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# The long-term influence of past land use on the Walker Branch forest

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## Abstract

Forest structure and composition influence patterns of insect outbreaks and can be explained on the Walker Branch watershed by past land use (timber harvest and agriculture), soils, aspect, and slope. In particular, pine bark beetles caased large losses of pine on sites that had been used for agriculture, on Fullerton silt loam soils, and on north-to-northeast and east-to-southeast exposures. Hickory bark beetles had a high impact on hickory biomass on Bodine soil areas that were forested in 1935 and sloped greater than 11%. Thus, prior land use can have an indirect effect on future disturbances.

Because forest disturbances can affect nutrient distribution, land use can also indirectly affect nutrient availability. For example, locations of hickory bark beetle outbreaks experience a large flux of calcium from dead wood to soil because hickory accumulates large amounts of calcium in woody tissue. The research demonstrates a link between past land use, insect outbreaks, and calcium cycling.

## Introduction

Short and long-term changes in patterns of forest cover, composition, and structure are influenced by past land uses (Pyle and Schafale 1988), frequency and intensity of disturbance (White 1979; Picket 1980; Romme and Knight 1982; Sousa 1984; Foster 1988a,b), and environmental constraints (Borman and Likens 1979). The short-term effects on forest ecosystems of land-use activities such as timber harvesting and agricultural abandonment are well known. For example, timber harvesting influences the nutrient status of the forest (Mann ***et al.*** 1988) and the amount of debris on the forest floor (Harmon ***et al.*** 1987). Removal of forests by logging activities can change runoff and nutrient conditions and sets back the successional sequence (Boring ***et al.*** 1981; Silsbee and Larson 1982). Past land use also influences productivity (Turner 1987a). The rate of vegetation recovery of abandoned agricultural land depends on available seeds, distance to a seed source, soil conditions, climate, and random events (***e.g.***, Oosting 1942; Keever 1950; Odum 1969; Drury and Nisbet 1973; Connell and Slatyer 1977).

The long-term influence of past land use on forest composition and structure is less well known. Past land use can have an indirect effect on subsequent management activities or disturbance because land use influences forest species composition and size structure. For example, a forest is not harvested until the trees attain a certain size, and fires

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spread more readily when the forest has an abundant fuel load. Past land use affects spatial heterogeneity (Burgess and Sharpe **1981;** Forman and Godron **1986;** Krummel *et al.* **1987;** Turner and Ruscher 1988), which can, in turn, influence the onset and spread of disturbance (Romme **1982;** Romme and Knight **1982;** Turner 1987b; Turner *et al.* **1989;** Franklin and Forman **1987).**

Few studies directly link changes in spatial heterogeneity caused by land-use practices with subsequent disturbances and their effects on the ecosystem. Documenting this linkage is important because of the need for ecologists and land managers to realize possible long-term implications of human activities.

The purpose of this paper is to examine the long-term effects of past land use on subsequent disturbances and ecosystem changes. We consider the effects of both past land use and site conditions on stand-type distribution and outbreaks of bark beetles decades after the land-use activities have stopped. It is well known that bark beetles select for particular tree species, and outbreaks are influenced by climatic conditions and site characteristics (*e.g.*, Martinat **1987;** Michaels *et al.* **1986).** Stand density and age also affect the timing of bark beetle outbreaks (Graham and Knight **1965;** Waring and Pitman **1983;** Dale and Franklin **1989).** The question we are addressing is, "Does past land use affect those site and stand characteristics which increase the susceptibility of **a** stand to bark beetle outbreaks?''

We extend the analysis from examining changes in live and dead biomass of select species to considering how nutrients in dead trees affect reservoirs of nutrients available to the residual trees in a stand. Although all nutrients in dead trees eventually become available, we focus on calcium because accumulation of calcium in stem wood and bark varies by species, its availability to trees from the soil is affected by harvesting and acidic deposition (Johnson *et al.* **1982,** 1985), and, perhaps most importantly, about 97% of all calcium in vegetation is found in wood (Johnson *et al.* **1982).** Nutrients in wood are tied up for long time periods compared to nutrients in foliage. The growth of species that readily take up calcium can reduce soil calcium levels (Johnson *et al.* 1988), and death and decay of those species may alter calcium availability. Calcium is a nutrient likely to be depleted by whole tree logging (Boyle *et al.* **1973;** Hornbeck and Kropelin **1982;** Johnson *et al.* **1982)** and, in such cases, can only be replenished by mineral weathering (Mann *et al.* **1988).**

We have used a geographic information system (GIS) in a creative way to demonstrate the relationship between prior land use, soils, slope, aspect, and tree mortality and to examine the effects of mortality on calcium distribution. This demonstration of the use of a GIS to deal with complex components of spatial patterns is a major contribution of this paper. The analyses were not designed to examine the environmental variables controlling either tree species distribution or the stresses contributing to their mortality. We, instead, examine the relationship between tree mortality and site characteristics readily available from map sources. These map units are presumed to be related to (1) environmental variables such as soil moisture, evapotranspiration, and soil fertility (soil type, aspect, slope) and **(2)** stand dynamics as a function of stand age or canopy closure (prior land use).

