THE RELATIONSHIP OF SITE CONDITIONS TO THE INVADING CAPABILITY OF *MELALEUCA QUINQUENERVIA* IN SOUTHWEST FLORIDA

BY

RONALD L. MYERS

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Ronald L. Myers

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Chairman: John J. Ewel
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The ability of the introduced tree *Melaleuca quinquenervia* (Cav.) Blake to invade disturbed and undisturbed sites in Southwest Florida was investigated by field experiments involving seeding and planting trials at regular intervals on a variety of sites. In conjunction with these field studies, greenhouse experiments were undertaken to determine moisture requirements for seed germination, plus seedling growth under artificially induced hydroperiod variation and under high and low dissolved oxygen in the soil water.

In the field studies, sites representative of common vegetation types and various histories of land use were selected. The sites were (1) longleaf pine flatwoods, (2) mixed hardwood--cypress forest, (3) recently burned cypress forest, (4) dwarf-cypress forest, (5) wet prairie, (6) mature cypress forest, (7) mangrove, and (8) recently drained cypress forest.

One gram of seed (approx. 34,000 individuals) was sown monthly on each of five randomly chosen 0.2 m^2 subplots within a 20 X 20 m plot at each site. Periodic plantings of seedlings were also carried out on each site. Seed germination, seedling survival, growth and survival of planted seedlings, water level changes, soil moisture,

dissolved oxygen content of the water on flooded sites, and species composition of the extant vegetation were recorded at each site.

No successful *Melaleuca* establishment occurred on any of the undisturbed sites, but a few germinated seedlings have survived on the disturbed sites. Survival and growth of planted seedlings were greatest on sites that were either recently disturbed or on those without dense forest canopies.

The greenhouse experiments demonstrated that seeds germinate in three days, even underwater, but that they are sensitive to drying and die if not kept moist. Greater height growth was obtained under saturated soil conditions than under moist, well-drained soil conditions, but there was no significant difference in the average dry weight of the seedlings from the two treatments. The height growth of seedlings subjected to various schedules of submergence was retarded, and little or no growth occurred while the plants were underwater. There was no significant difference in the height growth of seedlings grown under anaerobic soil conditions and those grown in flooded but aerated soil.

It appears that site disturbance coupled with periods of time in which the soil is either wet or saturated but not subjected to extensive flooding are requirements for the successful invasion of *Melaleuca*. The displacement of native vegetation by *Melaleuca* seems unlikely in those areas where these conditions do not frequently occur.

Chairman

INTRODUCTION

This study is an attempt to define the important environmental and biological factors that determine which sites in South Florida are susceptible to the development of new ecosystems dominated by the introduced tree, Melaleuca quinquenervia (Cav.) Blake.

The South Florida environment has been particularly susceptible to the introduction and successful establishment of exotic plant and animal species. These successful invasions have been brought about by human-caused alterations of the environment augmenting the effects of recurring natural ecosystem stresses, and by the fact that Florida, with its unique geographic position, is like a subtropical island supporting many species that are characteristically colonizers from both the tropical and temperate biomes, plus a number of endemic species that are only found in South Florida.

Besides the ever-abundant naturalized roadside weeds and the aquatic weed species, much of South Florida classed as wetlands has been invaded by several aggressive exotic tree species. These include Melaleuca quinquenervia (Cajeput), Shinus terebinthifolius (Brazilian-Holly), Casuarina equisetifolia (Australian-Pine), Colubrina asiatica, Ardisia solanacea, and Psidium guajava (guava). These species were originally introduced for either ornamental or commercial purposes and have subsequently become naturalized; in some areas they have become the most conspicuous species in the landscape. Generally speaking, these species exhibit characteristics of early successional invaders of abandoned farm fields, roadside ditches, hurricane-stressed coastal areas, and other disturbed areas. These characteristics include rapid growth, short life span, and the production of large quantities of small, easily disseminated seeds.

Most of South Florida has been altered by massive drainage projects, water control programs, and the introduction of nutrient rich waters from agricultural runoff and sewage effluent. The lowered water tables and hydroperiod changes resulting from these alterations have increased the severity and frequency of fires, altered vegetation types, changed nutrient availability and soil characteristics by the oxidation of muck and peat soils, and reduced the duration of annual flooding. These alterations have opened the door to significant long term changes in the plant and animal communities of South Florida: changes that will include exotic tree species well adapted to these new conditions.

Of particular concern is the tree, Melaleuca quinquenervia. It seems to be well adapted to both the periodic fluctuations in water level and frequent burning. Federal and State land management agencies and local conservation groups feel that the native flora and fauna are threatened by such an aggressive invader, and that drastic changes in the Florida landscape will occur if its spread is allowed to continue. Cursory observations of the dense stands and the rapid spread of Melaleuca in some areas have led to its being labeled as a "menace" or "threat" without effectively assessing its present and future role in the South Florida ecosystem. For example, the observations made in the following statement are in need of thorough study:

> "Should the Melaleuca continue to spread it could do incredible damage. For one thing it could destroy the Everglades as a wildlife habitat. It is difficult to

> see how any form of aquatic life could live in flooded areas covered by Melaleuca. For the colonies already established permit no sunlight to filter through. Once the trees covered the glades, the area would become a biological desert from the standpoint of animal life." (Smiley, 1973).

At present it may be more realistic to consider Melaleuca as an indication that the Florida environment has already been significantly changed by human activities. Melaleuca might better be considered as a symptom, not the cause, of vegetation changes and wildlife habitat destruction. Elton (1958) pointed out that "invasions and outbreaks most often happen in habitats and communities very much simplified by man", while Odum (1971) noted that "an invader may be filling a void in a new situation created by man although men are tempted to blame the invader for causing the disruptions". Melaleuca may have to be accepted as a new species in South Florida playing an active role in the functioning of the ecosystem. Perhaps instead of designing species-oriented control programs we should not only be attempting to identify this role but also to be concentrating control efforts toward environmental manipulation that would tend to correct or reduce the effect the man-induced ecosystem simplification that has favored exotic weed species.

Some basic questions that need to be asked and investigated are: (1) What environmental conditions are conducive to Melaleuca establishment? (2) Which ecosystems or communities are susceptible to invasion? (3) What effect will these changes have on both the natural and human systems and their interaction? For example, what benefits or detriments will vegetation changes have on natural and urban water supplies, wildlife, recreation, and overall image of South Florida as an attraction to tourists and future residents? (4) What present and future land use activities will encourage or hinder these changes?

Included in this report are a general review of the characteristics of Melaleuca, its history in South Florida, and the description of several greenhouse and field investigations that attempt to, if not answer, at least shed some light on these questions and provide a basis for more thorough studies in the future.

Characteristics of Melaleuca

Melaleuca quinquenervia (Cav.) Blake is a member of the Myrtaceae family which is comprised of about 80 genera, including Eucalyptus, Callistemon, and Psidium, each of which has been introduced into South Florida, and in the case of Psidium, successfully naturalized. Although there are numerous species of the genus Melaleuca grown as ornamentals in Florida, only Melaleuca quinquenervia has become naturalized (Sachet, 1953). Until recently, many authors have described the species as Melaleuca leucadendron Linn. Commonly, it is known as cajeput, cajuput, cajaput, punk tree, swamp tea tree, brown tea tree, paper-bark, broad-leaved tea tree, white tea tree, white bottlebrush, whitewood, and milkwood (Meskimen, 1962). The most frequently used common names in Florida are cajeput and punk tree; many people use the generic name, Melaleuca, as a common name.

There may be as many as 130 species of Melaleuca with all but Melaleuca quinquenervia restricted to Australia (Corner, 1951), and some authors doubt that this species occurs naturally there (Baker, 1913). There has been much confusion about its classification, with 27 distinct names, including Melaleuca quinquenervia, having been applied to Melaleuca leucadendron with numerous varieties and contradictory descriptions

(Ewart, 1917). It was originally described from specimens collected in India where it is not believed to be native (Ewart, 1917).

Melaleuca quinquenervia is a slender upright tree, 12 to 30 m in height and very often found with multiple stems apparently resulting from frost or fire damage when young. The stems are often contorted and covered with layers of thick, spongy white bark. The leaves are alternate. The flowers are white, sessile and borne on many flowered spikes from 3 to 12 cm long consisting of 30 to 70 flowers (Fig. 1). Each flower contains a single stigma subtended by 30 to 40 stamens and five white petals. The spikes are borne on the terminal ends of the branches, with new branch growth and leaves appearing after flowering (Meskimen, 1962; Long and Lakela, 1971).

Flowering in South Florida has been observed to occur throughout the year, with generally heavy blooms during the wet season, June through November, but with only sporadic flowering occurring during the dry season which occurs from December through May. Meskimen (1962) noted that individual trees may bloom as many as five times in a single year and individual branches will support three or more blooms annually. Young trees were observed to bloom in their first year.

Although Melaleuca seeds are minute (34,000/gram) (Meskimen, 1962), they are unwinged and it is very common to find dense Melaleuca reproduction around the base of a seed tree with only scattered individuals any distance away. However, the rapid growth of these trees and their ability to produce seed within a year or two suggests that it can spread rapidly from any isolated individual.

A twig or branch may support several seed crops of different ages, which can be easily delineated. Flowers are always produced on the

Figure 1. Melaleuca inflorescence and sertinous fruits.

present season's growing tips, and branch elongation continues beyond the inflorescence. Thus, the seed capsules from each bloom form unique clusters that are separated from previous and future capsules by the stem elongation occurring between blooming periods.

The seeds have been shown to remain viable for at least several years within the seed capsule (Meskimen, 1962). Indications are that a vascular break between the seed capsule and branch with subsequent drying of the capsule is necessary for seed release (Meskimen, 1962). Thus, sporadic seed release may occur at any time of the year by occasional capsules being separated from their vascular connection by radial stem growth, stem breakage, frost damage, and natural pruning; massive seed release occurs after burning. Meskimen (1962) showed that seed capsules on branches whose leaves were merely browned, the seed capsules took somewhat longer to open. Meskimen (1962) also noted that several million seeds can be shed by a single tree. In Java, where Melaleuca is native, forests are regenerated after logging by cutting off the branches and burning them. According to Burkill (1935), many Javanese believe that fire makes Melaleuca grow more luxuriantly.

The ability of Melaleuca to aggressively invade various types of sites is in part a result of its tolerance to brackish water, flooding, complete submergence, and fire. Melaleuca possesses several anatomical and morphological adaptations that facilitate its ability to thrive under these conditions and to rapidly invade suitable sites. These adaptations or characteristics include the thick, fire-insulating bark, a fire-triggered seed release mechanism, the storage for extended periods of millions of seeds on a single tree, the production of adventitious roots, and the ability to sprout from stumps and stems after felling.

Native Range and Distribution

Melaleuca quinquenervia has been described in Australia (Bailey, 1913), New Caledonia, Borneo, Java, Burma, Malaysia, and Viet Nam (Swain, 1928). In Australia, where it is known as weeping or river tea tree, it is found in brackish coastal swamps and along coastal river banks up to 16 km inland from southern New South Wales through Queensland and into the Northern Territory (Coaldrake, 1961), between 35° South latitude to 25° South latitude (Maiden, 1904). The climate is described as sub-humid to humid-tropical with marked wet and dry seasons. The annual precipitation ranges from 900 to 1300 mm per year. The annual pan evaporation is 1500 to 2300 mm per year and the mean temperature ranges from 21 to 24°C in June and July and from 26 to 30°C in December and January (Galloway, 1970).

In Queensland mixed stands of several species of *Melaleuca* have been described growing along the sandy banks of the large rivers that normally flood during the wet season. Here, *Melaleuca quinquenervia* reaches a maximum height of 10 m. It was noted, however, that it was impossible to distinguish one species from another in the field, but that data seemed to indicate that *Melaleuca quinquenervia* grew in isolated pure stands within the mixed communities (Coaldrake, 1961).

Melaleuca also forms pure dense stands in the low swamplands on both the east and west coasts of Malaysia where it is known as "gelam". Occasionally it is found as isolated stands inside the mangrove swamps (Coulter, 1952).

Malaysian peasants will not use soil that has supported *Melaleuca* because they believe that the tree secretes some substance into the soil that prevents their rice from developing. Studies by Coulter

(1952) and Chow (1969) have shown that these "gelam" soils are extremely acid: a result of the high concentrations of sulfides in the soil. During the dry season, or after drainage, the sulfides are oxidized, forming sulfates, sulfuric acid, and toxic levels of iron and aluminum. Although *Melaleuca* appears to tolerate very high concentrations of sulfur in the soil, Coulter (1952) found that it does not absorb particularly large amounts of it and that it is not limited to soils with high sulfur contents.

In Viet Nam, where it is known as "tram", *Melaleuca* is located directly behind the mangroves and is called "backmangrove" (Williams, 1967). Here, again, it grows to about 10 m in height on sandy soils inundated with fresh to slightly brackish water during the wet season while being drained and subject to frequent burning during the dry season. Some botanists consider *Melaleuca* to be a successional species following mangrove and they feel that it occupies sites similar to those occupied by *Pterocarpus officinalis* in Puerto Rico (Williams, 1967).

Outside of its native range, *Melaleuca* has become naturalized in the Philippines (Sachet, 1953), India (Dastur, 1951), Madagascar (Louvel, 1951), Zaire (Neybergh, 1953), and Hawaii (Neal, 1948). In the continental United States it has become established in Southern Florida, California, and Texas (Mortan, 1966).

Uses of Melaleuca

Melaleuca was originally introduced into South Florida as a possible source of raw material for a new forest industry. Although it has never achieved commercial value it is not devoid of possibilities. Throughout its entire native range the primary use of *Melaleuca* has been as a source of fuel. In certain areas of Viet Nam and Malaysia where mangrove is not available, Melaleuca forests have been set aside as sources of fuel for local villagers (Burkill, 1935).

Melaleuca wood has been described as hard, durable, and close grained, but checks readily upon seasoning and tends to be brittle (Schory, 1958). The wood is resistant to termite attack, is durable in water and has been used for wharf piles, boat knees, and railroad ties. It has been recommended for furniture, cabinets, flooring, gunstocks, framing, boat trim, and novelty items (Schory, 1958). It is not particularly well suited for pulp. Pulping tests have shown that the paper is strong, but high bleaching treatments are required (Curran, 1934).

Numerous local uses have been found for Melaleuca bark and leaves. In India, the bark was originally used as a form of paper for sacred writings (Dastur, 1951). The bark is chemically similar to cork (Wilks, 1953) and has been used as packing material, floats for fishing nets, insulation, and bedding. It is mildew proof and has been suggested for use in mattresses, upholstery, pillows, and life preservers (Schory, 1958). It is also used locally for leak-proofing roofs and for caulking boats (Corner, 1951). In New Caledonia a tea is made from the leaves (Burkill, 1935).

The aromatic volatile oil, cineol, is commercially distilled from the leaves and is used to treat a variety of illnesses and symptoms. These include headache, toothache, earache, rheumatism, and cramps. It is most commonly used in ointments for skin diseases and as an expectorant. The islands of Boeroe and Ceram in Malaysia have been the chief exporters of the oil. However, it is more expensive than eucalyptus oil and the quality specifications are quite rigid in the United States, so its commercial importance here is limited (Mortan, 1966).

The oil has also been promoted as an excellent mosquito repellent for certain species of mosquitoes, and it has been used to rid animals of lice and fleas (Guenther, 1950). In Florida, trees have been planted near homes and around pastures with the hope of reducing the mosquito problem. Some success has been reported (Schory, 1958).

Recently it has been noted that Melaleuca has become a respiratory irritant to sensitive people and causes allergic reactions in some people who come into physical contact with it (Mortan, 1969).

When Melaleuca honey started showing up in beehives, Florida bee keepers were concerned that it would destroy their industry. The honey was reported to have a distinctive taste and to be foul smelling. Since then, it has been found that by blending the honey it is salable to bakeries and health food stores, and Melaleuca has become important for producing package bees and wax (Mortan, 1966).

Introduction and Spread of Melaleuca in South Florida

Meskimen (1962) compiled a comprehensive narrative describing the people and areas involved in the introduction and cultural spread of Melaleuca in Florida. To review the sequence briefly, Melaleuca was introduced into Broward County near Davie by Dr. John C. Gifford in 1906 from seed he obtained from the Sidney Botanical Gardens in Australia. He specifically requested a species with the characteristics of the Eucalyptus that could withstand both the flooding and fires of the Florida environment.

At approximately the same time, A. H. Andrews of the Koreshan Unity Nurseries at Estero in Lee County obtained seed from Melbourne, Australia. Meskimen (1962) pointed out that, from two independent descriptions of the South Florida climate and topography, two Australian authorities independently recommended Melaleuca. Several other introductions may have occurred, possibly from seed obtained outside of Australia, but the authenticity of these introductions has been disputed. When Melaleuca first escaped is not known but presumably it occurred within a few years after its introduction. There are indications that Andrews may have scattered seed on various sites and even today the Koreshan Unity consider Melaleuca important in reforestation.

In 1936, H. Sterling of Davie scattered seed from an airplane over large areas of western Broward County. Its use as an ornamental, as windbreaks, and for fence rows has led to the establishment of many isolated pockets of reproduction. In 1940 and 1941 the U. S. Army Corps of Engineers operated a Melaleuca nursery and planted the species along the levees of the Lake Okeechobee Project to protect them from erosion.

Areas Being Invaded in Lee and Collier Counties

Several ecologists have described the natural features of South Florida and have noted with concern the introduction and spread of exotic tree species including Melaleuca. The most comprehensive descriptions have been written by Davis (1943), Craighead (1971), and Alexander (1973). The following is a summary of their descriptions.

South Florida is characterized by flat topography and low elevation supporting diverse plant communities delineated by slight changes in elevation and the concommitant effects of drainage, salinity, and fire that the different water regimes provide. Annual rainfall is about 1700 mm, with the majority falling between May and October.

Vast flatlands on either side of Lake Okeechobee support open pine flatwoods of Pinus elliotii (slash pine) and extensive areas of palmetto, grasses, sedges, and forbes, called wet prairies or dry prairies, depending on the extent of surface flooding during the wet season. Within the flatwoods and prairies are scattered cypress domes, sloughs, hardwood hammocks, and marshes. The Western Flatlands, as described by Davis (1943), extend as far south as northern and western Collier County where they gradually give way to cypress swamps and wet prairies in the Everglades Basin, the Big Cypress Swamp, and the mangroves.

Alexander (1973) described in detail the vegetation changes that have taken place in South Florida over the past 30 years due largely to the activities of people. The Western Flatlands, where they extend into Lee and Collier Counties, were lumbered extensively starting in 1925. At present large areas near Naples and Fort Myers have been urbanized or are slated for development. Because the Western Flatlands are generally higher than other areas and have well-drained sandy soils, the need for large drainage projects has been limited. The extensive Golden Gate Canal System does extend into the southernmost part of the Flatlands. Increasing amounts of land are being converted to farming, citrus, and cattle ranching, but these have generally spared the cypress stands and sloughs. Fires have played an active role in maintaining vegetation types and locally cause heavy damage during drought years. As for Melaleuca, Alexander (1973) stated that "The greatest threat to what is left of the original ecosystem is the rampant invasion of cajeput. The fate of the natural succession in the invaded areas of cypress and pine is unknown. Very few if any native woody species are seen under the dense cajeput canopy."

The Big Cypress area south of the Western Flatlands has been subjected to various degrees of manipulation and subsequent vegetation changes. Logging of the cypress and pine occurred between 1940 and 1957. The removal of most of the mature cypress from the large stands has changed their species makeup. Farming in the Big Cypress has been limited and generally unsuccessful except for cattle ranching in the north. Drainage canals have probably been responsible for the greatest changes in the western portion of the swamp. Drainage has lowered water levels, extended the dry period, and subjected the region to more frequent fires. These changes appear to have enhanced the movement of pine into areas formerly occupied by cypress.

The Big Cypress watershed has been divided into three subregions delineated by the direction of water flow and the extent of man-caused drainage. Subarea A covers about 1165 square kilometers (450 square miles) in the northeastern part of Collier County. It drains in a southeasterly direction into Conservation Area 3 and ultimately into Everglades National Park. Subarea B includes 1425 square kilometers (550 square miles) at the western end of the Big Cypress and is drained to the south and west by an extensive system of canals within the Golden Gate and Fahka Union Canal complex. These canals, which were completed in 1970, have accelerated runoff and possibly lowered water levels as much as 1.2 meters in a 140 square kilometer (54 square miles) area east of Naples. Subarea C covers 3755 square kilometers (1450 square miles) of eastern Collier County and except for the Tamiami, Turner River, and Baron River Canals, drains naturally to the south into the western half of Everglades National Park (Klein, 1970).

Much of the cypress swamp in subarea C remains inundated or wet for all but three or four months of the year. Even though fire causes some damage during drought periods, little vegetation change has been noted over the past 30 years (Alexander, 1973). Much of subarea B was formerly inundated each year during the wet season but now, with the completion of the Fahka Union Canal and the Golden Gate System, this area is effectively dry throughout the year. The primary function of these canals is to lower peak water levels to prevent flooding. The Fahka Union System contains about 30 weirs to control flow and reduce the possibility of overdrainage. Because the canals are shallow it has been stated that drainage from the shallow aquifer that supplies water to Naples is limited (McCoy, 1972).

The soils in Collier and Lee Counties consist of sands and marls of various depths overlying limestone rock. In many places the rock is exposed or just below the soil layer. In the Western Flatlands the soil depth to limestone ranges from 3 to 100 m, while in the Big Cypress and coastal areas the limestone may be exposed and pitted with solution holes. Generally the soil depth is from 0.6 to 1.5 m. These soils are predominantly fine sands, but in depressions and sloughs the amount of organic matter may change the texture considerably (Leighty, 1954).

The most common soil types in the pine lands of Western Lee and Collier Counties are Arzell and Pompano fine sands. These are characterized by being nearly level, slightly acid, and poorly drained. Much of the Big Cypress region that is not rockland or organic is occupied by various phases of Ochopee fine sandy marls. These consist of mixtures of marine sands and recent deposits of marl. The depth may range from 15 to 90 cm (Leighty, 1954).

Organic soils are found in the cypress swamps, sloughs, and ponds. In areas that have been drained and aerated or burned, the depth of these soils is greatly reduced. The organic soils vary from 5 to 8 cm layer of mucky fine sand to peaty muck, to deep deposits of brown peat. There is usually a layer of fine sand below the peat or muck (Craighead, 1971).

The vegetation of South Florida is subject to several environmental influences that check the successional sequence and maintain a situation of permanently deflected climaxes. These environmental influences include fire, drought, flooding, frost and hurricanes. The effect of extended drought (caused by the artificial drainage) is enhanced by the increased incidence and severity of fires, and this is particularly important to consider when studying the spread of Melaleuca. Historically, fire has played an important role in checking hardwood encroachment into the pinelands, prairies, and cypress swamps, and it has undoubtedly been related to many more subtle factors in the development and maintenance of the South Florida landscape. The increased frequency and severity of fire, on the other hand, may have significantly reduced the ability of the native vegetation to compete with an aggressive fire-adapted species like Melaleuca.

As previously stated, Melaleuca is associated with fire throughout most of its native range. The increase of fire in South Florida has undoubtedly aided its spread. In New Caledonia it has been suggested that Melaleuca is maintained by fire and would be succeeded by Acacia, *Psidium*, and *Lantana* in the absence of fire (Sachet, 1953). Whether the elimination of fire in South Florida would halt the spread of *Melaleuca* and allow succession to reclaim *Melaleuca*-dominated sites is not known, but any attempt to eliminate fire in order to control *Melaleuca* would lead to drastic changes within the native communities, which also burn under natural conditions.

The Fort Myers District of the Florida Forest Service, which includes Lee and Collier Counties, annually has the largest acreage burned by wildfires in the State of Florida. It also supports some of the largest stands of *Melaleuca*. Much of this area is subject to burning at any time of the year. For example, in the Fort Myers district in 1972, 21% of all fires occurred in March, 21% occurred from June through August, and 40% of all fires occurred from May through September (Hofstetter, 1973). Data on the acreage burned during these periods is not available, but generally the fires in the wet season are lightning caused, almost always burn out at night, are usually much less damaging; presumably the total acreage burned during the wet season is much less than the acreage burned during the dry season.

Objectives

To develop an overview of the role of a *Melaleuca* ecosystem in South Florida, several basic questions need to be investigated. For example, does the existence of *Melaleuca* significantly alter the ecosystem that it occupies or is there just a one-to-one replacement of cypress for *Melaleuca*, each providing the same function in the same manner? Does *Melaleuca*, through increased transpiration, reduce water levels, accelerate organic matter oxidation and reduce water storage capacity? Will *Melaleuca* perpetuate itself and facilitate its own spread by altering the hydroperiod, drying surface soils, and producing conditions conducive to fire? What are the effects of having a continually closed canopy over an ecosystem that normally (in the case of cypress) sheds its leaves, resulting in high light intensities at ground level during the winter?

To provide a basis for others to later answer these proposed questions, this study attempts to identify the conditions required by *Melaleuca* for successful establishment and to ascertain if there exists a relationship between the spread of *Melaleuca* and human-caused environmental changes. By defining the types of sites and conditions that are favorable for the invasion of *Melaleuca*, a more realistic evaluation of the role that *Melaleuca* will eventually play in South Florida can be made.

For the past year several laboratory and greenhouse experiments have been integrated with ongoing field studies, field observations, previous studies, and models to provide insight into the invading capability of *Melaleuca* under various site conditions. Descriptions of experiments and field investigations presented include (1) modeling; (2) germination tests under different moisture conditions; (3) initial seedling growth and response to various hydroperiods; (4) *Melaleuca* establishment on a variety of sites during different seasons of the year and under varying moisture conditions; and (5) seedling survival of naturally established *Melaleuca*. Field studies also included the notation of invasion patterns, and observation of site conditions at the border between *Melaleuca* stands and native vegetation.

