ECOLOGICAL EFFECTS OF FOREST FIRES

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INTRODUCTION

Fire has been a significant factor in determining the vegetation of North America for many centuries. This is evident from the numerous published references to telltale layers of charcoal in soil under forests, and to other evidences of past fires. This paper is an effort to bring together the literature concerning the extent of forest fires and their effects on soil and various forms of life.

Among the references to evidence of past fires is that of Soper (300) who discovered charcoal in different strata of peat in northern Minnesota, showing the periodic recurrence of fire in that region long before its settlement. From pollen analyses of peat from northern Idaho, Hansen (134) determined that severe and frequent fires inhibited the development of post-Pleistocene climax forests in that area. The importance of fire as a major natural factor contributing to forest succession was also stressed by Lee (201).

Evidence of pre-settlement fires is also inferred from the type and distribution of the present vegetation in many places. Maissurow (232) maintained that the typical northern-Wisconsin forest, consisting of a variety of uneven-aged, fire-tolerant hardwoods, developed between fires, and of even-aged, post-fire stands of conifers indicates that there have been fires in 95% of the virgin forest for at least five centuries. Chapman (59) believed that most of the old, even-aged white pine stands throughout the Lake States region originated on burned areas. Jones (172) also related the occurrence of even-aged stands throughout the north temperate zone to the occurrence of fire. Linteau (209) believed most of the extensive white pine stands north of the St. Lawrence to be the result of fire. In reviewing Land Office survey notes, early travellers' records and other evidence, Spurr (302, 303) was able to relate the pine forests of Itasca, Minnesota, to records of specific fires. Daubermire (78) also related the big pine woods of northern Minnesota to the occurrence of fire. Allen (7), however, believed fire to be completely deleterious to forest succession in the Lake States.

Lutz (221) described the extensive forest fires which have swept forested portions of Alaska in the past and cited references to similar, extensive fires in regions of Siberia and Alaska (241, 273). Rubner (281) believed that almost all of the forests of Finland showed evidence of past fires. Muller (252) found similar evidence in Bulgaria. Haig (129) presented as evidence of the importance of past fires in the United States, the fact that no other type of clearing occurred extensively before white men, yet sub-climax associations are found everywhere in the country. Iverson (165), from pollen analysis, determined that considerable clearing of neolithic forests occurred by burning, and this was followed by weeds, then hazel and birch.

General observations have often indicated that fire has been selective in the species it favors. MacKenzie (230), in his 18th century explorations from Montreal, noted as curious the fact that where areas of pine, spruce and birch were destroyed by fire, only aspen were produced, even though none was there before the fire. Along the Alaskan Highway, in British Columbia, Hansen (133) ascribed the persistence of lodgepole pine and aspen to frequent fires, and the presence and increase of spruce to the reduction of fires in modern times. Oosting and Reed (261) cited fire as a major factor in determining the vegetation of the central Rockies, favoring lodgepole pine. Weaver (341, 342, 343) believed that fire has been a natural agent for thinning and improving ponderosa pine stands in the west for many years.

There are cases, however, where pre-settlement fires are believed responsible for the absence of forests. Asa Gray (124) and Stewart (308) believed that the grasslands or prairies of the Midwest were developed or increased because of annual fires. One of the major causes of the treeless barrens of Kentucky was probably the spring burning of grass by the Indians (277). In the western states, grasslands were frequently replaced by mesquite and chaparral as a result of fire (308).

In pre-settlement times, lightning was probably a major cause of fire (60), although the Indian practice of setting fires appears to have been very important (80, 120, 124, 216, 227, 308). The Indians used fire to improve visibility and travel in forests, to drive and trap game, to clear land for better pasturage and crops, to increase the berry supply, for communication, and to eliminate mosquitoes and flies.

Fire, then, has been a major factor in the ecology of forests and grasslands in North America. In many places throughout the country, large and profitable forests have developed following fire. In other places permanent scrub or grasslands developed. Under various conditions, prescribed or controlled burning is used to maintain or develop grassland, shrubland or forest. The following review of literature dealing with observations of the effects of fire on vegetation and soil is aimed at determining the extent and nature of findings concerning the factors involved in such effects.

The majority of the investigations of fire deal with the changes it produces in the frequency or growth of certain species or groups of plants and animals. Most of the papers concerning possible mechanisms causing such biotic changes deal with fire's effect upon the soil. One must bear in mind, however, that the same principles do not necessarily apply in widely different regions and soil types, although it would appear that some general conclusions may be drawn from similar studies in widely separated areas.

EFFECTS OF FIRE ON SOIL

MOISTURE RELATIONS

The role of fire in increasing erosion and surface run-off, and in changing soil-moisture characteristics has been a subject of much concern in studies of the effects of burning on soils. It is logical to assume that, since fire often changes the vegetation and forest floor suddenly and drastically, by these actions, it also would change the reaction of the forest area to rainfall. However, the changes wrought naturally vary greatly with the conditions of the soil, forest floor, topography, region and type of soil.

Few workers disagree with the idea that extensive burning increases erosion, surface run-off and the possibility of flood on many sites. In Oklahoma, Elwell et al (97) reported that, over a nine-year period, water and soil losses were 12 to 31 times as great on burned as on unburned woodlots. In the pine region of the Sierras, run-off was 31 to 463 times as great and erosion was two to 239 times as great in burned areas (129). Increased erosion of wooded land has also been reported by many other workers (11, 25, 43, 67, 139, 181, 217, 220, 228, 247, 323, 325). Lutz (221) and Preble (274) reported the slumping-in of stream banks following fires, as a result of the destruction of steam bank vegetation.

On certain types of sites, however, erosion and run-off do not seem to be affected by burning. In California it has been reported that the burning of brush and woodland grazing lands apparently had no effect on run-off and erosion (2, 30, 331). Other studies of burned brush and grassland, however, have revealed increased erosion (90, 109, 256, 257, 285). Horton and Kraebel (157) reported increased erosion in brush plots in California following burning but stated that it is stopped if the proper pre-fire species re-invade the burned land. Brown (44) found that heavy rain in burned brushland in California brought down much debris and soil, whereas the run-off from unburned brushland was essentially clear. Tedrow (320) emphasized that where the land is flat and the soil sandy, run-off is negligible, as is the case where controlled burning is usually applied. In the New Jersey pine barrens, fire did not affect the physical properties of the soil (49).

Erosion and run-off are the result of lower infiltration rates and decreased water absorption. Specific studies of these latter soil characteristics usually agree with the more general observations on erosion. In a study of infiltration rates on seven types of soil in Missouri, Arend (13) found burning reduced infiltration rates 38%, compared to an 18% reduction when litter was removed by raking. Similarly, Kittredge (178) found infiltration one-fourth as intense on land burned annually as on unburned land, and Meginnis (239) reported lower water absorption capacity for burned oak forests in Mississippi. Reduced water absorption as a result of burning has also been reported by other workers (16, 17, 164, 256, 257, 265, 333). However, Veihmeyer and Johnson (331) found infiltration rates of brushlands in California unimpaired by burning. Ferrell and Olson (107) reported that, in the western white pine area, burning had little or varying effects on infiltration rates.

A change in the reaction of soil to precipitation, with resultant erosion, may be caused by the alteration of the forest canopy, thereby changing the force and rate at which rainfall hits the ground (46). It might also be caused by a direct alteration of the soil texture, making it less permeable (164, 178, 284), or by reduction in frequency of soil fauna burrows and the channels produced by decay of roots.

A diminution of the actual moisture content of the upper layer of soil following fire is reported for different regions (22, 31, 91, 130, 147, 148, 151, 270, 284). Kivekas (179) found that a reduction in humus content after burning correlated with a decrease in the percent of moisture, and that this reduction continued for 50 years or more. However, at lower mineral soil levels, greater or unchanged moisture content was reported in several of these and other cases (91, 130, 270, 284, 319). A variety of methods for determining changes in moisture content have been used. In some of these reports (20, 31, 151) wilting point or moisture equivalent was used, while in others (91, 130, 270, 284) actual moisture content was determined. Blaisdell (31), studying burning of sagebrush and grasslands in the West, found that any reduction in moisture content, even in the top one-half inch of soil, was only temporary. No differences in moisture content between burned and unburned plots were reported by Green (125), Wahlenburg et al (335), Wahlenburg (333) and Wicht (350) on various types of sites.

The importance of moisture-holding capacity in determining survival of forest trees was stressed by Kell (175) and Daubermire (79). Although Austin and Baisinger (16) reported that after burning there was a 33.7% reduction in the moisture-holding capacity in the top one-half inch of soil, many investigators agree that the moisture-holding or field capacity of soil is seldom affected by burning (22, 23, 151, 219, 307, 319). In the Douglas fir region, the field capacity of the duff and top 0.3 inch of soil was decreased with burning, but no change was noted below that (164). The presence of charcoal in sandy soil increased the moisture-holding capacity, while in clay soil, charcoal may have decreased it (317, 326).

