# Natural Biological Control of Oak Wilt in Arkansas

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ABSTRACT

Three species of red oak and two species of white oak (*Quercus* spp.) were inoculated with a spore suspension of *Ceratocystis fagacearum* and then harvested monthly. The fungus was recovered at a very low rate after 14 months. All inoculated red oak trees wilted and died. In the red oak group, *C. fagacearum* spores apparently moved rapidly upward into branches of the crown, and the pathogen was readily isolated up to 8 months after inoculation. Lowered survival of the oak wilt fungus after 8 months is believed due to high summer temperatures, drying of the branches, and sapwood invasion by species of *Hypoxylon* (mostly *H. atropunctatum*). *C. fagacearum* seldom colonized trunk sapwood or formed mycelial mats and pressure pads. Within 2 months after inoculation with *C. fagacearum* the conidial stage of *Hypoxylon* was apparent under sloughing bark on the trunks of several red oak trees; within 4 months *Hypoxylon* had begun to produce in many trees a characteristic yellow decay with black zone lines which probably prevented subsequent colonization by *C. fagacearum*. Trunks of trees containing *C. fagacearum* pressure pads were about 50% wetter than were trees with *Hypoxylon* decay.

Few trees of the inoculated white oak group wilted, but *C. fagacearum* was recovered at low levels from branches during the entire 14-month period. *Hypoxylon* was never found colonizing white oak trees inoculated with *C. fagacearum*.

Maps associating the southern distribution of oak wilt with isotherms and land forms are presented.

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Oak wilt, caused by *Ceratocystis fagacearum* (Bretz) Hunt, has been present in 21 states for decades and has caused serious losses to shade and forest trees in the midwestern and northeastern United States. In the southern portion of its range, however, oak wilt does not spread or develop as intensively as in northern states. The range of the disease in Arkansas has been static since its discovery 22 years ago (33) and is limited to the northern tiers of counties (F. H. Tainter & M. C. Tucker, *unpublished*). In Arkansas, infections are scattered and individual wilted trees usually die with no subsequent development of infection centers (F. H. Tainter, *unpublished*).

The purpose of the research reported here was to identify factors influencing the distribution and intensity of oak wilt in the southern states. In particular, we investigated: (i) the longevity of *C. fagacearum* and development of competing fungi as related to moisture content of branch and trunk sapwood in artificially inoculated trees; and (ii) the known southern range of oak wilt as related to climate and landform. A preliminary report has been published (26).

MATERIALS AND METHODS.—Approximately 900 oaks of five species, ranging from 7.5- to 35-cm diam at breast height (DBH), were used. Half of these were inoculated with an Arkansas isolate of *C. fagacearum* in April 1971, by introducing an aqueous spore suspension into an axe wound made at the base of each tree. The other trees were left as controls. Three oak species: black (*Quercus velutina* Lam.), southern red (*Q. falcata* Michx.) and blackjack (*Q. marilandica* Muenchh.), represented the subgenus *Erythrobalanus* or red oak group, members of which are highly susceptible to oak wilt. The subgenus *Leucobalanus* or white oak, resistant to oak wilt, was represented by post oak (*Q. stellata* Wangenh.) and white oak (*Q. alba* L.).

Each month for 14 months, five inoculated and five control trees of each species were felled and cross sections 4-cm thick were cut at ca. 1.52-meter intervals from 0.46 m above ground to a top diameter of 7.5 cm. Four blocks of 20-60 g fresh weight each were chipped out of the sapwood of each disc and the moisture content (oven dry basis) of these was determined. Four more chips were plated on nutrient agar to isolate fungi. In addition, four branches of 2.5-cm diam from the crown of each felled tree were selected and moisture contents determined and isolations made. Eight to 80 moisture determinations and isolations were made per tree, depending on tree size. Decay of sapwood of trunk discs and branches by *Hypoxylon* spp. was identified on the basis of characteristic color changes.

For the second aspect of the investigation, literature on southerly distribution of oak wilt was reviewed and geographical locations of infections were related to climate and landform.