PRELIMINARY MODELING

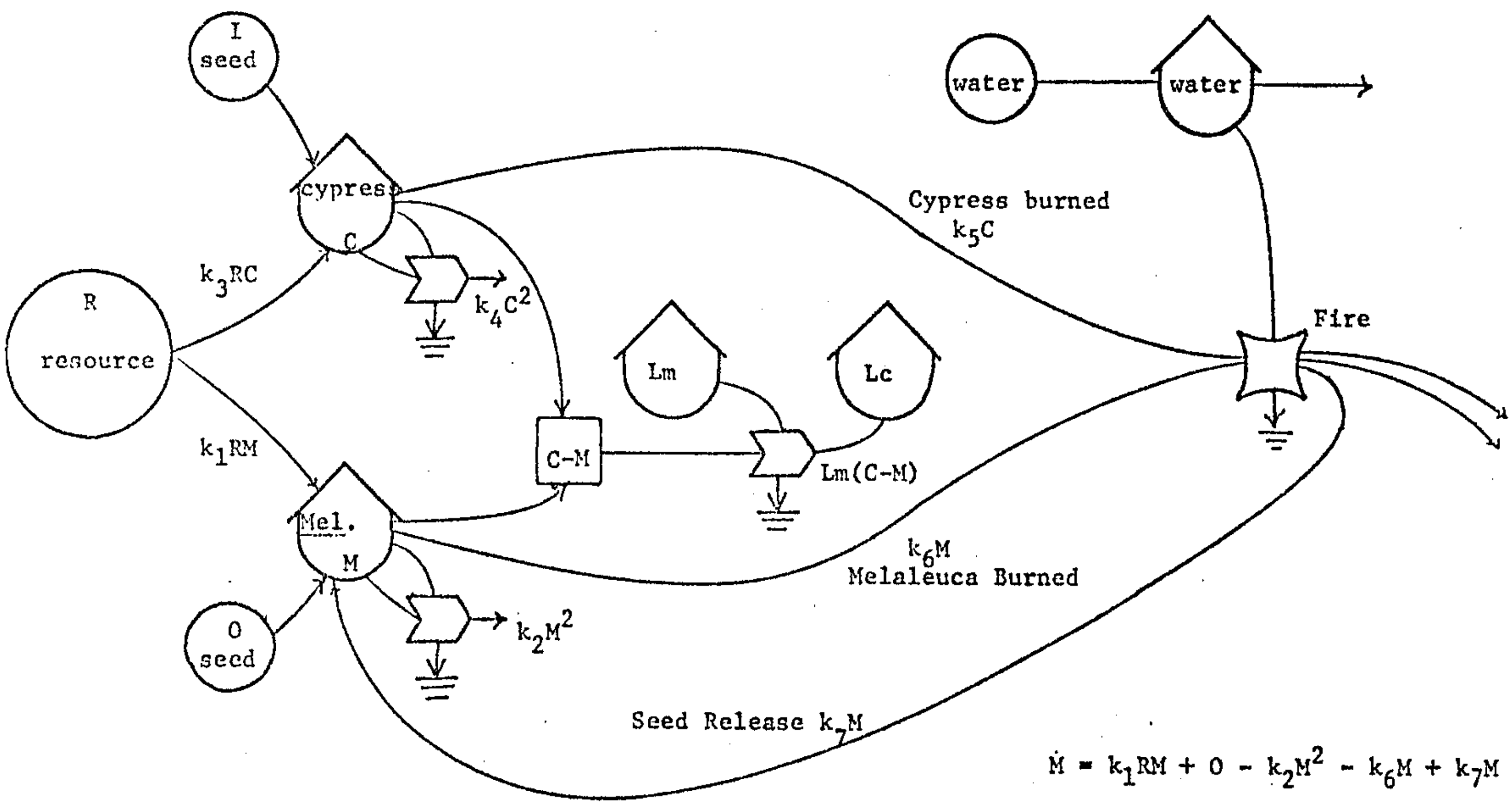
Modeling and computer simulation are important tools for looking at an entire ecosystem and trying to tie together various components of a problem. Models can be used both for illustrating expected responses under varied conditions and for providing clues to important parameters and various avenues of approach that may be utilized in investigating a particular problem.

Preliminary modeling is usually done when an investigation is in its initial stages of formulation and development. Modeling at this time forces the investigator to identify those aspects of the problem that are probably significant. If the model is then supported by field observation and measurement, the data collected can be used to develop more complex models, to extend the scope of a model simulation beyond the time restrictions encountered in the field study, and to manipulate different parameters for predictive purposes. In the case of this study a preliminary model was developed during the initial phase of the field and laboratory investigations.

Procedure

Figure 2 is a simple preliminary energy flow model of cypress and *Melaleuca* as they are affected by water level and fire. The model illustrates the two species utilizing an unlimited resource. Periodic drought-induced fire burns both cypress and *Melaleuca* biomass, while

Figure 2. Preliminary model showing *Melaleuca* and cypress utilizing an unlimited resource but being differentially affected by fire.



$\dot{M} = k_1RM + O - k_2M^2 - k_6M + k_7M$

$\dot{C} = k_3RC + I - k_4C^2 - k_5C$

$\dot{Lc} = L - Lm$

at the same time triggering *Melaleuca* seed release. The model was scaled using generalized biomass and energy flow figures (Table 1). Fire was induced by setting a threshold level for the water table. In other words, below a certain amount of water storage, conditions would be such that destructive fire would occur. The severity of the fire was controlled by the amount of biomass consumed. Water level fluctuations were simulated by using a sine wave: the undulation representing the rise and fall of water levels. In this case each cycle was time-scaled to represent a six-year drought cycle. Because biomass loss or increase does not signify an actual increase in area occupied or being invaded, a land occupancy factor is included. Land occupied by one species is dependent on its own biomass increase or loss, on the increases and losses of the competing species, and on the land occupied by the competing species.

Results

The three simulations presented (Figs. 3-5) show the increasing effects of lowering the water level and subjecting the two species to various degrees of fire severity. In the first simulation (Fig. 3) the drought was not severe enough to trigger a fire and no excess losses occurred on either species. Both continued to produce biomass within the confines of the sites that they already occupied. Growth continued until a steady state was reached.

As the severity of the drought increased (Fig. 4) destructive fires occurred. During each drought period both species lost biomass. *Melaleuca* sustained less loss due to its fire released seed and fire resistance. Cypress, although significantly burned during each drought

TABLE 1. Estimates of values used in the model simulation and pot settings

Variable	Coefficient	Unit	Estimated Value	Pot Setting
Resources	R	$Kcal/m^2/yr.$	1,460,000	----
Cypress	Initial C	$Kcal/m^2$	40,000	.660
Melaleuca	Initial M	$Kcal/m^2$	20,000	.330
Cypress seed	Initial I	$Kcal/m^2/yr.$	730	.007
Melaleuca seed	Initial O	$Kcal/m^2/yr.$	730	.007
Resource Utilization by Cypress	K_3	$Kcal/m^2/yr.$	18.250	.270
Resource Utilization by *Melaleuca*	K_1	$Kcal/m^2/yr.$	18.250	.540
Cypress Respiration	K_4	$Kcal/m^2/yr.$	10,950	.250
Melaleuca Respiration	K_2	$Kcal/m^2/yr.$	7,300	.650
Cypress burned	K_5	$Kcal/m^2$	20,000	.030
Melaleuca burned	K_6	$Kcal/m^2$	4,000	.010
Melaleuca seed released	K_7	$Kcal/m^2$	1,825	.005
Drought Threshold			.2 (highwater level)	.2
Land in Cypress	Lc	percent	90	.900
Land in *Melaleuca*	Lm	percent	10	.100
Total land	L			

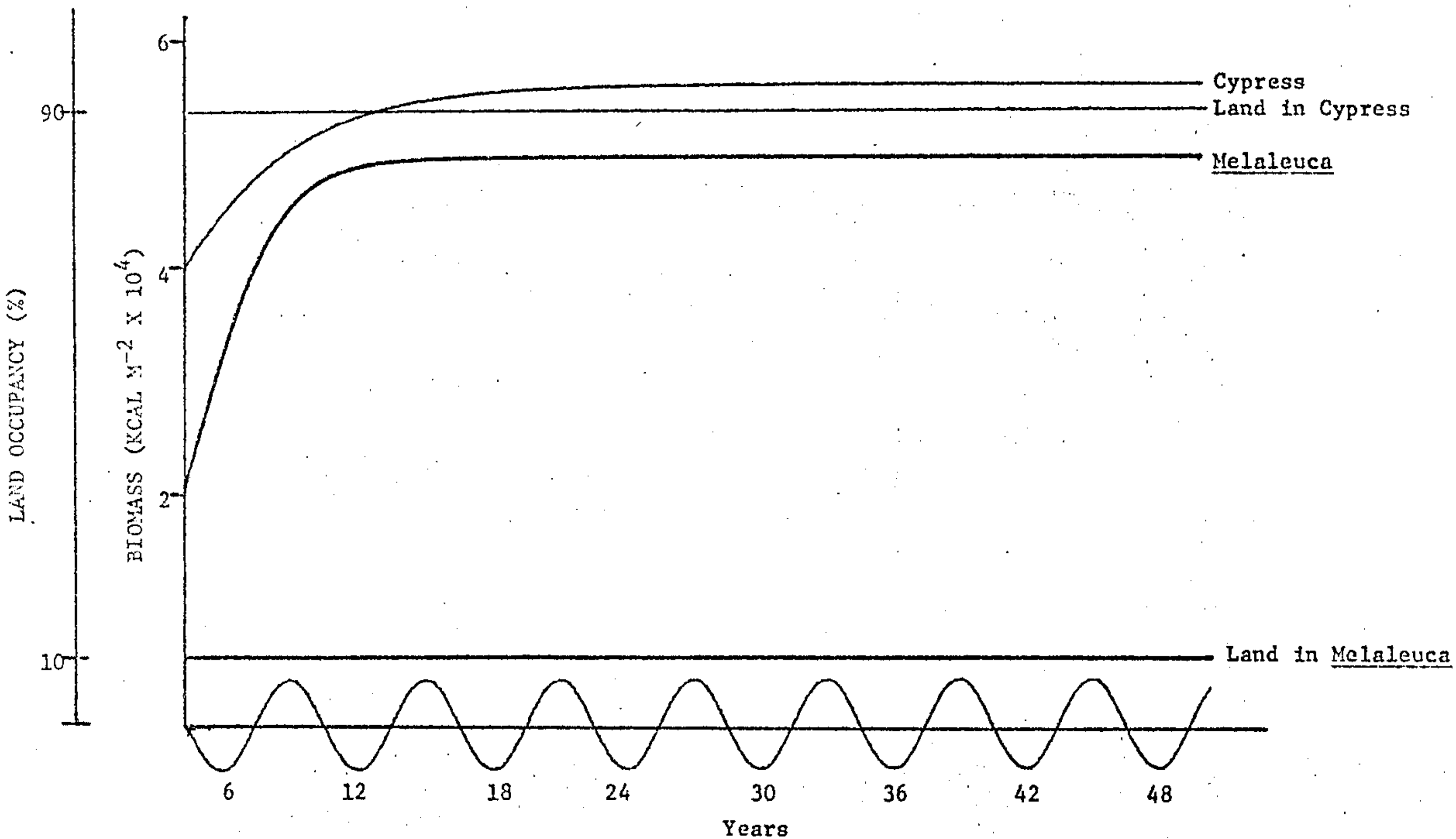


Figure 3. Simulation #1 showing cypress and *Melaleuca* growth without fire.

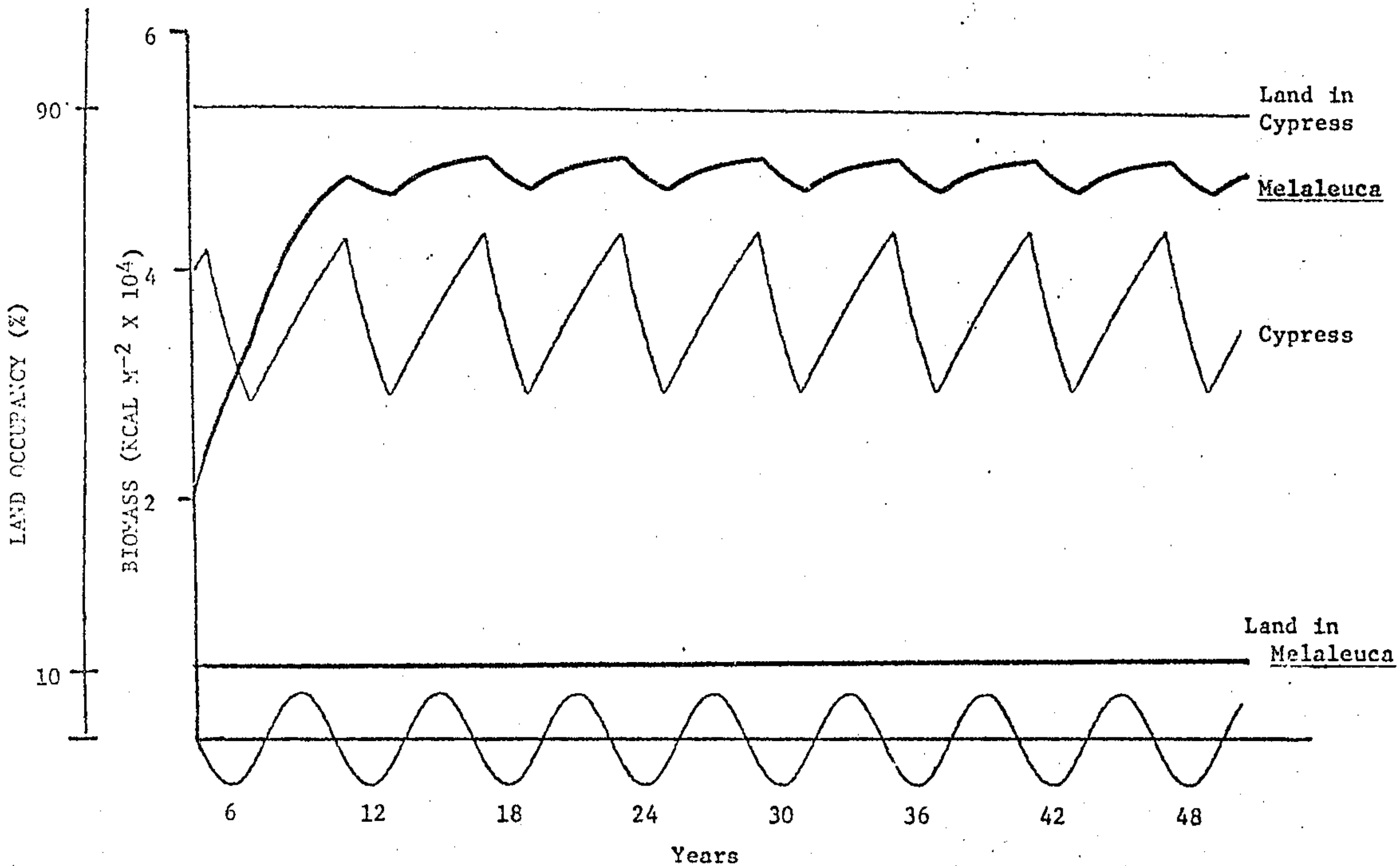


Figure 4. Simulation #2 showing both *Melaleuca* and cypress being burned by periodic fires, but with no *Melaleuca* invasion taking place.

period, quickly returned to its initial condition, thus preventing any change in the amount of land occupied by either of the two species. In other words, cypress biomass in the form of leaves, branches, and seedlings was readily consumed during burning, but the fire resistance of the larger trees and seed input prevented any change in the occupancy of the land.

As droughts became more severe due to artificial drainage (Fig. 5), fire caused more damage to cypress than to *Melaleuca*. The trees were destroyed to such an extent that the cypress forest did not recover before the next drought period and the site was open to *Melaleuca* invasion.

The three simulations illustrate the increasing effect of hydroperiod shortening upon the cypress ecosystem, and the importance of fire as a principle factor reducing the capacity of cypress to maintain itself on a site where the hydroperiod is altered and drought severity increased. On the other hand, fire may have a stimulating effect on *Melaleuca* growth and site invasion.

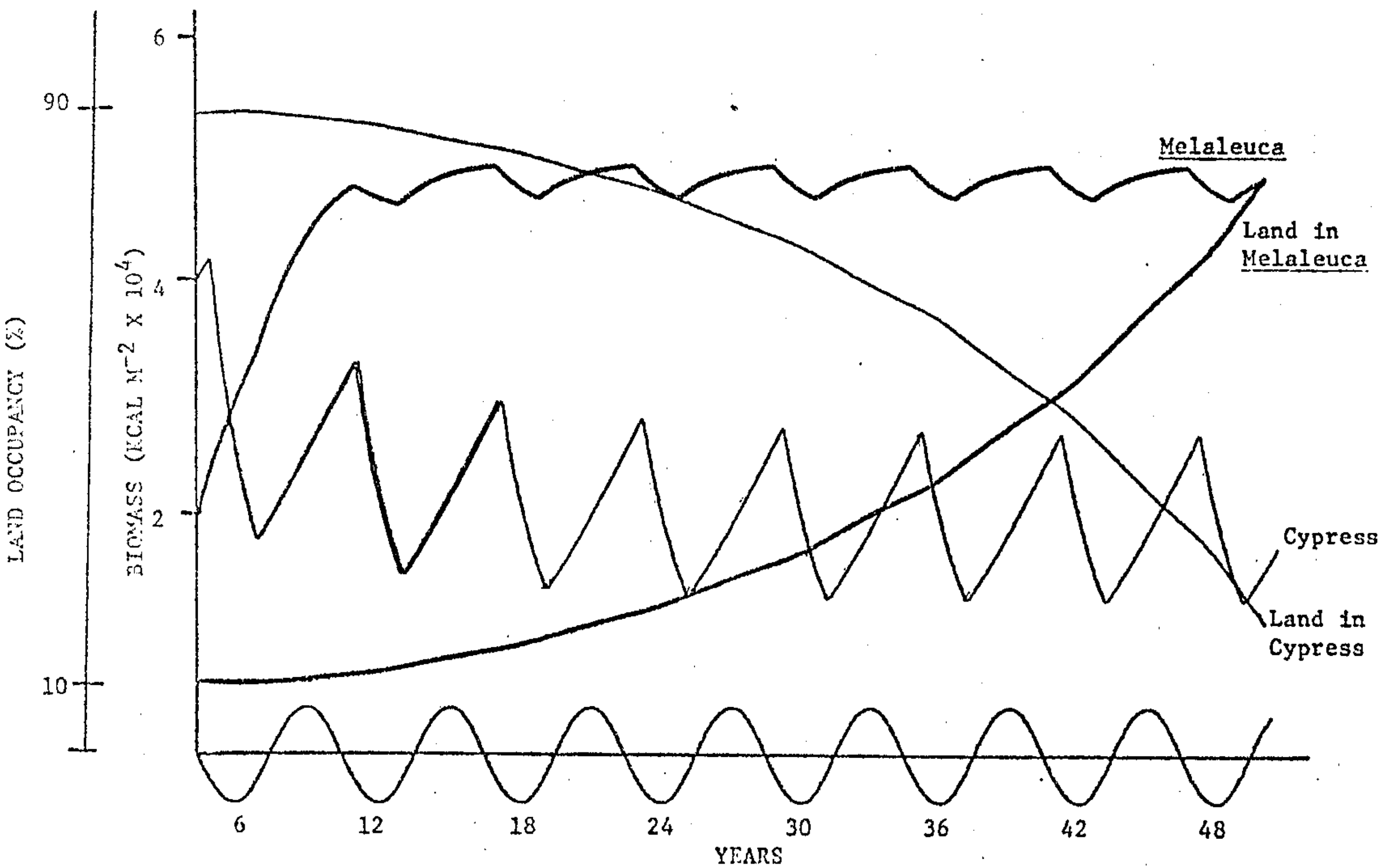


Figure 5. Simulation #3 showing *Melaleuca* invasion of cypress forests after periodic severe fires.

SEED GERMINATION IN THE LABORATORY

Meskimen (1962) suggested that the different-aged seed crops on a tree may exhibit different degrees of viability. He selected eight seed crops from one branch and germinated them under controlled conditions. His results showed that the most recent seed crop exhibited the least germination while the third and fourth crops produced the best results. The second crop was midway between these while the older crops germinated more slowly and produced slightly less than the average germination rate of 20 to 28%. The results suggest that the seeds require a ripening period within the capsule and that older seeds require slightly longer exposure to favorable conditions in order to effect germination. Jakimova (1965) showed that stratification retarded the germination of Melaleuca seed.

Objectives

Melaleuca seed requires only a few days to germinate. The moisture requirements to initiate germination are thus probably easily satisfied. However, for successful establishment, moist conditions must be maintained over a long period of time. This suggests that successful germination and establishment may be limited to certain seasons of the year when adequate moisture is available, and that seed can be easily destroyed if initial moisture levels are not maintained.

The experiment described in this section was attempted to gain information on (1) the amount of germination to be expected under ideal conditions; (2) the number of days needed to effect germination; and (3) the effect of an initial period of moisture followed by drying on germination.

Procedure

Five batches of three hundred Melaleuca seeds were selected randomly from seed collected near Estero in Lee County. Each batch was placed in a petri dish on filter paper moistened with distilled water, covered, and placed under a light bank (2000 F. C., 12 hour light/dark cycle) in an air conditioned room (23 to 26°C). A sixth batch was prepared in a similar manner but the seeds were submerged under approximately 1 cm of distilled water. The seeds would sink if surface tension was broken by agitating the water. A seventh batch was prepared with 300 seeds selected from seed capsules located on an 8-cm diameter main stem, thus insuring that the seeds were at least several years old. The first four batches of seed were subjected to different schedules of wetting, drying, and rewetting by removing the glass covers. Treatments 5, 6, and 7 remained covered for the duration of the experiment. Daily seed germination was tabulated for ten days. The treatment schedules and results are summarized in Table 2.

Results

Germination was initiated on the third day in the control (#5) and the submerged (#6) treatments. Germination was delayed one day in treatments #1 and #2 and 2 days in treatment #3. Thirteen seeds germinated in treatment #4 before the dry period, all of which died before

TABLE 2. Daily, total, and percent germination obtained from seven batches of 300 seeds subjected to different moisture regimes.

GERMINATION TESTS

No.	Treatment	Day 1/2	1	2	3	4	5	6	7	8	9	10	Total	%
1	Wet 12 hours then air dried 12 hours before rewetting	0	dry 0	0	0	66	21	16	16	2	0	0	121	40
2	Wet 24 hours then air dried 24 hours before rewetting	0	0	dry 0	0	13	35	2	17	3	0	0	70	23
3	Wet 48 hours then air dried 24 hours before rewetting	0	0	0	dry 0	0	19	24	3	1	0	0	47	16
4	Wet 72 hours then air dried 24 hours before rewetting	0	0	0	13	dry 0	0	0	15	13	8	0	36	12
5	Control---moist conditions	0	0	0	12	62	11	4	11	15	0	0	115	38
6	Submerged	0	0	0	14	40	2	3	15	4	0	0	78	26
7	Seeds from old capsules--moist conditions	0	0	0	0	23	28	7	11	6	0	0	75	25

rewetting and further germination was delayed 2 more days. Treatments #1 and #5 (Control) exhibited the greatest germination percentage. Less germination occurred as the dry period came later. The older seeds in treatment #7 and the submerged seed in treatment #6 exhibited approximately 35% less germination than the control.

HYDROPERIOD VARIATION IN THE GREENHOUSE

Melaleuca exhibits a preference for sites that are periodically flooded and, at least under some conditions, its seeds will germinate under water; the seedlings will tolerate total submergence for an undetermined amount of time. Trees growing in flooded areas develop a fibrous mat of roots just below the high-water level, and this root mat is apparently sloughed off at the end of each wet season. Large, permanent, woody adventitious roots have been observed on trees growing in the impounded waters of Conservation Area 3 in Dade County, where the soil surface may remain saturated even during the dry season.

Adventitious roots may develop on any part of the tree that is in contact with the water, including branches, horizontal stems, and leaves. Greenhouse experiments conducted by Meskimen (1962) indicated that *Melaleuca* will grow better in undrained conditions, and that plants submerged for 84 days did not lose their capacity for normal growth once the excess water was removed.

Objectives

This greenhouse experiment was designed to (1) determine the effect of different water regimes on seedling growth and development, and (2) gain information on the length of time *Melaleuca* seedlings can withstand submergence.

Procedure

Batches of approximately 300 seeds were placed in a total of 35 13-cm clay pots containing a greenhouse soil-sand mixture. The pots were divided into seven groups, each group consisting of five pots. Each group was subjected to different treatments of water level fluctuation by placing the groups under different schedules of submergence using large galvanized steel tubs filled with Gainesville tap water (Fig. 6). Water level was maintained at least 10 cm above the soil in the pots and the water was replaced once a week. The different treatments (Fig. 7) were as follows:

Treatment #1 - Soil maintained moist but well drained for the duration of the experiment.

Treatment #2 - Soil maintained saturated for the duration of the experiment by raising the pots within the basins so that the water level corresponded to soil level in the pots.

Treatment #3 - The pots were alternated on a two week basis, being submerged for two weeks in the tub then removed and maintained moist but well drained for two weeks before resubmergence for another two weeks.

Treatment #4 - Pots alternated every three days from submerged to drained.

Treatment #5 - Soil kept moist but drained for two months and then submerged for the duration of the experiment.

Treatment #6 - Soil kept moist but drained for one month and then submerged for the duration of the experiment.

Treatment #7 - Pots continuously submerged for the duration of the experiment.

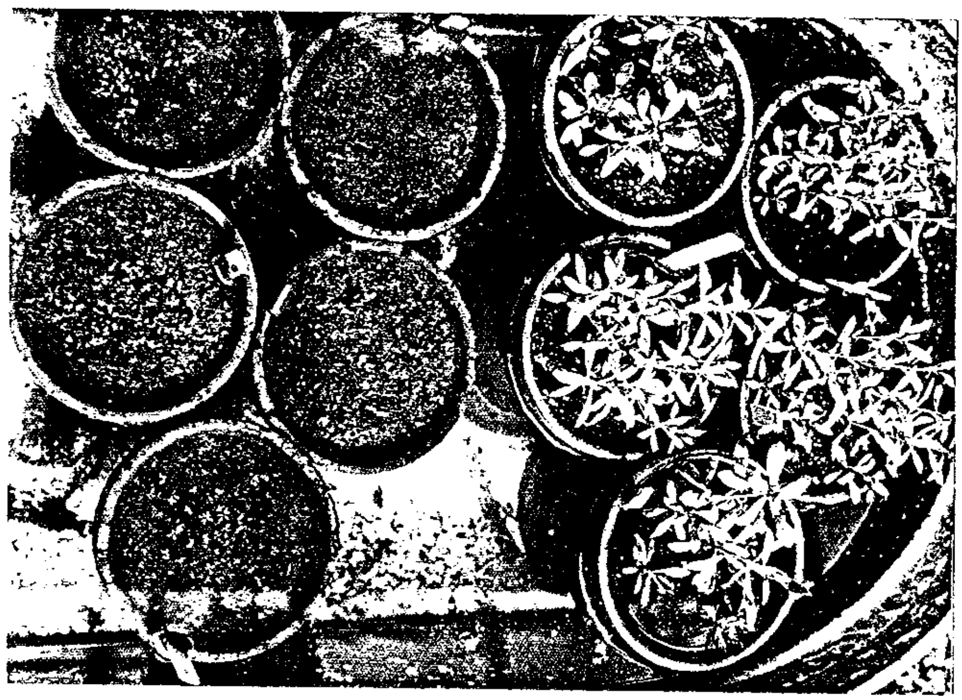
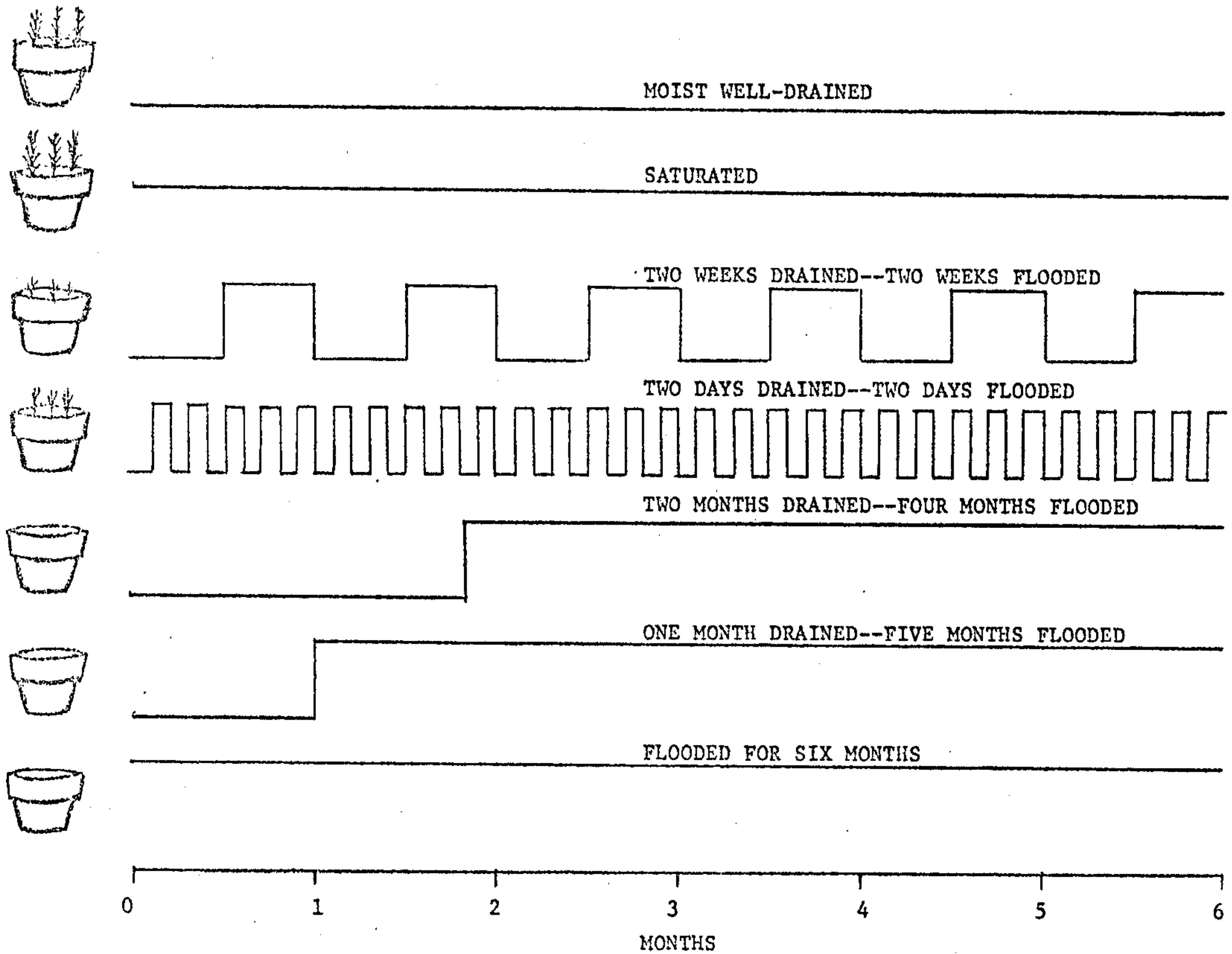


Figure 6. Two treatments in the hydroperiod variation experiment.
Left: Five replications of the submerged treatment.
Right: Five replications of the saturated treatment.

