The Role of Magnolia and Beech in Forest Processes in the Tallahassee, Florida, Thomasville, Georgia Area*

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INTRODUCTION

THE Tallahassee Red Hills area, once described as having "abundant groves of oak, hickory, beech and magnolia" covering its slopes (Williams, 1827), is now covered with vegetation representing a vast array of successional stages: recently abandoned fields inhabited by herbaceous plants; stands of pines (loblolly, shortleaf and longleaf), some of which possess a thick understory of encroaching hardwoods; areas dominated by hardwood mixtures (sweetgum, hickory, oaks), often including some remnant pines;

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and various combinations or mixtures of these species. In certain stages a considerable number of these woody communities have a large number of magnolia seedlings and saplings in them. Less frequently they include beech seedlings and saplings. Only rarely is there a forest community which has been undisturbed or unburned long enough to show an overstory predominately comprised of magnolia (*Magnolia grandiflora* L.) and beech (*Fagus grandifolia* Ehrh.). Generally such stands occur in ravines that are too steep for logging, farming, or grazing and are mesic enough so that fire rarely occurs in them. In a few instances relatively mature magnolia-beech forests of limited extent occur on other kinds of sites.

The generally very much disturbed communities characteristic of the area under consideration are typical of the coastal plain area as a whole. There is evidence that the vegetation here was burned on a considerable scale by Indians before the settlement by white men (Hilgard, 1860, Harper, 1914, Cotterhill, 1936). During the period since white man's settlement, burning of vegetation has continued. This, combined with the varied and extensive modifications of the landscape associated with human occupation, has yielded a complex mosaic of vegetational patterns and it is unlikely that any forest stands are without some effects of disturbance. Interpretations of successional processes and of climax vegetation vary considerably as a consequence.

Gano (1917) and Kurz (1944) both concluded that magnolia-beech is climax vegetation in the Tallahassee Red Hills area. Pessin (1933) suggested an oak-hickory association would probably develop into a magnolia-beech climax on moist sites. Hubbell, Laessle and Dickinson (1956) accepted the magnolia-beech climax, as did Braun (1950), who considered it transitional between the deciduous and broad-leaved evergreen forest formations. Harper (1906, 1911), cited by Quarterman and Keever (1962), described a mixed deciduous and evergreen forest as the probable climax on sandy mesic sites. Both sites studied by Harper were, however, in areas where beech does not occur. Quarterman and Keever (1962), considering that all preceding workers based their interpretations on subjective observations, undertook a quantitative analysis of the forest vegetation of the southeastern coastal plain as a whole. They found fourteen species to be "structurally important," and that although a number of these species shared dominance, they were not seen to form "association segregates." Five to nine species were found by them to be co-dominant and reproducing in the older, less disturbed stands. Their conclusion was that the climax forest for the pine belt of the southeastern coastal plain is mixed-hardwood.

The several interpretations of these workers seem to infer a single climax community which develops from the existing flora under the influence of the natural climatic forces existing throughout the lower coastal plain. It is important to emphasize that these authors apparently exclude fire as a natural ecological factor. Chapman (1932), in considering the effects of fire in this area, said ". . . fire at frequent but not necessarily annual intervals is as dependable a factor of site as is climate or soil." That fire is itself a natural climatic factor, as well as one attributable to human activities, is a view for which evidence is given by Robertson (1953) and Komarek (1962, 1964). Thus fire must be considered an important ecological factor affecting vegetational development and structure and is so considered in this study. It may affect both successional processes and forces responsible for stability of climax type. Interpretation of actual community types, or potential community types, will depend in part upon the role of fire (or the absence of fire) either during development or in relation to stability.

This study is designed to show by quantitative analyses and by subsequent interpretative observations based upon the results of the quantitative studies the role of *Magnolia grandiflora* and *Fagus grandifolia* in forest processes in parts of northwestern Florida and adjacent Georgia where they both occur.

PROCEDURE

Five vegetational stands were selected for quantitative analysis. Each of these stands appeared to represent a different stage in the development of a magnolia-beech forest.

Before any quantitative sampling was attempted, each stand was thoroughly explored. In this way sampling was restricted to areas well within the stand, thus avoiding non-representative transitional zones.

The overstory was sampled on each site by the following plotless method: The diameters of a number of overstory trees were first measured to get an idea of the relative diameters of the average overstory trees. A minimum diameter was then chosen and all trees with this diameter or greater were considered representative of the trees whose crowns comprised the canopy.

At one end of the stand a tree was selected which was in the chosen diameter class. The species and d.b.h. (diameter at breast height) were recorded. From this first tree, the nearest tree of this diameter class in the general direction of the opposite end of the stand was sighted. The distance between the two trees was measured, and the d.b.h. and species of the second tree were recorded. Then from the second tree the nearest tree in the general direction of the far end of the stand was again sighted, the distance between the second and third tree measured, and the d.b.h. and species of the third tree recorded. This process was repeated until the opposite end of the stand was reached. Sometimes it was necessary to use a compass to keep in the proper hemisphere, and therefore insure a progression toward the opposite end of the stand.

The data obtained from this sampling procedure were used to compute the relative dominance, relative density and distance frequencies for each stand. The relative dominance is the basal area of one species divided by the basal areas of all species, and the relative density is the number of one species divided by the number of all species. The distance frequency is an expression of the number of trees that are separated by a certain distance. For example, Figure 1 shows that for the particular distance of 45 feet, magnolia has a distance frequency of 30. This means that of the magnolia trees in that part of the sample, 30 of them were separated by a distance of 45 feet. To obtain the distance frequencies of a particular species, it was necessary to resample for that species. Resampling usually only included the dominants because the distances between non-dominant kinds of trees was so great that sampling was impracticable.

In this method not utilizing plots, distance frequency is substituted

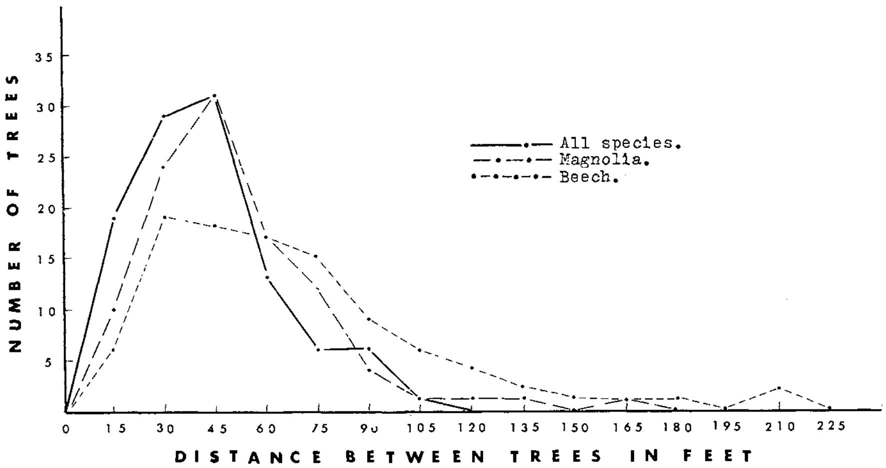

FIG. 1. Distance frequencies of overstory trees in Tall Timbers Woodyard Hammock.

for the more commonly used relative frequency. We feel that in using this procedure we are presenting a concept (distance) which mirrors the structure of the stand more closely and that this makes it possible to form a more accurate mental image of the forest being described.