RESULTS.—*Longevity of pathogen in red oak group*.—All inoculated trees of black, southern red, and blackjack oak wilted and died. Slight leaf-curling on scattered upper branches was visible 1 month after inoculation, when the pathogen was recovered from 5 to 40% of the branches. By June small branches in the upper crown had died and positive isolations rose to 80-95%. The rate of recovery of *C. fagacearum* from branches then began decreasing, especially for black and southern red oaks, and reached zero in December to March (Fig. 1-a, b, c). Moisture contents of branches of inoculated trees dropped from ca. 70% when extensive leaf wilting began in May to ca. 20% in November. In August, when the moisture content of wilted branches was ca. 30%, a yellow decay caused largely by *Hypoxylon atropunctatum* (Schw. ex Fr.) Cke., became noticeable and the average volume of decaying wood increased slightly during the remaining 10 months of the test.

*H. atropunctatum* invaded sapwood of trunks more extensively than branches. The conidial stage of this fungus was noted on a few trees within 2 months after inoculation, but no decay was evident then. Large patches of bark sloughed off by July and stromata of *H. atropunctatum* developed in the cambial zone and produced masses of grayish or brownish powdery conidia. In September, 30 to 95% of the samples were decayed (Fig. 1), and the perithecial stage of *H. atropunctatum* was abundant (Fig. 2-a).

In at least one tree, a small zone of sapwood colonized by the oak wilt fungus produced pressure pads whereas adjacent sapwood was decayed by *H. atropunctatum* (Fig. 2-b).

*C. fagacearum* was isolated at least once from trunk sapwood of only 14 trees of the red oak group (four blackjack, eight southern red, and two black) during the 14-month study. Of these, only six were found with pressure pads and spore-bearing mycelial mats.

The pressure pads, or cushions, are specialized fungus structures which form in the center of a mat of tightly woven mycelium at the cambium. The pads are formed in pairs back to back, and as they increase in thickness, create enough pressure to raise and rupture the bark. A moist cavity is thus produced in which the mats develop and spores are produced (29). Presumably, insect vectors enter and leave through the crack in the bark.

Pressure pads and mycelial mats matured on two trees in November and December. Adults and larvae of sap-feeding beetles (Nitidulidae) were found on two of these pads. The pads, however, were not so plentiful or large as those the senior author has observed in Minnesota. The remaining four trees with pads and mats were observed in February through April but the pads were old and disintegrating. Usually only one or two sets of pads were found on a tree, but in one case seven were observed.

Survival of the oak wilt fungus was associated with high moisture content of the sapwood. Figure 1-d shows that the sapwood moisture content 46 cm above ground in six red oak trees with pressure pads was about 50% greater than in inoculated trees affected only with *Hypoxylon* decay. Whether *Hypoxylon* caused the lower moisture content in the trunk sapwood, is not known. In one blackjack oak (Fig. 1-f) the moisture content was ca. 70% where *C. fagacearum* had colonized the lower 2 m of the bole. Higher in the tree, where *Hypoxylon* was invading the bole, moisture content was only about 25%.

Approximately 90% of the trees showing yellow discoloration and decay exhibited fruiting structures of *H. atropunctatum*. In the remaining 10% *H. mediterraneum* (De Not.) Mill. was observed. Occasionally both species occurred on the same bole. Figure 1-e summarizes the incidence of fungi from all inoculated trees for the entire 14-month study. Black oak had a low percentage of *C. fagacearum* in the trunk but

