PATTERNS OF OAK WILT MORTALITY IN MIDWESTERN OAK FORESTS

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ABSTRACT

Prediction of long term community interactions with a particular disturbance first requires quantification of both the effects of an individual episode of perturbation and temporal aspects of the disturbance regime. An analysis of patterns of oak wilt mortality was undertaken with these ends in mind. Data sets from northern Illinois and southern Wisconsin were used. Mortality, especially that resulting from root graft transmission, was highest in sites dominated by the red oak group, in young stands, on poor sites, and on sandy soils. Local root graft spread is predicted by regression equations in which the probability of transmission from one tree to another is directly proportional to the combined size of the two trees and inversely proportional to the distance between them. Overland spread rates are presented, and the tendency of this vector mediated infection to act locally is hypothesized. In the Illinois forest, this resulted in recognizable waves of disease movement through the area; with a periodicity of seven years. The rates and relationships garnered from data analyses will be incorporated into an empirically based stochastic simulation model.

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INTRODUCTION

Margalef (1968) has stated that "an ecosystem is a historical construction, so complex that any actual state has a negligible a priori probability." Although this statement is undoubtedly true, ecologists have traditionally searched for patterns in these states over time. Traditionally, the focus has been on forest communities, and has recognized both succession and disturbance as factors influencing changes in forests. The concept of succession was once envisioned as primarily unidirectional, resulting in a climatically determined community controlled steady state (Clements 1936, Braun 1950, Daubenmire 1966, Odum 1969). As more exceptions to the determinism implied by this model have accrued, the original notions of succession have been modified and challenged (Drury and Nisbet 1973, Pickett 1976, Connell and Slatyer 1977). Recently, the term "species replacement" has been used, reflecting the search for causes of succession focusing at the population and lower levels (Drury and Nisbet 1973, Pickett 1976).

A disturbance, or perturbation, may be defined as an episodic phenomenon resulting in unusually high mortality to some segment of a plant community. The dominant paradigm in ecology that relates disturbance to succession is that perturbations reset the successional clock, allow persistence of seral types in evolutionary time, and specify the state of the system at times subsequent to the perturbation (Loucks 1970, Heinselman 1973, Denslow 1978). When specific cases are observed, individual differences in the effects of a particular perturbation are evident; these depend on the type of disturbance, the state of the system perturbed, the frequency regime of the disturbance, and possibly the interactions of several types of disturbances. Examples of these specific cases include: the different sizes of trees affected by windthrow and fire respectively (Spurr 1956); the species specific nature of diseases; the effect of fire (Henry and Swan 1974) and windthrow (Stearns 1951) in providing opportunities for specific species; the contrasting effects of disturbances of various sizes and intensities (Oliver and Stephens 1977, Swan 1970, Heinselman 1973); and the requirements of certain species such as jack pine on fire frequencies of a specified length (Ahlgren 1960). Among possible interactions are those of windthrow and fire, and spruce budworm and fire (Blais 1968).

Important disturbances in midwestern forest communities include fire, windthrow, grazing, and insect and disease caused mortality. Disease caused perturbations have several attributes that make then unique and interesting. They are usually fairly species specific, removing one species or group selectively, and thus will have contrasting effects on stands with differing compositions. Therefore they may be unusually effective at changing the species composition (e.g. chestnut blight). At the same time, diseases cause less significant changes in soil properties than either fire or windthrow (Oliver and Stephens 1977). Finally, many diseases leave particular spatial patterning in their wake. The importance of the size of light gaps on regeneration is frequently cited (Bray 1956, Fox 1977, Oliver and Stephens 1977, Richards and Williamson 1975).

To analyze the effect of a disturbance on a community, one must:

1) describe the effects and patterns of mortality resulting from an episode of disturbance.
2) identify the temporal characteristics of the disturbance regime.
3) identify population reactions to the disturbance "opportunity" that may change the state of the community.

This paper will approach the first two of these points, through a study of patterns of mortality resulting from oak wilt.

