

SUBMERSION TOLERANCE OF SELECTED SEEDLING TREES

by 6791

WILLIAM LEROY LOUCKS

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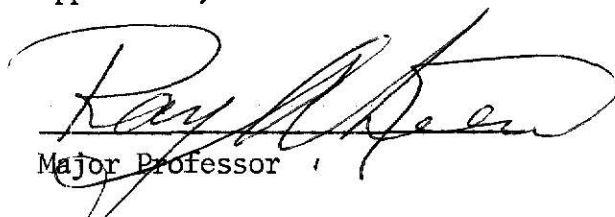
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INTRODUCTION

Flood control and irrigation reservoirs varying from relatively simple Soil Conservation Service watershed detention structures to the vast projects being constructed by the U. S. Army Corps of Engineers and Bureau of Reclamation, are being used as settings for hundreds of recreational developments throughout the United States. These developments range in size from single family picnicking or camping sites to large areas capable of supporting enormous crowds engaged in numerous activities.

Due to the sparsity of native woodlands in many of these recreational areas, large tree planting programs are being conducted to provide a cool and attractive environment. A large portion of the money spent in these programs is for establishing trees on the shore due to the public pressure to provide the benefits of trees near the water. Unfortunately, many of these areas are frequently flooded. The frequency and depth of floods varies by reservoir; however, many of them exceed their normal pool level several times each growing season inundating numerous acres and completely covering recently transplanted trees. Adverse effects of inundation results in poor tree survival and growth.

This study was designed to determine the relative tolerance to submersion of twelve tree species commonly used in recreational areas in the Great Plains Region.

Four frequently used terms must be understood before proceeding. Although the following definitions are not universally accepted, they will be used in this report for the sake of clarity:

1. Saturated soil refers to the soil being completely saturated with all pore space filled with water, but with no water standing on the soil surface.

2. Flooding refers to covering the soil surface and part of the stem with water.

3. Submersion refers to covering the entire plant with water.

4. Inundation is a general term including all three of the preceding conditions.

REVIEW OF LITERATURE

Causes of Injury to Trees Resulting from Inundation

Numerous investigators have found that prolonged inundation adversely affects the physiological processes of mesophytic plants. Oxygen deficiency is generally accepted as the single most important cause of injury (5, 36, 40, 44, 67). Kramer (47) and Jackson (44) believe, however, that the causes of injury are complex and are a combination of many factors.

Effect of Inundation on Photosynthesis, Transpiration, and Respiration

Childers and White (21) showed that transpiration and apparent photosynthesis is reduced within 2 to 29 days after apple tree roots are flooded. They found that in some cases the rate of transpiration and apparent photosynthesis becomes so small with continued flooding that they can not be measured.

Several investigators have observed a sudden increase above the expected rate of transpiration in many species just after flooding, which is followed by a decrease to well below the expected rate (10, 21, 47, 51, 56, 73). Parker (56) suggested that the increased rate of transpiration is due to the soil moisture being somewhat limiting to absorption even though it is near the field capacity before it is flooded. In some species, after the rate of transpiration reaches a low point, the rate will increase somewhat even though the plants remain flooded (56). The increase in transpiration is probably due to the formation of new leaves and adventitious roots.

In reviewing the literature pertinent to oxygen deficiency as a cause of disease in plants, Bergman (5) concluded that there have been few investi-

gations on the effect of oxygen deficiency on respiration. The few investigations that have been conducted show a great variation in results. The extent of the variation is represented by Childers and White (21) and Loustalot (51). Childers and White reported a definite increase in the apparent respiration of young apple trees when flooded. Loustalot reported that the apparent respiration of flooded pecan seedlings is reduced. Bergman (5) believes that the affect of oxygen deficiency on respiration varies with the species of plant and part of plant being tested.

Effect of Inundation on Absorption

It is generally agreed that inundating trees results in reduced water and mineral absorption (45, 47, 48, 56, 73, 79). Kramer (45) discovered that when the root systems of woody and herbacious plants are killed by heat or ether, the plants remain alive and unwilted for several days, which suggests that plants are able to absorb water through dead root systems. However, he found that absorption is quickly reduced by plugging of the xylem by deposits of substances which, he believes, are given off from dead cells in the roots.

Kramer (46) indicated that an excess of carbon dioxide reduces absorption much sooner than a deficiency of oxygen. He concluded that excessive carbon dioxide results in a decrease in permeability of the protoplasm and an increase in resistance to water movement across the cortex from epidermis to xylem. Hoagland and Broyer (37) found that after the initial decrease, there is an increase in permeability to inorganic solutes and water. Clements (23) reported that excessive carbon dioxide is common in saturated soils.

Effect of Inundation on Translocation

Kramer (47) believes that although dessication, due to the decrease in water absorption, may account for some symptoms, it can not fully explain such symptoms as rapid development of chlorosis and death of leaves, curvature of leaves, and formation of callus tissue on the stem and adventitious roots near the water surface. Mason and Phillis (54) and Curtis (26) suggested that if the exclusion of oxygen is adequate, translocation may be completely checked; however, they noted that oxygen may be obtained in some species through the transpiration current. Exclusion of oxygen may also prevent the movement of auxins as shown in Dubuy and Olson's (29) investigation on the movement of auxins in *Avena coleoptiles*. Kramer (47) suggested that hypertrophy and formation of adventitious roots are possibly due to the accumulation of carbohydrates and auxins near the water surface. The accumulation of auxins may also be responsible for curvature of leaves and petioles.

Effect of Inundation on Toxic Substances in the Roots and Soil

Kramer (47) indicated that yellowing and death of leaves may in some instances be due to dessication, but he believes that toxic substances moving up from the dead roots or from surrounding soil are at least partly responsible for injury or death of leaves. The eventual increase in permeability of the protoplasm of inundated roots, Kramer believes, corresponds with the death of the roots and results in whatever solutes are in the soil being absorbed with the water, since the dead root cells are no longer differentially permeable. He concluded that it is unlikely that deficiency of nitrogen or other mineral nutrients is an important factor in injury to flooded plants. One investigation, Jackson (43), supports Kramer's conclusion.

Jackson (44) found, however, that a severe oxygen deficiency, which causes death of roots and prevents the development of adventitious roots,

causes the maximum degree of chlorosis regardless of attempts to remove excess carbon dioxide, toxins, and microorganisms. He noted that epinasty of leaves and petioles is induced by only a slight deficiency of oxygen.

In comparing the influence of dessication and toxic substances on the internal structure of the cell, Hosner and Boyce (41) showed that the death of cherrybark oak (Quercus falcata var. pagodaefolia Ell.) seedlings in saturated soil is due to leaf moisture deficits rather than toxic substances as suggested by Kramer (47).

The characteristically low content of oxygen in inundated soils adversely affects chemical and biochemical processes which occur in well aerated soils, which results in some necessary mineral nutrients being unavailable for normal plant growth. Some investigators attribute some of the injury to plants inundated for prolonged periods to one or more of these compounds. Compounds produced under such conditions include nitrites, sulfides (particularly hydrogen sulfide), ferrous iron, and marsh gas (Methane) (5).

Plant Characteristics Affecting Survival of Trees Subjected to Inundation

It is generally accepted that tolerance to inundation varies greatly between tree species. The difference in tolerance, according to Bergman (5), is due to physiological and/or anatomical differences between species. Hosner and Boyce's (41) investigation supports this belief. They concluded that seedling tolerance to saturated soil is dependent on (1) whether the root system can adjust to poorly aerated conditions and continue to function, (2) whether the seedlings can form adventitious roots to replace the initial root system, and (3) whether the stems and leaves are sufficiently drought

resistant to withstand high moisture stress.

Role of Initial Root Systems in Tolerance to Inundation

Working with reciprocally grafted plants of peach and plum, Rowe (63) found that sensitivity to saturated soil is a property of the root system. Hosner (39) discovered that all of the established secondary roots of seedlings die during 38 days of flooding. His investigation included hackberry (Celtis occidentalis L.), eastern cottonwood (Populus deltoides Bartr.), sycamore (Platanus occidentalis L.), green ash (Fraxinus pennsylvanica Marsh.), pin oak (Quercus palustris Munenchh.), and cherrybark oak (Quercus falcata var. pagodaefolia Ell.). The only species in the study that formed new laterals while flooded was green ash. In a later investigation, Hosner and Boyce (41) found that the secondary roots of water tupelo (Nyssa aquatica L.) and green ash (Fraxinus pennsylvanica Marsh.) continue to grow after 60 days of flooding. The remaining species in the study did not have any actively growing roots; however, after 23 days of well drained soil the roots reoccupied the soil indicating that the roots were still alive. All of the plants that were living when the water was drained, except four sycamore (Platanus occidentalis) and three hackberry (Celtis occidentalis), resumed root and shoot growth.

Kramer (47) suggested that roots developed in water are different anatomically and/or physiologically from roots in well aerated media. He believes that the difference is possibly due to a different respiratory enzyme system which allows the plant to function with a lower oxygen supply. Bergman (3) believes that some plants are able to grow in saturated soil because of specialized tissue which permits oxygen to diffuse through the

shoot to the root system. Willow seedlings continue root growth at about one-half of the normal rate in complete lack of oxygen according to Leyton and Rousseau(49). They presented evidence that willow roots apparently obtain oxygen or oxidized substrate from the shoot. Bergman's and Leyton and Rousseau's observations are supported by Cannon (19), Conway (24), Bergman (5), and Hosner (39).

In investigating planted hardwood seedlings in saturated soil, Bonner (8) indicated that seedlings growing in saturated soil maintains a balance between the shoot and root system, so that they don't develop the large leaf moisture deficit commonly observed in plants flooded after a period of growth. This suggests that some tree species may be planted in saturated soils where trees of the same species were growing prior to the soil being saturated even though the original trees were killed.

Role of Adventitious Roots in Tolerance to Inundation

The importance of the formation of adventitious roots to the survival of flooded trees or trees growing in saturated soil has been stressed by numerous writers. Adventitious roots commonly form near the soil or water surface. Penfound (57) observed black willow (Salix nigra Marsh.) with huge platforms of roots eight feet across. In some cases there were two sets of roots, one at the summer and one at the winter flood level.

Bergman (3) reported that the only mesophytes that survive when flooded do so by developing adventitious roots near the water surface. In a later investigation (5), his conclusion was less emphatic. He stated that some species are able to survive flooding due to naturally shallow root systems, or development of adventitious roots.

Hosner (39) believes that the growth and survival of eastern cottonwood (Populus deltoides Bartr.) and sycamore (Platanus occidentalis L.) seedlings in saturated soil are directly related to the development of adventitious roots. He observed that green ash (Fraxinus pennsylvanica Marsh.) is able to produce new secondary roots as well as adventitious roots. Other species that do not produce new secondary roots or adventitious roots do poorly in saturated soil. Kramer (47), Bourdeau (10), and others presented additional evidence showing the importance of adventitious roots in reducing injuries due to saturated soil and flooding.

