



**Forest Structure Dynamics Following Wildfire and Prescribed Burning in
the New Jersey Pine Barrens**

Ralph E. J. Boerner

American Midland Naturalist, Volume 105, Issue 2 (Apr., 1981), 321-333.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0031%28198104%29105%3A2%3C321%3AFSDFWA%3E2.0.CO%3B2-3>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Midland Naturalist is published by The University of Notre Dame. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/notredame.html>.

American Midland Naturalist
©1981 The University of Notre Dame

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

Forest Structure Dynamics Following Wildfire and Prescribed Burning in the New Jersey Pine Barrens

RALPH E. J. BOERNER¹

Department of Botany, Rutgers University, New Brunswick, New Jersey 08903

ABSTRACT: The New Jersey Pine Barrens mosaic is made up of species exhibiting numerous adaptations to wildfire, including the dominants, *Pinus rigida* and several species of *Quercus*. To evaluate community change and recovery from two disturbance intensities (wildfire and prescribed burning), a site unburned for 53 years, two sites burned by wildfire in 1977 and 1978 and two sites burned by prescription in 1977 and 1979 were examined for species composition, horizontal and vertical structure and biomass relations. Wildfire killed the aboveground portions of oaks and removed needle and branch tissue from pines, but almost all individuals of trees and shrubs resprouted, to form a dense canopy ca. 1 m high after one growing season. While biomass and canopy height recovered slowly, total cover > 100% was established in 1½ growing seasons, effectively eliminating gaps for pioneer tree species. Prescribed burning had little effect on community structure other than opening areas in the dense heath-shrub layer, where herbaceous species could establish themselves for one to two growing seasons before the resprouting heath cover eliminated light gaps. Few tree seedlings were observed. Adaptations to a regime of frequent disturbance have resulted in a species assemblage that minimizes both species turnover and the period of time necessary to re-establish the predisturbance community structure.

INTRODUCTION

Recent studies of the role of wildlife in determining community structure, and the distribution of communities on the landscape, have resulted in two distinct views of the role of fire. In regions where fire has historically been frequent, such as grasslands (Daubenmire, 1968; Vogl, 1974), southern pine forests (Komarek, 1974) and chaparral (Wells, 1962; Hanes, 1971), fire has come to be viewed as a factor which, through its action as a consistent selection pressure, has resulted in communities made up of fire-adapted (Keeley, 1977) or even fire-promoting (Mutch, 1970) species. In areas where fire has been relatively rare, such as Maine spruce-fir forests (Lorimer, 1977) or northern hardwood forests (Bormann and Likens, 1979), however, fire is not considered a significant selection pressure and is only important as a creator of gaps, much as extensive windthrow or ice storms (White, 1979; Bormann and Likens, 1979). In general, the communities exposed to frequent fire are dominated by shrubs or herbaceous plants which resprout quickly following fire. One of the relatively few forest community types that combine large investment in persistent biomass with fire adaptations is the Pine Barrens of New Jersey (Little, 1979).

The Pine Barrens of New Jersey are part of a larger Atlantic Coastal Plain region whose soils are dominated by Miocene sands (Tedrow, 1952; Robichaud and Buell, 1973; Rhodehamel, 1979). The plants of these predominantly excessively drained soils have adapted to low soil nutrients and moisture, and fire to produce a unique ecosystem which covers over 30% of New Jersey's land area.

The upland forest of the New Jersey Pine Barrens is commonly dominated by pitch pine *Pinus rigida*, which often accounts for over 80% of the canopy trees (Robichaud and Buell, 1973; McCormick, 1979). Oaks (*Quercus* spp.) comprise the remainder of the canopy and also dominate in some areas. The shrub cover is dense and dominated by heaths (*Gaylussacia* spp. and *Vaccinium* spp.), and in places by the shrub, *Q. ilicifolia*. In general, herbs and other ground covers are sparse, covering less than 10% of the ground (McCormick and Andresen, 1975).

¹Present address: Department of Botany, The Ohio State University, 1735 Neil Avenue, Columbus 43210.

The combination of excessively drained surface soils and thick litter/humus layers makes wildfire common; in fact, this area of 450,000 ha has over 1100 wildfires annually (Forman and Boerner, 1980). The postfire recovery of relatively fire-adapted species such as *Pinus rigida*, *Quercus velutina*, *Q. marilandica* and *Q. ilicifolia* is rapid since much of the biomass survives the fire. These fire-adapted species, as well as a number of other tree oaks, including *Q. prinus*, *Q. stellata*, *Q. falcata*, *Q. coccinea* and *Q. alba*, and shrub oaks, such as *Q. prinoides*, exhibit basal sprouting, high early growth rate of sprouts, prolific early seed production and development of large root crowns under a regime of frequent fires (Little, 1974, 1979). Pitch pines sprout from stem tissue as well as from below-ground buds (Little, 1974, 1979). The bryophyte and lichen species found commonly in the New Jersey Pine Barrens are also typical of areas subjected to frequent fires (Moul and Buell, 1955). So, while adaptation to frequent fires occurs independently in separate species, the result of such adaptation has been a fire-adapted community whose dominant vegetation has been stable for at least 8 millennia (Heusser, 1979).

Since 1928, relatively cool, prescribed winter burns have been used in the Pine Barrens to improve pine stands for harvest and to reduce the potential for wildfire (Little and Somes, 1961; Little, 1979). The long-term effects of repeated prescribed burning have been described for the soils (Burns, 1952), ground cover and litter (Bernard, 1963; Moul and Buell, 1955), and shrubs and trees (Little and Somes, 1961), though no overall treatment of ecosystem structure and function following either wildlife or prescribed burning is available.

