THE EFFECT OF LAND USE PRACTICES ON THE VECTOR OF CALIFORNIA ENCEPHALITIS (LACROSSE) IN NORTH CENTRAL UNITED STATES

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INTRODUCTION. Of the 8 container breeding dipterans of northern United States only *Aedes triseriatus* is known to be of public health importance. The female feeds on man, many other mammals, some birds and even reptiles (Wright and DeFoliart 1970). LaCrosse virus, a member of the California encephalitis group, has been repeatedly isolated from the mosquito, and sentinel rabbits develop antibody to the virus when caged near tree holes where they can be fed upon by the mosquito. Disease in man develops only in individuals who have been exposed to bites of mosquitoes in woods in which *A. triseriatus* is present (Thompson *et al.* 1963). The species is also believed to be a vector of eastern equine encephalitis (Jenkins and Carpenter 1946).

Tree holes are found in almost any oak woods which has trees with multiple stems. This report will describe the history of a Wisconsin woodlot in which the biology of *Aedes triseriatus* was studied in 1967 and 1968. It is believed that the sequence of events in this woodlot is typical of what has happened in many areas of the midwest and that knowledge of the history of land use is of great importance to medical entomologists.

HISTORY OF THE SITE. The history of the site was obtained from records of the Wisconsin State Land Survey, abstract to the property described, and interviews with older residents.

The county in which the study site is located was an oak savanna when first surveyed in 1832. Still in evidence in 1969 are a few of the prairie oaks now over 300 years old, and more than 80 species of prairie herbs as defined by Curtis (1959). The initial homesteader reached the property in 1855. He cut firewood, cultivated small patches of corn and potatoes, and herded his cattle over the unfenced countryside. Although the country remained relatively open for the next several decades, fences were being built during this period and young trees were sprouting among the prairie oaks as the inhibiting fires became less frequent. The last big fire, according to residents, occurred about 1910.

After 1940, the farm could no longer support its owners and it was finally abandoned in 1945. This reflects the fact that less than 20 percent of the farm is classed by the U. S. Soil Conservation Service as suitable for cultivation and much of the 20 percent is rated as marginal (Figure 1). A similar history could be obtained for many farms on the steep rocky hills of countless other tributaries of the Wisconsin and upper Mississippi Rivers. Two other tracts in Wisconsin where we studied *A. triseriatus,* one located 30 and the other 120 miles from the farm being described, differed mainly in the fact that they were abandoned a little later.

HISTORY OF THE TREE HOLE. Holes in the basal plate were developed in trees (Table 1) primarily the white oak, *Quercus alba,* and the black-Hills oak complex, *Quercus velutina-Q. ellipsoidalis,* that regenerate by sprouting following damage to the primary or secondary trunks (Rogers and Rogers 1959). Trees with fire scars still visible at the base and usually on the uphill side are not uncommon near the study area and some tree holes could be traced to this origin (Rogers 1959). During the last century, cutting by man was the principal cause of the damage-regeneration cycle. The intensity of cut-

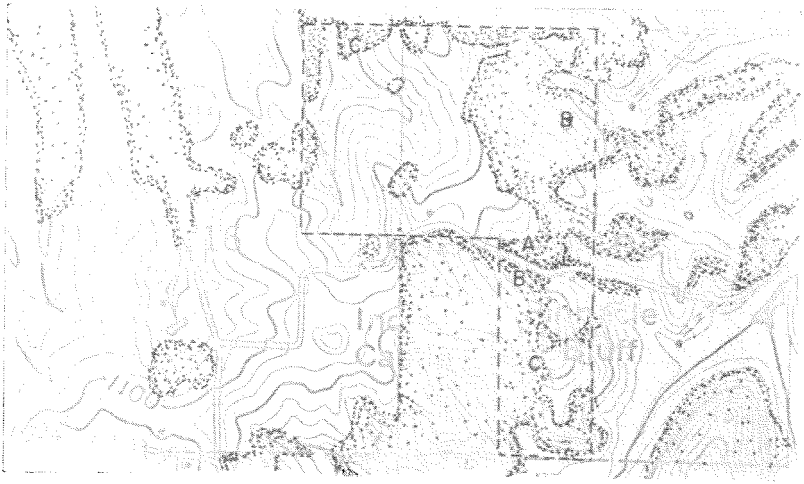

FIG. 1.—A portion of USCG quadrangle showing location of a study site (A). The farm circumscribed by a dashed line is 6 miles south of the Wisconsin River and contains 2 properties homesteaded in 1855; location of woodlots free of tree holes (B), other woodlots with tree holes (C).