The effect of these various changes in soil moisture relations upon the water table apparently vary greatly with different site conditions. Lutz (221) cited references (48, 128, 351) to indicate that where the ground water is close to the surface, destruction of forest by fire or other agencies will cause a rise in the water table, resulting in the production of swamp conditions, at least in Alaska. In Finland, Kolehmainen (180), however, did not believe that this occurred. He believed that the great numbers of plants which develop following a burn keep the water table normal, retaining the water where it will be available for later tree use. He further reported that in Sweden, burning has lowered the water table in some previously wet sites. This is because the unburned areas with thick moss cover do not freeze completely in the winter. Consequently, the spring surface thaw is absorbed into the ground and the water table is kept too high. When these areas are burned, however, they freeze in winter, the surface water runs off, and the water table is thus lowered to a more desirable level.

TEXTURE

The majority of studies indicate that most fires are not hot enough to produce a direct effect upon the texture of the soils, except where complete removal of duff and litter and subsequent exposure of mineral soil to rain result in puddling and baking of the surface (164, 178, 325, 221, 284). Garren (17), however, reported burned soil in southern states to have a more massive structure and to be less permeable to water. Similarly, Wahlenburg et al (335) reported that burned soil was up to five times as harder as unburned soil. Heyward (149) stated that the absence of fire for a period as short as ten years in the longleaf pine forests results in a more porous, penetrable soil. Soils of sandy loam or heavier texture may exhibit fine crumb structure, and the humus layer will become mull-like. Kittredge (178) believed soil porosity is greatly reduced because of destruction of insects and other macroorganisms which channel the soil. Edwards (92) reported better tilth in soils in India as a result of high temperatures during slash burning, and Ehrenberg (93) ascribed similar findings to the fact that the heat of fire could make clay more friable. Stepanov (307) and Sreenivasan and Aurangabadkar (304) reported lumping and hardening of clay soils after burning, the result of colloidal aggregation.

TEMPERATURE DURING BURNING

Temperatures recorded during fires cover a wide range, as might be expected in fires at different seasons, weather conditions, type and quantity of fuel. Long recognized as among the hottest and most destructive are the heavy slash fires in the coniferous forests of the Pacific Northwest. Hoffman (155) found that in such fires of Douglas fir, cedar and hemlock, temperatures above the ground reached 850°F, while below 0.75 inch of duff, temperatures attained 120°F. The mineral soil under one and one-half inches of duff rose no higher than 60°F, while one inch below exposed mineral soil, temperatures reached 75°F. Isaac and Hopkins (164), in similar area, recorded temperatures of 1841°F above the forest floor and 608°F one inch below. Heyward (150), reporting soil temperatures during fires in the longleaf pine region, found that in the upper one-quarter inch of soil, temperatures reached 150° to 175°F for only two to four minutes. At the one-half inch depth, the rise in temperature was negligible, or in some cases reached 190°F. At one inch there was only a slight and insignificant rise. Elpatievsky et al (96) reported that the upper sandy mineral soil in large spruce and pine slash pile burns in Russia reached 500°F, and that the depth of heat penetration was greater in sand than in heavier soils. Beadle (22) found temperatures of sandy top soil in New South Wales varied from 178° to 415°F during fires, while at one inch depths, temperatures rose to a maximum of 153°F. Bentley and Fenner (28) recorded temperatures between 200° and 250°F at mineral soil surface when burning grassland with light litter, and temperatures below 200°F when the land was covered with heavy litter. Where brushland was burned, mineral soil surface temperatures rose to 350°F.

Uggla (330) reported little or no temperature rise in the humus layer of forest soil during burning because of the thermo-insulating properties of the moisture condensation barrier between litter and duff layers.

Investigations of the effects of such temperatures on soils and on subsequent plant life grown on the heated soils are contradictory. It has been reported (251, 290) that high temperatures induced chemical changes in the soil. They found the amount of soluble material beneficial to plant growth in extracts from heated soil was six to ten times greater than that from unheated soil. However, Pickering (272) reported that a non-acid, nitrogenous material harmful to plant growth was formed in soils heated without drying to between 60° and 150°C or higher. The greater quantity of this substance which inhibited seed germination was formed at 200°C, the amount diminishing at greater temperatures. Coults (73) found little change in soils heated to 250°C, but above that there was a 20% reduction in buffering capacity. Sreenivasan and Aurangabadkar (304) noted that the clay content of soils was reduced by heating, due to the aggregation of colloids.

Increased fertility of burned soils has been believed by some workers to be caused directly by the high temperatures during the fire, not by the addition of plant ash (131, 182, 304). Pickering (271, 272) however, reported that growth of broad-leaved species was less vigorous on heated soils, although growth of grasses was better. Seaver and Clark (290) found that heating soil to 194°F favored growth of oats, while temperatures above 248°F reduced growth. Wilson (355) found that heating soil to 96°C accelerated the growth and vigor of plants, while heating to 175°C delayed germination, retarded growth, and increased susceptibility to disease. Johnson (171) reported that heating soil increased germination by eliminating certain fungi pathogenic to seeds and seedlings. It is evident that the differences in the effect vary with the plant species used and the type of soil treated.

While Sampson (284) reports that most dry seeds are killed by exposure to temperatures of 250° to 300°F, for five minutes or more, seed of certain plant species may be stimulated to germination by heat. Among shrubs, Stone and Juhren (312) observed that germination of *Rhus* spp. seeds was 17 to 60 times as great after heating the soil containing the seeds because the high temperatures made the seed more water-permeable. Wright (357) found *Rhus* spp. germination increased by the action of temperatures up to 260°F. Germination of *Cheonathus* seeds was also stimulated by heat (275, 357), in some species by temperatures as high as 280°F. *Rhamnus californica* increased in germination at temperatures up to 180°F (357). Wright (357) reported that heating the seeds of *Abies magnifica* to 180°F increased germination, the optimum being between 100 and 120°F. *Pinus ponderosa* showed slightly increased germination after exposure to temperatures up to 200°F, while *Pseudotsuga taxifolia* increased in germination rate only slightly at temperatures up to 160°F. No changes in germination with application of higher temperatures were detected for *Pinus contorta* and *P. lambertiana.* Stone (311) reported flowering of Brodianiae species to be stimulated by heat.

Among grasses, *Avena* species were stimulated by temperatures up to 220°F, while *Bromus* showed insignificant results (357).

POST-FIRE TEMPERATURE

Burning also affects the temperature of soil for some time after fire. This is partially the result of removing the insulating vegetation; more significantly, it is the result of increased light absorption by the blackened surface and by the presence of charcoal in the soils (36, 162, 221, 293, 326). Isaac (163) reported that at an air temperature of 89°F, the temperatures of surface yellow mineral soil rose to 125°F or higher, while in similar soil which had been charred, temperatures rose to 144°F. Hensel (140, 141) found that in burned over grasslands, at a one-inch depth, soil temperatures were 12 degrees higher maximum and two degrees higher minimum, while at three-inch depths, miximum and minimum temperatures were four to five degrees higher. Higher soil temperatures after burning were also reported by other workers (36, 135, 293, 335). Phillips (270) reported higher day but lower night temperatures in the top six inches of burned savanna soil in South Africa. In the Duke Forest, Pearse (264) found that similar, greater temperature extremes occurred on burned forest soil, and that these differences could be detected for at least five years after burning.

This change in temperature extremes affects various species differently. Hensel (141) believed that it would account for the earlier spring development of vegetation on burned plots. Shirley (293) found that it stimulated growth of aspen suckers. Often the increase in soil temperature is sufficient to kill very young tree seedlings and impede reforestation (36, 162, 225, 326). Undoubtedly other differences in vegetation and succession plant and animal life reported on burned lands might, if more fully investigated, be found related to these temperature differences.

FERTILITY

Observations on the effect of fire on soil productivity and fertility vary widely with region, soil and type of plant growth studied. Of more probable significance are those studies in which the change in fertility has been related to changes in specific soil substances or properties as reviewed in later sections. In many cases, however, a change in the plant yield of soil was observed after fire, but it was not identified with any specific soil constituent or property. Corson (71) noted that fire, by changing vegetation and fertility, interferes with the classification of soils into their adaptation to existing forest types.

