especially among the oaks of this study, survival curves were drawn based on two separate criteria: survival of crowns alone, that is, excluding basal sprouts; and survival of trees including basal sprouting. The survival curves for trees reported here include sprouting from the base as a criterion of vitality. In the data of 1962 no distinction was possible between the survival curves of white oak and scarlet oak and both curves are indicated by a single line in Fig. 6. LD_{50} values for the oaks and pine on the basis of these curves were 84 R/day and 61 R/day, respectively at midsummer. This was reduced to 16 R/day for pine by October 12, 1962. No such change during the summer was obvious for the oaks.

In the summer of 1963 there was a conspicuous increase in the circle of damage around the source. Scarlet oak was slightly more resistant than white oak although the difference does not appear to be great in the curves of Fig. 7. The LD_{50} for scarlet oak in midsummer of 1963 was 66 R/day and for white oak, 60 R/day. The LD_{50} for pine at this time was 15 R/day, substantially the same as for the previous fall.

By summer of 1964, the average exposures at which mortality was 50 per cent of the control had declined further, to 55 R/day for scarlet oak, 35 R/day for white oak and to 7.4 R/day for pine and

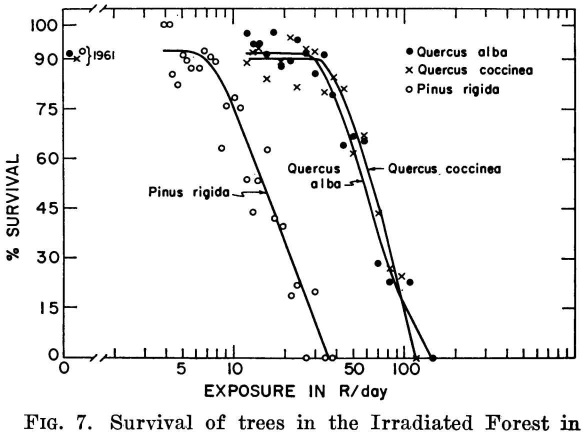

Fig. 7. Survival of trees in the Irradiated Forest in summer 1963. The survival curve for *Pinus rigida* was approximately the same as for the previous October (Fig. 6). *Q. coccinea* was at this time slightly more resistant than *Q. alba*, as predicted from the volume of the cell nuclei.

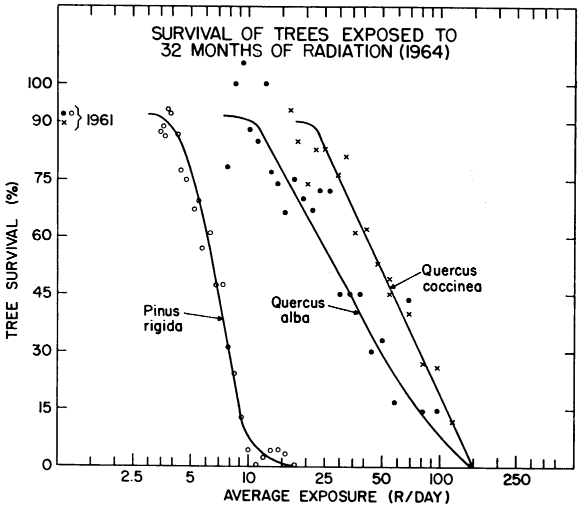

FIG. 8. Survival of trees in the Irradiated Forest in summer 1964.

the curves of scarlet and white oak had become distinct (Fig. 8).

Effects on crown condition. Survival percentages for even dominant species provide only a partial measure of change in structure of a community. Another criterion especially useful in estimating degree of disturbance is crown condition, which was in this work the proportion of living twigs within the living crown.

The crowns of trees normally vary markedly within species, with tree height, with position in the stand relative to other trees and with a host of environmental and historical factors. In closed-canopy stands death of the lower branches of tall pitch pines produces a relatively short, high crown, while in oaks, especially white oaks, branches low on the bole remain alive, even on very old trees. In 1961 before irradiation the crowns of pitch pines in this forest over 3 m tall extended along an average of 44% of the stem. The averages for scarlet, black and white oak were 62, 69 and 78%.

The short crowns of nonirradiated pines and scarlet oaks were also more dense, with fewer dead twigs within them than those of black and white oaks. Black and white oak each had an average of about 62% living twigs in their crowns in 1961; scarlet oak had 68% and pine, 75%.

Crown condition in normal trees is also related to the size of individuals. Dominant pines and scarlet oaks had a greater proportion of living twigs than smaller individuals. Pines 10 m and taller, for example, had 86% living twigs on the average, while those under 5 m had only 71%. White and black oak showed no such clear distinction with size, but fewer trees of these two species were dominants.

