Naturalistic Control: W. T. Penfound, T. F. Hall, and A. D. Hess and Malaria Control in Tennessee Valley Authority Reservoirs

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ABSTRACT

Wetland and aquatic plants in the shallow water in new Tennessee Valley Authority (TVA) reservoirs provided food and shelter for the larvae of the anopheline mosquito that spread malaria. The resulting increase in malaria in counties adjacent to these reservoirs triggered TVA studies to determine what could be done to reduce mosquito populations. One of these was their control by reservoir water-level manipulation. William Penfound and his colleagues at the TVA used their studies of the life histories of common wetland species and their habitat requirements to develop a water management schedule for the reservoirs that minimized the area suitable for mosquito larvae. In these reservoirs, it was possible to increase or reduce water depths to limit the spread and growth of common wetland species. By manipulating water levels to control the distribution of wetland vegetation, TVA biologists Penfound, Hall, and Hess in their pioneering papers demonstrated that their "naturalistic" approach to vegetation management was effective in controlling mosquito populations. It demonstrated, for the first time, that the distribution of wetland vegetation at any time is dependent on recent and current hydrology. However, their work, which was published in obscure journals, was unknown to other ecologists of their generation.

INTRODUCTION

On May 18, 1933, U. S. President Franklin D. Roosevelt signed the Tennessee Valley Authority Act, part of his New Deal. The new Tennessee Valley Authority (TVA) was charged with controlling flooding along the Tennessee River and its tributaries, improving navigation, and generating hydroelectric power for the region. Within three months of the TVA Act being signed, the construction of dams began, and by 1939, there were five hydroelectric facilities in operation. The TVA project converted significant sections of the valleys of the Tennessee River and its tributaries into reservoirs (Figure 1). This conversion of flowing water into standing water had serious unintended consequences: the rapid spread of aquatic and wetland plants along the shallow margins of the new impoundments and a significant increase in malaria in the Tennessee River watershed. These unintended consequences also had their own unintended consequence, contributing to the development of wetland science.

This increase in malaria around TVA impoundments created serious public health problems (Kitchens 2013). The TVA quickly responded by sponsoring numerous studies of aquatic and wetland vegetation, the biology of mosquito species that was the malaria vectors, the interactions between aquatic plant species and mosquito breeding and reproduction, and both mosquito and aquatic plant control. These studies were summarized in a joint U.S. Public Health Service/Tennessee Valley Authority publication, *Malaria Control on Impounded Water* (1947). Although mostly forgotten today, this report was an important milestone in the development of wetland science.

Historically, mosquito-borne diseases like malaria historically had been the major reason wetlands were feared. In the United States, malaria had been a public health problem and in the 1860s malaria occurred from the Gulf of Mexico to the Canadian border, but by the early 1930s it was restricted primarily to the southeastern U.S. (Figure 2). Because they were major breeding grounds for anopheline mosquitoes that spread malaria, the reduction of mosquito populations initially focused on wetlands. Wetland drainage was one of the most important tools in the management of malaria. However, drainage was not an option to reduce mosquitoes produced in TVA reservoirs. The TVA needed to find other ways to reduce mosquito populations in its reservoirs. To this end, it began to conduct studies of the biology of mosquitoes and the ecology of the mosquitoes' breeding habitat to try to find innovative approaches to mosquito control. In doing so, the TVA sponsored the research of the proto wetland ecologists Dr. William T. Penfound at Tulane University and its own staff biologists (Thomas F. Hall and A. D. Hess) with whom William Penfound collaborated.

PENFOUND, HALL AND HESS

William Theodor Penfound was born in Elyria, Ohio, on November 8, 1897, and died on September 31, 1984 in North Carolina. He obtained an A.B. from Oberlin College in 1922 and an A. M. in 1924. His Ph.D. in 1931 was from the University of Illinois where his major professor was W. B. McDougall (Sprugel 1980). Penfound's dissertation had nothing to do with wetlands and was entitled "Plant anatomy as conditioned by light intensity and soil moisture." During his professional career, he held three academic positions: Tulane University, 1927-47; University of Oklahoma, 1947-67; and Warren Wilson

