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EFFECTS OF IONIZING RADIATION AND FIRE ON GAYLUSSACIA BACCATA

AND VACCINIUM VACILLANS¹

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A B S T R A C T

Fire and ionizing radiation have parallel effects on survival of natural populations of Gaylussacia baccata and Vaccinium vacillans. Vaccinium is substantially more resistant. The differential sensitivity is due to differences in regenerative capacity; buds of Vaccinium are more resistant to damage, occur at greater depths in the soil and are better protected from both radiation and heat. This pattern of radiation and fire resistance lends further support to the general observation that in plants radiation resistance is related to ecological hardness.

THE RESPONSES of plants to ionizing radiation have been shown to depend on a variety of environmental and intrinsic characteristics. The principal intrinsic characteristic appears to be the average size of the chromosome at interphase (Sparrow and Woodwell, 1962; Sparrow, 1964). Type of life cycle, growth rate, life form and various environmental factors are also important. Limited field observations suggest that the same morphological characteristics facilitating survival after burning also confer resistance to ionizing radiation. The objective of this study was comparison of the effects of fire and ionizing radiation on the two ericaceous shrubs that are principal species of a shrub community common in eastern North America.

Opportunity for the study arose as part of the Brookhaven Irradiated Forest Experiment in which an oak-pine forest is being irradiated chronically with gamma radiation (Woodwell, 1963). The forest is similar to the oak-pine forests common on certain coastal plain sands in New Jersey, New York and New England. These forests have developed under frequent burning and appear to be particularly well adapted to fire. Both of the dominant shrubs, Gaylussacia baccata and Vaccinium vacillans, sprout readily in response to fire and apparently thrive under its influence if damage is neither frequent nor severe.

Previous research in the pine region of New Jersey has shown that burning more than once every five years increases the relative abundance of Vaccinium vacillans and depresses Gaylussacia baccata, although absolute stem densities of both species are reduced (Buell and Cantlon, 1953). Rebeck (1964) has reported parallel changes in shrub layer structure and composition due to

ionizing radiation (Fig. 1). He has also reported a decline in relative abundance of Vaccinium vacillans at high chronic exposures. The parallel between the effects of fire and radiation extends still further to an increase in the cover of Carex pensylvanica under intense radiation and under frequent burning.

Thus, fire and ionizing radiation appear to have similar effects on structure and composition of the shrub layer. That such a parallel should exist is surprising, since there is no basis for believing that ionizing radiation has played any role in the selective processes of evolution, at least in higher plants. The objective of this study was comparison of the effects of fire and radiation on the regenerative mechanisms responsible for these shifts in shrub populations.

Propagation of shrubs in the pine region of southern New Jersey and central Long Island is commonly by sprouting from rhizomes (McCormick, 1955; Reiners, 1964). Reiners (1964) observed that the rhizome system of Gaylussacia baccata on Long Island is usually restricted to the upper 5 cm of mineral soil, while the rhizome system of Vaccinium vacillans extends well below this depth. Laycock (1958) found rhizomes of Vaccinium vacillans in southern New Jersey concentrated in the top 5 cm of the A_1 horizon and occasionally as deep as 15 cm. Gaylussacia baccata in contrast tends to be restricted to the organic horizons. It usually occurs either in the A_0 horizon and top 2.5 cm of the A_1 or in the top 5-8 cm of the organic and mineral horizons where no A_1 layer is present.

Both species sprout readily in response to damage, buds nearest the stem apex normally producing the new shoots (Fig. 2). Thus the position of

growth initiation on the stem relative to the soil surface indicates the extent of damage to that stem. When damage to above ground parts is extensive, new shoots are initiated from below the soil surface.

Normally, lateral buds below the terminal bud remain dormant unless the stem apex is damaged. Thus the differential effects of both fire and ionizing radiation on these two shrubs appear to be related to their capacity for vegetative propagation. The objective of this work was a test of this hypothesis.

METHODS--The study was conducted at Brookhaven National Laboratory, Upton, Long Island, New York during August, 1964, after shoot elongation of both species had been completed.

Aerial stems were divided into categories based on the time and site of growth initiation. Categories were: 1) stems produced by axillary buds of 1963's above-ground stems, i.e., normal growth from the previous year's buds; 2) stems produced from axillary buds set in 1964, a common occurrence in both species; 3) sprouts from basal positions not normally producing shoots in undamaged aerial stems; and, 4) sprouts from rhizomes. These categories of stem types are illustrated in Fig. 2.

The number of stems in each category was counted in sample plots and the length of each shoot from (and including) the apex to the point of origin was measured to the nearest millimeter as was the position of its origin relative to the soil surface. Additional measurements of the position of growth initiation were taken to allow comparisons between plots of different treatments.