Oak Wilt

The disturbance considered here is caused by the oak wilt fungus, *Ceratocystis fagacearum* (Bretz) Hunt, which has been important in the Midwest and the East for decades. *C. fagacearum* causes a systemic disease, resulting in rapid wilting of trees of the red oak group (Erythrobalanus) and more gradual damage to white oaks (Leucobalanus). *Ceratocystis* stimulates tylose formation, which is currently thought to be the chief cause of wilting symptoms (Dimond 1970). The disease is very efficient in local spread. Conidia in the vascular system are transmitted by intraspecific root grafts (usually between trees in the red oak group) from a dead or dying tree to a nearby healthy one by the transpiration stream (Kuntz and Riker 1950, Beckman and Kuntz 1951). Conidia and ascospores are produced on

fruiting mats that form under proper conditions of temperature and moisture between the bark and the wood in recently killed oaks (Curl 1955, Boyce 1957). Various vectors, notably beetles of the family Nitidulidae, carry the spores, which have been shown to cause mortality, to healthy trees at longer distances from the source tree (Bretz 1951, Norris 1953, Dorsey et al 1953). Oak bark beetles are important vectors in some areas (Rexrode and Jones 1970). A recent review by Nair and Kuntz (1975) provides additional morphological, etiological, and physiological information.

The vector mediated spread, also termed overland spread, is notably inefficient when compared to root graft transmission, or local spread. The results, especially in the Midwest, are characteristic foci (or pockets or patches) of dead oaks, with recently killed or dying oaks on their expanding edges. Despite the slow rate of new pocket formation (Anderson and Anderson, 1958a) and the slow rate of pocket expansion (Anderson and Anderson 1958b, 1963), the efficacy of local spread has made oak wilt one of the major economic problems, as well as one of the notable ecological disturbances, of oak forests in the U. S.

METHODS

Data Sets

A 17-year record of oak wilt mortality in a northern Illinois forest was collected by E. B. Himelick and H. W. Fox of the University of Illinois between 1955 and 1971 (Himelick and Fox 1961). The area, Sinnissippi Forest, is located on the Rock River in northwest Illinois about 40 miles south of the Wisconsin border. There are 1648 acres of oak forest on sandy loam, sand, and silt loam soils. The area has been intensively managed since 1938, with selection cuts proceeding on a 10-year rotation. Himelick and Fox's oak wilt program included areas with various oak wilt control regimes, and check areas that were untreated. Data were gathered by these investigators on trees affected by oak wilt, using air and ground surveys, up to 6 times annually. Most of the information in this paper is the result of analyses performed on this data set by this author, and will be referred to as Sinnissippi data.

Data from four southern Wisconsin sites, two in Dane County and two in Sauk County, were gathered by J. E. Kuntz and associates and analyzed by this author. Complete maps of the areas were made, and oak wilt progress monitored annually for periods of up to six years.

Data Analyses

This paper treats data analyses of two types: phenomenological and fundamental (Wilson 1969); the former being descriptive and using correlations, while the latter seeks to estimate rates and quantify patterns. The fundamental data were shaped by the requirements of an empirically based simulation model built to predict oak wilt mortality. The model itself will not be treated here.

The phenomenological data taken from Sinnissippi Forest correlates total mortality and mortality by root graft transmission and vector spread to such factors as location in the forest, control regime in the pocket, species, composition, site type, soil type and tree size. Chi square tests were used to detect differences between observed and expected numbers of dead trees among treatments. Degrees of freedom in these tests were the number specified by each particular table, although a piece of raw data might be included in several tables. The expected number of dead trees is based on a single inventory made in Sinnissippi in 1972, and thus assumes that cutting regimes and other factors did not markedly change the composition or size class distributions over the course of the study. This is reasonable given the constant cutting cycle, but only for fairly large areas of the forest. Other descriptive data include temporal and spatial patterns of new pocket formation.

The rate estimates are at the scale of individual trees. Predictive equations for root graft transmission probabilities, as a function of summed diameter and intertree distance for the two trees, are summarized from previous work (Menges and Kuntz 1978). Arc sine transformations were performed on all data to homogenize variance for tests of significance (Sokal and Rohlf 1969). The equations are derived from southern Wisconsin data and include time independent and time specific (i.e. spread in a certain amount of years) probabilities for several sites. Similar data is available from Sinnissippi and is compared, as is the effect of site on these regressions.

The dynamics of overland spread are explored in both temporal and spatial senses. Characteristic rates of overland spread have been calculated from Sinnissippi data, as well as the variation in these rates over time and the spatial patterning of this long distance spread within the forest.

