The Effects of Late Winter Litter Burn on the Composition, Productivity and Diversity of a 4-Year Old Fallow-Field in Georgia

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ONE of the most articulate students of vegetation, fire and man in this century has been the geographer Carl Sauer. Beginning with his first doubts about the climatic origin of the Midwestern prairies he has ranged the field and the literature of ecology, history, anthropology, archeology and agriculture, documenting the role of fire in the coevolution of man and plants. In his words,

> ". . . man learned ways of setting fires so as to facilitate his appropriation of flora and fauna, thereby modifying both, by accident and also deliberately. It has been to his advantage to bring about what the ecologist calls secondary or deflected successions. A fully-grown forest, fully stocked with large trees, is a vegetation

in its least useful condition for man. Except for lumber he has little benefit from the big trees. Together with other creatures that live on the ground his harvest is restricted to low-growing things, his interest is in a retarded or degraded 'plant succession'. He sets up and keeps up ecologic disturbance and drives the primary forest back. His unending attempt is to master and manage the living environment, and this he does by substituting lesser and short-lived plants for the great ones, by breaking down the forest margin into brush and herbs and widening more and more the zone of disturbance and diminution. This he has done most easily and most frequently by fire, to make easier the harvest of plants and animals and also to manage his land for greater productivity. The practices of Indian burning make clear that purpose and result were understood, be they agricultural, hunting, or collecting. Attrition and alteration in significant part have been deliberate" (see Leighly, 1963, pp. 189–190).

Since aboriginal times fire has been a major tool in landscape management, used by hunters, ranchers, and foresters, to manipulate succession. This ancient empirical technology has evolved in recent decades into the organized science of fire ecology, well documented by the proceedings of the annual conferences sponsored by Tall Timbers Research Station. While this accumulated experience has now clarified many aspects of the role by fire in terrestrial ecosystems, there has yet been little attempt to quantify the impact of fire on basic ecological functions, such as productivity, mineral cycling and diversity. Experimental studies of an intensive nature are obviously appropriate for investigation into such matters. This paper reports on a small scale, but intensive, experiment designed to determine the impact of a late winter litter burn on basic properties of ecological systems.

CONCEPT OF "SUCCESSION SETBACK"

As earlier perceived by Sauer and others, the overall impact of fire on vegetation is to set back the developmental process to an earlier, or younger, stage. In this study attention was focused on four basic ecosystem properties which should theoretically provide measures of the degree of succession setback, if any. Referring to the tabular model for ecosystem development, as described by Odum (1969), burning the accumulated organic matter at the onset of a growing season could have any, or all, of the following effects: (1) plant species characteristic of earlier stages return to dominance, (2) net primary production increases, (3) species diversity decreases, and (4) the inorganic mineral pool in living plants increases, at least temporarily, as nutrients are released from the organic detritus pool.

THE HORSESHOE BEND STUDY AREA

Since 1966, experimental studies have been conducted on 1-acre tracts of fallow-field ecosystems in early stages of succession on a University of Georgia field study area known locally as Horseshoe Bend. Special emphasis has been given to the effect of specific perturbations on productivity, diversity and nutrient exchanges within the plant-arthropod-mammal component of the intact ecosystem. The rationale for applying experimental perturbations is three-fold: (1) To determine what properties of intact ecosystems are most appropriate for quantifying the impact of specific stresses, (2) to clarify relationships between diversity and productivity, and (3) to test certain parameters in Odum's 1969 model for ecosystem development.

The experimental tracts were enclosed by meter high sheet metal fences which proved convenient "black box" boundaries for the ecosystem and permitted control of emigration and immigration of small mammal populations. To start a successional series, a grain crop (millet: *Panicum ramosum*) was planted in 1966 in two adjacent enclosures, located in an area where other grain crops had been planted each year for several previous years. In the first study an acute insecticide stress, consisting of a single application of Sevin (a carbamate insecticide), was applied to one plot mid-way in the growing season and the impact on vegetation, litter decomposition, arthropods and small mammals assayed by comparison with an adjacent untreated plot. Results of this study have been fully reported by Barrett (1968) and a note on equitability concepts published by Pulliam, Odum and Barrett (1969).

Following the grain crop, the plots were allowed to undergo natural succession. In 1967 the effects of an unplanned flood stress was studied when a nearby river rose unusually high and inundated the plots with more than 3 feet of water. Part of the results of the second year's study (the first year of natural succession) have been outlined by Richardson (1968). During 1968 and 1969 regular sampling was continued without further perturbations, in order to chart the course of natural succession. This paper reports on a 1970 experiment in which a "controlled burn" was used as a perturbation on the "old-field" ecosystem, then in its 4th year of natural succession.

METHODS

On March 5, 1970, the litter in one-half of each of two 1-acre fenced plots was burned. There were thus two burned ½-acres to compare with two adjacent unburned ½-acres. As already indicated, the burn occurred at the beginning of the fourth growing season in a natural succession following a grain crop.