Figure 7. Diagram of the treatment schedules in the greenhouse hydroperiod variation experiment.


MOIST WELL-DRAINED
SATURATED
TWO WEEKS DRAINED--TWO WEEKS FLOODED
TWO DAYS DRAINED--TWO DAYS FLOODED
TWO MONTHS DRAINED--FOUR MONTHS FLOODED
ONE MONTH DRAINED--FIVE MONTHS FLOODED
FLOODED FOR SIX MONTHS
0
1
2
3
4
5
6
MONTHS

Once germination occurred the seedlings were thinned to ten trees per pot. Height growth measurements were made after 3 months and 6 months. After 6 months, treatments 1, 2, 3, and 4 were harvested for root and shoot dry weight determinations. Two pots each from treatments 5, 6, and 7 were removed from the tubs and maintained moist but well drained. The other three pots of these treatments are still being maintained under flooded conditions after 12 months.

Results

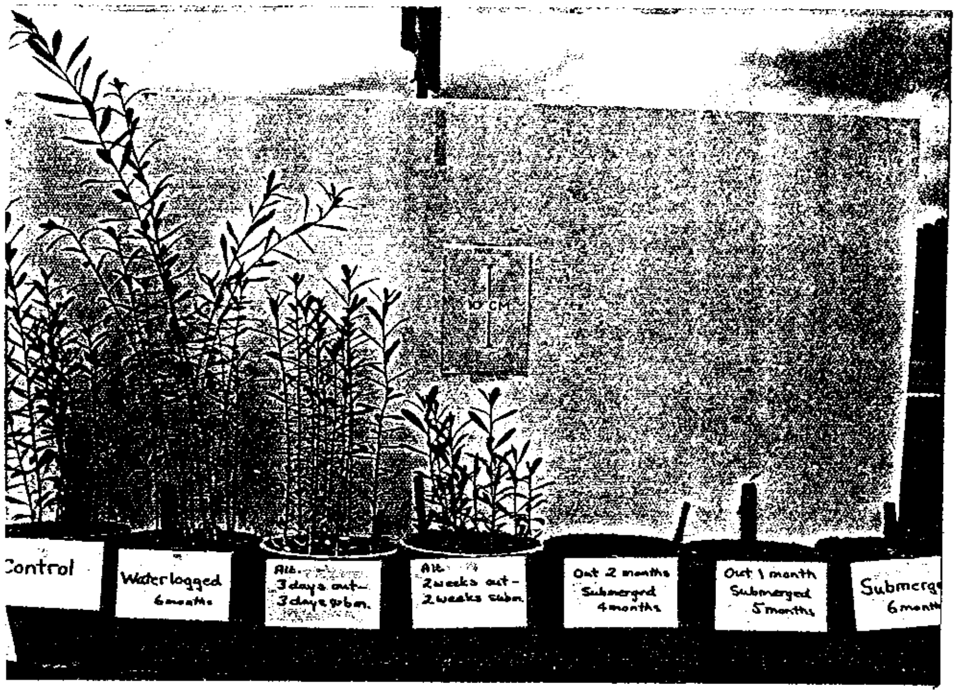
The seeds in each of the treatments exhibited no gross differences in germination rate or total germination. No counts were made because the amount of seed sown was only approximate. After thinning, some seedlings were lost by the mechanical disturbance encountered while removing the pots from the water and vice versa. These losses were not included in the calculation of average height growth and average dry weight; therefore, it is possible that the seedling growth may have been greater in those pots with less than 10 seedlings due to less crowding and competition, but this is unlikely to have affected the results significantly. No losses occurred that could be attributed to the detrimental effects of a particular treatment.

The comparative growth differences after three and six months are shown in Figure 8. Average height in each of the seven treatments is illustrated in Figure 9 with the measurements taken after 3 and 6 months. After 3 months the height was greatest in the well-drained treatment (#1) which averaged 13.0 cm per tree, while the trees in the saturated treatment (#2) grew an average 11.9 cm per tree.

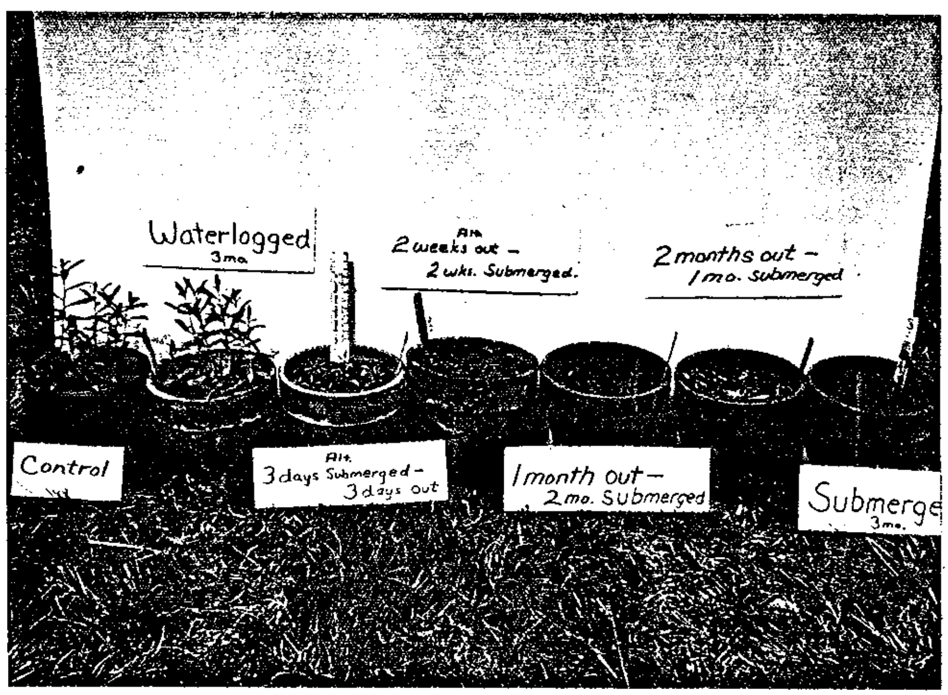
Measurements taken after 6 months showed that the average height

Figure 8. Growth differences in the hydroperiod variation experiment after (a) three months; and (b) six months.

(a)


ontrol
Waterlogged
6 months
Alt.
3 days out–
3 days subm.
Alt.
2 weeks out –
2 weeks subm.
Out 2 months
Submerged
4 months
Out 1 month
Submerged
5 months
Submerg

(b)


Waterlogged
3mo.
Alt.
2 weeks out –
2 wks. Submerged.
2 months out –
1 mo. submerged
Control
Alt.
3 days Submerged –
3 days out
1 month out –
2 mo. Submerged
Submerge
3mo.

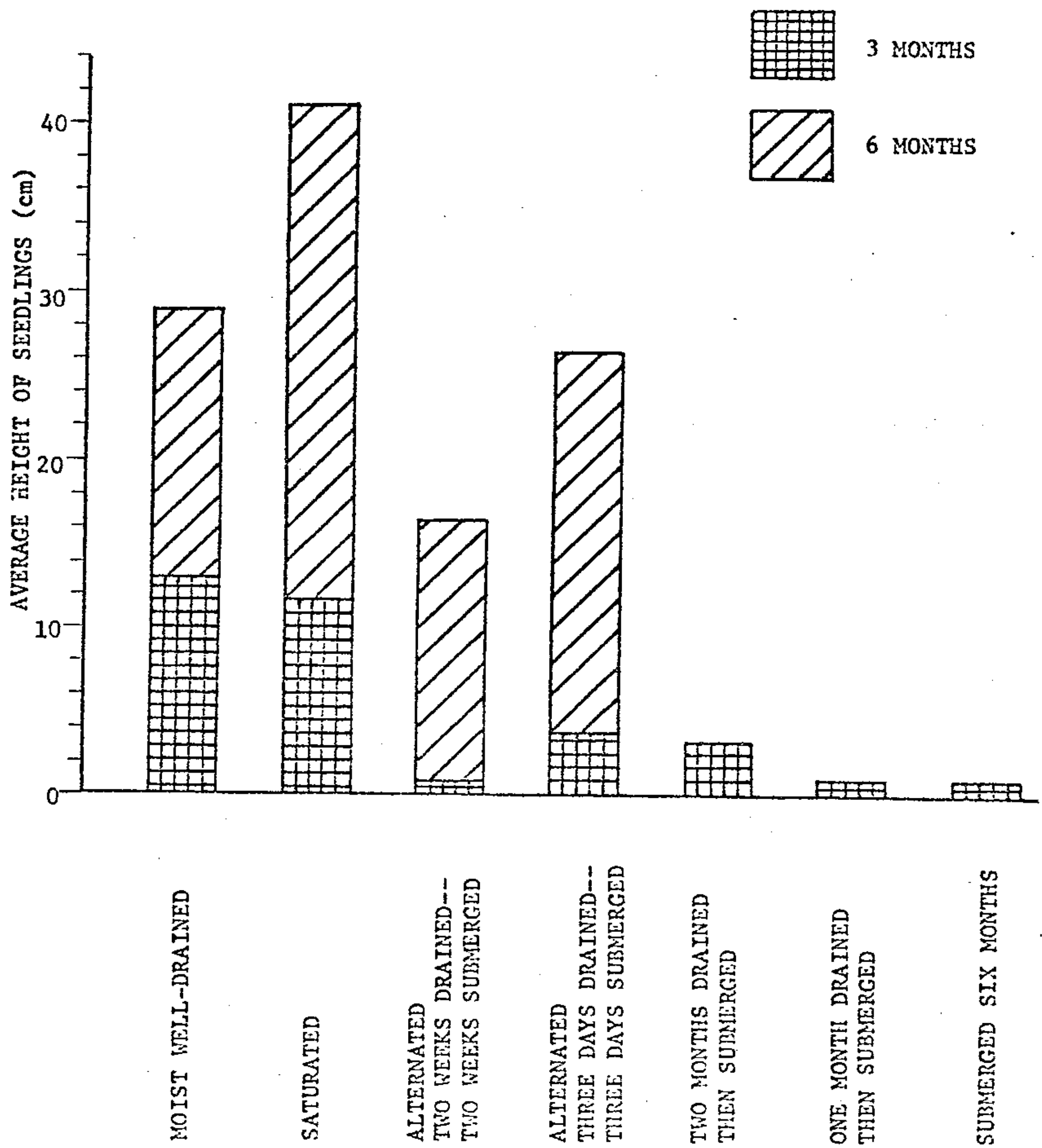


Figure 9. Mean height of the seedlings in each treatment after three and six months.

of the seedlings grown in the saturated soil (#2) exceeded by 12 cm the average height of the seedlings grown in moist well-drained soil (#1). Using a t-test, the difference between the means was determined to be significant to the 99.5% confidence level.

Although the seedlings growing in the saturated soil were considerably taller than those in the moist well-drained treatment, they seemed to produce weaker stems that were unable to support the aerial portions in an upright position. This may be a normal response in a rapidly growing tree; however, it appears from the very little difference exhibited between the average dry weights of the shoots and roots from these two treatments (Fig. 10), that less biomass is produced under saturated soil conditions. Possibly more intercellular spaces are produced under saturated soil conditions to facilitate the diffusion of oxygen through the stem to the roots. The roots in treatment #2 (saturated soil) also protruded above the soil level around the edges of the pot. When the seedlings in this treatment were harvested, it was found that a considerable portion of the root system was between the soil surface and a dense algal mat that developed over it.

The seedlings in treatments 6 and 7 (submerged most or all of the time) produced leaves that appeared to be morphologically distinct from normal leaves. They were considerably smaller than the normal leaf, more lanceolate in shape, and developed in a tight rosette without any apparent lengthening of the internodes. The seedlings in treatment #5 (moist 2 months then submerged) lost their normal leaves after submergence, then produced similar clusters or rosettes of leaves at the end of the stem. A thick algal mat developed over the soil surface in each of the treatments that were submerged for a considerable

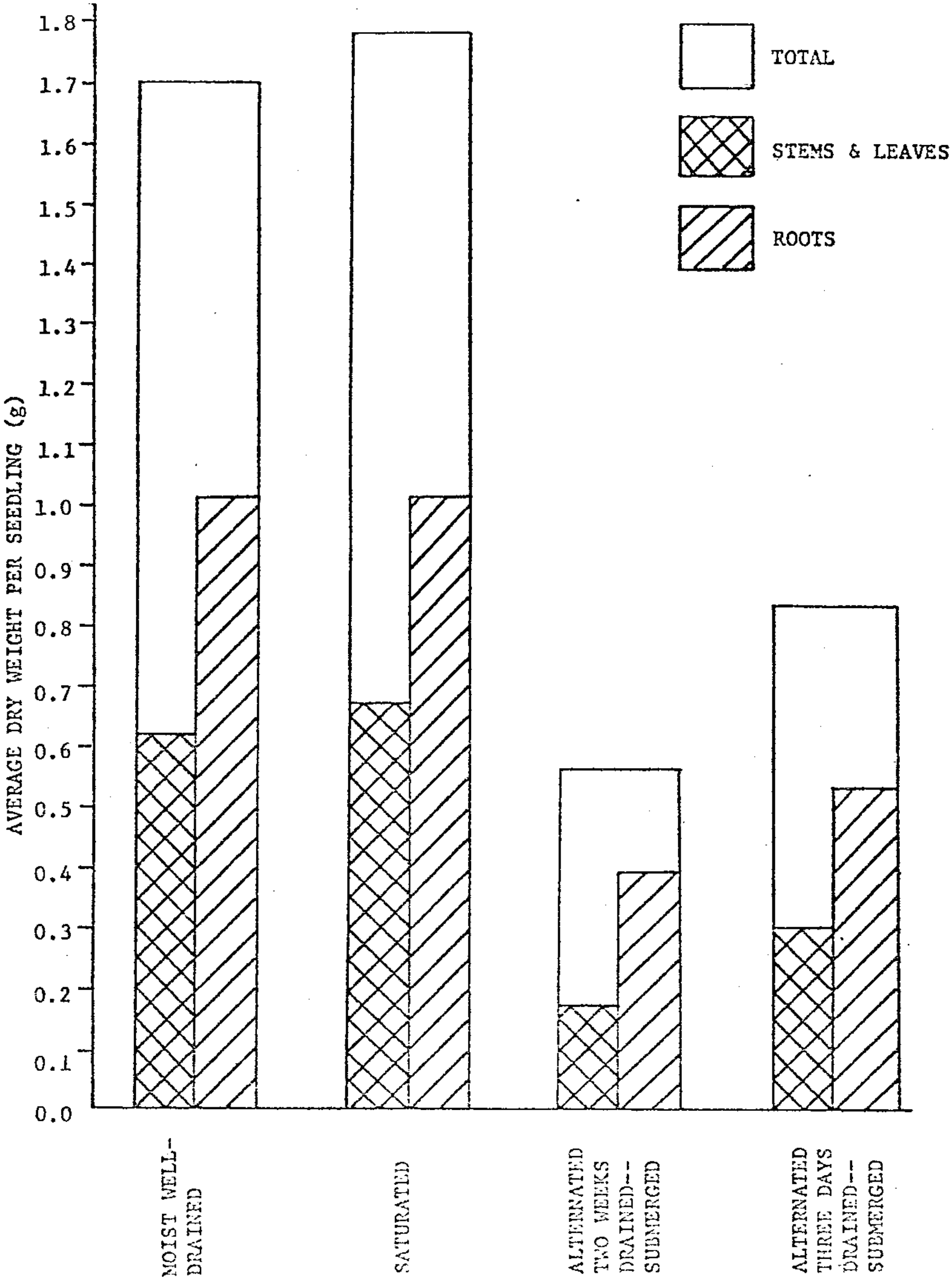


Figure 10. Average shoot, root, and total dry weights of seedlings after six months.

amount of time; in some cases the algal mat almost completely covered the seedlings.

After ten months only two seedlings remained in the treatment that was continuously submerged. In the other two submerged treatments no surviving seedlings could be detected. Two months later, or after one year of total submergence, only one seedling, which was almost completely covered with algae, remained. The seedlings that were in the pots that were removed from submergence after six months appeared to resume normal growth.

THE RESPONSE OF MELALEUCA TO ANAEROBIC SOIL CONDITIONS

From the results of the previous experiment, it seems likely that *Melaleuca* can grow at least equally as well under saturated or flooded conditions as under moist, well-drained conditions; however, observations in the field seem to indicate that *Melaleuca* prefers seasonally flooded sites over those which are continuously flooded. This suggests that long term flooding may be detrimental to *Melaleuca* growth, or at least it may be unable to compete with cypress on continuously flooded sites and that low dissolved oxygen levels in the water may be a determining factor. Generally, in aquatic ecosystems, the amount of dead organic matter present has a strong affect on the amount and distribution of dissolved oxygen (Ruttner, 1963). Fires during seasonal droughts can consume the muck and peat, thereby reducing the amount of oxidizable organic matter in the water when the site is flooded and probably increasing light intensities for photosynthesis by eliminating some of the vegetation shading a site. Drainage aerates organic soils which increases their oxidation. This suggests that dissolved oxygen levels may be higher in floodwaters on sites that are relatively open, are flooded for short periods, and have been recently burned.

Objectives

The following experiment was set up in an attempt to find out whether *Melaleuca*, at least in the short run, is adversely affected by anaerobic soil conditions caused by low oxygen levels in flood waters. If so, this would suggest that the continuing growth of Melaleuca on a site may be dependent on fire and the maintenance of relatively short periods of flooding.

Procedure

Ten Melaleuca seedlings were grown from seeds in the greenhouse. They were divided randomly into two groups and each group was planted in a 19-liter glazed crock. The two crocks contained organic soil collected from a cypress strand in southern Collier County. Both crocks were flooded with distilled water, leaving about 8 cm of water standing above the soil level. The crocks were covered with cardboard to prevent algal photosynthesis, and the trees protruded through holes in the cardboard. Air was bubbled through the surface water of one of the treatments. The dissolved oxygen content of the water of both treatments was monitored periodically using a YSI Model 54 Oxygen Meter. Height growth of the seedlings was recorded at the beginning of the experiment and after 34 days.

Results

The surface water of the aerated treatment remained saturated with dissolved oxygen for the duration of the experiment, while in the unaerated treatment dissolved oxygen averaged 1.1 ppm. Table 3 shows the initial height of each seedling, height after 34 days, the change in height and mean height. Seedlings in the nonaerated treatment exhibited a mean height growth of 43.4 cm while the mean height growth of the aerated seedlings was 41.5 cm. A t-test of the hypothesis

TABLE 3. Seedling growth under aerated and anaerobic soil conditions.

	TREATMENT					
	NON-AERATED			AERATED		
	Initial Height (cm)	Height after 34 days (cm)	Diff. (cm)	Initial Height (cm)	Height after 34 days (cm)	Diff. (cm)
	40.0	84.2	44.4	26.0	70.8	44.8
	35.5	78.5	43.2	47.8	101.8	54.0
	34.9	81.0	46.1	44.1	88.1	44.0
	35.1	78.6	43.5	32.6	58.2	25.6
	53.5	88.4	34.9	39.8	79.0	39.2
Mean	39.8	82.1	43.4	38.1	79.6	41.5

that the treatments did affect height growth indicated that there was no significant difference between the mean height growth of the two experiments.

The trees in the nonaerated treatment produced a massive amount of adventitious roots between the water level and the soil, and the roots within the soil penetrated only 8 cm. The soil, when removed, produced the distinctive smell of hydrogen sulfide, indicating that it was anaerobic.

Roots in the aerated treatment extended to the bottom of the crock, indicating that the air supplied at the surface was able to diffuse into the soil. Only a few adventitious roots were produced. Root biomass measurements were not taken due to problems in extracting the roots from the soil. However, there was no distinctive differences in root appearance.

FIELD STUDIES

Although greenhouse and laboratory experiments can provide some indication of what to expect under field conditions, one is hesitant to draw conclusions based on these results alone. The important question still remains: under what field conditions will *Melaleuca* successfully invade a site? Site conditions favorable to *Melaleuca* invasion were studied by Meskimen (1962). He seeded several sites having different soil characteristics and supporting various vegetation types. In the greenhouse, he simultaneously ran germination tests on soil samples collected at each site. His results indicated that *Melaleuca* did well on acid sandy soils, while alkaline marl soils did not generally induce germination. Good germination was obtained on soils already supporting *Melaleuca*, indicating that the large stands in Lee County are not only the result of the initial introduction there but also a response to favorable soil conditions. Ochopee marl soils did not generally induce germination, even though some of the sites already supported *Melaleuca* plantations. This indicated that even on unfavorable sites, conditions at times may be conducive to establishment. This is apparent when one considers that Meskimen (1962) pointed out that by 1960 a 14-year-old plantation growing on Ochopee marl near Monroe Station in Collier County had not produced any reproduction. Since then it has reproduced and spread several miles from the original plantation. This may be an indication that soil characteristics are not as significant as previously believed and that moisture conditions present at the time of seed release and during initial establishment may be at least as important. Meskimen (1962) concluded that his results supported the hypothesis that germination and establishment may be controlled by soil pH and its ramifications, and that much of South Florida's wetlands that are underlain by alkaline marls are not as susceptible to Melaleuca invasion as are those areas underlain by acid sands.

The present distribution and direction of spread of Melaleuca in South Florida are along the east and west coasts, and centered around the areas of original introduction. It has been generally assumed that these distribution patterns are an expression of prevailing winds and drainage patterns that act as seed disseminators. This explanation has led to the conclusion that the vast inland areas of South Florida are relatively free of Melaleuca due to the paucity of seed reaching these areas and that it is only a matter of time before Melaleuca will become a conspicuous part of these inland ecosystems.

Thus the two predominant explanations for the present distribution and future spread of Melaleuca are (1) Melaleuca will be largely limited to the east and west coasts by differences in the soil characteristics, and (2) the present distribution and direction of spread are controlled by biogeographical influences, including the availability of a seed source.

Objectives

It seems unlikely that Melaleuca would be adapted to practically all sites in South Florida. Obviously there are sites that have been more susceptible to *Melaleuca* invasion than others. I feel that certain definable site conditions, both biological and physical, are prerequisites for *Melaleuca* establishment, and that *Melaleuca* will be largely limited to these sites in South Florida.

Field studies were set up to determine what types of sites are suitable for successful *Melaleuca* establishment and to delineate some of the important parameters that influence germination and provide for subsequent growth and survival. The factors considered were the time of year of seed release, soil moisture requirements, the influence of water level and hydroperiod, the effect of site disturbance and land use history, and vegetation type.

Procedure

Initially six study sites were selected, one in each of the following vegetation types: pine flatwoods, mixed hardwood--cypress, dwarf cypress, sawgrass wet prairie, mature cypress, and mangrove. Four sites were established in January 1974. Studies were begun in the mature cypress forest and sawgrass sites in February. Two more sites were later established as conditions and preliminary results presented new problems. A mixed hardwood--cypress site burned in April, so a plot was established there in May. An eighth site was established in late July 1974 as water conditions on the other sites indicated that the water levels on these sites were probably not significantly altered by drainage. This new site was established in a well-drained cypress stand with two drainage canals located within 200 m of the plot, one to the south and the other to the west.

Plot numbers, date of establishment, location, vegetation type, and general characteristics of the field plots are listed in Table 4. Figure 11 shows the location of the eight sites.

At each site a 20 m by 20 m plot was arbitrarily chosen and marked off with a north-south, east-west orientation. An attempt was made to lay out the plots over an area exhibiting varying degrees of cover, vegetation changes, and topography that appeared common and representative of conditions found in Southern Florida. The plots were divided into 0.2 m subplots, each a meter apart, with five subplots chosen for each month of the study. Each of the five subplots were seeded monthly with 1 g of seed. The seed was collected from a large uniform *Melaleuca* stand near Estero, Lee County, and was periodically tested for viability. Other subplots on the same plots were randomly selected for the planting of greenhouse-grown seedlings. The original plan was to seed 5 subplots on each plot approximately once a month for at least a year and record germination and survival. The longest time between seedings was 57 days, the shortest was 23 days, and the average was 34 days.

Plantings were not carried out on a monthly basis. It was intended to get at least 5 seedlings established as soon as possible on each plot and observe their growth through the year. The first planting did not take place until March 31. This was well into the dry season and practically all of the seedlings did not survive their first month. A second planting was made on May 25. At this time the soil on all sites was moist, due to several early wet-season storms. Nevertheless, only about half of the seedlings survived the planting. Five subplots on each plot were again planted in July, when most of the sites were flooded. In this case, survival was 100% after the first month. Also, plots #2, #3, and the newly established plot #8 were planted in August with both

TABLE 4. Study plot locations, dates of establishment, and descriptions.