Previous studies of forest dynamics following large disturbances have focused on communities where such disturbance occurs at frequencies much lower than those observed in the Pine Barrens (Heinselman, 1973; Lyon and Stickney, 1976; Lorimer, 1977; Ohmann and Grigal, 1979; Bormann and Likens, 1979). In such communities, the initial postdisturbance dynamics are often dominated by species uncommon in the predisturbance assemblage (*cf.*, Marks, 1974). The large number of fire-adapted species observed in the Pine Barrens, however, suggests that the initial postfire dynamics of these upland forests should be dominated by the regrowth of prefire individuals with relatively little recruitment from either seedbanks or outside sources. The postfire dynamics of these forests would, therefore, be more similar to those observed in the chaparral (Wells, 1962; Hanes, 1971) than other forests. To determine if this is the case, species composition, biomass, horizontal and vertical structure and cover patterns in an unburned site and two sites burned by wildfire were analyzed. To evaluate the relationship between fire intensity and postfire community structure, the postfire dynamics of two sites burned by prescription were also analyzed.

METHODS AND MATERIALS

Description of the study area.—Despite the proximity of the Pine Barrens to the Atlantic Ocean, the prevailing NW winter winds and SW summer winds prevent the maritime influence from penetrating more than 4-6 miles (6.5-9.7 km) inland, resulting in a predominantly humid, temperate, continental climate (Robichaud and Buell, 1973). Summer temperatures average about 23 C and winter temperatures about 1 C (Tedrow, 1979), with the soils generally freezing for all or part of the winter, especially in burned sites where the insulating effects of the vegetation and forest floor have been obviated (Johnson, 1978). Precipitation averages 100-120 cm annually and falls in a fairly uniform pattern; but since it is the soils' ability to hold water rather than the amount of precipitation that limits plant growth in the region, the typically small seasonal variations in precipitation observed are likely of small importance (Robichaud and Buell, 1973). Extended periods of drought, however,

may influence seedling mortality (Ledig and Little, 1979) and fire frequency and extent (Forman and Boerner, 1980).

The upland soils that have developed on the extensive Tertiary and Quaternary sands of the region are well to excessively drained podzols (Tedrow, 1952, 1979). The heavily reworked soil material is very low in clay minerals and the soils generally have a cation exchange capacity less than 5 meq/100 g (Markley, 1979) and very low base saturation (Tedrow, 1952, 1979). The Lakewood and Downer soil series are the most common upland soils of the New Jersey Pine Barrens.

Five study sites were established in November 1978 as part of a larger study of postfire patterns in the Pine Barrens (Boerner and Forman, 1979; Boerner, 1980; Forman and Boerner, 1980). The sites occur in three groups: a control site, two wildfire sites and two prescribed burn sites. All five study sites are located on Downer loamy sands or sandy loams.

The control site and the wildfire sites are located 10 km SE of Mays Landing and 0.6 km S of McKee City in southeastern Atlantic County. These three sites are all within 9 km². The control site (hereafter called C) is an old pine-oak woods which, based on tree core evidence, New Jersey Bureau of Forest Fire Management records and the owner's recollections, last burned in May 1926. The two wildfire sites near this unburned control burned in April 1977 and May 1978, respectively. The 1977 site will be referred to as W+3 since it was monitored during its third postwildfire growing season while the 1978 wildfire site will hereafter be referred to as W+2. Both fires exceeded 400 ha and are officially listed as unknown in origin. These sites were chosen from approximately 35 major wildfire sites surveyed during the autumn of 1978 and were chosen to correspond to the pine-oak community type (McCormick, 1979; Little, 1979), which is characterized by a mix of tree oaks and pines in the canopy.

The prescribed burn group is made up of two sites located in Lebanon State Forest, near the border between Burlington and Ocean counties. Both of these sites were burned in a large wildfire in 1963 (described in Banks and Little, 1963) and are believed to have remained unburned until burned by prescription as follows: one site (P+3) was burned by prescription in early spring 1977 while the other (P+1) was burned on 16 March 1979. Detailed descriptions and locations of all sites are given by Boerner (1980).

Field methods.—Cover of the major vascular species was determined during July 1979. At each site, five parallel 30-m line intercepts were laid out at random, at least 10 m apart and perpendicular to the contours. The maximum elevation covered by a line never exceeded 3.0 m. Percent cover of pine and oak trees (≥ 2.5 cm dbh), oak shrubs/sprouts (< 2.5 cm dbh) and other species were estimated along the entire length of each line intercept by noting the starting and ending points of each individual or patch on a transect tape. Cover of heath shrubs was estimated by counting the number of times the tape crossed a leaf or stem in four randomly chosen meters of each line intercept, and then multiplying by an average cover length per leaf or stem determined by measuring 50 randomly chosen leaves and stems. Since the coefficient of variation of both these correction factors was less than 10%, the percentages obtained were considered reliable.