Sampling procedures were similar to those described in detail in Barrett's (1968) report of the first study in this series. Litter (including standing dead vegetation) and living vegetation were sampled each month from March through November, the first sample taken the day before the experimental burn. Sixteen $0.1m^2$ quadrats laid out in a grid pattern were sampled in each ½-acre tract at each monthly period—totalling 32 samples in both burned and unburned areas. Vegetation was clipped at ground level, and representative whole plants, including roots, were dug up to determine root-shoot ratios; from these ratios root weights could be calculated for clipped samples. All plant material (including litter) was dried before weighing in a large, forced-air drying oven at 100°C. Thus, all biomass values shown in tables and graphs represent oven-dry weights.

Arthropods were sampled by placing an open-ended barrel, enclosing a $0.25m^2$ area, over the vegetation and removing insects and spiders with a vacuum sweeper device designed and described by Barrett (1968). Two "sweeps" were made at each location, one with the hose in the vegetation and one with the hose down over the litter.

In subsequent analyses these are designated as "vegetation arthropods" and "litter arthropods", respectively. Only macroscopic organisms that could be effectively removed from samples by hand-sorting were considered, since this type of sampling was not appropriate for microarthropods (mites, collembola, etc.). As with plants, 16 quadrat samples were taken in each ½-acre at each of the monthly sample periods.

The concentration of mineral nutrients, especially nitrogen and phosphorous in the above ground plant biomass, was determined by Keldahl method (N) and atomic absorption spectrometry (other minerals) of extracts of vegetation. These analyses were made in the laboratory set up for the Institute of Ecology's component of the Eastern Deciduous Forest Biome segment of the International Biological Program, funded by the National Science Foundation. Soil samples were also analyzed for nutrient levels in the University of Georgia's soil test laboratory.

All small mammals in the fenced areas were removed before the March litter burn. On April 12, six pairs of each of four species, *Sigmodon hispidus*, *Mus musculus*, *Reithrodontomys humulis* and *Peromyscus polionotus* were introduced into each of the two 1-acre enclosures. Live traps were placed near each of the grid stakes used in the plant sampling program and these were operated for 2 or 3 consecutive nights each week from April 17 to September 9. The mammalian aspect of the study was carried out by Susanna Wilson and is reported in her Master's thesis (Wilson, 1970). Only population trends and weight gains in relation to the burn will be noted in this paper.

Three measures of diversity were calculated for plants and arthropods. Each index brings out a different characteristic of diversity in the population (for a discussion of these diversity concepts, see Odum, 1971, pp. 148–154). The first measure can be designated as a "species richness," which relates a number of species (S) to the log of the number of individuals (N):

$$D = \frac{S - 1}{\log_e N}$$

The second measure is the Shannon index of general diversity,

$$\overline{H} = -\sum \left(\frac{ni}{N} \right) \log_e \left(\frac{ni}{N} \right)$$

where ni is the importance value of each species and N the total of importance values. Importance may be determined by number of individuals, biomass contribution, etc. In this paper plant biomass, plant productivity; and arthropod numbers were used as importance values. The Shannon index is less affected by sample size than most indices and it permits statistical comparison of two samples for a test of significance, as described by Hutcheson (1970). The third measure of diversity was an evenness index

$$e = \frac{\overline{H}}{\log S}$$

where $\overline{H}$ is the Shannon index previously described and S the number of species. Values of e range from 0 to 1, the maximum value occurring when all species are equal in importance. Low values, therefore, indicate strong dominance by a few species.

ACKNOWLEDGMENTS

The division of labor in this team research effort was roughly as follows: The design of the experiment and analyses of data were the responsibility of the senior author. Pomeroy carried out the sampling program and supervised several research assistants in the sorting and weighing of plant and arthropods material. Dickinson tended to the nutrient cycling aspects of the study and assisted in the writing of the manuscript. Hutcheson calculated the diversity indices and all statistical tests to determine variance and confidence levels, using an extensive computer program previously set up for a wide range of diversity analyses. We are especially indebted to Linda Deuver for her patience and skill in sorting numerous arthropod samples. This study was supported by a Grant (GB-16507, renewal of GB-6113) from the National Science Foundation.

RESULTS

The two ½-acres which received the same treatment were first compared in regard to all of the measurements. In no case was there a significant difference; therefore, the two replicates could be considered together and data presented in terms of a direct comparison of burned and unburned areas. In all graphs a-a on paired points indicates no significant difference, a-b indicates a significant difference at the 0.05 level.

