SEP 10 1965

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H.C. $ 1.00; MN .50

BNL 9437

MASTER

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EFFECTS OF CHRONIC GAMMA IRRADIATION ON LICHEN COMMUNITIES OF A FOREST[1]

G. M. WOODWELL AND T. P. GANNUTZ[2]

Biology Department, Brookhaven National Laboratory, Upton, N. Y. 11973

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[1] Received for publication

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

[2] Graduate Student, Biology Department, Clark University, Worcester, Mass.

This paper was submitted for publication in the open literature at least 9 months prior to the issuance date of this Microcard. Since the U.S.A.E.C. has no evidence that it has been published, the paper is being distributed in Microcard form as a preprint.

ABSTRACT

Chronic gamma irradiation of an oak-pine forest on Long Island reduced populations of corticolous and terrestrial lichens in approximate proportion to the rate of irradiation. The decline in species diversity was approximately linearly related to logarithmic increases in daily radiation exposure. While a daily exposure of 800 R/day was estimated to have reduced diversity by 50% in the first year, a linear extrapolation of diversity, coefficient of community and similarity curves to zero suggested that certain lichen populations would survive 3 years' exposure at daily rates up to 15,000-20,000 R. There was an apparent threshold at 100-200 R/day for radiation effects on the composition of lichen communities. The crustose forms were more resistant than foliose or fruticose forms, an observation which parallels previous observations that the most radioresistant higher plants tend to be of short stature.

THE RELATIVE resistance of microorganisms to ionizing radiation has led to the assumption that lichens are also highly resistant, although few data have been available. Brodo (1964) measured growth and survival of corticolous lichens along the radiation gradient in the Brookhaven Irradiated Forest and showed that there was growth of individual thalli and an apparent increase in numbers of thalli at radiation exposures which killed all higher plants. Thalli of Physcia stellaris, Lecanora chlarotera and L. caesiorubella survived exposures in excess of 1000 R/day during more than 1½ years. These observations, plus consideration of patterns of growth and chromosome size in fungi and algae, led Brodo to the conclusion that lichens in general are indeed highly resistant to radiation damage and are probably among the most radioresistant plants. He believed the changes he observed in sizes of thalli and density of thalli to be related primarily to changes in the higher plant vegetation and not to the direct effects of irradiation on the lichens. He did not, however, do a systematic study of the distribution of lichen populations along the radiation gradient to determine whether diversity, density or other aspects of community structure had been affected. The objective of the present study was an extension of Brodo's observations to measure the changes in the lichen communities along the radiation gradient.

METHODS--The Irradiated Forest Experiment was established in 1961 and irradiation was commenced in November of that year (Woodwell, 1963). The stand selected for the experiment was a relatively homogeneous oak-pine forest characteristic of glacial outwash sands in central Long Island. The principal trees were Quercus alba,[*] Pinus rigida, and Q. coccinea. Shrub cover was the Vaccinium-Gaylussacia synusia described by Reiners (1965). The survey reported in this study was completed in July, 1964, about 32 months after the start of the experiment. At this time there was a gradient of damage to the higher plant vegetation from mortality of all indigenous species at exposures above about 300 R/day (at 15 m from the source) to minor effects on growth and reproduction at exposures below 1 R/day. The gradient was apparent in the spring of 1962, although it spanned a very narrow zone of 10-20 m depth at that time. Continued exposure has merely expanded the area of damage, not altered the pattern of the gradient. The gradient of damage to the higher plant vegetation follows closely the life forms of the species; the species with smallest stature are the most resistant, the largest the most sensitive (Woodwell, 1965). The lichen populations sampled for this study occurred along this gradient of damage to the higher plant vegetation.

Sampling procedure--Lichen populations were sampled on the plots marked in the original land survey of 1961 (Woodwell, 1963). At 5 and 7 m from the source the ultimate sampling unit for lichens was one rectangular plot ½ m x 8 m, arranged with the long dimension forming a chord of a circle around the source. At 10 m the ultimate sampling unit was 1 x 4 m, and at 25, 30 m, and in the community called "control," 2 x 2 m. A plot of numbers

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[*] Higher plant nomenclature follows Fernald (1950).

of species per unit area showed that a sample of four, 2 m x 2 m plots (16 m^2) contained more than 90% of the species in seven such plots (28 m^2) indicating that four plots were the minimum sample to describe the flora (Fig. 1). In practice the numbers of plots were limited by the area available. One such minimal-area plot was taken at 5 m from the source, two at 7 m, four at 10 m and three at 25 and 30 m and in the control community.