Crown conditions of all species declined with increasing radiation exposures. In no instance did irradiation at any level improve tree vigor. An example of the pattern of the decline appears in Fig. 9, where the probit of bud survival of scarlet oak was plotted against the logarithm of the daily radiation exposure. The sharp break in the curve for 1963 was characteristic of the oaks after 2 yr irradiation and reflects different rates of bud mortality in different ranges of exposure rates.

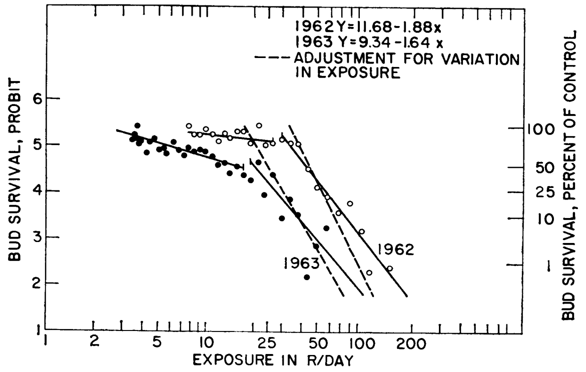

FIG. 9. Survival of buds of scarlet oak in 1962, 1963. Dotted lines are the survival curves when a correction for shielding has been entered (see text).

Shielding by the stems of trees introduces systematic variation into survival curves such as these. This variation can be removed in part by the following correction.

Within any species the pattern of survival of buds in space is closely correlated with the pattern of radiation exposure, if the lethal exposure is the same for all buds. This assumption seems justified inasmuch as there was less than 5% variation in the daily exposure to prevent buds at tips of the white oak twigs from opening during the first year of the experiment. Thus the proportion of buds surviving at any distance [distance is equivalent to an average exposure (Woodwell 1963a)], is a measure of the frequency of sublethal exposures at this distance. If 1.3% of the buds survived, it was because approximately 1.3% of the exposures were at sublethal levels. In 1963, 1.3% of scarlet oak buds survived at an average exposure of 63 R/day. But 1.3% of the exposures at this distance were actually 54 R/day or less. Presumably buds receiving exposures greater than 54 R/day died. Therefore, the lethal exposure for scarlet oak buds exposed to chronic irradiation for 18 months was closer to 54 R/day than to 63 R/day. Similarly, 62% of scarlet oak buds survived in 1963 at an average exposure of 18 R/day. However, 62% of the exposures at this distance were actually 22.5 R/day or less. The lethal exposure for chronic irradiation for 18 months was probably closer to 22.5 R/day than to 18 R/day. With this analysis, based on the frequency of bud survival and measured frequencies of various exposures, it is possible to correct the bud survival curves as shown to curves approximating those which would occur if there were no shielding.

Slopes of the bud survival curves ranged between 1.17 for *P. rigida* in 1962 to 2.60 for *Q. ilicifolia* in

1963, but otherwise lay between 1.4 and 1.8. This shows that at the higher exposures the increase in bud mortality (in probit units) per unit increase in the total exposure (as the common logarithm) was approximately equal among all species. A similar relationship appears to hold among the much lower slopes of the curves characteristic of low exposure rates. The occurrence of these two sharply different survival rates at different exposure rates suggest that there are at least two mechanisms by which radiation damage occurs in plants but how these work is not known.

Relationship between mortality and size of trees. The mechanisms by which mortality from ionizing radiation occurs in plants are far less well known than for mammals. One of the most attractive hypotheses is that irradiation simply kills the meristematic tissue, especially the buds in perennials, reducing the plant's capacity for growth. This hypothesis is based on the widely accepted observation that irradiation has its most important effects on the chromosomes. Indeed, it is now widely accepted that radiosensitivity is correlated at least in plants with the average volume of the chromosomes (Sparrow 1962). Since chromosomes in actively growing tissue tend to be large, these cells are assumed to be the most vulnerable, and centers of active growth, such as the buds, are the most sensitive tissues.

If this hypothesis is correct, size of a plant in terms of numbers of buds should be an important factor influencing survival, the more buds the greater the chance that a plant will survive. Large trees would seem to have a decided advantage over small trees, and indeed, a previous study of a small population of *Pinus rigida* trees along the perimeter of a gamma irradiated garden at Brookhaven National Laboratory suggests that such may be the case (Sparrow *et al.* 1965). If so, the probability of tree survival should be simply p^n, where p is the probability of bud survival and n is the number of buds. The objective of the study reported here was to test this hypothesis among the tree populations of the irradiated forest.

Dosimetry proved a major consideration in this study. The lateral variation tended to be random; vertical variation was systematic with a regular increase in average exposure with height to the point where there was an unobstructed line of sight to the source. This meant that the average exposure at 1.0 m above the ground was a fair estimate of the mean exposure for the above ground portions of the tree, but that certain portions of a large tree, such as the crown, received higher exposures, while other portions, such as buds along the stem on the shielded side, received lower exposures. The variability meant that species which commonly sprout from the root crown or the base of the stem had a relatively high probability of producing sprouts from buds shielded by the thick base of the tree.