Litter

As shown in Figure 1 (upper graph) the March burn reduced litter to less than 200 g/m², compared to 350 g/m² on the unburned

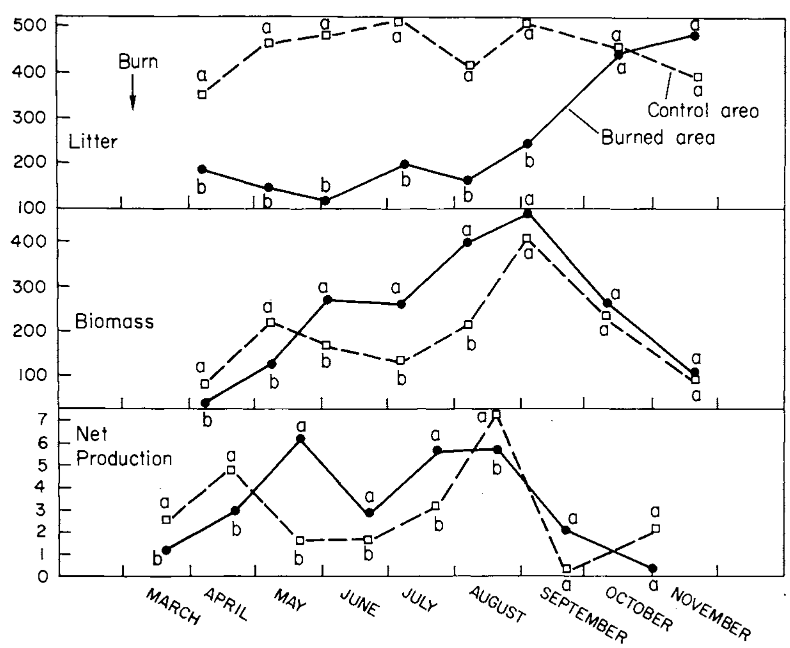

FIG. 1. The effect of an early March litter burn on the quantity of litter (upper diagram, figures in grams dry weight/m²), the biomass of vegetation, including roots (middle diagram, figures in grams dry weight/m²), and daily net primary production rate (lower diagram, figure in grams m^{-2} day^{-1}.

control. By June the difference had increased as the litter on the unburned plot rose, and that on the burned area declined, presumably because of higher surface temperatures in the latter area. In August, litter in the burned area began to increase rapidly and by October there was no statistically significant difference in the amount of litter on the burned and control plots. The recovery of litter in the burned area can be accounted for by increased net production of spring and summer annuals, as outlined below.

Plant Biomass

The seasonal pattern of plant biomass changes in both burned and unburned plots was bimodol with first peak in late spring and a second one in August (Fig. 1, middle graph). This pattern reflects the existence of two crops of annuals, one maturing in late April or May and the other in late summer or early fall. Such a pattern is characteristic of Georgia "old-fields." Something of the species composition of seasonal groups is shown in Table 1. As indicated in Figure 1, (middle graph), the fire delayed, but prolonged and elevated the late spring peak so that biomass was significantly higher in May, June and July.

Net Production

Net primary production was calculated by summing monthly growth increments for each species. The alternate method of summing the maximum standing crop of each species gave somewhat lower values, because some species have two growth periods (spring and fall, for example). Comparison of the seasonal pattern of net production in burned and controlled areas is shown in Figure 1, lower diagram. In this graph the mean rate for the monthly period is plotted mid-way between two successive sample dates on which the rate calculations were based. For the first 2 months net production was depressed in the burned area, but from May to about August the rate was significantly increased. By the end of the growing season (September and October) no difference could be detected between burned and unburned areas. As shown in Table 1, the total net production for the season was 837 g/m^2 in the burned area as compared with 714 g/m^2 in the unburned area.