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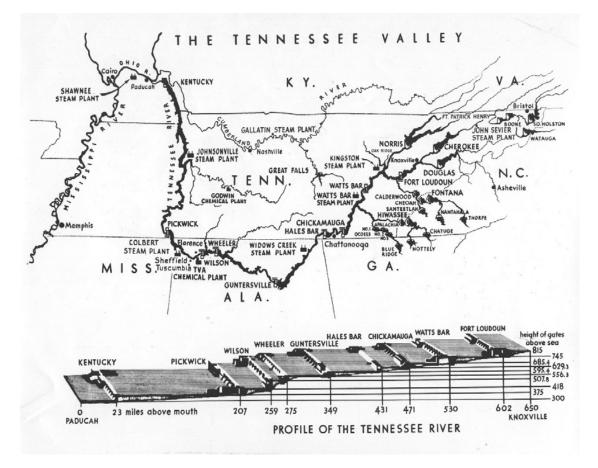


Figure 1. Map of the Tennessee River valley showing the TVA reservoirs. (Source: Tennessee State Library and Archives.)

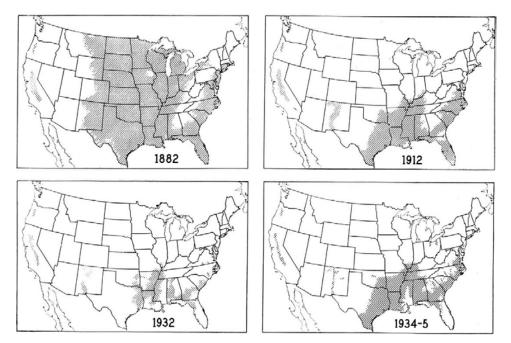


Figure 2. Malaria in the United States. (Source: U. S. Public Health Service and Tennessee Valley Authority (1947) Malaria Control on Impounded Waters.)

College, 1967-77. In 1950, he served as treasurer of the Ecological Society of America and in 1957 as its vice president (Burgess 1977).

At Tulane University in New Orleans, Penfound began to work on wetlands. His early wetland papers included: "Comparative structure of the wood in the "knees," swollen bases, and normal trunks of the Tupelo Gum (Nyssa aquatica L.)" (Penfound 1934); and "Plant communities in the marshlands of southeastern Louisiana" (Penfound and Hathaway 1938). In 1939, he also published three papers with Thomas F. Hall: 1) "A phytosociological study of a Cypress-Gum Swamp in southeastern Louisiana" (Hall and Penfound 1939a), 2) "A phytosociological study of a Nyssa biflora consocies in southeastern Louisiana" (Hall and Penfound 1939b); and 3) "A phytosociological analysis of a tupelo gum forest near Huntsville, Alabama "(Penfound and Hall 1939c). At the time of publication of the first two papers, Hall was a teacher at Lyon High School in Covington, Louisiana, near New Orleans. By the time the third was published, Hall was working for the Tennessee Valley Authority as was Penfound in some capacity. Their affiliations are given as "Botanist [Penfound] and Junior Biological Aid [Hall], respectively, Division of Malaria Studies and Control, Tennessee Valley Authority, Wilson Dam, Alabama." Penfound had begun his association with the TVA's malaria control program in the spring of 1937. Presumably, Penfound recommended him to the TVA. According to Hess and Hall (1945), "his [Penfound's] participation in the [malaria] research program is responsible in a large measure for the progress which has been made."

During the 1940s, Penfound and Hall published a series of life-history studies on common aquatic and wetland species in Tennessee Valley Authority reservoirs. These included studies of *Saururus cernuus* (Hall 1940), *Dianthera americana* (Penfound 1940a), *Achyranthes philoxeroides* (Penfound 1940b), and *Nelumbo lutea* (Hall and Penfound 1944). These studies were initiated because these species had become widespread in the shallow margins of TVA reservoirs. In their studies, Penfound and Hall identified the conditions under which these species became established from seed and spread vegetatively. In effect, they pioneered the life-history approach to the study of wetland plants. Their studies culminated in Penfound's 1952 paper, "An outline for ecological life histories of herbaceous vascular hydrophytes."

When Penfound left Tulane for the University of Oklahoma in 1947, he was the most productive and best-known American ecologist working on wetlands. Although Penfound published a few minor papers on wetlands, e.g., "The Vegetation of Stock Pond Dams in Central Oklahoma" (Kelting and Penfound 1950) while at Oklahoma, his research after leaving Tulane was focused mostly on terrestrial vegetation (prairies, woodlands, and old fields).