Role of Stems and Roots in

Tolerance to Inundation

Wilted leaves frequently found on inundated plants are probably at least partly due to moisture stress. Species that are resistant to moisture stress in the leaves and stem may be more tolerant to inundation. Hunt (42) found that although injury occurs to the root systems of flooded one year old seedlings of shortleaf pine (Pinus echinata Mill.), loblolly pine (Pinus taeda L.), and pond pine (Pinus rigida var. serotina [Michx.] Loud.), little injury to the shoots results even when the soil is allowed to dry out. He suggested that the lack of injury to the shoots reflects their resistance to moisture stress, which is supported in part by Ursic (71). Kramer (47) reported that wilted leaves is a common, but not the most characteristic symptom of injury due to flooding. Perhaps lack of wilt is related to greater drought resistance.

Role of Individual Tree Characteristics

in Tolerance to Inundation

The tolerance of individual trees of the same species will vary (25,28).

Dickson (28) believes that much of the variation is due to differences in genetic characteristics.

Age. Tolerance to inundation generally increases with the age of the tree until it begins to lose vigor with overmaturity. During the first 30 days following germination, Briscoe (14) found that tolerance to submersion increases with age in the tree species he tested. He believes that it is due to having more food reserves, changing enzymatic systems, and greater mechanical strength or possibly a more efficient vascular system. In investigating the effects of flooding on mature trees, Yeager (78) observed that healthy vigorous trees show the greatest resistance to flooding and saturated soil and that the very small class and overmature class show the greatest susceptibility. Hall, Penfound, and Hess (14) in contrast, concluded that generally mature plants succumb more readily than immature plants.

Height. Many authors (27, 34, 35, 38, 40, 50, 53, 73) have shown that the relationship between the height of plants and water becomes increasingly important as the water begins to cover the foliage. The greater degree of injury caused by submersion compared to flooding or saturated soil shows the importance of this relationship.

According to Walker, Green, and Daniels (73), submersion mortality is inversely related to the height of seedlings. They reported that the terminal buds on slash pine (Pinus elliotii Engelm.) and loblolly pine (Pinus taeda L.) must be above water to survive more than a few weeks of inundation. Maisenhelder and McKnight (53) suggested that cottonwood seedlings, rather than cuttings, should be planted so that their foliage will be high enough to stay above water where floods are likely in the early growing season.

Growth rate. The rate of growth and vigor are important to the survival of trees. Bonner (8) suggested that faster growing seedlings use

more water and suffer sooner from moisture deficiency than the slower growing seedlings. Bonner's conclusion supports Caughey's (20) report. She found that inundated plants with a high transpiration rate are more seriously injured than those with low rates. Bergman (4) correlated the greater injury to submersed growing tips of cranberries with a higher respiratory rate.

Some investigators believe vigorous plants have better survival. Yeager (78) observed greater survival in vigorous mature trees than low vigor trees growing in continuously saturated soil and flooded conditions. Hosner (38) indicated that silver maple (Acer saccharinum) is the least tolerant to submersion of the six species tested, but later Hosner (40) found that silver maple was the most tolerant to submersion of the 14 species tested, which included most of the species in the previous investigation. He believes that the difference in results was due to low vigor of silver maple in the initial investigation.

Other Factors Affecting Survival of Trees Subjected to Inundation

Numerous investigators have reported other factors that affect the survival of trees subjected to inundation. Most of the following factors are concerned with the availability of oxygen, and the response of trees to various environmental conditions.

Water Characteristics

Dissolved gases, physical properties, and other water characteristics directly and indirectly affect the gaseous exchange and some physiological processes in the plant. That the water characteristics vary between bodies of water was established by Birge and Juday (6) in their investigation of inland lakes of Wisconsin. A special problem occurs in some bodies of water

caused by industrial pollution. For instance, 850,000 fish were killed on the Cottonwood and Neosho Rivers near Emporia, Kansas, in 1966, due to organic matter in feed-lot waste runoff depleting the oxygen (31).

Availability of oxygen. Submersed plants absorb oxygen and carbon dioxide from the water or give them into solution through the processes of photosynthesis and respiration. Therefore, the oxygen content of the water increases during the day in proportion to the amount of vegetation in the water and light intensity, and carbon dioxide decreases under the same conditions. Oxidizable organic matter tends to decrease oxygen and increase carbon dioxide (4, 6, 21, 50, 58, 79, 80). Broadfoot (17) discovered that dissolved oxygen in impounded waters is rapidly depleted in periods of no rain, but even small showers fully recharge the supply. He believes that ground wells also contribute dissolved oxygen.

Birge and Juday (6), in a detailed study of several inland lakes in Wisconsin, found that there is a zone of photosynthesis. Its depth varies with the turbidity of the water. They observed that in highly turbid lakes the zone is about two to three meters deep, while in clear lakes it may be as deep as ten meters. The oxygen content of this zone varies with the rate of photosynthesis and that absorbed from the air to that consumed by respiration and decomposition of organic matter. They believe that decomposition of organic matter accounts for the greater portion of oxygen consumption. On clear days, according to Birge and Juday, photosynthesis produces more oxygen than is consumed and the quantity of oxygen may rise above the saturation point. They suggest that wind plays an important part in maintaining high oxygen content by mixing and exposing a greater absorbing surface to the atmosphere.

Decomposition of organic matter occurs at the bottom. Birge and

Juday (6) observed that this pattern of decomposition results in an accumulation of carbon dioxide that increases with depth, and a corresponding reduction of oxygen. Their findings are supported in part by Yelenoski (79), Childers and White (21), Bergman (4), and Broadfoot (17). Although photosynthesis consumes a volume of carbon dioxide equal to the volume of oxygen produced, Birge and Juday found no evidence of this relationship in the lake water because of the obscuring affect of other processes taking place simultaneously.

Temperature of water. Briscoe (14) found that tree seedlings suffer less injury due to submersion in water with a water temperature of 68°F than at 95° or 41°. He suggested that the increased injury at 95° may be due to an increased rate of respiration, less dissolved oxygen at 95°, a destructive effect of enzymatic systems of plant cells at higher temperatures, or activity of pathogenic organisms being greater at high temperatures. The 41° treatment caused more injury to the leaves than the 68° treatment, but it did not cause greater reduction in growth or an increase in mortality. His findings are supported in part by Birge and Juday (6), Bergman (4) (5), Brink (13), Hosner (40), Putman (60), Van Camp (72), and Bonner (9).

Depth of water. Many investigators have reported depth of water as a factor affecting tree survival following inundation, but few have presented evidence to support their conclusions. Briscoe (14) compared the effect of flooding and submersion on cherrybark oak (Quercus falcata var. pagodaefolia) seedlings, and found that 34 days of submersion reduced growth more than flooding for a similar period. Although his findings did not clearly show the difference between flooding and submersion, he concluded that submersion will more severely reduce seedling survival. His findings are supported in part by Hosner (40) and Walker, Green and Daniels (73). Welch (74) found

that baldcypress (Taxodium distichum) seedlings do not grow when submersed, but they will resume growth as soon as the tips of foliage extend above the water.

Yeager (78) and Green (33) observed that in continuously flooded mature bottomland trees, the depth of water makes little difference as long as the root crown is covered and the foliage is not covered. Trees in four feet of water survived as well as those with their root crowns just covered. Hall, Penfound, and Hess (34) however, concluded that there is a correlation between water depth and survival of swamp trees. They observed baldcypress (Taxodium distichum) left standing in a reservoir at approximately ten feet below the top summer pool that were sickly or dead after five years of continuous flooding, but baldcypress located four feet or less below the top summer pool were in a healthy condition.

Williston (76) found that survival of loblolly pine (Pinus taeda) seedlings flooded to the root crown is not significantly different from submersion.

On lands near permanently flooded areas, the rise in ground water level may adversely affect tree survival. Yeager (78) observed differential rates of dying in parts of the same bottomland tree growing in such a position that the root crowns were flooded on the stream side, but lay above the water on the land side. Green (33) found that after seven years impoundment, most species of trees growing two feet above the permanent water level were still hardy; but some of them were beginning to show a decrease in growth and may eventually die.

The variations in reports on the effects of water depth is probably due to a combination of several factors related to the availability of dissolved gases (4, 6, 13). Relative rates of photosynthesis, respiration, decomposition

of organic matter, diffusion of gases, wind, rainfall, and supply of ground water as well as species characteristics probably determine the effect of water depth.

Range of oxygen in water. The dissolved oxygen may range from above the saturation point to near exhaustion (6). Broadfoot (17) found that in a shallow water impoundment (approximately 90 centimeters deep), dissolved oxygen was depleted in 15 days of dry weather, but it was quickly replenished after a light rain. The dissolved oxygen at the surface ranged from 2.98ppm to 6.38ppm during a period from March 21 to August 7, 1963. The oxygen concentration at the surface in a Wisconsin Lake, according to Birge and Juday (6), ranged from eight cubic centimeters per liter in May to five in August. Bergman (3) reported that the oxygen concentration at Lake Hubert, Minnesota, was about six cubic centimeters per liter, and a swamp lake tested at about 3 cubic centimeters per liter.

Plant Oxygen Requirements

Cannon (19) found that there is a level of oxygen concentration below which root growth will not continue. The "lower critical concentration" varies by temperature and by species. It is greatest at high temperatures and least at low temperatures. The range of lower critical concentration of oxygen for root growth of different species was found not to vary over one to two percent at a given temperature. The range of the lower critical concentration for any species appears to be about one percent. He noted that the range of lower critical concentration between the extremes of normal root temperatures is similar to the difference in oxygen absorption capacity in water at the same temperatures.

There is also a level of oxygen concentration at which normal growth

will just be sustained. The range in the "upper critical concentration" may be from about two to eight percent for any species. He suggests that the difference between the lower and upper critical concentrations is specific and is the greatest in those species most dependent on a good oxygen supply.

Cannon (19) noted that of the 30 species tested many maintain a slow rate of growth in as little as one-half percent oxygen for a limited time.

The lower and upper critical concentrations of oxygen may be put into perspective by reviewing the oxygen concentration of normal soil air. Russell and Appleyard (64) found that the oxygen content of free soil air in cultivated fields is normally above 18 percent, except just above the water table. Lyon, Buckman, and Brady (52) report that the oxygen in the soil air may get as low as 10 percent.

Cannon's (19) findings are supported in part by several investigators. In one and two year old budded apple trees grown in a sandy loam, Childs (22) found that neither photosynthesis nor transpiration of individual healthy leaves decreases until the oxygen concentration around the roots is two percent or less, and the leaf and terminal growth decreases with a decrease from 12 to 2 percent oxygen concentration around the roots. Conway (24) concluded that the upper limit of oxygen concentration which is likely to be low enough to injure the roots of most plants is about 10 to 11 percent. A somewhat greater lower critical concentration of oxygen was reported by Boynton and Reuther (11). They observed that 12 percent oxygen inhibited root initiation on apple trees and less than ten percent stopped all root growth.

The lower critical concentration of oxygen for root growth in some species is apparently much lower than reported by Cannon (19). Willow cuttings will form roots in water if the dissolved oxygen concentration is at

least one part per million (80).

Cannon's (19) investigation of the relation of roots to aeration of soil suggested that it is the rate of supply rather than the partial pressure of oxygen that influences the rate of growth. He showed that if a plant were in a soil so deficient in oxygen that it could not continue to grow, it would resume growing if the oxygen deficient air were caused to pass slowly through the soil. This may partially explain the observations of several investigators who reported plants inundated with moving water having less injury than those in stagnate water (4, 5, 13, 40, 47). Bergman (5) suggested that Cannon's (19) findings apply only to soils of good structure with below normal moisture content. He believes that in poorly drained or flooded soils, the rate of oxygen supply is too slow to provide the minimum requirements of many plants due to oxygen dependence upon diffusion to move through water. Loustalot (51), Kramer (47), and Bonner's (9) observations of plants growing better in coarse-textured, well-drained soils than in fine-textured, poorly drained soils supports Bergman's (5) conclusion.