Biomass estimates for trees and large shrubs were generated using a slight modification of the methods used to study the dimension and production relations of trees and shrubs in the Brookhaven, New York, pine-oak forests (Whittaker and Woodell, 1968). Three 10 x 10 m quadrats were randomly placed, without overlap, in each site. All trees ≥ 2.5 cm dbh were tallied for species, height and dbh, while all shrubs, sprouts and saplings with diam 0.5 cm \leq dbh < 2.5 cm were tallied for species, height and basal diameter. Heights were determined using a Ranging 120

Opti-Meter. Estimates of aboveground biomass of trees and shrubs were generated using the allometric dimension regressions given by Whittaker and Woodwell (1968). For those oak species for which regression coefficients were not presented (*Quercus velutina*, *Q. prinus*, *Q. falcata* and *Q. stellata*), estimates were made using the mean regression coefficient values for the two oak species (*Q. alba* and *Q. coccinea*) which resemble them most in growth form. The regressions for total aboveground biomass were used in all cases except for the pines in the sites recently burned by wildfire (W+3 and W+2). In these sites, regressions were used to estimate stem and bark biomass of the pines, while biomass for branches, twigs and needles was determined directly by clipping the material, drying at 60 C for 48 hr and weighing. All herbs and shrubs < 0.5 cm diam were clipped from six 0.5 x 2.0 m randomly placed quadrats in each site, dried as above and weighed to determine biomass.

The number of pine seedlings was determined in six 0.25 m² quadrats in each site at 2-week intervals throughout 1979. Nomenclature follows Fernald (1950).

RESULTS

Biomass and species composition.—Tree species composition and community structure among the five sites were generally similar before the fires described above (McCormick and Jones, 1973). In each site, pines and oaks were intermixed with the pines emerging above a dense oak canopy. The impact of the wildfires which occurred on two of the sites changed the community structure quite drastically, while prescribed burning on two other sites seemed to have little effect on tree biomass or survival.

While the biomass of oaks and pines was almost equal to the control site, C (Table 1), no living oaks ≥ 2.5 cm dbh were found at the wildfire sites. There were large numbers of both standing and fallen dead oak boles between 5 and 25 cm in diam, however, at the wildfire sites. The biomass of oaks < 2.5 cm dbh showed the opposite trend (Table 1). There were no oaks of this size at the control site and only a very small biomass at the prescribed burn sites, while the entire biomass of oaks at the wildfire sites was sprout stems. So, while the wildfire effectively killed back the aboveground portion of oaks, the crowns quickly resprouted and produced oak biomass exceeding 20% that of the other sites in 2-3 growing seasons.

The biomass of oak trees was similar among the prescribed burn sites and the control site (Table 1). The dominant oaks in the control woods were *Quercus velutina* and *Q. coccinea* while *Q. velutina* and *Q. prinus* were important at the prescribed burn sites. Like the control site, pines made up more than half the tree biomass at P+3 and P+1. The shrub oaks *Q. marilandica* and *Q. ilicifolia* were not important biomass components in these three sites.

Biomass of pines varied considerably, both between and within sites (Table 1). Biomass of *Pinus rigida* was significantly lower at the two wildfire sites than at the prescribed burn sites and the control woods. Presence of many dead pine stems in the wildfire sites (W+3: 23.1% dead; W+2: 17.3% dead) was consistent with earlier estimates of mortality rates in *P. rigida* from severe headfires (Little, 1946). The prescribed burns, however, did not appear to increase mature pine mortality over that of the control woods, as no standing dead pines were observed at either the control or prescribed burn sites.

Total canopy biomass was somewhat higher at the control site than at the prescribed burn sites (Table 1) with most of the difference attributable to oak biomass. Since the prescribed burn sites had been burned by wildfire 16 years ago, compared to 53 years ago at the control site, the lower oak biomass was to be expected. The total pine and oak biomass was much lower at the wildfire sites, reflecting the greater reduction in aboveground parts of canopy trees, especially oaks, caused by the

wildfire (Little, 1946; Little and Moore, 1949).

The dominant undergrowth species at all sites was a heath, *Gaylussacia baccata*. Its biomass was similar among the control site and the two wildfire sites (Table 2), attesting to the ability of this heath to resprout from underground buds following severe fire (Whittaker and Woodwell, 1969; Woodwell and Rebeck, 1971). The prescribed burn sites had similar *Gaylussacia* biomass but were significantly lower than the other three sites. *Vaccinium vacillans* was present in significant quantities only at the prescribed burn sites. When this biomass was added to that of *Gaylussacia*, the heath shrub totals for the five sites were similar.

Pteridium aquilinum bracken fern has been cited as a postfire colonizer in coniferous forests (Lyon and Stickney, 1976). In this study, its biomass was greatest at the wildfire sites and the most recent prescribed burn site (Table 2). While *Pteridium* was present at the older prescribed burn site (P+3) and the control site (C), it did not approach the biomass present at the more recently and/or severely burned sites. *Comptonia peregrina* sweetfern, also cited as a species favored by fire (Ahlgren, 1974), had a pattern similar to *Pteridium aquilinum*.

Only in the most recent prescribed burn site were significantly more species

TABLE 1.—Aboveground biomass in kg/ha of trees and oak shrubs/sprouts. Values are means of three 10 m X 10 m quadrats per site; standard errors of the means are listed in parentheses. Species present at a site but not in the sample quadrats are listed as (+) while those absent are listed as (-). Site codes are as follows: C: old control site unburned for 53 years; W+3: 1977 wildfire site, W+2: 1978 wildfire site, P+3: 1977 prescribed burn site, P+1: 1979 prescribed burn site