Transgressors and understory species were sampled in 35 foot square plots in each of the five stands. The species, height and/or d.b.h., were recorded for all plants 1 foot and over in height. Seedlings of potential overstory were recorded regardless of height. Except in the Tall Timbers Woodyard Hammock, all plots were laid out at random. In the Woodyard Hammock stand, some of the sampling plots were placed so that either a mature magnolia or beech was situated in the center of these plots. Because of this placement, any specificity between transgressors and overstory species was indicated. Relative frequency

$$\left(\frac{\text{number of plots containing a particular species}}{\text{total number of plots used}}\right) \times 100$$

was calculated from data taken in these plots.

Increment borings were taken from a large number of trees in order to estimate some general relationships between tree ages and tree diameters. Two increment borings were taken from some magnolia trees to correct for errors caused by lenses which have been shown to occur in magnolia (Flanders, 1950). In two stands (Ireland's Uncut Ravine and Woodyard Hammock at Tall Timbers) diameters of magnolia trees were sampled in order to obtain diameter frequencies. The estimated relationship between age and diameter was then used to compute the frequency with which magnolia of different ages occurred in each stand. The magnolia age frequencies of the two stands were then compared, to provide some insight into the development and maintenance of each stand.

Several soil samples were taken at 6 inch depths in each stand. The percentage of moisture was determined by weighing, drying at 103° C. for 24 hours, and reweighing. The samples were then sent to the Florida Agricultural Extension Service at Gainesville, Florida, for analysis of pH, organic matter, calcium, magnesium, phosphate, potash, and nitrogen.

RESULTS

Mill Pond Loblolly Pine Stand

This stand is located on Mill Pond Plantation near Thomasville, Georgia. The area considered here is a fairly flat ridge of about 15 acres with an evenly distributed overstory of loblolly pine (*Pinus taeda* L.) (Table 1.).

Although there is a hardwood understory, the stand is still relatively open so that it is possible to see large portions of it at once. On three sides the ridge slowly slopes down to several small streams. On the stream banks or beds are a number of mature magnolia and beech trees and these provide a source of seeds for this area.

According to Mr. Gibson, the overseer for the plantation, the site of this stand was once in cultivation. The older pines are of fairly even age indicating that cultivation ceased simultaneously over the entire site. Increment borings of the larger pines indicate an age of about 100 years. Growth of the large pines is at present

TABLE 1. RELATIVE DOMINANCE AND RELATIVE DENSITY OF ALL OVERSTORY SPECIES

Potential Overstory	Mill Pond Loblolly Stand		Mill Pond Longleaf Stand		Ireland's Cut Stand		Tall Timbers Woodyard Hammock		Ireland's Uncut Stand	
	Rel. Dom.	Rel. Den.	Rel. Dom.	Rel. Den.	Rel. Dom.	Rel. Den.	Rel. Dom.	Rel. Den.	Rel. Dom.	Rel. Den.
Magnolia grandiflora	1	1	7	23	19	8	44	43	55	57
Fagus grandifolia			1	3	12	3	31	29	19	21
Liquidambar styraciflua	9	17	16	13	40	53	7	9	15	15
Nyssa sylvatica					1	3	5	4	5	4
Pinus glabra							4	7	3	2
Quercus laurifolia							3	2		
Carya sp.	1	3	4	8	4	6	2	3		
Quercus prinus							1	1		
Magnolia virginiana							1	1	3	2
Ulmus alata							1	1		
Ulmus americana							1	1		

TABLE 1. (CONTINUED)

Oxydendrum arboreum			11	13		
Pinus taeda	77	60	13	5	16	11
Pinus palustris			36	13		
Quercus nigra	5	7	3	5	6	8
Quercus shumardii					1	3
Quercus alba			5	8		
Quercus velutina			3	5		
Quercus hemisphaerica	5	8				
Quercus falcata	1	1				
Ostrya virginiana					1	3
Ilex opaca			1	3	1	2
Cornus florida	1	4	1	5		

very slow as evidenced by the annual increments of the last few years. Thus one may assume that the pines are essentially mature. Mr. Gibson also said that the stand was regularly burned until about 50 years ago, and has been fire free subsequently. This is corroborated by increment borings of the oldest hardwoods in the stand which show them to be about 50 years old.

While the overstory at this stage in this stand (trees about 10 inches in diameter) is clearly dominated by *Pinus taeda*, there are representatives of a few hardwood species of the same and smaller size classes present (Table 1). Assuming the continued absence of fire and that the pines are mature and will soon begin to die, the next successional stage will have an increasingly greater percentage of hardwoods of the species now present, but of uneven ages, in its overstory. The four hardwoods now present in appreciable numbers (Table 2) are *Quercus hemispaerica* Bartr., *Q. nigra* L., *Carya* sp., and *Magnolia grandiflora*. Of these magnolia is readily seen by inspection on the site to be the most recent invader. *Quercus hemisphaerica, Q. Nigra, Nyssa sylvatica* and *Carya* sp. grow well under the less severe shade conditions provided by the pines. This means that they can ultimately produce an overstory in which they share dominance. While seedlings or saplings of these species do continue to be produced, as the shade becomes more intense they appear much less vigorous than the early invaders of the same species and tend to die before they become very large. Godfrey (personal communication) states that neither *Quercus hemisphaerica* nor *Q. nigra* are long-lived oaks. On the other hand, magnolia which is extremely shade tolerant, begins to invade these stands when the shade is heavy and can continue to reproduce when the canopy is closed (see data from Woodyard Hammock). In addition to the foregoing hardwoods present in this stand and in relative abundance, there are lesser numbers of trees of *Liquidambar styraciflua* L., and *Q. alba* L.