PLOT	DATE ESTABLISHED	VEGETATION TYPE	LOCATION	CHARACTERISTICS
1	January 18	Longleaf pine flatwood	Estero, Lee County.	Sandy well-drained soil.
2	January 19	Mixed hardwood--cypress swamp (not burned within two years)	South of Alligator Alley on the east side of the Fahkahatchee Strand.	Shallow sandy peat soil; drained in dry season with 15-35 cm of surface water during the wet season.
3	May 25	Mixed hardwood--cypress swamp (burned in April 1974)	Adjacent to the south side of plot #2.	Same as plot #2 except slightly higher topography with 5-25 cm of surface water in the wet season.
4	January 19	Dwarf cypress	North of the Dade-Collier Training Jetport in eastern Collier County.	Shallow sandy marl soil; drained in the dry season, 5-25 cm of surface water in the wet season.
5	February 16	Saw-grass wet prairie	One mile west of 40 Mile Bend in western Dade County.	Shallow marl soil over limestone; drained in the dry season, 10-20 cm of standing water during the wet season.
6	February 16	Mature cypress strand	Three miles east of Monroe Station in Collier County.	Muck to peat soil; drained in the dry season, 20-70 cm of surface water during the wet season.
7	January 19	White mangrove--*Spartina* swamp	Five miles NW of Carnestown in Collier County.	Brown fibrous peat; saturated in the dry season, 10-30 cm of surface water during the wet season.
8	August 12	Drained cypress	Four miles NE of Golden Gate in Collier County.	Deep sandy soils; artificially well-drained throughout the year.

Figure 11. Map of southwest Florida showing the location of the study sites.

1 Longleaf pine flatwood

2 Mixed hardwood--cypress forest

3 Burned mixed hardwood--cypress forest

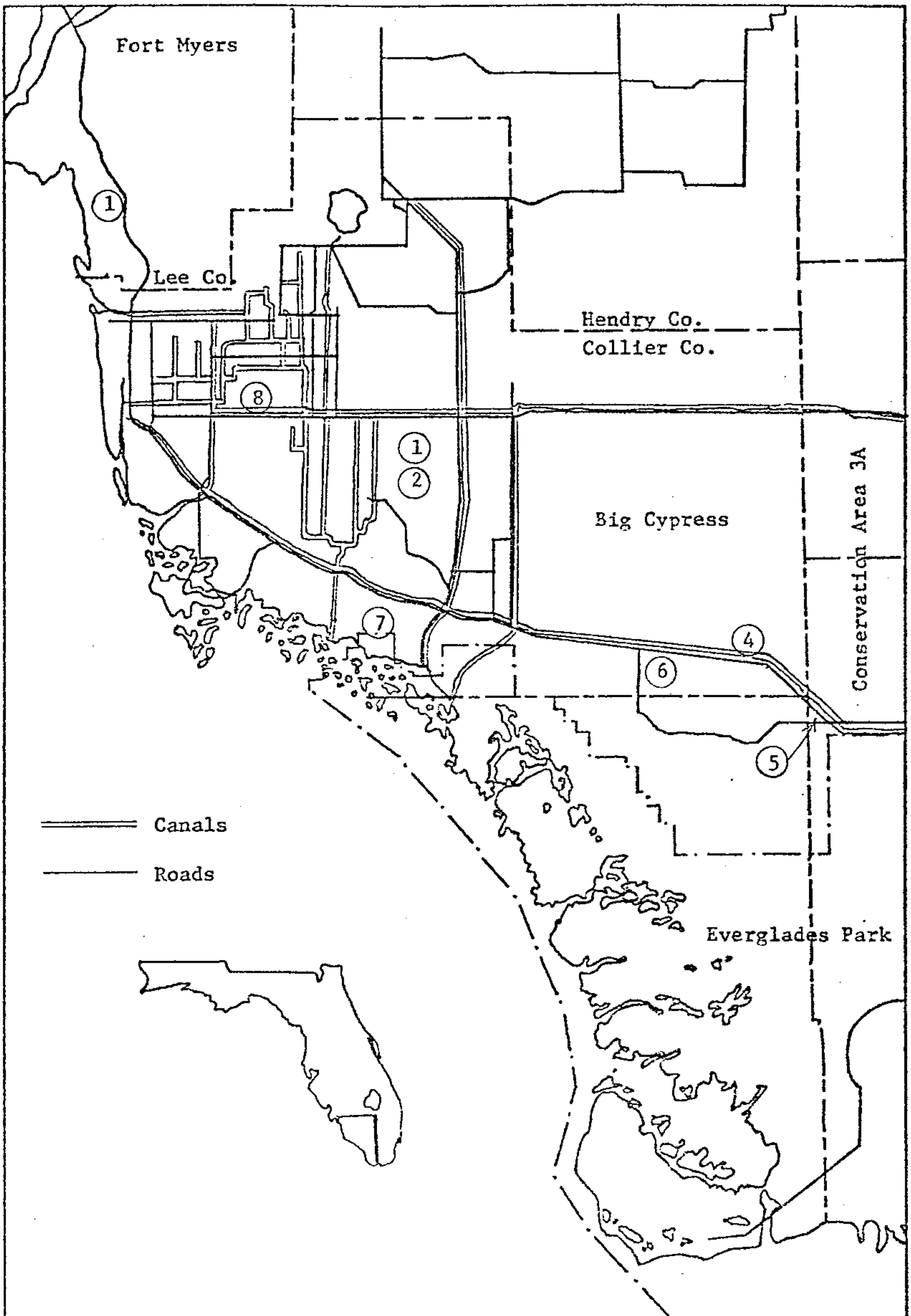
4 Dwarf cypress forest

5 Wet prairie

6 Mature cypress forest

7 Mangrove

8 Drained cypress forest


Fort Myers
Lee Co.
Hendry Co.
Collier Co.
Big Cypress
Conservation Area 3A
Everglades Park
Canals
Roads
1
1
2
4
5
6
7
8

a *Melaleuca* and a cypress seedling on each of the five subplots, in order to obtain a comparison of cypress and *Melaleuca* seedling growth under nearly identical field conditions. The cypress seedlings were obtained in February from the dwarf cypress site and kept in the greenhouse until they were replanted in the field. Only three sites were selected for planting because of lack of cypress seedlings. All seedlings were planted bare-root, the soil being washed off just prior to planting. Initial height and monthly growth increments were recorded and growth responses were noted.

During each visit one surface soil sample was taken for soil moisture determination. This was by no means a representative sample, but the time limitations of weekend trips precluded the design of a more sophisticated sampling procedure; nevertheless, an indication of monthly changes was obtained.

During the March trip 3.8 cm diameter galvanized iron pipes were driven into the ground for water level determinations. An attempt was made to place each pipe as close to the center of the plot as possible, but where bedrock was near the surface, several borings were made to set the pipe as deep as possible. No pipe was placed either on site 5 (sawgrass), due to the shallowness of the soil, or on site 3 (burned), due to its proximity to site 2 where one pipe served both sites. Monthly water level changes were recorded. In July and August weekly measurements were made. Also, water depth measurements were made at each of the seeded or planted subplots on the flooded sites to get an idea of the topographic changes within each plot.

Starting in July, when most of the plots were flooded, weekly dissolved oxygen measurements were made of the surface water using a modified Winkler method. The samples were taken from the plot centers. Again, only one sample was taken per site each week, and the time of day when the sample was taken varied, so the data can only be considered an indication of the dissolved oxygen contents under which seedling establishment was attempted.

In addition to a qualitative description of the vegetation on each site, forty 1 m^2 subplots were randomly selected, and the terrestrial and rooted aquatic plant species that occurred on each subplot were recorded.

Results

Site descriptions

The longleaf pine flatwood site is located just south of the Koreshan State Park in Estero, Lee County. It is dominated by *Pinus palustris* Mill (longleaf pine), *Serenoa repens* Hook. f. (saw palmetto), and *Befaria racemosa* Vent. (tarflower) (see Fig. 12). *Melaleuca* is abundant around the site and there have been numerous seed crops released in the vicinity. However, no *Melaleuca* is growing on the site except where there are obvious depressions in the topography. The 20 m by 20 m plot is free of *Melaleuca*. The predominant species on this site are listed in Table 5.

The soil is a well-drained deep sand, probably low in fertility. Monthly soil moisture measurements presented in Figure 13 illustrate that peak moisture levels were reached during a three month period between May and July. The rest of the year the moisture levels were low and the soil surface dry.

Figure 12. Longleaf pine flatwood site.

TABLE 5. List of common plants on the longleaf pine flatwood site and their abundance expressed as a percent of the total number of sample plots where they occurred.

WOODY PLANTS	ABUNDANCE
Befaria racemosa	97.5
Serenoa repens	82.5
Pinus palustris	7.5
Ilex glabra	7.5
Quercus myrtifolia	7.5
HERBACEOUS PLANTS	
Hypericum brachyphyllum	45.0
Andropogon capillipes	26.5
Aristida spiciformis	12.5
Aristida tenuspica	10.0
Lachnanthes caroliniana	5.0

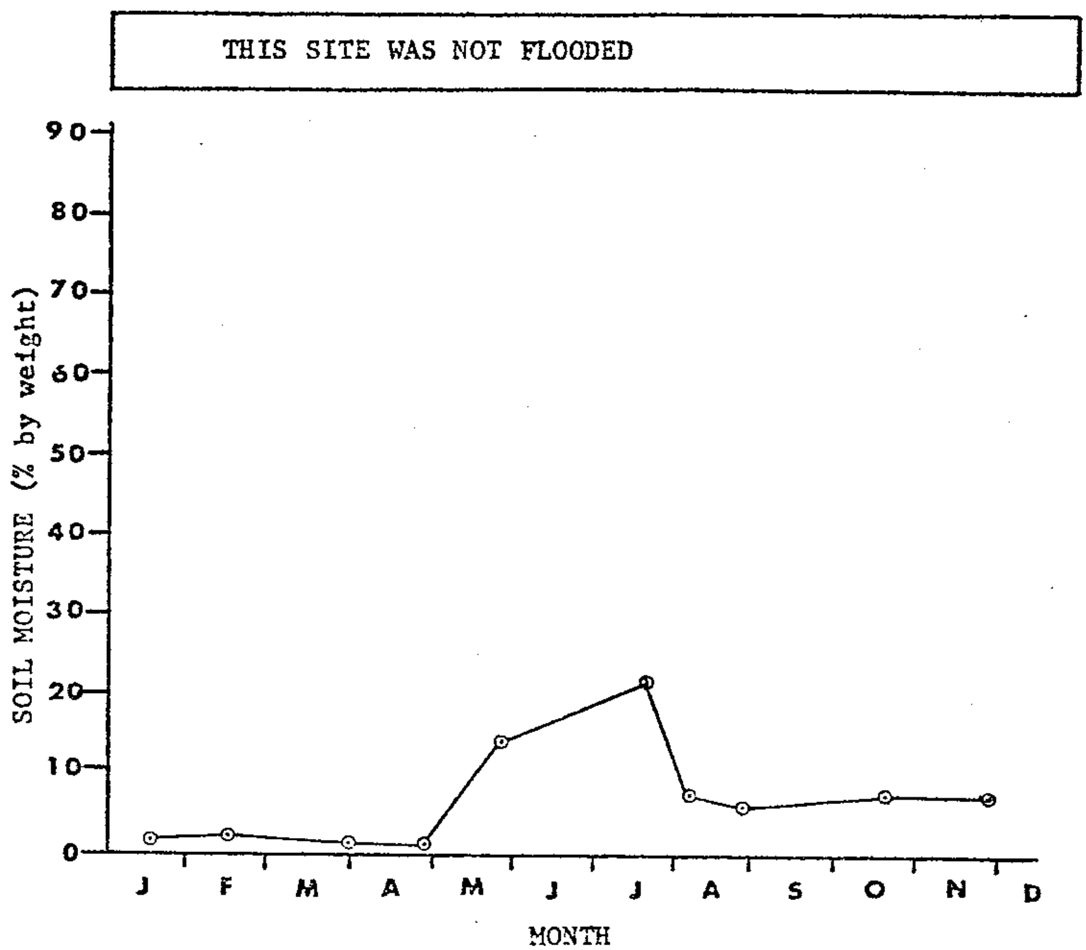


Figure 13. Monthly soil moisture changes and length of flooding on the longleaf pine flatwood site.

The water level (shown in Fig. 14 for all sites) at this site was subsurface except for a one-week period in July when heavy rains occurred in Lee County and the water level rose to the surface, causing some puddling. The lowest water table recording was in late April when it dropped to 172 cm below the surface. The highest reading of 2.0 cm of surface water was recorded in July. This site, with the possible exception of the drained cypress forest site, had the lowest average water level and the shortest period of flooding of any of the study areas.

The mixed hardwood--cypress forest site is located just south of Alligator Alley, along the west edge of the Fahkahatchee Strand in Collier County. It is dominated by Taxodium ascendens (pond cypress), Fraxinus caroliniana Mill. (pop ash), and Acer rubrum L. (red maple). The site apparently burned a few years ago and many hardwood snags are now present. The loss of these trees have made the canopy relatively open and the soil is densely covered with herbaceous plants (see Fig. 15). The more abundant species are listed in Table 6. No Melaleuca was located on the plot or near the site. The closest observed Melaleuca trees were at least 15 km away.

Approximately 1 m of sandy peat soil overlies limestone bedrock. The topography change from high to low point within the plot is 21 cm. Soil moisture measurements, as shown in Figure 16, indicate that relatively high moisture was present in the soil during January and February. It was reduced in March and April and the soil surface became dry. Early wet season rainstorms caused the soil moisture to increase in May. By June, the site was flooded.

Water level on this site fluctuated from 1 m below the surface

Figure 14. Water level changes on the eight study plots.

- Longleaf pine flatwood
- Mixed hardwood--cypress forest
- Burned mixed hardwood--cypress forest
- Dwarf cypress forest
- Wet prairie
- Mature cypress forest
- Mangrove
- Drained cypress forest

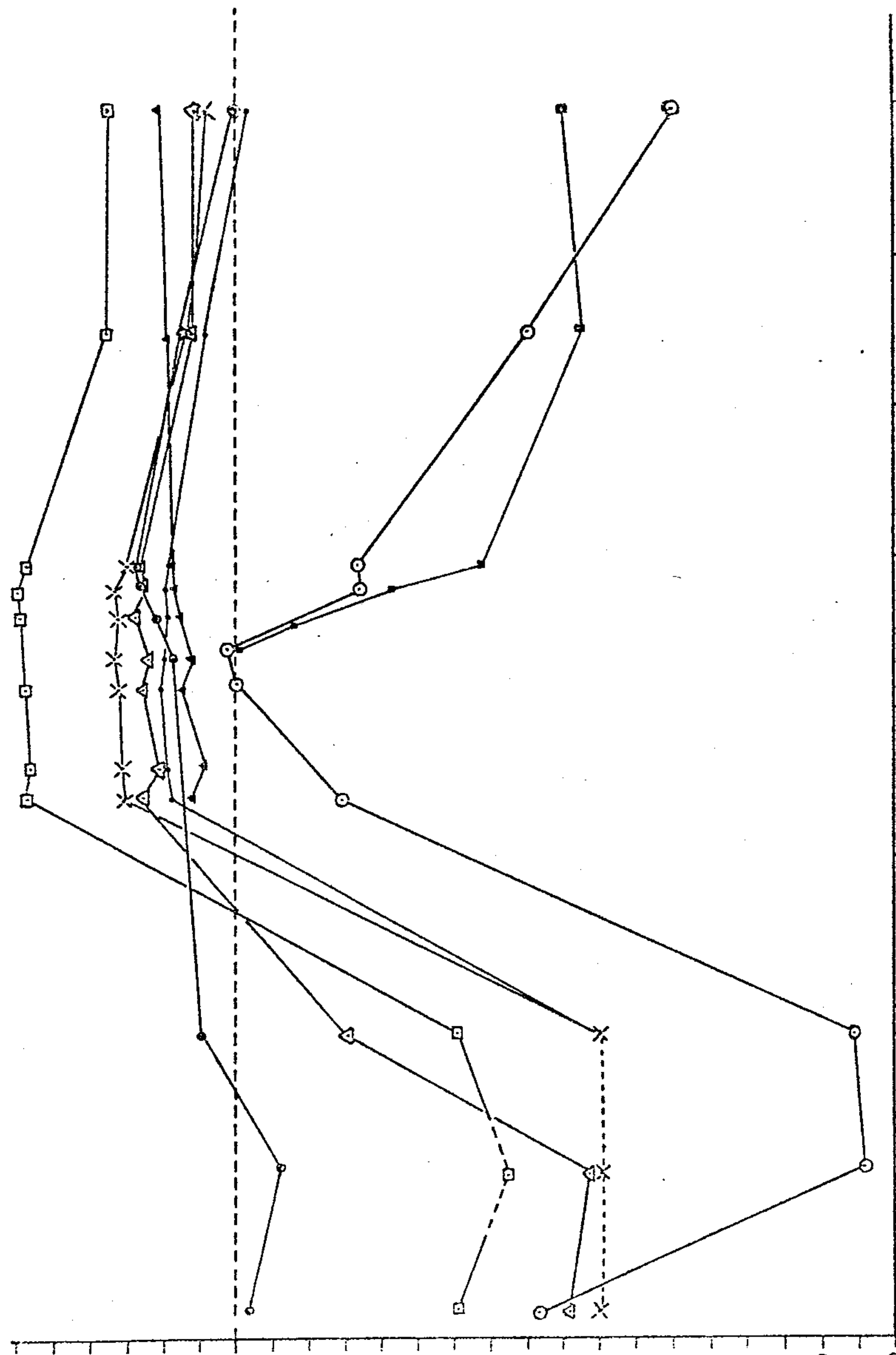

WATER LEVEL IN CENTIMETERS
60
40
20
0
20
40
60
80
100
120
140
160
180
APR 1
MAY 1
JUN 1
JUL 1
AUG 1
SEP 1
OCT 1
NOV 1
DEC 1

Figure 15. Mixed hardwood--cypress forest site.

TABLE 6. List of common plants on the mixed hardwood--cypress forest site and their abundance expressed as a percent of the total number of sample plots where they occurred.

WOODY PLANTS	ABUNDANCE
Taxodium ascendens (trees)	32.5
Taxodium ascendens (seedlings)	5.0
Acer rubrum	25.0
Salix caroliniana	22.5
Baccharis halimifolia	10.0
Fraxinus caroliniana	2.5
Myrica cerifera	2.5
Ficus aurea	2.5
HERBACEOUS PLANTS	
Blechnum serrulatum	90.0
Mikania batatifolia	65.0
Ludwigia repens	42.5
Boehmeria cylindrica	32.5
Polygonum hydropiperoides	22.5
Cladium jamaicensis	12.5
Cyperus haspen	10.0
Pontederia lanceolata	7.5

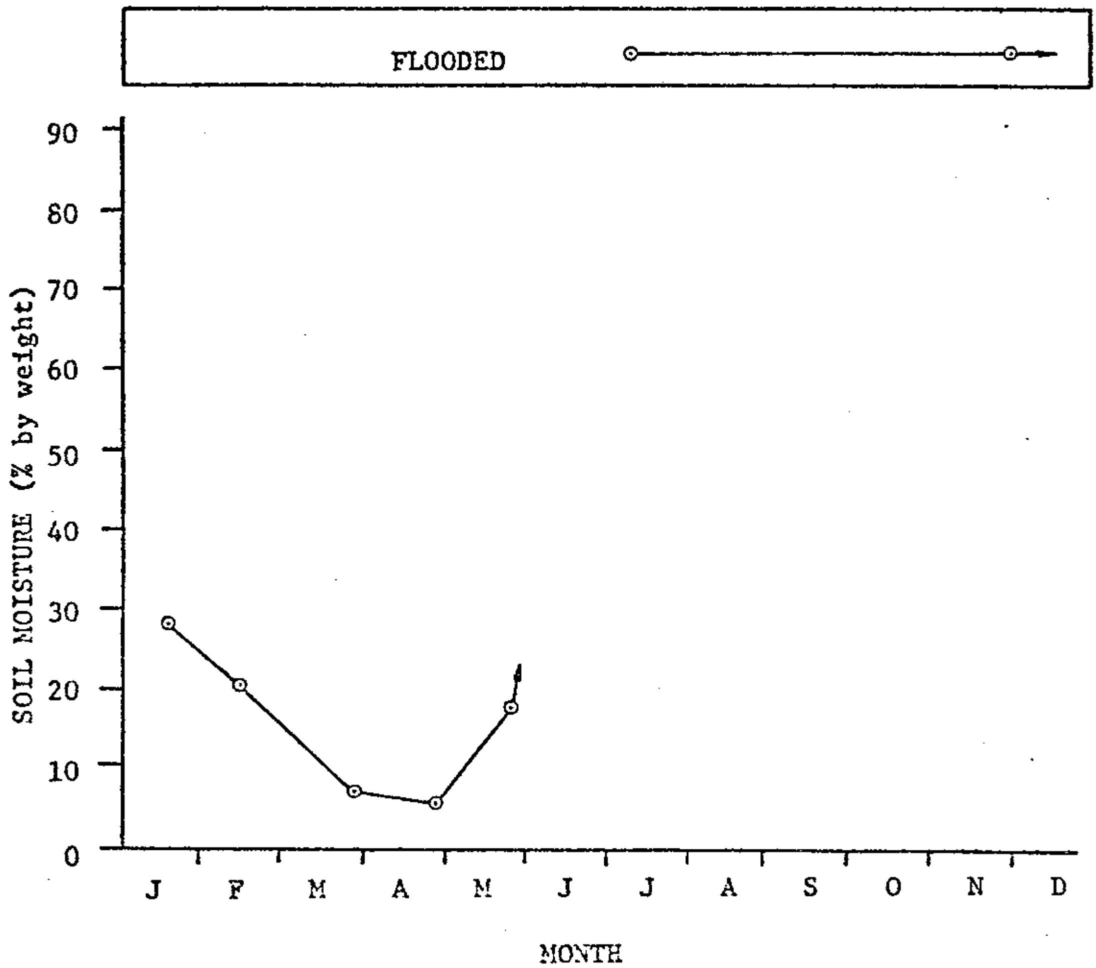


Figure 16. Monthly soil moisture changes and length of flooding on the mixed hardwood--cypress forest site.

during the dry season to a relatively constant level of 20-25 cm above the surface in June, July, and August. It began to drop off again in September. By late November approximately three-fourths of the plot was still flooded, making the hydroperiod about six months long.

Dissolved oxygen readings for all sites are given in Table 7. The dissolved oxygen content of the flood waters at the mixed hardwood--cypress forest site was fairly low. The greatest amount recorded was 2.56 ppm, taken from an afternoon sample. The other measurements were taken at midmorning and this may account for the lower values.

The burned mixed-hardwood-cypress forest plot is located adjacent to the previous plot, within the same vegetation type. This plot was established after a fire had burned up to the edge of the other plot on March 31. This presented an opportunity to observe differences between a recently burned site and one that had had a few years to recover. The fire completely eliminated the ground cover and/or killed many of the hardwoods. The plot was established on May 25, after a few days of rain, and only a few grasses and herbs had sprouted. The predominant woody vegetation on the plot was pond cypress (Fig. 17). A list of the other abundant species are given in Table 8.

No soil samples were taken on this plot. Topography change within the plot from high to low point is 17.5 cm. This plot is slightly higher than the adjacent plot and the soil is shallower. Therefore, the length of the flood period may be as much as a month shorter than on the adjacent plot.

The water level measurements presented in Figure 14 show that the surface water during the wet season averaged slightly less than 20 cm deep. The water table was more than 1 m beneath the surface during

TABLE 7. Dissolved oxygen measurements taken on flooded study sites.

MIXED HARDWOOD--CYPRESS FOREST SITE

Date	Time	Dissolved Oxygen Content of Water (ppm)
August 10	1500	2.09
August 18	1100	1.08
August 24	1000	0.65
August 29	1100	1.32
October 15	1500	2.56
November 30	1400	2.76

WET PRAIRIE SITE

Date	Time	Dissolved Oxygen Content of Water (ppm)
August 11	1600	9.49
August 18	1600	8.17
August 24	1400	3.17
August 30	1000	3.74
October 17	0900	3.15
November 30	1200	6.54

MIXED HARDWOOD--CYPRESS FOREST (BURNED) SITE

Date	Time	Dissolved Oxygen Content of Water (ppm)
August 10	1500	2.09
August 18	1100	1.08
August 24	1000	0.87
August 29	1100	2.42
October 15	1500	4.14

MATURE CYPRESS FOREST SITE

Date	Time	Dissolved Oxygen Content of Water (ppm)
August 9	1500	3.64
August 18	1500	1.51
August 24	1300	0.87
August 31	1600	1.32
October 17	1000	1.38
November 30	1300	1.09

DWARF CYPRESS SITE

Date	Time	Dissolved Oxygen Content of Water (ppm)
August 9	1400	4.45
August 18	1000	1.94
August 24	0900	2.62
August 29	1500	2.99
October 16	1400	2.56
November 30	1100	2.67

MANGROVE SITE

Date	Time	Dissolved Oxygen Content of Water (ppm)
August 18	1400	1.72
August 24	1200	0.65
August 29	1600	5.97
October 17	1200	1.97

Figure 17. Burned mixed hardwood--cypress forest site.

TABLE 8. List of common plants on the burned mixed hardwood--cypress forest site and their abundance expressed as a percent of the total number of sample points where they occurred.

WOODY PLANTS	ABUNDANCE
Taxodium ascendens	15.0
Sabal palmetto	7.5
Baccharis halimifolia	2.5
Persea borbonia	0.5
Salix caroliniana	0.5
Acer rubrum	0.5
Cephalanthus occidentalis	0.5
HERBACEOUS PLANTS	
Blechnum serrulatum	72.5
Sacciolepis striata	40.0
Nymphaea odorata	25.0
Polygonum hydropiperoides	22.5
Hyptis alata	17.5
Pontederia lancelolata	12.5
Diodea virginiana	10.0
Mikania batatifolia	7.5
Canna flaccida	7.5
Ludwigia repens	7.5
Boehmeria cylindrica	5.0
Solidago stricta	2.5
Hydroles corymbose	2.5
Melothria pendula	2.5

the dry season. By late November the water level was again subsurface and the soil was soggy. The dissolved oxygen measurements averaged slightly higher here than on the adjacent plot (samples were taken at the same time). This was possibly due to the more open canopy and sparser ground cover, which may have resulted in a greater amount of algal photosynthesis in the water.

The dwarf cypress forest site is located just north of the Collier-Dade Training Jetport in eastern Collier County. The vegetation is predominantly widely scattered dwarf (pond) cypress (Taxodium ascendens) with a herbaceous ground cover (Fig. 18). The plot includes part of a small cypress dome. No Melaleuca were located on the plot; the closest individuals were located along a disturbed roadside about 2 km south of the plot. Common species on the plot are listed in Table 9.

The soil is an Ochopee fine sandy marl that ranges in depth from only a few centimeters to over a meter. The topography change within the plot is 22 cm. Much of the soil is covered with a thick algal mat. During the dry season as it became separated from the soil surface the mat dried out. Seedlings which germinated on this mat were subject to dessication as this process occurred. On sites in which the mat was burned during the dry season, the chances of successful germination would be enhanced. Burning would eliminate the mat, which acts as an effective barrier between the Melaleuca seed and mineral soil. Soil moisture levels presented in Figure 19 show that moisture content dropped steadily from January, reaching its lowest level in April when the soil surface and algal mat were dry.

The water table (Fig. 14) dropped to 90 cm below the surface during late March, April, and early May. This corresponded to the

Figure 18. Dwarf cypress forest site.