Species	Sites				
	C	W+3	W+2	P+3	P+1
<i>Pinus rigida</i>	42,089 (28,986)	9,692 (4,975)	22,121 (9,494)	31,488 (12,570)	35,923 (7,911)
<i>P. echinata</i>	-	-	-	300 (300)	-
<i>Quercus alba</i>	5,017 (1,578)	+	1,773 (1,167)	+	3,017 (1,830)
<i>Q. velutina</i>	11,993 (3,189)	+	+	16,706 (13,865)	15,130 (6,211)
<i>Q. coccinea</i>	15,990 (5,668)	386 (386)	+	-	-
<i>Q. stellata</i>	-	2,905 (963)	3,277 (1,038)	-	909 (533)
<i>Q. prinus</i>	-	-	-	11,243 (1,126)	6,649 (3,634)
<i>Q. falcata</i>	830 (830)	-	-	-	-
<i>Q. marilandica</i>	-	-	-	-	65 (65)
<i>Q. ilicifolia</i>	-	1,396 (202)	471 (216)	160 (91)	37 (37)
Total oak shrubs and sprouts*	0	4,687	5,521	841	297
Total oak trees**	33,830	0	0	27,949	25,705
Total tree biomass	75,919	9,692	22,121	59,437	61,628

* < 2.5 cm dbh

** ≥ 2.5 cm dbh

found than at the unburned control site (Table 2). Only two of these taxa, *Gaultheria procumbens* and *Smilax* spp., are considered common or widespread in the upland forests of the Pine Barrens (Ferren *et al.*, 1979), and as a group, herbaceous plants made up less than 1% of the total community biomass.

Cover patterns.—Many of the same trends seen for biomass applied to cover patterns. The two wildfire sites had less pine cover than the other three sites, due to fewer stems per unit area and the smaller resprout crowns of the survivors (Table 3). While oak tree cover was absent at the wildfire sites, oak shrub/sprout stems covered more than half of each recent wildfire site (Table 3). Oak sprout cover was significantly higher ($p < .01$) at W+3 than at W+2, reflecting the additional year's growth.

The control woods and the prescribed burn sites had similar cover of canopy pines ($p > .20$). Oak tree cover at the control site was significantly greater than that of the prescribed burn sites ($p < .01$), again reflecting the difference in the length of the wildfire-free period. The two prescribed burn sites were similar in cover of all major trees and shrubs, differing only in the cover of *Pteridium aquilinum*, which was significantly greater at the more recent prescribed burn site (Table 3).

TABLE 2.—Aboveground biomass, in kg/ha, of small shrubs and herbs. Means are based on sampling of six 0.5 m × 2.0 m quadrats per site; standard errors of the means are listed in parentheses. Species present at the sites but not in the sample quadrats are listed as (+) while those not present at a given site are listed as (-). See Table 1 for site codes

Species	Sites				
	G	W+3	W+2	P+3	P+1
<i>Gaylussacia baccata</i>	961 (197)	755 (104)	802 (223)	478 (96)	574 (94)
<i>Vaccinium vacillans</i>	-	+	1 (1)	162 (52)	35 (23)
<i>Lyonia ligustrina</i>	-	+	+	16 (16)	18 (18)
<i>Ilex glabra</i>	-	-	-	6 (6)	27 (23)
<i>Pteridium aquilinum</i>	1 (1)	382 (14)	74 (66)	+	82 (40)
<i>Gaultheria procumbens</i>	-	2 (1)	43 (18)	149 (84)	1 (1)
<i>Carex pensylvanica</i>	-	-	-	-	10 (6)
<i>Smilax</i> spp.	1 (1)	18 (1)	+	+	4 (2)
<i>Comptonia peregrina</i>	-	101 (101)	+	-	57 (41)
<i>Clethra alnifolia</i>	-	-	-	-	6 (6)
<i>Prunus serotina</i>	-	-	-	-	2 (2)
<i>Solidago odora</i>	-	+	+	-	11 (9)
<i>Tephrosia virginiana</i>	-	-	-	-	3 (2)

TABLE 3.—Cover of major vegetation components, expressed as mean percent cover, based on measured overlap lengths of individuals on five 30-m transects/site. Standard errors of the means are indicated in parentheses. Species comprising < 0.5% cover are indicated by (+). See Table 1 for site codes

Site	Pines	Oak trees*	Oak** shrubs/sprouts	Heaths	<i>Pteridium</i>	Other shrubs	Total tree cover	Total cover
C	23.1 (12.1)	78.3 (5.9)	0.6 (0.6)	91.8 (7.3)	+	0.8 (0.8)	101.4 (18.0)	194.1 (26.2)
W+3	5.1 (3.3)	+	88.4 (1.6)	71.2 (9.6)	9.0 (2.3)	2.8 (1.6)	5.1 (3.3)	176.4 (17.7)
W+2	5.1 (1.3)	+	65.8 (3.2)	53.4 (4.9)	5.6 (2.2)	1.7 (1.1)	5.1 (1.3)	131.5 (13.0)
P+3	18.0 (6.2)	47.4 (7.1)	12.2 (1.7)	49.7 (2.6)	+	+	65.4 (13.4)	127.4 (20.6)
P+1	30.3 (4.4)	45.8 (2.2)	7.3 (1.3)	39.4 (4.9)	16.9 (4.1)	+	76.1 (6.6)	139.6 (16.7)

* ≥ 2.5 cm dbh ** < 2.5 cm dbh

Cover of heaths, especially *Gaylussacia* and *Vaccinium*, was relatively high at all sites, ranging from ca. 40% at P+1 to 90% at C (Table 3). The heath cover was significantly lower at the 1979 prescribed burn site than at the 1977 prescribed burn site though the biomass at the two sites was not different. This apparent difference was due to fire-induced differences in plant architecture. The heath stems observed at P+1, formed since the prescribed burn some 6 months before, were upright and sparsely branched, with leaves borne all along the stem and branches, while those at P+3, up to 3 years old, were heavily branched and had leaves only near the tips of branches, so that while the biomass of the sites did not differ, the pattern of leaf and branch display at P+3 resulted in higher cover. The cover of heaths at the control site was greater, though not significantly so, than that of the 1977 wildfire site. Both of these sites had significantly higher cover than the 1978 wildfire site.