Germination and very young tree seedling growth has some times been reported to be poorer on burned soil. In clarifying this, Fabricius (104), growing trees in pots of soil, found that covering the soil with ash reduced germination and early growth of all species studied. He noted, however, that the inhibition by ash was less on sandy soil than on loam. Heikinheimo (137) also carried out extensive tests in which ash was added to neutral sand and to peat, and the germination and growth of pine, spruce, birch and alder were studied. He recorded that the higher concentrations of ash hindered germination and growth of all four species, but that spruce and alder were more seriously affected. This, he believed, corresponded with the fact that spruce is often slow to return after fire. Schmidt (286), performing similar experiments with Scots pine, found that germination was improved by ash, although subsequent growth was reduced. Tryon (326) reported decreased germination of white pine seed in soil to which charcoal had been added. Perry (267) found growth of both white and red pine better on unburned soil. In France, Arnould (14) found that trees grew poorly for 100 years after fire on clay soil, and he believed this to be the result of compaction of the soil as a result of burning. Similar, shorter term results with redwood seedlings on clay soil were reported by Fritz (114).

Reduced growth of other plants is also reported. Without the presence of ash, heating soil resulted in less vigorous growth of most vegetation, according to Pickering (271, 272). While heating soil to 90°C was beneficial to growth of oats, heating to above 120°C was injurious to their growth. Thompson (322) reported burned soils less productive for oats and potatoes than unburned soils. Poor productivity of burned soil was also noted by other workers (97, 164, 279, 333, 356).

Alway (8) and Alway and McMiller (9) reported that burning had no effect on productivity of crops on sandy loam in Minnesota, and Thompson (322) found that yields of hay and sunflower were similar on burned and unburned soil. From phytometer studies of pitch pine plantations in New Jersey, Lutz (220) found no consistent differences in fertility of unburned and burned soils, and, in the same area, Somes and Moorehead (299) reported no significant differences in growth of pine-oak stands as a result of burning. In South Africa no appreciable difference in soil fertility in brushlands could be detected after burning (23). In the southern Appalachians, fire had no significant effect on radial growth of shortleaf pine for two to 13 years after fire (169). Heyward and Barnette (152) found no marked change in soil fertility after burning in the longleaf pine region. Although productivity of steep slopes and rocky ledges is lessened by fire in Alaska (221), other sites do not seem to be affected in productivity.

On the other hand, reported stimulation of germination and growth of tree species has been reported frequently. Schmidt (286) reported Scots pine germination stimulated by application of wood ash to the soil, while in Madras, India, Laurie (194) reported that slash burning was beneficial to germination and height growth of most tree seedlings except teak. Kessel (176) also reported increased growth of tree seedlings around ash beds in Australia. In India height growth of tree seedlings was reported to be greater on burned than on unburned plots, especially the first year (126, 168).

The beneficial effect of burning on growth of herbaceous plants has also been cited frequently. While some of these reports may seem contradictory, to those reported above, it must be remembered that different species and soils are usually involved. Wahlenberg (333) reported that forage plants and corn grew better on burned soil in the longleaf pine region. Corn also produced better yields on burned soil in tropical Africa, according to Topham (324). The number and size of forage plants in the longleaf pine region was found by Greene (125) to be increased by prescribed burning. Fowells and Stephenson (110) reported a stimulation of plant growth after burning, but believed it to be very temporary. Blaisdell (31) found stimulation of grasses and herbs by fire to disappear after two to three years. Fertilizing action of ash on grasses was also reported by Curtis and Partch (76), together with an increase in grass flowering heads caused by the higher soil temperatures resulting from removal of the insulating cover of old litter. Kivekas (179) conducted experiments in which oats grown in pots under greenhouse conditions yielded twice as much dry substance when grown on burned soil as when grown on unburned soil. Garren (117) also believed that burning increased growth of ground cover plants as a result of the return of minerals to the soil by way of ash. Beneficial effects of burning on plant growth were also reported briefly by other workers (94, 131, 143, 144, 182, 194, 202, 219, 293, 304, 332).

Conclusions on this subject are difficult, since soil productivity is dependent upon many factors, and fire may affect each of them differently. For example, erosion and run-off are generally increased by fire, with the resultant washing away of nutrients. However, under some conditions these harmful aspects may be more than compensated for by the stimulatory effect of ash on subsequent plant growth and on the growth of micro-organisms in the soil. These, in turn, replenish soil, both physically and chemically, and cut down on erosion and run-off.

CHEMICAL COMPOSITION

The sudden release to the soil via ash and subsequent rainfall of soluble mineral salts previously incorporated in plant tissue and usually returned very slowly by the decay processes is undoubtedly responsible for many of the changes in plant growth found on burned soils. Therefore, the temporary effect of burning may be helpful, but, since soil productivity depends on gradual mineralization and utilization of fallen litter, it would not be reasonable to expect continued and repeated burning to improve soil fertility (110, 117) unless this sudden, large supply of mineral nutrients were in some way immediately incorporated into the biological cycle before it could be leached away. Stephanov (307), working with Scots pine forest soils in Russia, and Katz (174), working on peat soils, and Burns (49) in the New Jersey pine barrens found that there was an increase in both water-soluble compounds of alkali and alkaline earth metals, sulfates and carbonates after burning. Haines (130), on the other hand, working on heathlands in England, found that two months after burning, the soluble salts in the soil were reduced by leaching 70% in the top two inches, and 86% below this. Heyward and Barnette (152), studying the effect of frequent fires on mineral soil in the longleaf pine regions, found the general chemical composition improved by burning, while Lutz (220), working in the New Jersey pitch pine region, found very little general change in soil chemistry. Improved soil fertility following fire has been reported in many other areas (3, 4, 42, 98, 220, 288). More may be learned by investigations of the various elements separately. These are discussed in the following sections.

ACIDITY

It is reasonable to assume that the considerable amounts of ash left on the ground after burning will decrease the acidity, since ash is rich in alkaline material, and, according to Heikinheimo (137), 7% of the potassium carbonate and other similar salts will dissolve in cold water. However, no significant change in soil acidity as a result of burning was reported on various sites (22, 23, 220, 268, 332). Perry (226) reported a decrease in acidity as a result of burning in hardwood forests in Pennsylvania to be very temporary. The majority of the studies, however, indicate that fire usually decreases acidity (8, 16, 18, 21, 96, 99, 107, 117, 119, 125, 130, 152, 164, 179, 183, 212, 219, 236, 328, 330).

This change in acidity may vary with the depth and type of soil. Hess (143) found that burning lowered acidity of acid soils in Switzerland but had no effect on neutral soils. Alway and Rost (10) reported that, in Minnesota, acidity was lowered in the top three inches but unchanged below that after fire. Perry and Coover (268) found that the A horizon of frequently burned areas had the same pH as infrequently burned areas, but that there was a lower acidity in the B horizon, attributed to the leaching downward of ash materials.

The length of time these changes persist after fire differs. Eneroth (99) found that in Sweden, an increased pH of surface soil following burning lasted ten years. In English heaths, Haines (130) found that the lowered acidity of surface soils returned to normal in a few months after fire. Finn (108) burned organic material which had been placed on boxes of sandy and loamy soil, and found it resulted in a change to an alkaline condition which reverted to acid after one year.

The change in acidity, as previously mentioned, is usually believed to be caused by the presence of ash and by the resultant release of soluble mineral salts, especially those containing calcium (126). Subsequent leaching of these salts from the top layers results in eventual return of them to the original acidity. Reported differences in degree of acidity following burning and in the rate of return to normal indicate that the quality of the soil, type and amount of ash are important in determining the extent to which fire effects acidity. Eden (91) pointed out the possibility that the heat of fire may also destroy buffers, especially organic ones, as well as organic acids in the soil. Coults (73) reported a 20% reduction in buffering capacity of soils when heated to above 250°C. Munste (255) and Hessleman (145) found that after a burn, the alkaline materials from the ash neutralized free humic acid; when this happens, leaching of salts from the soil will be minimized. Svenhufruid (315) reported that up to 25% of the ammonia produced in burning can be absorbed if conditions are right.

ORGANIC CONTENT

The extent to which soil organic matter is destroyed by fire is very largely a factor of the fire intensity and temperature, the extent to which the organic matter is incorporated in the soil, and the type of pre-burn vegetation. Although Hosking (158) demonstrated that organic material heated to 100°C without combustion lost weight significantly, Heiberg (136) stated that fire does not affect organic material incorporated in the soil, probably because soil temperatures below the top inch of soil are not raised high enough during most fires.