Inundation Duration

Many investigators have reported that an increase in duration of inundation results in increased mortality and decreased plant growth following the cessation of inundation (12, 25, 34). Briscoe (14) and Bonner (9) also obtained evidence supporting this general concensus; however, they found that in some species a relatively short period of inundation may result in greater growth than in the controls.

Inundation Season

Many plants vary in their tolerance to inundation with the time of year. Many observers agree that most deciduous trees suffer little if any

adverse effects to inundation during the dormant season.

Silker (68), Hall and Smith (35) and U. S. Department of Agriculture (69) observed that several bottomland tree species which are periodically subjected to long periods of submersion during the dormant season show little or no adverse effects. Silker states that the inherent increased soil moisture may result in increased growth. He suggested that areas that are unfit for agricultural use because of inundation offers considerable potential for commercial **timber** production.

American beech (Fagus grandifolia), according to Hall, Penfound, and Hess (34), is very intolerant to inundation during the growing season, but there are apparently no adverse effects from dormant season inundation.

Heinicke (36), Broadfoot (15) and Williston and McNaughton (77) found that many deciduous trees can be flooded from late fall until late spring without apparent injury as long as the water is drained prior to any noticeable growth.

Inundation Frequency

The author found little information directly applicable to the accumulative influence of repeated periods of inundation to hardwood trees, but some investigations give an insight of the effects to be expected. It appears that repeated periods of inundation have more adverse effects on tree form than on survival.

According to Hall, Penfound and Hess (34), short periods of inundation during the growing season do not result in serious injury to most woody species, even though the total length of the periods equals one continuous lethal period of inundation. They found that alternating inundation and drainage provides almost ideal conditions for some swamp species due to the

elimination of competition and to a good supply of moisture and air. Further, they found that woody species which are defoliated by short periods of inundation recover rapidly when the water is drained. When the original shoot is killed back to the ground, they found that new shoots are often produced. They suggested that younger plants will sprout better generally than older plants.

Hunt (42) compared the flooding effects of three treatments for seven months: (1) one group was flooded continuously with standing water, (2) another group with running water, (3) and a third group was alternately flooded for two weeks and kept at field capacity for two weeks. Three seedling species were used in the investigation including shortleaf pine (Pinus echinata), loblolly pine (Pinus taeda), and pond pine (Pinus rigida var. serotina). He found no significant difference in mortality in the three treatments.

Some investigators indicated that drainage generally benefits inundated plants (2, 34, 65), but there is some evidence that additional problems may develop with drainage.

Bonner (9) suggested that, due to a decline in root growth and an increase in leaf moisture stress, a drought immediately after drainage may be especially damaging to trees growing in saturated soil.

Drainage may not solve the immediate need for oxygen. The dissolved oxygen in a saturated soil may be depleted very rapidly, according to Scott and Evans (66). Furthermore, the reducing condition that develops in a soil deficient in oxygen is not readily removed by adding oxygen. They believe that the effects of deficient oxygen on the plant may persist for some time after a soil is drained.

Tolerance of Trees to Inundation

Tolerance to inundation varies greatly between tree species and between individual trees due to the factors previously discussed. Some tree species die after only a few days or weeks of inundation and others may survive several years of continuous inundation.

Williston (75) found that six upland hardwood species that were continuously flooded during the summer of 1958 near Oxford, Mississippi, had relatively poor survival. His observations included 15 to 25 trees each of pole-size and larger white oak, southern red oak, yellow poplar, red maple, blackgum, and sweetgum. All yellow poplars flooded for as long as 10 days were damaged, and all of those flooded 19 days died. Twenty-one days of flooding resulted in the death of 60 percent of the southern red oak and 62 percent of the white oak. All of the blackgum, 86 percent of the sweetgum, and 73 percent of the red maple survived 21 days of flooding. Hall and Smith (35) observed that in the West Sandy Dewatering project at Kentucky Reservoir the lowest healthy black cherry (Prunus serotina), was flooded only six tenths of a percent of the growing seasons during eight years of intermittent flooding.

The other extreme in tolerance to inundation was shown by Shunk (67). He believes that after baldcypress (Taxodium distichum) seedlings have obtained a certain amount of growth, the roots and lower parts of the stem may be flooded indefinitely without harm. Applequist (1) indicated that swamp blackgum (Nyssa sylvatica) and tupelogum (Nyssa aquatica) not only tolerate but actually thrive in near flooded conditions. However, Egglar and Moore (30) found that after impounding water in Lake Chicot, Louisiana, the original swamp species are gradually dying after eighteen years of flooding during the

growing season. Survival of the longest period of submersion of any terrestrial plant noted by the author was reported by Porterfield (59). Buffalograss (Buchloe dactyloides) reportedly survived 19 months of submersion in Texas from October 21, 1941 to the end of May, 1943. He suggested that the exceptional survival was possibly due to especially favorable growth the previous season. Buffalograss normally fails to survive more than two to eight weeks of flooding during the growing season.

Tolerance of a species to inundation is generally related to the frequency that its natural site is inundated (14, 38, 55). Brown (18) described a correlation between the vegetation zones and lake levels and elevation of land surfaces at Catahoula Lake, Louisiana. Catahoula Lake has an extreme variation in water elevation of 40 feet and a normal season variation of more than 25 feet. The high and low water levels are not the same each year. For instance, in 1804, the lake bed was dry except for the meandering stream. During periods when the water is low, some species may become established at a lower level than normal. Later, when the water rises, their fate depends upon their ability to tolerate inundation. Four distinct zones of woody vegetation have developed as a direct result of the variation in water level. Brown found that the lowest zone of woody plants is composed of dwarf shrubs located just above the normal low water level. The species are chiefly bushy water elm (Planera aquatica) two to five feet in height. Brown believes that water elm is normally found on drier sites. The dwarf shrubs grade into the water elm-swamp privet zone of medium sized trees and shrubs. The species include water elm, swamp privet (Forestiera acuminata), water locust (Gleditsia aquatica), and small baldcypress (Taxodium distichum). This zone varies in width depending on the slope of the land. It occupies the level between the normal low and normal high water. The baldcypress

zone developed at the normal high water level and consists of large, old trees. The mixed hardwood zone is located above the normal high water level. It includes red gum (Liquidambar styraciflua), water oak (Quercus nigra), cherrybark oak (Quercus falcata var. pagodaefolia), deciduous holly (Ilex decidua), chittumwood (Bumelia spp.), persimmon (Diospyros virginiana), red haw (Crataegus spp.), and an occasional baldcypress.

Hall, Penfound, and Hess (34) noted that there are three general types of forests in the Tennessee River system: upland, floodplain, and swamp. Prior to their investigation, they believed that all of the component woody species of each of the respective forest types would be intolerant, moderately tolerant, and tolerant to inundation. They found that the swamp species are tolerant; however, floodplain and upland forest species do not always follow the pattern. They observed trumpet vine (Campsis radicans) and persimmon (Diospyros virginiana), both upland species, to be tolerant of continuous flooding in the growing season. Certain species of the floodplain forest, notably American beech (Fagus grandifolia), were found to be very intolerant. In an investigation of the relative tolerance to submersion of 14 bottomland tree species, Hosner (40) noted that red maple (Acer rubrum) exhibited less tolerance than silver maple (Acer saccharinum), even though Fowells (32) indicated that red maple is a wet site species and silver maple grows best on better drained sites. Hosner (40) also found sweetgum (Liquidambar styraciflua) less tolerant than is indicated by the flooding frequency of its natural site. Hunt (42) reported that even though pond pine (Pinus rigida var. serotina) grows naturally on wetter sites than shortleaf pine (Pinus echinata) and loblolly pine (Pinus taeda), pond pine seedlings failed to survive seven months of flooded soil as well as the other seedling species. Similar investigations have also shown that although the tolerance to inundation is

generally related to the frequency that its natural site is flooded, there are some species which show greater or lesser tolerance (14, 56, 78). These differences are probably at least partially due to differences in plant characteristics and the season of year that the natural sites are normally flooded.

Tolerance of Trees to Flooding

Numerous investigations have been conducted of the tolerance of trees to flooding, but it is very difficult to compare results due to the variation in conditions, species, and investigative procedures. Since survival is influenced by numerous variables, which are difficult to evaluate and control, the number of days that a tree survives in different investigations may vary considerably. However, the relative tolerance of several species probably will not vary much with minor changes in investigative procedure. Therefore, rather than study results in number of days that a species survived a set of conditions, it is more significant to evaluate the relative tolerance of the tested species. In reviewing the following investigations, the reader is advised to compare the relative tolerance rather than the absolute tolerance as reported in some investigations.

Construction of a series of pools on the upper Mississippi River during the 1930's provided Green (33) an opportunity to investigate the effect of permanent flooding on tree mortality. His findings are presented in table 1.

The table lists 17 species of trees and shrubs in ascending order of tolerance to permanent flooding. It includes the number of years each species survived. Green found that buttonbush (Cephalanthus occidentalis) and red osier dogwood (Cornus stolonifera) were the only two species that survived four years. It is interesting to note that buttonbush makes good growth

Table 1. Tolerance of various trees and shrubs to permanent flooding.
Green (33)

Species	Years Survived	Remarks
Sand bar willow <u>Salix fluviatilis</u>	2	Mostly dead in first year.
River birch <u>Betula nigra</u>	2	Survived well first year.
Cottonwood <u>Populus deltoides</u>	2	Survived well first year.
Silver maple <u>Acer saccharinum</u>	3	Mostly dead in second year.
Elm <u>Ulmus americana</u>	3	Mostly dead in second year.
Hackberry [sic] <u>Celtis occidentalis</u>	3	Fair growth in second year.
Red oak [sic] <u>Quercus borealis</u>	3	Scarce in bottoms.
Bur oak [sic] <u>Quercus macrocarpa</u>	3	Mostly dead in second year.
Swamp white oak [sic] <u>Quercus bicolor</u>	3	Fair growth in second year.
Pin oak <u>Quercus palustris</u>	3	Mostly on higher ground.
Alder [sic] <u>Alnus rugosa</u>	3	Hardy to second year.
Green ash <u>Fraxinus pennsylvanica</u>	4	Hardy to second year; fair in third year.
Black willow <u>Salix nigra</u>	4	Hardy to third year; all die in fourth year.
Deciduous holly <u>Ilex decidua</u>		Hardy to fourth year.
Swamp privet <u>Foresteria acuminata</u>		Hardy to fourth year.
Button bush <u>Cephalanthus occidentalis</u>		Hardy after four years.
Red osier dogwood <u>Cornus stolonifera</u>		Hardy after four years.

even where it is almost completely submerged. Green (33) observed that river birch (Betula nigra) and silver maple (Acer saccharinum) were the first to show loss of vigor and that occurred in the second year. Nearly all of the species died in the second and fourth years.