The total cover of major species exceeded 100% at all sites. Since there was significant crown overlap of oaks and pines over heaths, especially at C, P+3 and P+1, probably little bare ground was open to full sunlight in midsummer, even in the recent wildfire sites.

Density of pine seedlings varied markedly between and within sites. No pine seedlings were observed at the control site during the sampling period. Mean densities of seedlings per hectare (\pm standard error) observed at the wildfire sites were 15,825 (\pm 2700) at W+3 and 289 (\pm 289) at W+2. The prescribed burn sites also had appreciable pine seedling densities: 6675 (\pm 2015) at P+3 and 3350 (\pm 1214) at P+1.

Vertical structure.—In the control site, the oaks, which varied in height from 2-12 m, were 23-86 years old. The pines overtopped the oaks and ranged from 12-22 m in height (Table 4). While no shrub oaks were present, the heath layer, together with a very thick litter accumulation, effectively prevented most light from penetrating to the mineral soil surface.

A widely scattered, very open pine canopy was found in the wildfire sites as well (Table 4). Whereas such an overstory distribution would suggest a large amount of available space for new colonization, the large numbers of sprout stems 2 m or shorter likely inhibit colonization (Table 4). Indeed, a very dense canopy at 1-2 m height, shown both by the stem height distributions and by cover estimates (Table 3), existed at these wildfire sites. While sprouts of tree oak species made up a minority of the stems <2 m in the prescribed burn sites, they dominated these size classes in the wildfire sites, accounting for 78% at W+3 and 75% at W+2.

The height distributions for the prescribed burn sites also showed a scattering of large pines up to 17 m in height, with a thick oak subcanopy between 4 and 10 m (Table 4). The two prescribed burn sites differed from the control woods in the presence of a significant cover of small oak shrub/sprout stems <2 m in height. The smaller stems of tree oak species were usually found in gaps between taller oaks, often formed after the death of a central oak leader followed by rootcrown sprouting.

DISCUSSION

Since 1940, there have been approximately 1100 wildfires per year in the Pine Barrens (Forman and Boerner, 1980). While there may have been fewer fires prior to 1940, the area burned was considerably greater, averaging ca. 22,000 ha (55,000 acres) annually from 1906 to 1939 (Forman and Boerner, 1980). Estimates of the frequency of wildfire in the upland areas range from approximately 40 years for oak-pine stands (Little and Moore, 1949; Little, 1979) to 8 years for the pitch pine plains, a dwarf pitch pine area in the center of the Pine Barrens (Lutz, 1934). Forman and Boerner (1980) found the fire-return interval for the uplands as a whole to be approximately 20 years before 1940, and approximately 65 years since

that time. In fact, the oak and pine upland forest types which cover the major part of the Pine Barrens are made up chiefly of sprout oak and pine stands typical of recent postwildfire areas (Little and Moore, 1945). A similar pattern of vegetative recovery resulting in a mosaic of sprout forests differing in postfire age has been reported for coniferous forests in the northern Rocky Mountains (Lyon and Stickney, 1976) and for dry oak forests in the N-central United States (Ahlgren, 1974).

The pattern of colonization of postdisturbance sites depends on the mosaic of available resources presented to potential colonists, especially light and space. Since most of the oak and heath species in the Pine Barrens sprout quickly from underground, unburned buds (Little, 1979), much of the space available immediately after a wildfire is quickly reoccupied by individuals present before the disturbance. My data suggest that prefire cover is attained 1-2 years after a wildfire while biomass and vertical structure recover more slowly (Fig. 1). Within one growing season, total cover generally exceeds 100% (Table 3) with the cover of individuals <2.5 cm dbh and generally <1 m in height approaching 60% (Table 3). There is, therefore, a relatively limited amount of light and space available for colonization after a major wildfire. In addition, since little humus is consumed in a fire, little clean mineral soil is available for seedling establishment.

There was a large difference in pine seedling density between the two wildfire sites, with the 1977 site having 50 times as many seedlings as the 1978 wildfire site. The large difference between these densities can be accounted for by predicted differences in new seed input. Since the wildfires occurred after seed fall (Fowells, 1965; Ledig and Little, 1979), and since no cone serotiny was observed in the part of the Pine Barrens that included the control and wildfire sites, it is unlikely that

TABLE 4.—Height distributions and densities (stems/ha) of pines, oak tree species and oak shrub species. Three 10 m × 10 m quadrats were sampled at each site. See Table 1 for site codes

Height classes	Sites				
	C	W+3	W+2	P+3	P+1
0.2 - 1.9 m					
pines	0	67	0	0	0
oak tree species	0	30,467	36,467	2,900	1,667
oak shrub species	0	12,867	5,100	4,467	3,867
total for class	0	43,401	41,567	7,367	5,534
2.0 - 3.9 m					
pines	0	0	0	0	0
oak tree species	67	133	533	400	300
oak shrub species	0	0	0	33	67
total for class	67	133	533	433	367
4.0 - 9.9 m					
pines	0	67	233	166	0
oak tree species	767	0	0	667	833
oak shrub species	0	0	0	0	0
total for class	767	67	233	833	833
over 10.0 m					
pines	200	67	100	133	200
oak tree species	267	0	0	0	67
oak shrub species	0	0	0	0	0
total for class	467	67	100	133	267
Total stems per ha	1,301	43,668	42,433	8,766	7,001

a large, viable seed bank was available for establishment during the first postfire growing season. The number of seeds, and therefore seedlings, would be expected to increase during the subsequent growing seasons as seeds disperse in from other stands and as the surviving pines begin to reproduce. The probability of seedling survival, however, would begin to decrease during the second and third growing seasons as the dense oak-sprout cover closes over these shade-intolerant seedlings.