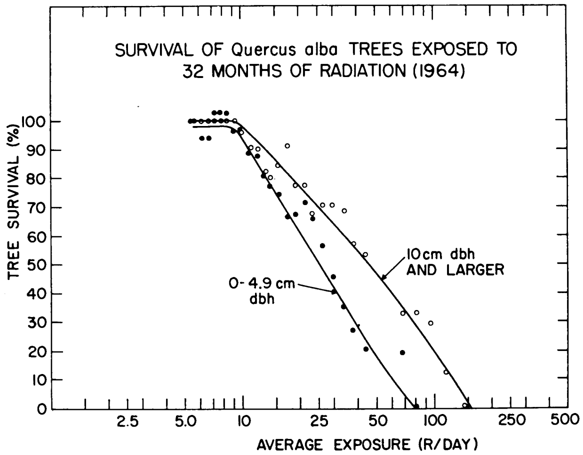

FIG. 10. Survival of large and small *Q. alba* trees exposed for 32 months to chronic irradiation (1964). Basal sprouting was included as a criterion of survival.

The effect of this type of shielding was particularly conspicuous in the oaks. Survival curves for white oak trees of different sizes, based on the presence of one or more green leaves in any position on the tree including basal sprouts, appear as in Fig. 10. There is little question that larger trees survived greater average exposures than smaller trees. The LD_{50} (in 1964) for trees with a dbh of 4.9 cm or less, taken from this graph, was 26 R/day. For trees 10 cm or more in diameter it was greater by a factor of 1.7 or 45 R/day. No small trees survived exposures above 80 R/day, while larger trees survived to 160 R/day. The curves, moreover, diverge, showing that at high exposures the size effect was intensified.

If similar survival curves are constructed eliminating basal sprouting as a criterion of survival, the larger trees still appear to be more resistant but the LD_{50}s occur at substantially lower average exposures (Fig. 11). Here the LD_{50} for crowns of trees 4.9 cm or less in diameter was 17 R/day; that for trees 10

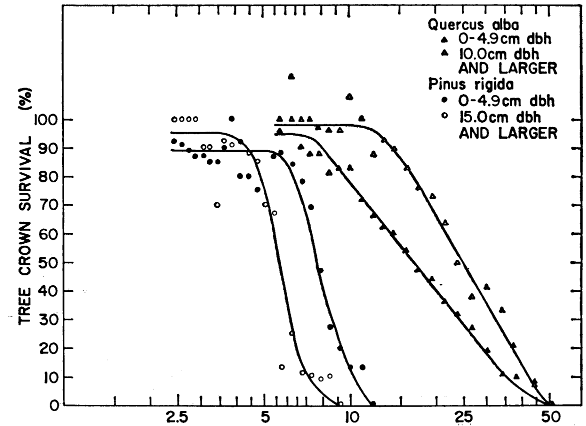

FIG. 11. Survival of large and small *Q. alba* and *Pinus rigida* trees exposed for 32 months to chronic irradiation. Criteria of survival based entirely on crown condition, omitting basal sprouting.

cm dbh and more, 25 R/day. The new curves, free from any effects of sprouting at the base on the survival of trees, converge at the highest exposures, showing that the size effect in crowns is reduced at increasing exposures.

A similar pattern occurred in scarlet oak, although basal sprouting is much less common in this species than in white oak.

In *Pinus rigida* persistent sprouting from the base of the tree is unusual. Most, perhaps all, trees arise from seeds, not from sprouts. This meant that the pattern of apparently greater resistance to irradiation due to basal sprouting as seen in the oaks did not occur. The survival curves for tree crowns, shown here, are survival curves for the entire tree as well. But the pattern of size-effects was reversed! In pine trees 4.9 cm dbh and smaller had an LD_{50} of 7.7 R/day. Trees 15 cm dbh and larger had an LD_{50} of 5.7 R/day, about 26% less than that for the smaller trees. The curves, moreover, are parallel, showing that there is no change in apparent relative sensitivity of large and small trees with change in daily exposure.

Thus, in oaks and pines survival of crowns of large and small trees was reversed: in oaks large trees appeared to be more resistant; in pine small trees were more resistant. In oaks the difference due to size declined toward higher exposures; in pine there was no such effect.