Austin and Baisinger (16) found that the organic content of the top one-half inch of soil in western Oregon and Washington was reduced as much as 75.5% after fire. Two years later the organic content was still 50% below normal. Blaisdell (31) found a significant reduction in organic content in the top one-half inch of burned soil in sagebrush and grasslands, but the effect was temporary and disappeared after a few years. Isaac and Hopkins (164) found organic matter reduced one-third by burning in the top three inches, while below that the changes were insignificant. Always (8) stated that in a bad fire in Minnesota, the loss of organic matter ran from seven to 26 tons per acre in the surface layer, with little change below that. Barnette and Hester (18) compared soils burned annually for 42 years with unburned soil and found a loss of 2,088 pounds of organic matter per acre. In English heaths, Haines (130) found a loss of 60% of the organic matter in the top soil layers and an eight per cent reduction at lower levels. Minckler (243) reported fires can destroy as much as two feet of pure organic soil in spruce forests of the southern Appalachians. Ferrell and Olson (107) reported that the organic matter lost to burning in western white pine regions takes 50 years or more to be replaced. Diebold (85), in the Adirondacks, found the forest floor burned to an average depth of two inches. There are many other references to loss of soil organic matter with burning (87, 97, 110, 179, 263, 266, 304, 325, 344), although Beard and Darby (23), Bruce (41) and Wicht (350) reported no significant loss in soil humus in their studies.

In Alaska, Lutz (221) found the loss of organic matter varied with the intensity and frequency of fires, but that deep burning to mineral soil, even in fires severe enough to kill all the trees, occurred on 30% to 40% of the total burned surface. Lovejoy (215) quoted an opinion of Dr. Marbut of the U.S. Soil Survey that any accumulation of forest debris is injurious to soil and forest growth, and that any method which removes it is good. Lovejoy holds, however, that there is insufficient evidence of the advantage of this to advocate extensive, controlled burning. Muller (252) also emphasized the beneficial importance of burning in reducing excessive raw humus, particularly in pine stands, although Lowdermilk (217) pointed out that the great reduction of forest litter caused by burning is a serious factor in the increase of erosion. Williamson (354) reported that annual burning of forests in Florida reduced organic content seriously, to a depth of four to five inches.

NITROGEN

One major factor controlling soil productivity is available nitrogen, and there is little doubt that in most cases fire affects the quantity available. At the same time, fire may cause changes in other soil conditions which in turn stimulate or inhibit the nitrification process carried on by soil and nodule bacteria and soil fungi. The activities of these organisms may obscure tests of the direct destruction or increase of soil nitrogen by fire, and this may be one of the reasons for contradictory reports in the literature.

Reports of lower nitrogen content following burning are frequent. In Florida, Barnette and Hester (18) reported an estimated annual loss of 27 pounds of nitrogen per acre when land was burned annually. In New Jersey, Lutz (220) found a slightly lower nitrogen content in frequently burned soils as compared with soils burned infrequently. A loss of nitrogen from the upper two inches of clay and loam soils after burning of wattle litter in Africa was reported by Osborn (263). Finn (108) reported loss of nitrogen by leaching in experiments in which sand and loam soils placed in boxes were covered with organic matter and burned. Losses of from 450 to 1,500 pounds of nitrogen per acre through losses in the surface cover were reported by Alway (8) in Minnesota. He found, however, little change in the upper mineral soil.

Austin and Baisinger (16) discovered a 67% loss of nitrogen in the top 12 inches with a 75% recovery of this loss two years later in burned soils in the Pacific Northwest. Lovejoy (215) cited Snyder's figure of a loss of 1,600 pounds of nitrogen per acre from forest fires in the northern Lake States region. Blaisdell (31), Elwell et al (9) and Wahlenberg (334) also reported losses of nitrogen from soil after burning. In Finland, Kivekas (179) found loss of ammonia from the top layer of soil with burning, but he believed this loss was much greater in brush fires than in sod burning because hotter fires oxidize organic material more rapidly with greater vaporization. Svenhufruid (315) reported that up to 25% of the ammonia formed during burning of peat can be absorbed by the soil after burning.

On the other hand, increased soil nitrogen as a result of burning is also reported frequently in the literature. Heyward and Barnette (152) reported higher total nitrogen after burning in soils of the longleaf region. Isaac and Hopkins (164) found no significant change in the nitrogen content of soils in the Douglas fir region after burning, and Chapman (58) reported similar results in loblolly pine stands. Garren (117) reported nitrogen increases in the southeastern states after burning, and Lunt (219) found higher total nitrogen after burning under red and white pine stands in the northeastern states. Tryon (326) found that coniferous charcoal in the soil increased the total nitrogen, but he detected no change in the amount of available nitrogen with such addition. Vlamis et al (332), conducting controlled fertility tests on soil from the ponderosa pine region, found that heavy burning increased nitrogen slightly. An increase in soil nitrogen after fire has been reported in many other areas (4, 10, 107, 117, 144, 220, 278, 284).

In discussing the effect of burning on the biological processes which restore available nitrogen to the soil in Finland, Kivekas (179) reported that, while ammonification is less, the nitrification process is greatly increased due to the effect of the changed pH on bacterial growth. Green (125), working with longleaf pine soils, found a large increase in growth of legumes after fire. These plants, he feels, were responsible for subsequent increases in nitrogen. Hesselman (144) also felt that burning increased soil nitrification and that such increases after burning could last from 12 to 25 years, depending on the type of soil and other conditions. He also found increased denitrification, oxidation of ammonia to nitrate, and reduction of peptones to ammonia—or increased bacterial activity in general. In Russia, Sushikna (314) found that an increased nitrification rate was detectable two days after fire and lasted at least five years. Fowells and Stephenson (110) also reported increased nitrification by burning. In the Cameroon, control of the nitrogen cycle by burning, known as "ecoubage", is practiced in places where the nitrogen cycle is completed too rapidly (167). To conserve nitrogen, soil is allowed to remain fallow for two years. It is then allowed to grow up into brush, and the brush is burned. Three or four crops are then grown on the land, and the process is repeated. This burning is believed to "mobilize" the minerals, especially the nitrogen. Kivekas (179) found that the proportion of amino acid nitrogen to protein and amide nitrogen was much higher on burned land. He also found that the total nitrogen was reduced by burning, but not to a critical level.

CALCIUM

As would be expected, changes in soil calcium content correlate fairly closely with changes in acidity as a result of burning.

In the southeastern United States, significant increases in replacable calcium following burning were reported by Garren (117), Heyward and Barnette (152) and Barnette and Hester (18). Vlamis et al (332) reported similar increases in the ponderosa pine region as do Isaac and Hopkins (164) and Fowells and Stephenson (110) for soils of Douglas-fir regions. Hess (143) found that burning increased the calcium carbonate in acid soils in Switzerland but had little effect on the calcium content of neutral soils. Uggla (329) reported increased calcium after burning in Lapland. Lunt (219) reported an increase in exchangeable calcium under red and white pine forests after burning. Lutz (221) found a seven-fold increase in exchangeable calcium following fires in Alaska. Kivekas (179) found that after burning in Finland, there were significantly higher amounts of calcium in soil down to a depth of ten centimeters. Tryon (326) found that addition of charcoal to soil caused an increase in available calcium.

Austin and Baisinger (16), working with soils in the Pacific northwest, found that, as a result of mineral release from ash following burning, the soil calcium content increased as much as 830%, and that two years later it was still 327% as high as before burning. Wahlenberg et al (335) reported burned soil to have up to 100% more calcium than unburned soil in the longleaf pine region. Finn (108), however, in experimental studies, found that leaching after burning caused a loss of calcium in both sandy and loamy soils. Sreenivasan and Aurangabadkar (290) found that heat, in the absence of ash, lowered the amount of replaceable calcium.

PHOSPHORUS

In a complete fertility test using sandy loam and loam from the ponderosa pine region, Vlamis et al (332) found that on sandy loam there was a marked increase in available phosphorus following fire, while on loam there was no significant change. These different results were believed to be due to the fact that one type of soil tends to bind phosphorus and make it unavailable. Such binding may be the reason for other conflicting reports. Kivekas (179), in Finland, and Uggla (329, 330) in Sweden and Lapland reported an increase in available phosphorus as a result of burning, as did Lunt (219) and Lutz (220, 221) in the United States and Alaska. Austin and Baisinger (16) found, in the northwestern states, that soil phosphorus was twice as high after burning.

Tryon (326) reported increases of phosphorus with addition of charcoal to clay, loam and sand, while Lutz (221) observed no significant change in phosphorus content in pitch pine soils of New Jersey after burning, as did Isaac and Hopkins (164), Fowell and Stephenson (110) in the Douglas-fir region, and LeBlanc (199) in Quebec.

POTASSIUM

Available potassium was increased with burning in the Douglas-fir region (164), in Finland (179), Lapland (329) and in Alaska (221). Austin and Baisinger (16) reported potassium increase up to 166% following burning of soils in Oregon and Washington, with a drop to 112% two years later. Finn (108), however, stated that the leaching which follows most burning decreases soil potassium.