Within plots a total inventory of lichen populations was attempted, including both lichens on the soil and corticolous forms up to 2 m. An arbitrary definition of "thallus" was established for measurement of density. For this purpose a colony of small thalli of the same species, all members of which were separated by less than 1 cm, was counted as a single thallus.

Lichens were identified to species where possible. Identifications were checked by V. A. Ahmadjian, I. Brodo, and G. W. Thompson. Responsibility for accuracy of determinations remains with the authors. Voucher specimens are in the Herbarium, Brookhaven National Laboratory. Nomenclature follows Hale and Culberson (1963).

Criteria for appraising lichen vitality were necessarily arbitrary. In general, lichens with normal form and color were assumed to be alive. Thalli which were apparently moribund were examined microscopically and the presence of the green algal symbiont was accepted as the criterion of vitality.

Average exposures of sampled plots were 2250, 1250, 620, 100, 50 R/day and about 40 mR/day in the community adopted as control. These were the exposures at the mid-point of each set of plots 1 m above the ground.

RESULTS--Of the 51 species identified in this study, 33 occurred in the control community and 11 in the community sampled at 2250 R/day. Between these extremes there was a continuous decline in species diversity and an over-all decline in the numbers of thalli per unit area (Table 1). The decline in species-diversity was approximately linear on a semi-log plot, an exposure of about 600 R/day reducing the number of species to ½ those in the nonirradiated community (Fig. 2). The most resistant species included some of the most abundant lichens of the forest: *Arthonia caesia*, *Lecidea varians*, *Cladonia chlorophaea*, *Parmelia sulcata*, *Physcia millegrana*, and *Cladonia cristatella*. Densities declined irregularly from about 17 thalli/m^2 in the control community to about 2/m^2 at 2250 R/day (Fig. 3).

Separation of lichen species by growth form (Fig. 4) showed substantially greater numbers of crustose species surviving high exposures than either fruticose or foliose forms. There were about 7.0 crustose species per 16 m^2 in the control community and 10 at 2250 R/day. Numbers of foliose and fruticose species declined along the gradient of increasing exposure from about 9 species per sample in the control community to one or less per sample at exposures of 2250 R/day. It is clear that the major decline in diversity occurred among the fruticose and foliose species. ¶Densities of foliose and fruticose species declined consistently along the radiation gradient while densities of crustose species increased erratically at intermediate exposures (Fig. 3) and declined abruptly at intermediate exposures above 1000 R/day.

DISCUSSION--The gradients of diversity and density of lichen populations at exposures above 50 R/day (Figs. 2 and 3) appear to be direct effects of irradiation and not effects of mortality of trees. Most trees were killed throughout this central zone during the first six months of the experiment (Woodwell, 1962) and lichens were consequently exposed to similar changes in microclimate by the opening of the tree canopy throughout this area. Differences in lichen diversity and density along the radiation gradient within this zone were presumably responses to the radiation gradient, not to the microclimatic effects of the death of trees.

Support for the hypothesis that radiation exposures were of primary significance for the change in lichen communities comes also from curves of coefficient of community and percentage similarity. Coefficient of community is the number of species shared by two communities as a percentage of the total number of species in both communities (Jaccard, 1902, 1912). Percentage similarity (Odum, 1950; Whittaker, 1952) weights each species by a measure of abundance to compare two communities in terms of relative similarity in quantitative composition. Both indices have been used previously to examine species populations along environmental gradients (Whittaker and Fairbanks, 1958; Whittaker, 1960; Woodwell and Oosting, 1965; Woodwell, 1965). These curves (Fig. 4) decline approximately linearly with logarithmic increase in daily radiation exposure. However, both curves show plateaus, with community similarity values of 55-65% at exposures below 50-100 R/day. These values represent absence of significant difference from the control; comparison of replicate samples from the control stand, no two of which are identical, gives similarity values in this range. The breaks in the curve at around 50-100 R/day consequently represent a threshold: at radiation exposures below this range there is no effect on lichen communities significant enough to be expressed in community similarity values; at exposures above this range the slopes of the curves express increasing departure of community composition from that of the control with increasing intensity of radiation.