Some insight is gained into this apparent paradox by consideration of bud survival apart from tree survival. This was done by measuring the survival of buds on each tree as a fraction of the total number of buds on the trees. These data can then be plotted to determine an LD_{50} for buds. In all species the LD_{50} for buds declined with increase in tree size as shown in Fig. 12. Thus, in larger trees of all species a smaller fraction of the buds present survived, raising the question of whether buds of large and small trees vary in radiosensitivity. Evidence available from an extensive series of studies of bud sensitivity in this forest early in the experiment suggests that terminal buds from various parts of the crowns of trees of all sizes vary little in sensitivity. In this study in 1962 all buds of white oak receiving 41 R/day or less survived; those receiving 43 R/day or more died, and the variability spanned about 2 R/day. There appears to be no basis for assuming that buds of large and small trees have different radiosensitivities.

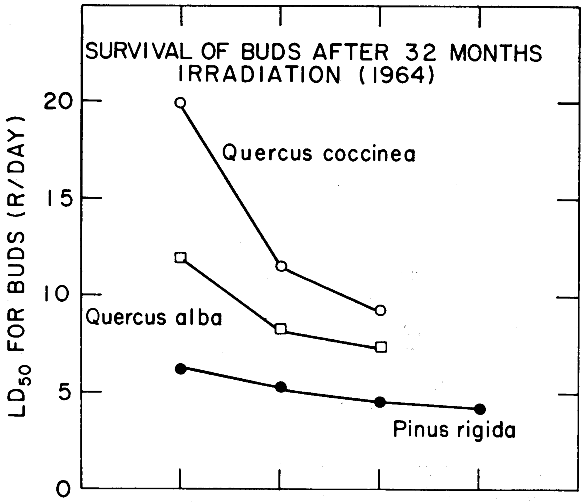

FIG. 12. LD_{50} for buds of trees of different sizes. The differences appear to be a complex function of size and the shape of the tree crown in relation to variation in the radiation field; not due to intrinsic variability in the sensitivity of buds.

It seems more probable to assume that the patterns observed are a complex function of tree size and its effect on shielding. Support is gained for this conclusion from a detailed study of the variability of the radiation field and from consideration of the form and regenerative capacity of the trees. The radiation field varies due to shielding from the stems of trees (Fig. 2). It is clear that there may be a factor of 3 variability in exposure at 1 m above the ground. At greater heights in the forest, the lower end of this span becomes abbreviated, since the trees contain less total mass near their tops and shielding is reduced. Thus, the crown receives a higher average exposure than the average at 1.0 m above ground. From detailed measurements of dose in the forest it is possible to calculate that at 80 m from the source where the 1 m mean exposure is 6.1 R/day the mean exposure for 10 m is 1.42 times greater or 8.6 R/day. Thus, any tree 80 m from the source whose living crown was entirely above 10 m in height would be receiving 6.1 R/day at 1 m above ground but 8.6 R/day in the crown. Any estimate of the LD_{50} of a population of such trees would be low if based on the 1.0 m exposures.

This specific example appears to apply to the larger pines and not to the oaks because of differences in the structure of their crowns. Large pines tend to have short living crowns in the top of the tree with little or no sprouting from the stem below the living crown. The oaks, especially white oak, tend to have sprouts all along the stem. Thus, in the oaks the living crown usually extends to within 1.0 m above ground and the 1.0 m mean exposure is a fair estimate of the exposure of the tree. In the larger pines the 1.0 m exposure is an underestimate of the exposure of the crown. This means that for pines whose crowns occur principally above 10.0 m the LD_{50}s must be corrected for the vertical variation in dose. No such correction is necessary in the oaks.

Entering this correction for tree form and for the measured variability in radiation field reverses the survival patterns for pine trees of different sizes, showing that the larger trees of pine do survive mean exposures equal to or greater than the exposures survived by smaller trees and that the observations are, in fact, consistent among both oaks and pines.

Thus, it seems that bud survival is an excellent criterion of vitality in trees and the hypothesis that mortality of buds is a primary effect of irradiation appears here to be supported. In general, trees with large populations of buds have a higher probability of survival, not only because of the larger numbers of buds, but also because tree size itself contributes shielding for buds, increasing the probability that any bud will survive. The simple theoretical relationship that the probability of death of a tree is expressed by p^n, where p = the probability that a bud will die and n = the number of buds on a tree is not borne out in detail simply because the probability of bud survival varies not only with the average dose but also with size of the tree.

DISCUSSION

RADIATION EFFECTS ON STRUCTURE OF THE FOREST

The effects of 3 yr irradiation of the oak-pine forest have in general been closely related to the reduction in diversity of species at increasing radiation exposures. Invasion was restricted to a few individuals of a very limited number of species of radiation resistant and rapidly reproducing herbs (Wagner 1965). Densities of invading populations have been so low that adventives were not represented in most of the samples used for diversity measurements. Thus, reduction in diversity (Fig. 5) has been progressive and cumulative over the 3 yr period, reflecting accurately the advance of the perimeter of radiation damage. There is every reason to expect that the rate of invasion by herbaceous plants will increase within the next two to three years, changing diversity relationships along the gradient markedly as the more radiation resistant herbaceous plants of early successional communities accumulate. Wagner (1965) has shown that there is an abundant rain of seeds of many successional species in the central area of the forest and that populations of herbaceous species are in fact accumulating. Invasion has been slow, however, and it is true that through the first three years of chronic irradiation the principal effects on the vegetation have been reduction in the diversity of species and that this reduction has been to all practical purposes unaffected by succession.