ting varied greatly from property to property and was accelerated during certain periods, particularly the agricultural depressions of the 1890's and 1930's. Before 1960, oak fence posts used on each farm were cut there, and split and pointed by the owner. Only in the 1960's with more extensive use of steel posts and the conversion of most farmhouse heaters to oil, did cutting of the oak woods essentially cease. Logging had been an exceptional practice in the county, occurring only a short period in the 1940's when many of the surviving 2–3 century old prairie oaks were cut for barrel staves. No regeneration has been observed from these stumps.

At the present with the cessation of fires and development of a true oak forest with a continuous canopy, the struggle for light results in increasing numbers of failures among the smaller stems of clumps (Curtis 1959). The dying stem invaded by fungi weakens and eventually breaks off close to the root leaving the site for tree hole formation.

Damage by fire, cutting, or death from

TABLE 1.—Trees on the Five Acre Study Site.

Species		No.	No. Tree Holes
Quercus alba	White Oak	284	15
Quercus velutina-Q. ellipsoidalis	Black-Hill's Oak	100	5
Populus tremuloides	Aspen[1]	61	0
Juglans cineria	Butternut	50	0
Carya cordiformis	Hickory	25	0
Pyrus ioensis	Crab[1]	7	0
Celtis occidentalis	Hackberry	5	0
Quercus macrocarpa	Burr Oak	4	0
Betula papyrifera	Birch[1]	2	0
Prunus serotina	Black Cherry[1]	1	0

[1] Aspen, crab, birch, cherry grew only on periphery of the area, other species were scattered over the entire area.

shading is followed by entry of microbial organisms that break down the structure of the wood, rendering it friable and subject to removal by wind and frost, or animal action. How long this process takes is not known, but it probably takes several decades, if interpolation can be made from decay of fence posts. Sapwood of oak fence posts is usually destroyed at the ground line in 10 years, the rate of decay being delayed at very dry or wet sites and accelerated at places subjected to frequent fluctuation in soil moisture. The initiating cause of most of the present tree holes at the study site was probably cutting that occurred in the last depression, 35 to 45 years ago.

At some point in the decay process, a cavity develops that can hold water. The process then probably accelerates as the cavity fills at each rain and dries out in periods of fair weather.

If the root of the injured tree did not remain viable and send up circumferential sprouts, the decay would destroy all wood and no cavity would be formed (Table 2). One or more of the secondary stems survive, grow into trees, and form a callus of live tissue around the rim of the cavity which occupies the position of the old trunk just above or often below the ground line (Figure 2). If growth is rapid and the mouth of the cavity small, the callus may close the opening. The surrounding stems divert rain down their surfaces into the tree hole and in this way even large cavities with small openings (an inch or less in diameter) receive an ample supply of water.

Most of the tree holes are probably temporary. Decay either eventually penetrates deep enough to perforate the bottom of the cavity and drain it or the hole is filled with falling debris (twigs, leaves, and dirt) that is blown in by the wind. Seeds that land in the developing soil germinate and speed the process of eutrophication. Nevertheless, for a period of ten years or more a special environment is provided for the aquatic stage of several dipterans.

The living forms within the tree hole have not been inventoried, but they certainly include bacteria, certain algae, a variety of protozoa, infusoria, nematodes, and small annelids which provide an abundant food supply for the developing mosquito larvae. Jenkins and Carpenter (1946) list rotifers, vorticella, paramecium, hypotriches, cyclops, and nematodes, all of which were eaten by *A. triseriatus* larvae. At the same time, the cavity is free of mosquito predators found in large bodies of water.

TABLE 2.—Dimensions of 10 representative trees and tree holes in a five acre study area in Iowa County.