RESULTS

Mortality

The oak wilt control program in Sinnissippi had profound effects. The practical implications of control on a stand basis are not a subject of this paper (see Himelick and Fox 1961). However, it is important to note the effects of control at the pocket level. The effects of control in a pocket reduced both total mortality and root graft transmission mortality significantly ($p \leq .01$, 1df). Since control in a pocket cannot proceed until there has been an overland infection, it is not reasonable to test the effect of control on vector spread on a pocket basis. Himelick and Fox (1961) showed that control measures at the stand level had little effect on the number of new infection centers initiated in Sinnissippi. In the following analyses, efforts have been made to compare areas receiving similar control regimes.

It is well known that trees of the red oak group are more susceptible to oak wilt than trees of the white oak group, and that members of the former are, at least in the Midwest, more commonly root grafted (Kuntz and Riker, 1956, Beckman and Kuntz 1951). Chi square results on Sinnissippi data confirmed this; trees of the red oak group, followed by bur oaks, and finally white oaks, showed decreasing amounts of total mortality, root graft mortality, and vector mortality (differences significant at $p \leq .01$, 2df). The latter fact is not entirely expected, but appears sound due to the special efforts of Himelick and Fox to identify the causes of the sometimes various symptoms seen in white oaks, and to the frequency of surveys, unusual in oak wilt studies, that allowed better distinction between sources of the fungus. The moderate susceptibility of bur oak is consistent with recent observations of local pocket formation in this species in the Midwest (A. Prey-personal communication).

The effects of composition, age, site type, and soil on total mortality, on root graft transmission, and on vector spread in Sinnissippi are shown in Table 1. As might be expected, stands dominated by trees of the red oak group showed significantly higher mortalities than mixed stands, which in turn had higher death rates than stands dominated by white oak. Root graft transmission differences were the most significant. Young stands less than 30 years old showed higher local and total mortality, but no significant difference in

TABLE 1 - Levels of Significance for Chi Square Tests Comparing Different Compositions, Ages of Stands, Site Types, and Soil Types, on Oak Wilt Mortality in Sinnissippi Forest, Illinois.

		Levels of Significance, p≤value shown, for mortality from:		
Factor	Levels	All O.W. Mort.	Root Graft	Vector
Composition	Red oak group (R.O.G.)* vs. Mixed vs. White oak dominated	.01	.01	.01
	R.O.G.* vs. Mixed	.05	.01	.01
	Mixed* vs. White	.01	.01	.01
Age of Stand	Poles and Repro.* vs. Stands older than 30 years	.01	.01	NS
Site Type	White Oak Dominated			
	Poor vs. Medium	NS	NS	NS
	R.O.G. Dominated			
	Poor* vs. Good	NS	.05	NS
	Mixed Oaks			
	Poor* vs. Medium vs. Good	.01	.01	.01
	All Compositions	.01	.01	.01
	Poor* vs. Medium vs. Good			
Soils	Sands* vs. Sandy Loams vs. Silt Loams and Loams	.01	.01	.01

* Highest mortality in this factor.
NS = Not significant

vector transmission compared to older stands. Site also seemed to play an important role in oak wilt mortality. Sites typed as poor showed a significantly higher mortality, especially by root graft spread, than better sites. This may partially reflect a greater abundance of trees of the red oak group on such sites. On sites dominated by trees of the red oak group, there are less, but still significant, differences. Anderson and Skilling (1955) show that there is higher mortality in scrub oak types, while Cones and True (1967) found more wilt on poor sites, in agreement with the results of this study. Since differences in root graft transmission are the most significant, it is possible that differences in overland spread are due to local differences in inoculum due to higher root graft transmission mortality, and not due to site itself.

Soil types were also compared by Chi square tests in Table 1. Trees on sands had more mortality of all types than those on sandy loams or silt loams and loams. Sandy loams and loams showed a similar level of mortality. In the soil comparisons, the expected values were made proportional to the area occupied by these soils rather than depending on the timber inventory, since the cutting regimes were dissimilar. Control regimes also differed between soil types; loams were more often check areas, perhaps inflating mortality on these soils relative to others. Results agree with True and Gillespie (1961, Gillespie and True 1959), who found that shallow soils favored local spread of the disease in West Virginia, with Craighead and Nelson (1960) who found more mortality on sandstones, and with observations (J. E. Kuntz, personal communication) that sandy areas in Wisconsin show most extensive damage. Anderson and Anderson (1959) also found a slower rate of patch expansion on heavier soils in Central Wisconsin.