The life history information and growth requirements for the kinds of trees enumerated above enables one to predict that the loblolly pine overstory will initially be replaced by a mixture of hardwood species but that ultimately magnolia will increasingly

TABLE 2. RELATIVE DENSITY AND RELATIVE FREQUENCY OF ALL POTENTIAL OVERSTORY SPECIES

Potential Overstory Species	Mill Pond Loblolly Stand		Mill Pond Longleaf Stand		Ireland's Cut Stand		Tall Timbers Woodyard Hammock		**Ireland's Uncut Stand**	
	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.
Magnolia grandiflora	27	100	24	100	87	100	9	39		
Fagus grandifolia					3	100	8	61	15	71
Liquidambar styraciflua	5	20	7	100	9	66	28	89		
Carya sp.	14	60	10	100	21	100	23	89	24	29
Quercus laurifolia							5	33	22	29
Pinus glabra							1	33		
Quercus nigra	16	40	11	50	14	100	6	72	28	57
Nyssa sylvatica	2	40					2	29	4	29
Quercus hemisphaerica	30	80	17	100	6	66				
Quercus alba	3	20	10	100			71	6		
Quercus stellata			10	50						
Quercus shumardii									2	14
Quercus prinus					2	100	17	89	4	29
Fraxinus pennsylvanica							1	6		
Pinus sp.			7	50						

replace many or most of them. Beech is here conspicuous by its absence and we can only suggest that this may be a consequence of too low seed pressure.

Mill Pond Longleaf Pine Stand

This stand, also on Mill Pond Plantation, was chosen because of its longleaf pine (*Pinus palustris* Mill.) overstory. This stand is of particular significance because longleaf pine is considered a climax species over large areas of the Southeast in which fire is a naturally recurring phenomenon (Chapman, 1932).

According to Mr. Gibson, the site of this stand was never cultivated and has been protected from fire for about 50 years. Increment borings of the older hardwoods suggest that the stand has been free from fire perhaps slightly over 60 years—about 10 years longer than the loblolly stand discussed above. The actual area of longleaf overstory is only about ½ acre and quickly blends into a much larger loblolly stand (on a site formerly cultivated), which runs for about 200 yards down a gradual slope to a small stream. Mature magnolia and beech are common along this stream and provide the area with a source of seed of both species.

Samples of the overstory show longleaf to be the dominant overstory species with a fair number of hardwoods just making their appearance in the overstory (Table 1). Most significant perhaps is the presence of one beech tree in the overstory sample. The information available about beech indicates that it has specific growth requirements. Some requirements which have been suggested are: the presence or absence of certain unknown flora or fauna in the soil (Harper, 1928); availability of moisture (Harlow, 1941); a pH ranging between 4.1 and 6.0, seldom exceeding 7.0; and leaf litter or mineral soil for germination (Fowells, 1965). There are at least two possible explanations for the occurrence of only one beech tree in the stand with no signs of beech seedlings. One explanation is that this single beech is the result of chance. By this we mean that the general conditions of the stand are not yet suitable for the establishment of beech, but that conditions just happened to be right in the particular spot, at the particular time that a beech seed happened to fall some years ago. The other explanation is that beech dispersal is so poor that only one seed was dispersed to that area in the last 60 years. It is also possible that both of these explanations are applicable.

A clue to the next successional overstory is again given by the young hardwoods which are presumed to be potential representatives of the overstory species (Table 2). There are nine such species represented in the understory. The most abundant is *Magnolia grandiflora*. Others are *Quercus hemisphaerica, Carya sp., Quercus nigra, Pinus sp.,* and *Liquidambar styraciflua*, which, as already indicated, are all either shorter-lived or intolerant of shade and will not continue to reproduce themselves and contribute to the ultimate overstory to any appreciable degree; *Quercus stellata* Wang., and *Quercus alba*, which because they are long-lived, will remain, but will be outnumbered by the more rapidly reproducing magnolia. Although there are presently no beech seedlings in the stand, there is a seed source, and analysis of other stands show that beech does come into a stand some time after magnolia has become established. (See data on Woodyard Hammock, Tables 1 and 2). Beech is both long-lived and shade tolerant (Fowells, 1965; Harlow, 1941).

In summary, it appears from the life histories of the species present that the stand will at length become dominated by magnolia, and possibly much later will share this dominance with beech.

Ireland's Cut-Over Stand

This site, a few miles north of Tallahassee, was once inhabited by a "mature hardwood stand." During the early 1940's the government contracted with the owner, Mr. Kenneth Ireland, to cut out hardwoods suitable for use in making crates.

On one side of the stand is a field of *Andropogon* and pine seedlings, with clumps of *Liquidambar* and *Rubus*. From the field the cut-over stand is on a gradual slope which finally drops abruptly to a stream. For a few hundred yards the stand runs lengthwise between the stream and the field and eventually is adjunct to an uncut area discussed later.

Samples of the overstory show *Liquidambar styraciflua* to be the dominant overstory species and magnolia and loblolly pine to be the next most significant species (Table 1). The larger trees of this overstory are those which were unsuitable for lumber and were therefore left standing. In sampling, a minimum d.b.h. was chosen which would include the new overstory that has grown up since the lumbering 24 years ago. This explains why occasional permanent understory trees are found in the overstory sample, e.g., dogwood.

Among the young, successional, potential overstory trees, the preponderance of magnolia is shown by the very high relative density value for magnolia (Table 2). All the magnolias in this sample were seedlings less than 7 years old, and most of them were from 2 to 3 years old. The striking absence of magnolia seedlings in a mature magnolia stand, specifically in the area beneath the parent trees, has been commented on by both Kurz (1944) and Quarterman and Keever (1962). The period of 21 to 22 years from the time the presumed magnolia overstory was removed (1942) until the time the seedlings began to germinate (1963–64) is evidently the approximate time required by the stand to recover from the inhibitory effects of the former magnolias.

Although there are not a large number of young beech trees (Table 2), the age distributions indicate that the reproduction is continuous. The recovery of beech may be described as "slow but steady."

The other young overstory species, *Carya sp.*, *Quercus nigra*, *Liquidambar*, and *Quercus hemisphaerica*, have already been described as either short-lived or intolerant of shade. *Quercus prinus* L. is intermediate in shade tolerance (Fowells, 1965). This leaves only magnolia and beech, as the only long-lived, shade tolerant species, to eventually dominate the overstory.

The permanent understory is shown in Table 3. The presence of *Albizza julibrissin* Dur. indicates the openess of the stand and also the influence of the bordering field.