Circumference of base plate in inches	Number of surviving stems	Circumference of opening in inches	Depth in inches
132	5	8	8
104	6	42	6
82	3	11	7
76	2	24	4
60	2	20	11
54	2	19	6
41	3	14	6
41	3	17	4
30	1	5	5

FACTORS AFFECTING DISTRIBUTION. Tree holes are found in large numbers in restricted sectors of a woodland, even when the initiating damage, fire or cutting, occurred over a much larger area. Environmental factors apparently contribute to the formation of tree holes. Greatest numbers of tree holes are found on south and

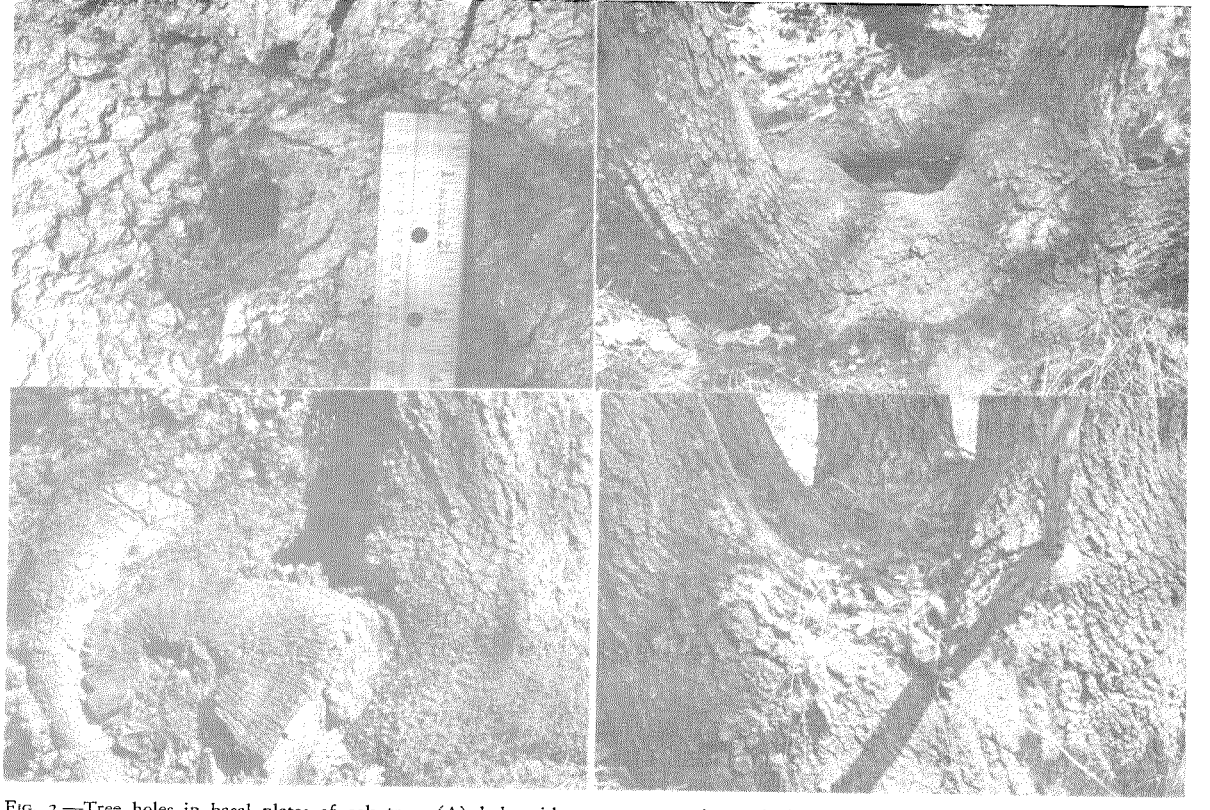

FIG. 2.—Tree holes in basal plates of oak trees (A) hole with a narrow opening, 3 inches in circumference, 8 inches deep, (B) hole with a wide opening, 24 inches in circumference, 6 inches deep, (C) hole with partially rotted stump still in place, surface of the stump shows marks of sawyer, (D) hole filled with accumulation of soil.

southwest-facing slopes, smaller numbers on southeast slopes and a few on north-facing slopes or level areas. Twenty tree holes were located in the 5-acre, southwest-facing study site and none in an adjoining 5-acre northeast-facing area (Figure 3). Some microclimatic differences between these areas are marked (Van Arsdel, 1954). Snow cover is intermittent most winters on south-facing slopes of 15–30 degrees, while it remains continuous on equally steep north-facing slopes. The temperature differences are reflected in such phenological events as the blooming time of bloodroot which is 14 days earlier on south-facing slopes than it is on the opposite slope, a hundred yards away. In climate, this corresponds to a latitudinal displacement of 100 miles (Curtis 1959).