Pocket Dynamics

A pocket at Sinnissippi was defined as including wilting or dead trees within approximately 50 feet of each other. Expansion of a pocket presumably is accomplished mainly through root graft transmission, although vector spread may play a role.

Is a wave of new pocket formation detectable across the forests? Areas of between 80 and 400 contiguous acres with greater than 1.5 new pockets per 40 acres in a given year were tallied. The number of new pockets in the following year in this area decreased 0.895/40 acres, but the number of new pockets

in the subsequent year in neighboring areas increased in 23 of 30 instances, an average of 0.537 pockets/40 acres. Both values are significantly different from zero (t tests, $p < .01$).

The overall annual new pocket formation in Sinnissippi Forest varied between 20 and 69 between 1955 and 1971 (0.000714/acre/yr to 0.00246/acre/yr) with a mean of 41.9 and a standard deviation of 12.6. The values for check areas were somewhat higher.

Are there any patterns of new pocket formation over time? Results of run tests ("above and below the median" and "up and down" (Sokal and Rohlf 1969)) on different sized blocks of the forest did not detect significant patterns, but these non-parametric tests are not particularly sensitive to quantitative data or to sudden peaks. The three highest peaks in new pocket initiation were chosen objectively from runs in various sized blocks on the basis of absolute height and difference from neighboring years. The high proportion of periodicities in the 6-7 year range (38%) was most pronounced in blocks of between 120 and 400 acres. This is evidently the return time for the waves of infection over the forest, and will be discussed in light of overland infection periodicities, in a later section.

Root Graft Transmission

Seven models for predicting root graft transmission probability between trees of the red oak group were considered by Menges and Kuntz (1978) for southern Wisconsin data. These included various combinations of combined dbh and intertree distance as independent variables or predictors, and probability of root graft transmission under those circumstances as the dependent variable.

Best fits were to the following models:

$$P = m(CDBH/D) + b$$
$$p = m(CDBH-D) + b$$

where P is the probability of root graft transmission
CDBH is the combined dbh in inches
D is the intertree distance in feet
m is the slope of the linear regression
b is the intercept of the linear regression

Models that predicted spread independent of time included:

(1) $p = 12.7\ (CDBH/D) + 2.64$ $r = .797^{**}$ (Dane County)
(2) $p = 1.20\ (CDBH\text{-}D) + 14.0$ $r = .763^{**}$ (Dane County)
(3) $p = 20.4\ (CDBH/D) - 3.59$ $r = .758^{**}$ (Sauk County)
(4) $p = 1.89\ (CDBH\text{-}D) + 18.8$ $r = .786^{**}$ (Sauk County)

Equations for spread in a specific number of years (time specific) at one of the sites in Sauk County were:

(5) $p = 1.37\ (CDBH\text{-}D) + 11.3$ $r = .819^{**}$ (same year)
(6) $p = .896\ (CDBH\text{-}D) + 9.68$ $r = .733^{*}$ (one year)
(7) $p = 1.02\ (CDBH\text{-}D) + 10.9$ $r = .906^{**}$ (2 years)
(8) $p = 1.23\ (CDBH\text{-}D) + 6.94$ $r = .884^{**}$ (3 years)

In general, equations using the same model for time specific spread at a particular site did not show significant differences in regression parameters (m and b) between different number of years (all comparisons of regression parameters at $p < .05$). Apparently, at least with regard to the effects of distance and size on transmission probability, there is little fundamental difference between rapid and slow root graft transmission between two trees.

When results of the same model from two sites are compared, significantly different intercepts imply that the overall level of infection is different. If slopes differ significantly, this implies that distance and diameter are interacting differently with transmission probability between sites. In Wisconsin data, the former was often found when comparing different sites for time specific relations, while slopes differed in time independent data (Menges and Kuntz 1978). However, the similarity of models giving best fits does indicate that the overall relationships, and possibly mechanisms, are similar in the sites considered.