MINOR ELEMENTS

Worley (356), reporting on studies in New Zealand, believed that burning in general decreases soil fertility. Such elements as copper and manganese are usually brought to the surface very slowly by tree growth and are gradually returned to the humus at a rate at which the plants can utilize them. When burning occurs, these elements are released rapidly into the soil from the plant tissues as ash, and they are then allowed to leach out or down to the layers of soil unavailable to plant roots, thus destroying the work of centuries in maintaining a delicate balance of these elements.

LeBlanc (199) pointed out the necessary balance of such minerals as manganese and magnesium in the maintenance of black spruce in Quebec. He stated that increases in manganese to very high levels is detrimental. However, excess manganese is made insoluble if calcium is added, so that the harmful effect of increased manganese is lessened after burning if calcium as well as manganese is released to the soil via the ash. Austin and Baisinger (16) reported a 337% increase in available magnesium following burning, with a return to normal in two years.

Very little work has been done on the content of the minor elements in ash and their effect on plant growth in burned-over areas. It is very possible that such investigations might prove very significant, since these elements, necessary in very small quantities and often toxic in large quantities, may be critical in plant succession.

EFFECT OF FIRE ON LIVING ORGANISMS

LOWER PLANTS

Special attention has been given to these lower forms of plant life in connection with forest fires. Since they are among the most frequent living components of the forest floor, their destruction or increase as a result of fire is important in the problem of water conservation and in competition or assistance to seedlings of higher plants.

Rainfall interception by mosses and lichens has been investigated in the New Jersey Pine Barrens, where Moull and Buell (240) found that mosses, especially the turf type, frequent after burns, can intercept and hold an average of 50% of the rainfall, while lichens intercept 25%. Together, these plants frequently cover 90% of burned land and are, therefore, important in determining whether rainfall reaches mineral soil. However, the authors do not believe that the mosses and lichens intercept as much water as does the thick, continuous layer of litter found on forested land not subjected to burning. Mosses are often completely destroyed by fire because they lack firm connection with the soil. Some species which form deep tufts may survive (327, 330).

Kujala (185) believed fire to be more destructive of lichens and mosses than it is of higher plants. Buell and Cantlon (45), however, in the New Jersey Pine Barrens, found that burning stimulated growth of mosses and lichens greatly, and that increased light caused by removing the upper vegetation favored lichens over mosses. Lutz (221) believed that most moss reproduction following fire was vegetative, coming from fragments which survived fire instead of from spores. Hustich (160) believed that in northeastern Canada, recovery of the lichen cover following fire required at least 40 years. Lewis (207) and Lewis et al (208) did not believe that fire was a critical factor in the retrogression of sphagnum or muskeg areas in Alberta, while Stallard (306) stated that in northern Minnesota, fire very frequently causes a shift from sphagnum to grass in bog land.

Smith (298) believed that, as a seedbed for white pine, *Polytrichum* spp. and similar mosses and the moist mineral soil below them make better conditions than exposed, dry mineral soil or forest litter. This is partially because of the insulation furnished by the moss, but more significantly because seedling roots can penetrate moss and get into the mineral soil more successfully than they can penetrate litter.

In those cases where they have been studied, certain moss and lichen species have been found characteristic of burned areas, and typical post-fire succession occurs which corresponds to the succession found among higher plants (1, 74, 160, 174, 185, 285, 296). *Ceratodon purpureus, Funaria hygrometrica* and *Marchantia polymorpha* (122, 123, 334) are typical fire followers in many widely scattered regions, as are *Pohlia* spp. and *Polytrichum* spp. Among lichens, *Biatora, Baeomyces* and *Cladonia* species are frequently mentioned.

The fungus flora of the forest floor also changes with burning. In the Transvaal, Cohen (65) found that burning and light grazing stimulated the production of fungi and favored active spore production. Sarvas (285, 289) also noted an increase in fungi resulting from fire, especially those belonging to *Peziza* (Discomycetae). Moser (249) found that the Agaricaceae and Discomycetae were increased most markedly on burned soils. In comparing different kinds of burned soils, the difference in fungi was largely quantitative and not qualitative, and the differences occurred with different intensity of burning. A characteristic succession of fungi after fire was also noted, that is, the fungus flora differed in newly burned land as compared with land burned further in the past. Tryon (326) found the presence of charcoal in the soil did not appreciably affect the fungi present. No detailed studies of the effect of fire on the smaller, non-fleshy fungi were available.

PLANT DISEASES AND PESTS

In some cases fire may aid in the control of plant diseases. Muller (252) pointed out the value of fire in purging the forest of insect and fungus enemies, and in restoring vigorous, fast growing species. Siggers (295) reported that a single winter fire may almost eliminate brown needle spot, caused by *Septoria acicola,* on longleaf pine, although the disease reappears the second season, and by the third post-fire year is as frequent as before the burn. The reduction of disease for at least two years, however, results in a greater foliage retention and better seedling development. Chapman (55) and Garren (119) also reported the use of fire in the control of *Septoria* on longleaf pine.

Markim (234) found that burning controlled red leaf *(Exobasidium)* disease of blueberries and blueberry leaf spot *(Septoria)*. Cantlon and Buell (52) presented the idea that fire may reduce the occurrence of some virus diseases by destroying the insect vectors, notably leaf hoppers. LeBarron (197) and Weir (347) reported that fire effectively controls dwarf mistletoe which can be spread only by seeds from infected, living host plants (spruce). Haig (129) mentioned the use of fire to control bark beetles, nectria canker and other forest pests. Muller (252) also cited the use of fire in Bulgaria to control several fungus and insect enemies.

In some cases, however, fire may favor the increase of disease by producing thick stands of the host plant and thereby induce multiplication and spread of the pathogen. Demaree and Wilcox (82) believed this to be the case with certain leaf diseases of blueberries, such as powdery mildew *(Microsphaera alni)* and a rust *(Pucciniastrum myrtilli)*. Davis and Klehm (81) reported increase of *Ribes* after burning unless the *Ribes* was eliminated by a second burn or other eradication methods. This, of course, would affect the spread of white pine blister rust. Schmitz and Jackson (287) reported that, in Minnesota, fire scars on aspen are the main port of entry for *Fomes ignarius,* the pathogen causing heart rot. Richmond and Lejeune (280) reported a large increase in wood boring insects in fire-killed white spruce in northern Saskatchewan. Kirkpatrick (177) believed that, by eliminating the proper habitat for birds which prey on insects, many insect pests are allowed to thrive after burns. The weakened or dead trees on the burned area may provide a medium on which fungi and insects thrive. Basham (19) reported extensive growth of *Fomes* spp., causing heart rot, on fire-damaged jack, red and white pine. Richmond and LeJeune (280) reported an increase of wood-boring insects in burned white spruce stands in northern Saskatchewan. Schmitz and Jackson (287) found that fire scars on aspen are the chief portals of entry for heart rot in that species.

Wilson (336) reported that heating soil to 175°C resulted in increased susceptibility to disease on host plants later grown on this soil.

BACTERIA

A change in soil bacterial population with burning would be expected, since burning frequently raises the soil pH, a factor critical in bacterial growth. Indirect evidence of an increase in bacteria is contained in the reports described earlier, that nitrification—a process largely dependent upon soil bacteria—often increases after fires.

On the Malay Peninsula, Corbet (70) studied the effects of felling and burning virgin timber and found that the number of microorganisms rose immediately after fire but fell to the preburn level one week later and remained there for nine months or longer. In Switzerland, Dugelli (88) discovered that mixing ash with mineral soil did not significantly change the number of bacteria, and Wahlenberg et al (335), in the long leafpine area, were not aware of any significant increase in number of bacteria per acre after burning. Similarly, Jacques (167) reported that, in the Cameroon, burning did not disturb the microflora. Hall (131) found that if soil was heated for one hour to 100°C, there was an initial decrease in bacterial count followed shortly by a significant increase. Destruction of microorganisms in the top soil layers was cited by Kivekas (179) and Fritz (114). Hesselman (144) believed that charcoal in soil favored growth of bacteria. He stressed the fact that burning causes a complete change in bacterial flora. Tryon (326), however, claimed that addition of charcoal to soil did not appreciably change the abundance of bacteria. Isaac and Hopkins (164) asserted that, in the Douglas-fir region, slash burning and the subsequent calcium release favored growth of *Azotobacter,* an important nitrogen fixing genus. Lutz (220) also believed that *Azotobacter* and *Clostridium* increased after fire, as well as the nodule bacteria in wild legume roots.