Yeager (78) investigated the effect of permanent flooding on bottomland hardwood trees in the Pere Marquette Wildlife Experimental Area, Illinois. The area was formed by the confluence of the Mississippi and Illinois rivers. A dam on the Mississippi River was closed for the first time in 1938 causing the area to flood. The investigation began in 1939 and ended in 1946. Six transects, each 50 feet wide and varying in length from 600 feet to 1.1 miles, were established. They were laid out to cross as many as possible of the sloughs and vegetation types. No attempt was made to space them in an uniform or random manner. Maps were drawn of each transect showing the location of all trees and large shrubs, diameters of trees, and size of shrubs. Each living tree and shrub was tagged for future inspection. A total of seven inspections were conducted. The original forest type was the typical bottomland hardwood forest found in the upper Mississippi River Valley. The stands varied from saplings to large overmature trees. The more significant results of this study are presented in table 2.

Yeager reported that pin oak (Quercus palustris) is the most susceptible tree to injury by flooding. Most species showed a high loss one year before the time that Yeager reported a 100 percent mortality. Although the injury due to saturated soil differed only in degree to that of flooding in most species, he observed that white ash (Fraxinus americana), river birch (Betula nigra), and cottonwood (Populus deltoides) were not greatly affected by the saturated soil.

Hall and Smith (35) conducted an investigation of the effects of

Table 2. Approximate period of flooding in up to three feet of water, required to kill all trees of various species in six study transects, Calhoun County, Illinois.
Yeager (78)

Species	Years of Flooding							
	Two	Three	Four	Five	Six	Seven	Eight	

Pin oak	x						
<u>Quercus palustris</u>							
Bur oak		x					
<u>Quercus macrocarpa</u>							
Hackberry		x					
<u>Celtis laevigata</u>							
Persimmon		x					
<u>Diospyros virginiana</u>							
River birch		x					
<u>Betula nigra</u>							
Hawthorn			x				
<u>Crataegus spp.</u>							
Cottonwood			x				
<u>Populus deltoides</u>							
Holly			x				
<u>Ilex decidua</u>							
Silver maple				x			
<u>Acer saccharinum</u>							
American elm				x			
<u>Ulmus americana</u>							
Pecan					x		
<u>Carya illinoensis</u>							
Waterlocust						x	
<u>Gleditsia aquatica</u>							
White ash							x
<u>Fraxinus americana</u>							
Buttonbush							x
<u>Cephalanthus occidentalis</u>							
Water privet							x
<u>Forestiera acuminata</u>							
Black willow							x
<u>Salix nigra</u>							

intermittent flooding on woody plants adjacent to Kentucky Reservoir. Their unique study determined the percent of all growing seasons between September 1, 1944 to July 1, 1952 that the lowest healthy plant and the highest sickly plant of 39 species of trees and shrubs were flooded. The sampling entailed locating the lowest healthy plant and the highest sickly plant of each species and determining their elevations. The percent of growing season that each plant was flooded was determined by comparing its elevation with historical water level records. Since survival is greater if the top of plants project above the water, Hall and Smith selected specimens three inches d.b.h. or larger whenever possible. Smaller specimens were selected for the shrubs and smaller trees.

They considered as healthy those specimens with well developed foliage of normal color, retention of fruiting bodies, absence of adventitious roots, and no die-back. Sickly specimens were those affected beyond recovery.

No attempt was made to conduct a statistical analysis of the results. The results of this investigation is shown in table 3.

All observed species were killed when 54 percent of the growing seasons (of a possible 1,402 days) were flooded. The normal forest shows little effect at elevations flooded less than 16 percent, other than dead specimens of the most intolerant species.

The vegetation around Lake Chicot, Louisiana, was investigated by Eggler and Moore (30) after eighteen years of flooding. This investigation is a continuation of the report by Penfound (57). The lake is normally about seven feet deep and is drawn down about four feet starting early in September until about the first of January. The original woody vegetation consisted mainly of baldcypress (Taxodium distichum), tupelo gum (Nyssa aquatica), water elm (Planera aquatica), and buttonbush (Cephalanthus

Table 3. Effect of flooding on trees at Kentucky Reservoir.
Hall and Smith (35)

Species	Percent of Time Flooded During all Growing Seasons	
	Lowest Healthy Tree	Lowest Sickly Tree
Black cherry <u>Prunus serotina</u>	0.6	13.4
Flowering dogwood <u>Cornus florida</u>	0.8	11.6
Hornbeam <u>Ostrya virginiana</u>	1.8	11.6
Sassafras <u>Sassafras albidum</u>	1.8	5.6
Beech <u>Fagus grandifolia</u>	3.2	16.1
Yellow poplar <u>Liriodendron tulipifera</u>	4.5	16.1
Christmas holly <u>Ilex opaca</u>	9.7	17.0
Pawpaw <u>Asimina triloba</u>	11.6	11.6
Redcedar <u>Juniperus virginiana</u>	14.0	24.4
Black alder <u>Alnus rugosa</u>	15.8	24.6
Shagbark hickories <u>Carya</u> spp.	16.0	22.4
Loblolly pine <u>Pinus taeda</u>	16.1	16.1
Blackgum <u>Nyssa sylvatica</u>	16.3	25.3
Water oak <u>Quercus nigra</u>	16.3	23.9
Catalpa <u>Catalpa</u> spp.	18.6	23.9
Pignut hickories <u>Carya</u> spp.	19.4	20.2
Ironwood <u>Carpinus caroliniana</u>	23.2	26.1
Birch <u>Betula nigra</u>	23.2	34.5
Sycamore <u>Platanus occidentalis</u>	23.9	31.2
Winged elm <u>Ulmus alata</u>	24.6	24.9
American elm <u>Ulmus americana</u>	24.6	38.8
Hackberry <u>Celtis</u> spp.	24.9	24.9
Swamp blackgum <u>Nyssa sylvatica</u> var. <u>biflora</u>	26.1	26.1
Cow oak <u>Quercus michauxii</u>	28.6	34.0
Honeylocust <u>Gleditsia triacanthos</u>	29.1	35.0
Persimmon <u>Diospyros virginiana</u>	30.4	36.2
Willow oak <u>Quercus phellos</u>	30.6	41.6
Hawthorn <u>Crataegus</u> spp.	31.7	36.9
Sweetgum <u>Liquidambar styraciflua</u>	34.3	43.3
Cottonwood <u>Populus deltoides</u>	34.5	34.5
Deciduous holly <u>Ilex decidua</u>	35.2	36.9
Red maple <u>Acer rubrum</u> var. <u>drummondii</u>	36.4	40.7
Water tupelo <u>Nyssa aquatica</u>	38.4	53.0
Ash <u>Fraxinus</u> spp.	38.4	41.6
Pin Oak <u>Quercus palustris</u>	39.2	40.3
Buttonball <u>Cephalanthus occidentalis</u>	39.2	53.0
Overcup oak <u>Quercus lyrata</u>	40.3	41.2
Black willow <u>Salix nigra</u>	42.5	58.8
Swamp ironwood <u>Planera aquatica</u>	42.9	53.9

occidentalis). The shallower portions of the lake originally supported upland vegetation. Penfound selected two sites for quantitative studies. The swamp vegetation was located in over two feet of water and the upland vegetation was in zero to two feet of water. Penfound determined the number of trees of each species at the time of impoundment in 1943, and in 1945 and 1947. Egglar and Moore recorded their observations in 1960. The data for the swamp vegetation is presented in table 4 and the upland vegetation in table 5. All species decreased in numbers in both areas, except for tupelo gum and baldcypress. Baldcypress actually increased in numbers indicating that its seeds are able to germinate during a period when the area is not flooded and obtain sufficient growth the first year to keep some of their foliage above water during the growing season.

Hosner and Boyce (41) compared 45 flooded seedlings each of 17 species of trees with well drained, but well watered controls. The potted plants were flooded by placing the pots in a large tank with sufficient water to cover the soil with one inch of water. They found that relatively few of the tested species die when flooded for 60 days. Four sycamore (Platanus occidentalis) and three hackberry (Celtis occidentalis) died when the pots were removed from the tank. Their death is apparently due to poorly functioning root systems below the ground and rapidly dying adventitious root above the ground. All other plants extended their roots and continued to grow. Hosner and Boyce classified the seedlings to tolerance to flooding as follows: tolerant - green ash (Fraxinus pennsylvanica), pumpkin ash (Fraxinus nigra), water tupelo (Nyssa aquatica), and black willow (Salix nigra); intermediate - eastern cottonwood (Populus deltoides), boxelder (Acer negundo), red maple (Acer rubrum), silver maple (Acer saccharinum), pin oak (Quercus palustris), and sycamore (Platanus occidentalis); intolerant - Shumard oak (Quercus

Table 4. Survival of swamp trees in water two to ten feet deep.
Egglar and Moore (30)

Species	Original No. 1943	Oct. 12, 1945 No.	Percent 1943	Apr. 28, 1947 No.	Percent 1943	Nov. 2, 1960 No.	Percent 1943
Buttonbush <u>Cephalanthus occidentalis</u>	8	3	37	1	14	0	0
Tupelo gum <u>Nyssa aquatica</u>	98	55	56	33	33	27	28
Water elm <u>Planera aquatica</u>	12	10	83	10	83	0	0
Baldcypress <u>Taxodium distichum</u>	148	146	98	144	97	74	50

Table 5. Survival of upland trees in water zero to two feet deep.
Eggler and Moore (30)

Species	Original No. 1943	Oct. 12, 1945 No.	Percent 1943	Apr. 28, 1947 No.	Percent 1943	Nov. 2, 1960 No.	Percent 1943
American hornbeam	7	0	0	0	0	0	0
<u>Carpinus caroliniana</u> Walt.							
Persimmon	41	27	66	3	8	2	5
<u>Diospyros virginiana</u> L.							
Pecan	2	0	0	0	0	0	0
<u>Hicoria pecan</u> (Marsh) Britton.							
Yellow poplar	1	0	0	0	0	0	0
<u>Liriodendron tulipifera</u> L.							
Red gum	31	4	13	2	7	1	3
<u>Liquidambar styraciflua</u> L.							
Tupelo gum	1	1	100	1	100	1	100
<u>Nyssa aquatica</u> L.							
Black gum	2	1	50	0	0	0	0
<u>Nyssa sylvatica</u> Marsh.							
Water oak	13	0	0	0	0	0	0
<u>Quercus nigra</u> L.							
Overcup oak	2	1	50	1	50	1	50
<u>Quercus lyrata</u> Walt.							
Black willow	4	3	75	3	75	2	50
<u>Salix nigra</u> Marsh.							
Baldcypress	60	59	98	55	90	230	385
<u>Taxodium distichum</u> (L.) L. C. Rich							
Winged elm	9	1	11	0	0	0	0

shumardii), cherrybark oak (Quercus falcata var. pagodaefolia), American elm (Ulmus americana), willow oak (Quercus phellos), sweetgum (Liquidambar styraciflua), hackberry (Celtis occidentalis), and sugarberry (Celtis laevigata).

Tolerance of Trees to Submersion

It is generally accepted that submersion is more injurious to trees than flooding. Even baldcypress (Taxodium distichum), which is usually considered the most tolerant to inundation of the swamp trees, will survive relatively few days of submersion (27, 61, 74).