Similar data for Sinnissippi (in lieu of mapped data, expected frequencies of each combined diameter and distance class were calculated from 1972 inventory figures for density, composition, and size) shows best fits to the 'CDBH/D' model. Models weighing CDBH more heavily performed better at Sinnissippi, perhaps reflecting the inclusion of a greater range of tree sizes than Wisconsin data. Regressions using data from check (non-control) areas showed higher slopes, and are hence more sensitive to changes in diameter and distance, than control areas where the information was obscured due to removal and poisoning of oaks around oak wilt killed trees. Control measures also

TABLE 2 - Oak Wilt Mortality by Vector Spread in Selected Blocks of Sinnissippi Forest, by Year

Block	Acres*	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
ALL	1648	40	57	40	62	59	41	29	44	51	37	75	89	66	63	44	49
126	154	4	5	2	5	10	3	2	2	13	8	17	14	6	16	7	7
35	56	4	0	5	3	1	0	5	3	2	1	3	5	1	2	1	5
100	129	4	2	3	2	0	1	3	2	5	1	1	1	14	7	7	3
A3	303	11	6	8	8	5	1	8	6	8	5	6	9	16	9	10	11
81	157	1	3	0	4	10	2	0	3	2	0	3	9	3	4	5	0
85	146	4	5	5	6	10	7	0	3	2	1	4	10	8	2	0	5
115	147	3	2	2	5	3	4	3	2	3	3	2	3	4	3	1	3
A21	384	9	9	8	11	9	13	6	7	13	11	11	20	13	22	11	14
A22	301	10	15	16	22	11	8	9	13	14	9	29	22	16	11	10	13

* Approximate acreage on oak types
Circles designate peaks. See text.

TABLE 3 - Periodicities in Vector Spread, Sinnissippi Forest, Blocks of 120-400 Acres

Number of Years Between Peaks	Frequency- (Highest Peaks)	Frequency- (All Peaks)
2	3	7
3	1	7
4	1	7
5	1	5
6	1	3
7	6	8
8	0	3
9	3	6
10	0	1
11	0	0
12	1	2
13	0	

lowered the intercept, or the overall level of transmission, significantly. Comparison of the effects of site showed that better sites had significantly lower slopes and higher intercepts. Size and distance may be less important factors here. However, different sites had different ranges of tree sizes, and this will affect the regression parameters.

Knowing that the oak wilt fungus moves gradually through root grafts (Yount 1955, Skelly and Wood 1974), one would expect that root graft spread between smaller trees and over longer distnaces would not only be less likely, but would take a longer time. However, time to spread in Sinnissippi was not predicted by either CDBH or D individually, or by a multiple linear regression of these factors. This lack of a relationship was also reflected in the previously cited absence of differences in the time specific regressions predicting probability of root graft transmission.

Vector Transmission

The amounts of vector induced oak wilt mortality are summarized in Table 2. Overall, the variability in overland spread for the whole of Sinnissippi is fairly low relative to the larger variation in smaller areas.

Run tests (Sokal and Rohlf 1969) were used with the vector data on blocks of various sizes, and, as with the analysis of patch patterns, did not give significant results. Peaks were chosen objectively in a manner identical to that of the pockets, (Table 2) and the results (Table 3) indicate a preponderance of seven-year periodicities at the scale of 120-400 acres. Therefore, the periodicity in new pocket formation seems to be mainly a function of vector spread.

If population dynamics of the vector itself were responsible for peaks in overland transmission, or if the patterns could be related to weather, one would expect the whole forest to show a distinct pattern. This is not the case, although 1967 is a peak year for many parts of Sinnissippi. The fact that the peaks are abrupt may indicate the highly variable nature of the overland spread, which is influenced heavily by local weather (Curl 1955).

Curl (1955) has shown that trees dying in a given year will most likely provide inoculum for trees that will die from

vector spread the following year (in trees of the red oak group). One would expect that the number of trees dying in a given year would be a good predictor of overland mortality in that area in the next year. Regressions on data from blocks ranging in size from 40 acres to the entire forest did not show this relationship, however.