## Study area

The Walker Branch watershed (WBW) was chosen as the study area because its land-use and disturbance history is known, and there are 20 years of vegetation data from permanent plots that cover the period before, during, and after bark beetle outbreaks on the watershed. WBW is in the eastern deciduous forest of East Tennessee, U.S.A., at latitude 35°58′N, longitude 84°17′W. The 98-ha watershed is underlain by dolomite from which highly weathered Fullerton and Bodine soils are derived. WBW ranges in elevation from **285** m to **375** m. Precipitation averages **151** cm/year (Henderson *et al.* **1978).** The watershed is in the Ridge and Valley Physiographic Province and the Oak-Chestnut Forest Region (Braun **1950).**

Vegetation on WBW is currently dominated by mixed oak-hickory with scattered pine stands. Broad-scale vegetation categories are not distin-

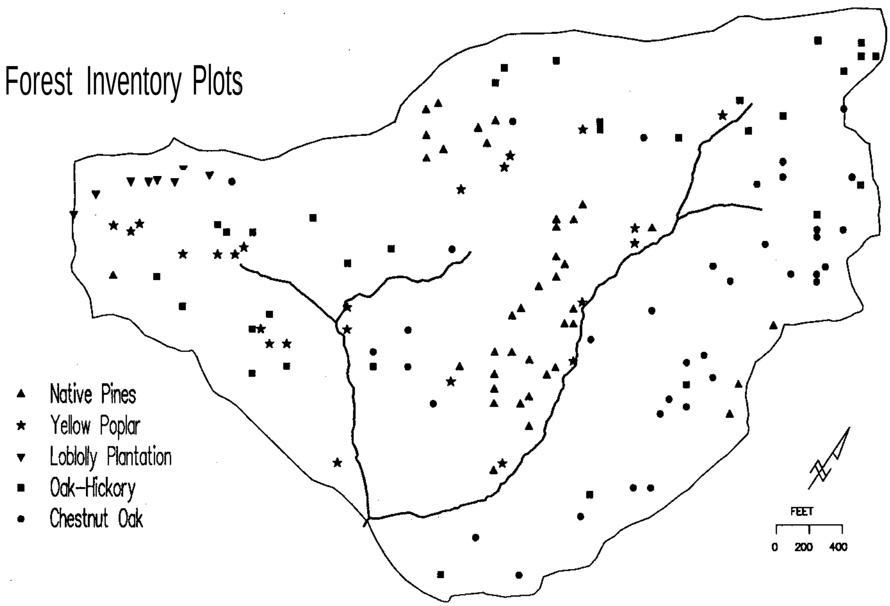

*Fig. 1.* Spatial distribution of stand types on Walker Branch watershed based upon the classification of 130 permanent plots measured in 1967.

guishable on the WBW because there is no strong environmental gradient other than stream drainages. Individual plots are distinguished by the dominance and abundance of particular species. The plots on the watershed can be grouped into five stand types according to the classification of Grigal and Goldstein (1971), which is based on 1967 stand inventory data (Fig. 1). Although each group consist of several non-contiguous plots, we refer to these groups as stand types. The yellow-poplar, oak-hickory, and chestnut oak types are widely distributed on the watershed. Native pines are concentrated along the central part of the watershed. **A** loblolly stand was planted in the northwestern corner of WBW in 1952. The oak-hickory stands consists of hickory *(Carya glabra, C. cordiformis, C. ovata,* and *C. tomentosa),* chestnut oak (*Quercus prinus),* white oak *(Q. alba),* and red maple (*Acer rubrum*), with lesser amounts of sourwood *(Oxydendrum arboreum*), blackgum *(Nyssa sylvatica),* and yellow-poplar *(Liriodendron tulipifera* L.). The pine stands are primarily composed of shortleaf pine (*Pinus echinata* Mill.) and Virginia pine *(P. virginiana* Mill.).

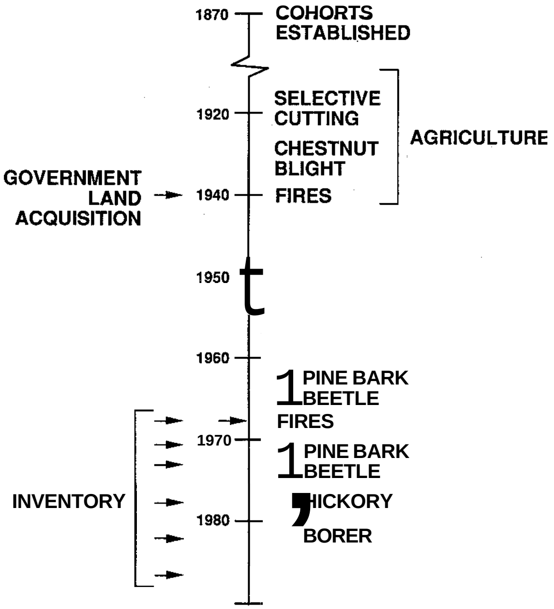

*Fig. 2.* Disturbance history of Walker Branch watershed.

WBW has a complex land-use and disturbance history (Fig. 2). Human disturbance was prevalent on the WBW until the land was purchased by the U.S. government in 1942. Before that time some of the area was farmed or subjected to selective cutting