TABLE 9. List of common plants on the dwarf cypress forest site and their abundance expressed as a percent of the total number of sample plots where they occurred.

WOODY PLANTS	ABUNDANCE
Taxodium ascendens (trees)	45.0
Taxodium ascendens (seedlings)	35.0
Myrica cerifera	2.5
Chrysobalanus icaco	2.5
Ficus aurea	2.5
HERBACEOUS PLANTS	
Cladium jamaicensis	67.5
Panicum virgatum	45.0
Paspalum monstachyum	25.0
Proserpinaca palustris	22.5
Cassytha filiformis	7.5
Nymphaea odorata	7.5
Stillingia sylvatica	5.0
Bacopa caroliniana	2.5

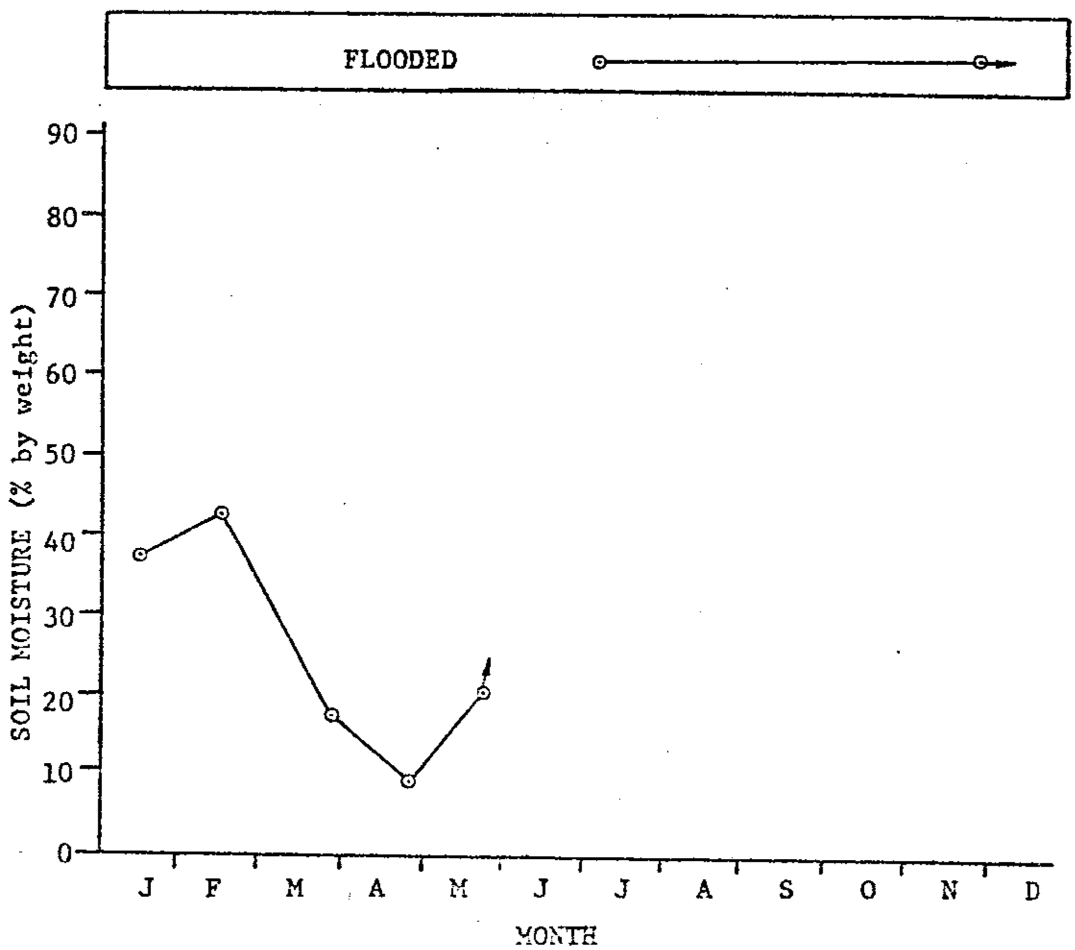


Figure 19. Monthly soil moisture changes and length of flooding on the dwarf cypress forest site.

period when both the soil surface and algal mat were dry. During the wet season the surface water level fluctuated between 25 and 30 cm and began to recede in early September. The period of flooding was five to six months long. Dissolved oxygen contents (Table 7) were higher than those recorded on the previous plots. The highest measurement was 4.45 ppm recorded at 2:00 PM. Other measurements taken in the afternoon were at least 1.50 ppm less than this. If the higher levels are significant they can probably be attributed to the openness of the cypress forest and the resulting photosynthesis of the submerged algal mat.

The wet prairie site is located just south of U. S. 41, 1.5 km northwest of Forty-mile Bend in Western Dade County. The dominant species is Cladium jamaicensis (sawgrass). No woody vegetation was located on the plot (Fig. 20). Other common species are listed in Table 10.

The soil is a marl (probably of the Ochopee series) with an average depth of 15 to 30 cm to limestone bedrock. The topography change from the high to low point within the plot is 8 cm. Soil moisture measurements presented in Figure 21 show that there was considerable moisture still present in the soil in March, April, and May, but due to the fine texture of this clay soil, the moisture may not have been readily available to seeds.

Water table depths during the dry season were not obtainable because the shallowness of the soil made it impossible to drive a pipe into the ground. The water level after June is illustrated in Figure 14. The surface water averaged about 20 cm in depth during the wet season. This site is probably flooded longer than any of the other seven sites due to the release of water into the Everglades National

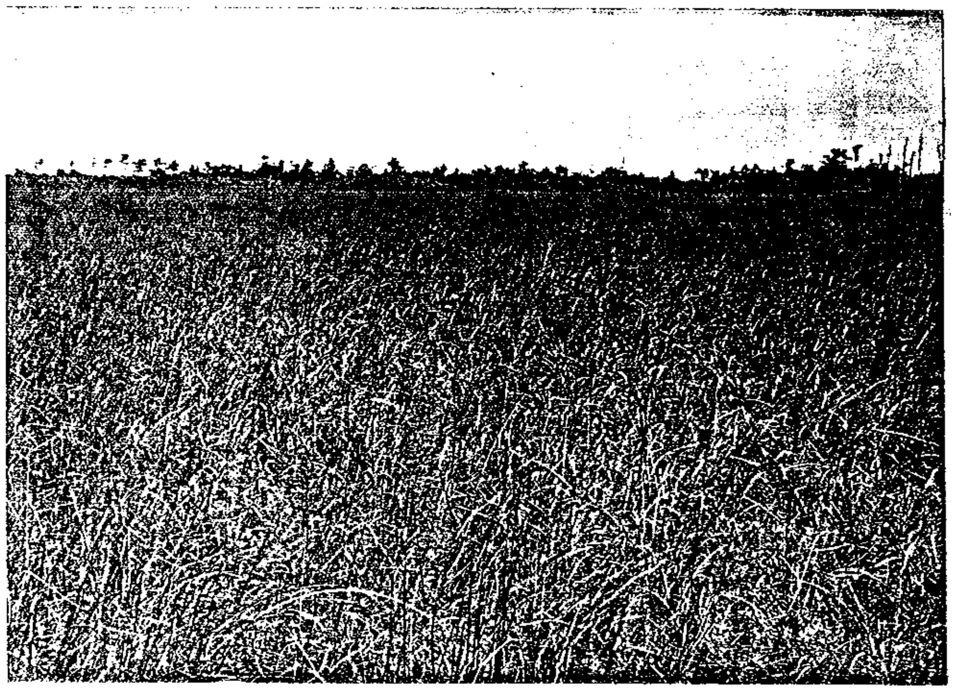


Figure 20. Wet prairie site.

TABLE 10. List of common plants on the wet prairie site and their abundance expressed as a percent of the total number of sample plots where they occurred.

HERBACEOUS PLANTS	ABUNDANCE
Cladium jamaicensis	97.5
Rhynchospora tracyi	87.5
Utricularia biflora	72.5
Muhlenbergia capillaris	25.0
Bacopa caroliniana	5.0
Sagittaria graminea	2.5
Eleocharis cellulosa	2.5

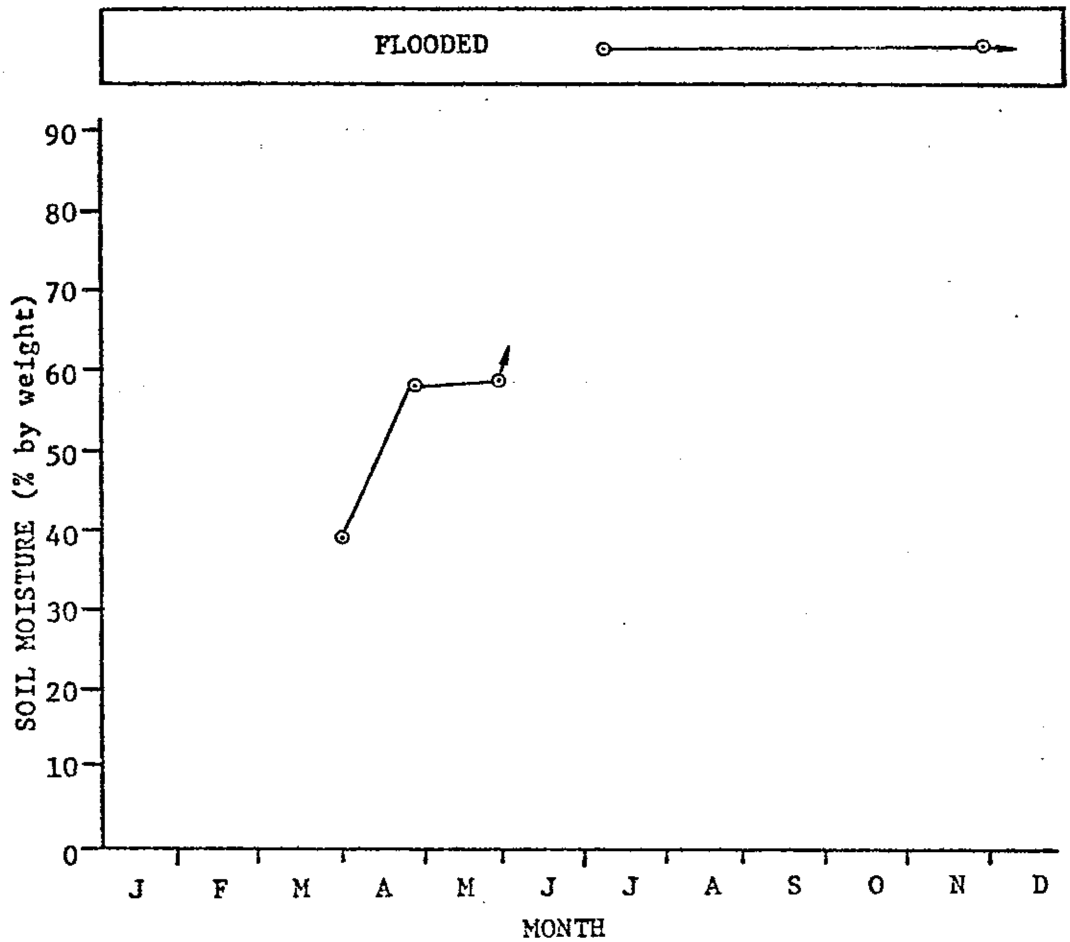


Figure 21. Monthly soil moisture changes and length of flooding on the wet prairie site.

Park from Conservation Area 3. This tends to maintain high water levels through the fall in this particular area. As of November 30 this site was still flooded with 19 cm of water. Dissolved oxygen measurements (Table 7) were the highest recorded on any plot. In some cases the surface water was saturated, as indicated by late afternoon readings as high as 9.49 and 8.17 ppm. Two of the lower readings were recorded in the morning while a third was taken on a cloudy day. Presumably the high dissolved oxygen levels resulted from the photosynthesis of the algal mat.

The mature cypress forest site is located within a cypress strand approximately 5 km east of Monroe Station and south of U. S. 41 in Collier County. The predominant woody species are Taxodium ascendens, Annona glabra L. (pond apple), and Fraxinus caroliniana. The more abundant species are listed in Table 11. The strand is characterized by a tall overstory of mature cypress trees with a scattered understory of hardwoods, a few reaching into the lower canopy. The strand follows a long depression running in a northeast-southwest direction and accounts for a considerable amount of water flow from the Big Cypress Watershed. The plot is located at the edge of a pond in the center of the strand. Part of the plot extends into the shallower portion of the pond where full sunlight is available, while most of the plot is in dense shade (Fig. 22).

The soil is variable in depth and consists of a mucky peat mixed with sand which overlies limestone bedrock. Topography change within the plot is 49 cm. In February and March the soil was quite wet and, except for the surface litter, remained moist throughout the dry season (Fig. 23).

TABLE 11. List of common plants on the mature cypress forest site and their abundance expressed as a percent of the total number of sample plots where they occurred.

WOODY PLANTS	ABUNDANCE
Fraxinus caroliniana	7.5
Annona glabra	7.5
Ficus aurea	2.5
Taxodium ascendens	2.5
Sabal palmetto	2.5
Chrysobalanus icaco	2.5
HERBACEOUS PLANTS	
Ludwigia repens	27.5
Nymphaea odorata	20.0
Blechnum serrulatum	10.0
Asclepias incarnata	7.5
Thalia geniculata	2.5
Rhus radicans	2.5
Mikania batatifolia	2.5
Hydrocotyle umbellata	2.5
Proserpinaca palustris	2.5

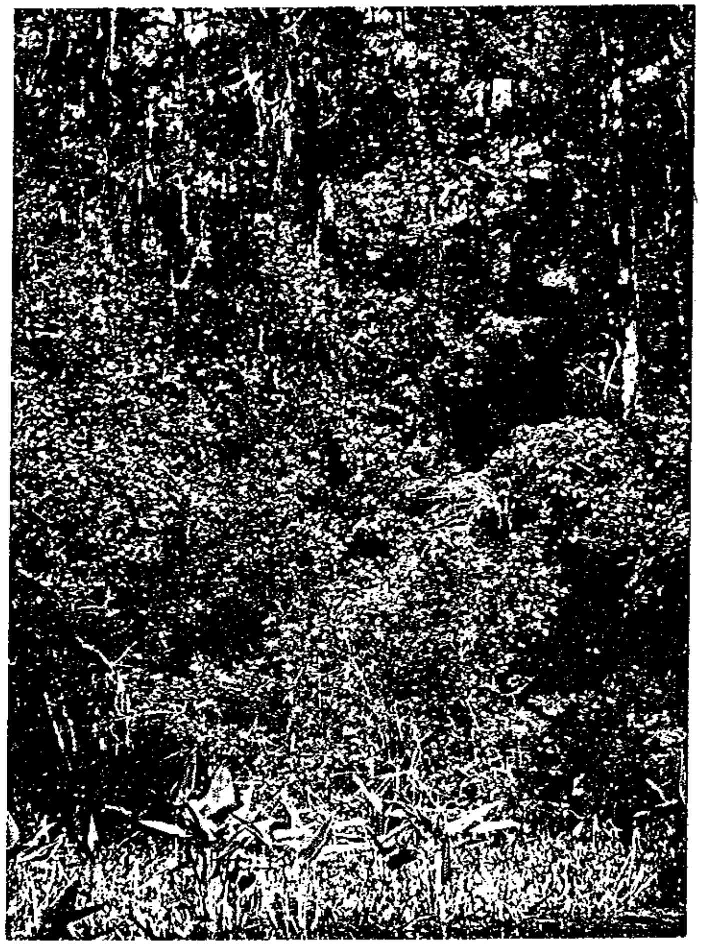


Figure 22. Mature cypress forest site.

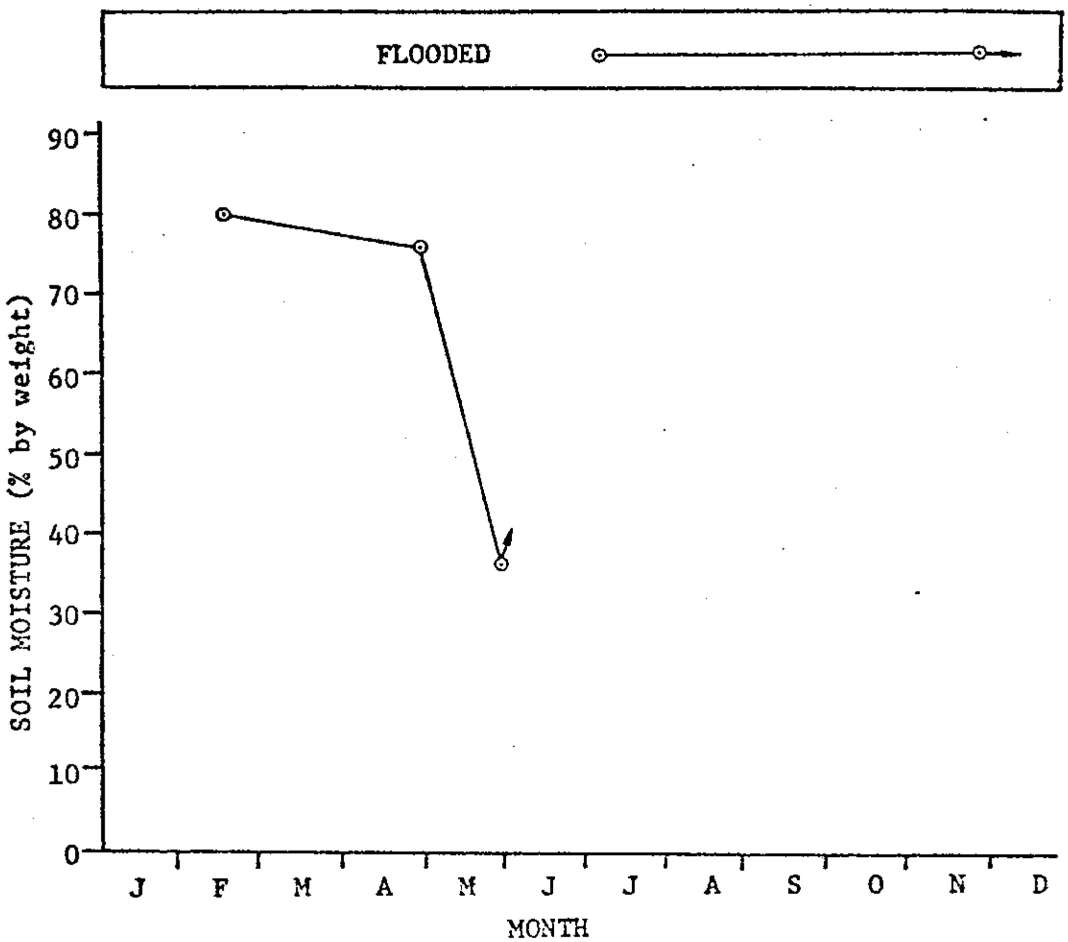


Figure 23. Monthly soil moisture changes and length of flooding on the mature cypress forest site.

The water level (Fig. 14) during the dry season dropped below the depth of the pipe (75cm). The surface water rose to about 58 cm during the summer months and then began to drop off in September. By late November most of the site was still flooded with 35 cm of standing water at the center of the plot, giving most of the plot at least a six-month hydroperiod. Dissolved oxygen contents (Table 7) were quite low. The highest measurement was 3.64 ppm, with most of the measurements taken in the late afternoon when dissolved oxygen levels would be expected to be at their highest.

The mangrove site is located about 7 km northwest of Carnestown, along U. S. 41 in Collier County. The dominant species (Table 12) are white mangrove (Laguncularia racemosa Gaertu. f.) and open marshes of Spartina spartinae, and Salicornia bigelovii. It is characterized by dense patches of white mangrove that abruptly change to open salt marsh (Fig. 24). Shallow mangrove creeks or estuaries meander through both vegetation types.

The soil is a fibrous brown peat that held enough moisture even during the dry season so that water could be squeezed out of it by hand. The topography change within the study plot is 12.5 cm.

Water level changes are illustrated in Figure 14. The water table remained at or near the surface during the dry season and the water was probably brackish. During the wet season an influx of fresh water was received from the Fahkahatchee Strand area and the water level rose continuously during the summer months, reaching a maximum of 28 cm in late August. Flooding began a month sooner here than on the other sites, but by late November the plot was no longer flooded.

TABLE 12. List of common plants on the mangrove site and their abundance expressed as a percent of the sample points where they occurred.

WOODY PLANTS	ABUNDANCE
Laguncularia racemosa	45.0
HERBACEOUS PLANTS	
Salicornia bigelovii	50.0
Spartina spartinae	42.5
Paspalum vaginatum	12.5

Figure 24. Mangrove site.

Dissolved oxygen measurements were variable, with the results ranging from 0.65 ppm to 5.95 ppm.

The drained cypress forest site, which was established in August, is located about 8 km northeast of the community of Golden Gate in western Collier County. It is an artificially well-drained site characterized by a relatively open stand of pole-sized cypress trees (Fig. 25). No pine is located on the study plot, but the site area includes a patchwork of scattered pine (Pinus elliotii) and cypress stands delineated by slight undulations in the topography. The understory on the study plot is mostly grasses and herbs which include many weedy species such as Baccharis halimifolia, Hypericum sp., and Foeniculum vulgare. The more abundant species are listed in Table 13.

The soil is a deep sand that was moist (Fig. 26) through August, but by October the surface was very dry. The November soil sample was taken during a rainstorm which accounts for the increase obtained.

The water table (Fig. 14) was near the surface at mid-summer, and for a brief period in August there was puddled surface water. Otherwise, the plot was effectively drained throughout the year.

Seeding Trials

Accurate seedling counts from seed sown on the study plots were difficult to make due to the small size of the seedlings and the fact that site conditions changed considerably from visit to visit due to vegetation growth, water level changes, and in some cases the development of an algal mat that covered the seedlings. Consequently an indicated loss of seedlings actually may have resulted from my inability to relocate a seedling and not actual mortality. Only as the

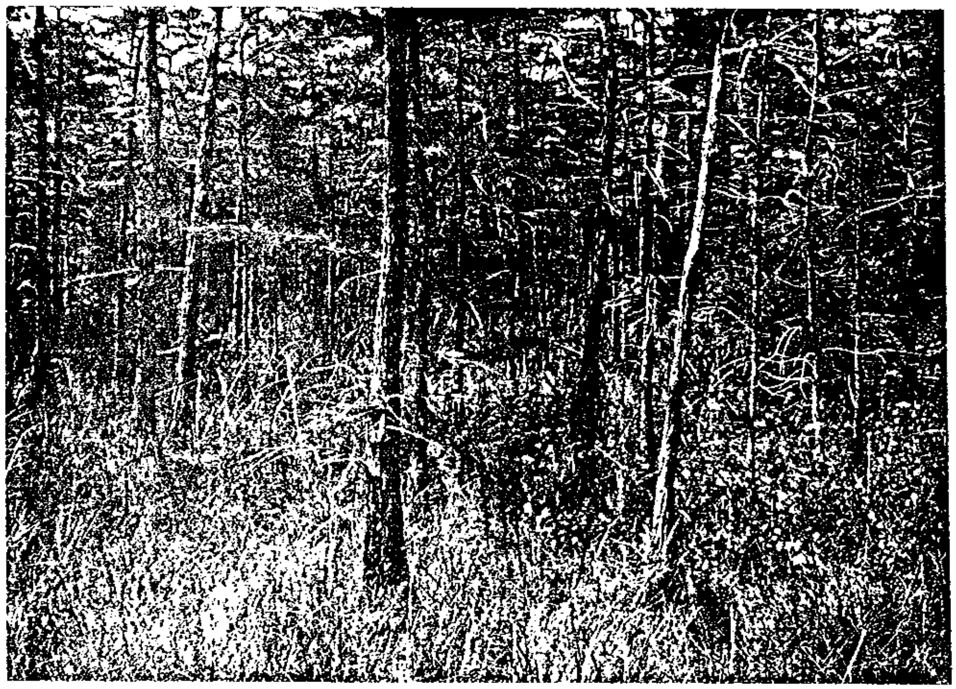


Figure 25. Drained cypress forest site.

TABLE 13. List of common plants on the drained cypress site and their abundance expressed as a percent of the sample points where they occurred.

WOODY PLANTS	ABUNDANCE
Taxodium ascendens	27.5
Baccharis halimifolia	7.5
Myrica cerifera	2.5
HERBACEOUS PLANTS	
Eupatorium mikaniodes	57.5
Chloris neglecta	47.5
Pluchea rosea	45.0
Hyptis alata	40.0
Foeniculum vulgare	40.0
Eupatorium capillifolium	17.5
Cladium jamaicensis	17.5
Vitis aestivalis	10.0
Mikania batatifolia	7.5
Hypericum fasciculatum	7.5

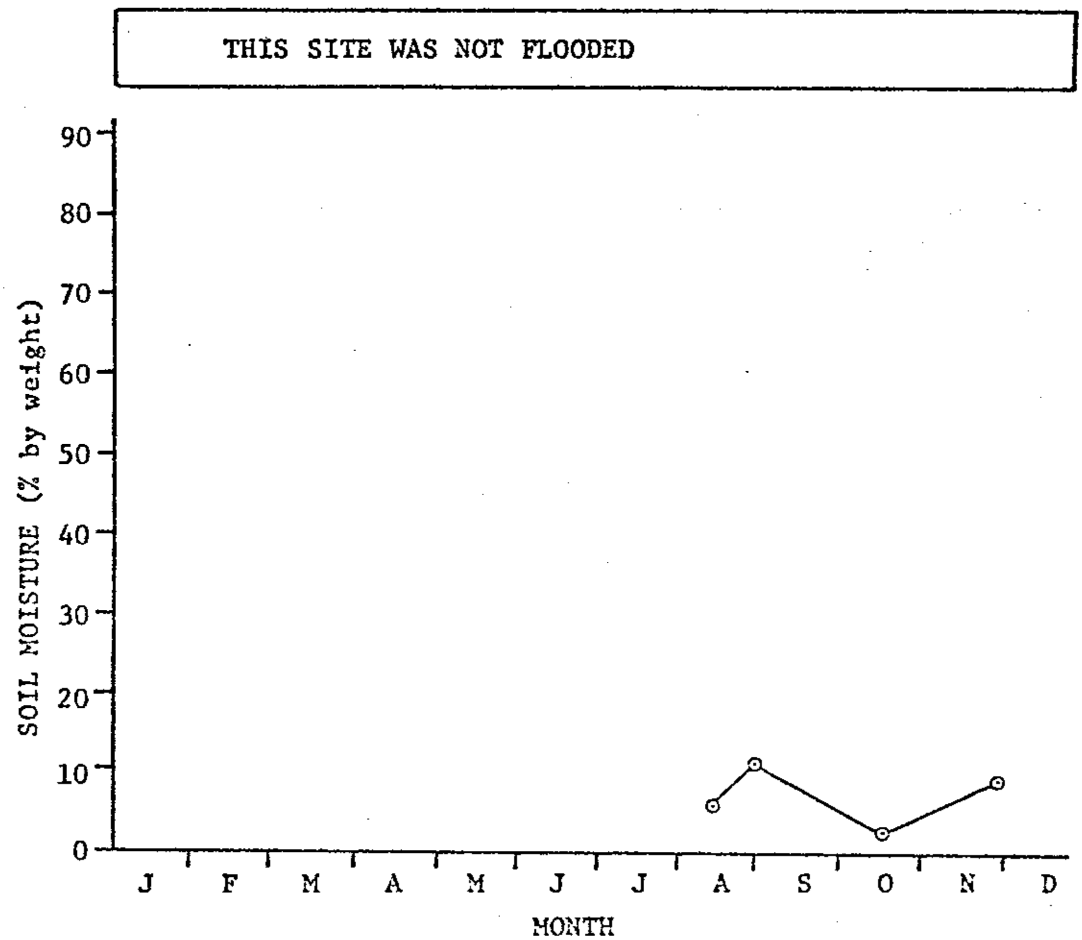


Figure 26. Monthly soil moisture changes and length of flooding on the drained cypress forest site.

water level drops and seedlings grow will actual survival be known.