Species diversity appears to be a particularly useful criterion of disturbance because of its linearity in relation to the logarithm of daily radiation exposure and its close relationship to exposure in this and other studies (Woodwell and Oosting, 1964; Woodwell, 1965). The radiation exposure to reduce diversity to 50% of that in a control community is analogous to the LD_{50} of toxicology and can be a measure of the sensitivity of a community to radiation damage.

Diversity of lichens was reduced to 50% of that in the nonirradiated community by exposures of about 400 R/day (Fig. 2). We can compare this to data from other studies. In an old field, for instance, an exposure of approximately 1000 R/day reduced diversity to 50% and approximately 150 R/day had the same effect on the higher plant community of a forest (Woodwell, 1965). On this basis the lichen community would appear to be more sensitive than anticipated.

This observation, however, may be somewhat misleading. The data on lichens were taken during the third year of irradiation; the data for the vascular plants of the forest and field were taken during the first year of exposure. Thus the lichen communities accumulated damage over a 3-year period and appear to be more sensitive when sensitivity is measured as daily exposure over 2 years than if irradiation had been for a shorter time. Observations of the progression of radiation effects on higher plants of the irradiated forest (from year to year) show that the daily exposure to cause any specific effect declined by 40-60% of the 1962 exposure over the following 2 years (Woodwell and Rebuck, 1965). If the decline were exactly one half, then the 50% reduction in diversity occurred in the first year at an exposure of about 800 R/day. By this criterion the lichen community was approximately as resistant to radiation as the old field.

Extrapolation of the diversity line to exposures higher than the maxima at which substrata for lichens are available in the irradiated forest (Fig. 2) suggests that the lichen community was, in fact, more resistant to ionizing radiation than either the forest or the herbs of the field. A linear extrapolation indicates that zero diversity would be approached at 15,000-20,000 R/day. Extrapolation of coefficient of community and percentage similarity graphs to zero also indicates that exposures in this range would be required to produce zero similarity. These are very high exposures indeed and can be compared with the 300 R/day to reduce diversity in the forest to zero and the more than 3,000 R/day required in the first year old field (Woodwell, 1965). Despite the uncertainty of this extrapolation, it seems clear from the diversity data that although the 50% diversity exposure is of the same general range as that for the herbaceous community, its slope is low, indicating that certain lichen populations are in fact substantially more resistant than higher plant communities.

The decline in total density at increasing radiation exposures suggests that niches opened by mortality of sensitive species were not filled by resistant species, at least within three years. The density data of Table 1 support this conclusion in general. Densities of most species declined linearly with logarithmic increase in radiation exposure. This generality applied throughout the radiation gradient for such species as *Parmelia sulcata* but for many others such as *Cladonia cristatella*, applied only above 50 R/day. The pattern was not universal however. Densities of other species such as *Lecidea varians* and *Pertussaria xanthodes* increased at intermediate exposures and declined at exposures above 1000 R/day (Table 1). Thus, in contrast to the old field (Woodwell and Oosting, 1965) we do not see in the lichen community a rapidly shifting mosaic of species, shifting in response to subtle changes in environment. Instead, replacement of radiosensitive species by resistant species, if it occurs at all, is slow and undramatic.

No clear reason exists for the apparent radioresistance of crustose lichens as opposed to foliose and fruticose forms. It is interesting that in communities of vascular plants the species that have been the most resistant have usually been low-growing forms (Woodwell, 1965). It now appears that within the lichen populations of the oak-pine forest a similar relationship exists, with the close-growing crustose lichens being more resistant than the upright foliose and fruticose species. This contributes still another parallel to the several already shown between the effects of radiation on lichen communities and those on vascular plant communities.