The tolerance of loblolly pine (Pinus taeda L.) to submersion was investigated by Williston (76). He used potted one year old seedlings and submerged them in a spring-fed pond. The control seedlings were also in pots and were kept on the bank of the pond. He found that loblolly pine seedlings will survive 12 days submersion in May and early June, that 50 percent will survive 21 days, and that nearly all seedlings will succumb to one month submersion. The correlation coefficient ($r = -.932$) indicates a highly significant correlation between the days of submersion and survival.

Hosner (40) attempted to relate the relative tolerance to submersion of 14 bottomland tree species to the reproduction of these species in southern Illinois forests. The test seedlings were grown from seed collected from trees in southern Illinois and grown in seven inch unglazed clay pots. The samples consisted of three replications of five seedlings randomly selected from the seedlings growing in the pots. The excess seedlings were removed prior to the test. Similar pots were kept as controls. Three large tanks, one for each replication, capable of holding 24 inches of water, were used to submerge the potted seedlings. The assignment of pots to the tanks and their

location within the tanks was done in a random manner. The tanks were filled with tapwater. He added enough clay and silt to the container to produce a turbidity level of more than 200 units per thousand, however, it dropped to less than 25 the third day after the test began. The only agitation to the water occurred when he added tapwater to replace that lost due to evaporation. The tanks were in a partially shaded greenhouse. The seedlings were removed from the tanks at 5, 10, 20, and 30 days and placed on partially shaded benches in the greenhouse with the control plants. The test began on July 2 and the observations continued until October 1, 1958. The mean minimum and maximum temperatures were 78°F and 83°F. Hosner recorded his observations of the rate of recovery, development of sprouts, loss of terminals, and survival. The rate of recovery and loss of terminals of all species generally related to their tolerance as measured by survival. American elm (Ulmus americana) and hackberry (Celtis occidentalis) seedlings developed sprouts in the 20 day and 10 day treatments respectively. Hosner found that the greatest increase in seedling mortality is between the 10 and 20 day treatments. All seedlings of silver maple (Acer saccharinum) and buttonbush (Celphalanthus occidentalis), and some of boxelder (Acer negundo), black willow (Salix nigra), eastern cottonwood (Populus deltoides), and green ash (Fraxinus pennsylvanica) survived 30 days submersion. Considerable variation in tolerance was shown by the other species. Hosner reported a definite range from most to least tolerant as follows: silver maple, buttonbush, boxelder, black willow, cottonwood, green ash, American elm, pin oak, (Quercus palustris), sycamore (Platanus occidentalis), red maple (Acer rubrum), Shumard oak (Quercus shumardii), red gum (Liquidambar styraciflua), hackberry, and cherrybark oak (Quercus falcata var. pagodaefolia). He concluded that high water exercises a selective killing effect on reproduction and thereby influences the makeup of

individual stands. He made no attempt to conduct a statistical analysis of his data.

In an earlier investigation, Hosner (38) followed a similar procedure in determining the effects of submersion on six bottomland hardwood tree species. The relative tolerance of the species in decreasing order was as follows: black willow, green ash, red gum, boxelder, eastern cottonwood, and silver maple. Hosner (40) believes that the change in relative position of silver maple is due to it being rather low in vigor in the first study, and that in the second study the silver maple seedlings had greater height, which probably resulted in the foliage being in oxygen rich water.

Growth of Trees Subjected to Inundation

As with other aspects of the effects of inundation of trees, the growth of trees following inundation varies greatly with the extent of inundation and various other factors. Several investigators have presented information on the growth of trees following specific conditions of inundation.

Growth in First Year Following

Planting in Saturated Soil

In investigating first-year growth of one year old hardwoods planted in saturated soil, Bonner (8) found that when soil temperatures are increasing in mid-April, more than 10 to 12 weeks of saturation severely reduces height, root, and stem-diameter growth. The species studied included sycamore (Platanus occidentalis), sweetgum (Liquidambar styraciflua), and Nuttall oak (Quercus nuttalli).

Hosner and Boyce (41) found that the roots of some seedlings continue to grow in saturated soil for at least 60 days. They reported that tupelo

(Nyssa aquatica), black willow (Salix nigra), and green ash (Fraxinus pennsylvanica) grow better in saturated soil than in well-drained, but well-watered controls.

Growth of Established Trees

Following Flooding

Green (33) investigated the effect of flooding trees in an upper Mississippi River floodplain. The hardwood forest was permanently flooded when water was impounded by a downstream dam in the 1930's. He observed the diameter growth, based upon increment borings, of 10 trees of each species growing in three different situations: high ground where they were flooded for only short, intermittent periods; two feet above the normal water level; and permanently flooded lands. The investigation included the following species: American elm (Ulmus americana), silver maple (Acer saccharinum), river birch (Betula nigra), eastern cottonwood (Populus deltoides), green ash (Fraxinus pennsylvanica), black willow (Salix nigra), and pin oak (Quercus palustris).

Green found that there was little effect on trees growing on high ground where they were flooded for only short periods. In an area that was flooded once, with measurements taken five years later, American elm, silver maple, and pin oak showed a depression in growth, but they had recovered by the end of five years. River birch, eastern cottonwood, and green ash showed a marked stimulation of growth rate which gradually decreased after the first year. Black willow also showed a marked increase in growth the year of the flood, but the following years' growth was consistently below pre-flooding rates. Bonch and Penfound (7) found that, in the bottomlands of the New Orleans area, bottomland tree species continue shoot elongation even though flooded four to seven feet from May 22 to July 10.

All of the trees growing just over the two foot contour, except American elm, black willow, and pin oak, increased in growth rate the year of impoundment, and all of the trees, except green ash, and pin oak had a greater rate of growth five years after impoundment than they did five years before impoundment. The average annual growth before and after flooding of the trees growing on high ground and just above the two foot contour are shown in table 6.

Green observed that on permanently flooded land the growth rates following impoundment compared favorably with those prior to flooding as long as the trees lived. The absence of a period of stimulated growth rate is probably due to these trees having sufficient moisture prior to impoundment. Green noted that death was abrupt rather than, as might be expected, being preceded by a gradual decrease in growth rate. Green's findings on the effect on trees of permanent flooding is supported in part by Broadfoot (16).

Growth of Seedlings Following

Submersion

Lindsey, Petty, Sterling, and Asdall (50) conducted an investigation of the effect of submersion on one year old seedlings of red maple (Acer rubrum), silver maple (Acer saccharinum), and Drummond's maple (Acer rubrum var. drummondii). The period of submersion was eight weeks and it was conducted in May-July, 1960. Tapwater was used to submerge the seedlings. The water temperature was maintained at 75°F. In order to reduce the diatom accumulation, the water was replaced at one week intervals. They found that shoot elongation and young leaf enlargement ceases during submersion. However, after draining the water, the test plants surpassed the controls in average height and vigor on August 8. All of the plants survived the test. The exceptional survival

Table 6. Average annual growth before and after flooding.
Green (33)

Species	On High Ground		Just Above 2-foot Contour	
	5 Years before Flooding	Year of Flooding	5 Years before Flooding	Year of Flooding
				5 Years after Flooding
(Measurements in units of 1/80 inch)				
Elm <u>Ulmus americana</u>	5.6	3.2	5.4	7.2
				5.6
				8.2
Maple <u>Acer saccharinum</u>	9.3	12.2	11.2	6.6
				9.8
				9.2
Birch <u>Betula nigra</u>	10.0	10.7	9.2	7.3
				7.6
				7.7
Cottonwood <u>Populus deltoides</u>	15.3	20.2	18.4	8.0
				11.5
				13.5
Green ash <u>Fraxinus pennsylvanica</u>	4.5	5.7	5.2	6.8
				7.4
				6.1
Black willow <u>Salix nigra</u>	8.2	8.8	5.5	12.8
				10.4
				9.7
Pin oak <u>Quercus palustris</u>	7.5	7.8	8.1	10.0
				9.7
				13.3

is probably due to the relatively low water temperature, and to replacing the water every week. Their findings are supported in part by Welch (74), Hosner (40), and Hosner and Boyce (41).

MATERIALS AND METHODS

The relative tolerance to submersion of selected seedling trees was determined by covering the seedlings with 2 feet of water for periods of one, two, three and four weeks.

Description of Seedlings

The age, average height and source of the 12 tree species studied are shown in table 7. They were selected because of their local reputation as the most tolerant species commonly used in recreational plantings in the Great Plains Region. All of the trees were one year old seedlings, except bur oak and American sycamore, which were two years old. One year bur oak and American sycamore seedlings were not available. All seedlings of a species were approximately uniform in size and condition when planted. Since several of the rapidly growing species were well over 18 inches in height by the time the ponds were filled with water, they were pruned to 18 inches to make sure they would be adequately submerged.

Description of Study Area

Five flat bottom ponds were constructed at the Wheeler Evergreen Farm northeast of the Manhattan Municipal Airport, Manhattan, Kansas. The inside dimensions were 22.5 by 52.5 feet and about three feet deep. All ponds were contiguous, being separated by approximately 18 foot dikes as shown in plate I. Four treatments and a control were randomly assigned to the five ponds.

The soil is a Wymore silty clay loam. The seven inches of topsoil was a silty clay loam with a pH of 6.3. The bottom of the ponds, however,

Table 7. Tree species included in this study.*

Common Name	Scientific Name	Age	Initial Height (Centimeters)	Source
Baldcypress	<u>Taxodium distichum</u> (L.) Rich.	1-0	24.6	Illinois
Black walnut	<u>Juglans nigra</u> L.	1-0	24.7	Indiana
Boxelder	<u>Acer negundo</u> L.	1-0	26.2	Iowa
Bur oak	<u>Quercus macrocarpa</u> Michx.	2-0	17.8	Kansas
Green ash	<u>Fraxinus pennsylvanica</u> Marsh.	1-0	21.3	Oregon
Eastern cottonwood	<u>Populus deltoides</u> Bartr.	1-0	26.3	Nebraska
Honeylocust	<u>Gleditsia triacanthos</u> L.	1-0	19.3	Kansas
Pecan	<u>Carya illinoensis</u> (Wangenk.) K. Koch	1-0	10.7	Kansas
Pin oak	<u>Quercus palustris</u> Muenchh.	1-0	27.0	Missouri
Siberian elm	<u>Ulmus pumila</u> L.	1-0	23.2	Kansas
Silver maple	<u>Acer saccharinum</u> L.	1-0	24.4	Missouri
American sycamore	<u>Platanus occidentalis</u> L.	2-0	24.5	Nebraska

*The Check List of Native and Naturalized Trees of the United States (Agr. Handbook 41, U. S. Gov. Printing Office, Washington, D. C.) is the authority for tree names.