The burned community was on the northeast boundary corner of the Brookhaven National Laboratory tract. The stand was very similar to the irradiated

forest described by Rebeck (1964). It consisted of Quercus alba, Q. coccinea and Pinus rigida trees with a discontinuous understory of Q. ilicifolia and the shrub layer. The 1964 growing season was the first year of regeneration following an intense crown fire on September 1, 1963. The fire completely destroyed the canopy except for a few scattered stems of Pinus rigida (Fig. 3). Records of the Fire Department indicate that the stand was burned previously by an intense ground fire in 1942, and by a crown fire on May 31, 1961. The large number of pitch pine and small oak stems in the stand suggested that the 1961 fire caused considerable damage.

Two intensities of burn damage were recognized--light and heavy. The intensity of burn was probably controlled by the amount of fuel prior to burning. Light burns were common and generally were in relatively open areas away from tree bases. Heavy burns averaged 1 m in diameter and usually occurred at the bases of trees where more litter tends to collect. Such sites tend to be heavily burned repeatedly.

The distinction between a light and heavy burn was necessarily somewhat arbitrary. Judgement was based on position relative to stems of trees, on the amount of charcoal in the soil, on the amount of litter remaining, on the frequency of charred standing stems of the shrubs and on the amount of Carex pensylvanica present. Heavy burns were characterized by little or no Carex, a large amount of charcoal and no litter or charred standing shrub stems.

Sampling was by four 25 x 40 cm plots in the geometric center of a site, the long axis of the plots oriented north-south. For each burn intensity nine sites were sampled, making a total of 36 plots per burn intensity.

The irradiated forest has been described by Woodwell (1963) and Rebuck (1964). Sampling here was in the third growing season since the introduction of the gamma radiation source in November of 1961. Plots were arranged with the short axis parallel to a radius from the source and were taken between 20-52 m from the source. Exposures at 20 m (180 R/day) were the highest at which living stems of either species occurred. The approximate end of the zone of total tree canopy death in 1964 occurred at 52 cm (16 R/day), although there were some tall oak sprouts at this distance.

Plots were in areas free from shielding by the stems of trees at the following distances from the source: 20 m (180 R/20 hr day), 24 m (105 R/20 hr day), 30 m (64 R/20 hr day), 34 m (47 R/20 hr day), 40 m (33 R/20 hr day), 46 m (23 R/20 hr day) and 52 m (16 R/20 hr day). These exposures were average exposures at 1 m above the ground (Woodwell, 1963).

Nomenclature of plants follows Fernald (1950). Voucher specimens were placed in the Rutgers University Chrysler Herbarium and in the Herbarium at Brookhaven National Laboratory.

RESULTS--Effects of fire--Sprouting from rhizomes produced most of the new growth following both light and heavy burns. Under heavy burning, sprouting of Gaylussacia was restricted to rhizomes and occurred most frequently from depths between 1.5 and 2.5 cm (Fig. 3). A few above-ground stems of Vaccinium vacillans survived the fire, suggesting that the Vaccinium vacillans stems are intrinsically more resistant to heat than the huckleberry. Moreover, sprouting occurred from Vaccinium rhizomes at depths as great as 5 cm, further contributing to the greater regenerative capacity of Vaccinium as opposed to Gaylussacia after fire.

Densities of above-ground stems of Vaccinium and Gaylussacia also varied with intensity of burning. The change in density of Gaylussacia was most pronounced. Populations declined from 72 ± 17 stems/m² (limits indicated define 95% confidence interval) in the light burn to 22 ± 11 stems/m² in the heavy burn. Vaccinium populations showed an opposite tendency with a slight but statistically insignificant increase from 117 ± 27 stems/m² in the light burn to 138 ± 24 stems/m² in the heavy burn.

Shoot elongation in both species was slightly less in the heavy burns than in the light burn, but none of the difference was statistically significant.

Effects of irradiation--Chronic gamma irradiation caused a similar pattern of damage and regeneration in these two shrubs (Figs. 4 and 5). At 33 R/day shoot growth was initiated principally from aerial shoots. At higher radiation exposures a progressively higher proportion of the regeneration was from rhizomes. Aerial exposures of 105 R/day excluded Gaylussacia. Vaccinium at this exposure produced sprouts only from rhizomes 1.0 cm or more deep. At aerial exposures of 180 R/day sprouts occurred only from rhizomes 2 cm or more deep. Measurements of radiation exposures at various depths in soil indicated that sprouting of Vaccinium shoots and rhizomes did not occur in 1964 when rhizomes were receiving more than 65-70 R/day. Gaylussacia was more sensitive. There was no sprouting from above-ground stems receiving more than 45-50 R/day and there were no sprouts from basal buds or rhizomes in areas receiving aerial exposures above 65 R/day (Fig. 5). Thus shoots of Vaccinium were about 1.5 times more resistant than shoots of Gaylussacia.