It is clear now that, contrary to previous indications, irradiation has had direct effects on lichens of the Irradiated Forest. Effects include a progressive, linear decline in diversity with logarithmic increase in daily radiation exposure; an apparent threshold at 100-200 R/day for effects on composition of the communities; differential mortality of crustose, foliose and fruticose forms, the crustose appearing the most resistant; and a progressive decline in density with logarithmic increase in radiation exposure, although striking increases occurred in densities of certain species at intermediate exposures. Diversity appears to have been reduced by 50% during the first year of the experiment by exposures of about 800 R/day, although the slope of the diversity curve would suggest that if suitable substrata were available certain species would survive to exposures as high as 15,000-20,000 R/day. This relationship indicates that there is considerable variation among lichen populations in sensitivity to radiation and that it is probably incorrect to say that all lichens are radiation resistant, although it is most certainly true that certain lichens are substantially more resistant than most higher plants.

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TABLE 1. Density of lichens in an irradiated forest

	Average number of thalli per 16 square meters Exposure in R/day					
Species	Nonirradiated control	50	100	620	1250	2250
Lepraria chlorina	3.33					
Cladonia cinetra	1.33					
C. nemoxyna	4.00					
Baeomyces roseus	7.33					
Cladonia pyxidata	0.33					
Lecanora sp. a		1.66				
L. sp. b		0.66				
Parmeliopsis placorodia		2.33				
Parmelia borreri		1.66				
Physcia orbicularis		1.00	0.33			
Parmelia aurulenta			0.66			
P. livida			3.00			
P. subaurifera	13.33	6.00	3.00			
P. physodes	2.33	2.66	4.66			
Cladonia incrassata	3.33		0.33			
C. squamosa	13.33		0.33			
Parmelia caperata	1.33	3.66	1.33	0.75		
P. rudecta	6.00	2.66	0.33	1.25		
Physcia aipolia			0.33	0.25		
P. setosa			9.00	0.25		
P. stellaris	6.33	7.66	5.00	1.75		
Cladonia sp.(primary thallus)		12.00	4.66	25.25		
C. atlantica	1.00	3.00	3.33	0.75		
C. delicata			0.33	0.25		
C. coniocraea	9.00	10.33	9.66	2.50		
C. piedmontensis	5.66	1.33	2.66	0.75		
C. pityrea	0.66	0.33	2.33	1.00		
C. subcariosa			0.33	0.25		
C. subtemuis	1.33		0.66	0.25		
Lecanora sp. c			1.00		0.50	
L. caesiorubella	0.66	7.66	5.66	4.75	1.50	
Buellia curtisii	2.00	4.00	0.33	8.50	4.50	
Candelaria concolor	8.00	7.33	4.00	4.25	1.00	
Physcia millegrana	15.33	29.00	3.00	2.75	2.00	
Parmelia sulcata	31.33	18.33	14.33	0	1.00	
P. galbina					1.00	
Cladonia bacillaris					0.50	
C. macilenta	17.66	1.00	1.00		0.50	
C. cristatella	13.33	20.66	13.33	8.50	1.50	
C. clavulifera		0.66	1.00		0.50	
Arthonia caesia	60.00	84.66	17.00	14.25	13.00	3.00
Lepraria aeruginosa	1.00	4.00	0.33	0.25	0	3.00
Lecanora chlarotera	2.33	4.66	0.33	2.00	1.00	1.00
Lecidea anthracophila	1.00	21.00			0	1.00
L. varians	23.66	44.00	24.66	82.25	0	2.00
Buellia stillingiana		1.66		0.25	0	1.00
Bacidia chlorococca				0.75	0	2.00
Buellia polyspora	1.66		6.66	1.00	4.00	3.00
Pertusaria xanthodes	2.66	15.66	6.00	13.75	3.50	1.00
P. trachythallina	0.33		1.00	1.50		1.00
Cladonia chlorophaea	16.00	31.66	19.33	7.50	5.00	8.00
Sum	276.90	352.88	171.22	187.50	41.00	26.00