As shown in Table 14, seedlings were not observed on the pine flatwood site until August 5, when four seedlings were recorded on two subplots that were seeded in July. Apparently none of the previously sown seed remained viable during the dry season to germinate when moisture requirements became favorable. A seedling crop was recorded on August 31 from seed sown on August 5, but by October all of these seedlings had died and only one seedling remained from the July 14 seeding. As of November 28 only one seedling that germinated from seed sown in October was observed on the entire plot.

The results of the seedings on the mixed hardwood--cypress site are given in Table 15. The only germination recorded was between January and February when the soil was moist. In this case a total of 70 seedlings were observed on a total of four subplots. All of these were lost either during the dry season, in the summer while the site was flooded, or in the fall when the water level dropped.

The seeding results for the burned mixed hardwood--cypress site are shown in Table 16. Twenty-eight seedlings were counted on July 12 resulting from the May seeding. Losses were recorded each succeeding month. By October 17 only two of these seedlings remained. The heavy algal bloom (which may have resulted from nutrients released by the fire) made these counts unreliable by obscuring the seedlings. No germination occurred underwater subsequent seedings. By late November the site was no longer flooded and seed germination was recorded on subplots that had been seeded as early as July 12. All five subplots seeded in October supported seedlings, and as many as 850 seedlings

TABLE 14. Results of field seedings on the longleaf pine site.

DATE WHEN SEEDED \ DATE OF SEEDLING COUNTS	JAN 18	FEB 15	MAR 30	APR 26	MAY 24	JUL 14	AUG 5	AUG 31	OCT 17	NOV 28
JAN 18	Seeded	0	0	0	0	0	0	0	0	0
FEB 15		Seeded	0	0	0	0	0	0	0	0
MAR 30			Seeded	0	0	0	0	0	0	0
APR 26				Seeded	0	0	0	0	0	0
MAY 24					Seeded	0	0	0	0	0
JUL 14						Seeded	4	1	1	0
AUG 5							Seeded	70	0	0
AUG 31								Seeded	0	0
OCT 17									Seeded	1
NOV 28										Seeded

TABLE 15. Results of field seedings on the mixed hardwood--cypress forest site.

DATE WHEN SEEDED	DATE OF SEEDLING COUNTS									
	JAN 19	FEB 16	MAR 31	APR 27	MAY 25	JUL 12	AUG 4	AUG 29	OCT 17	NOV 30
JAN 19	Seeded	70	0	0	0	0	0	0	0	0
FEB 16		Seeded	0	0	0	0	0	0	0	0
MAR 31			Seeded	0	0	0	0	0	0	0
APR 27				Seeded	0	0	0	0	0	0
MAY 25					Seeded	0	0	0	0	0
JUL 12						Seeded	0	0	0	0
AUG 4							Seeded	0	0	0
AUG 29								Seeded	0	0
OCT 17									Seeded	0
NOV 30										Seeded

TABLE 16. Results of field seedings on the burned mixed hardwood--cypress forest site.

DATE WHEN SEEDED	DATE OF SEEDLING COUNTS: MAY 25	JUL 12	AUG 4	AUG 29	OCT 17	NOV 30
MAY 25	Seeded	28	18	9	2	1
JUL 12		Seeded	0	0	0	95
AUG 4			Seeded	0	0	5
AUG 29				Seeded	0	36
OCT 17					Seeded	1330
NOV 30						Seeded

were recorded on a single subplot. This particular subplot was very wet but not flooded when it was seeded in October.

The results of the seeding trials on the dwarf cypress forest site are given in Table 17. Seedlings were recorded from both the January and February seedings; however, all of the seedlings died during the dry season. No further germination was recorded until October 16, when six seedlings were found growing on one of the subplots that was seeded at the end of August. This particular subplot is located on the edge of the 20 m by 20 m plot where the topography is highest; consequently, as water levels began to drop this subplot was one of the first to be exposed. When this subplot was seeded in August it was covered with 5 cm of water. When this subplot was monitored on October 16, this particular subplot was no longer flooded. The soil was saturated and the seedlings were growing on the wet algal layer. It is not known how soon after the seeding the water receded or if the seeds germinated underwater. On November 30, 215 seedlings were recorded on a total of four of the five subplots seeded in October. Two of these subplots were still flooded. One hundred and fourteen seedlings were counted on four subplots that were seeded as early as August 28.

The results of the seeding trials on the wet prairie site are shown in Table 18. In March, 19 seedlings were recorded from the seeds sown in February. In March the soil was soggy wet with a thick algal mat on which the seedlings were growing. None of these seedlings survived the dry season and no further germination was noted from seed sown either during the dry season or while the site was flooded.

Germination results on the mature cypress forest site are given

TABLE 17. Results of field seedings on the dwarf cypress forest site.

DATE OF SEEDLING COUNTS

DATE WHEN SEEDED	JAN 19	FEB 16	MAR 31	APR 27	MAY 25	JUL 12	AUG 3	AUG 28	OCT 16	NOV 30
JAN 19	Seeded	180	120	0	0	0	0	0	0	0
FEB 16		Seeded	42	0	0	0	0	0	0	0
MAR 31			Seeded	0	0	0	0	0	0	0
APR 27				Seeded	0	0	0	0	0	0
MAY 25					Seeded	0	0	0	0	0
JUL 12						Seeded	0	0	0	0
AUG 3							Seeded	0	0	3
AUG 28								Seeded	6	114
OCT 16									Seeded	215
NOV 30										Seeded

TABLE 18. Results of field seedings on the wet prairie site.

DATE OF SEEDLING COUNTS

DATE WHEN SEEDED	FEB 16	MAR 31	APR 27	MAY 25	JUL 12	AUG 5	AUG 30	OCT 17	NOV 30
FEB 16	Seeded	19	0	0	0	0	0	0	0
MAR 31		Seeded	0	0	0	0	0	0	0
APR 27			Seeded	0	0	0	0	0	0
MAY 25				Seeded	0	0	0	0	0
JUL 12					Seeded	0	0	0	0
AUG 5						Seeded	0	0	0
AUG 30							Seeded	0	0
OCT 17								Seeded	0
NOV 30									Seeded

in Table 19. Seedlings were recorded in March from seed sown in February. A month later the soil surface was still moist, but none of the 75 seedlings could be relocated. Between March and April a lush growth of herbaceous plants developed on the forest floor, particularly in the more open part of the plot. Presumably the _Melaleuca_ seedlings could not compete with these rapidly growing plants. No further germination was recorded either during the dry season or while the site was flooded.

There was a noticeable water flow through this plot during the wet season; this flow would have been capable of floating seeds out of the plot if they had been directly on the surface. Therefore, the seeds were presoaked for 24 hours before sowing, enabling them to be placed directly on the soil surface under the water. On the other flooded plots the water was considerably shallower with no noticeable flow, so the seed could be sown on the water surface. Then, by agitating the water by hand the seeds would sink.

The seeding results for the mangrove site are shown in Table 20. No germination was recorded on this plot at any time during the year.

The results of the seeding trials on the drained cypress forest site are given in Table 21. On August 28 a total of 280 individuals were recorded from the five subplots. These germinated from the August 12 seeding. By October 15, only eight of these seedlings remained alive; many of the others were found in a dessicated state. Five other seedlings were recorded in October from the August 28 seeding; however, in late November no seedlings remained on the plot.

TABLE 19. Results of field seedings on the mature cypress forest site.

DATE WHEN SEEDED	DATE OF SEEDLING COUNTS: FEB 16	MAR 31	APR 27	MAY 25	JUL 12	AUG 3	AUG 31	OCT 17	NOV 30
FEB 16	Seeded	75	0	0	0	0	0	0	0
MAR 31		Seeded	0	0	0	0	0	0	0
APR 27			Seeded	0	0	0	0	0	0
MAY 25				Seeded	0	0	0	0	0
JUL 12					Seeded	0	0	0	0
AUG 4						Seeded	0	0	0
AUG 31							Seeded	0	0
OCT 17								Seeded	0
NOV 30									Seeded

TABLE 20. Results of field seedings on the mangrove site.

DATE WHEN SEEDED	DATE OF SEEDLING COUNTS: JAN 19	FEB 16	MAR 31	APR 27	MAY 25	JUL 14	AUG 9	AUG 29	OCT 17	NOV 30
JAN 19	Seeded	0	0	0	0	0	0	0	0	0
FEB 16		Seeded	0	0	0	0	0	0	0	0
MAR 31			Seeded	0	0	0	0	0	0	0
APR 27				Seeded	0	0	0	0	0	0
MAY 25					Seeded	0	0	0	0	0
JUL 14						Seeded	0	0	0	0
AUG 9							Seeded	0	0	0
AUG 29								Seeded	0	0
OCT 17									Seeded	0
NOV 30										Seeded

TABLE 21. Results of field seedings on the drained cypress site.

DATE WHEN SEEDED	DATE OF SEEDLING COUNTS: AUG 12	AUG 28	OCT 15	NOV 29
AUG 12	Seeded	280	8	0
AUG 28		Seeded	5	0
OCT 15			Seeded	0
NOV 29				Seeded

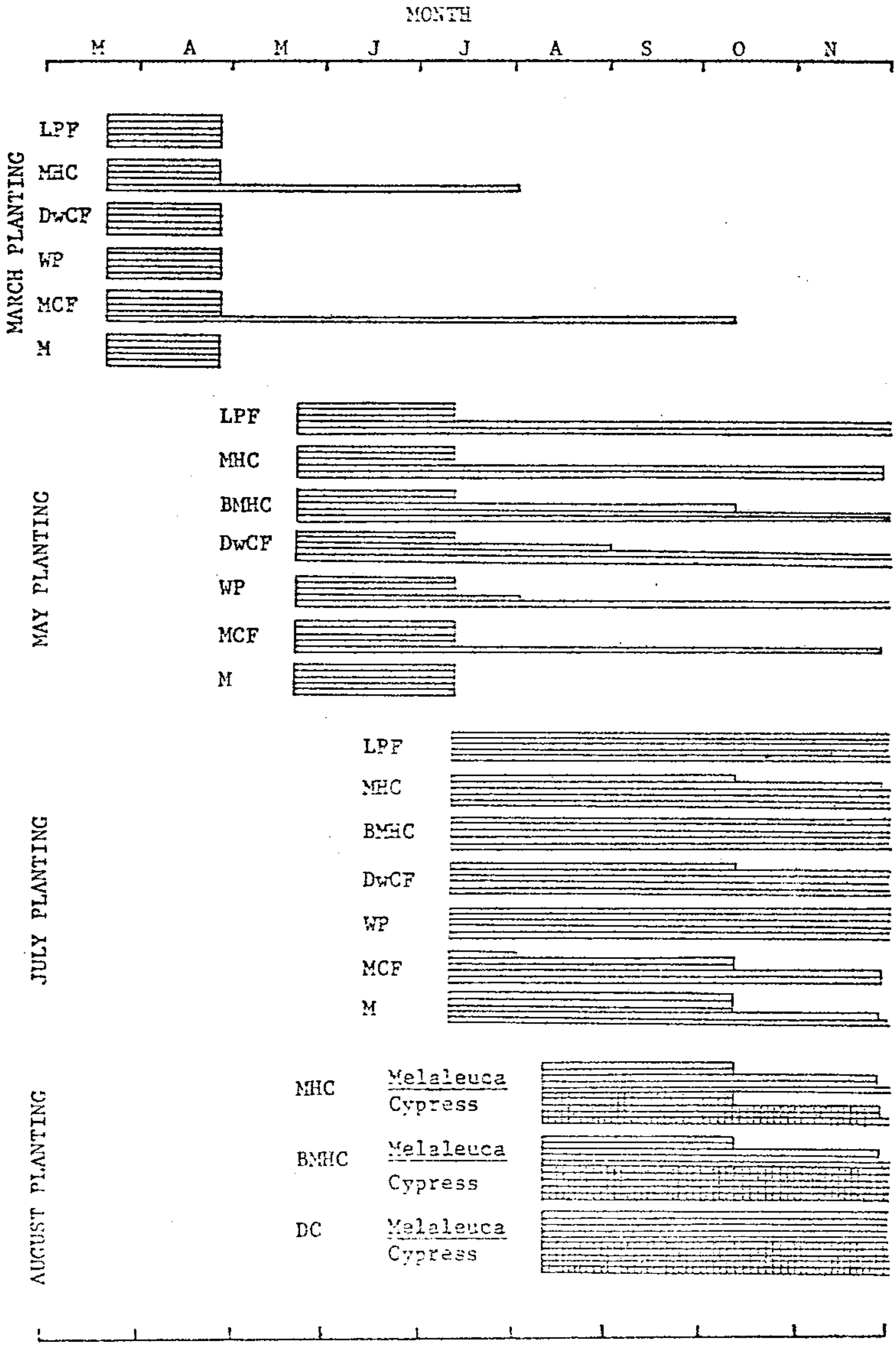
Field Plantings

Tree seedling survival for each consecutive planting on each study plot is illustrated in Figure 27. Mean height growth as of November 30 for the surviving trees from each planting is shown in Figure 28. In many cases the trees had several months of growth--either positive or negative--before dying. Gains and losses of individual seedlings that eventually died were not included in the calculation of mean height growth. In other words, only those trees that survived until November 30 were used.

The seedlings from the March planting on the longleaf pine flatwood site did not survive the first month. This mortality was probably the result of transplantation shock during a time when the soil moisture content was very low. Two seedlings survived the May planting and as of late November exhibited an average growth of minus 4.5 cm. The negative growth signifies that the tops of most of the trees died back. All five seedlings from the July planting have survived and they exhibited a growth of minus 8.8 cm. None of the trees from this planting had positive growth. The seedlings appeared to be deficient in nutrients; they produced small, pale yellowish-green leaves. Several of the trees were badly damaged by insects.

On the mixed-hardwood cypress forest site one seedling from the March planting survived until July. Two other seedlings have survived from the July planting. Their mean height growth as of late November was minus 11 cm. From the August planting, which included five cypress seedlings in addition to the *Melaleuca*, only one individual of each species has survived. The single *Melaleuca* seedling has grown 21.5 cm, while the cypress seedling had a growth of minus 28.0 cm.

Figure 27. Seedling survival on each study plot from the four planting trials. Each bar represents one seedling. The length of the bar indicates the time before the seedling was observed to had died. The open ended bars indicate that the seedlings were still alive on December 1. (LPF, longleaf pine flatwood; MHC, mixed hardwood--cypress; BMHC, burned mixed hardwood--cypress; DwCF, dwarf cypress forest; WP, wet prairie; MCF, mature cypress forest; M, mangrove; DC, drained cypress).


MONTH
M A M J J A S O N
MARCH PLANTING
LPF
MHC
DwCF
WP
MCF
M
MAY PLANTING
LPF
MHC
BMHC
DwCF
WP
MCF
M
JULY PLANTING
LPF
MHC
BMHC
DwCF
WP
MCF
M
AUGUST PLANTING
MHC
Melaleuca
Cypress
BMHC
Melaleuca
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DC
Melaleuca
Cypress

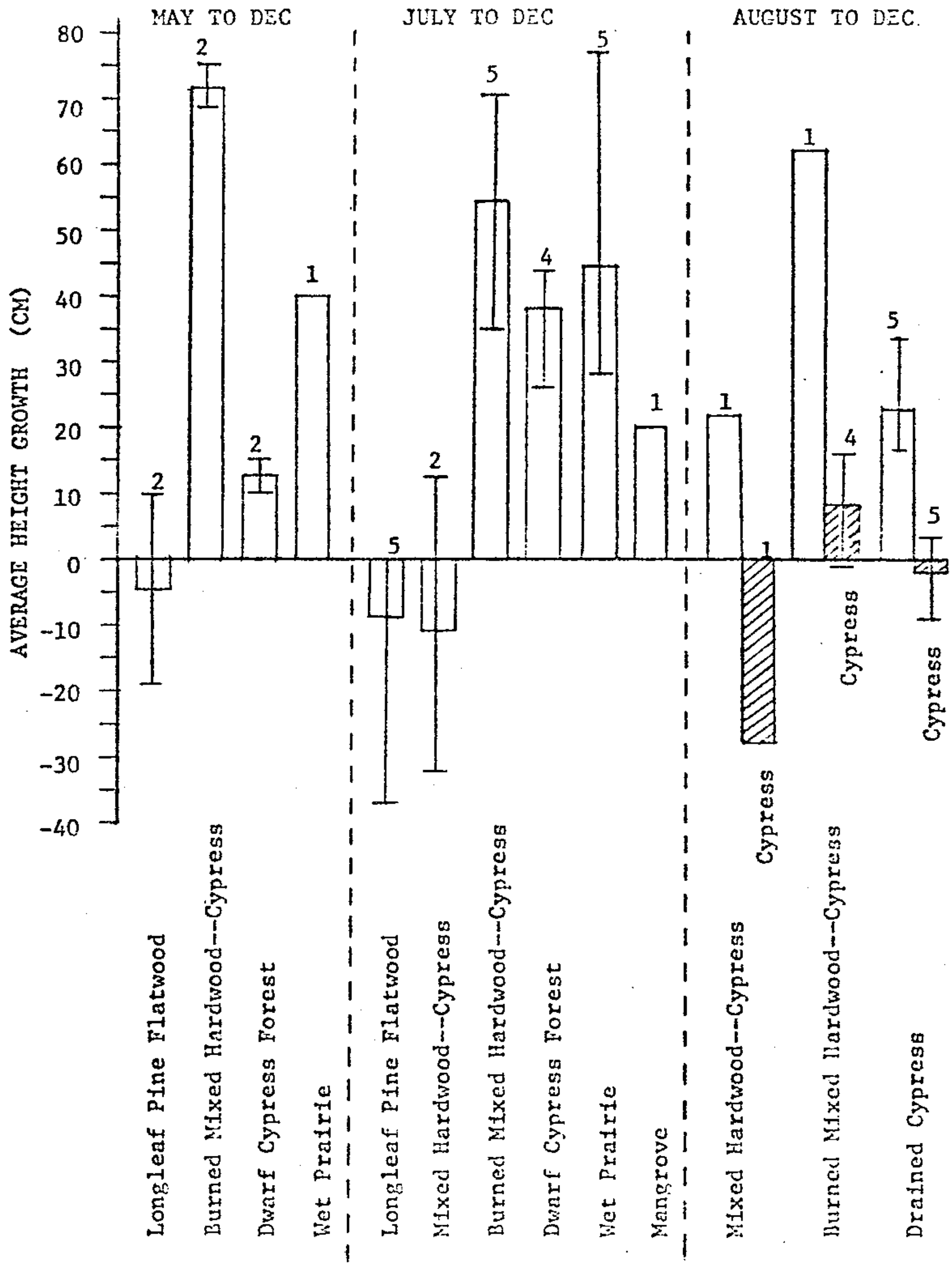


Figure 28. Mean height growth of seedlings which survived each planting. The line with each bar represents the range of height growth The associated number represents the number of surviving trees.

The seedlings planted on the burned mixed hardwood--cypress forest site exhibited the greatest height growth of any of the plots planted. It also had one of the best survivals. From the May planting, two seedlings have survived. Their average height growth was 71.8 cm. All five seedlings from the July planting have survived, with an average height growth of 54.5 cm, but only one of the August-planted Melaleuca seedlings has survived, growing 61.5 cm in three months. Four out of five of the cypress seedlings are still growing and their average growth as of late November was 8.5 cm. The results obtained so far on this plot are in sharp contrast to those of the adjacent plot described above. Obviously, the burning with subsequent reduction in competition and release of nutrients has had a noticeable effect on both seed germination and seedling growth.

All five seedlings planted in March on the dwarf cypress forest site did not survive the first month. However, two of the five seedlings planted in May survived and grew an average of 12.5 cm between May and late November. From the July planting only one seedling was lost. The remaining seedlings averaged 37.6 cm of height growth. No plantings were undertaken in August. Most of the surviving seedlings appeared healthy throughout the summer months, but in late November all were severely insect damaged. Most of the seedlings on this site developed a ball of adventitious roots at the water surface.

None of the seedlings planted in March on the wet prairie site survived the first month. One seedling has survived from the May planting and as of late November had grown 40 cm. All five seedlings from the July planting have survived. They had an average height growth of 44.5 cm. This was the second best growth response obtained from any of the plantings on any of the sites. In November several of the trees were badly insect damaged.

One seedling from the March planting on the mature cypress forest site survived beyond September 1, but it could no longer be located on October 17. One seedling from the May planting survived for five months. Both the March and the May plantings took place while the soil was moist. All of the seedlings were planted underwater in July and remained completely submerged until they died. Two of these submerged seedlings developed the dimorphically distinct leaves exhibited by the submerged seedlings grown in the greenhouse. None of the seedlings on this site exhibited any positive growth after they were submerged, and all were dead by late November.

In addition to the seedlings planted on the mature cypress forest plot, 12 large seedlings averaging 125 cm in height were planted in July in the center of the open pond just outside of the study plot. Most of the trees were completely submerged but a few had their tops out of the water. In October all of the trees were still alive, but by November 30 they were dead.

On the mangrove site no seedlings survived either the March or May planting. All five seedlings from the July planting survived through August, but as of October 17 only two seedlings remained alive. On November 30 one seedling was left and it had grown 20.0 cm since it was planted in July.

One hundred percent survival was obtained on the drained cypress forest site for both the cypress and *Melaleuca* seedlings that were planted in August. The *Melaleuca* seedlings averaged 23.3 cm of height growth between August and November, while the cypress seedlings averaged a minus 1.8 cm (Fig. 29).

Figure 29. Planted cypress and Melaleuca seedlings on the drained cypress forest site.

SURVIVAL OF NATURALLY REGENERATED SEEDLINGS

The tremendous amount of *Melaleuca* reproduction observable in many areas of Lee and Collier Counties usually results from massive seed release following the burning of sites that already support at least widely scattered mature *Melaleuca* trees. The question arises as to the susceptibility of these sites to *Melaleuca* establishment. In other words, do these sites regularly and uniformly present conditions favorable for *Melaleuca*, or is the proper timing of seed release accompanied with fire and proper moisture conditions only infrequently met?

Objectives

The vast acreage of Lee and Collier Counties that burned during the drought of 1974 presented an opportunity to observe *Melaleuca* seedling establishment after burning. This simple experiment was set up to: (1) observe natural seedling survival on established *Melaleuca* sites, and (2) to study seedling establishment on the same sites from seed sown later in the season.

Procedure

Three different sites were located where *Melaleuca* was already established and which had burned during the dry season. Massive seed release had occurred on each of the sites and seedlings literally carpeted the ground. The site locations were: #1, due west of Monroe Station in Collier County in an open glade surrounded by scattered pine, cypress, and clumps of Melaleuca; #2, south of Highway 846 northeast of Naples in Collier County, in mixed cypress and pine and scattered Melaleuca; and #3, two miles south of Estero in Lee County along U. S. 41, next to an old cypress dome now dominated by large Melaleuca trees. On each of the sites, four 20 cm by 20 cm plots were arbitrarily chosen so that naturally established seedlings were uniformly dense on each of the plots. At the beginning of the experiment, the seedlings on one plot on each site were merely counted and recorded. On the other three plots the seedlings were counted and removed. Immediately, one of the cleared plots was seeded with 0.25 gram of Melaleuca seed. The second cleared plot was seeded in the same manner after one month, and any response on the control and the initially seeded plots was noted at that time. The third cleared plot was seeded after approximately two months. Water level and dissolved oxygen content measurements were also taken.

Results

The dates of initial establishment and successive treatments, along with results and measurements, are summarized in Table 22. On site #1, near Monroe Station, the control plot supported 45 seedlings at the time of establishment. The water level was approximately 13.5 cm above the surface and six of these seedlings were emergent, the tallest being 16 cm. After approximately one month no seeds had germinated underwater and a second seeding plot was set up. A month and a half later the soil surface was moist and the originally seeded

TABLE 22. Survival of naturally regenerated *Melaleuca* seedlings on burned sites and the results of seedings on the same sites carried out later in the wet season.

Site 1
Monroe Station (wet prairie, pine, cypress)

Date	Control	Number of Seedlings Treatment 1	2	3	Water Depth (cm)	Dissolved O_2 Content (ppm)
July 25	45	seeded	---	---	13.5	4.95
Aug. 31	45	0	seeded	---	13.0	1.76
Oct. 17	40	3	30	seeded	soil moist	----
Nov. 30	37	2	13	3	soil moist	----

Site 2
Highway 846 (Pine--cypress)

Date	Control	Number of Seedlings Treatment 1	2	3	Water Depth (cm)	Dissolved O_2 Content (ppm)
July 25	78	seeded	---	---	1.0	----
Aug. 31	74	12	seeded	---	0.2	----
Oct. 15	50	21	45	seeded	soil moist	----
Nov. 30	50	0	1	0	soil moist	----

Site 3
Estero (cypress dome)

Date	Control	Number of Seedlings Treatment 1	2	3	Water Depth (cm)	Dissolved O_2 Content (ppm)
July 27	90	seeded	---	---	12	----
Aug. 31	90	0	seeded	---	10	6.19
Nov. 28	63	0	4	seeded	soil dry	----

plot supported three seedlings. The second seeded plot supported thirty seedlings. A third plot was seeded at this time. After four months 37 seedlings remained on the control plot. The first, second, and third seeded plots contained 2, 13, and 3 seedlings respectively.

On site #2, near Highway 846, the control plot supported 78 seedlings at the time of establishment. There were 2 cm of standing water at the time and all of the seedlings were underwater. A month later 74 seedlings remained on the control plot. There was only 0.2 cm of standing water and all of the seedlings were emergent. From the seeds sown on the first seeding plot, 12 had germinated. By October 15, the soil was moist and 50 seedlings remained on the control plot; 21 on the first seeding plot; and 45 on the second plot. A third seeding plot was established at this time. By late November there were still 50 seedlings on the control plot, but only one seedling remained on any of the seeded plots.

On the third study site, near Estero, 90 seedlings were growing under 12 cm of water on the control plot. One month later there were still 90 seedlings on the control plot, all still growing under 10 cm of water. No germination had occurred on the initial seeding plot. By late November there were 63 seedlings remaining on the control plot, while the only seedlings established from seedings occurred on the plot seeded in late August, which contained four seedlings.

DISCUSSION

Seed Germination and Seedling Survival

Several major factors control _Melaleuca_ seed germination and seedling survival. These factors include moisture availability, water level, hydroperiod, soil fertility, salinity, light, and competition with natural vegetation. In other words, a certain set of biological and physical influences interact to define the conditions necessary for _Melaleuca_ germination and growth. Only in those areas where these conditions are found will _Melaleuca_ become successfully established.

Moisture Requirements

The germination experiments carried out in the laboratory demonstrated that under ideal conditions _Melaleuca_ seed germination was initiated rapidly, within three days, and that the germinating seeds were very susceptible to dessication if moisture conditions were not satisfactory. The fact that no germination occurred from seed sown on the study plots during the dry season suggests that a seed crop released and on the ground may be extremely vulnerable to the seasonal vagaries of moisture availability. Germination may be triggered by a brief dry season rain, or possibly by dew or fog; but moisture levels would not be sufficient for continued growth and survival.