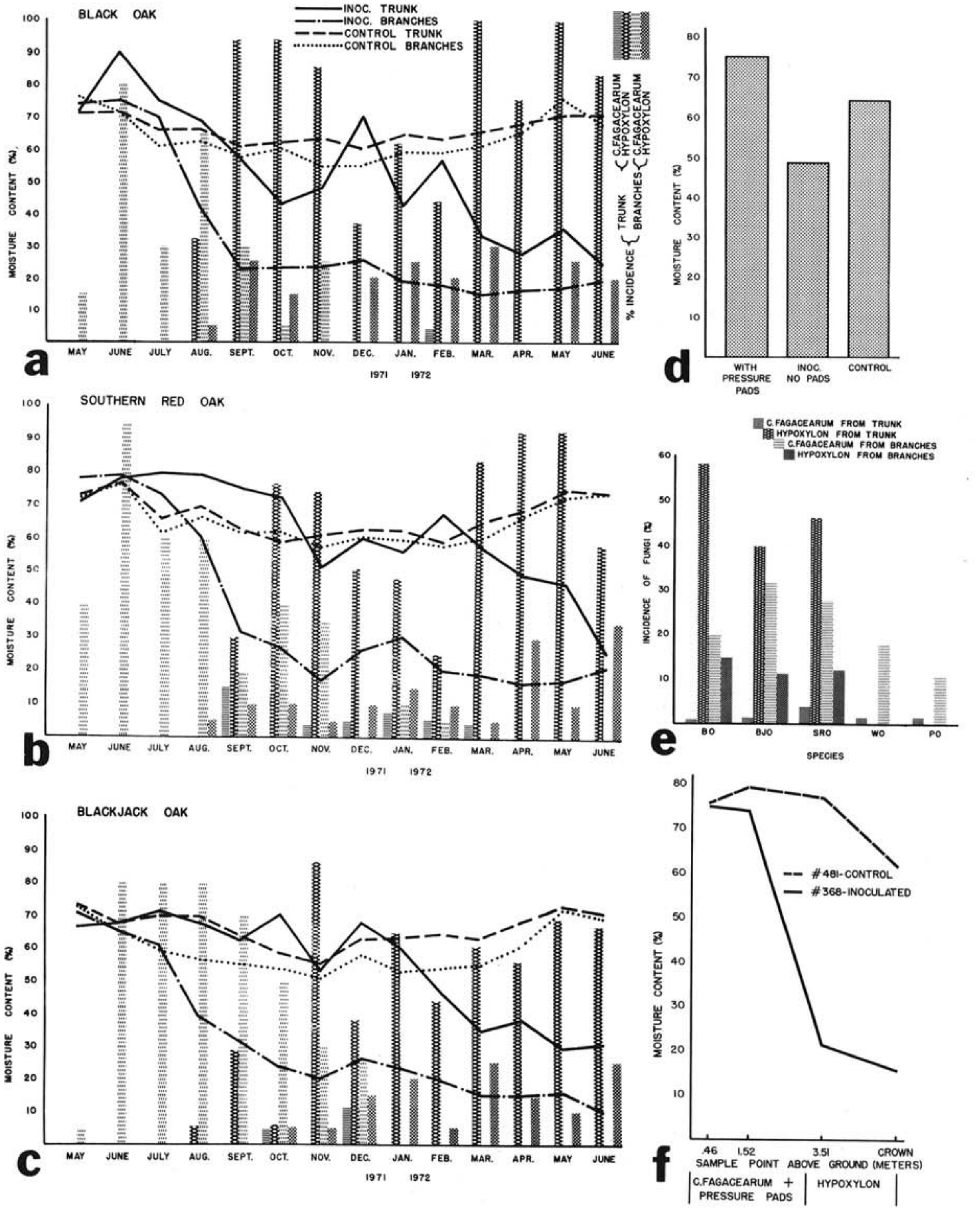



**Fig. 1. a, b, c).** Moisture contents (oven-dry basis) of red oak species inoculated with *Ceratocystis fagacearum* in April 1971, and incidence of *C. fagacearum* and *Hypoxylon* spp. in trunk sapwood and branches. **d)** Mean sapwood moisture content at 46 cm above ground of red oak trees that were inoculated with *C. fagacearum* and developed pressure pads, were inoculated but developed *Hypoxylon* decay and no pressure pads, and were uninoculated controls, six trees per group. **e)** Average percentage incidence of colonizing fungi in all inoculated trees (data from isolations and observations of 1464 trunk sapwood samples and 1400 branch samples during a 14-month period. **f)** Relationship of colonizing fungi to sapwood moisture content in trunk of a blackjack oak tree, 12 months after inoculation with *C. fagacearum*. Pressure pads were evident in the lower, wetter portion of the trunk, whereas *Hypoxylon* was present in the upper, drier portion.