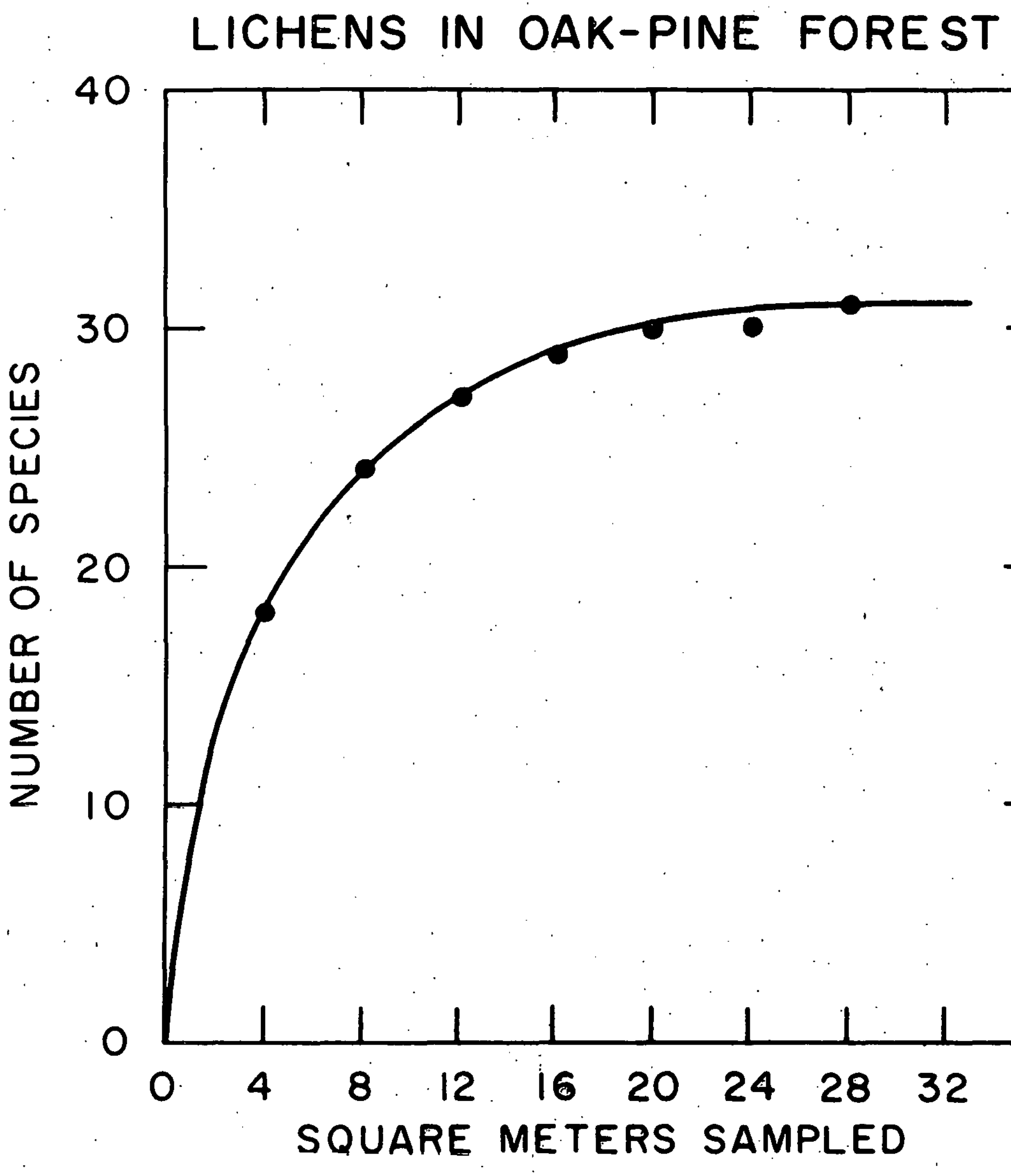
FIGURE LEGENDS

Fig. 1. The species-area curve for lichens.

Fig. 2. Diversity of lichens along the radiation gradient.

Fig. 3. Diversity of lichens of different growth forms along the radiation gradient.

Fig. 4. Coefficient of community and percentage similarity for lichen communities along the radiation gradient.