Archie Davilla Hess (1911-2004) was born in Weatherford, OK, received his Ph.D. from Cornell University in 1939, and died in Fort Collins, CO. His Ph.D. was in entomology, a study of the round-headed apple-tree borer (Hess 1939). Hess worked for the TVA during the 1940s as a biologist in their malaria control program and then moved to the U.S. Public Health Service in the early 1950s. At the TVA, his research focused on mosquito ecology and control, and it ranged from biological controls using fish (Hess and Tazwell 1941) to the use of DDT (Metcalf et al. 1945) as well as his work with Penfound and Hall on using "naturalistic" control, i.e., water level manipulations, in TVA reservoirs to reduce mosquito larvae populations by limiting their breeding habitat.

MALARIA

Malaria is caused by a single-celled parasite of the genus *Plasmodium*. This parasite is spread only by mosquitoes of the genus *Anopheles*. Female anopheline mosquitoes acquire the parasite from infected people and transmit it to unaffected people. When the parasite *Plasmodium* is injected into people by an infected mosquito, the parasite enters a red blood cell and multiplies to produce 16 to 24 new parasites. The parasitized red cell eventually bursts, freeing the parasites which enter other red cells, and anemia results. An infected person typically suffers from chills, fever, and nausea. Sometimes, malaria can result in death. Although several species of *Anopheles* can carry the malaria parasite, in the American Southeast only one species is involved, *Anopheles quadrimaculatus*.

Anopheles quadrimaculatus lays its eggs in shallow, still water. Its larvae require plant parts and plant litter in and on the surface of the water on which they feed and in which they shelter. The new TVA reservoirs created large areas of ideal habitat for mosquito larvae. Consequently, TVA biologists began to do research on the biology and ecology of Anopheles quadrimaculatus and on the relationships between the mosquito larvae and wetland and aquatic plants (Hess and Hall 1945), and on ways to reduce the amount of favorable habitat for mosquito larvae (Hall et al. 1946). Field studies and observations on the habitats of mosquito larva had demonstrated repeatedly that larval densities were highest in shallow water that had both aquatic plants and plant litter. The number of larvae varied with the dominant place species as well as the amount of live and dead plant material (Penfound 1942; Hess and Hall 1943, 1945). These findings were summarized in a TVA mantra: a clean water surface does not produce "quads" (Hess and

Hall 1945). Consequently, the main goal of TVA reservoir management was to manipulate water levels to maximize the amount of "clean" water.

NATURALISTIC CONTROL

In the early 1940s, William Penfound and his TVA colleagues designed and conducted a pioneering series of studies of how water depth and water-level fluctuations could limit plant growth and "flotage" (plant debris) to reduce mosquito larval populations. Their studies looked at ways to control the abundance of unwanted upland, wetland, and aquatic plant species around the margins and in the shallow waters of TVA impoundments (Penfound 1942; Hess and Kiker 1944; Hess and Hall 1945; Hall et al. 1945; Carter 2014). Over a four-year period, they examined the distribution of all common woody and herbaceous species around and in eleven reservoirs as well as in three natural and two experimental ponds. The goal of their study was to use water-level manipulations to manage the vegetation of the TVA reservoirs to minimize mosquito larval populations. Studies of the relationship of various plant types (flexuous, submerged, carpet, floating mat, etc.) to mosquito larval densities had demonstrated larval densities could range from as few as 1 (in floating leaved vegetation) to 8 (flexuous stemmed) per square foot (Hess and Hal 1945). Thus, by manipulating water levels to promote the abundance of some species or to decrease that of others, it would be possible to minimize mosquito larval production in the reservoirs. The resulting program for controlling malaria through water level manipulations was dubbed "naturalistic" (U.S. Public Health Service and Tennessee Valley Authority 1947).

Hall et al. (1946) identified the key life-history features that could be used to predict the establishment and spread of each species under different water regimes: seed germination conditions (inundated vs dewatered), vegetative growth (sprouting) at different water depths, plant survival at different water depths, and growth form and water depth. It is the last section of this paper on the "Application of knowledge concerning the water level relationships of plants to a program of malaria control..." that makes this one of the most important papers in the history of wetland science. This paper transformed wetland ecology from a descriptive to a predictive and prescriptive science. They demonstrated that that it was feasible to manage wetlands for specific purposes, in this case, malaria control. Water level management involves increasing water depth (progression), lowering water depth (regression or recession), or holding water depth constant. Water-level management schedules for TVA reservoirs were developed by combining periods of progression, recession, and constant

water level. For the TVA reservoirs four water management schedules were developed (Figure 3): 1) flood surcharge (progression of water depths above the top summer pool level and into forested areas in winter or early spring), 2) constant pool, 3) cyclical fluctuations, and 4) regression (gradual seasonal drop in water level). Natural cyclical fluctuations during the growing season occur due to precipitation and evaporation. They have an upward and downward phase. The upward phase retards the growth of emergent species and promotes submerged species. The downward phase promotes seed germination and growth of species whose seeds cannot germinate while submerged and is unfavorable for submerged species. Plant zonation patterns and the vertical extent of plant species are heavily influenced by cyclical fluctuations, as is mosquito larval abundance.