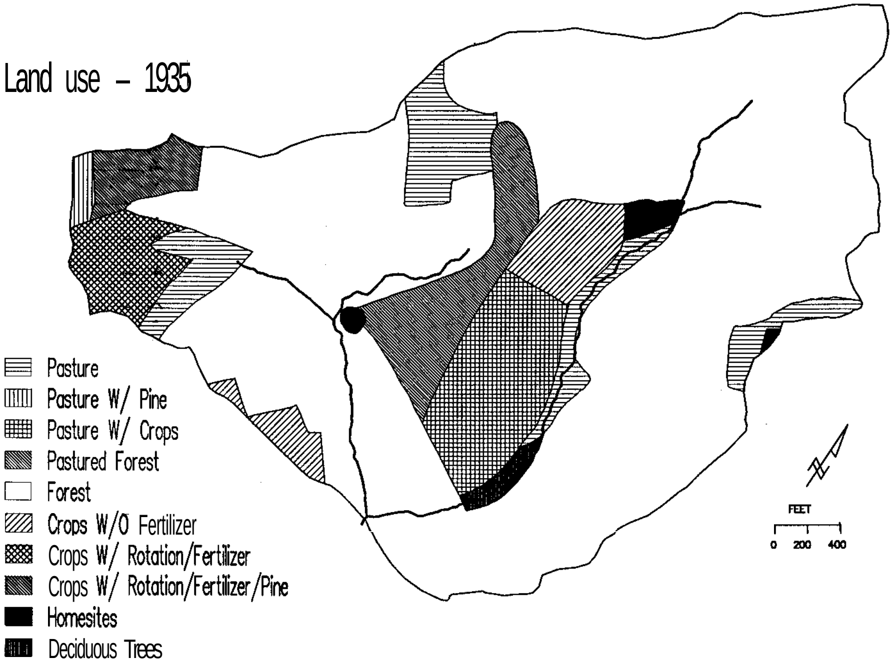

***Fig. 3.*** **Land-use history on Walker Branch watershed derived from interviews of local residents and a 1935 aerial photograph interpreted by Henderson and others (see Johnson and Van Hook 1989).**

(Fig. 3). Fires and selective cutting on WBW have affected tree growth rates and forest biomass (Dale and Doyle 1987). In 1935 the largest part of the watershed was forest (70 ha), but 19 ha was pasture, and 8 ha was planted with crops (Johnson and Van Hook 1989). Prior to 1935 much of the forest was probably selectively cut for firewood, fence posts, and building material, which removed many of the large or accessible oak, hickory, and pine trees. This pattern of forest use is consistent with known practices in the region prior to 1935 and to the present time (Hett 1971). The 19-ha of pasture was a heterogeneous land use group with 27% of the pasture occurring within open forest and 36% planted with a rotation of agricultural crops. Of the 8 ha of cropland, 13% was not fertilized, and 87% was fertilized (probably with manure) and had the crops rotated. About 2 ha of the area, which was fertilized and planted with a rotation of crops, was planted to loblolly pine plantations in 1952. Scattered homesites and orchards accounted for less than 1 ha each.

Trees on the WBW have been killed by both pathogens and insects during recent decades. Chestnut trees were killed by chestnut blight in about 1930, and no mature chestnut trees have reestablished; instead, chestnut oak has become a dominant species (Woods and Shanks 1959). Outbreaks of pine bark beetle (***Dendroctonus frontalis*** Zimm.) occurred during 1964–67 and in the early 1970s on the WBW. During the late 1970s and early 1980s, hickory bark beetles (*Scolytus quadrispinosus*) killed more than half of the hickory on WBW.

Significant increases in standing dead biomass, nutrient content in standing dead biomass, and nutrient return via tree fall on WBW are correlated with insect preferences for the pine and hickory stand types (Johnson *et al.* 1990). However, not all stands dominated by pine or hickory were affected by pine bark beetle or by hickory bark beetle, respectively. In this paper we show that affected sites can be better characterized by past land use, soils, aspect, and slope class than by stand type for the purposes of explaining patterns of insect outbreaks. Past land use on the WBW affects the spatial distribution of stand ages and types and, therefore, influences patterns of bark beetle outbreaks. It is important to know conditions under which large amounts of standing dead wood occur, because the decay of wood can influence changes in availability of soil nutrients. The two species considered in this paper contain very different amounts of calcium and their demise will have different effects on future availability of calcium.

## Methods

Stand biomass and calcium content of the wood were obtained by using regression equations, diameter at breast height (DBH) measures from permanent plots on WBW, and calcium concentrations from sampled trees. Forest inventory plots were established on WBW in **1967** based on a stratified random design (Grigal and Goldstein **1971).** Species, diameter, and status (live or dead) were recorded for individual trees on **130** core plots that were measured in **1967, 1973, 1983,** and **1987.** Tree biomass was calculated from DBH using pine, hardwood, and yellow-poplar allometric equations of Sollins ***et al.* (1973)** and loblolly pine (*Pinus* ***taeda)*** equations of Van Lear ***et al.* (1984).** Estimated calcium content of dead trees was obtained by multiplying average concentrations of calcium in branch and bole components by the biomass of each component as determined from tree DBH (Johnson ***et al.* 1990).** Stand biomass and calcium were obtained by summing the estimates for individual trees on a plot and dividing the sum by the area of the plot.

Stand type classifications were determined from the **130** core plots based on four numerical classifications and canonical analysis (Grigal and Goldstein **1971).** That classification gives the stand types that were subjected to insect outbreaks that occurred in the **1960s** and **1970s.**

Each of the plots was assigned a soil type and land-use history by digitizing soils and land-use maps and intersecting the plot locations with each map coverage by using a geographic information system. The soil map for WBW developed by Peters ***et al.* (1970)** contained seven soil types and was produced at a scale of **1:3163.** The land-use history of WBW was determined by Henderson and others in **1967** based on a **1935** aerial photograph and other records, including interviews with previous residents (Johnson and Van Hook **1989).** We digitized the coarse land-use boundaries (at a scale of approximately **1:5000)** from the **1935** aerial photograph.

The slope and aspect on the WBW were estimated by digitizing the 40-ft (12-m) contours from a **1987** contour map drawn at a scale of **1:1200** with 2-ft **(0.6-m)** contours. **A** digital elevation model was developed using a bivariate quintic interpolation method with a triangulated irregular network of elevations filtered from the digital contour data (ESRI **1988).** Slope and aspect were calculated for 228-$m^2$ triangles and aggregated into six slope and eight aspect classes for analyses.