It seems especially significant that the reduction in diversity is correlated with the gross morphology of plants. There is a cline of life forms from mosses, lichens, algae and decay organisms at the highest exposures to the sedge zone, a zone of low shrubs and finally, the high shrub and tree zones at the lowest exposures. Observations from numerous other studies of radiation effects (Platt 1965; McCormick & Platt 1963; Woodwell & Oosting 1965; Sparrow & Woodwell 1965; Sparrow & Sparrow 1965; Woodwell & Gannutz 1965; and others) have shown beyond question that in general, among plants the lower forms are more radioresistant, herbs somewhat more sensitive, and woody plants most sensitive of all. The pattern of survival in the irradiated forest is no coincidence, therefore, but appears to reflect a general pattern of radiosensitivity within the plant kingdom. This pattern in itself would seem to be incidental and probably of little consequence except that similar patterns of life forms occur commonly in nature.

Perhaps the most conspicuous parallel with the cline of radiation effects is the gradation of life forms from tundra to forest. Here, in the north at least, even many of the genera are the same, with lichens, especially Cladonia, in the high Arctic and on the most exposed mountain peaks; in sheltered spots Carex and numerous low-growing shrubs occur, followed at slightly lower latitudes or less severe exposures by ericaceous shrubs including especially species of *Vaccinium,* and then, trees. The parallel is striking and is repeated with less fidelity of genera along such other common environmental gradients as occur in boreal bogs (Gates 1942) and on marine sand strands (Boyce 1954).

These parallels are striking and important in that they emphasize that the gross patterns of radiation effects on vegetation are by no means unique but have abundant precedent in nature despite the fact that radiation levels have been so low as to have had little or no influence on the selective processes of evolution, at least in the period in which the higher plants have evolved. This means that the evolution of radiosensitivity in all of its various ramifications has been controlled not by radiation but by other factors, or combination of factors, that have had the same selective influence that ionizing radiation might have had. The result is a very wide range of radiosensitivities among species of plants (Sparrow & Woodwell 1963), and a clear correlation between radiosensitivity and the distribution of plants along environmental gradients in nature. The generality appears true that radioresistant plants tend to be resistant to environmental extremes other than radiation, although the specific relationships between radioresistance and ecological amplitude in terms of drought tolerance, tolerance of heat and other factors and combinations of factors remain to be established.

One of the most important factors influencing radiosensitivity appears to be chromosome size and number (Sparrow 1962) and the inference seems justified that the evolution of radiosensitivity must be closely related to the factors influencing the evolution of the size and number of chromosomes. A logical extension of this inference is that the size and number of chromosomes influences susceptibility to environmentally induced mutations, using "mutation" here in its broadest sense, and that the evolution of mutability is what has in fact determined the patterns observed. While there are many other factors including both environmental factors and factors intrinsic to plants that influence radiosensitivity, this

TABLE 3. Daily and cumulative exposures to reduce average crown condition to 50% of nonirradiated trees.

Species	1962		1963		1964		1965	
	R/day	Total	R/day	Total	R/day	Total	R/day	Total
Quercus alba	39	7410	12.0	6600	10.0	9150	7.8	9984
Quercus coccinea	42	7980	16.0	8800	12.5	11438	6.2	7936
Pinus rigida	37	7030 (July)	6.1	3355	4.75	4346	3.9	4992
	11.2	2131 (Oct.)						

general hypothesis offers the most logical and generally satisfactory explanation of the striking relationship between the distribution of radiosensitivity among species of plants and their ecology.

DIVERSITY AND ABUNDANCE

The experiment provided an unusual opportunity to study the effects of disturbance on the diversity and abundance of plants in a forest. During 4 yr irradiation there was no substantial shift in the species list reported for the entire area of the forest prior to irradiation (Rebuck 1964). Adventives after irradiation was started probably included *Erigeron canadensis, Erechtites hieracifolia, Euphorbia Ipecacuanhae, Carex umbellata, Bulbostylis capillaris* and *Juncus tenuis*. Certain of these, such as *Juncus tenuis* and *Bulbostylis capillaris* were restricted to the road, where disturbance was severe during installation of the source, and their presence is probably not attributable to irradiation. The other "adventives" are usually extremely rare within the forest but do occur in areas where the vegetation and soil have been disturbed. It is of course possible that some were in the area in 1962 and overlooked. In any case, despite the drastic changes in the forest by irradiation, there has been no large influx of successional species and those populations that have become established have been very small. Succession has been slow and it is clear that the major effect of irradiation has been a reduction of diversity at high exposures.