DISCUSSION--The principal effects of fire and ionizing radiation on both Vaccinium vacillans and Gaylussacia baccata appear to be damage to perennating buds. The greater resistance of Vaccinium is due to both the greater resistance of its buds to heat and to ionizing radiation and to its capacity for originating shoots from greater depths in the soil where buds are protected (Figs. 3 and 4).

The relative resistance of Vaccinium is of particular interest because the average volume of its nuclei has been reported to be approximately 30% greater than that of Gaylussacia (Sparrow and Woodwell, 1962). According to the correlation between radiosensitivity and nuclear volume as summarized by Sparrow (1963), Vaccinium would be expected to be more sensitive to radiation than Gaylussacia. It seems abundantly clear from this study and from the previous study by Woodwell and Sparrow (1963) that quite the reverse is true. Such an observation merely emphasizes that determinations of nuclear volumes are subject to variation occasionally exceeding 100% and there is probably little basis for discriminating between these two species from nuclear volumes alone. It does, however, seem well established now that Vaccinium is more radioresistant than Gaylussacia and that part of this resistance is due to the higher intrinsic resistance of buds and part to the greater depth of Vaccinium rhizomes. It also appears to be true that buds of Vaccinium are more resistant to fire than those of Gaylussacia, since Vaccinium stems survived burning where Gaylussacia did not (see above). Thus there is a striking coincidence here between radioresistance and resistance to fire. The reasons for the resistance appear to be the same for each species, namely intrinsic characteristics of buds and the relative position of rhizomes in the soil.

It has been shown in a previous study (Woodwell, 1965) that the most radioresistant species tend to be plants that are normally of low stature, prostrate or decumbent forms. Along the radiation gradient in the irradiated forest, for example, the most resistant higher plants were herbaceous species including Carex pensylvanica; at lower exposures the shrubs survived, then the trees. A similar pattern was observed in an irradiated first-year field. It is interesting that the Vaccinium is usually one-third to one-half the height of Gaylussacia and that the pattern of greater radioresistance among lower-growing forms applies to these two species as well.

The general pattern emerging from these studies shows that the effects of radiation are related not only to such intrinsic characteristics of cells as nuclear size and chromosome number, but also to the gross morphology of plants, including their growth habit, depth of roots or rhizomes and number of buds. Morphologies which protect from fire would seem to contribute as well to resistance to radiation. Thus, the evolution of radioresistance has probably been controlled not by the selective action of ionizing radiation but by the selective action of other environmental factors, such as fire itself, which have been much more persistent parts of the environmental complex and which have exerted selective pressures parallel in at least certain ways to those which radiation would exert.

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FIGURE LEGENDS

Fig. 1. Comparison of the effects of fire (Buell and Cantlon, 1953) and ionizing radiation (Rebuck, 1964) on the low shrubs and ground cover of the oak-pine forest.

Fig. 2. The growth habits of Gaylussacia baccata (a) and Vaccinium vacillans (b) in response to damage. From left to right: underground sprouts, above-ground sprouts from the bases of damaged stems, and normal undamaged growth. Note the secondary shoot in the middle picture of Vaccinium vacillans (b) arising from the axil of an existing leaf. The horizontal line in each illustration represents the soil surface.

Fig. 3. The position of growth initiation in relation to soil surface under two intensities of fire. Sample sizes were as follows: Gaylussacia, light burn, N = 67; Gaylussacia, heavy burn, N = 78; Vaccinium, light burn, N = 92; Vaccinium, heavy burn, N = 78.

Fig. 4. Position of 1964 growth initiation of Gaylussacia and Vaccinium under four aerial exposures in the irradiated oak-pine forest. Exposures in R/20 hr day. Sample sizes were: 33 R--N = 42 for Gaylussacia and 38 for Vaccinium; 64 R--N = 40 for Gaylussacia and 38 for Vaccinium; for both 105 R and 180 R--N = 31 for Vaccinium.

Fig. 5. Densities of Gaylussacia and Vaccinium shoots produced from 1963 axillary buds, above-ground sprouts and below-ground sprouts in the irradiated oak-pine forest.

GROUND COVER IN AN IRRADIATED FOREST (1963)

GROUND COVER IN A CONTROL-BURN FOREST

FIGURE 1

(a)

(b)

FIGURE 2

POSITION OF 1964 GROWTH INITIATION IN A FIRST YEAR BURN

FIGURE 3

POSITION OF 1964 GROWTH INITIATION IN AN IRRADIATED FOREST

FIGURE 4

DENSITY OF STEMS PRODUCED IN 1964

FIGURE 5