The relationship between land use, soils, slope, and aspect class and mortality of pine **and** hickory was determined by comparing the mean live biomass, dead biomass, and percent mortality within each of the classes. Percent mortality was calculated as the biomass of dead wood divided by total live plus dead biomass-for each year. Because pine and hickory trees occurred in plots that were not necessarily classified as pine or oak-hickory stand types, respectively, all plots that contained trees of the genus of interest were included in the analysis.

## Results

### *Factors affecting stand-type distribution*

Spatial patterns of past land use partially explain the distribution of stand types (Table **1). As** was expected, native pines occur primarily on areas that were pastures or agricultural fields rather than in areas that were forests in **1935.** Pines are found on recently disturbed sites because the seeds require high light levels for germination (Oosting **1942).** Loblolly pine was planted only in open or pastured areas. The oak-hickory and chestnut oak stand types are found primarily on sites that were forested in **1935.** These two stand types are characteristic of mature forests in East Tennessee (Whittaker **1956).** Their rarity on areas that had been cropland or pasture is because not enough time has elapsed for the establishment and maturation of the slower-growing trees. Distribution of the yellow-poplar

*Table 1.* Distribution of 130 inventory plots on the Walker Branch watershed by land use, soil type, slope, and aspect.

| | Stand type | | | | | Total |
|---|---|---|---|---|---|---|
| | Native pine | Loblolly pine | Yellow-poplar | Oak-hickory | Chestnut oak | |
| ***Land use** in **1935*** | | | | | | |
| Homestead | 0 | 0 | 1 | 0 | 0 | 1 |
| Cropland | 9 | 4 | 2 | 1 | 0 | 16 |
| Pasture with crop | 15 | 0 | 2 | 0 | 1 | 18 |
| Pasture | 11 | 2 | 4 | 1 | 0 | 18 |
| Pastured forest | 0 | 0 | 2 | 0 | 2 | 4 |
| Forest | 1 | 0 | 9 | 30 | 33 | 73 |
| ***Major soil type*** | | | | | | |
| Bodine cherty silt loam | 5 | 0 | 10 | 24 | 14 | 53 |
| Claiborne cherty silt loam | 4 | 0 | 2 | 0 | 0 | 6 |
| Fullerton silt loam | 4 | 3 | 2 | 0 | 0 | 9 |
| Fullerton cherty silt loam | 23 | 2 | 5 | 8 | 20 | 58 |
| ***Slope*** | | | | | | |
| 3–10% | 7 | 3 | 7 | 0 | 2 | 19 |
| 11–22% | 15 | 3 | 8 | 17 | 22 | 65 |
| 23–46% | 14 | 0 | 5 | 15 | 12 | 46 |
| ***Aspect*** | | | | | | |
| N–NE | 8 | 0 | 6 | 6 | 1 | 21 |
| E–SE | 25 | 9 | 6 | 10 | 3 | 53 |
| S–SW | 3 | 0 | 3 | 11 | 14 | 31 |
| W–NW | 0 | 0 | 1 | 5 | 18 | 24 |

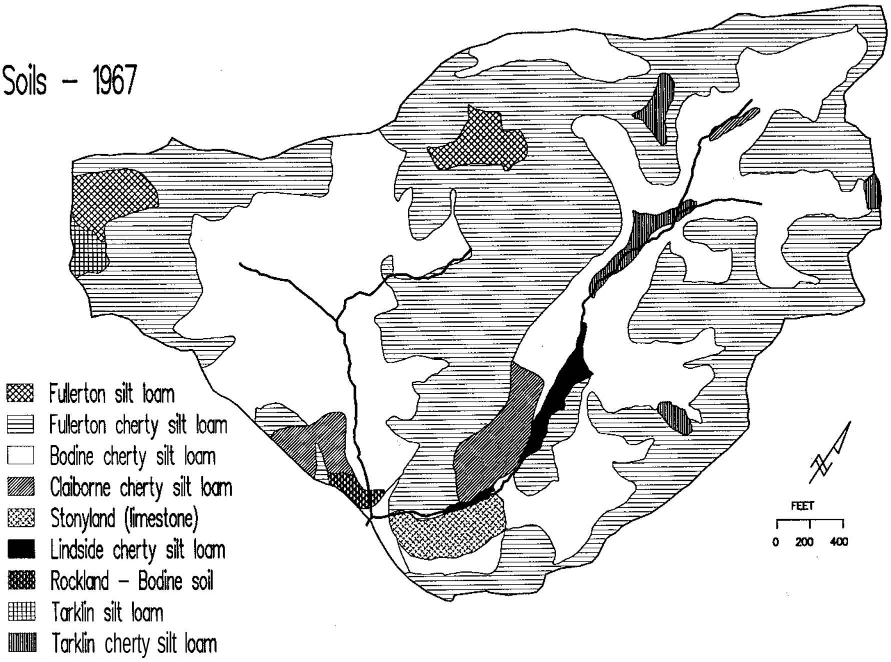

*Fig. 4.* Soil map of Walker Branch watershed (based on Peters *et al.* 1970).

stand type is independent of past land use. The widespread distribution of the yellow-poplar type may reflect the ability of yellow-poplar to be a pioneer species on abandoned land and yet continue to persist in the mature forest (Fowells **1965).** Thus the yellow-poplar type can occur over a range of the stand ages present on the WBW.

The influence of soils on stand-type distribution is largely modified by prior land use. For example, plots on the Claiborne soils (Fig. **4)** were all planted to crops prior to **1942,** which generally did not allow enough time by **1967** for trees characteristic of the oak-hickory or chestnut oak types to attain dominance on those sites. Neither of those stand types was identified on the Claiborne soils (Table **1).** The Claiborne soils tended to be in cultivation because they are relatively fertile and occur on accessible sites and relatively flat terrain. For similar reasons, the oak-hickory and chestnut oak types did not occur on the Fullerton silt loam soils which had been used primarily for pasture. Some of the Fullerton soils were subsequently planted to loblolly pine. The native pine and yellow-poplar stand types were found on the four most common soil types.