"Information on the water level relationships of marginal plants has been used by the [Tennessee Valley] Authority to design more favorable water level management schedules for malaria control. These schedules have a dual function of managing vegetation by planned water levels to prevent the development of favorable habitats for *Anopheles quadrimaculatus* and to control the larvae of this species" (Hall et al. 1946: 50). Specifically, the TVA developed a Combined Schedule for Main River Reservoirs (Figure 3) with a spring flood surcharge, constant pool, cyclical fluctuations, and seasonal regression phases (Hall et al. 1946). Each phase of the combined schedule had a specific purpose (Hess and Kiker 1944).

The flood surcharge phase (Figure 3) occurs in winter or early spring. During this phase, water levels are raised above the summer maximum pool elevation. This results in floating plant debris (flotage) that accumulated during the winter being deposited in the zone above the summer pool. This ensures that this debris is not in the reservoir during the mosquito breeding season. Any plants along the shoreline are removed prior to the flood surcharge stage so that they do not trap the debris. The removal of this floating debris from the summer pool of the reservoirs helps to reduce the number of mosquito larva. The flood surcharge phase ends before the start of the mosquito breeding season. During the constant pool phase (Figure 3) water levels are kept at the maximum summer pool elevation. High water along the margins of the reservoirs during this phase keeps aquatic and wetland species from spreading lower into the reservoir. The result is a narrower vegetated zone around the margin of the reservoir.

Cyclical fluctuations (Figure 3) are used to lower water levels by about one foot. During this phase, mean water levels are reduced gradually (ca. 0.1 feet per week) so that fluctuations move downslope during the summer. Mean

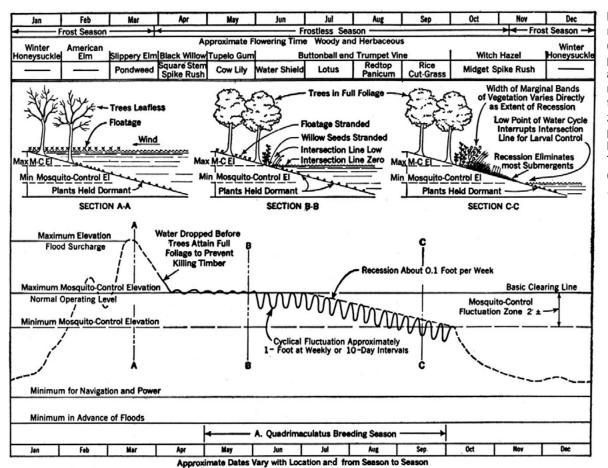


Figure 3. Combined water management schedule (flood surcharge, constant pool, cyclical fluctuations, and regression) for main river TVA reservoirs and their impacts on plant zonation (three upper panels). (Source: U. S. Public Health Service and Tennessee Valley Authority (1947) Malaria Control on Impounded Waters.)

water levels fluctuate about 1 foot during this phase. Water level fluctuations reduce the number of mosquito larvae indirectly by making their habitat less suitable and directly by killing mosquito larvae that are stranded during low water.

The last phase of a combined schedule is the seasonal regression phase. As noted, this phase begins during the cyclical fluctuations phase, i.e., in late spring. Mean water levels typically drop two feet during the summer months, and, when the mosquito breeding season is over, are allowed to decline naturally because of a drop in precipitation in the region during the fall.

To examine the effectiveness of their naturalistic control of mosquito populations, Hall et al. (1946) also describe two reservoirs: one with a "favorable" water management schedule and the other an "unfavorable" schedule. In the reservoir with the favorable schedule, the band of marginal vegetation extended down to only 1.3 feet below the top summer pool level while in the reservoir with the unfavorable schedule it extended to a depth of 5.2 feet. The reservoir with the favorable water management regime did not require any larvicide treatment to control mosquito populations.