This reduction in diversity of plants was progressive and cumulative over the 3 yr period. The rate of change declined with time and, hence, with increase in cumulative exposure. Between 1962 and 1963 there was a drop of 65 R/day in the exposure to reduce diversity to 50% of normal but in the following year the decline was only 5 R/day, or about 1/13 that of the previous year (Table 3), suggesting that in terms of diversity alone an equilibrium was being established rapidly by the third year of the experiment.

No completely satisfactory explanation of the increase in diversity observed in 1963-1964 at 10 R/day is possible (Fig. 5). While the peak may represent the normal variability encountered in a forest, it occurred in a zone in which the ground cover was more than usually luxurious and where the tree canopy has been substantially reduced (Fig. 3). The luxuriance of the ground cover was a consequence of the reduction in the canopy (Reiners 1964) and it seems reasonable to assume that the rise in diversity measured in 1963 and again in 1964 was also due to this opening of the canopy. If true, the effects of irradiation do not appear to be simply a reduction in diversity, but, at relatively low exposures where disturbance has been less, an increase in diversity as well. It seems quite possible that once a succession has been re-established involving herbaceous species that are adventives to the forest, diversity will increase.

The various indices of abundance and growth of woody species declined in close parallel with the decline in diversity along the radiation gradient. This relationship was in sharp contrast to the behavior of herbaceous species of old fields, where removal of one species by irradiation opened a niche for more radiation resistant species whose populations expanded rapidly (Woodwell & Oosting 1965). Woody species doubtless show similar responses but their generation time is great enough that the trend toward replacement was not measurable in as short a time as 3.5 yr. An analogous situation occurred in the Southern Appalachian Mountains during the latter part of the first half of this century when the chestnut blight (*Endothia parasitica*) selectively removed the chestnut from extensive oak-chestnut stands. In that instance the oak populations appear simply to have expanded to use the resources released by the chestnut (Keever 1953). Selective mortality of pine in the oak-pine forest would probably result in a similar replacement by oak, no matter the cause of death of the pine. The replacement would be slow, especially in comparison with the replacement observed in the old field, where there appear to be several species with broadly overlapping niches capable of replacing one another within one growing season. Responses of the forest to this type of disturbance thus appear sluggish and the reduction of diversity remains for several years the best single index of disturbance.

The nature of the relationship between the degree of disturbance and species surviving in this forest is shown even more clearly by consideration of coefficient of community (Jaccard 1912, 1932). Coefficient of community is the number of species shared by two communities expressed as a percentage of the total number of species in both communities and is thus an index of the similarity in species composition. It has been used previously in connection with ionizing radiation by Woodwell & Oosting (1965) to examine community relationships along a gradient of radiation in old field communities. Coefficients of community, computed between the communities at various radiation exposures and the community at the lowest exposure for whach data were available in the forest each year, appear in Fig. 13. There was an approximately linear decline in the curve of coefficients of community when this curve was plotted on semi-logarithmic paper, a relationship similar to that for diversity (Fig. 5). The curve of coefficients of community, moreover, spans approximately the same radiation exposures that the diversity curve spans, showing that the communities persisting at the higher radiation exposures contain the same species as occur at lower exposures except that there are fewer species surviving the high exposures. This relationship is in contrast to the old fields where the communities surviving high exposures were substantially different in species from those at lower exposures, a relationship which shifted the coefficients of community curve to much lower exposures than the diversity curve. Thus there is a sharp difference between the response of forest and the field, again based principally on the capacity of the herbaceous plants to replace one another rapidly.

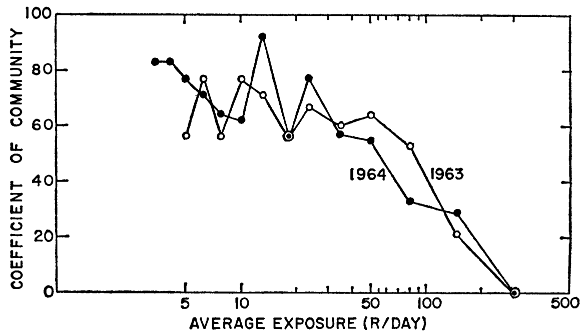

FIG. 13. Coefficient of community for 1963 and 1964.

The observation that diversity, abundance and, now, coefficient of community, all decline linearly with a logarithmic increase in exposure rate shows that change in these community parameters is proportional to the increase in radiation exposure rate as a fraction of the initial rate ($\frac{\Delta R}{R}$) rather than to absolute values of radiation alone (R). A similar relationship has been observed along radiation gradients in old fields (Woodwell & Oosting 1965) and along other environmental gradients as well (Whittaker & Fairbanks 1958).