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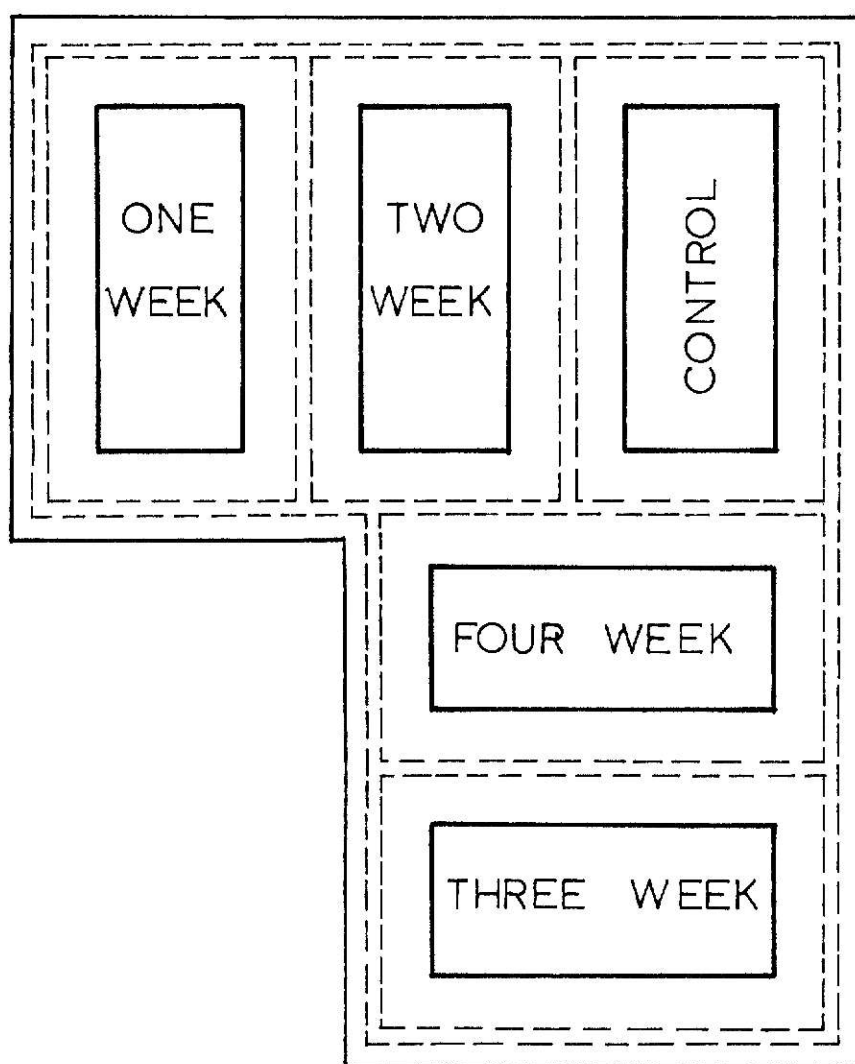
EXPLANATION OF PLATE I

The design of the five contiguous ponds and the periods of submersion randomly assigned to each pond.

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PLATE I



PLAN



was a silty clay with a pH of 6.6. The permeability of this soil was slow.

The trees were submerged with well water which had a pH of 7.6 and a dissolved oxygen content of 8.0 ppm, according to the sulfamic acid modification of the Winkler method of oxygen determination (70). The well water's electrical conductivity was 0.61 millimhos per centimeter and its soluble sodium was 17.2 percent of all the salts present. Although its initial temperature was 15.0°C., it increased rapidly when pumped into the ponds.

A border row of black willow was planted around each pond just inside the dikes. Each pond was divided into three sections to provide three replications of the treatments. Each replication consisted of three seedlings of each species. The three seedlings were planted together in a plot as shown on plate II. The twelve plots were located randomly within each replication. All seedlings were planted 30 inches between and within the rows. Due to the heavy texture of the soil in the bottom of the ponds, the seedlings were planted in a hole 12 inches in diameter and 12 inches deep and back-filled with topsoil. The seedlings were transplanted in mid-April, 1970. Due to mortality, some seedlings were replaced in mid-May.

Heavy rains in late May and early June resulted in the seedlings being flooded occasionally. However, by pumping out the excess water no serious injury was noted.

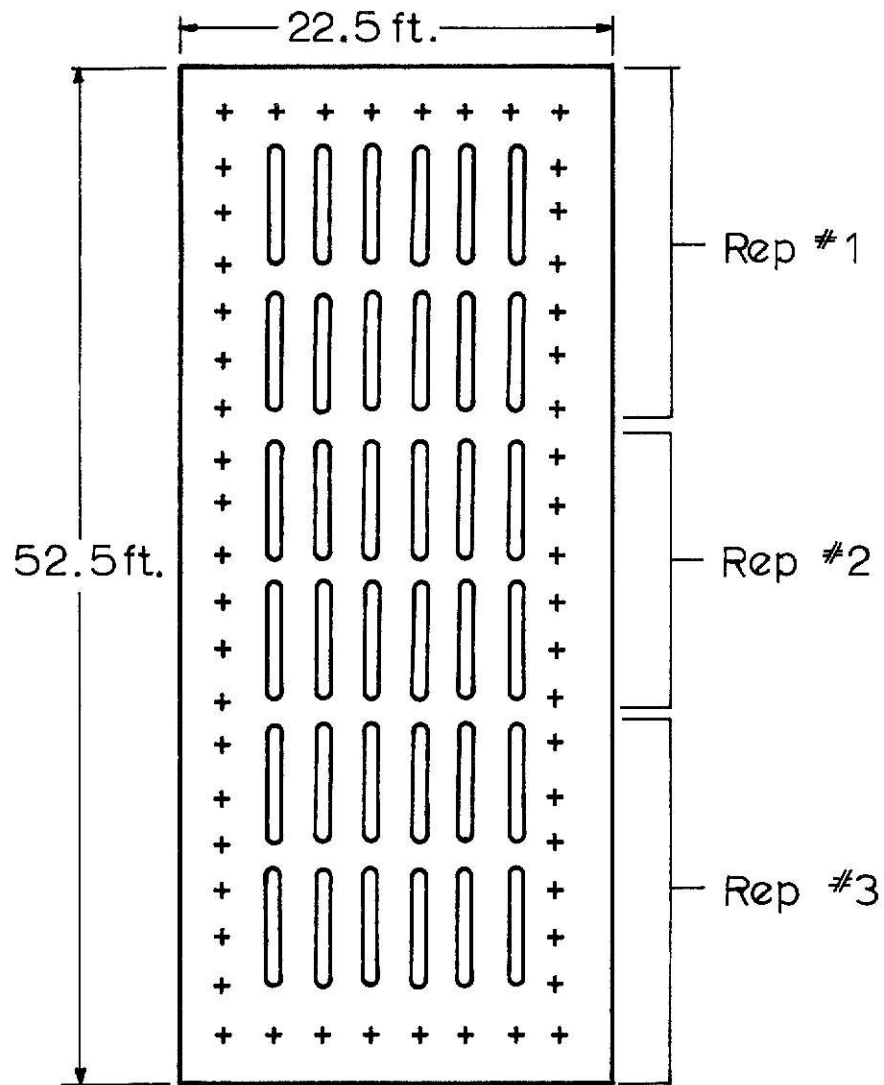
Submersion Procedure

Four ponds were filled to a depth of 24 inches on June 13, 1970. The fifth pond remained unflooded for use as the control. Since evaporation and seepage caused a loss of water, the ponds were refilled once or twice each day. The water level fluctuated from 20 to 24 inches.

EXPLANATION OF PLATE II

The interior design of each pond.

PLATE II



+ Border plants
Plot of 3 seedlings

In an effort to maintain a constant level of dissolved oxygen, the water nozzle was directed through the air to carry as much oxygen into the water as possible. The force of the water stream caused considerable agitation of water in the ponds. The dissolved oxygen changed from an initial concentration of 8.0ppm to a high of 11.8ppm on June 27 and to a low of 5.5 ppm on July 11.

Although the initial water temperature was 15.0°C., the mean high was 27.8°C. and the mean low was 23.9°C.

The ponds were successively drained at seven day intervals: June 20, June 27, July 4 and July 11.

Measurement of Results

The condition of each seedling in a treatment was recorded at the time that each pond was drained. The seedlings were rated according to the following scale: 3.00 indicated no defoliation, 2.00 indicated partial defoliation, and 1.00 indicated complete defoliation. These figures were used as an indication of the degree of injury caused by submersion.

Terminal growth was recorded at the end of the growing season in order to compare the amount of growth following submersion with the control. This measurement was used as an indication of how well each species recovers from a flood and how rapidly it can grow to get its foliage above the high water level so that it will be more tolerant of future floods.

Survival was recorded three times: immediately after the water was drained from the ponds to determine the rate of mortality that occurred during submersion; at the end of the growing season in October, 1970, to determine the ability of the seedlings to adjust to the summer drought; and again in May, 1971, to determine the effect of freezing temperatures on trees after they had survived submergence.

RESULTS AND DISCUSSION

Green Ash

At the time of submergence, all of the green ash seedlings (table 8) were growing vigorously. At the time the ponds were drained, most of the leaves were light green and slightly wilted on the margins. The degree of wilt increased with the duration of submersion; however, no leaves were lost except in the four week treatment and then only a few seedlings were partly defoliated.

All of the seedlings survived in the control and all of the treatments. However, the terminal growth decreased as the duration of submersion increased to a low of 52.1 percent of the terminal growth obtained in the control.

Green ash's tolerance to submersion and drought (32) makes it an ideal tree for recreational plantings on the Great Plain Region reservoirs. Once it is well established with its foliage above the high water level, it will tolerate the length of floods that normally occur on the flood control and irrigation reservoirs (35). Hosner and Boyce (41) reported that green ash will gain more height growth in a saturated soil over an extended period than a well-aerated and well-watered control; therefore, perhaps established green ash may grow faster with an occasional flood than it would without the excess moisture supply.

Baldcypress

Baldcypress seedlings (table 9) were very tolerant of four weeks submersion. The seedlings did not wilt or lose any leaves in any of the treatments. All of the seedlings survived in the control and every treatment.

The terminal growth in the four treatments wasn't significantly less

Table 8. The effects of submersion on green ash.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	3.0	3.0	2.8	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	33.0	24.9	22.3	19.3	17.2	15.5
Survival following submersion (percent).	100.0	100.0	100.0	100.0	100.0	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	100.0	100.0	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	100.0	100.0	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

Table 9. The effects of submersion on baldcypress.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	3.0	3.0	3.0	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	29.8	28.0	34.3	26.1	23.4	15.5
Survival following submersion (percent).	100.0	100.0	100.0	100.0	100.0	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	100.0	100.0	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	100.0	100.0	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

than in the control. Although the seedlings did not grow while submerged, they did resume growth shortly after the water was drained. Apparently the high soil moisture following submersion supported rapid growth through the summer drought which offset the delay caused by submersion.

Due to its high rate of survival and growth following submersion, baldcypress seems to be well adapted to areas subject to intermittent floods.

Boxelder

All of the boxelder seedlings (table 10) were growing vigorously at the time they were submerged. When the water was drained, the leaves were severely wilted at the margins and some had dropped in the three week treatment. Most of the seedlings were defoliated in the four week treatment. The seedlings in the control and the one and two week treatments showed no serious adverse effects due to submersion. All of the original leaves in the three and four week treatments abscised in late summer; however, new leaves were formed before the original leaves dropped.

All of the boxelder seedlings survived in the control and the one and two week treatments. Survival in the three and four week treatments, however, decreased significantly to 66.7 and 33.3 percent respectively.

The terminal growth decreased significantly in the three and four week treatments.

These results indicate that boxelder has some potential in areas that are flooded for short periods; however, its low rate of growth following submersion and numerous pests may limit its use.

Bur Oak

Since the bur oak seedlings (table 11) were later in initiating growth

Table 10. The effects of submersion on boxelder.