DISCUSSION

Penfound and his colleagues advanced the development of wetland ecology in three ways:

- (1) They demonstrated the importance of the life history features of wetland plant species for understanding their establishment, spread, and growth at different water depths.
- (2) They linked the hydrology to the life histories of aquatic and wetland plant species to predict the distribution of these species. Because of their research, wetland ecology became a predictive science.
- (3) They demonstrated that wetland ecology had practical applications for solving societal problems.

The most highly visible publication that included a detailed account of the TVA studies of the control of aquatic and wetland plants by water-level manipulation was Chapter V, Water Level Management, in the 422-page report Malaria Control on Impounded Waters published jointly by the U. S. Public Health Service and the Tennessee Valley Authority (1947). It contains detailed summaries of Hess and Hall (1945) and Hall et al. (1946). This publication was reviewed in public health and medical journals. A reviewer (Anonymous 1949) in the Journal of the American Medical Association (JAMA) noted that "Methods used to change the natural environment to make it unsuitable for mosquito propagation are given in detail. They include discussions of engineering methods, vegetation control, water level fluctuation methods and maintenance of proper conditions after the more permanent control measures." It was also reviewed in the American Journal of Public Health (Gray 1949). Gray also pointed out that there was a chapter on the control of aquatic plants by altering the hydrology of TVA reservoirs. I have not been able to find any reviews of this report in an ecological journal. Because of its importance in the history of public health in the United States, the University Press of the Pacific reprinted Malaria Control on Impounded Waters in 2005.

The pioneering studies by TVA biologists linking lifehistories of plant species to the hydrology of the TVA reservoirs that enabled them to alter the distribution of plant species were rarely cited by their ecological contemporaries. Even today (2022), both classic papers, Hall et al. (1946) and Hess and Hall (1945), are unavailable in digital form, e.g., as a pdf. Publishing their work in a regional journal, the Journal of the Tennessee Academy of Science, and in the narrowly focused and short-lived Journal of the National Malaria Society, may have ensured that very few ecologists would ever see them. According to Google Scholar, Hall et al. (1946) has been cited less than 100 times and Hess and Hall (1945) less than 40 times. However, the small number of citations of these works may only reflect the paucity of ecologists working on wetlands in the 1940s, 1950s, and 1960s, not the visibility of the journals in which they were published. For example, L. R. Wilson's important paper on the aquatic vegetation of the lakes of Vilas County, Wisconsin (Wilson 1935), which was published in Ecological Monographs, has been cited less than 80 times.

What is striking about Hess and Hess (1945) and Hall et al. (1946) is the absence of a theoretical framework for their studies. During the 1930s and 1940s competing models of vegetation dynamics (succession) proposed by F. E. Clements, H. A. Gleason, A. G. Tansley, among others were hotly debated (van der Valk 2014). Penfound was certainly familiar with contemporary discussions of competing theories about the classification and dynamics of vegetation. He had co-authored a paper with Stanley Cain, a leading participant in these discussions (Cain and Penfound 1938), and this paper deals with some of these issues. The TVA papers could have played a significant role in resolving these debates. It would be another 35 years before comparable, but less sophisticated studies (van der Valk 1981) demonstrated again that combining information about life histories of wetland species and water-level changes makes it feasible to predict changes in the composition and distribution of wetland vegetation.

After the end of World War II, the naturalistic control of vegetation in TVA reservoirs for malaria control was replaced by chemical control of both the vegetation and Anopheles quadrimaculatus larvae. As early as 1943, the TVA was experimenting with aerial spraying of DDT as a larvicide (Krusé et al. 1944; Metcalf et al. 1945). A. H. Hess was a co-author of these initial reports on the use of DDT by the TVA. By 1950, Hall and Hess are no longer writing about water-level control of impoundment vegetation, but the use of the herbicide 2,4-D for this purpose. The integrated approach to the management of the malaria vector, Anopheles quadrimaculatus, in the TVA reservoirs that was inaugurated by the Authority's biologists would eventually become endorsed by the World Health Organization (WHO) as the best framework for the management of parasitic diseases in aquatic systems (WHO 2004, 2011). There is a link between the TVA studies of malaria control in the 1940s and the WHO framework, A. D. Hess. Hess, who worked for the U.S. Public Health Service for most of his career, was a WHO consultant. The manipulation of water levels to reduce mosquito larval populations in reservoirs is still being used, e.g., Reis et al. (2011). However, the pioneering work of Penfound and his TVA colleagues remains unappreciated and unacknowledged by wetland ecologists, hence the reason for highlighting their accomplishments in this paper.

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