Slope and aspect partially explain stand-type distribution (Table **1)** although their effects relate to patterns of past land use. The oak-hickory and chestnut oak types occurred primarily on the steeper slopes, probably because of the difficulty of cultivating steep slopes. Loblolly pines were only planted in a single location in the northwestern corner of the watershed. The site was likely chosen because of the relative ease of planting on its flat terrain. The native pines were found more frequently on the east- and southeast-facing slopes.

### *Pine mortality*

Pine mortality caused by pine bark beetles was associated with specific past land use, soil type, aspect, and slope factors (Fig. *5).* There was virtually no pine mortality on the WBW in **1970,** but by **1973** about **15%** of the total pine biomass was in dead wood, and by **1983** the percentage had increased to **40%.** The amount of dead pine biomass was highest on the areas that were previously planted or pastured because the live pine biomass was initially higher on those areas. Pine trees died on all soil types, but both the percent of mortality and live and dead pine biomass were greater on the Fullerton silt loam soils than on other soils. More dead pine were found on the north-to-northeast and east-to-southeast aspects. Percent pine mortality was significantly less on the south-to-southwest facing slopes. The gentle slopes **(<11%** slope) tended to have higher live pine biomass prior to the pine bark beetle infestation and more dead pine afterwards. Thus, the gently sloping areas had the greatest loss of biomass, although there was no significant difference in percent mortality between slope classes.

In summary, most of the high pine mortality (both total and percent) occurred on sites that were gently sloped **(<11%),** were planted or pastured in **1935,** or were on Fullerton silt loam soil (Fig. **6).** The stands with high pine mortality that did not occur in sites with one or more of those conditions were either on Fullerton cherty silt loam or on east-facing slopes.

### *Hickory mortality*

Bark beetle-induced hickory mortality on the WBW was associated primarily with past land use (Fig. 7a). Areas that were forested in **1935** had the greatest amount of dead hickory wood by **1983.** Percent mortality was significantly higher ($p < 0.05$) in **1987** on the **1935** forested sites than on prior croplands and pastures. If the sample sizes were larger for the pastured forest (n = 4) and pasture (n = **9),** we expect the percent mortality would have been significantly less for those areas as well, since the mean mortalities were much smaller.

Not all of the stands with high hickory biomass suffered significant mortality. There was little hickory mortality on areas that had been cropped or farmed, even though high hickory biomass occurred on a few of those sites (note that these plots are not of the oak-hickory stand type). There was actually an increase in live hickory biomass to amounts previously found on plots in the former