Tall Timbers Woodyard Hammock

The Woodyard Hammock is a large lowland stand on the property of the Tall Timbers Research Station about 20 miles north of Tallahassee. The hammock is flat, with its southern portion ending

TABLE 3. RELATIVE DENSITY AND RELATIVE FREQUENCY OF ALL PERMANENT UNDERSTORY SPECIES

Understory Species	Mill Pond Loblolly Stand		Mill Pond Longleaf Stand		Ireland's Cut Stand		Tall Timbers Woodyard Hammock		Ireland's Uncut Stand	
	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.	Rel. Den.	Rel. Freq.
Symplocos tinctoria	3	60	11	50	1	33	11	44	32	100
Hydrangea arborescens									15	100
Ostrya virginiana	1	20			6	66	29	94	12	100
Halesia diptera					4	66			11	100
Euonymus americanas					34	100	2	6	8	100
Callicarpa americana	10	100	11	100	1	33			6	100
Morus rubra					2	33	2	27	5	86
Prunus caroliniana	14	80	15	100			1	11	4	43
Cornus florida	23	80	15	100	6	100	10	61	1	29
Sambucus canadensis									1	14
Ilex coriacea									1	14
Celtis laevigata									1	14
Bumelia lanuginosa									1	14
Aralia spinosa			22	100	22	66			1	14
Gordonia lasianthus									1	14
Ilex opaca	4	40					24	89		

Carpinus caroliniana					1	33	10	72
Oxydendron arboreum							3	27
Itea virginica							1	6
Vaccinium elliottii	2	40					1	6
Diospyros virginiana					1	33	1	6
Rhododendron canescens							1	6
Cercis canadensis					4	33		
Prunus serotina	4	40			1	33		
Osmanthus americana	4	40	6	100	1	33		
Cinnamomum camphora			1	50				
Myrica cerifera	6	60	3	100				
Rhus copallina	3	60	3	100				
Crataegus uniflora	2	40						
Acer rubrum	11	60	11	100			5	38
Albizzia julibrissin					8	66		
Sassafras albidum	15	60	4	50	6	33		
Vaccinium arboreum							2	22

in a hyacinth-choked lake, Andrew's Flat. For most of its length, about 700 yards, the site gradually rises until it reaches an uneven area of pine-oak hills and gum-swamp pockets. The uneven northern end of the stand has obviously been subject to much disturbance and was therefore not included in the sampled area. The stand is bordered on the east side by hilly fields and on the west by a dirt road with some *Liriodendron tulipifera* L. along the side of the road. The actual area sampled is about 45 acres with an apparent overstory of magnolia and beech. In most places the canopy is well closed and the understory is open. At one time some spruce pines (*Pinus glabra* Walt.) were cut from the stand, but other than this there has been no lumbering. On the forest floor are mounds and depressions left by the uplifted roots of fallen and now decayed trees, with columns of mosses outlining the decayed remains of the trunks where they fell across the ground. A few rotting stumps still have shells of characteristic pine bark.

The overstory is composed almost entirely of magnolia and beech, although there are at least ten other species in the canopy (Table 1). The frequency distribution of magnolia shows that most of the magnolias are 30 to 45 feet apart, but that there are some areas that have relatively few magnolia. The distribution of beech is more spread out than that of magnolia; most of the beech are between 30 and 75 feet apart and the areas of the stand with relatively few beech are greater than the areas with relatively few magnolia. The closeness with which the distance frequencies of magnolia and beech parallel the distance frequencies of the overstory sampled as a whole (all overstory species) indicates the prevalence of magnolia and beech (Fig. 1). This, combined with the high relative dominance and relative density values for the two species, clearly shows that the stand is dominated by magnolia and beech.

Besides the trees forming the canopy, the stand contains young trees of the following kinds (Table 2): *Liquidambar styraciflua*, *Carya sp.*, *Quercus prinus*, *Q. nigra*, *Q. laurifolia*, *Pinus glabra*, *Nyssa sylvatica*, *Fraxinus pennsylvanica* Marsh., and *Quercus alba*, *Magnolia grandiflora*, *Fagus grandifolia*. The first three are the most abundantly represented but the plants were mostly seedlings.

With the exception of the magnolia and beech, the plants do not appear to be vigorous and flourishing to the extent that they may be expected to be more than ephemeral. In the stand as a whole then, it is our interpretation that the magnolia and beech will contribute to the overstory to about the same extent as presently represented.

In this stand a study was also made of the effect overstory beech and magnolia have on beech and magnolia reproduction. In this study 18 plots were sampled. Six of these plots had a beech overstory; six had a magnolia overstory; and six plots had an overstory of both magnolia and beech. In each of these groups of six plots, the percentage of plots having either magnolia or beech seedlings were recorded (Table 4).

TABLE 4. OVERSTORY INFLUENCE ON BEECH AND MAGNOLIA REPRODUCTION

Overstory tree present	Percentage plots with beech seedlings	Percentage plots with magnolia seedlings
Beech	33%	100%
Magnolia	83%	0%
Beech and Magnolia	67%	17%

Table 4 shows that beech reproduces fairly well under canopy-forming trees of both magnolia and beech, whereas magnolia reproduces well under a beech overstory but very poorly under a magnolia overstory. It is significant that in the magnolia and beech plot which had magnolia seedlings the magnolia seedlings were definitely under a parent tree. The parent tree was, however, leaning to one side so that it dropped its leaves on the side opposite the seedlings. This suggests that the inhibitory effect of a magnolia overstory on magnolia reproduction is probably closely associated with the magnolia leaves, which in many areas completely cover the ground. Also, we have never seen magnolia seedlings growing in magnolia leaf litter. A critical test for this might be to rake a section clear of magnolia leaves and see if there were any magnolia germination in the next few years.

IRELAND'S UNCUT STAND

This stand, adjoining Ireland's Cut Stand, covers the valleys and ridges of two small, branching, springfed streams that flow eastward about ¼ mile and empty into Lake Jackson. According to Mr. Ireland, this area has not been cut since he purchased it about 35 years ago, and at that time the stand looked much as it does now. There is no sign of cutting in the stand, although depressions and mounds in the forest floor indicate that fallen trees have been removed from the stand.

Although this is the oldest of the stands sampled, it has certain features which may be accounted for because of its small size. These features cause it, as a forest, to seem different at first sight than a much larger example such as the Woodyard Hammock. Analysis of its structural dynamics, however, lead one to the view that essentially the same processes are occurring but that size relations are important.

In this smaller stand, if a large, mature magnolia or beech falls or dies a successional process sets in within the opening created. Relative to the size of the whole area, such an opening and the vegetational development taking place there is very much more noticeable. There results a patchwork quilt kind of pattern in the structure of the vegetation which can be seen to be similar to that in a relatively large stand. It is simply that the developmental dynamics taking place in one or several openings of a given size in a much smaller total area are more conspicuous than one or a few such openings of the same size in a much larger total area.

In an opening caused by the death or fall of a large beech or magnolia, conditions are favorable for reproduction and vigorous growth of trees like *Liquidambar*. These then come to form a patch of overstory in such places.