	Weeks of Submersion					LSD _{.05}
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	3.0	1.6	1.2	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	33.5	27.2	20.0	10.4	12.1	15.5
Survival following submersion (percent).	100.0	100.0	100.0	88.9	44.4	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	77.8	33.3	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	66.7	33.3	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

Table 11. The effects of submersion on bur oak.

	Weeks of Submersion					LSD _{.05}
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	1.0	1.3	1.2	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	7.0	7.1	4.8	4.3	5.0	15.5
Survival following submersion (percent).	100.0	100.0	88.9	66.7	66.7	25.8
Survival in Oct., 1970 (percent).	88.9	100.0	88.9	66.7	55.6	21.5
Survival in May, 1971 (percent).	88.9	77.8	88.9	55.6	55.6	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

than most of the test species, they were not as well established. All of the seedlings had leafed out, however, and appeared to be adjusted to the site except for one seedling in the two week treatment that was planted just one week prior to submersion since the original seedling had not survived.

When the water was drained, the leaves in the one week treatment were wilted on the margins, but none of the seedlings were defoliated. Seedlings in the two, three and four week treatments, however, were nearly completely defoliated. All of the surviving seedlings produced new leaves in one to three weeks.

The seedling that was planted one week prior to submersion in the two week treatment was the only dead seedling in the two week treatment when the water was drained. The only significant mortalities occurred while the seedlings were submerged when three died in both the three and four week treatments.

The amount of terminal growth was quite low compared to most of the other species. There was no significant decrease in terminal growth in any of the treatments.

Bur oak's relatively low tolerance to submersion and its slow rate of growth makes it adapted only to areas flooded infrequently for short periods. However, once established with its foliage above the high water level, it would be quite tolerant of the intermittent floods and droughts (32).

Eastern Cottonwood

When submerged, the eastern cottonwood seedlings (table 12) were growing vigorously. The seedlings survived very well through the three week treatment. None of the seedlings died in the control or the one, two or three week treatments. The four week treatment, however, had two dead

seedlings when the water was drained, and one other seedling died during the summer drought.

In the one week treatment, the terminal growth equalled the control. However, in the two week treatment, there was a significant decrease, and the three and four week treatments had significantly less terminal growth than the two week treatment.

Although the four week treatment had only 49.8 percent as much terminal growth as the control, the seedlings still grew 60 centimeters. Such rapid growth following submersion would allow eastern cottonwood seedlings to rapidly grow above the normal high water level. Once established with its foliage above the high water level, they would survive the length of floods common in the reservoirs (32).

Siberian Elm

At the time of submergence, the Siberian elm seedlings (table 13) were growing vigorously. The seedlings withstood the one week treatment very well. Although the original leaves had no wilt or other signs of adverse effects when the water was drained, new buds had formed while the seedlings were submerged and the buds opened as the water receded. The seedlings were completely defoliated in the three and four week treatments.

All of the seedlings survived in the control and the one and two week treatments. In the three and four week treatments, however, four seedlings were dead in the three week treatment and two in the four week treatment at the time the water was drained. Six seedlings also died during the summer drought in the four week treatment.

In the one and two week treatments, the terminal growth equalled the

Table 12. The effects of submersion on eastern cottonwood.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	3.0	2.3	2.8	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	119.2	119.4	89.9	63.4	59.3	15.5
Survival following submersion (percent).	100.0	100.0	100.0	100.0	77.8	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	100.0	66.7	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	100.0	66.7	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

Table 13. The effects of submersion on Siberian elm.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	2.8	1.0	1.0	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	87.5	91.9	88.5	66.1	15.1	15.5
Survival following submersion (percent).	100.0	100.0	100.0	55.6	77.8	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	44.4	11.1	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	44.4	11.1	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

control; however, there was a significant decrease in the three week treatment and another significant decrease in the four week treatment where the terminal growth was at a low of 17.2 percent of the control.

Although the Siberian elm seedlings had poor survival in the three week treatment, their terminal growth was impressive at 66.1 centimeters. This suggests that the seedlings that did survive would rapidly grow above the normal high water level, and, therefore, continue to survive the normal floods. Siberian elm seedlings' rapid growth combined with its tolerance to drought (63) makes it suitable for all areas except those flooded for exceptionally long periods.

Honeylocust

At the time they were submerged, all of the honeylocust seedlings (table 14) were growing vigorously, except those in the three week treatment. Three of the seedlings in the three week treatment were partially wilted. The wilted seedlings accounted for the honeylocust seedlings' poor performance in the observations in the three week treatment.

Following submersion, the seedlings had some wilted leaves in all of the treatments, and they were partially defoliated in the three and four week treatments. Most of the original leaves in all treatments eventually defoliated and the surviving seedlings formed new leaves.

The only significant mortality occurred in the four week treatment. Three seedlings died during the summer drought.

The honeylocust seedlings had an excellent rate of growth following three weeks submersion; however, it decreased significantly following four weeks submersion.

This study indicated that honeylocust seedlings are well adapted to

areas subject to infrequent floods of short duration. Honeylocust's drought tolerance (32) makes it especially adapted in areas that tend to be droughty between floods.

Silver Maple

The silver maple seedlings (table 15) survived all of the treatments very well, although they did develop symptoms of injury after only one week submersion. When submerged, all of the seedlings were growing vigorously. Then the water was drained from all four treatments, most of the petioles curved so that the lower side of the leaves were turned upward. Wilted leaves developed for the first time in the three week treatment. The seedlings were partly defoliated in the four week treatment.

Although there was no significant mortality in the control or any of the treatments, the terminal growth declined with the duration of submersion. The terminal growth in the four week treatment was only 35.9 percent of the terminal growth in the control. However, this still represents 22.9 centimeters of growth which will enable it to eventually extend its foliage above the high water level.

The silver maple seedlings' good survival rate indicates that it is adapted to areas subject to flood. However, its lack of drought tolerance may limit its use in areas that are droughty between floods.

Pecan

When submerged, all of the pecan seedlings (table 16) were growing vigorously. At the time the water was drained, only a few leaves had dropped in the two, three and four week treatments; however, most of the seedlings that were submerged had some symptoms of injury which increased with the

Table 14. The effects of submersion on honeylocust.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	2.6	2.6	2.0	2.1	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	35.9	36.3	30.4	33.4	11.7	15.5
Survival following submersion (percent).	100.0	100.0	100.0	66.7	100.0	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	55.6	66.7	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	55.6	66.7	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

Table 15. The effects of submersion on silver maple.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	3.0	3.0	2.0	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	63.6	53.7	38.7	27.0	22.9	15.5
Survival following submersion (percent).	100.0	100.0	100.0	100.0	100.0	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	100.0	100.0	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	100.0	88.9	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

length of submersion. All of the seedlings had a thick layer of algae on the leaves. Most, but not all, of the original leaves eventually abscised.

All of the seedlings resumed growth following submersion; nevertheless, there was a marginally significant mortality in all of the treatments. However, there wasn't any significant difference in survival in the one, two, three and four week treatments.

The amount of terminal growth was very low in the pecan seedlings. There was no significant difference between the control and the treatments.

Although their slow rate of growth would result in the seedlings being subject to submersion the first few seasons, after they are well established, pecan seedlings can grow as much as three feet per year on a good site (32). Further study is needed to determine whether pecan seedlings can survive frequent floods for several years until they can grow sufficiently to get their foliage above the high water level.

American Sycamore and Pin Oak

American sycamore and pin oak were deleted from this study due to the lack of any significant results.

Both species had very poor survival prior to being submerged. All of the original American sycamore were replaced with older seedlings, but the replacements' survival was also very poor. Although some of the seedlings of both species were still dormant when submerged, some of them commenced growing for the first time following submersion only to die in the summer drought.

Black Walnut

When submerged, all of the black walnut seedlings (table 17) were growing vigorously. The black walnut seedlings developed symptoms of injury

Table 16. The effects of submersion on pecan.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	3.0	2.7	2.6	2.9	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	7.4	6.6	7.2	8.5	5.6	15.5
Survival following submersion (percent).	100.0	100.0	100.0	100.0	100.0	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	66.7	88.9	21.5
Survival in May, 1971 (percent).	100.0	77.8	77.8	55.6	77.8	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

Table 17. The effects of submersion on black walnut.

	Weeks of Submersion					LSD .05
	0	1	2	3	4	
Mean condition following submersion (nine observations in each treatment).*	3.0	1.8	1.0	1.0	1.0	0.5
Mean terminal growth in centimeters (mean based on surviving seedlings).	7.7	14.8	3.7	4.0	0.0	15.5
Survival following submersion (percent).	100.0	100.0	100.0	77.8	0.0	25.8
Survival in Oct., 1970 (percent).	100.0	100.0	100.0	66.7	0.0	21.5
Survival in May, 1971 (percent).	100.0	100.0	100.0	55.6	0.0	23.4

*Condition scale: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

in all of the submersion treatments. Although the control seedlings were vigorous throughout the study, the seedlings in the one week treatment were severely wilted when the water was drained, and those in the two, three and four week treatments were completely defoliated. Even in the one week treatment, new leaves began developing in about one week and the original leaves eventually dropped.

Although they were defoliated by the submersion, all of the seedlings in the one and two week treatments quickly resumed growth and survived throughout the study. In the three week treatment, however, there was a significant increase in mortality. All of the seedlings were dead when the water was drained from the four week treatment.

The black walnut seedlings' amount of terminal growth was very low. There wasn't any significant difference between the control and the treatments.

This study indicated that black walnut seedlings do not tolerate prolonged floods and should be considered only in areas that are not subject to more than an occasional flood of short duration.