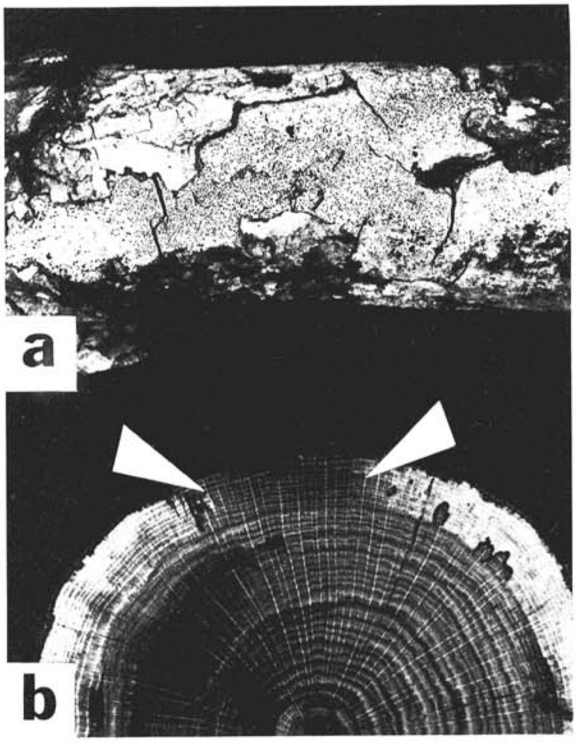



**Fig. 2. a)** Perithecial stage of *Hypoxylon atropunctatum*. **b)** Typical yellowish decay with black zone lines produced by *H. atropunctatum*. The area delimited by arrows was not decayed but was colonized by *C. fagacearum*, with a mycelial mat and pressure pads. The wood in this area was noticeably wetter than adjacent decayed sapwood.

nearly a 60% incidence of *Hypoxylon*. Blackjack oak had a 40% incidence of *Hypoxylon*. Our preliminary report (26) indicated that stems of this species had not been colonized by *Hypoxylon*. Only a few cases of fruiting had been observed when that report was written. Later examination of wood samples showed that decay was indeed present, even in August collections. There was a noticeable lag in production of the perithecial stage on this host.

*Longevity of pathogen in white oak group.*—Only a few small trees of post and white oak died. If wilting was evident, it usually was restricted to only one or two branches. Surprisingly, the oak wilt fungus was isolated from branches of white oak almost every month of the study, even from trees which showed no wilting (Fig. 3-a, b). *C. fagacearum* was recovered from branches of post oak until January. The pathogen was infrequently isolated from trunk sapwood of both white oak species. In contrast to Van Arsdel's findings (32) we found no evidence of *H. atropunctatum* in white oaks.

*Range of oak wilt related to climate and landform.*—Figure 4-a illustrates the distribution of oak wilt in the southern states as determined from a variety of sources [1, 10, 22, 34; also in the 1969 and 1970 South Carolina oak wilt survey and control reports (J. E. Graham & W. Witcher, *unpublished*)].

We initially interpreted the southerly limit of oak wilt to be due to high summer temperatures. The highest temperatures in the southern states usually occur during July (31). The 27 C isotherm for average daily temperature in July (Fig. 4-b) reflects the distribution of oak wilt in the Mississippi river valley in southeast Missouri, northeast Arkansas, and western Kentucky. This isotherm swings southward into northern Alabama and Georgia, where oak wilt is unknown. The infections in northern South Carolina are just south of the 27 C line. An examination of this map, moreover, does not explain why there are no infections in eastern Virginia and central North Carolina or why there are not more infections in central Tennessee. Apparently *C. fagacearum* has the potential for survival far south of its present general occurrence, since 15 positive oak wilted trees were found in Dallas, Texas, several years (14) after the initial report (9).

We also compared the general southerly limit of oak wilt with major upland features (Fig. 4-c). The eastern and southwestern limits of the range of oak wilt are also the boundaries of mountainous regions, but in the south-central region in central Tennessee and northern Alabama and Georgia the expected relationship does not occur.

DISCUSSION.—Reports in the literature indicate that oak wilt does not rapidly spread or intensify in the southern part of its range. In Kentucky and Tennessee where no oak wilt control was attempted, no increase in rate of spread occurred during a five-year period (16). In similar no-control areas in Pennsylvania, Maryland, and West Virginia, incidence of the disease has been higher and rate of spread has increased (17). In Oklahoma, where no control is attempted, only occasional cases of oak wilt are observed (R. V. Sturgeon, *personal communication* 1972).

Lack of intensification of oak wilt in the south is partially attributable to poor survival of the pathogen, both in growth and spore production.

Relatively dry conditions are detrimental to the fungus. Spilker & Young (24) noted that as the moisture content of stored wooden blocks decreased, viability of the fungus in them decreased.

High temperature is detrimental to the oak wilt fungus. The results reported by Houston et al. (15) were in agreement with those of earlier workers who found that growth of the fungus was maximum at 24 C and decreased abruptly above 32 C. These temperatures coincided with those which favored or restricted growth of the fungus in seedlings in the greenhouse. In larger, exposed trees, internal temperature became higher than ambient air temperature, especially in northern pin oaks. Higher temperatures were reached for longer periods of time in wilted than in healthy trees. The fungus was isolated from the shady but not from the sunny side of infected northern pin oak logs after periods of exposure to direct sunlight (15). Bretz & Morison (4) felt that high summer temperature was responsible for low recovery of the oak wilt fungus from twigs collected in Arkansas in 1952. They found that survival of the fungus was brief in small diam material stored more than 6 days at temperatures above 20-25 C. They also noted more secondary organisms in twigs stored at high temperature. Spilker & Young (24) observed that the oak wilt fungus lived 3 to 5 weeks in small wooden blocks stored at 25-27.5 C.