The 1977 prescribed burn site has less than half as many pine seedlings as the wildfire site of the same age. Both of the prescribed burn sites, however, had much higher seedling densities than the 1978 wildfire site. Since the prescribed burns occurred before spring seed fall and did not burn down into the humus layer and destroy whatever seedbank was present, the potential for seedling establishment was much higher than at the wildfire sites. The heavy oak, pine and heath shrub cover at these sites, however, left few sunlit gaps over clear mineral soil in which these pine seedlings might grow to maturity (Ledig and Little, 1979).

In a study of postfire dynamics in *Pinus banksiana* stands in Minnesota, where the average fire-return interval is ca. 100 years (Heinselman, 1973), Ohmann and Grigal (1979) found some of the same postfire patterns as were evident in the Pine Barrens, including the sprouting of some shrubs and the increase in cover of *Pteridium* and *Comptonia*. However, the lack of resprouting of the pines, oaks and other hardwoods resulted in herb biomass exceeding tree biomass for the first 4-5 years, a uniform 0.1-0.2 m canopy after one growing season, and a large number of well-established pine seedlings. Much of the 1st 5 years' production was by species not present in the prefire assemblage (Ohmann and Grigal, 1979). While the same

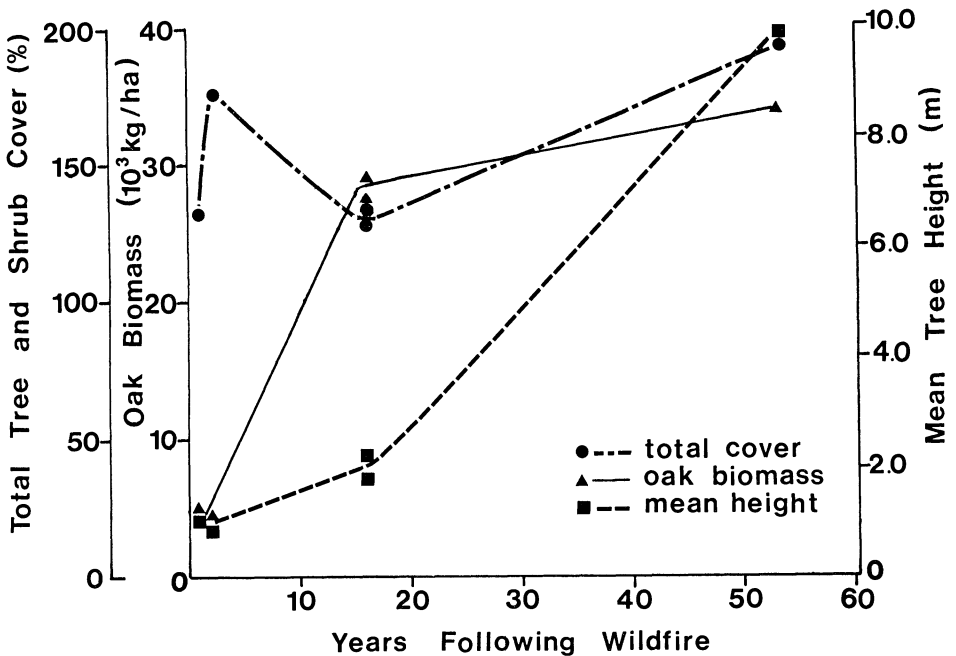


Fig. 1.—Changes in oak biomass (▲), total cover (●) and mean tree height (■) as a function of the length of the wildfire-free period, based on analysis of five New Jersey Pine Barrens stands. The 2-year point corresponds to site W+2, the 3-year point to W+3, the 16-year points to P+1 and P+3, and the 53-year point to C. See Table 1 legend for site codes

species of trees dominate these *Pinus banksiana* sites 5 years after burning, the lack of tree sprouting resulted in a complete turnover of genotypes, a result very different from that observed in the New Jersey Pine Barrens, where pine biomass is persistent and both pine and oak genotypes are effectively conserved. Were the recovery of the Minnesota pine forests plotted on Figure 1, all three parameters would, through the 1st 5 years at least, parallel the Pine Barrens recovery of canopy height rather than total cover. Thus, the reestablishment of tree and shrub cover is a key indicator of the postfire dynamics of the Pine Barrens community.

Only in the most recent prescribed burn site were significantly more species present than at the unburned control site. Such a postprescribed burn increase in herbaceous species richness is thought to be common following repeated treatments (Little and Moore, 1945; Buell and Cantlon, 1953). The majority of these species fell into one of two groups: wind-dispersed, forest edge or roadside species (e.g., *Carex pensylvanica*, *Solidago odora*), or animal-dispersed shrub or pioneer tree species (e.g., *Smilax* spp., *Sassafras albidum*, *Prunus serotina*, *Clethra alnifolia*, *Lyonia ligustrina*). Few of these plants will likely persist after the heath cover closes near the end of the first postfire growing season. The autumn allelochemic actions of *Pteridium* (Gleissman, 1976) may also affect survival of these seedlings. None of the shrub or tree species listed above is considered common or widespread in the upland forests of the Pine Barrens (Ferren *et al.*, 1979).