Species composition is also different, prairie plants being not uncommon in the woodland with a steep south exposure but rare or absent in those facing north.

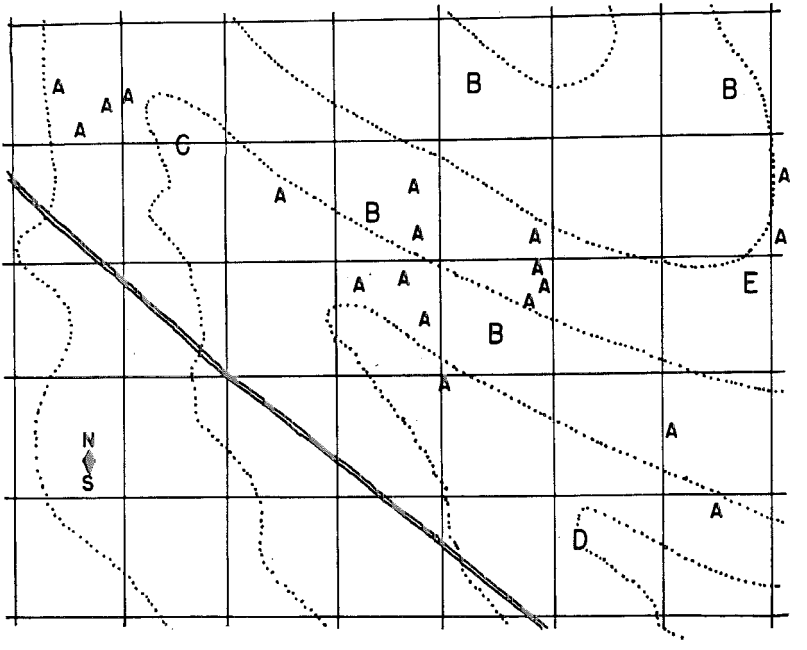

FIG. 3.—Map of the 5-acre site that was used by Loor in his 1967–1968 study of *A. triseriatus*. The grid is 100 feet. Twenty foot contour lines show the general southwest exposure of the section containing tree holes. The town road parallels the bottom of the hollow. Symbols: (A) tree hole, (B) cages of sentinel rabbits that did not develop antibody, (C) cage of a rabbit that developed LaCrosse antibody 31 August, (D) cage of 3 rabbits that developed LaCrosse antibody 28 July, 3 August, and 21 September, (E) cage of 2 rabbits that developed trivittatis antibody 28 July. The tree canopy over cages C and D provided greater shade and humidity than was true of any other cage site.

Isolation, soil temperature and transpiration are all higher on south-facing slopes. As surface drainage is rapid, the shallow surface soil is almost always dry. On some of the steepest hillsides (25–45 degree slope—goat prairies) the aridity is so extreme that no trees or shrubs will grow. In less extreme exposure tree growth is affected as evidenced by stunting and a short life span. The adverse

environmental conditions apparently play a role in tree hole formation probably by reducing resistance of trees to invasion by fungi and bacteria.

The type of tree hole that has been described is by far the most abundant in all of the areas studied in Wisconsin. Other types do occur. A hole containing larvae of *A. triseriatus* was found 4 feet above the ground in a white birch ¼ mile west of the study area. It has persisted for at least 4 years. Another was found 8 feet above the ground in an oak, and one was located in a central cavity of a stump cut at least 10 years earlier. Other natural containers, including rock cavities, are utilized. In July 1969, *A. triseriatus* larvae were collected from a water filled crevice in a rock bluff ¼ mile south of the study area. (Personal communication Charles Porter, Department of Entomology, University of Wisconsin.)