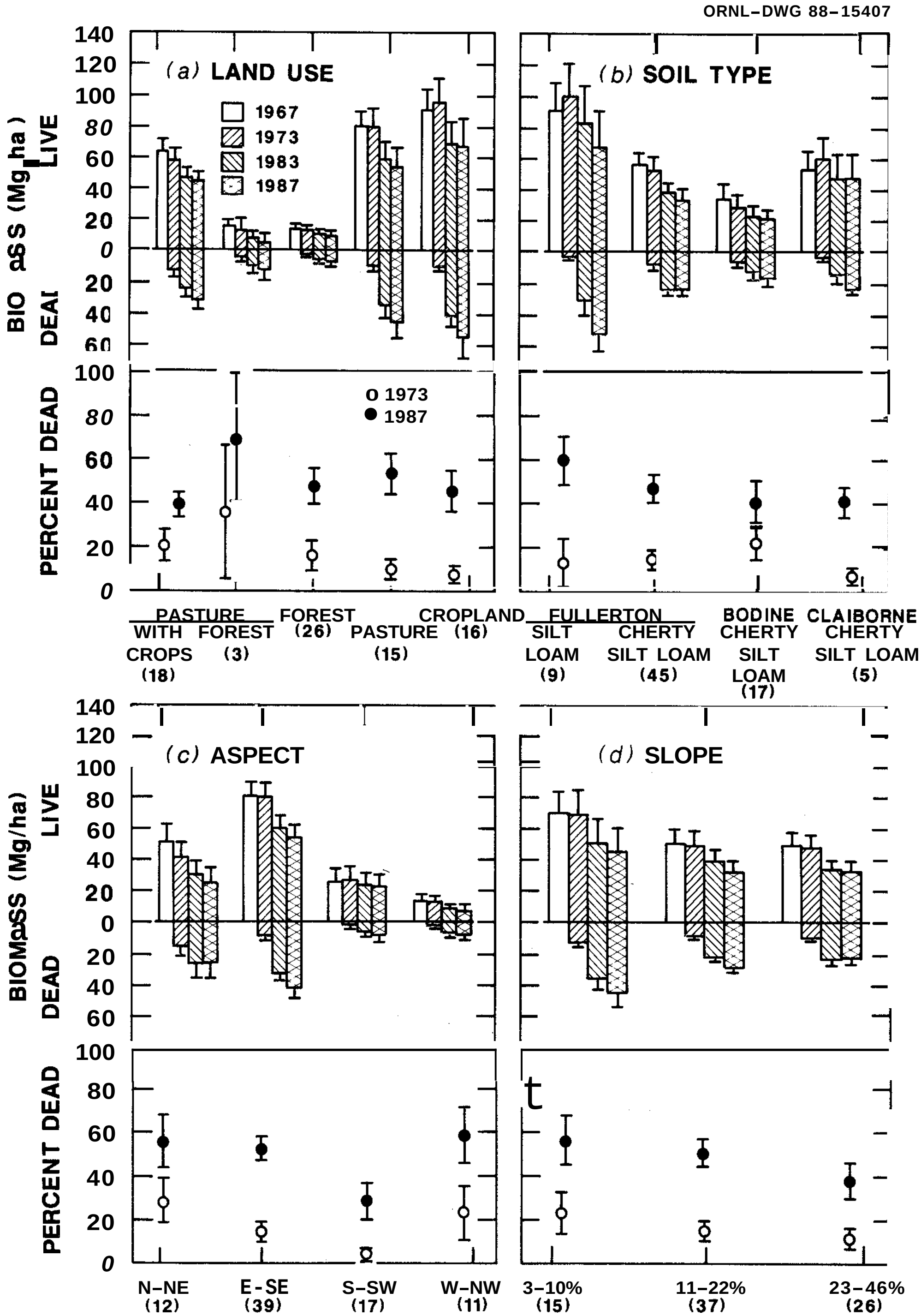

Fig. 5. Relationship between the mean (+ s.e) of live and dead pine biomass and percent cumulative mortality (± s.e.) over time by (a) land use, (b) soil type, (c) aspect, and (d) slope. Percent mortality is the proportion of dead biomass to total biomass (live plus dead) for the given year. Sample size is given in parenthesis.

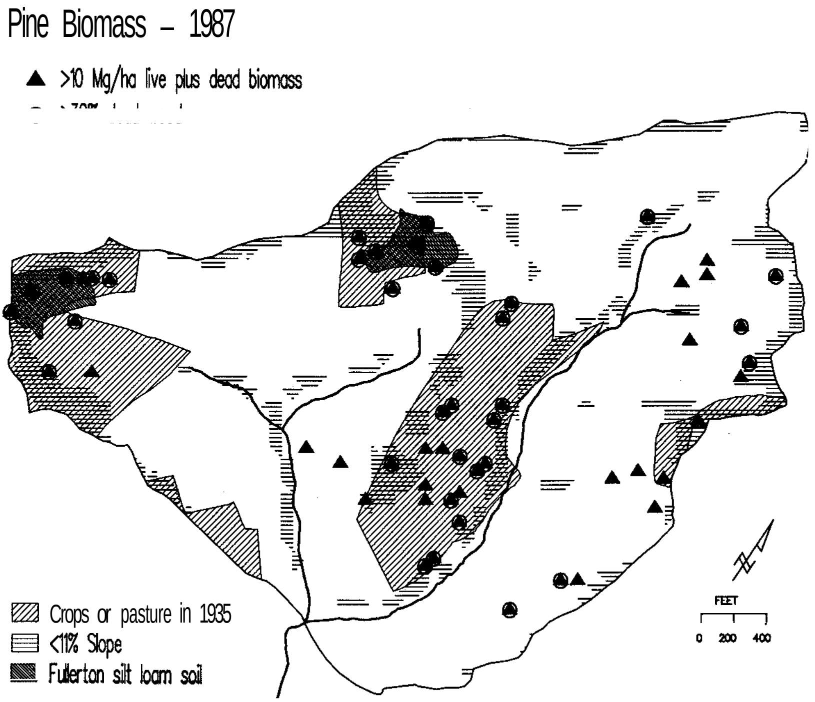

*Fig.* **6. Spatial distribution of plots with > 10 Mg/ha total pine trees and with >30% pine mortality in 1987 on the WBW. The overlap of stands experiencing severe mortality with the cross-hatched areas (where all three factors occur) indicates that the areas with >30% dead pine were flat (sloped <11%), planted or pasture in 1935, and/or on Fullerton silt loam.**

forests on plots located on former farmland. Thus, over the two decades of measurement (1967 to 1987), the areas that had highest hickory biomass shifted from the continuous forest to the former croplands because many of the pines on those stands had died due to pine bark beetle which allowed the hickories to succeed.

Soil type, aspect, and slope also influenced the pattern of hickory mortality (Fig. 7b). The greatest biomass loss and percent mortality occurred on the Fullerton and Bodine cherty silt loams. There was little hickory mortality on the Claiborne cherty silt loam even though that soil type supported a high biomass of hickory. The low rate of mortality could have occurred because the Claiborne soil is extremely fertile (Johnson *et al.* 1988) and thus less likely to support bark beetle infestations (Campbell and Smith 1980; Kroll and Reeves 1978). Percent mortality was greatest on south-to-southwest facing slopes, although plots on all aspects lost more than 8 Mg/ha of hickory by 1983. The highest biomass loss and percent mortality occurred on sites sloped greater than 10%.

Combining the past land use and site conditions which are most susceptible to hickory bark beetles depicts the areas of highest hickory borer impact on **WBW** (Fig. 8). The greatest mortality occurred on pastured sites, on stands forested in 1935, on sites sloped >10%, and on Bodine cherty loam soils.