RADIOSENSITIVITY AND CHROMOSOME VOLUME

Prior to establishment of this experiment an attempt was made to predict the effects on the vegetation of the first years' irradiation (Sparrow & Woodwell 1962). The prediction was based on correlations between nuclear size, chromosome number and radiosensitivity as established by Sparrow & Miksche (1962). The prediction was in general correct, although most plants in the forest were more sensitive than anticipated (Woodwell & Sparrow 1963). Certain differences predicted did not become apparent the first year. Scarlet oak for instance was expected to be substantially more resistant than white oak, since there is a factor of nearly 2 between them in nuclear volume. Mortality of these two species in the first year of the experiment was identical (Fig. 6) and the observations of mortality fell precisely intermediate between the two predictions (Woodwell & Sparrow 1963). Subsequently, however, the differences in radiosensitivity predicted did in fact appear (Figs. 7, 8), showing the prediction of greater resistance for scarlet oak to have been correct, although the difference did not span a factor of 2. In 1964-1965, however, secondary effects appear to have increased mortality of scarlet oak appreciably (see below).

The predictions for the ericaceous shrubs were less accurate. On the basis of nuclear volume alone for instance, *Gaylussacia baccata* was expected to be the most resistant of the shrubs. It was in fact the most sensitive (Figs. 4, 5). The reasons for its relative sensitivity appear to be several, among them greater intrinsic sensitivity at the cellular level, and a comparatively low capacity to regenerate from sprouts after damage to the shoots. Interestingly enough, the effects of irradiation on the shrub synusia and ground cover parallel quite closely the effects of burning. High frequency of fires depresses populations of Gaylussacia most severely, the Vaccinium least, and usually results in an increase in the cover of Carex. It is also interesting, although perhaps coincidental, that the pattern of radioresistance and resistance to fire in this shrub and sedge community follows the gross pattern of life forms established in the forest as a whole: the largest form, the Gaylussacia, is most sensitive, the smallest, the sedge, most resistant. This observation would seem to add support to the general hypothesis that gross morphology plays a far more important role in determining radiosensitivity than has been recognized heretofore (Brayton & Woodwell 1965).

RELATIONSHIP BETWEEN CHRONIC, CUMULATIVE, ACUTE AND FALLOUT EXPOSURES

The experiments reported here have been based on chronic exposures averaging 20 hr daily and dosimetry has been expressed in R/day. This treatment of dosimetry has become conventional for studies of chronic irradiation principally because of its convenience. It has the disadvantage of emphasizing the effects of exposure rate as opposed to cumulative exposure, an emphasis which may be in some respects misleading. We can examine, for example, the daily and cumulative exposures to reduce average crown condition to 50%, a sensitive measure of radiation damage (Table 3). While there was a progressive decline from year to year in the exposure rates to reduce crown condition to 50%, the cumulative exposures were far less consistent. Indeed, the cumulative exposure for white oak and pine declined appreciably between 1962 and 1963, while that for scarlet oak increased. In the following years there was a general increase for all species in the cumulative exposures to reduce crown condition to 50%. This was broken in 1965 for scarlet oak, which was subject to sudden mortality late in the season in 1964 (after the inventory) and again in 1965. The effect of this unusual mortality, the specific cause of which is yet unexplained, was to reduce the exposure at 50% crown condition to 6.2 R/day and the total exposure to 7936 R, slightly less than the 1962 total. Thus, for scarlet oak, due to a unique pattern of mortality that is doubtless related to secondary effects of irradiation, total exposure to reduce the crown by 50% approached a constant value over four years of about 7900 R. In the other species after the 1962 decline in total exposure, there was an annual increase through 1965, the annual increase approximating 25% of the 1963 total.

These data show clearly that under certain circumstances cumulative exposures required to produce any standard degree of effects may decrease, increase or even remain constant over periods of a year or two and there is good reason to examine in detail the significance of these changes. First, the only possibilities for real relationships between cumulative exposures and effects are limited to (a) the possibility that radiation exposure increases with time or (b) remains constant. In experiments where cumulative exposures decline with time as indicated above for 1962-1963 and as reported previously by Sparrow *et al.* (1964) for LD_{100} of *Pinus rigida,* the criterion of damage must lag by months, possibly many months, the accumulation of the damaging exposure. Thus the cumulative exposure measured at the time the damage appears exceeds the exposure causing the damage by a substantial amount. With increasing time damage progresses, "catches up" with the cumulative exposure. No general rule defining the lag-time seems possible since it appears to depend in large degree on the criterion of damage. Certainly for 50% bud survival in the trees of this study, lag-time was about 1 yr. For the LD_{100} used by Sparrow *et al.* for *Pinus rigida* around the Gamma Irradiated Forest at Brookhaven it exceeded 3 yr. The increase in lag-time when mortality of an entire tree is the criterion is understandable when one realizes that mortality of a tree, especially in a radiation field subject to shielding by tree stems is a far more complex and time consuming process than mortality of 50% of the buds. Thus it seems that those situations where cumulative exposures decrease with time are really instances where cumulative exposure is not a good criterion of the damaging exposure and in experiments using chronic irradiation and perennial plants this condition may obtain for as much as 3 yr, depending on the criterion of damage.