The actual data yielded from sampling this stand show (Fig. 2) a more closed stand than the Woodyard Hammock. Magnolia comprises most of the canopy. There is seen here a lesser percentage of overstory beech and *Liquidambar*. The data in Table 2 show that there is no *Liquidambar* reproduction but moderate beech reproduction in this stand. The other hardwood trees (Table 2)

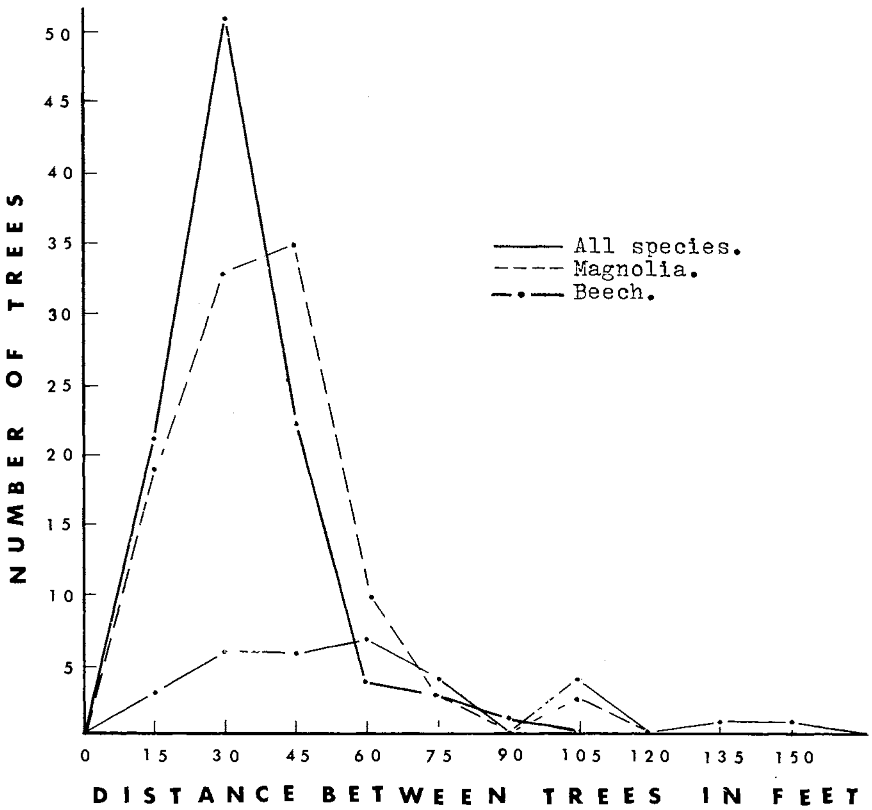

FIG. 2. Distance frequency of overstory trees in Ireland's uncut stand.

are, like *Liquidambar*, kinds which reproduce and grow vigorously in stronger light. If they reproduce in relatively dense shade they are not vigorous and do not reach appreciable size. Thus the younger or smaller trees of these species, if in the understory, are not considered to be significant insofar as the composition of the ultimate overstory is concerned. The data also show that magnolia is not reproducing very much in this stand and that is because of the density of mature magnolia at present and the corollary fact that magnolia does not reproduce from seeds under magnolia. Also, since beech shows a greater degree of reproduction, it is possible that there will eventually be some shift toward a greater density of beech. The latter may, however, be offset by magnolia reproduction by root sprouting. In this stand, of a sample of 125 magnolia trees, 45% were root sprouting. In one instance a leaning sprout which came in contact with the ground produced adventitious roots. Established, larger magnolias were also observed that appear to have started as sprouts from the bases of fallen or old decaying trees. It seems fairly evident that sprouting plays an important role in maintaining the percentage of magnolia as a co-dominant in the forest.

The evidence, indicates, then, that the hardwoods in this stand other than magnolia and beech are successional insofar as they constitute portions of the canopy and that they are but ephemerals as understory trees. Beech reproduction and magnolia reproduction, whether from seeds or sprouts, is sufficient so that one can predict that magnolia and beech will maintain dominance.

Understory

The permanent understory for all stands is compared in Table 3 which shows that many of the species which form the permanent understory in mature magnolia-beech stands are among the first to invade a pine stand which has been free from fire, such as the Mill Pond Loblolly Stand and the Mill Pond Longleaf Stand.

DISCUSSION

Habitat

From the stands sampled and observed in the Tallahassee-Thomasville area, it appears that a magnolia-beech forest will develop within this geographic area (where both kinds of trees occur together) on any site which is not regularly flooded or burned and is in range of a seed source. Both the Mill Pond Loblolly Pine Stand and the Mill Pond Longleaf Pine Stand are examples of areas where fire has been controlled by man and which are now supporting the early stages of a magnolia-beech forest. There are also upland areas which are naturally protected from fire. An example of this is cited by Harper (1939) in which he describes an area, the Alabama pocosin, that is protected on one side by a creek and on the other three sides by sand-hills. Under these conditions the hammock vegetation is slowly spreading into the sand-hill vegetation.

As a hardwood stand establishes itself on a sandy upland, conditions become more mesic, and the occurrence of fire becomes less likely. This is not, however, considered as evidence that hardwood stands are moving into the fire-maintained pine lands, but simply that there is a constant fluctuation between the two in marginal areas. If this is correct, the habitats that are supporting and will in the future support magnolia-beech stands are those areas which are between the frequently inundated lowlands and the frequently burned uplands.

The analyses of the soil samples did not indicate what role, if any, soil has in influencing the occurrence and development of a magnolia-beech forest. Except for the greater moisture content of the soil in the older hardwood stands, when compared with the pine stands, there are greater variations in soil composition within each stand than between stands. In a more complete study of soil influences (Monk, 1965), magnolia was found to respond to potassium, phosphorus, and moisture levels, but not to calcium and magnesium. Although a large number of samples may indicate some relationship between these elements and magnolia, there is as yet no strong evidence that soil, within the geographic range of magnolia-beech forests, limits the habitat of the magnolia-beech community. If soil is a factor which prevents the early establishment of beech, it is probably a more subtle relationship than has been tested for in either Monk's or this study. Since beech comes in after magnolia becomes established, and it so far appears that magnolia is not restricted by soil composition, then it can be generalized that soil is not one of the important determinants of the potential magnolia-beech habitat. Since magnolia and beech do occur in the area under consideration, and given the general forest dynamics prevailing based upon evidence from these studies, periodic fire and periodic flooding are seen to be the major factors limiting the development of magnolia-beech forests.

Development of a Magnolia-Beech Forest

The order of succession toward a magnolia-beech stand varies with the history of the site and availability of a seed source. In areas with nearby magnolia seed sources, magnolia seedlings may be among the first hardwoods to invade, as is seen in both the Mill Pond Loblolly Pine Stand and the Mill Pond Longleaf Pine Stand. In other areas with poor seed sources, observed but not sampled, oak, hickory, and sweet-gum may become well established in the overstory by the time the first magnolia appears. Ireland's Cut-over Ravine is an example of a stand in which the presence of a magnolia overstory 20 years ago delayed the reproduction of magnolia for about 20 years following selective cutting, allowing trees of other species to precede it successionally. It is characteristic of all of the stands that we have observed that beech is one of the last species to invade. The explanation for this will probably depend on further studies of seed germination and dispersal.