These postfire dynamics, dominated by resprouting species, have developed over an extended period during which the fire-return interval has been relatively short. Under such a regime, sprouting species will have an advantage over obligate-seeding species since seed banks remain sparse and openings in the canopy are small and short-lived (Keeley, 1977). Under the longer fire interval of approximately 65 years for the entire Pine Barrens region since 1940 (Forman and Boerner, 1980), however, the advantage shifts away from sprouting species. Were such a longer fire-return interval to be maintained in the future, sprouting species such as the oaks and pines found here could be expected to decline in importance. Factors involved in this decrease include a decrease in total density of mature trees with increasing postfire age (Keeley, 1977; Little, 1979), the decreased sprouting ability of older oak and pine individuals (Little, 1979) and the increased mortality resulting from more intense fires, which in turn, result from the larger fuel accumulation expected over a longer fire-free period (Keeley, 1977). Over an extended period of time, a longer fire-return interval would favor adaptations for postfire seedling establishment rather than the sprouting habit. This apparently has been the case in the *Pinus banksiana* forests of Minnesota, where the fire-return interval of 100 years (Heinselman, 1973) has favored such seed-oriented adaptations (Ohmann and Grigal, 1979).

The postfire dynamics in the upland forests of the New Jersey Pine Barrens is a redevelopment by existing genotypes, more similar to that in chaparral regions (Wells, 1962; Hanes, 1971) and grasslands (Daubenmire, 1968; Vogl, 1974), rather than a series of seral stages with differing species, as has been suggested for the Brookhaven, New York, oak-pine forests (Whittaker and Woodwell, 1969), as well as the piedmont areas of New Jersey (Bard, 1952) and North Carolina (Oosting, 1942). In the New Jersey Pine Barrens, only in rare sites where the majority of the oaks and pines are very old will resprouting and redevelopment be of less than major importance.

Acknowledgments.—I wish to thank R. T. T. Forman for his aid, discussions and ideas, as well as S. T. A. Pickett, S. Little, M. J. McDonnell, R. P. McIntosh and an anonymous reviewer for their criticisms of the manuscript.

LITERATURE CITED

- AHLGREN, C. E. 1974. Effects of fires on temperate forests: northcentral United States, p. 195-224. *In*: T. Koslowski and C. E. Ahlgren (eds.). *Fire and ecosystems*. Academic Press, New York.
- BANKS, W. G. AND S. LITTLE. 1963. The forest fires of April 1963 can point the way to better production and management. *Proc. Soc. Am. For.*, **1963**:140-144.
- BARD, G. E. 1952. Secondary succession on the piedmont of New Jersey. *Ecol. Monogr.*, **22**:195-215.
- BERNARD, J. M. 1963. Forest floor moisture capacity of the New Jersey Pine Barrens. *Ecology*, **44**:574-576.
- BOERNER, R. E. J. 1980. Post-fire mineral cycling and ecosystem stability in the New Jersey Pine Barrens. Ph.D. Thesis, Rutgers University, New Brunswick, New Jersey. 225 p.
- AND R. T. T. FORMAN. 1979. Post-fire mineral fluxes in New Jersey Pine Barrens sites. *Bull. Ecol. Soc. Am.*, **60**:86 (Abstract).
- BORMANN, F. H. AND G. E. LIKENS. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag New York, New York. 253 p.
- BUELL, M. E. AND J. E. CANTLON. 1953. Effects of prescribed burning on ground cover in the New Jersey Pine Barrens. *Ecology*, **34**:520-528.
- BURNS, P. Y. 1952. Effect of fire on forest soils in the Pine Barren region of New Jersey. *Yale Univ. Sch. For. Bull.* #50. New Haven, Connecticut. 53 p.
- DAUBENMIRE, R. 1968. Ecology of fire in grasslands. *Adv. Ecol. Res.*, **5**:209-266.
- FERNALD, M. L. 1950. *Gray's manual of botany*, 8th ed. Van Nostrand Reinhold Co., New York. 1632 p.
- FERREN, W. R., J. W. BRAXTON AND L. HAND. 1979. Common vascular plants of the Pine Barrens, p. 373-395. *In*: R. T. T. Forman (ed.). *Pine Barrens: Ecosystem and landscape*. Academic Press, New York.
- FORMAN, R. T. T. AND R. E. BOERNER. 1980. Fire frequency and the New Jersey Pine Barrens. *Bull. Torrey Bot. Club*, in press.
- FOWELLS, H. A. 1965. Silvics of forest trees of the United States. *U.S. Dep. Agric. Handb.* #271. U.S. Department of Agriculture, Washington, D.C. 762 p.
- GLEISSMAN, S. R. 1976. Allelopathy in a broad spectrum of environments as illustrated by bracken. *Bot. J. Linn. Soc.*, **73**:95-104.
- HANES, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.*, **41**:28-52.
- HEINSELMAN, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quat. Res. (N.Y.)*, **3**:329-382.
- HEUSSER, C. J. 1979. Vegetational history of the Pine Barrens, p. 215-228. *In*: R. T. T. Forman (ed.). *Pine barrens: Ecosystem and landscape*. Academic Press, New York.
- JOHNSON, J. H. 1978. Soil survey of Atlantic County, New Jersey. U.S. Dep. Agric. Soil Conserv. Serv., Washington, D.C. 61 p.
- KEELEY, J. E. 1977. Fire dependent reproductive strategies in *Arctostaphylos* and *Ceanothus*, p. 38-46. *In*: Proc. Symp. Environ. Consequences of Fire and Fuel Management in Mediterranean Ecosystems. Palo Alto, Calif.
- KOMAREK, E. V. 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States, p. 251-278. *In*: T. Koslowski and C. E. Ahlgren (eds.). *Fire and ecosystems*. Academic Press, New York.
- LEDIG, F. T. AND S. LITTLE. 1979. Pitch pine (*Pinus rigida* Mill.): ecology, physiology, and genetics, p. 347-368. *In*: R. T. T. Forman (ed.). *Pine Barrens: Ecosystem and landscape*. Academic Press, New York.
- LITTLE, S. 1946. The effects of forest fires on the stand history of New Jersey's pine region. *U.S. For. Serv. Northeast. For. Exp. Stn. Manage. Pap.* #2. 43 p.
- . 1974. Effects of fire on temperate forests: northeastern United States, p. 225-250. *In*: T. Koslowski and C. E. Ahlgren (eds.). *Fire and ecosystems*. Academic Press, New York.
- . 1979. Fire and plant succession in the New Jersey Pine Barrens, p. 297-314. *In*: R. T. T. Forman (ed.). *Pine Barrens: Ecosystem and landscape*. Academic Press, New York.
- AND E. B. MOORE. 1945. Controlled burning in south Jersey's oak-pine stands. *J. For.*, **43**:499-506.