THE TREE HOLE MOSQUITO. Eggs laid on the side of the tree hole by the female *Aedes triseriatus* in summer or fall are induced by the short day length to go into diapause, a state of arrested development which enables the egg to survive the winter. In late spring with the lengthening of the day, diapause is broken, the larvae hatch out late in April, develop into pupae and emerge as adults the middle of June (Loor and DeFoliart 1970). Mating occurs almost immediately and the female is ready to seek a blood meal to supply the nutritional requirements of her developing eggs. She will feed again and again to fill that requirement and lay more eggs.

Although she feeds on a variety of hosts, including man, squirrels, chipmunks, deer, rabbits, and other mammals, and takes blood from birds and snakes (Wright and DeFoliart 1970), the female stays within the shade of the woods. She feeds preferably in the afternoon and at dusk and does not bite after dark (Loor and DeFoliart 1970).

LaCrosse virus of the California group has been repeatedly isolated from female *Aedes triseriatus* in several areas (Ohio, Wisconsin, Indiana, and Minnesota) of the upper Mississippi and Ohio River Valleys (Thompson *et al.* 1970). In 1967, the virus was isolated from *A. triseriatus* in the tree hole study area, and from the blood of 2 out of 16 rabbits that were caged at selected points on the hillside (Figure 3). Five of the 16 rabbits developed antibodies to LaCrosse virus indicating that they had been infected 10 to 14 days earlier. Two rabbits developed antibodies to trivittatus virus, another member of the California group (Papadopoulos *et al.* 1970).

Tree holes probably were present in the oak savannas of the midwest before settlers arrived. As a result of changes that have occurred in the ensuing years, tree holes originally initiated by fire, subsequently, primarily by cutting, now arise largely from death of stems unable to survive the closing of the canopy.

Aedes triseriatus also readily uses suitable artificial containers. Loor and DeFoliart (1969) working in the study area, tested acceptance by the *A. triseriatus* female of cans with dark and light inner and outer surfaces and with and without organic debris. While preferences were shown, all types of containers were utilized. The mosquito larvae have been collected from cemetery urns (Jenkins and Carpenter 1946), and from a teakettle in a rural Wisconsin dump. (Personal communications, R. J. Dick, Department of Entomology, University of Wisconsin.) The potential of this species and the closely related *A. hendersoni* to benefit from the activities of man while parasitizing him is clearly evident. In the near future, we may find that the number of breeding sites has actually increased.

The most significant aspect of the natural history of tree holes is their abundance in many areas of scenic interest. The steep ridges and narrow valleys with an intermixture of woodland and green grassland, occasional cliff or rock pinnacle and spring-fed creeks are rich in game and scenic vistas. Opportunities for hunting,

hiking and camping, and relatively low prices for the land have led to a rapid conversion of the land from marginal farming to public and private development for recreation. Nearly half of the land in some of the Wisconsin river townships is now owned by the state for parks or hunting reserves or by individuals from cities who have built a second home on it for a weekend retreat. Cases of California encephalitis have occurred in children from the city who summer in the area. The introduction of large numbers of young susceptible children from urban centers into the tree hole woodland could lead to an increase in cases of California encephalitis.

It does not appear likely that tree holes will disappear in the near future as new holes are still forming. Tree holes could be eliminated by filling them with dirt in areas frequented by children such as the immediate vicinity of homesteads and around campsites and picnic grounds in parks. It would not be practical to do this over large tracts of land.

SUMMARY AND CONCLUSION. Tree holes in the basal plates of several species of oaks were found to be the most common breeding site of *Aedes triseriatus* in Wisconsin. Injury from fire and cutting led to resprouting of oaks in the past and initiation of a process which frequently resulted in the formation of a water-containing cavity. Death of secondary stems from shading that results from closing of the canopy in undisturbed woodlands is now initiating tree hole formation where fire and cutting have ceased. Socio-economic factors which have determined plant succession and created the oak woodlands of the North Central States are described. The significance of the conversion of the more rugged portion of these lands to recreational use is discussed in relation to the prevalence of California encephalitis.

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