In summary, the appearance of a heavy magnolia understory is the first sign that a stand is developing into a magnolia-beech forest (Table 2). The time when magnolia enters the stand is determined by the dynamics of community development on a given site and the availability of a seed source. The second stage of development is the appearance of beech seedlings, which depends first, like magnolia, on a seed source. The relative rates of appearance of magnolia seedlings versus beech seedlings, even given a seed source for both, is presumed to be related to different ways in which seeds of each are dispersed and/or by differing conditions limiting seed germination, or even by different total quantities of seeds produced by mature trees of each species, i.e., seed pressure. It has been observed in a number of instances, not only in the stands sampled but in others, that magnolia seedlings appear more or less randomly and simultaneously in a given forest whereas beech seedlings first appear near the mature seed trees and then gradually beyond.

Magnolia seeds are eaten by certain birds. The nutritive portion of the seed is the pulpy outer covering. The embryonic portion is covered by a hard coat and passes through the digestive tract and is eliminated in the feces. Thus magnolia may be effectively dispersed by birds and this doubtlessly accounts for seedlings appearing in developing forest as randomly scattered individuals. It is highly probable that the time of appearance of magnolia seedlings in developing forest is consequent upon succession of bird populations accompanying plant succession. Beech seeds have a very different morphology. The embryonic portion is within the nutshell and when the seed is consumed by an animal the embryo is in effect destroyed. We suggest that rodents are the principal predators on beech nuts. Inasmuch as they may carry some seeds short distances and bury them, perhaps never finding some of them again, this would account for the different manner in which establishment of beech seedlings occurs, especially if the seed source is limited.

Climax Consideration

To avoid a fruitless discussion of what ecologists mean by vegetational climax, we will define climax as it is used in this paper. A vegetational climax is a community of plants of a species or a distinct group of species that have a relatively stable association and are able to reproduce indefinitely under the existing environment (the environment being all factors which influence the vegetation, either directly or indirectly). This definition does not exclude the possibility of more than one climax occurring in a given area. This definition is considered valid because it is based on the vegetation, and not just selected elements of the environment, such as climate, which have been given special value.

It should be emphasized that fire is a natural part of the environment in some places. In the coastal plain of the eastern and southern United States, there is an average of 60 or more thunderstorm days a year (Komarek, 1964). In terms of lightning strikes, an area which has 50 storms yearly should expect from 50 to 100 lightning bolts to hit within a ½ mile radius of that area each year (Lightning Protection Institute, in Komarek, 1964). According to a map showing the distribution of lightning fires in Florida (Komarek, 1964) there were approximately 14 lightning-set fires south of Tallahassee in Leon County alone in the year 1962. In a fire-producing environment such as this, it is consistent with the above definition to consider the upland, fire-maintained longleaf pine forest as one of the climaxes of the southeastern coastal plain.

Before the magnolia-beech association is given climax status, certain criteria, imposed by the above definition, must be met. These conditions are: that it be a distinct association of species; that it be able to reproduce itself under the existing environment; and that it be a stable community. The first condition is met by the characteristics of the overstory in both the Woodyard Hammock and Ireland's Uncut Stand (Table 1).

The inability of magnolia to reproduce under the parent tree was noticed by Kurz (1944) and by Quarterman and Keever (1962). The inability of magnolia to reproduce in the leaf litter of the parent tree was verified by quadrat studies in the Woodyard Hammock stand (Table 4). The ability of magnolia to reproduce vegetatively, which was first noticed in Ireland's Uncut Stand and verified in the Woodyard Hammock, has not been mentioned by either Kurz or Quarterman and Keever. This reproductive characteristic is significant in relation to the definition of climax. The data obtained from Ireland's Cut Ravine shows that the time it takes for the inhibitory effect of a magnolia overstory to wear off is about 20 years. If this can be generalized to apply to other magnolia-beech stands, then when a mature magnolia dies and is not replaced by a sprout, some species other than magnolia will have about a 20-year head start. It is emphasized in this connection that beech seedlings or saplings do occur under both magnolia and beech trees (Table 4). The point to be made is that gaps which occur in the magnolia-beech stand are eventually reclaimed by one or the other of the dominant species. An example of this is seen in the Ireland's Uncut Stand where magnolia seedlings are coming in under a portion of the canopy which has been filled with a clump of sweet-gums. It is noteworthy that we did not see these magnolia seedlings until after the stand had been visited about 20 times although it was suspected that magnolia seedlings would be found in such successional spots.

We are led to think that the stand which Kurz was studying may also have had a scattered occurrence of magnolia seedlings in similar places but that they were not observed. The combination of vegetative reproduction of magnolia by sprouting and sexual reproduction, as described, fulfills the second requirement of the climax definition, that a climax species be able to reproduce itself under the existing environment.

The third, and last, requirement is that the stand remain stable, that is, that the dominant species should maintain their dominance. Whether a stand remains stable or not is related to the rate of death versus the rate of reproduction. The rate of death is related to the distribution of different age trees in the stand. Consider, for example, the Woodyard Hammock. In the forest now present, the overstory is predominately magnolia and beech. Thus it is a magnolia-beech forest. (It is emphasized here that it is the forest as a whole at which one looks, not a given small area or patch within it.) If the forest has, or is approaching, stability, then the distribution of different age trees of these species should be such that one can predict its continued general present composition. This would appear to follow if the ages of trees of the dominant species tend to become more evenly distributed as the age of the stand increases. In this case, using magnolia as an index (from inspection the same is seen to be true of beech), the frequency of different diameters of trees in the Woodyard Hammock and Ireland's Uncut Ravine were plotted (Fig. 3). This shows a high peak at about 100 years (d.b.h. 14–20″) in the Woodyard Hammock and several peaks ranging over 200 years in the (much smaller) uncut forest of Ireland's Ravine. The spread indicates that the present composition of Ireland's Uncut Stand will be maintained, and that the magnolia in the Woodyard Hammock are approaching stability, but may fluctuate some before this stability is reached. If the same may be assumed for beech, then one can predict that Ireland's Stand will remain relatively stable, and that in time the Woodyard Hammock will become stable.