Although there is no conclusive evidence that any insect is the direct vector of *C. fagacearum* (20), both oak bark beetles (*Pseudopityophthorus* spp.) (21) and sap-feeding beetles (*Nitidulidae*) (29) have been implicated as vectors. Since the latter are attracted to the spore-bearing mats, any climatic factor which suppresses the formation of these mats could effect a reduction in disease (13). Boyce (3) obtained a positive correlation between precipitation and frequency of mat formation on wilted oaks in North Carolina. In 1955, when the total rainfall in August-December was 22.5 cm, only 9% of the stems had mats the following January-April. In comparison, in 1958 the total rainfall during the same period was 40 cm and 79% of the stems had mats the following January-April.

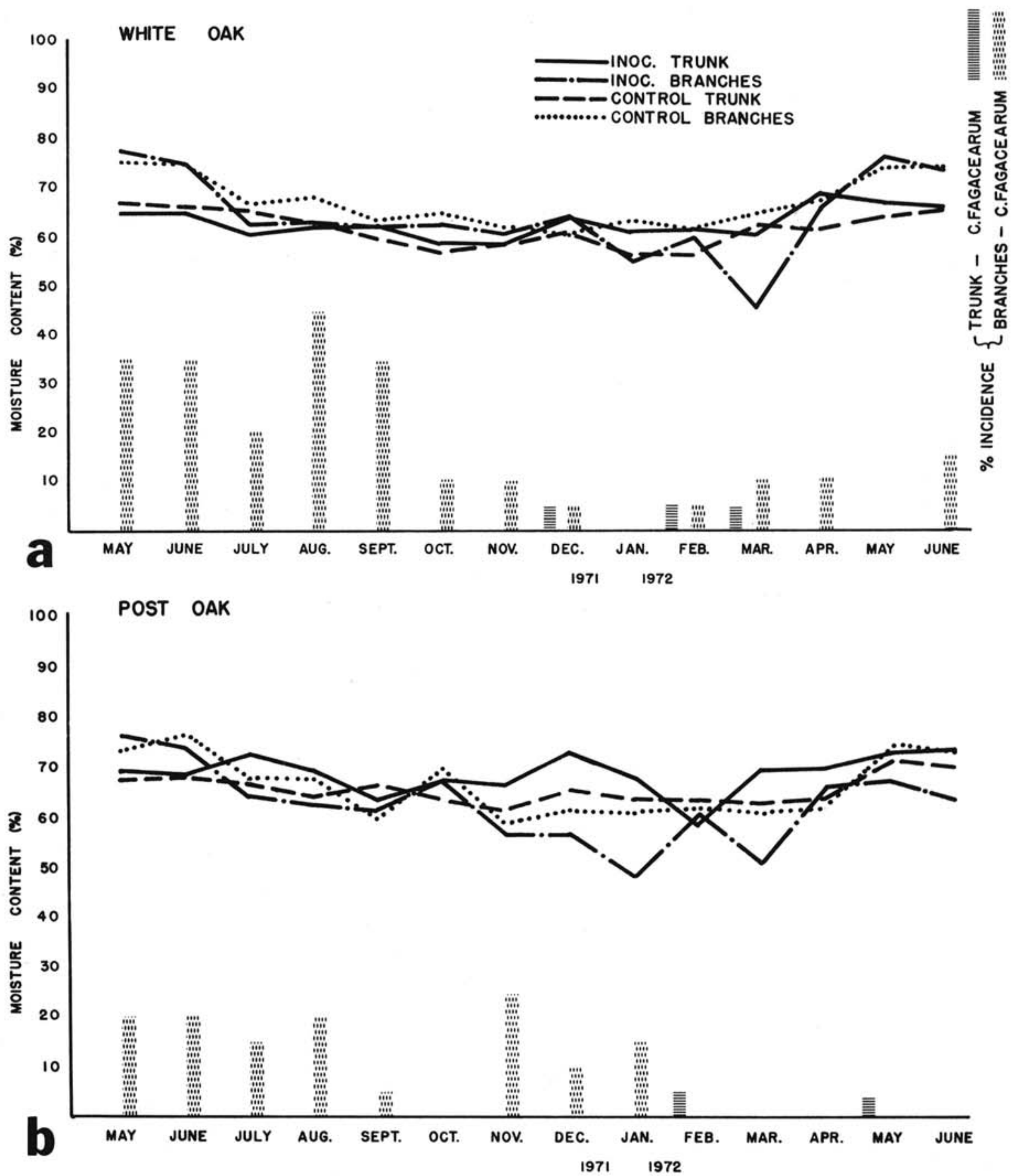
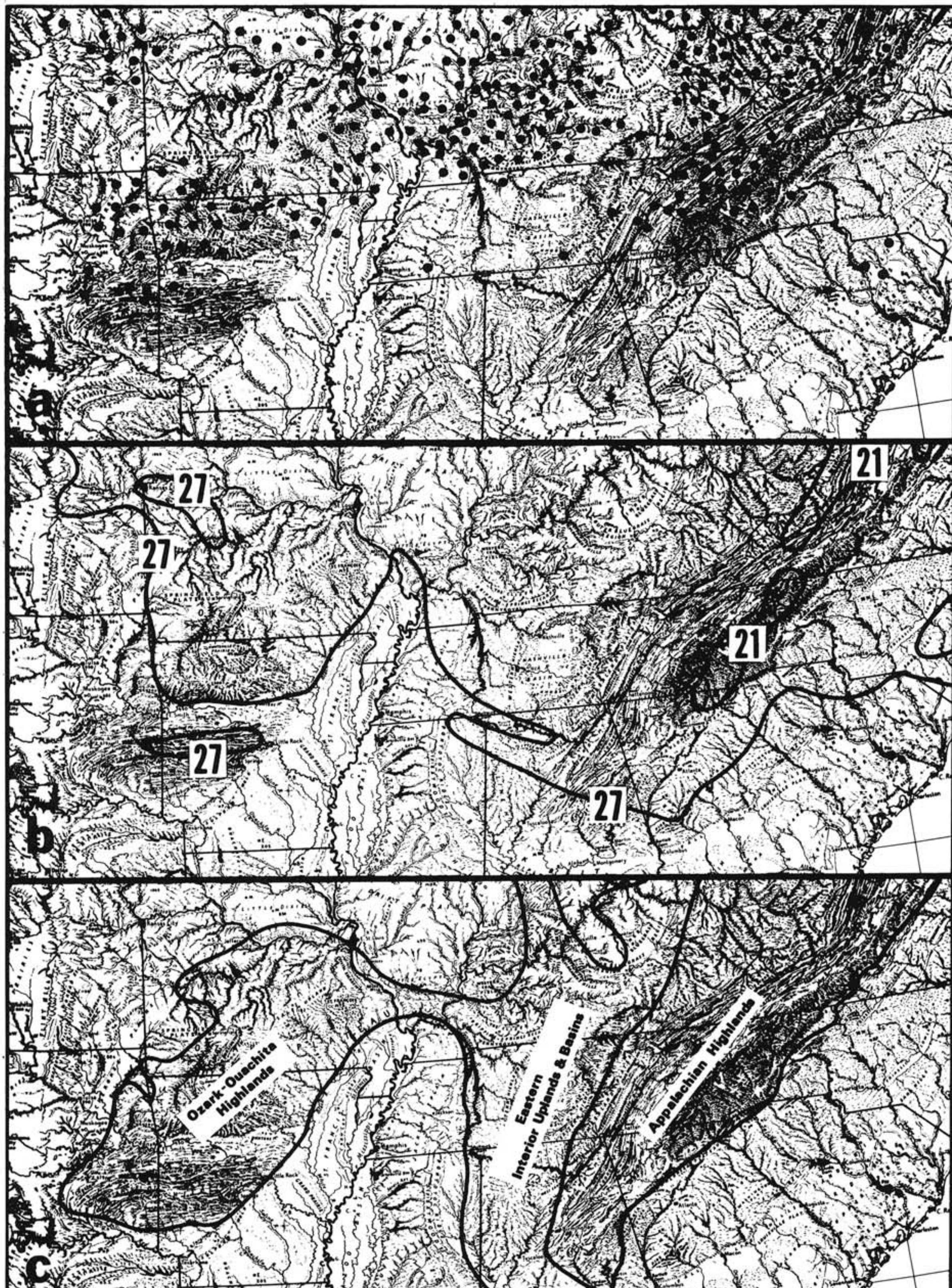