INVERTEBRATES

In studying the soil microfauna in burned veld in South Africa, Coults (73) stated that the majority of the population in the top inch of soil survived ordinary burning processes. Heyward (149) reported that excluding fire from the longleaf pine forest for as short a time as ten years resulted in a more active soil fauna. Heyward and Tissot (153) determined the microfaunal population of unburned A_0 horizons to be five times as great as that of burned soil, while the top two inches of unburned mineral soil had 11 times larger population than burned soil. In general, the species or organisms in the two areas were the same, although fire significantly reduced the proportion of earthworms to other organisms. In the Duke Forest, earthworms, centipedes, millipedes and ants were significantly reduced in number after burning (264). Of ecological significance also was the fact that important soil nesting pollinators, such as bumble bees, were also seriously reduced in number. Burning, however, was not as detrimental to soil fauna as mechanical removal of litter by raking.

VERTEBRATES

Damage to wildlife has been much publicized (e.g., 89, 125, 204). Animals, in their dependence on vegetation for food and cover, are variously affected by fire. Deer, for example, are usually associated with post-fire vegetation. Leopold (206) pointed out that deer are most frequently found on the sub-climax forest characteristic of burned-over areas, and that a climax forest does not favor their existence. Leopold, Sowls and Spencer (205) pointed out that fire stimulates the production of browse and results in an increase in the deer population. Ten years after fire, if there is no further burning or logging, tree crowns close in, reduce browse supply and result in a lowered carrying capacity and a deer population too large to be supported by this reduced food supply. Lay (195) reported that in east Texas prescribed burning did not damage habitat for deer and would improve the quantity and quality of deer forage, while Dasman (77) emphasized that such improvement or possible damage to deer forage depends on a number of area conditions.

Lloyd (214) emphasized the association between the quick growth of deciduous species which sprout abundantly after fire and the abundance of deer, in contrast to the almost complete lack of wildlife in unbroken forests. He pointed out that fires favor deer and grouse, although some other species disappear with fire—as in the case of caribou in northern Ontario. He stressed the complexity of the problems of wildlife and fire, and the fact that each case must be considered individually. For example, fire rarely results in a significant direct loss of wildlife because the fires are usually too small to destroy an appreciable number of individuals. However, there are cases where the destruction of individual nests may be important to the survival of a rare or local species, for example, the heath hen which was exterminated by scrub fires on Martha's Vineyard. Fires increased the browse and were beneficial to herds of moose on Isle Royal and in Alaska (6,301).

Lloyd (214) further pointed out that some birds find ideal nesting conditions in fresh burns. The house wren and bluebird for example, are typical fire-followers. Other species follow a few years later. Stoddard (309) found fire very beneficial in the management of quail in the southeastern states. Kirkpatrick (177), however, reported that spring burning of marsh areas in Wisconsin completely disrupted the breeding season of a variety of low-nesting birds, and that they were driven out of the burned areas, thus allowing insect pests to thrive. Leopold (204) pointed out that the greatest damage to bird life is done by spring and early summer fires which destroy eggs and young, and ruin cover and food.

In Missouri, Terril and Crawford (321) reported that fires which follow logging eliminate squirrels from an area for ten to 25 years, unless a sufficient number of den boxes are immediately placed in the area. Nagel (258) reported that flood and lack of food which limit development of the beaver population in Missouri are due, in part, to forest fires. Destruction of fur-bearing animals has been emphasized by Lutz (221), Brabant (37) and Seton (291). Michaelis (240) reported that rodents were completely eliminated from a young hardwood plantation in Pennsylvania by fire. Destruction of small mammals by fire is also stressed by Gabrielson (115). Cook (68) reported that lack of cover following burning is the restricting factor in reducing mouse populations, especially for *Microtus* which requires one year mulchl for runways. He found shifts in species corresponding with fire—induced changes in vegetation from grassland to seed-produced annuals or from brush to grass. Similary, in the longleaf pine region, rodent damage can be reduced by prescribed burning which destroys grass cover necessary for seedling destroying rat species (238).

Leopold (204) and Kirkpatrick 177 have reported that, because of the wash of ash into lakes and streams after fire, fish are frequently killed.

PLANT SUCCESSION

Very few generalizations can be derived from the literature concerning plant succession following fire, since so many conditions in addition to the actual burning come into play as factors in the process. Typical post-fire sequences are inferred in many of the references, and characteristic fire-following plants are mentioned frequently for various regions. Lutz (221) stressed the necessity for evaluating quantity of seed produced, adaptations for dispersal, and efficiency of dispersing agents as well as such site factors as light and exposure of mineral soil.

Buell and Cantlon (45) believed that fire was a factor quite secondary to climate in controlling plant succession and the establishment of maple-basswood after pine-oak, common on the prairie in northwestern Minnesota, although Buell and Niering (47) recognized the destruction of pine forests in northeastern Minnesota as a major factor in the establishment of fir-spruce-birch forests. In Alaska fire has been more important than soil types and superficial geology in the establishment of forest patterns (276). In Finland, Sarvas (285) believed the appearance and subsequent spread of various plants on burned areas was dependent on the previous forest type. However, this does not mean that post-fire vegetation would necessarily develop into the same forest type or even the same major vegetational group as was present before the fire, at least not for many years.

In Switzerland, Ludi (218) reported that in a *Pinus-Larix-Picea* forest, the flowering plants which appeared after fires were mostly ones which were present in the pre-burn vegetation. However, he predicted that a long period would elapse before willow, birch, larch and finally pine would return. In the loblolly pine region, Oosting (260) reported that changes in herb and shrub vegetation following burning were very temporary. Growth of sapling or larger pines was slightly reduced, while that of lower strata hardwoods, especially oak and hickory, was increased. New reproduction of pines, however, was good and could compete successfully with hardwoods.[(5)] In following the revegetation of a burn in British Columbia, McMinn (229) found that the succession took varied courses and progressed at different rates because of pre-burn vegetation, edaphic conditions, available seed and microclimatic variations. LeBrun (200) believed the savannahs of central and eastern Africa to be of fire origin, woody species appearing only in the long absence of fire.

In Nova Scotia, on a burn of spruce-birch-oak-maple sites, Martin

(237) found that the herds and shrubs appearing during the first two years were all of sucker origin or developed from seeds which survived in the soil. However, Kujala (184, 185) divided the fire followers into four classes: *a*) plants provided with underground reproductive structures which survive the fire and produce sprouts; *b*) plants with seed which survive the fire in soil; *c*) plants with wind-disseminated seed; *d*) plants with a combination of fire-surviving or wind disseminated seed and vegetative sprouting.

GRASSES AND OTHER HERBS

A vigorous growth of herbs characteristically succeeds fire in many places. This lush, rapid growth may be related to the fertilizing action of mineral nutrients released by the ash, as discussed in earlier sections. In British Columbia, McMinn (229) reported that after a burn, bracken fern reached sufficient density to retard all forest regeneration. Martin (237), studying early development of plants following fire in Nova Scotia, also reported vigorous survival of bracken as the dominant plant because of its underground root system which survived the fire. Curtis and Partch (75) reported that after fire on prairie land, herbs increased markedly with the destruction of grasses and the increase of bare ground. Garren (117) found in the slash pine region that burning of both forest and open range resulted in great increases of herb growth, including wild legumes. Similar increases in legumes were also reported by Greene (125) in the longleaf pine region. Blaisdell (31), working on sagebrush land, found that herbs increased two to three times after fire, but he predicted the increase would be short-lived. Buell and Cantlon (46), in the New Jersey pine barrens, found burning to be followed by an increase in herbs, but they believed this increase to be caused mostly by an increase in light, since similar increases also occur after cutting. Hesselman (144) reported that the increase in the well known fire follower, *Epilobium,* is probably due to an increase in nitrogen in the soil, since this species is known to accumulate large quantities of nitrogen in its tissues. In New Zealand, Dick (83) found frequent 19th century burning of mountain beech resulted in a vegetation consisting largely of grasses. Mark (233) concluded that fire was not important in the maintenance of grass balds in the southern Appalachians, while Clements (63) believed fire to be crucial in their development.

Lutz (221) believed that, although many fire-following herbs reproduce vegetatively, the majority of species which invade burned areas have wind disseminated seed. As with shrubs, Kujala (185) and Petterson (269) held that fleshy-fruited species are rare on burned over lands because of the scarcity of animals necessary for their dissemination. These workers, however, apparently overlooked the possibility of dissemination by fire-following birds (214). Ahlgren (3, 4) found the majority of plants appearing on burned land in northeastern Minnesota to be of vegetative origin. Seed-reproducing plants on the burns were usually not found on nearby, unburned land. Many produced animal- or wind-disseminated seed.