TABLE 1. NET PRODUCTION BY SPECIES IN SEASONAL GROUPS

	grams/m²		
A. Spring Dominants[1]	Control (unburned)	Experimental (burned)	Effect of burn[2]
Lolium multiflorum (Rye Grass)	98.44	47.41	—
Allium vineale (Wild Onion)	49.46	21.96	—
Vicia angustifolia (Vetch)	25.68	4.94	—
Geranium carolinianum (Geranium)	10.06	3.92	—
Cerastium vulgatum (Chickweed)	3.68	2.52	
Trifolium incaratum (Crimson Clover)	3.64	0.42	—
Specularia perfoliata (Venus Lookinglass)	3.42	2.96	
Hordeum pusillum (Barley)	3.76	1.72	—
Oenothera crispus (Evening Primrose)	1.16	12.78	+
Rumex crispus (Curly Dock)	0.02	3.86	+
Others	7.94 (11 sp.)	6.70 (10 sp.)	
TOTALS	207.26	109.19	—
B. Summer Dominants[1]			
Cyperus sp. (Nut Sedge)	39.40	32.56	
Festuca sp. (Fescue)	10.60	0.36	—
Lactuca scariola (Prickly Lettuce)	9.70	5.90	
Lactuca canadensis (Wild Lettuce)	7.68	0.50	—
Oxalis stricta (Sorrel)	3.52	0.32	
Lepidium virginicum (Peppergrass)	3.08	5.22	
Solanum carolinense (Nightshade)	1.40	4.36	+
Sorghum halepense (Johnsongrass)	0.20	27.42	+
Senecio tomentosus (Bitterweed)	—	4.86	+
Others	5.06 (9 sp.)	2.44 (5 sp.)	
TOTALS	80.64	83.94	
C. Fall Dominants[1]			
Aster pilosus (White Aster)	172.78	47.06	—
Solidago sp. (Goldenrod)	130.98	213.38	
Heterotheca latifolia (Campher Weed)	89.28	172.62	+
Cynodon dactylon (Bermuda Grass)	14.70	0.24	—
Ambrosia artemisiifolia (Ragweed)	7.32	204.58	+
Erigeron canadensis (Horseweed)	2.48	4.94	+
Others	8.66 (12 sp.)	1.40 (5 sp.)	+
TOTALS	426.20	644.22	+
Total Annual Net Production	714.10	837.35	+
Total Number Species in Samples	56	45	—
Diversity, $\overline{H}$[3]	2.41	2.03	—
Diversity, e	0.60	0.53	—

[1] Species listed by name are those contributing 3 or more grams dry matter net production to one or both areas. Other species contributing 1–3 gms included: Spring—*Lamium amphexicule, Viola, sp., Trifolium procumbens, Mentha sp., Galium*

aparine, *Capsella bursa-pastoris*, and *Valerianella radiata*. Summer—*croton glandulosus*, *Cassia tora*. Fall—*Digitaria sanguinalis*, *Andropogon virginicus*, *Anthemis cotula*. Rare species contributing less than 1 gm. numbered 4 for spring, 8 for summer, 10 for fall.

[2] Minus sign (−) indicates significant reduction and plus sign (+) a significant increase in burned area, as compared with the control area.

[3] In these calculations, ni = net production of each species for whole season and N = total net production for the whole season.

Plant Species Composition

The litter burn had a striking impact on species composition. The unburned control could be considered reasonably typical of a 4-year "old field" successional stage, while the burned plot took on the characteristics of an earlier successional stage resembling roughly a 2-year stage. As shown in Table 1, eight dominant species, mostly annuals representative of very early successional stages, were more abundant in the burned area, while 10 species became less abundant. Seven species showed no significant change as a result of the burn. Another 36 species contributing less than 3 grams dry matter each were not important enough, in terms of production, to warrant comparison. The impact on these rarer species is best assayed in terms of diversity indices, as outlined in subsequent paragraphs.

The most striking effect of the burn was the return of ragweed (*Ambrosia*) to dominance. This species, which made a very minor dry matter contribution in the unburned area (only 7 g/m^2) became the second most important species in the burned area with an annual production of 205 g/m^2 (Table 1). In Figure 2 monthly standing crop values are plotted to illustrate the dramatic resurgance of this species in the burned plots. The terminal standing crop approaching 200 g was similar to that observed on these same plots in 1967 and 1968, the first and second year of natural succession. Camphor weed (*Heterotheca*) is another first and second year dominant that resurged in the burned area. Among spring and summer dominants the species which "came back" as a result of the burn were also characteristic of earlier stages—for example, evening primrose, dock and bitterweed. In contrast, asters, which are characteristic of older stages, were suppressed by the burn.

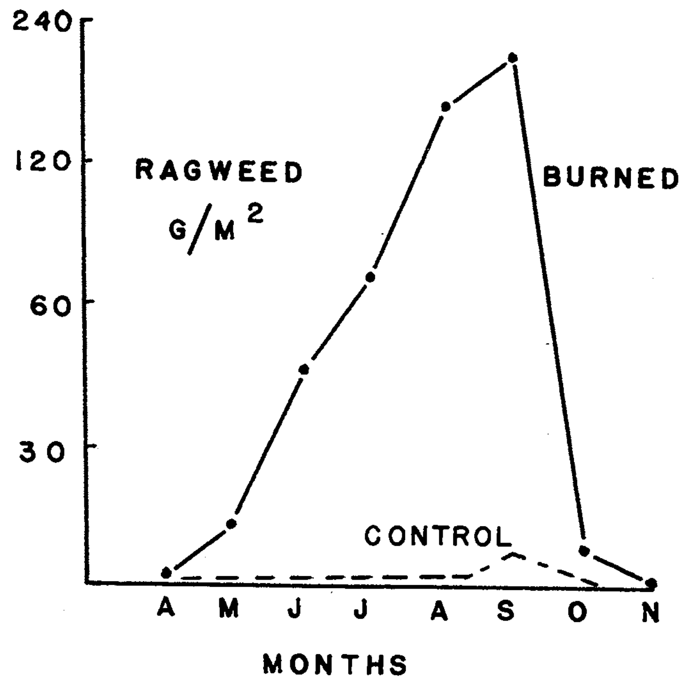

FIG. 2. Comparison of monthly estimates of the standing crop biomass of ragweed (*Ambrosia*) in burned and unburned (control) areas.