LICHENS IN OAK-PINE FOREST
NUMBER OF SPECIES
40
30
20
10
0
0
4
8
12
16
20
24
28
32
SQUARE METERS SAMPLED

FIGURE 1

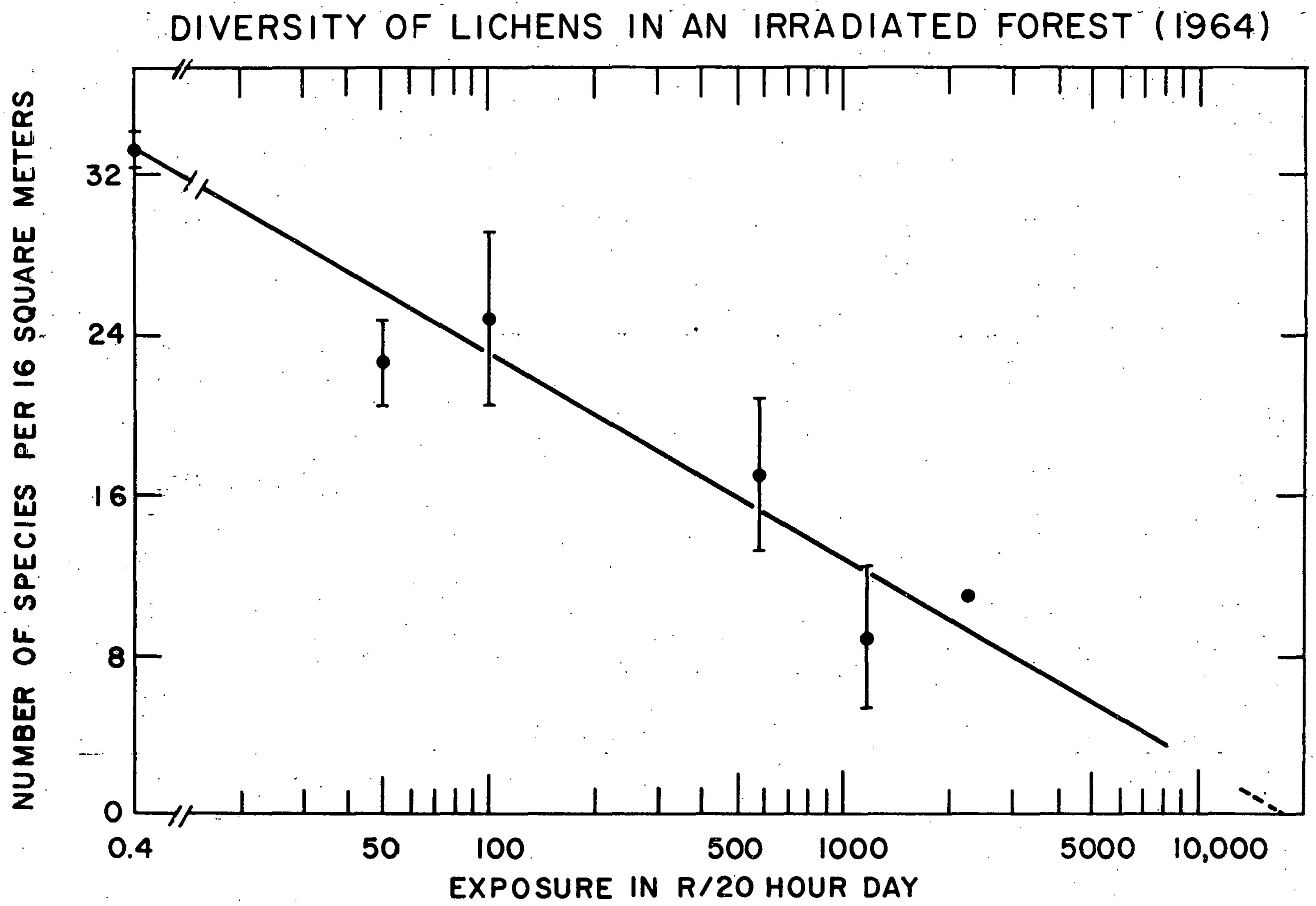

DIVERSITY OF LICHENS IN AN IRRADIATED FOREST (1964)
NUMBER OF SPECIES PER 16 SQUARE METERS
32
24
16
8
0
0.4
50
100
500
1000
5000
10,000
EXPOSURE IN R/20 HOUR DAY