**Fig. 3.** Moisture contents (oven-dry basis) of white oak and post oak inoculated with *Ceratocystis fagacearum* in April 1971, and incidence of *C. fagacearum* and *Hypoxylon* in trunk sapwood and branches.


a
27
27
21
21
27
27
b
Ozark-Ouachita Highlands
Eastern Interior Uplands & Basins
Appalachian Highlands
c

In the southern Appalachians, summer cutting of wilting trees resulted in fall fruiting only, whereas more than half of wilting trees left standing produced mats the following spring (2). Presumably the moisture content of the wilting trees left standing was higher and allowed mats to develop later. Campbell & French (7) found that the moisture content of the sapwood of northern pin oak remained high when the tree wilted and bore mats in the same season and concluded that the pathogen required a high sapwood moisture content. Girdling, especially deep girdling in June-July causes the sapwood to dry out quickly, limits the production of mats, and shortens the life of the fungus in wilted oaks (12, 19, 30). Campbell & French (6) observed that the period of mat formation was of short duration on trees that began to produce mats during hot weather. They hypothesized that high temperature may reduce the growth rate of the fungus or increase the rate of desiccation, so that the sapwood becomes too dry for development of the mats. In Missouri, pressure pads seldom develop sufficiently to crack the bark of wilted trees (5). This is true in Arkansas as well. In oak logs stored at different temperatures, spore-bearing mats formed at 6.1 to 20.5 C, but not at 32.2 C (11). Optimal temperatures for perithecium formation and ascospore extrusion were 18-24 C (25).

The production of mycelial mats on red oaks in Pennsylvania (8) by isolates of *C. fagacearum* from Arkansas, Missouri, and Ohio indicates that factors other than genetic differences in the pathogen account for the rare occurrence of mats in the latter states.

The presence of competing fungi such as *H. atropunctatum*, may be an important limiting factor. Miller (18) reported that this species is especially common on species of *Quercus* in the southern states following drought or injury. Thompson (27) described the decay produced by *H. atropunctatum* in Georgia and found the optimum temperature for growth to be about 30 C. He later described it as a sapwood decayer, occurring naturally on suppressed trees, or on those suffering from drought (28). The stromata may appear within 4 months following inoculation with *H. atropunctatum* and they may form almost any time of the year (27). Shigo (23) isolated *H. atropunctatum* with great frequency from branches on healthy trees killed as a result of ice breakage, from branches of nongirdled, oak-wilted trees, and on isolation plates, it overgrew *C. fagacearum*. He isolated *H. punctulatum* (Berk. & Rav.) Cke. from girdled oak wilt trees and observed a rapid rot of sapwood. *H. mediterraneum* was isolated frequently from branches of all trees (23). We have never found *H. punctulatum* on wilted oaks in Arkansas.

True et al. (29) have shown that *H. punctulatum*, while not exerting any repellent effect on *C. fagacearum*, quickly exhausted the carbon and nitrogen sources required by *C. fagacearum*, which provided it a marked nutritional advantage over the oak wilt fungus.

Van Arsdel (32) reported that in Texas *H. atropunctatum* causes the death of many oak trees injured by various agents. It frequently occurs on live oaks (*Q. virginiana* Mill.) and post oaks, usually as a secondary pathogen on trees infected with Cephalosporium wilt or suffering from root damage.

Although high temperature and desiccation may directly affect growth and survival of the oak wilt fungus, we believe that the primary determinant of survival of *C. fagacearum* in the south, especially in Arkansas, is the rapid invasion of wilted trees by species of *Hypoxylon*. Growth of *H. atropunctatum* is favored by the same high temperatures which inhibit growth of the oak wilt fungus. It causes rapid decay and is able to colonize and survive in wilted trees much more successfully than is *C. fagacearum*. Research is continuing to elucidate this competitive relationship more fully.

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**Fig. 4. a)** Distribution of oak wilt in the southern states, compiled from sources given in the text. Each dot indicates one county in which presence of oak wilt has been confirmed. **b)** 30-year average July isotherms (data from reference 30). **c)** Major mountainous or upland regions in the southern states. The landform maps are presented with the permission of Mrs. Erwin Raisz.

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