Anecdotal accounts indicate that oak wilt spread over large distances is rare. Often one woodlot shows extensive damage with many pockets, while another is essentially free of the disease. If composition and site of the two woods are similar, this observation would further support the contention that overland spread primarily initiates foci near old pockets, and that occasional longer distance spreads are highly stochastic.

There are few studies of nitidulid behavior (Morris et al 1955), but one can approach the problem statistically. In Sinnissippi, where oak wilt has been established for quite some time, is most of the inoculum coming from within the stand or is there an "edge effect" commonly seen in crop diseases dispersed over long distances? A comparison was made of vector mortality in the interior of the forest with areas facing the Rock River, facing open fields, and facing areas of mixed fields and woods outside of the Sinnissippi boundaries. There was no significant difference, using t-tests for 2 independent samples, between compartments partly on the borders of the forest and those in the interior. Apparently, the amounts of inoculum in the forest over the 17 years has been evenly distributed.

The direction that a compartment on the border of Sinnissippi faced (i.e. river vs. fields vs. mixed woods and fields) did not affect its rate of vector mortality.

How local is the pattern of overland spread within the forest from year to year? A map analysis was undertaken on Sinnissippi data. Minimum distance, in classes, was measured from each tree of the red oak group dying of overland spread to the nearest oak wilt killed tree dying the previous year. Most inoculum takes a year, from death of the donor tree, to cause death of the recipient (Curl 1955). Linear regression provided the distribution equation for nearest neighbors of the previous year:

$$p = (0.628 \text{ X LOG X}) - 0.980$$

$$r = .999^{***}$$

where p is the proportion of trees found up to that distance,
d is the distance in feet.

Although the fit is very good, there is no guarantee that such a fit is anything more than a statistic associated with random nearest neighbors. However, it can be shown that these distances are closer than expected (Chi square test, $p < .05$, 1 df) based on considerations of plotless sampling theory (Menges 1978, Cottam and Curtis 1956). The importance of vector transmission in fairly local spread has been mentioned in the literature (Boyce 1957, Jones and Bretz 1958).

Other factors that may be associated with overland mortality include cutting and increased tree size (Craighead and Nelson 1960, Brinkman 1952). Selective cutting in a compartment at Sinnissippi did not increase the overland mortality in the year of cutting or in the following two years. Presumably, cutting took place after the season of greatest vector activity. The size of trees infected by overland spread was compared to the size, by species, of trees in the 1972 inventory. Trees of the red oak group killed by oak wilt were significantly larger (average 3 inches dbh more) than the overall population ($p < .01$, t test), while white oaks and bur oaks showed no significant differences.

DISCUSSION AND CONCLUSIONS

Although descriptive statistics cannot demonstrate causality, the variety of manipulations outlined in this paper can provide a picture of how oak wilt works. Local spread occurs in a probabilistic manner, but this can be modelled. The model that includes tree size and intertree distance will parameterize differently for each stand, so that the constants involved can reflect significant factors such as soil and age. Vector transmission levels are highly variable, but their spatial pattern tends to be more concentrated in local areas.

Much of the data included here was gathered in part for inclusion in a simulation model. The model is stochastic in nature, which reflects the disease dynamics. Given the makeup of a stand and choice of parameters reflecting edaphic or climatic conditions, model simulations can provide predictions on the range of probable results. Manipulation of model parameters can provide clues to the boundary conditions necessary for survival of the disease. How much vector spread is required to sustain an epidemic? What is the density of susceptible oaks that limits damage below a certain level?

A model parameterized for the Midwest in the 1950's and 1960's can answer further questions when compared to data of other regions or times. For example, is the small average patch size in the eastern United States (Staley and True 1952, Gillespie and True 1955) a reflection merely of composition, or of some difference relating to less frequent root grafting, given the same combined dbh and distance? Could oak wilt have survived in the savanna communities that predated fire suppression in large parts of Wisconsin (Cottam 1949, Curtis 1959)?

I have not considered the third part of the early outline on analysis of the effects of disturbance on a community. The question to be asked is, "How do populations of oaks and other species react to the opportunity caused by oak wilt?" The answers so far appear incomplete (but see Auclair 1975). However, in approaching them, one can, given more knowledge concerning the exact nature of the opportunity, make a connection between disturbance effects on a plant community and the population responses of its species to this perturbation.

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