This prediction is not intended to indicate a precise or absolute stability, but arrives by extrapolating generally from the data of

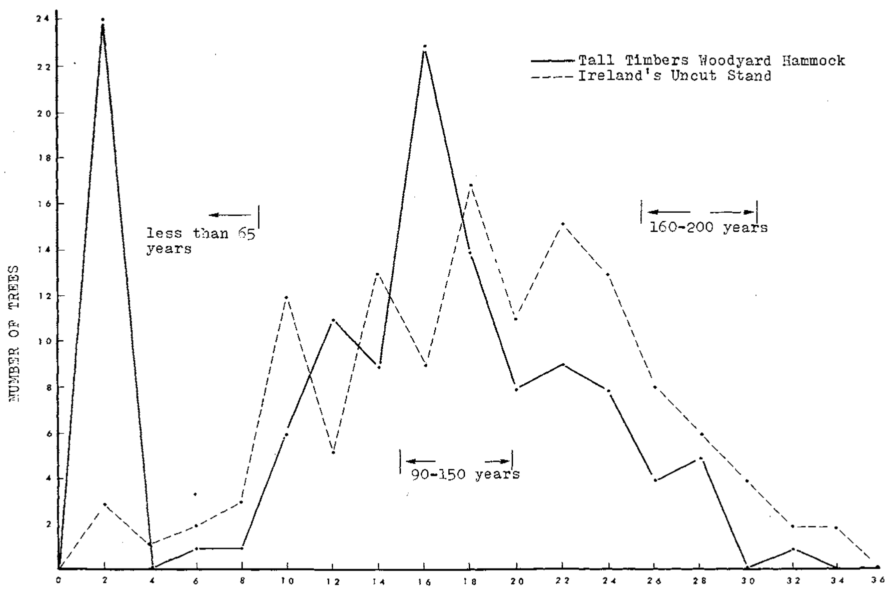

FIG. 3. Comparison of Magnolia diameters.

the samples and from observation of community dynamics. If a given large dominant tree dies or falls, obviously a developmental process will occur in the small included area as a consequence. The exact nature of vegetational change in time in these small areas will depend upon circumstances such as how large the opening is, what may have been growing under the tree at the time of death or fall, whether or not there is sprouting from the old base, and the like. The important question is whether or not the forest as a whole will be stable. We conclude that it will in this instance and that a magnolia-beech climax does occur in the general area under consideration.

Geographic Overlap of Magnolia and Beech

The objectives of this report did not include consideration of the overall distribution of a magnolia-beech climax. Its geographic limits are, of course, within the limits of the area of overlap. From herbarium specimens, personal observation, the literature, and personal correspondence we have indicated on a map (Fig. 4) the counties of the Southeast in which both *Magnolia grandiflora* and *Fagus grandifolia* occur. In all probability the spottiness of the distribution as shown is a reflection of the inadequacy of the sample but the overall area encompassed may be very nearly correct. The sources of information did not make it possible to distinguish in many counties whether or not trees of the two species grow together there.

According to Evans (1933), the northward range limits of

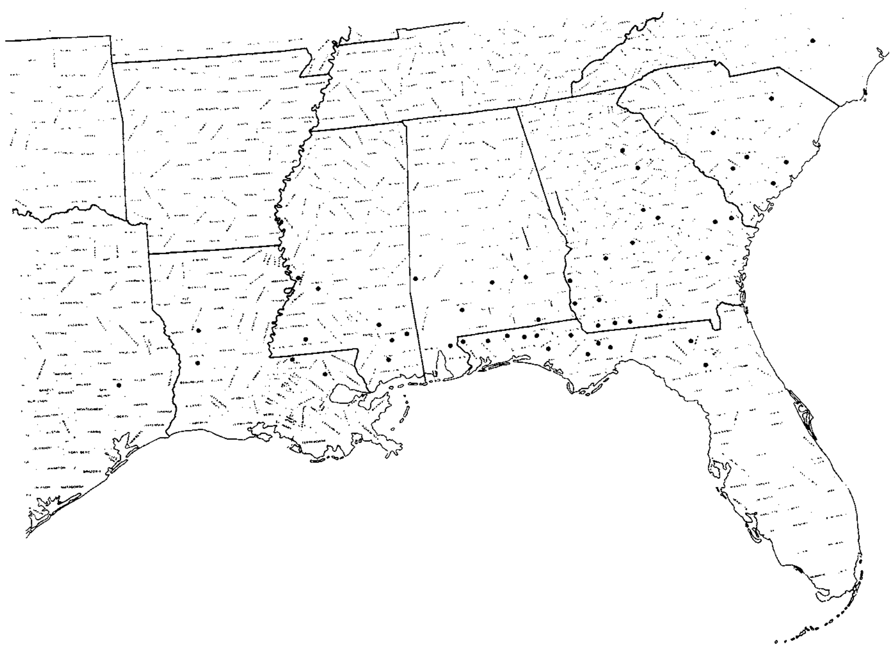

FIG. 4. Distribution overlap of beech and magnolia in the southeastern United States. Source: Sidney McDaniel, Mississippi State University, Daniel Ward, University of Florida, Wilbur Duncan, University of Georgia, and herbarium specimens, Florida State University.

magnolia occur where seeds and seedlings are not subject to freezing for more than 48 hours. Fowells (1965) reports that beech seeds are released from the burs after the first heavy frost and Diller (1935) indicates that high summer temperatures may be unfavorable to growth of beech, thus limiting its southward range.

In any event, if the magnolia-beech climax forest potentially occurs elsewhere than in the particular area in which these studies were made, it would be within the area of overlap. Throughout this area the landscape is generally in a great state of flux at present owing to the activities of man. In the Tallahassee, Florida-Thomasville, Georgia, region the potential for a magnolia-beech forest is seldom reached because of this flux. It is emphasized, however, that with the understanding of forest dynamics revealed by this study one can look at a great many stands of second growth or successional forest here and see that if fire were long excluded the eventual development of a magnolia-beech forest would seem to be inevitable. This may or may not be equally observable elsewhere within the overall range of overlap of the two species.

SUMMARY AND CONCLUSIONS

In the Tallahassee, Florida-Thomasville, Georgia region, a magnolia-beech climax vegetation type develops on sites free from periodic burning or periodic inundation.

Soil does not appear to be an important restricting factor with respect to development of this climax.

Vegetative reproduction of magnolia plays a role in maintaining numbers of this species in the stabilized community.

Magnolia leaf litter is suspected of having an inhibitory effect upon seed germination and upon seedling development of the magnolia.

Beech seeds germinate and seedlings develop under old trees of either species. Magnolia seeds germinate and seedlings develop under beech.

Trees of the two species appear to become more evenly distributed in age throughout the climax over time after it approaches the climax stage initially. This accounts for its reproductive stability.

The order of succession toward a magnolia-beech climax relates to the specifics of vegetational development on the site and requires, of course, a seed source for the climax species.

In the area here considered, the magnolia-beech climax is seldom realized owing to the prevalent, general state of vegetational flux related to man's activities.

Inasmuch as the whole southeastern area of overlap of the two dominant species of this climax is in a dramatic state of vegetational flux, the potential for this climax may exist elsewhere in the southeastern United States.

EPILOGUE*

A Wildfire in a Beech-Magnolia Hammock

Some considerable time subsequent to the acquisition of the data in the previous section, i.e., in March of 1968, just prior to the break of winter dormancy, a managed burn in a pine forest on Spring Hill Plantation, Thomas Co., Georgia, became unmanaged and swept through a stand of hardwood forest. This forest, on rolling terrain, is approximately 50 acres in extent. Trees which form the overstory include principally *Magnolia grandiflora*, *Fagus grandifolia*, *Liquidambar styraciflua*, *Pinus glabra*, *Carya glabra*, *Quercus alba*, *Q. hemisphaerica*. The mix of trees forming the canopy is uneven as regards the stand as a whole but one may readily see by inspection local areas where beech and magnolia together dominate. There are beech and magnolia trees throughout the stand even though in given places they are not dominant. The overstory trees belonging to these two species vary from about 18 inches to 36 inches d.b.h.