## Discussion

Past land uses, soils, aspect, and slope on the **WBW** combine to influence the distribution of tree species, stand age, and stand structure. Past land use is particularly important because clearing the forest sets back or restarts the successional sequence and thus is a primary determinant of stand age and type. Pines are most common in younger stands that have recently been used for crops or pasture. The flatter, Fullerton and Claiborne soils were selected for agricultural uses prior to 1935. In 1942 both croplands and pastures were abandoned and pine stands became established, including a 2-ha loblolly pine plantation planted in 1952. In contrast to pine,

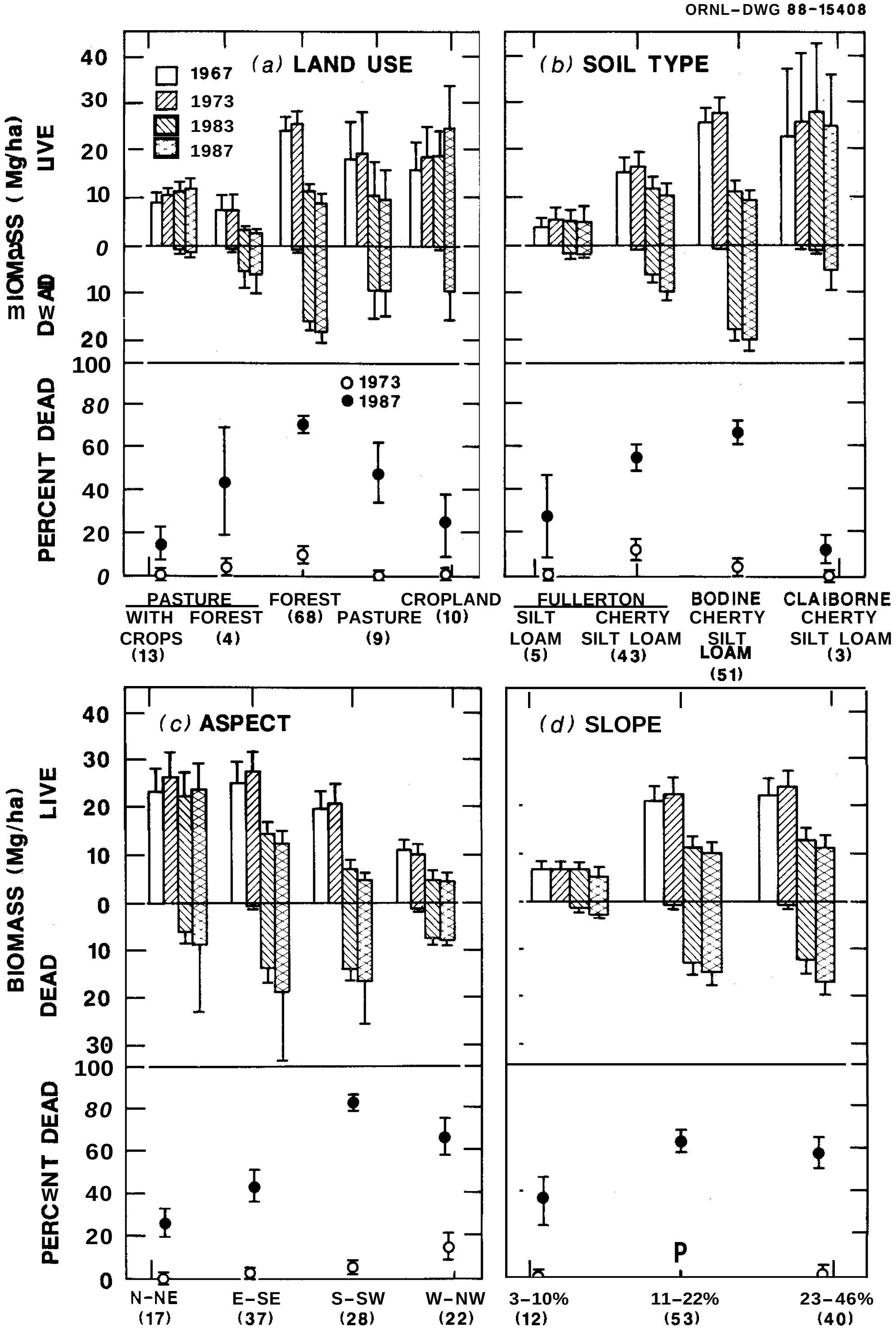

*Fig. 7.* Relationship between the mean (+ s.e) of live and dead hickory biomass and percent cumulative mortality (± s.e.) over time by (a) land use, (b) **soil** type, (c) aspect, and (d) slope. Sample size is given in parenthesis.

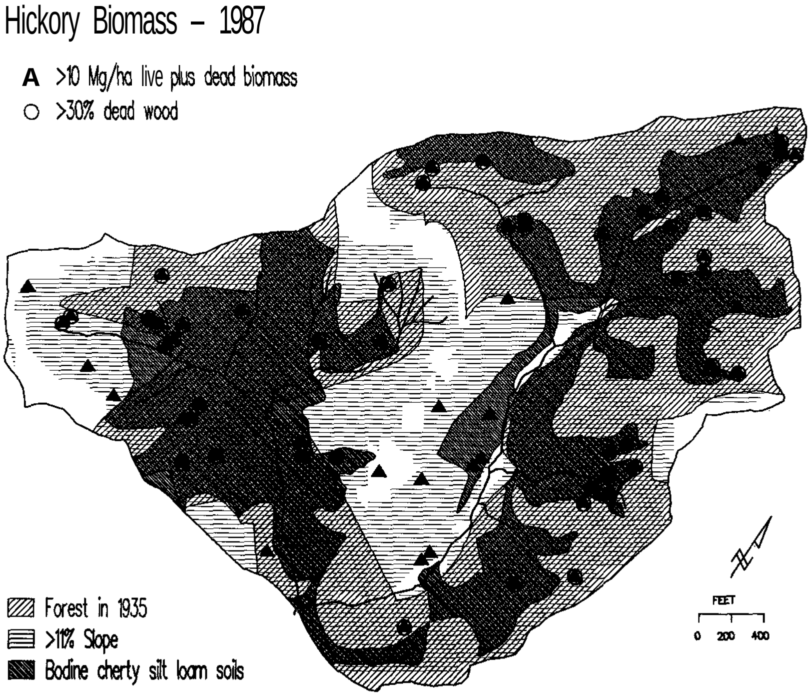

*Fig.* 8. Spatial distribution of plots with > 10 Mg/ha total hickory trees and with >30% hickory mortality in 1987 on the **WBW.** The overlap of stands experiencing severe mortality with the cross-hatched areas (where all three factors occur) indicates that the areas with >30% dead hickory were steeply sloped (>11%), forested in 1935, and/or on Bodine cherty silt loam.

hickory were well established on the steeper Bodine soils that were forested in 1935.