Plant Species Diversity

As shown in Figure 3, plant species diversity was higher 1 to 3 months after the litter burn. Species richness (d) was higher only during the May sample and then actually dropped below the control level during the summer and early fall (Fig. 3, upper graph). In contrast, evenness (e) was markedly increased (i.e., dominance decreased) for 3 months, May through July. As a consequence the Shannon index was also elevated for this period. The fire actually reduced the total number of plant species and diversity indices for the whole season (see bottom three lines, Table 1), but the marked decrease in dominance during the early part of the season had the

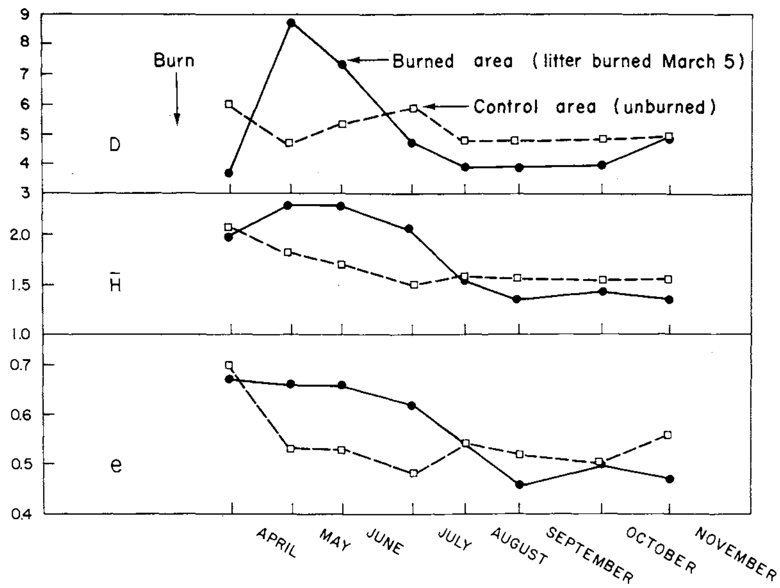

FIG. 3. Comparison of three measures of species diversity of vegetation in burned and unburned (control) areas. $D = S - 1/\log_e N$; $\bar{H} = -\sum ni/N \log_e ni/N$; $e = \bar{H}/\log_e S$, where S = number of species, ni biomass of each species and N = total biomass. See text for further explanation.

effect of increasing diversity immediately following the litter burn (Fig. 3).

Arthropod Density and Diversity

As might be expected (see Fig. 4, upper graph), the density of animals in the litter stratum was much reduced in the burned area during the spring and early summer, correlated, no doubt, with the reduced quantity of litter (see Fig. 1, upper graph). By the end of the season when the accumulation of new litter in the burned area reached a level equal to that of the unburned area, arthropod population density also returned to the same level, (Fig. 4, upper graph).

There was no clear-cut difference in regard to density of vegeta-

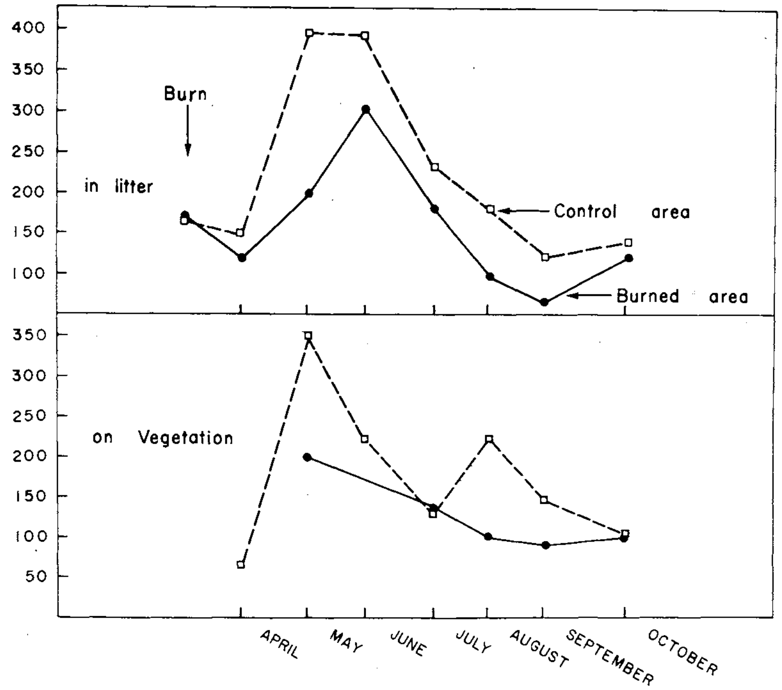

FIG. 4. The effect of an early March litter burn on density of arthropods in the litter (upper diagram) and in the vegetation (lower diagram). Figures are numbers of individuals per square meter.

tion arthropods in the vegetation. Only in the May sample was there a significant difference with burned areas showing almost twice the density in the control area, (Fig. 4, lower graph).