Rapid germination after initial moisture application would be an advantage to seed released at the beginning of the wet season.

Abundant moisture would be available as practically daily rainstorms develop and germination would probably occur before flooding. This would tend to follow the sequence of events that occurs in the monsoon climate where *Melaleuca* is native. Seasonal droughts provide conditions for fire, which in turn results in seed release and site preparation just prior to the onset of the monsoon rains. Much the same pattern exists in South Florida, especially as artificial drainage has shortened the length of the flood period and increased the incidence of fire.

Although both the laboratory and greenhouse experiments indicated that *Melaleuca* seeds will germinate underwater, this does not seem to be the case under normal field conditions. No germination was recorded on any of the sites while standing water was present. This indicates that areas which are continually flooded during the wet season do not normally present conditions favorable for *Melaleuca* seed germination.

The low dissolved oxygen content characteristic of most swamp waters may effectively inhibit or at least delay germination. Whether or not seed is destroyed under prolonged flooding is uncertain, but on the burned study plot some germination did occur, after the drop in water level, on subplots that were seeded as early as July.

Where seedlings were observed underwater, germination probably occurred prior to flooding, as for example from the May seeding on the burned plot. In November, seedlings were also observed that were growing underwater on the dwarf cypress forest site. However, this site probably was not flooded for at least a brief period between the

October and November visits, and germination most likely took place during this period. This is suggested by both the observation that newly germinated cypress seedlings were growing underwater on the site (cypress does not germinate underwater), and the fact that the site was visited just after a cold front had dropped over 2.5 cm of rain over much of South Florida.

Except on the wet prairie site, the dissolved oxygen levels in the water at each of the flooded study sites were relatively low. Because Melaleuca seeds are minute there is a possibility that they would lay entirely within a layer of anaerobic water that may exist at the soil surface where little water movement and mixing would occur. This may account for the lack of germination on flooded sites. In some preliminary experiments, it was found that Melaleuca seeds would germinate in six days in water with a dissolved oxygen content of 4.0 ppm, while no seed germination occurred after two weeks in water with 2.5 ppm of dissolved oxygen.

Apparently germination and successful establishment will not occur on sites while they are continually flooded during the wet season nor on sites where the seed has laid on the ground through most of the dry season. A favorable window for successful germination exists only for brief periods confined to either the onset of the wet season or after water levels recede in the fall. Prolonged conditions favorable for germination would be found, therefore, only on those sites where the soil surface is exposed but remains wet for long periods of time.

Hydroperiod and Water Level

In the varied-hydroperiod experiments undertaken in the greenhouse the seedlings in the treatment that was alternated between submergence and drainage every three days seemed less affected by submergence than those in the treatment that was alternated on a two week basis. The seedlings of the first treatment broke the water surface more than a month before those of the treatment that was alternated every other week. This suggests that, even though the total number of days of submergence was the same for both treatments, a fluctuating water level or "noisy" hydroperiod is more favorable for Melaleuca than a stable hydroperiod. These fluctuating water levels are characteristic of those areas in South Florida that have been artificially drained, and include those areas where Melaleuca has been actively invading. For example, maximum recession rates of groundwater levels within the Fahka Union--Golden Gate drainage system in Collier County are between 9.1 and 10.4 cm per day, while maximum rates for undrained areas of the Big Cypress Swamp are between 2.1 and 4.0 cm per day (Carter et. al., 1973). Drainage canals in some areas have also increased the rate of surface flow one order of magnitude over the average of 0.5 km per day in the Big Cypress Swamp (Carter et. al., 1973), effectively removing surface water at a rapid rate and causing dramatic fluctuations in water levels and length of hydroperiod.

The fact that Melaleuca growth ceases or at least is significantly slowed when plants are submerged was demonstrated in both the greenhouse experiments and in the field on the burned mixed hardwood--cypress site and mature cypress forest site, where both the germinated and some planted seedlings remained submerged throughout the wet season. Apparently, seedlings that do germinate underwater form morphologically distinct leaves. The greenhouse experiments also showed that seedlings established under drained conditions loose their normal leaves upon submergence, develop the tight clusters of morphologically distinct leaves, and cease further growth. Flooding seems to have little noticeable effect on seedling growth once the apex of the shoot breaks the water surface. An uninterrupted hydroperiod with a relatively constant water level would tend to inhibit seedling growth by keeping the seedlings submerged throughout the wet season. A fluctuating water level and sporadic flooding during the wet season would permit greater growth and improve a seedling's chances of surviving the dry season.

On the wet prairie site the planted seedlings have been (or will be) subjected to an eight to nine month inundation. Even so, both height growth and survival have been good. This success may be the result of two factors. First, there is an absence of any overtopping vegetation, and second, increased stem elongation may have occurred in response to the flooded conditions to facilitate gas exchange through a greater number of larger intercellular spaces. Also, none of these plants have produced any adventitious roots, indicating that the high dissolved oxygen levels recorded are sufficient to maintain the seedlings without their expending energy to produce adventitious roots. On the other hand, it seems that this type of site would rarely present conditions favorable for Melaleuca germination because the hydroperiod is maintained (in this case artificially) for a long period of time. The period when a newly germinated seedling could grow sufficiently to overcome the effects of the prolonged hydroperiod would be after burning, which would release nutrients and destroy the algal mat. Still, the seedling would have to pass eight to nine months under water in competition with a newly forming algal layer. These conditions would be similar to the completely submerged treatment in the greenhouse hydroperiod experiment where, over a period of a year, a thick algal mat developed over bare soil and completely covered the *Melaleuca* seedlings.

Where hydroperiods have been artificially extended, it seems unlikely that *Melaleuca* would ever become a problem. For example, parts of Conservation Area 3A have been continuously flooded for the past ten years. In fact, water levels have been maintained so high that flooding has caused damage to most of the tree islands in the lower third of Conservation Area 3A. This is readily apparent as one travels through this area. On the other hand, the canal system that drains this area tends to dry out the northern end of the Conservation Area. It is in the northern third where scattered *Melaleuca* trees are found. Biologists of the Central and Southern Florida Flood Control District have noted that *Melaleuca* rapidly invaded Conservation Area 2B only after the construction of a drainage canal lowered water levels (Dineen, 1972).

Fire

Fire undoubtedly plays an active role in determining the distribution patterns of *Melaleuca* in South Florida. It is common to find *Melaleuca* occupying the shallow portions of a cypress dome or strand, especially where water levels have been lowered. It can be conjectured that during dry periods surface soils are drier in the higher, better drained fringes of a strand or dome than at its lower center, and fire damage is incurred more frequently and severely at these fringes. In the absence of Melaleuca these burned sites are reclaimed by cypress, or, if affected by drainage, by pine. When a Melaleuca seed source is present the rapid growth of Melaleuca can effectively preempt the site from cypress. It should also be pointed out that after burning, which normally would occur in the dry season, Melaleuca seed would be released on the site at least six months before the cypress seed, which is not released until the fall.

The effect of fire in the ecosystems of South Florida is inseparably linked to hydroperiod. As hydroperiods are shortened, accumulated plant material and organic soils are subjected to greater degrees of dessication for prolonged periods of time and the chance for destructive fires is increased. The complete removal of annual flooding on the drained cypress study plot has resulted in a build up of a flammable ground cover (Fig. 30). Most of the cypress trees would probably be killed if this site burned, while the nutrients released would be available to plants colonizing the burned site. If these nutrients had been available to the Melaleuca seedlings established on the site, perhaps they would have stimulated enough growth during the brief period when moisture conditions were satisfactory to survive the dry season.

The influence of fire coupled with the effects of flooding seem to have allowed Melaleuca to become established on the burned mixed hardwood--cypress site, while a very similar adjacent site that had not been recently burned did not permit Melaleuca establishment and was not favorable for Melaleuca growth. Site preparation either by fire or

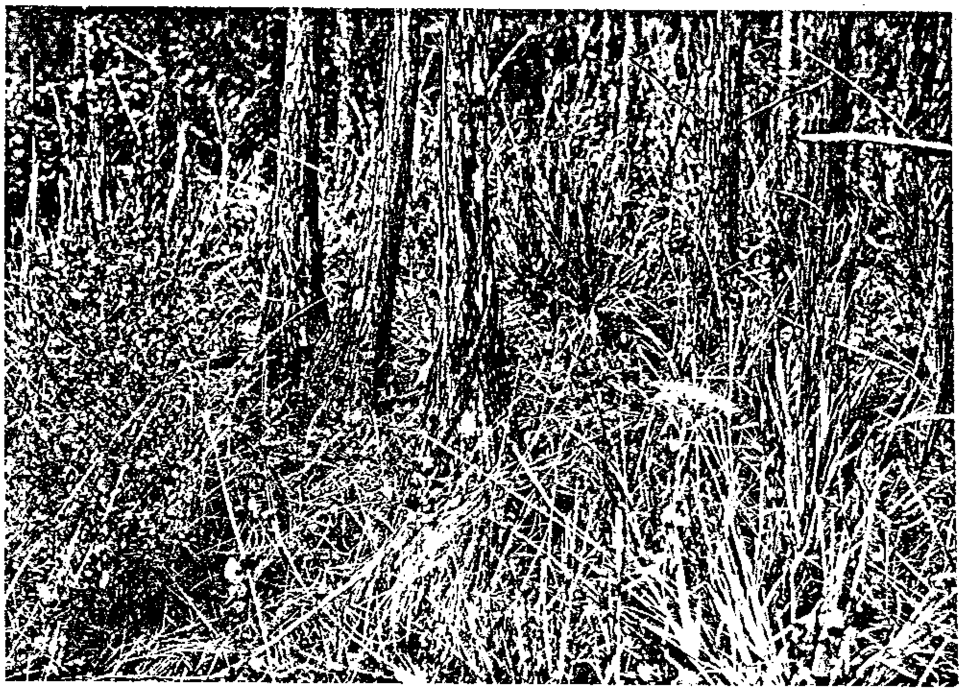


Figure 30. Drained cypress forest study site showing the dense herbaceous ground cover which increases the fire danger.

mechanical disturbance which removes litter and competing vegetation is probably a prerequisite for Melaleuca invasion. A litter layer on the forest floor may act as a physical barrier to Melaleuca seeds. Seeds sown on a layer of litter, if caught within the litter, would not encounter sufficient moisture for germination. Even seeds that fall or are washed through the litter to mineral soil would probably not be able to grow through the litter layer due to the minuteness of the seedlings and the small amount of food reserves within the seed. Fire effectively eliminates this barrier.

Even if a seedling does manage to get through the litter, it would still be overtopped by the extant vegetation. This overtopping and shading may have been the cause of both the poor survival and poor growth obtained on the unburned mixed hardwood--cypress site. Meskimen (1962) pointed out that Melaleuca tends to form even-aged stands, which suggests that Melaleuca is a shade intolerant species. In testing the effects of shading on Melaleuca, Meskimen (1962) found that a comparison of seedling diameter and shoot growth of field-grown sun and shade seedlings revealed little difference between the two. Using controlled shading regimes ranging from full sunlight through 36 percent shade, 64 percent shade, and 90 percent shade, height growth differences were also found to be insignificant; however, general observations suggested that stems of shade grown seedlings were weaker than sun grown seedlings. Dry weight measurements of the roots and shoots supported the hypothesis that more dry matter was being produced in the stems of the shaded individuals at the expense of root production.

Although Melaleuca could probably be considered shade intolerant, as are most successional tree species, it seems quite possible that *Melaleuca* could maintain and perpetuate itself on a site. Few shade tolerant species are observed growing within *Melaleuca* forests, possibly due to repeated fires sweeping through these stands. These fires would help maintain low amounts of litter, would release seed and nutrients, and eliminate any understory vegetation. Any canopy openings could probably be rapidly filled by newly germinated *Melaleuca* seedlings. In dense stands there is probably a constant rain of *Melaleuca* seeds released by natural pruning.

It is almost impossible to locate *Melaleuca* stands that do not show evidence of recent burning. Fire frequency may, in fact, be increased within stands due to the *Melaleuca* trees actually drying out the soil surface sooner than normally would occur. *Melaleuca* and other Myrtaceous tree genera, such as *Eucalyptus*, have reputedly been utilized to dry out wet areas. Whether the transpiration rate of *Melaleuca* is actually greater than cypress is not known, but in the case of *Melaleuca* it would be a year round process, while cypress, which loses its leaves, might tend to conserve moisture during the winter months.

Due to their location in topographic depressions and because they act as reservoirs of moisture, cypress strands and domes probably act as effective fire breaks. Very seldom would conditions exist for an entire undrained cypress strand to burn to the extent that the vegetation would be significantly altered. This would tend to limit *Melaleuca* to the fringes, which are more susceptible to fire damage.

Melaleuca, with its fire triggered seed release mechanism, thick insulating bark, and sprouting ability, is obviously a fire adopted species. In fact, Melaleuca may depend on fire for its competitive advantage over other species. Perhaps without the weakening effect of severe fires on the native vegetation the extent of Melaleuca in South Florida would be significantly less. Not only must the fire release Melaleuca seed and produce a favorable seed bed but also it must eliminate much of the competing vegetation.

For example, at the burned mixed hardwood--cypress site the fire and subsequent flooding had several marked affects which resulted in the successful germination and rapid height growth of Melaleuca. First, the fire effectively removed the ground cover and competing vegetation. Second, nutrients released from the burned vegetation and litter were available for both germinating seedlings and planted seedlings. Third, fire damage to overtopping trees and shrubs opened the canopy, resulting in a greater input of solar energy. Finally, flooding effectively checked the encroachment or reinvasion of many other herbaceous plants so that in the fall, after the soil was again exposed, much of the site was still unoccupied by competing vegetation. It remains to be seen if the many seedlings now established from seed can survive the dry season. The uninterrupted five to six month long flood period, which curtailed growth of submerged seedlings and postponed further germination until late fall, may still prove to be the factor that prevents Melaleuca from taking over the site.

It is impossible to find Melaleuca growing on sites where some sort of disturbance has not occurred. Changes in the hydroperiod and destruction of existing vegetation seem to be prerequisites for any sort of Melaleuca invasion. It seems unlikely that cypress would be able to reproduce and successfully compete with Melaleuca on drained sites, even if the cypress are not killed by fire. The alteration of the hydroperiod would make it extremely difficult for cypress to complete germination. The cypress seed, which is normally released in the fall, would encounter a dry soil surface or one that is only infrequently moist. Langdon (1955) noted that the main requirement for cypress seed germination is abundant moisture for a period of one to three months. The seeds will not germinate if submerged, but will remain viable underwater. Normally, cypress seed would either fall on wet soil or into receding flood waters and germinate as soon as saturated conditions were alleviated.

Site Susceptibility to *Melaleuca* Invasion

Field observations tend to support the hypothesis that the types of sites most suitable for *Melaleuca* invasion are those areas with periodic shallow surface flooding during the wet season. Here, even minor water level fluctuations periodically expose the higher areas, but the surface seldom if ever dries out or is subjected to extended flooding during the wet season (Figs. 31 and 32). The vegetation most commonly found under these conditions is either a mosaic of cypress and pine stands or mixed stands composed of these two species. These mixed stands and mosaics are commonly found on the acid sands of western Lee and Collier Counties and extend into the Big Cypress region. Much of the drained area of the Fahka Union--Golden Gate canal complex supports this type of vegetation. Some of the pine sites and excessively drained cypress stands may now be too dry for successful *Melaleuca* establishment, but much of this area is probably very

Figure 31. Melaleuca seedlings on an ideal site for successful establishment. These sites frequently support as many as 2000 seedlings per m^2.

Figure 32. Dense Melaleuca reproduction in a drained (but periodically flooded) and burned cypress forest.

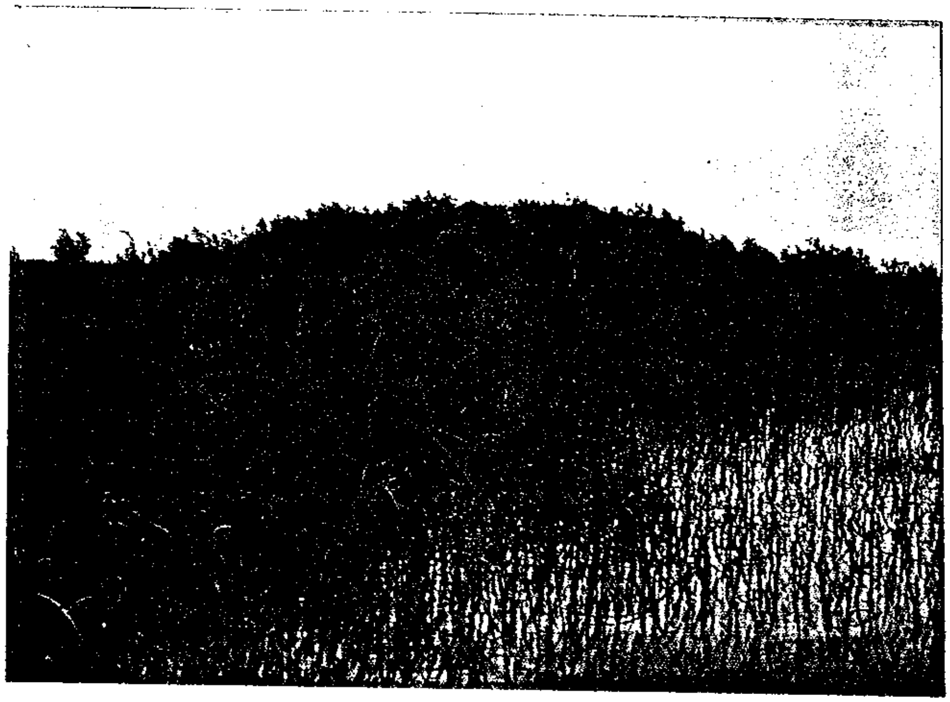
susceptible to *Melaleuca* invasion as moisture conditions are ideal and fires are now more frequent.

Observations made at the transition zone between *Melaleuca* stands and native vegetation seem to indicate that *Melaleuca* occupies the wet pineland sites and those cypress sites which are most frequently drained and burned. In other words, *Melaleuca* may be invading those parts of the habitats of both pine and cypress that are not particularly favorable for either.

The same thing can be said of the transition zone between cypress and wet prairie, and pine and wet prairie. *Melaleuca* is found to occupy the higher, more frequently exposed sites in the wet prairies. It would be extremely unlikely to find *Melaleuca* growing in a slough that is wet most of the year. A reconnaissance of Conservation Area 3A in Dade County by airboat during the wet season showed that only in a few places had *Melaleuca* become established. It can be conjectured that these few stands became established during a severe drought followed by fire, or when water manipulation produced unusually low water levels, and that their future spread is essentially held in abeyance until these conditions again present themselves. Water level at the time of observation was over a meter deep and the one large stand of *Melaleuca* that was found appeared to be breaking up. Many of the trees in the center of the stand had fallen, producing an impenetrable mass of dead or down trees (Fig. 33). The standing trees exhibited massive amounts of adventitious roots; some of the roots were woody and several centimeters in diameter, suggesting that water levels had been high for some time (Fig. 34). These trees could easily be pulled out of the ground by hand, even though some were over 15 cm

Figure 33. A *Melaleuca* stand in Conservation Area 3A. (a) View of dome-like appearance of stand. (b) Interior of stand showing fallen, dying trees. This stand appears to be dying because of continuously high water.

(a)



(b)

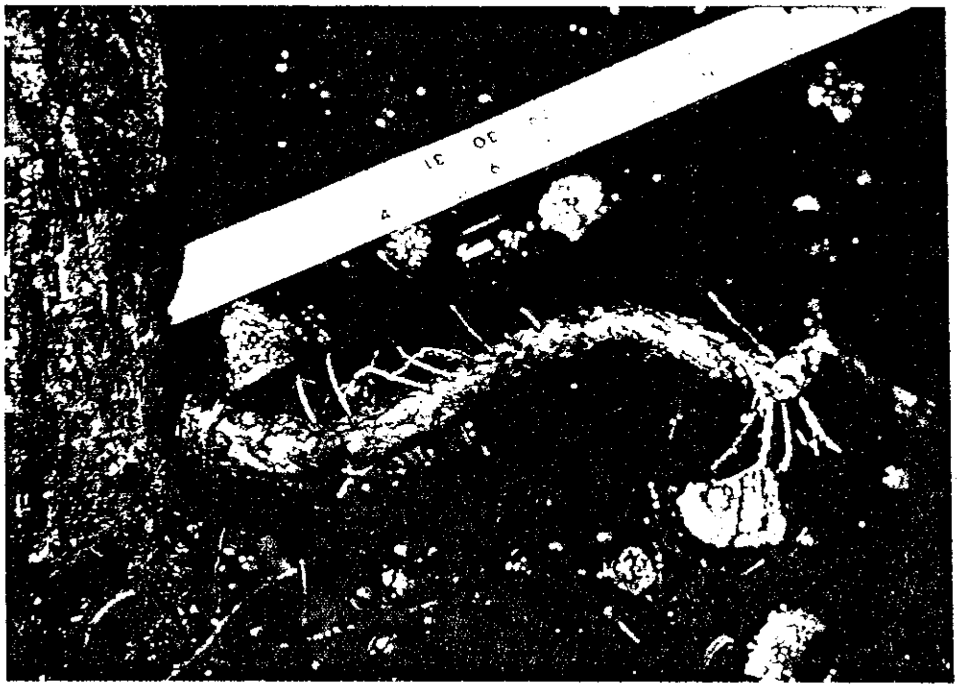


Figure 34. Large, woody adventitious root typical of those commonly found on Melaleuca growing on continuously flooded sites.

in diameter, indicating that they had either failed to produce adequate root systems or that their root systems had died due to the continuously flooded conditions.

Sites that are unflooded throughout the year may only present conditions favorable for germination for brief periods during the wet season, and would rarely exhibit satisfactory moisture conditions required for growth and survival. The longleaf pine flatwood study site is an example of an area that is normally too dry for Melaleuca. Slash pine flatwoods (Pinus elliotii) are probably more favorable for Melaleuca establishment because they tend to occupy soils that are not only subject to occasional surface flooding but also remain wet for longer periods of time.

Many of the artificially drained cypress and slash pine forests in Collier County are probably now very similar to the drier longleaf pine sites. A considerable portion of western Collier and Lee Counties consists of these dry longleaf pine flatwoods, and very little Melaleuca invasion has occurred. Those Melaleuca trees that are found to exist as either isolated individuals or stands that are usually restricted to definite depressions where moisture and possibly nutrients collect.

The longleaf pine site was not only unfavorable for Melaleuca seed germination (almost none occurred), but seedling growth was very poor there as well. Seedling survival was high, but the seedlings appeared to be nutrient-deficient, unhealthy, and insect-damaged. On the other hand, Melaleuca seedling growth on the drained cypress site was considerably better. This probably indicates that there are significant soil differences between these two dry sites and if moisture conditions occasionally become satisfactory on the drained cypress site, it would be much more susceptible to *Melaleuca* invasion.

The mature cypress forest obviously does not normally present conditions favorable for successful germination or subsequent growth of *Melaleuca*. Even though many of the planted seedlings survived a good part of the wet season underwater, the hydroperiod on this site is relatively long and as the water level drops in the fall, flow through the site practically ceases; the water then becomes stagnant and oxygen depleted. The dense shade over much of the plot would probably also be a factor limiting growth of any emergent seedlings.

Although *Melaleuca* seedlings have become established during the late fall on the dwarf cypress forest site, it seems unlikely that they will survive the dry season. Seedlings established from seed as early as November the previous year were all dead by March. Perhaps fire that would remove the thick algal mat and release nutrients would be sufficient to open this site to *Melaleuca*. Even though the planted seedlings have been heavily insect-damaged, growth has been good.

The general lack of any germination and the survival of only one planted seedling on the mangrove site suggests that, at least in this particular case, salinity may be an important factor limiting the encroachment of *Melaleuca* into mangrove-dominated areas. The survival that did occur resulted from a mid-wet-season planting when there was a significant fresh water input; however, the entire site was flooded at this time so favorable conditions for germination did not exist. The single surviving seedling has produced smaller, thicker than normal leaves in response to what is probably slightly brackish water. The possibility that *Melaleuca* might invade mangrove sites was suggested by the areas that it inhabits in Southeast Asia. Although no significant Melaleuca invasion of mangrove areas has yet been noted anywhere in Florida, mangrove sites do vary considerably as to salinity, soils, and species. Due to this variability the study site may not have been representative of much of the mangrove areas in South Florida. Perhaps seeding and planting trials should be tested on a buttonwood site (Conocarpus erectus) because this species occupies the "backmangrove" in South Florida.

Qualitative Melaleuca Model

The basic factors affecting the ability of Melaleuca to invade an ecosystem are summarized in the energy flow diagram in Figure 35. Water level is considered to be the principle factor controlling the type of vegetation that a site will support and the vulnerability of a site to Melaleuca invasion.

If water levels are high the native vegetation types, utilizing the nutrient resource released through decomposition, will continue to grow and perpetuate themselves. However, when water levels are lowered by artificial drainage and litter levels are high severe fires occur which consume the litter and destroy much of the vegetation. If Melaleuca is already on the site, seed will be released. If moisture levels then fall within the range described as favorable for Melaleuca establishment these seeds will successfully germinate. Even though drainage has occurred and fires are frequent the moisture levels required for Melaleuca may not be present and the seed crop will be lost.