On lightly used range in California, Hervey (142) and Sweeney (316) found that fire increased herbs and decreased grasses, although on heavily grazed land, burning had little effect on the proportions of herbs to grasses. Dix and Butler (86) stressed that the responses of grasses to fire varies markedly with species and that, therefore, each species requires special study. Oosting (260) reported that in the loblolly pine region, any change in herb population following fire is very temporary. Pickering (272) reported that grass grew more vigorously on heated soil than on unheated soil; while other herbs grew less vigorously.

On certain types of land, a stimulation in the production of grasses has been noted after burning. In western regions, with an elevation of 1,600 to 4,000 feet, burning did not injure perennial grasses and seemed to encourage their spread by removing the dense pine needle mats and killing back the competing shrubs, according to Weaver (341). Stahelm (305) also reported that in the Rocky Mountain coniferous forests, burning seemed to cause an increase in grasses and other herbs. In studying western sagebrush, Blaisdell (31) found the total yield of grasses to be increased for three years following fire, but this increase was not believed to be permanent.

Burning as a stimulant to flower and seed production in several species of grass was reported by Cornelius (72) and Burton (50). For several perennial grasses, Curtis and Partch (76) reported that removal of old litter either by fire or clipping increased flower production six times because the removal of the old insulation permitted earlier growth and build-up of food reserves before flowering time. They also found that there was further growth stimulation which could be attributed to the fertilizing action of ash.

Stallard (306) reported that in upland areas in northern Minnesota, repeated burning frequently may result in the production of a grass stage, while in bogs a reed or rush stage is produced. Either of these may delay the development of forest.

In bluegrass prairie land, when annual or biennial prescribed burning was done in March, May or October, the density of the bluegrass sod was reduced to one fifth the original after six years of burning, although the fruiting stems increased in number (75). Hervey (142) reported that on grazing land, fire had little effect on the proportion of grasses to herbs if the land was heavily grazed. On ungrazed or lightly grazed land, however, fire decreased grasses. Lemon (203), in studying post-fire succession in longleaf and slash pine areas, recognized bulky, perennial grasses with underground basal meristems which survive fire as one of the major plant types to appear immediately after fire.

In New Zealand, Sewell (292) attributed the deterioration of montane tussock type grassland, in part, to burning. He believed that burning killed tussocks and removed the protection of old leaves. After burning, two or more years were required to reproduce the proper microclimate for seed germination.

SHRUBS

Shrubs are generally believed to increase prolifically after fire. Lynton (223, 224) found this to be especially true after repeated fires on poor soils and believed the presence of such plants limited tree reproduction. Lutz (221) pointed out that because of their low stature and small stems, shrubs are very liable to destruction by fire, although they resprout vigorously. According to Petterson (269) and Kujala (185), shrubs with flushy or pulpy fruit regenerate slowly after fire, since they are dependent upon animals which are scarce in burned areas for their dispersal. Uggla (329), however, believed that many seeds survive the fire in the soil. Wind-disseminated plants such as willow come in rapidly. This, however, does not hold true for many shrubs which reproduce by suckering as, for example, *Vaccinium* (1, 113, 179, 285, 328).

Increase in shrubs may be due, in part, to the fact that heat stimulates the germination of seeds of some shrub species, as reported in previous sections (186, 275, 313, 349). Part of the increase in growth of shrubs may be caused by the increase in available nitrates and other minerals. Hesselman (144) and Uggla (330) reported that *Rubus idaeus,* a common fire follower, requires and accumulates very large quantities of nitrates in its tissues. McMinn (229), reporting on a burn in British Columbia, found dense tangles of *Rubus spectabilis* which attained sufficient density to retard regeneration of the forest. In the redwood region, Fritz (114) reported that controlled burning of logged-over land could increase the fire hazard by producing an extremely heavy mass of shrubs. In the Colorado headwaters area, Ives (166) found that brush reaches its maximum density 25 years after the burn.

A change in the relative frequencies of various species of shrubs following fire has also been reported. Cantlon and Buell (52) and Buell and Cantlon (46) reported that in New Jersey, the frequency of *Gaylussacia* decreased while *Vaccinium* increased rapidly. Horton and Kraebel (157) also reported changes in the relative abundance of various species of chaparral shrubs in southern California following burning. Oosting (260), however, reported that burns in loblolly pine forests produced very temporary changes in shrub frequency, except for a definite and long-lasting increase in Virginia creeper and poison ivy.

TREES

Because of the structural and physiological adaptations among them, the effects of fire vary with different species. Therefore, each must be considered separately. This review will treat the effect of fire on species characteristic of the northern boreal forest which have not been extensively subjected to prescribed burning as a management practice. The practical application of fire in the management of southern and western species has been under study for many years and will not be included here (12, 15, 16, 20, 33, 54, 56, 57, 58, 60, 66, 117, 127, 173, 193, 195, 247, 336, 338, 339, 340, 341, 342, 344, 345). The application of fire by prescribed burning in northern forests has not been extensive except in Europe (180, 297, 299).

In considering the effect of fire on a given species, it is necessary to consider the direct effect on the tree itself at different ages from seed to maturity, and the more indirect effect of fire in creating a beneficial or harmful environment for the growth of the species at different ages. Optimum conditions vary not only with species but also with age. Wright (357), for example, has shown that exposure of various conifer seeds to high temperatures for short periods can stimulate germination in some cases—i.e., *Abies magnifica* and *Pinus ponderosa*—but does not effect germination in others—i.e., *Pinus contorta* and *P. lambertiana.* Borman (35), studying *Pinus taeda,* found that young seedlings achieve maximum photosynthesis rates in low light intensity. However, after secondary needles mature, the maximum photosynthetic rate is achieved in relatively high light intensity. Therefore, this species, at least, requires different conditions for optimum growth at different ages.

Early stages of conifer growth are generally believed to be favored on burned land, mainly because seedbed conditions are improved (54, 57, 129, 210). Little and Moore (212, 213) reported that the ecological effect of burning on seedbed conditions for most conifers is mainly physical, the result of the removal of the forest floor, thus favoring survival of most conifer seedlings over that of deciduous species. The reason for the basic difference lies in the initial root system. In pines, this root is only about one inch long, with about the same length of stem. In many hardwoods, however, the fleshy cotyledons permit development of a five- to six-inch root system before the first leaves begin to function, on stems two to three inches tall. The roots of hardwoods thus are able to penetrate unburned, deep litter to mineral soil before the leaves have an increased water demand, while those of pines are shallow and can reach mineral soil before drying out only if the litter has been at least partially removed, as by burning. Similar explanation was given by Farrar and Fraser (105) for results of laboratory experiments which demonstrated that humus did not contain a chemical which inhibited germination, and that if jack pine seeds were sown on deep humus and were watered thoroughly, good germination was obtained. Bonner (34) found that pure stands of hardwoods were very infrequent after fire in northern Ontario. On swamps, spruce and larch seeded in, while on high ground spruce and mixed hardwoods appeared. While much of this seed is dispersed after fire, a significant amount is present in the soil prior to fire (154). Buell and Borman (44) found, in northern Minnesota, that in the absence of fire basswood, fir and black ash replaced fire-following paper birch and white pine.

Haig (129) believed that burning was of great value in exposing mineral soil for a seed bed. The exposed mineral soil dries more slowly, fluctuates less in moisture content and temperature than the humus layer, and thus is more favorable to seedling growth. Although the abundant ash released may be of nutritional value, he believed this to be of secondary importance. Frazer (111) pointed out that forest trees having low moisture requirements are most frequent fire followers.

Tryon (326) and Isaac (163) reported that seed bed conditions could be made poor by addition of charcoal which increases soil temperature sufficiently that it may kill seedlings. However, Retan (277) noted that under nursery conditions, the addition of charcoal to heavy clay soil produced a marked improvement in coniferous seedling growth. Ooyama (262) stated that extracts of unburned litter inhibited seed germination and seedling growth of some species, especially the pines. Gemmer et al (118) asserted that ash stimulated germination but inhibited radicle penetration of longleaf pine seedlings.

Burning as a method of slash disposal in order to eliminate the hazard of wildfires is frequently proposed (187, 192, 211, 222, 226, 235, 246, 254, 342, 343, 344, 345, 352, 353 also 33, 120, 132, 358), although it is considered costly and dangerous by others (61, 192).

JACK PINE. Of the northern species, jack pine is most often recognized as a frequent post-fire species (175, 199, 232 and others). The ecological adaptation to fire of the serotinous cones has been pointed out (60, 4, 100, 101, 197, 198). Seed remains viable within the cone for many years, and the cones are opened by heat. Consequently, when a jack pine forest burns, or when the slash in a cut-over area is burned, seed is readily available. However, Watson (337) believed that proper restocking could occur after fire only if there were at least 75 seed trees left per acre. On many sites, however, jack pine reproduction is prolific and many fewer seed trees are necessary. Eyre (101) also pointed out that a large number of seed trees is necessary for restocking jack pine stands after burning, and that the seed is often killed by fire. Eyre emphasized the possibility that seedlings which come up immediately after late summer and autumn fires will not be strong enough to survive the winter. Johnson (170) believed that all methods of slash disposal, including fire, were detrimental to jack pine reproduction. The Lake States Experiment Station reported (189, 190) that spring fires frequently do not damage merchantable trees but are responsible for lack of reproduction in older stands. Mitchell (244) reported damage to older trees and the elimination of smaller ones.