The question devolves to whether cumulative exposures to produce any standard effects are in fact constant over a range of chronic exposures of few to hundreds of R/day, or increase through this range. For this consideration the data above on white oak and pine and the earlier data from the Gamma Radiation Field (Sparrow *et al.,* 1964) seem especially significant. The pattern of survival of the scarlet oak above appears unusual; certainly the patterns of mortality have been erratic, suggesting secondary causes. Elimination of scarlet oak makes it appear that cumulative exposures to produce a standard effect (50% crown survival or LD_{50} of pine) in perennials do increase slowly with time when irradiation is chronic. Thus there seems to be good reason to use daily exposure (or exposure rate) and not total exposure as the primary criterion of radiation exposure, especially in experiments with chronic radiation and perennial plants.

There is persistent temptation to extrapolate data such as those from the Irradiated Forest to the types of radiation exposures that a bomb or a reactor explosion might produce. Such extrapolations are difficult and speculative for several reasons. First, the quality of the radiation is different. A nuclear explosion would produce a very short pulse of neutrons and the fallout would include as principal radiation hazards to life both beta and gamma emitters. The relative importance of these in bomb fallout have been discussed in various papers (see Woodwell 1965b). The best extrapolation of the Irradiated Forest data appears to be based on the 1962 data using one-half the total exposure accumulated in the first six months of the experiment (Woodwell & Sparrow 1965). This, of course, neglects the influence of the pulse of neutrons (important only near the explosion) and the beta component of the fallout. It also accounts only crudely for the difference in exposure rates, which would be initially high in the fallout field, declining exponentially with time. The effect of this shift in exposure pattern is not known. These considerations have been discussed in detail elsewhere and inferences drawn as to effects (Woodwell 1965b). Despite the precautions necessary in making quantitative appraisals of the effects of fallout fields, the observations are directly pertinent to qualitative assessments of potential effects of radioactive fallout from any source on natural communities. There can be little question that exposures of a few thousand Roentgens would produce damage equivalent to that of the most severely damaged areas of the Irradiated Forest. Such effects with their implications for man are clearly frightening and worth great cost to avoid.

SUMMARY

1. An oak-pine forest in central Long Island, New York, has been irradiated chronically with

gamma radiation from 9500 Ci of Cesium^{137} during 4 yr.

2. Effects on the structure of the community were expressed best by change in diversity (number of species per unit land area). There was a 50% reduction in diversity at 160 R/day during the first 6 months' exposure. Diversity declined regularly in subsequent years despite the influx of several herbaceous successional species in the damaged zones close to the source.

3. The reduction in diversity was systematic in that plants with large life-forms were most sensitive. This resulted in zonation of the vegetation around the source, five zones being conspicuous although not always clearly delineated. These were a Devastated Zone close to the source where all indigenous higher plants were killed; a Carex Zone where *Carex pensylvanica* was the principal survivor; a Shrub Zone where both Carex and the ericaceous shrubs survived; and Oak-Forest Zone where the pines had been killed; and an Oak-Pine Zone where the forest was intact. These zones persisted throughout the experiment.

4. Survival of trees varied with tree size, an increase in size contributing generally to increased resistance because of the greater number of buds and because of the increased probability that certain buds would be shielded. In these studies the survival of buds as opposed to survival of trees proved a particularly useful criterion of radiation damage.

5. It seemed particularly significant that radiation resistance was correlated with life forms of the plants, the most resistant being low growing species. The pattern of change down the radiation gradient paralleled that along other environmental gradients, especially the tundra to forest ecotone.

6. Radiosensitivity of plant populations in nature is also broadly correlated with the average size of the chromosomes at interphase as suggested by previous work.

7. The relationships between radiosensitivity and chromosome size and between radiosensitivity and the ecology of plants suggest that the evolution of radioresistance in plants has paralleled the evolution of other aspects of ecological amplitude. Indeed, since radiation has probably not been a selective factor affecting the evolution of the higher plants, it seems necessary to postulate that other environmental factors have had effects that would parallel the evolutionary effects of radiation. These would seem to affect the evolution of susceptibility to mutation.

8. The results of this study can be used to infer the effects of fallout radiation on other natural communities.

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