If Melaleuca does become established it is still dependent on the

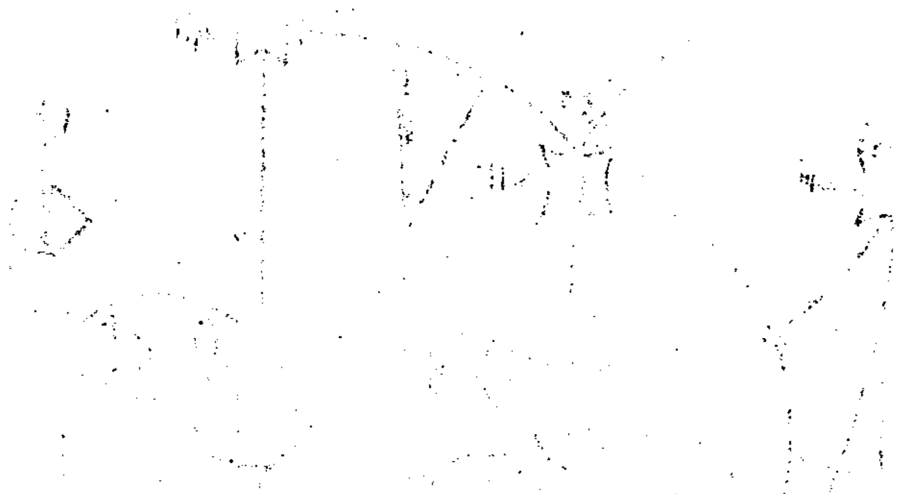
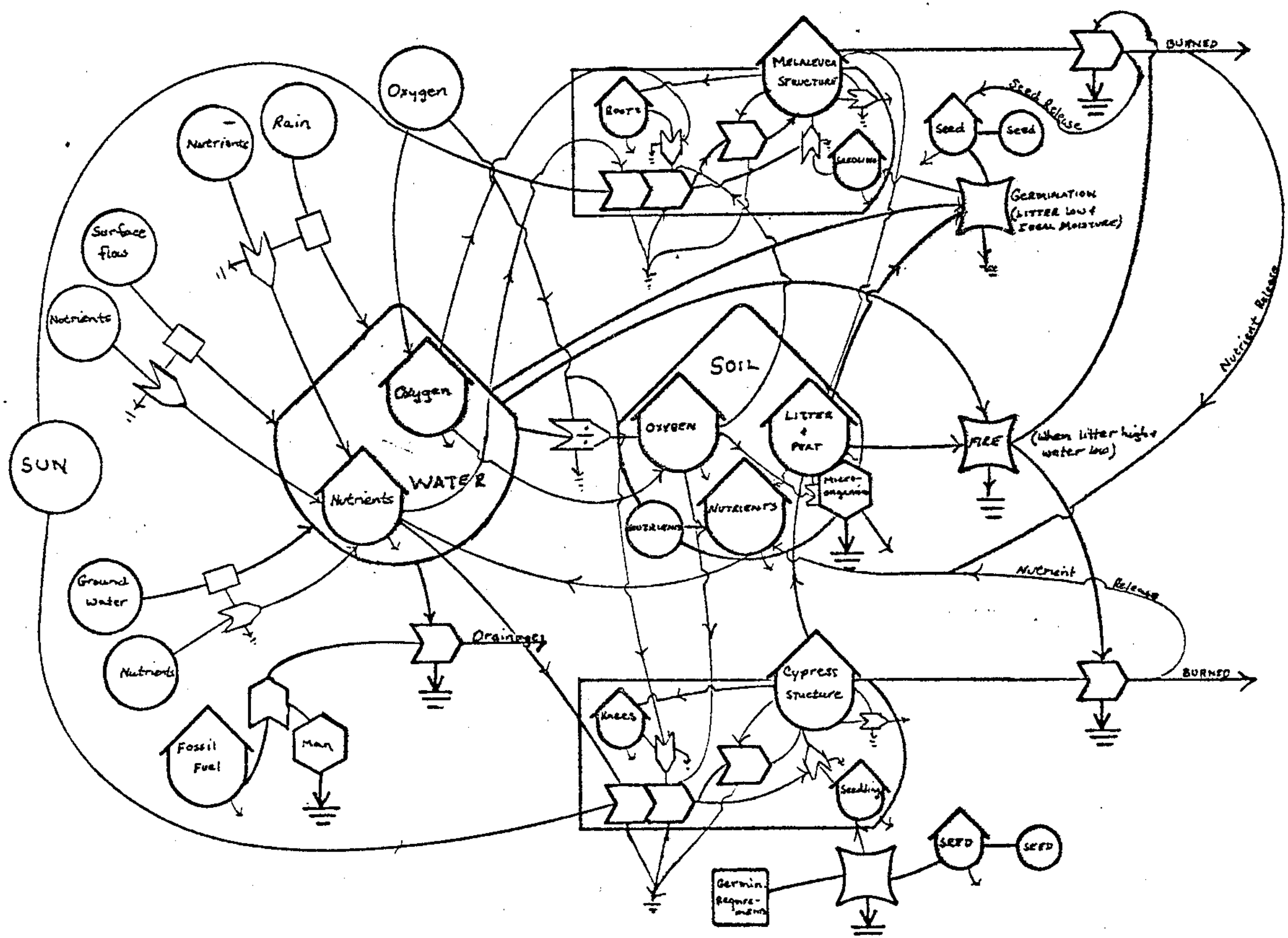


Figure 35. Qualitative energy flow diagram of Melaleuca--cypress competition.



SUN
Surface flow
Nutrients
Rain
Oxygen
Ground water
WATER
SOIL
Melaleuca Structure
Roots
Seed
Seed Release
Germination (litter low & ideal moisture)
Litter & Peat
FIRE
(when litter high & water low)
Nutrient Release
BURNED
Drainage
Fossil Fuel
Man
Cypress Structure
Knees
Seedling
SEED
Germin. Require-ments

water level for its continued ability to utilize the resources. If water levels again rise, conditions may become unfavorable for continued growth and the trees will die out. (These water conditions are independent of the conditions required for germination.) If Melaleuca is not present on a site at the time of burning any influx of Melaleuca is dependent on the outside seed source and favorable moisture conditions.

The crux of the Melaleuca problem in South Florida seems to be related to the presence or absence of these favorable moisture requirements for germination and the degree to which sites are subject to flooding and burning. Because this field study has not yet been carried through the complete cycle of wet and dry seasons it is difficult to draw any final conclusion about favorable sites for Melaleuca establishment and what combination of site conditions are required. However, certain trends are evident and tentative conclusions can be made.

(1) It seems unlikely that seed germinated during the winter months on any of the sites described will survive, while seeds released during the dry season may not remain viable for extended periods.

(2) Survival and growth seem to be better on open, disturbed sites than on undisturbed and densely vegetated sites.

(3) Seeds apparently do not normally germinate underwater under field conditions, thus, areas that are normally flooded quickly after the initial rains begin may not be conducive to germination; the higher, more irregularly flooded sites are probably more favorable.

(4) Soil fertility may affect the ability of seedlings to grow rapidly enough to survive dry periods; in many cases the nutrients released from burning may be a sufficient impulse to stimulate the required growth.

(5) Newly germinated seedlings appear to be able to withstand submergence for extended periods, while larger seedlings appear to be relatively unaffected by waterlogged soils, but will develop dimorphically distinct leaves and for all practical purposes cease growth if submerged.

This study, at its present development, tentatively supports the conclusion that conditions for *Melaleuca* establishment, even on disturbed sites, are present for only a limited amount of time each year and that these conditions are critical and must be met. Certain site conditions which may have been increased in area by human activities have resulted in an increase in the area occupied by sites which are susceptible to invasion. Due to these alterations in the environment, the effective range of *Melaleuca* has been extended and probably includes much of the drained areas of western and central Collier County, especially those sites that support cypress forest, while undisturbed areas of native vegetation will probably be relatively free of *Melaleuca*.

Management Alternatives

Direct control of *Melaleuca* is extremely difficult. The use of fire releases seed and normally does not kill the trees. Cutting and removal does nothing but stimulate sprouting, and *Melaleuca* is a prolific sprouter (Fig. 36). It sprouts from the mainstem and branches after the top has been killed by frost, fire, or felling. The sprouts

Figure 36. Burned stand of Melaleuca. (a) Immediately after the fire, (b) three months later.

(a)

(b)

usually occur just below the point of damage. Saplings less than a centimeter in diameter sprout at ground level (Meskimen, 1962). Root sprouts or suckers have not been observed by me, but nurserymen use cuttings of immature wood or bits of slender roots laid horizontally on the soil to propagate *Melaleuca* (Morton, 1966).

Due to its rapid growth, long succulent growing regions are maintained throughout the year, but these are invariably killed back during frost periods. The multiple-stemmed individuals are probably produced when seedlings are killed back to ground level and subsequently sprout. These multiple-stemmed trees are frequently observed in the more northerly extent of the range of *Melaleuca*, where frost is more frequent. Meskimen (1962) pointed out that in 1958, a group of 30 to 45 cm tall seedlings was planted in the Austin Cary Forest in Alachua County. In January 1959 they were all killed back to ground level by subfreezing temperatures, but by March each stem had produced sprouts, and within eight weeks these sprouts exceeded the height of the original seedlings.

Stump sprouts on large trees develop rapidly after felling, growing through several inches of bark. When trees are incompletely severed, bulldozed, or windthrown, sprouts develop along the dorsal surface of the stem, producing several new stems where only one had existed before (Meskimen, 1962). These sprouting characteristics preclude most conventional means of control. Complete cutting produces stump sprouts and releases seed, while bulldozing or incomplete felling produces a greater number of new vigorous stems. Burning releases seed, induces sprouting, and reduces competition. The success of herbicides has been limited. It is not uncommon to find *Melaleuca* stands greatly increased in size by an uninformed attempt to control them by cutting or burning (Fig. 37).

At this late date the probability of controlling Melaleuca over extensive areas is limited. Its outright elimination, except on a small scale, seems nearly impossible. Melaleuca will have to be accepted as part of the landscape. Beyond this acceptance there are possibilities for land and water management programs that may hinder its spread and provide for its exclusion from such areas as Everglades National Park, the Conservation Areas, and the undrained regions of the Big Cypress Swamp. These areas, relatively free from Melaleuca at the present time, could continue to be maintained in some semblance of their original vegetation.

From the data collected thus far, several management possibilities are apparent. The feasibility of the suggestions offered here, along with any other management schemes that may develop, should be tested on a small scale before their widespread application is considered. It must be remembered that due to South Florida's unique environment, the effects of any local manipulation of water levels, hydroperiods, fire, and the use of herbicides, etc. can have far reaching effects in both the natural and human aspects of the ecosystem.

Within the natural preserves of South Florida it appears likely that an integrated program of both water and fire management, coupled with vigilance and the assumption that an undisturbed ecosystem is relatively resistant to invasion, can exclude Melaleuca from these areas. In other words, those factors which give Melaleuca a competitive advantage over a particular native vegetation type could be controlled. This does not mean, for example, a return to fire control,

Figure 37. Melaleuca stump sprouts six months after a control cutting, Koreshan State Recreation Area, July 1974.

but rather the selective use of fire in those areas which regularly present favorable conditions for *Melaleuca* establishment and are close to a seed source. The rapid invasion of a burned site will not normally occur unless there are already *Melaleuca* trees on that site to provide an input of seed. Large areas of the Everglades National Park could burn severely without ever incurring anything approaching a *Melaleuca* replacement of the native vegetation, even if site conditions are favorable. A seed source does not exist within the park at this time. All that could occur is the establishment of a few individuals from errant seed. These could be eliminated either by uprooting and removing or by using a combination of cutting and direct application of herbicide. Only if this initial establishment is ignored would the possibility of uncontrollable invasion exist, assuming the other conditions, including site disturbance and appropriate soil and water conditions exist.

In susceptible areas supporting widely scattered *Melaleuca*, when soil conditions are such that an early seed fall would not encounter conditions favorable for survival, early season prescribed burning might be used as a seed release mechanism. Much of the drained cypress area in Collier County will burn in the fall. This would put the seed on the ground at a time when the seedlings would be subjected to unsatisfactory moisture conditions. Also, frequent fall burning in these areas would tend to favor pine. Fuel reduction and site preparation at the time of pine seed release would enhance pine establishment and reduce losses from severe burning. Unless attempts are made to slow runoff through drainage canals, either by special structures or possibly by using aquatic vegetation to slow water flow through the canals, the cypress forests in much of western Collier County can probably be written off to pine, hardwoods, or Melaleuca. The decision would have to be made whether to favor hardwoods through fire control, or pine by late fall burning. Neglect would open much of this area to Melaleuca.

Water management poses a problem in that much of South Florida has already been affected by drainage, and even in areas where a fair degree of freedom does exist, severe drought conditions periodically occur. Any water manipulation program must be designed to alter the hydroperiod so that the time between severe fires is lengthened and the loss of organic soils through burning and oxidation reduced. However, it is important to emphasize that the management of water levels and hydroperiod could have drastic effects on the desirable environmental characteristics which ecosystem managers are trying to maintain in South Florida. Manipulation for the sole purpose of checking the spread of Melaleuca should not be considered as a management goal.

There exists another management possibility that could be implemented on a limited scale. This would involve the use of existing Melaleuca stands, especially those around the Naples and Fort Myers areas, as receptors of secondary treated sewage (Fig. 38). The feasibility of using wetlands, especially cypress domes, as sewage receptors and nutrient filters is presently being tested at the University of Florida. Most wetland areas have been recognized as efficient nutrient filters and water purifiers. The possibility exists not only for the use of Melaleuca swamps for this purpose but also for using sewage effluent as an eventual means of eliminating Melaleuca over limited areas. Sewage effluent could be pumped into some of the large former cypress strands and domes that are now dominated by Melaleuca. The

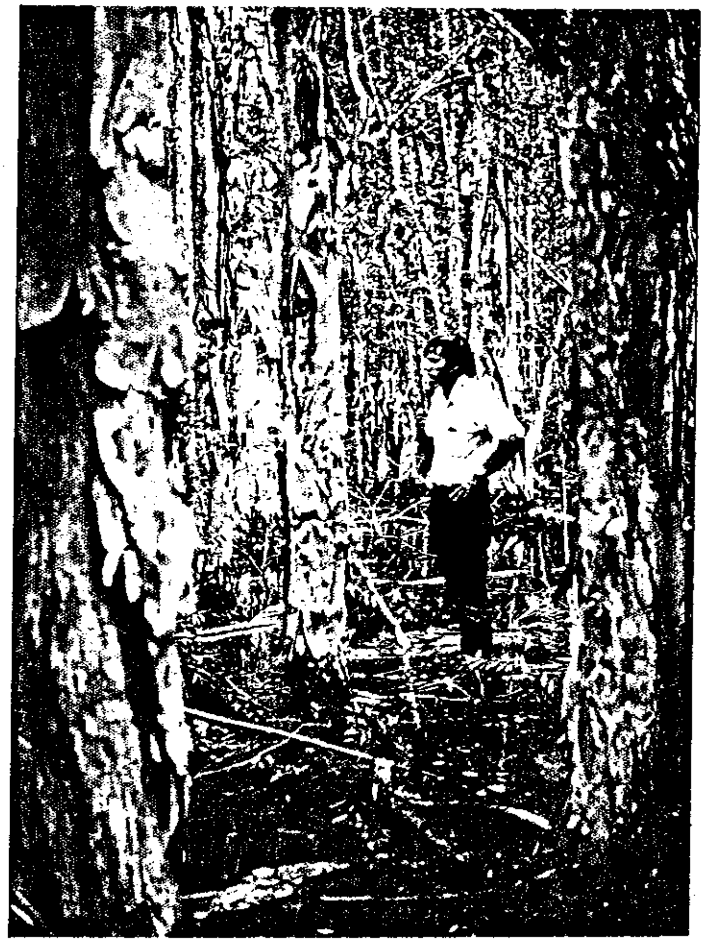


Figure 38. Mature _Melaleuca_ forest at Six-mile Cypress Strand, southeast of Fort Myers. This is the kind of _Melaleuca_ forest which might be useful for recreation or sewage disposal.

successional nature of *Melaleuca* would at the onset make it particularly suited to utilizing this nutrient input.

On the other hand, it has been found that the dissolved oxygen content in cypress domes receiving sewage effluent approached zero during a 24 hour period (Sidney Cowles, Center for Wetlands, University of Florida, per. com.). Perhaps if *Melaleuca* swamps were continuously flooded with water containing sewage effluent, the low dissolved oxygen levels might eventually kill the *Melaleuca*. The greenhouse experiment, involving the manipulation of dissolved oxygen levels, failed to demonstrate a short term effect of high and low dissolved oxygen levels on *Melaleuca* growth; however, it is suspected that this experiment may not have been carried out for a sufficient length of time to get a differential response. The field observations in Conservation Area 3A suggest that *Melaleuca* cannot tolerate a continuously flooded condition with low dissolved oxygen levels. In addition, if high water levels were maintained for extended periods of time the possibility of both frequent burning and successful reproduction would be greatly reduced. Once *Melaleuca* trees are killed in a stand receiving water containing sewage effluent, the water levels could be lowered briefly and the sites replanted or seeded to cypress. From then on water levels and sewage input could be manipulated in such a way that cypress would be favored.

Another management alternative might be the actual maintenance and use of existing *Melaleuca* stands for forest products and recreation. A mature *Melaleuca* forest provides an aesthetically pleasing environment with a relatively open forest floor. Forests such as these which are located near densely populated urban areas could be used as city and county parks and recreation areas.

Future Spread in South Florida and Environmental Impact

The consideration of the spread of *Melaleuca* as solely a biogeographical problem has been avoided in this study. I feel that alterations in the ecosystems of South Florida have been responsible for the rapid spread of *Melaleuca*, rather than the mere presence or absence of a *Melaleuca* seed source. Those areas in South Florida that do not at present support *Melaleuca* probably do not because their natural state has not been sufficiently altered to present conditions conducive to *Melaleuca* establishment, or at least the time lag between disturbance and invasion has been too short to realize the effects. The occurrence of prevailing winds, waterflow, and other geographical conduits and barriers are not looked upon as being the principal factors controlling the patterns of *Melaleuca* establishment that exist. The Everglades National Park, Conservation Area 3, and the eastern portion of the Big Cypress Swamp do not support large stands of *Melaleuca* because it cannot compete and cannot become established under the conditions that are normally present there. The isolated stands and individuals that are occasionally found are probably not the incipient precursors of a dramatic change taking place, but are remnants of what had once been a favorable site for a short period of time when a chance seeding took place. *Melaleuca* should be looked upon as a weed, an aggressive invader of unoccupied, disturbed sites, not as an active invader of undisturbed, natural ecosystems. It seems unlikely that any of the areas not presently being colonized by *Melaleuca* have not at some time received an input of *Melaleuca* seed. Only after a site has been disturbed will *Melaleuca* be successful. In other words, *Melaleuca* probably occupies, and will continue to occupy, those areas in South Florida that normally support weedy species; likewise, Melaleuca will, once established, probably occupy a site for a long time.

Casual observations have led to the conclusion that Melaleuca stands are practically devoid of animal life, and that its continuous spread will result in a pauperization of native fauna through the elimination of their habitat. The belief that direct destruction of wildlife habitat is caused by the replacement of native vegetation with Melaleuca is probably a fallacy. Much of the fauna of South Florida's wetlands is dependent upon and genetically programmed to a specific hydroperiod spectrum to carry out their life cycles. If indeed there is a paucity of wildlife in Melaleuca dominated ecosystems, the cause may well be the destruction of wildlife habitat through drainage and hydroperiod alteration. The fact that Melaleuca tends to invade these disturbed areas might be incidental to the loss of wildlife diversity. Perhaps the alligator is not normally found in Melaleuca swamps because the water so vital for its existence has already been drained away.

The difficulties encountered so far in the attempt to establish Melaleuca on a variety of undrained, unburned sites suggests that if an ecosystem is managed for these native vegetation types, and if major permanent disruptions in their natural influences are prevented, then they will be relatively effective in excluding Melaleuca. A difficult problem for the ecosystem manager is to determine what types and degrees of manipulation are necessary to maintain the native vegetation. A prevalent land management policy these days is to manage natural preserves not only as entities separate from their surrounding ecosystems but also as museums. This "as the first white man saw it" syndrome is inconsistent with basic ecological principles and probably is in the long run detrimental to the environment. Vegetation cannot be manipulated to remain in a static state or return to some historic condition without tremendous energy inputs to divert or reverse the natural energy flows within the ecosystem. Most natural preserves in South Florida are so tightly linked to the surrounding ecosystems that those changes occurring outside of their administrative boundaries greatly affect what happens inside. These areas should be looked upon as dynamic systems changing not only due to man-caused manipulation but also through long term climatic, geologic, and biologic changes. The ecosystems should be managed to maintain the diversity necessary for stability. In other words, they should be managed for healthy, not historic, ecosystems.

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BIOGRAPHICAL SKETCH

Ronald Lewis Myers was born in Palo Alto, California on April 6, 1946. He graduated from Morris Hills Regional High School in Rockaway, New Jersey in 1964. He received a Bachelor of Science degree in Forestry from the University of Montana in 1969. After working for two years as a Peace Corps Volunteer in Honduras, he was employed by the National Park Service as a Park Technician in Everglades National Park. In 1973 he was admitted to the Master of Science Program in the Department of Botany at the University of Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

John J. Ewel, Chairman
Assistant Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

Howard T. Odum
Graduate Research Professor of Environmental Engineering

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a thesis for the degree of Master of Science.

Daniel B. Ward
Associate Professor of Botany

This thesis was submitted to the Graduate Faculty of the Department of Botany in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Master of Science.

March 1975

Dean, Graduate School

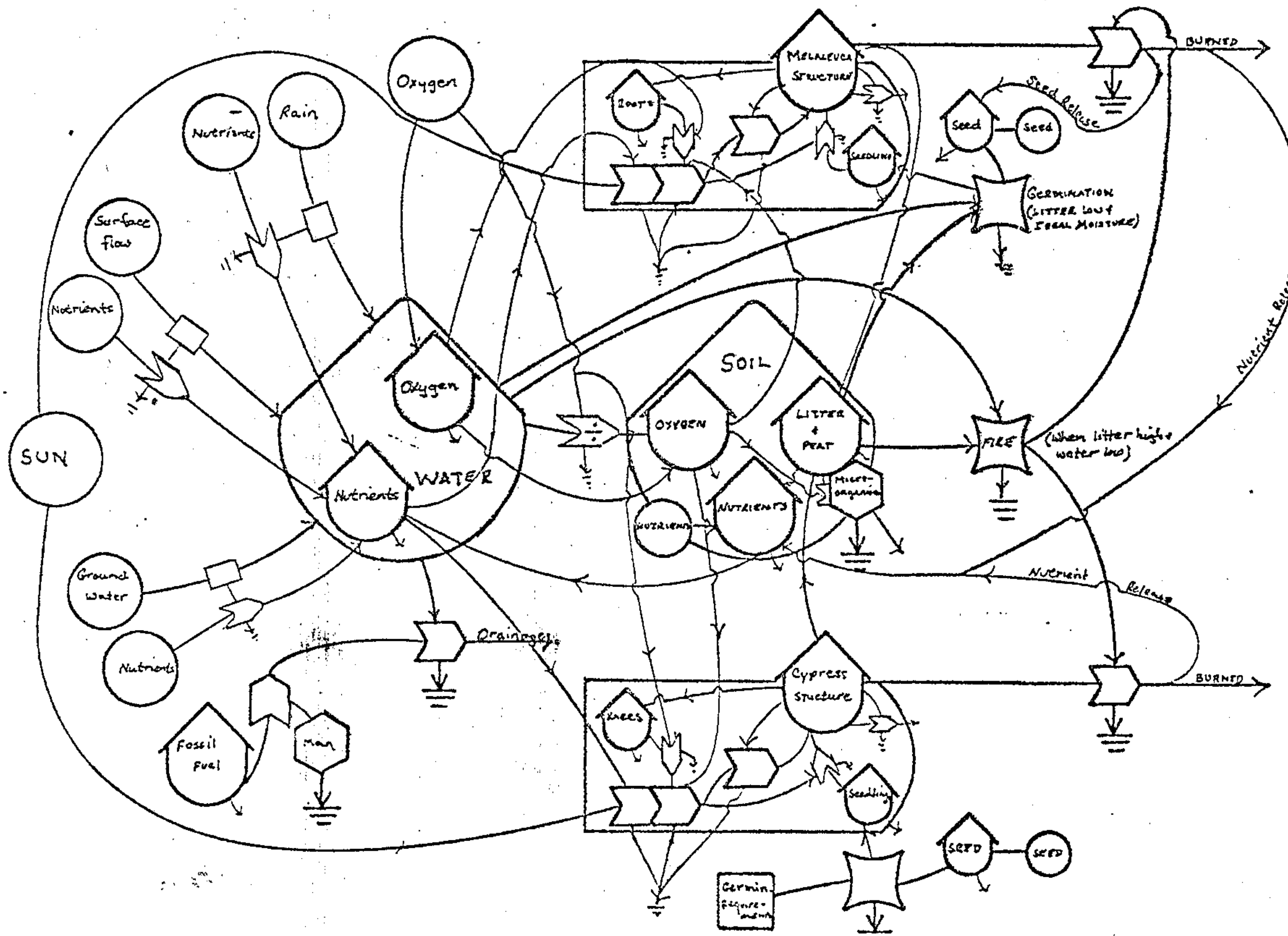

Fig. 35. Qualitative energy flow diagram of Melaleuca – cypress competition.

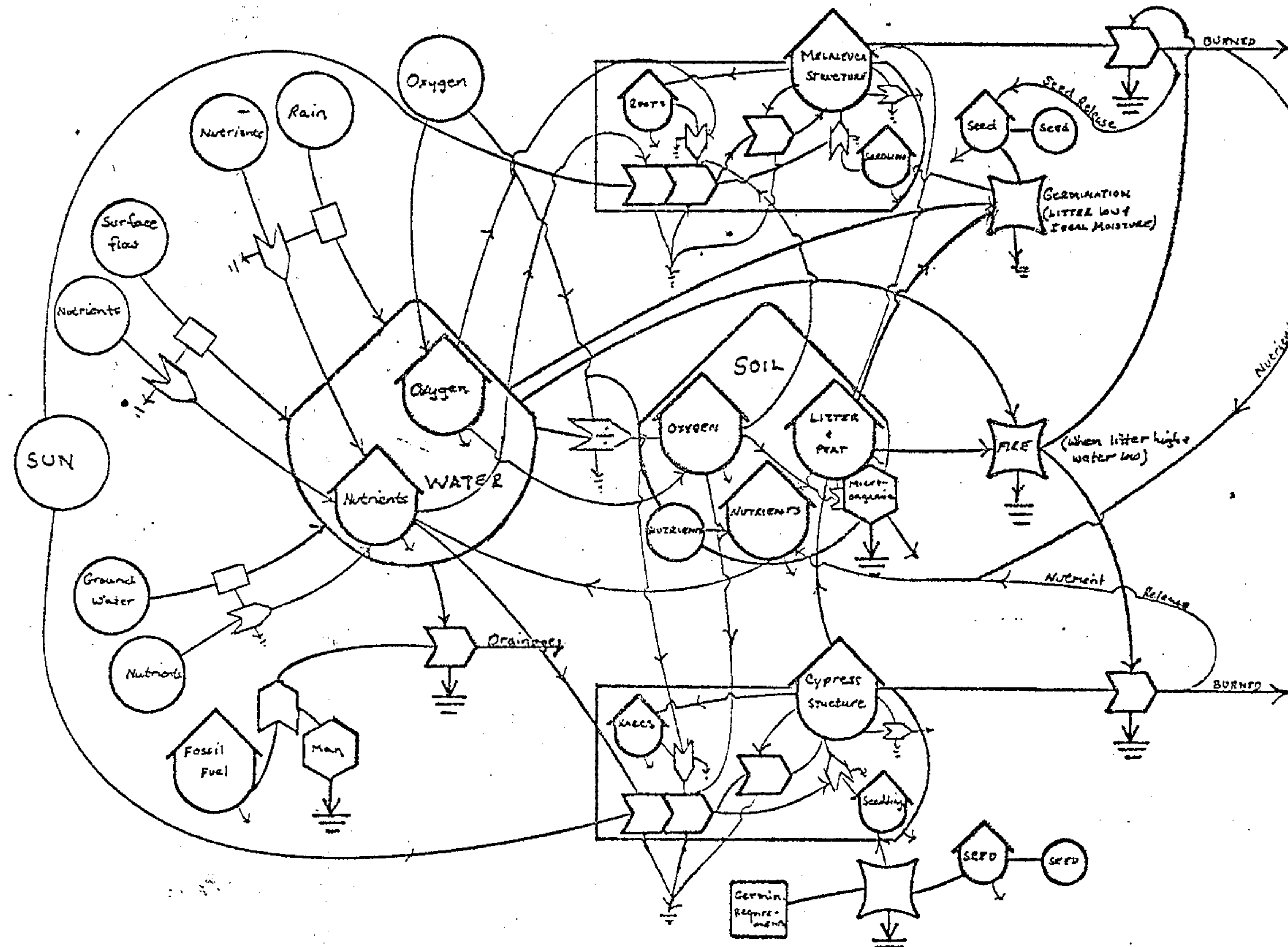

Fig. 35. Qualitative energy flow diagram of *Melaleuca* - cypress competition.