Requirements for germination and young seedling growth are often met ideally by post-fire conditions. The exposure of mineral soil as a seedbed is advantageous (4, 62, 91, 113) because it is necessary for the young roots to reach a more steady supply of moisture than exists in forest litter and humus. Partial shade is required for good germination (60, 112, 113), and this is usually furnished by the characteristic lush herbaceous growth the first year following fire[4]. Direct sunlight is advantageous for later seedling growth. This condition is usually present in the opening created by fire, once the seedlings rise above the herb-shrub layer. Bensend (27) found that jack pine seedlings require 200 to 250 ppm nitrogen for optimum seedling growth. Since fire is frequently reported to release nitrogen into the soil, this condition may also be met by fire.

There are frequent reports (102, 190) that spring fires were particularly destructive of seedlings and smaller jack pine trees but caused little damage to merchantable timber. Summer fires, since they are usually hotter, crown and burn deeper, did considerable damage to larger trees. Damage to trees of all size classes at any season was great enough, however, that burning to control brush, etc., in the productive stands could not be recommended. Rudolph et al (282) suggested that the distribution, in Minnesota, of jack pine having the fire-favored serotinous cones may have been influenced by the state's fire history.

WHITE PINE. Many worker have recognized that the existing white pine stands very frequently occur on burned-over land (39, 60, 64, 159, 196, 221, 245), although Cary (53) pointed out that fire is not necessary for the establishment of white pine on all sites. Kell (175) reported that white pine occurs as a pioneer on clay-loam sites after fire, while jack and red pine invade sandier, drier soils. Perry (267) found that white pine seed germinated best on burned soils, although subsequent growth was better on unburned soil. However, Lunt (219) reported that burning increased height growth by 8.1%, and volume growth by 18.8%, probably because of the higher pH, nitrogen, potassium and calcium concentrations in the topsoil. Cary (53) and Chapman (59) pointed out that white pine frequently comes in after blowdowns as well as after fires, so that the effect of fire may be largely one of opening an area to light. Maissurow (231) also held this view, since he maintained that white pine would reestablish after logging without burning if the areas were logged properly with due respect for good seed years.

RED PINE. Published references to the effect of fire on red pine are few, and it would appear that knowledge of fire and this species is very incomplete. Lunt (219) found fire stimulated height and volume growth of both red and white pine. Kell (175) observed that in Itasca Park, Minnesota, red pine was a post-fire pioneer on coarse soils, along with jack pine. Perry (267) reported that red pine seedlings grew better on unburned soil. Maissurow (232) believed that many good, mature red pine stands existing today are the result of fire. Ahlgren (4) reported good growth and survival of planted red pine on burned-over land. Eyre and Zehngraf (103) believed fire could be useful and not damaging in slash dispersed after red pine cutting.

PAPER BIRCH. The best paper birch stands almost always occur on burned or cutover land, according to Betts (29), Weaver and Clements (346) and Gibson (119). In Alaska, Lutz (221) reported that seedlings of birch thrived on burned land, since they require mineral soil and full sunlight. He also found that relatively few mature trees survived even quick fires, although sprouting in young stands was very vigorous, less frequent in older stands. On the whole, he believed that seedling growth was much more important than sprouting in the re-establishment of birch following fire. Heikinheimo (138) found that birch seeds and seedlings were less harmfully affected by the presence of ash in the soil than were those of spruce and alder. Ahlgren (4) reported best seedling germination in northeastern Minnesota on burned land in low-lying sites, two to three years after fire, with vigorous vegetative sprouting the first post-fire growing season.

ASPEN. Aspen is generally recognized as a fire type. Shirley (294) and Breitung (38) pointed out the difficulty in the conversion of fire-perpetuated aspen stands to more desirable pine and spruce stands. They believed frequent fires to be one of the main reasons while large acreages in Canada and the Lake States remain covered with unproductive aspen stands. The Lake States Forest Experiment Station (188) found that in aspen stands which were cut and planted with pine and spruce, burning stimulated both the production and height growth of suckers to such an extent that they would compete with planted stock. Stimulation of sucker growth was also reported by Lutz (221) and Shirley, (293) who believed it to be caused by increased heat absorption by the fire-blackened surface. Uggla (328) found that in Lapland aspen seed germination and growth was very vigorous on burned land. Ahlgren (4) found germination best on moist seed beds two to three years after fire, with vegetative sprouting the first year. Stoeckler (310) reported that repeated burning was bad for aspen site index.

BLACK SPRUCE. Although mature trees are easily killed by fire (221), black spruce is quick to re-establish on an area subsequent to fire (26, 32, 156, 196, 221, 253). Lebarron (196) pointed out that prompt reproduction following fire is the result of serotinous cones which retain viable seed for up to three years and open when exposed to heat. Trees begin producing seed at an early age and do so frequently, so that a good seed supply is almost always readily available in a burned stand. Fire also exposes peat and cuts down on competition of cedar and tamarack. LeBarron (197), Bellefeuille (26) and Millar (242) all reported that the best quality stands of black spruce occur on burned areas, so fire must be beneficial not only to initial reproduction but also to subsequent growth. Ahlgren (4) discovered good seedling growth after burns where the fire had not been sufficiently intense to destroy the cones in the tallest trees. Dickson (84) found spot seeding to be necessary to insure good re-establishment of black spruce following fire in Newfoundland.

WHITE SPRUCE. Lutz (221), observing forests in Alaska, reported that white spruce was very susceptible to fire. It was slow to return to burned areas because it seeded sparsely and not at an early age, in contrast to black spruce. Also, fire quickly destroyed the seed available in the nonserotinous cones so that it had to be blown in from unburned areas if it was to re-establish naturally. Heikinheimo (137) reported that ash inhibits germination and seedling growth. Saari (283) also reported that the species is easily damaged by fire. Holman and Parker (156) found white spruce to reproduce well after severe, late summer and early fall fires, but not after spring and early summer fires. Bedell (24) reported that in Manitoba, white spruce seemed to require a mineral seed bed and to reproduce well only on burned soil. Millar (242) also reported that white spruce reproduced following fire, especially on slopes. Hesselman and Schotte (146) and Nilsson (254) reported that in heaths in Europe, spruce species were slow to re-establish themselves after fires. Similar observations in North America were made by Breitung (38) and Minckler (243).

SUMMARY

In nearly every section of the preceding review, apparent contradictions as to the effect of fire can be found. These divergencies indicate that it is impossible to draw many general conclusions as to the ecological effects of fire. Rather, each combination of region, climate, forest tree association, soil type and plant species must be considered individually. However, the following points seem to be generally true:

1. Fire has been frequent in forest, shrub and prairie land for many

centuries, and has undoubtedly been a major factor in determining the direction and rate of plant succession.

2. In most cases, extensive, severe fires increase erosion by lowering the ability of the topsoil to absorb and retain water.

3. The ultimate effect of the changed moisture relationships on the water table apparently varies with different conditions and has not been investigated completely.

4. The temperature of the top soil during fire varies greatly, but below two inches the temperature rise is not great. There are some reports that this heat causes direct changes in the texture and chemistry of the soil as well as direct stimulation or inhibition of plant germination and growth.

5. Very frequently, by removing the insulating plant life or blackening the surface of the soil, burning results in greater post-fire soil temperature extremes for some time after the fire. These extremes may affect plant growth.

6. Reports of the effect of fire on soil productivity range from decreased plant growth to greatly increased growth, and each must be considered individually.

7. The acidity of the soil is usually lower after fire. Generally there is also increased soil calcium, phosphorus and potassium, but reports regarding increase and decrease in nitrogen are contradictory. Burning usually stimulates biotic nitrogen fixing activities in the soil.

8. Fire frequently results in an increase in moss, lichen and liverwort cover, certain species being characteristic of burned areas.

9. Fire influences the spread or destruction of numerous insect pests and plant disease organisms. Here again, each case must be considered individually.

10. Definite patterns of post-fire plant succession exist, but these are different for different sites and conditions.

11. A vigorous regrowth of herbs, grasses and shrubs occurs frequently the first few years following fire.

12. The effect of fire on tree reproduction varies with species, largely because of different methods of seed dispersal, seed survival, sprouting capacity and seedling requirements.

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