Patterns of pine and hickory mortality can be predicted by the spatial distribution of past land use because land use influences the composition, age, and size of forests. The distribution of pines and hickories affected the location of insect-induced mortality because the bark beetles are restricted to those genera. In the mid-1970s heavy mortality occurred in the 20- to 35-year-old, overstocked pine stands as a result of pine beetle outbreaks. The mature hickories in the older stands that experienced high mortality were primarily associated with hickory bark beetles in the late 1970s.

The trends in pine establishment and growth on the WBW are probably similar to those on the North Carolina Piedmont where pines readily establish on the cleared land and, over time, their density declines as the volume increases to a maximum at a stand age of about 40 years (Oosting 1942; Keever 1950; Christensen and Peet 1981). The pines on the WBW that established following agricultural abandonment in 1940 were likely to have been still approaching their maximum stand volume in the mid-1960s and early 1970s when the bark beetle outbreak occurred. The pattern of bark beetle outbreak in the WBW is similar to the pattern depicted by Schowalter *et al.* (1981), except that human use of the land has replaced fire as the factor that resets the successional sequence. Our results emphasize that anthropogenic disturbance must be included as a factor shaping age structure and stand type of the present landscape and thus its susceptibility to bark beetles.

The susceptibility of a stand to insect outbreak is influenced by conditions that vary over time and space. Bark beetles are particularly noted for attacking trees that have been stressed by drought, disease, or prior injury (Berryman and Wright 1978; Coulson 1979; Pittman *et al.* 1982; Schowalter 1985). Beetle outbreaks generally occur with the confluence of events that vary in time and frequency (*e.g.*, lightning strikes, climate regime, and availability of vulnerable stands) (Rykiel *et al.*

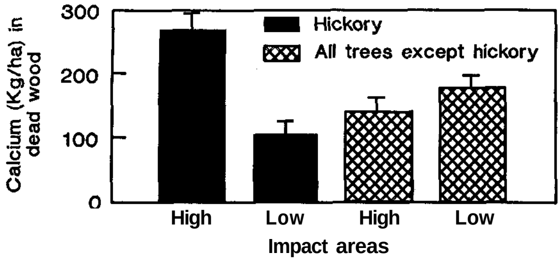

*Fig.* 9. Histogram of calcium in dead wood for stands with high and low impact by the hickory bark beetles in **1987.** The highly impacted stands were on sites that were forested in 1935, on Bodine soils, and sloped greater than 11%.

1988). Our results show that prior land use can affect stand age structure and type and thus combine with site conditions to influence the spatial distribution of vulnerable stands.

### *Secondary effects of bark beetle outbreaks*

Massive mortality of select species can induce secondary effects on forest function (Swank ***et al.*** 1981). For example, extensive hickory mortality can affect distribution of calcium because calcium concentrations are higher in hickory tissues than in other tree species (Johnson ***et al.*** 1990). Although rates of release of calcium from decaying hickory wood are not known, we hypothesize that greater amounts of calcium will eventually be available in parts of the watershed where more hickory have died. To explore this hypothesis, we compared calcium in dead wood in two hickory impact classes derived from our earlier analyses (Fig. 8) to estimate the magnitude of calcium stored in dead wood. These classes were (1) high impact – plots on Bodine soils, sites with slopes greater than **10%,** and lands forested in 1935 (where plots had experienced heavy hickory mortality), and **(2)** low impact – all other plots. Sixty-four percent of the plots that experienced heavy hickory mortality (>30% dead biomass) were in the high-impact category. The total calcium in dead hickory wood was significantly greater ($p < 0.05$) on the high-impact areas than on the low-impact areas (Fig. 9). There was no significant difference in calcium in the dead wood of all other species. Amounts of calcium stored in dead wood in the highly impacted areas are of the same magnitude as decreases in available soil calcium previously documented (Johnson ***et al.*** 1988).

We hypothesize that the large amount of calcium held in dead hickory will increase soil calcium availability as the hickory decay. Therefore, we suggest that the soil calcium availability, acidic deposition, and tree growth rates be monitored over the next decade on the high- and low-impact areas on the WBW. These factors are important because of the potential for calcium to naturally buffer the effects of acidic deposition (Johnson ***et al.*** 1985). Furthermore, a calcium-aluminum imbalance in the tree-rooting zone reduces the rate of wood formation, decreases the amount of sapwood and live crown, and increases the vulnerability of large trees to insects and pathogens (Shortle and Smith 1988).

### *Conclusion*

Patterns of forest composition and structure on WBW are influenced by prior land use, soil, aspect, and slope. Locations of bark beetle outbreaks on the landscape are determined by forest conditions and, thus, indirectly by prior land use and soil fertility. Prior land use is, therefore, a necessary factor to evaluate the potential for future landscape dynamics. For example, past land use can serve as an indicator of sensitivity to bark beetle outbreaks and potential changes in soil calcium availability. The general applicability of past land use as a predictor of landscape changes should be further explored. Quantifying the relationship between past land use and changes in disturbance regimes and ecosystem properties may require using a **GIS** approach and will enhance understanding of landscape processes and dynamics.

### Acknowledgements

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