FIGURE 2

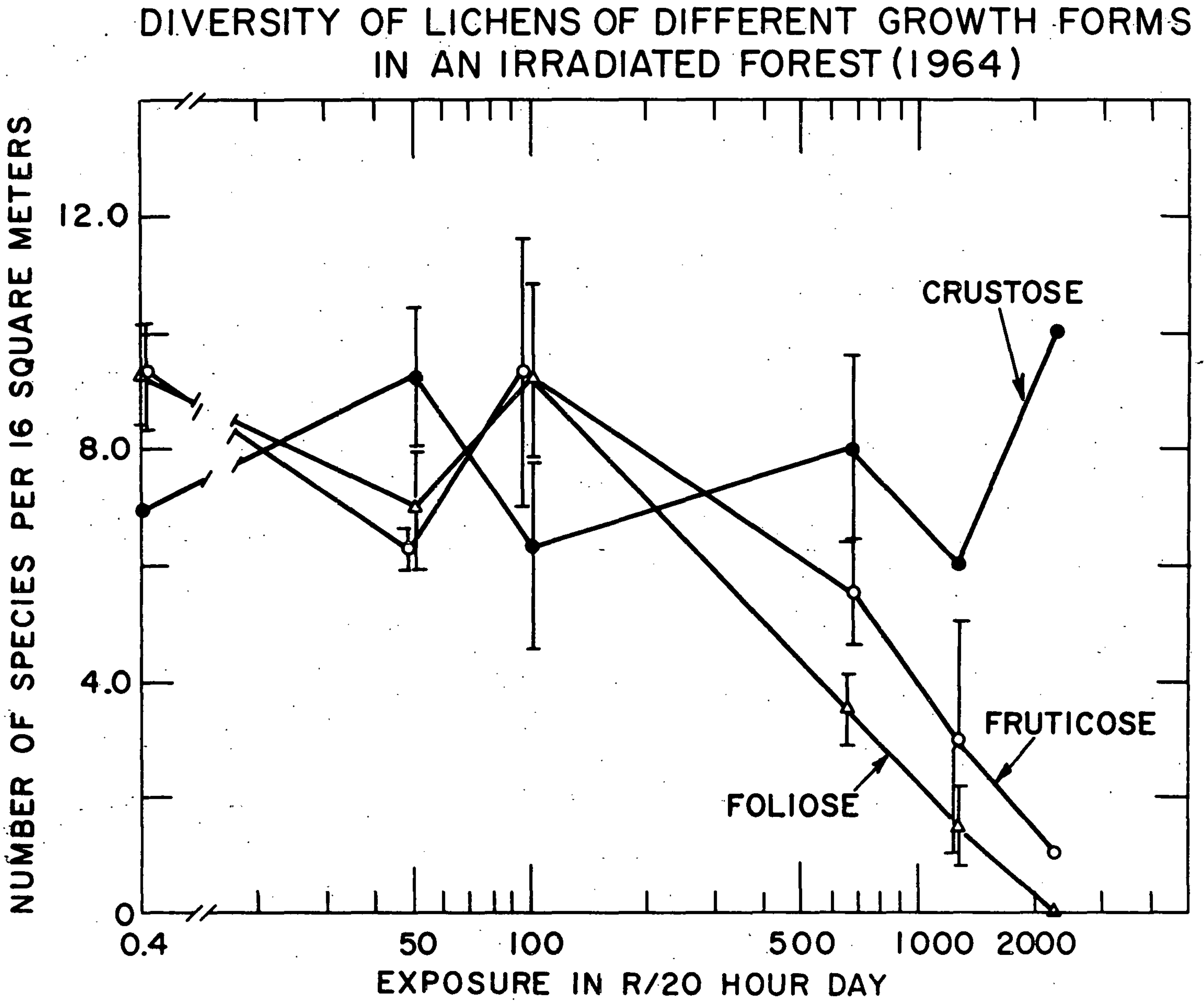

DIVERSITY OF LICHENS OF DIFFERENT GROWTH FORMS IN AN IRRADIATED FOREST (1964)
NUMBER OF SPECIES PER 16 SQUARE METERS
12.0
8.0
4.0
0
0.4
50
100
500
1000
2000
EXPOSURE IN R/20 HOUR DAY
CRUSTOSE
FRUTICOSE
FOLIOSE