- AND ———. 1949. The ecological role of prescribed burns in the pine-oak forests of southern New Jersey. *Ecology*, **30**:223-233.
- AND H. A. SOMES. 1961. Prescribed burning in the pine regions of southern New Jersey and eastern shore Maryland. *U.S. For. Serv. Res. Pap. NE #151*. 21 p.
- LORIMER, C. G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology*, **58**:139-148.
- LUTZ, H. J. 1934. Ecological relations in the pitch pine plains of southern New Jersey. *Yale Univ. Sch. For. Bull.* #38. 80 p.
- LYON, L. J. AND P. F. STICKNEY. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. *Proc. Mont. Tall Timbers Fire Ecol. Conf. Fire Land Manage. Symp.*, **14**:355-376.
- MARKLEY, M. L. 1979. Soil series of the Pine Barrens, p. 81-93. *In*: R. T. T. Forman (ed.). Pine Barrens: Ecosystem and landscape. Academic Press, New York.
- MARKS, P. L. 1974. The role of pin cherry in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.*, **44**:73-88.
- MCCORMICK, J. 1979. The vegetation of the New Jersey Pine Barrens, p. 229-243. *In*: R. T. T. Forman (ed.). Pine Barrens: Ecosystem and landscape. Academic Press, New York.
- AND J. W. ANDRESEN. 1975. New Jersey Pine Barrens shrub cover: stable for 42 years. *Bull. N.J. Acad. Sci.*, **20**:18-19.
- AND L. JONES. The Pine Barrens: Vegetation geography. N.J. State Mus. Res. Rep. 3. Trenton, N.J. 78 p.
- MOUL, E. T. AND M. F. BUELL. 1955. Moss cover and rainfall interception in frequently burned sites in the New Jersey Pine Barrens. *Bull. Torrey Bot. Club*, **82**:155-162.
- MUTCH, R. W. 1970. Wildland fires and ecosystems: a hypothesis. *Ecology*, **21**:451-459.
- OHMANN, L. F. AND D. F. GRIGAL. 1979. Early revegetation and nutrient dynamics following the 1971 Little Sioux forest fire in northeastern Minnesota. *For. Sci.*, **25**:1-80.
- OOSTING, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Midl. Nat.*, **28**:1-126.
- RHODEHAMEL, T. 1979. Geology of the Pine Barrens of New Jersey, p. 39-60. *In*: R. T. T. Forman (ed.). Pine Barrens: Ecosystems and landscape. Academic Press, New York.
- ROBICHAUD, B. AND M. F. BUELL. 1973. Vegetation of New Jersey. Rutgers University Press. New Brunswick, N.J. 340 p.
- TEDROW, J. C. F. 1952. Soil conditions in the Pine Barrens of New Jersey. *Bartonia*, **26**:28-35.
- . 1979. Development of Pine Barrens soils, p. 61-80. *In*: R. T. T. Forman (ed.). Pine Barrens: Ecosystem and landscape. Academic Press, N.Y. pp. 61-80.
- VOGL, R. L. 1974. Effects of fire on grasslands, p. 139-194. *In*: T. Koslowski and C. E. Ahlgren (eds.). Fire and ecosystems. Academic Press, New York.
- WELLS, P. V. 1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo Quadrangle, California. *Ecol. Monogr.*, **32**:79-103.
- WHITE, P. S. 1979. Pattern, process and natural disturbance in vegetation. *Bot. Rev.*, **45**:229-299.
- WHITTAKER, R. H. AND G. M. WOODWELL. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, N.Y. *J. Ecol.*, **56**:1-25.
- AND ———. 1969. Structure, production and diversity of the oak-pine forest at Brookhaven, N.Y. *Ibid.*, **57**:155-174.
- WOODWELL, G. M. AND A. L. REBUCK. 1971. Effects of chronic gamma radiation on the structure and diversity of an oak-pine forest. *Ecol. Monogr.*, **37**:53-69.