The effects of the late winter burn on arthropod diversity was quite marked in both strata (litter and vegetation), and the effects persisted until near the end of the growing season. In Figures 5 and 6, three diversity indices are plotted. In general, the three indices behaved in a parallel manner. Since the Shannon index lends itself to calculation of variance (Hutcheson, 1970), we will concentrate discussion on this measure (middle graphs, Figs. 5 and 6).

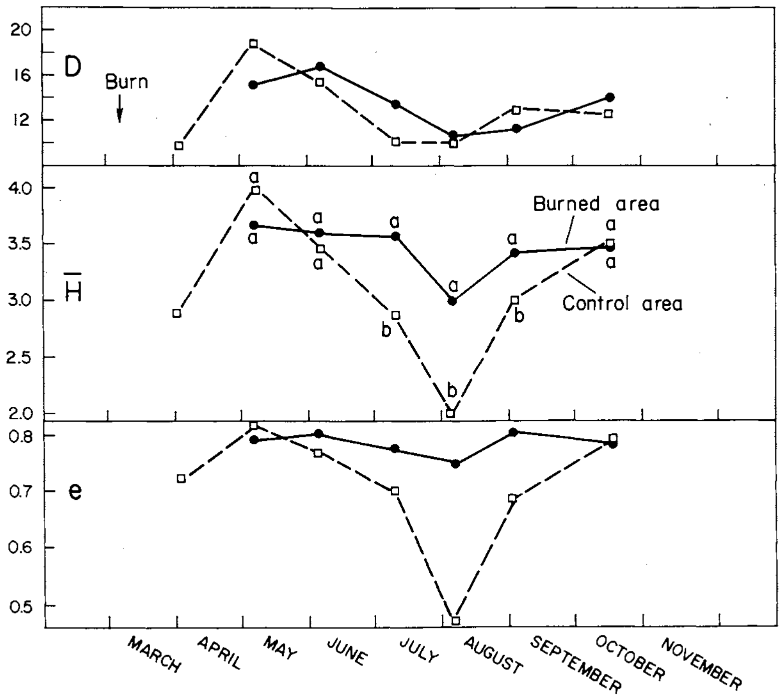

FIG. 5. Comparison of species diversity of arthropods in the vegetation of burned and unburned (control) areas. Diversity indices, as described in the legend of Figure 3 except that these calculations are based on numbers of individuals rather than biomass.

The diversity of litter arthropods was increased as a result of the fire from May to August and for vegetation organisms from July to September. Comparing the "species richness" index "D" and the "evenness" index "e", it is apparent that the evenness component of diversity was most affected by the early spring litter burn. The overall response of arthropods to the fire perturbation was similar to that of the plants—dominance was reduced during the spring and summer.

Mammals

Following the release of the six pairs of four species, the popula-

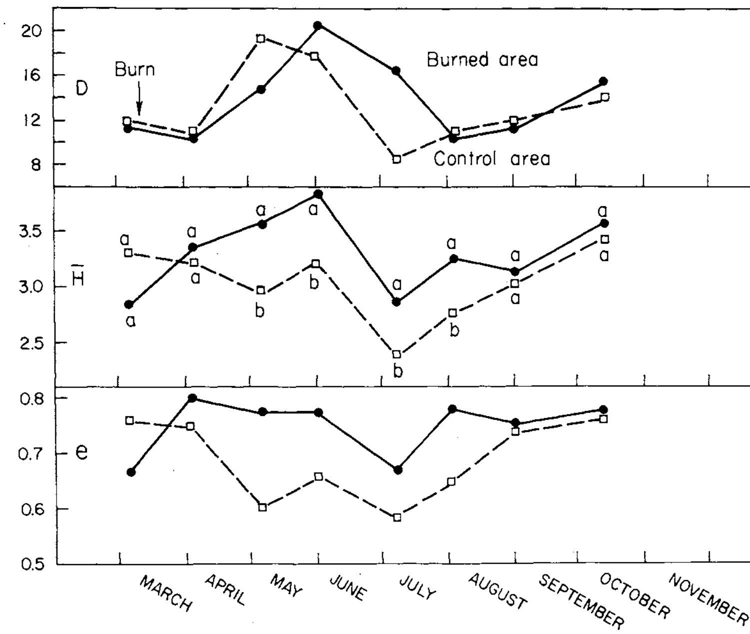

FIG. 6. Comparison of species diversity of arthropods in the litter of burned and unburned (control) areas. Diversity indices, as described in the legend of Figure 3, except that these calculations are based on numbers of individuals rather than biomass.