FIGURE 3

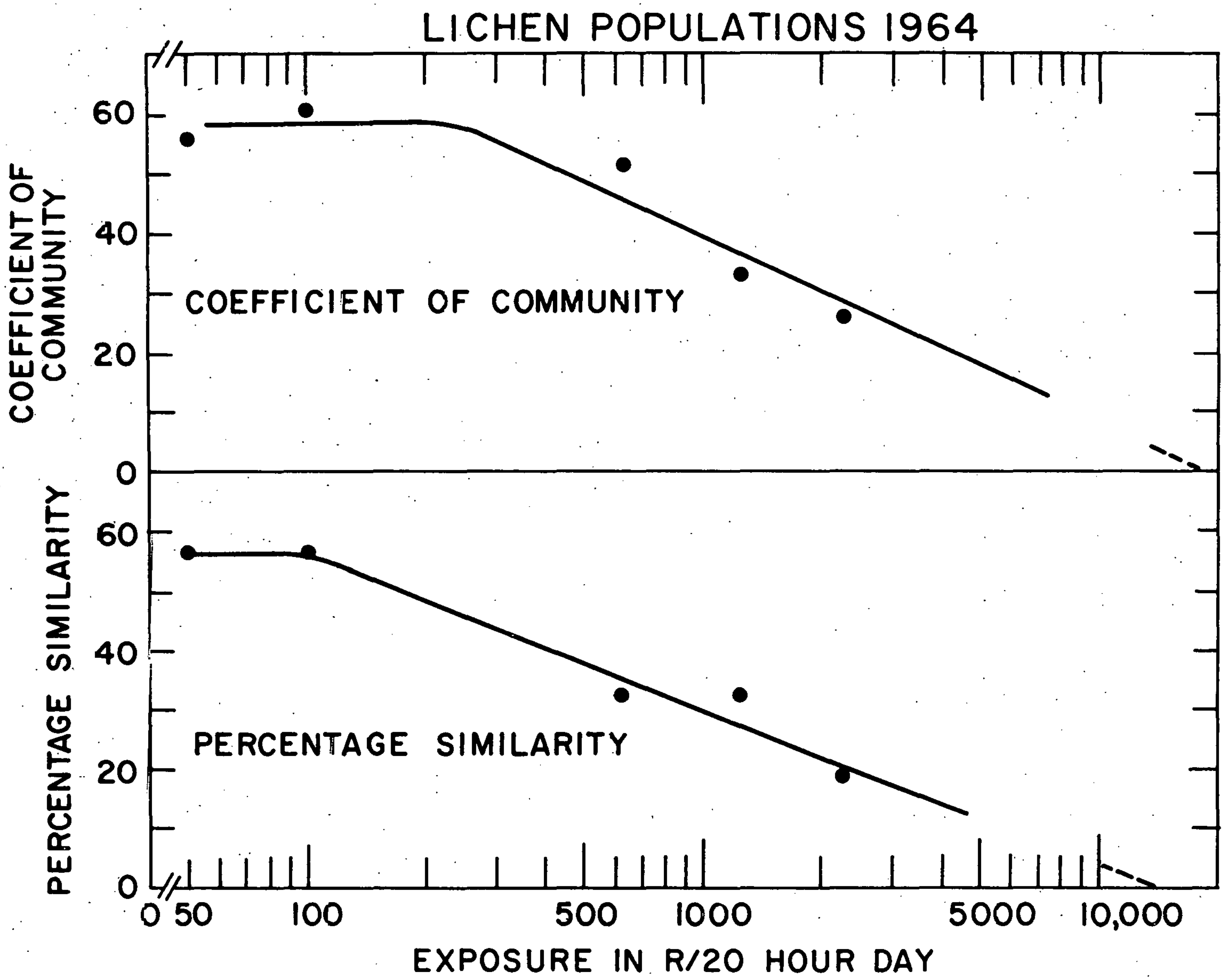

LICHEN POPULATIONS 1964
COEFFICIENT OF COMMUNITY
COEFFICIENT OF COMMUNITY
PERCENTAGE SIMILARITY
PERCENTAGE SIMILARITY
60
40
20
0
60
40
20
0
0
50
100
500
1000
5000
10,000
EXPOSURE IN R/20 HOUR DAY

FIGURE 4