A short time after the 1968 burn, Roy Komarek, E. V. Komarek Sr., and R. K. Godfrey visited this stand and noted that the leaf litter on the forest floor was well burned off except in a few

* Contributed by Robert F. Doren, Tall Timbers Research Station (present address: United States National Arboretum), Jean Wooten, and R. K. Godfrey.

isolated spots. The tree trunks were, most of them, to some degree charred on the side away from the direction from which the fire came. Low shrubs in the understory, such as horsesugar, *Symplocos*, and small hollies, *Ilex americana*, were killed back to the ground, larger ones damaged but not killed. There were numerous areas where young magnolias were relatively abundant; these were mostly 3–6 feet high but some were up to 12–15 feet. The shorter ones were killed back, at least to the ground, but the taller were scorched below, alive at the top.

In 1973, the Komareks, Richard Vogl, and Godfrey revisited the hammock. The immediate impression gained was that an extraordinarily high number of small beech seedlings existed in the area of the 1968 burn. Besides this it was observed that the basal portions of magnolia trunks seen to be charred just after the fire now exhibited no signs of damage, the charring had been sluffed off. The beeches, on the other hand, almost all showed permanent bark damage just at and just above ground level on most of the half-circumference earlier charred; some trunks showed bark-killing more or less in a v-shape above. Healing of the scar edges had by now taken place but there was rotting of exposed wood. The point we wish here to stress was that the beeches were in effect half-girdled by the fire.

Given that beeches, as is the case with certain other trees, do not have heavy mast crops every year, we were wont to question what age classes the seedlings might constitute; whether in similar forest stands known not to have been recently burned there were any such high number of seedlings; what were the age classes of whatever seedlings were to be found in comparable stands. An analysis bearing upon the foregoing considerations we felt might help to indicate whether or not there were any likely positive correlation between the incidence of the wildfire and the remarkable crop of beech seedlings.

PROCEDURE

We chose, as similar stands in which to seek information on beech seedlings to compare with that to be gained in the Spring Hill

Hammock, the following: Woodyard Hammock, Tall Timbers Research Station; Ireland Uncut Stand (± 15 acres) and Winewood Hammock (± 8 acres), adjacent to Indian Head Acres, Tallahassee. (The first two stands were a part of the study in the previous paper).

Seedlings were age-classed by counting annual nodes (terminal bud scale scars) on their stems, the oldest being recognizable for up to 10 years.

Within the Spring Hill Hammock, which had been burned in 1968 three plots were established, each circular and with a 30 foot diameter: (1) centered on a large magnolia tree; (2) centered on a large beech tree; and (3) in an area between magnolia and beech trees and outside the crowns of both.

Within Woodyard Hammock, four plots were established, three of them as at Spring Hill and a fourth in an opening created by the death of and subsequent recent fall of a large beech tree.

The total number of seedlings in each was determined and the age of each ascertained.

Plots were not established in either the Ireland Uncut stand or in Winewood Hammock. The data gained at Spring Hill and at Woodyard was dramatically different and by inspection we could readily see that at the Ireland Stand and at Winewood seedling density was very low as it was at Woodyard. Thus, instead of laying out plots only to get information roughly comparable, we counted and aged all seedlings near to and under the beeches having their crowns in the overstory.

RESULTS AND DISCUSSION

Within the Spring Hill Hammock, where the burn occurred, the three plots had a total of 576 seedlings, 554 of which were four years of age with the remaining 22 either two or three years old (Table 5). The Tall Timbers Woodyard Hammock plots yielded but 20 seedlings, 11 of them two years old, nine of them three years of age. Ireland's Uncut forest yielded 26 seedlings of from two to eight years of age (Table 5). Within the Winewood Hammock, 60 seedlings were found, 34 of four years of age, 12 eight years of age, the remaining 14 scattered from three to ten years of age (Table 5).

No seedlings one year of age were found in any of the vegetational areas sampled. This may have been owing to the effects of a prolonged drought on seed germination and/or seedling development during the latter part of 1972.

The presence of such a large number (554) of four year old seedlings within the Spring Hill plots confirmed visual observations. Recall that fire within this area was in spring of 1968, our sample in winter of 1972–73. Thus, subsequent to the fire there were four growing seasons after the first crop of seeds could have been produced (autumn, 1968). Within all other areas sampled there was both a strikingly lower number of seedlings (20, 26, 60) and the few seedlings present were distributed over age classes of two to ten years.

Comparing both the high number of beech seedlings in the Spring Hill Hammock, and the fact that most were four years of age (i.e., presumably established from the mast crop the autumn of the year of the spring burn), with the low density of seedlings of various ages in all other unburned stands sampled leads us to the view that there is some causative relation between the fire and the great seedling crop. A possible explanation is that fire alters the forest floor, site of seed germination and seedling establishment, either by removal of the litter and exposure of the mineral soil or by changing the mineral composition of the soil or both. If this were true, perhaps the substrate would retain some of the changed characters for more than a year and there would thus be a gradual diminution in numbers of established seedlings in several of the years to follow. In any case, the data does not reflect this.

Alternately, it is possible that fire in some way triggers production of an unusually large seed crop, a sufficiently greater crop than is produced even in cyclical high mast years. Forage of beech nuts by small animals inhabiting such a forest is, we assume, an important factor in the fate of seeds and thus of seedlings. Such an unusually large seed crop might provide for a maximal predation by animals present and for presence of a bounteous number of seedlings. This hypothesis becomes more tenable when coupled with the observa-

TABLE 5. NUMBER OF BEECH SEEDLINGS IN VARIOUS VEGETATION STANDS

Age	Spring Hill Hardwood			Tall Timbers Woodyard Hammock				Ireland's Uncut Hardwood	Winewood Hammock
	Plots			Plots					
	Under mag.	Under beech	Between trees	Under mag.	Under beech	Between trees	Beech tree fall	Whole forest (± 15 acres)	Whole forest (± 8 acres)
1									
2	10		6	4	4		3	1	
3		6			2		7	8	2
4	88	199	267					5	34
5								2	
6								6	3
7								3	5
8								1	12
9									2
10									2
Sub Total by Ages	98	205	273	4	6	0	10	26	60
Total Within Areas		576				20		26	60

tion that the fire in the Spring Hill stand dramatically and effectively partially girdled the bases of most beech trees in the stand at ground level or just above. This girdling may have had a physiological effect such that the first year, 1968, the beeches may have produced a phenomenally large seed crop.

We report the results of this small study for whatever interest they may have to the reader. It is not possible, of course, to predict what may be the long-range consequences of this one-shot event in forest processes in such a climax stand.

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