tions of *Sigmodon* (cotton rat) increased to a relatively high density in September (70/acre), while the density of *Mus* and *Peromyscus* populations remained low. The *Reithrodontomys* populations decreased to extinction in both fenced plots. Cotton rats at first concentrated their activity on the unburned portion of each plot where cover was greater, but as the season progressed, the animals increased their activity in the burned portion. A slightly greater weight gain was noted in cotton rats caught in the burned halves of each plot, which, together with a marked preference for the burned side of plot A, suggest that there may have been a food preference for the vegetation of the burned areas. The fact that mammal density at the end of the growth season was higher in the fenced plots than outside might be taken as an indication of the validity of the "patch burning" technic often used in game management. The unburned half of each fenced area provided cover, while the burned half provided better feeding conditions. On the other hand, greater density may have been the result of the partial protection from ground predators provided by the fenced enclosures.

MINERAL UPTAKE

Nitrogen levels in the first green plants to appear after the burn were definitely higher than in the same species in the control plots. In Figure 7 are plotted the mean differences in nitrogen between the burned and unburned samples of the above ground living vegetation. The highest difference occurred in April following the burn. By July there was no difference in nitrogen level. A paired difference test indicated that the April difference value was significant at the .05 level. Calculations for phosphorous also revealed a significant elevation in the burned plots in April followed by a decline to equality for the two areas. These results indicate that some of the nutrients released by the litter burn were immediately taken up by the early spring growth, as predicted by the ecosystem development model.

DISCUSSION

Three of the four properties of ecosystems which we singled out for special attention in this study were affected in the predicted manner by the late winter litter burn. Species characteristic of earlier successional stages (1 and 2 year "old fields") returned to dominance in the burned plots. These included *Oenothera* and *Rumex* in the spring, *Sorghum* and *Senecio* in the summer, *Heterotheca,* and most important, *Ambrosia* (ragweed) in the fall. The litter burn also increased total net production for several months and resulted in increasing the nutrient content of the early spring growth. Thus, both of these basic functions behaved according to theory.

The effect of the fire perturbation on species diversity was not so clear-cut. As shown in Table 1, the total number of plant species was reduced in samples from the burned areas (45 compared to 56 in the control areas) as was diversity in terms of the apportionment of net primary production among the species in line with the principle of "succession setback." However, the Shannon index of diversity ($\bar{H}$) was higher during spring and summer in the burned areas. Greater evenness (e) in the apportionment of individuals within each species was the chief difference. In other words, the litter burn "opened up" the habitat to allow certain early successional species to become more common and reduce the dominance of certain latter successional species during the first half of the growing season.

Trends in arthropod diversity were similar; there was an increase in evenness, resulting in a significant increase in overall diversity, as measured by the Shannon index. But unlike plants, the increase in in diversity persisted almost to the end of the season. As might be expected, the effect occurred sooner in the vegetation arthropods than in the litter arthropods (May, as compared to June, see Figs. 5 and 6.

Old (1969) reports on a series of experiments involving fire, clear-cutting, litter removal and mulching on an Illinois tall grass prairie. She reported that an early spring fire increased dry matter production and also stimulated flowering, and she cited eight other studies that report increased production following fire in midwest prairies. Nitrogen was also increased in the May samples of vegetation. Jordan (1965) reports an increase in soil phosphorous after fire in the old-fields of New Jersey. Old (1969) and also Hulbert (1969) contended that the increase in production on burned prairies is not the result of a sudden release of minerals by the fire itself, but a result of increased soil temperatures which increases decomposition and plant growth throughout the spring. No increase in production was obtained by both authors when ash was placed on clear-cut areas, but an increase was obtained when the litter was raked up and removed. The litter remaining after the March burn in this study did decrease rapidly in April and May, indicating a potential mineral release after the fire.

It is generally understood that the proportion of minerals in plant biomass relative to soil increases with decreasing latitude reaching a peak in the low humid tropics (for examples, see Ovington, 1963,

H. T. Odum, 1970, and Bormann and Likens, 1972). Therefore, on a gradient from the arctic to the humid tropics, fire will affect an increasing proportion of the total nutrients in an ecosystem releasing them in a highly mobile form for leaching or uptake by plants. Consequently, the direct nutrient release effect of fire would become more important, and the indirect microclimatic effect of litter removal would become less important, as one goes southward.

The higher cycling rate in warm, humid climates results in rapid successional growth following fire. Gordon Miller in this conference volume reports that burned Scottish moors took 3 years to reach the same relative level of minerals in vegetation that occurred in 3 months on the burned site in Georgia. The potential for leaching increases with increase in rainfall. One would expect mineral loss through leaching to be greater in Georgia than in a more northerly environment. However, leaching is minimized by the timing of the experimental burn in late winter, which coincides with the beginning of rapid vegetation growth in the Southeast, resulting in high uptake of minerals, such as phosphorous and nitrogen (Fig. 7). The higher May-July productivity on the burned plot (see Fig. 1, lower diagram) as compared with the unburned control could result from nutrients directly released by the fire or released by increased decomposition after the fire, or both. This illustrates the empirical wisdom of the hunter and cattleman burning at the end of winter, Vogl (1972).

Considering the experimental study as a whole, the most striking result was the pronounced and prolonged effect of one very small fire lasting only a couple of hours. Effects on productivity and species diversity of both plants and animals were demonstrateable until late summer, while species composition and dominance in the vegetation was altered to the very end of the growing season. The fact that the burn came at the beginning of the season, before there was much new growth, undoubtedly was a major reason why a relatively small perturbation had the effect of altering the pattern of seasonal development of the whole community. In this case, the burn set in motion an orderly pattern resembling that of earlier stages in the natural succession. Fire later in the season would be expected to produce disruptive and disorderly effects.

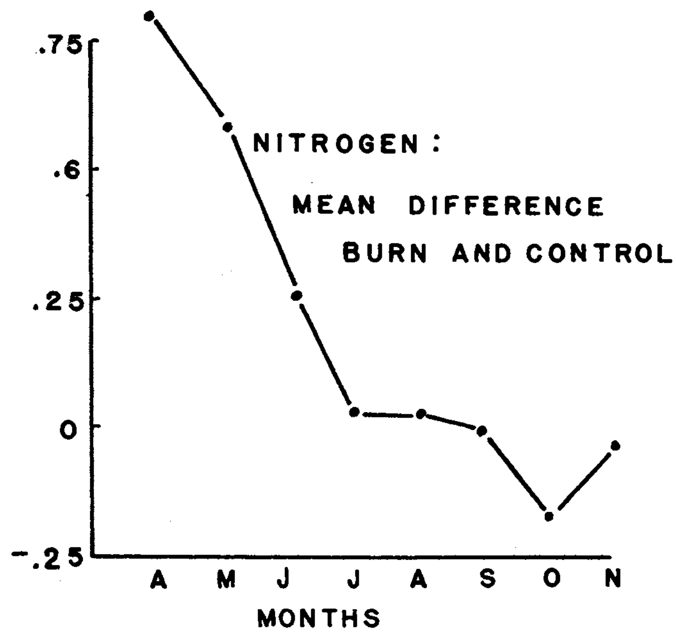

FIG. 7. Mean difference between burned and unburned (control) in nitrogen content of the above ground portion of living plants, as assayed in terms of ppm N.

The literature on "fire ecology," as well as this study, confirms the importance of the timing of controlled burns where specific effects or results are desired.

SUMMARY

Burning the litter on March 7 in one-half of each of two 1-acre fenced plots of a 4-year old natural succession following grain culture (in 1966), produced the following statistically significant effects:

1. The amount of litter remaining in the burned plots decreased until June, then increased rapidly to equal that in the control plot by September.
2. Standing crop biomass of vegetation on burned plots was less in March and April, more in May through July, and the same (as in control) in September through November.
3. Net primary production was less in March and April, considerably greater in May through July, less in August and the

same (as in the control) September through November. Total annual production was greater in the burned plots (Mean, 837 compared to 714 g/m^2 in control plots).

4. Ragweed (*Ambrosia*) and seven other species characteristic of earlier successional stages contributed more to net production on the burned plots, while 11 species were reduced in dominance, including Asters which are characteristic of older successional stages.
5. Species diversity of both plants and arthropods was increased by the litter burn May through July, but the total number of species of plants in samples collected from the burned area was less and plant species diversity in terms of annual primary production was lower for the season as a whole. Increased diversity during the summer was largely a function of increased evenness in the apportionment of individual in species.
6. Small mammals stocked in the experimental enclosures concentrated their activity in the unburned portions during the spring, but shifted to the burned portions later in the season.
7. The nitrogen and phosphorous levels in spring annuals were higher in the burned plots; by July there was no difference in mineral concentrations in the vegetation of burned and unburned plots. It is suggested that increased mineral uptake and productivity is a two-fold effect resulting from (1) direct nutrient release by the fire, and (2) increased decomposition following the fire. The former would be expected to become more important southward and the latter northward in an arctic to tropic gradient.

The overall effect of the late winter litter burn was to set back the succession from a 4-year stage to about a 2-year stage. Three basic properties of ecosystems, namely net production, species composition and nutrient recycling were effected by the fire in the direction predicted by Odum's model for ecosystem development. Effects on diversity were not clear-cut since the number of plant species and diversity of annual net production was reduced by the litter burn, but diversity ratios for both plants and arthropods were increased during the late spring and summer.

LITERATURE CITED

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