Relative Tolerance to Submersion of Some Tree Species

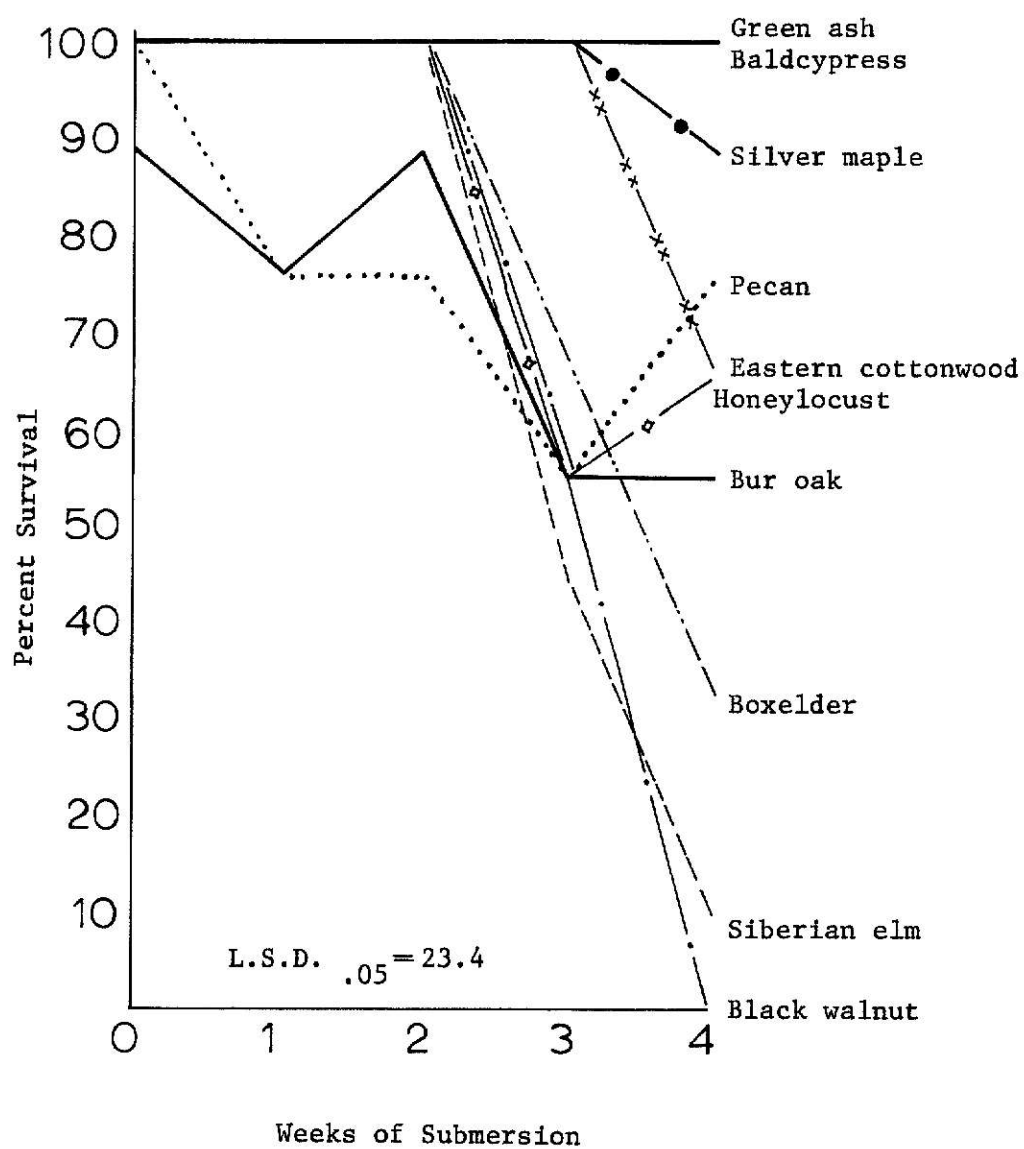
There was no significant mortality in any species in the one and two week treatments (plate III). However, the species were segregated into two groups in the three week treatment. The first group, green ash, baldcypress, eastern cottonwood and silver maple, had 100 percent survival; but the remaining species had only 44.4 to 66.7 percent survival. There was no significant difference between the species within the two groups.

In the four week treatment, there was a great difference in survival between species ranging from zero to 100 percent. The species were arranged in three groups. Except for pecan and boxelder, there was no significant

EXPLANATION OF PLATE III

Rate of survival in May, 1971, of ten tree species following submersion for periods of one, two, three and four weeks.

PLATE III



difference between species in a group. It is not clear whether pecan should be included in the first or second groups, and whether boxelder should be in the second or third group. The most tolerant group included green ash, baldcypress and silver maple. The intermediate group included pecan, eastern cottonwood, honeylocust and bur oak. The least tolerant group included boxelder, Siberian elm and black walnut.

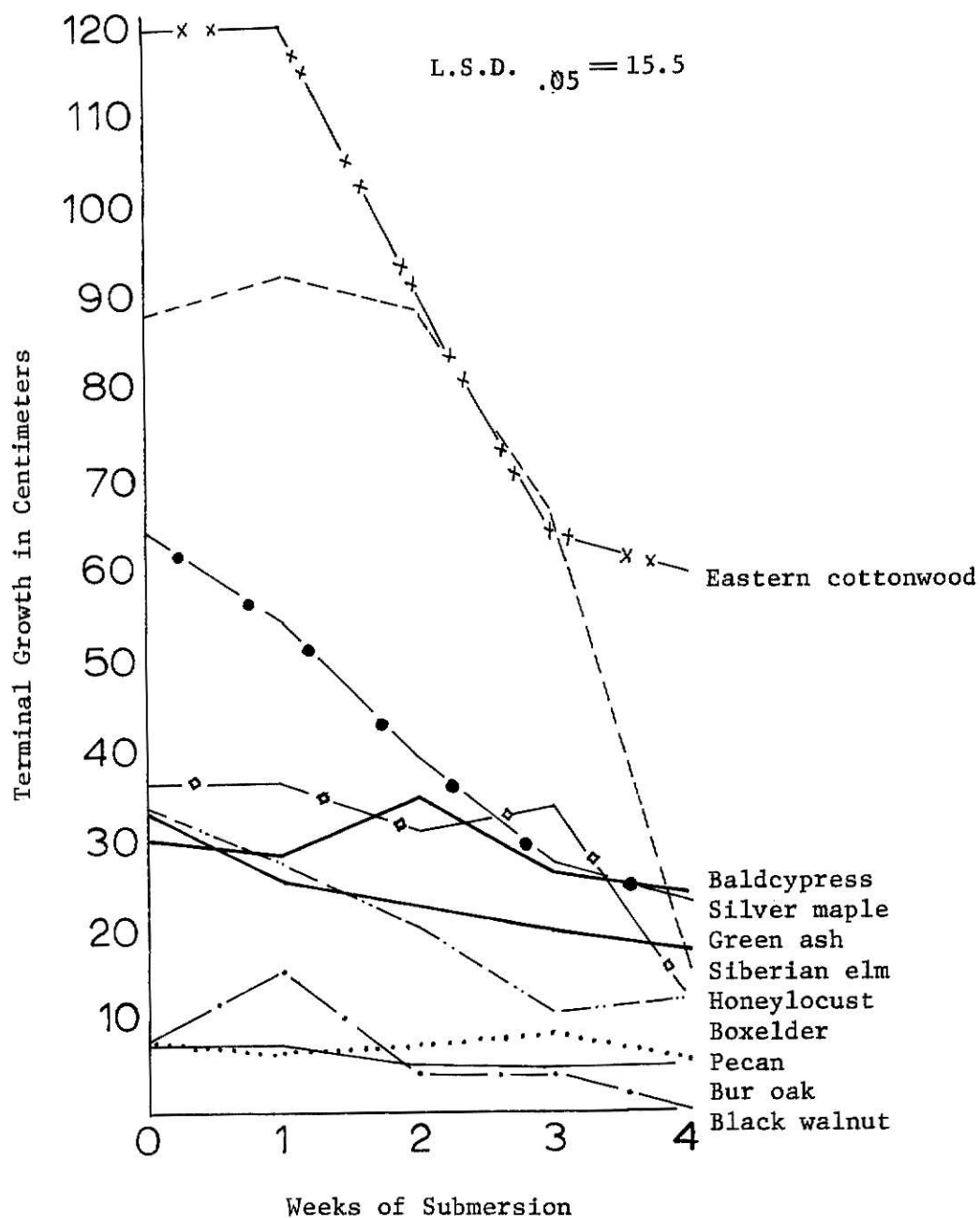
The success of tree plantings on flood control reservoirs is dependent not only upon the species' tolerance to submersion, but also upon their rate of growth. Species that can grow rapidly inspite of an occassional submergence will be subject to fewer periods of submersion than slower growing species and, therefore, less apt to suffer serious injury. Once their foliage is above the normal high water level so that their foliage is not submerged, the species included in this study will survive the intermittent floods common in the Great Plains Region.

In some species there was a slight increase in terminal growth after one or two weeks of submersion due to the inherent soil moisture benefitting the plants in the summer drought more than their growth was delayed by submergence. However, there was a general decrease in terminal growth with an increase in duration of submersion (plate IV). Except for silver maple and Siberian elm, the relative amount of terminal growth of each species corresponded closely to that in the control. Silver maple and Siberian elm had a comparatively large amount of terminal growth until the two and four week treatments respectively where their terminal growth decreased to compare with several other species. In the four week treatment, the species were arranged into three groups by the amount of terminal growth obtained. Eastern cottonwood grew much more than any other species. Baldcypress, silver maple, green ash,

EXPLANATION OF PLATE IV

Mean terminal growth in October, 1970,
on ten tree species following submersion
for periods of one, two, three and four
weeks.

PLATE IV



Siberian elm, boxelder and honeylocust compared very closely in terminal growth. The slowest growing group included bur oak, pecan and black walnut. There was little significant difference between species within the three groups.

Some species, such as pecan, bur oak and black walnut, are noted for growing very little the first season after being transplanted, but they usually increase their rate of growth in succeeding seasons. Further tests may show that these species' rate of growth following submersion in succeeding seasons after being transplanted may increase corresponding to the amount of growth obtained on plants not submerged.

CONCLUSION

When determining which tree species to plant in areas subject to flooding, in addition to basic considerations such as soil conditions, exposure and amount of precipitation, the species' rate of survival and growth following submersion should be considered.

This study determined the rate of survival and growth following submersion of ten tree species that were submerged after transplanting for periods of one, two, three and four weeks.

There was no significant decrease in the rate of survival of any species in the one and two week treatments. In the three week treatment, however, the species were segregated into two groups. The most tolerant group consisted of green ash, baldcypress, eastern cottonwood and silver maple; and the least tolerant group consisted of boxelder, bur oak, Siberian elm, honeylocust, pecan and black walnut.

In the four week treatment, the species were segregated into three groups. The most tolerant species were green ash, baldcypress and silver maple. The intermediate group included pecan, eastern cottonwood, honeylocust and bur oak. The least tolerant species were boxelder, Siberian elm and black walnut.

Although there was generally less terminal growth on the trees as the period of submersion was increased, the comparative amount of terminal growth by species generally corresponded to the comparative amount in the control. Eastern cottonwood, Siberian elm and silver maple had a significantly higher rate of growth than the other species; however, silver maple and Siberian elm's rate of growth declined in the two and four week treatments respectively where they compared with the intermediate group of species. The intermediate

group included baldcypress, green ash, boxelder and honeylocust. The group with the lowest rate of growth included bur oak, pecan and black walnut.

These results are based upon seedlings submerged only once during the growing season. However, many areas may be flooded several times during one growing season. Repeated floods may influence any conclusions based upon these results.

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APPENDIX

Table 18. Seedling condition following submersion.*

	Weeks of Submersion				Mean
	1	2	3	4	
Green ash	3.0	3.0	3.0	2.8	2.9
Baldcypress	3.0	3.0	3.0	3.0	3.0
Boxelder	3.0	3.0	1.6	1.2	2.2
Bur oak	3.0	1.0	1.3	1.2	1.6
Eastern cottonwood	3.0	3.0	2.3	2.8	2.8
Siberian elm	3.0	2.8	1.0	1.0	1.9
Honeylocust	2.6	2.6	1.9	2.1	2.3
Silver maple	3.0	3.0	3.0	2.0	2.8
Pecan	3.0	2.7	2.6	2.9	2.8
Black walnut	1.8	1.0	1.0	1.0	1.2
Mean	2.8	2.5	2.1	2.0	

*Condition class: 3.00 indicates no defoliation.
 2.00 indicates partial defoliation.
 1.00 indicates complete defoliation.

Analysis of Variance

Source	df	Mean Squared
Treatment	3	4.59*
Error (a)	8	0.11
Species	9	4.45*
Species x Treatment	27	0.69*
Error (b)	72	0.09

LSD_{.05} = 0.5

*Indicates significance at 0.01 level.

Table 19. Mean terminal growth in October, 1970.*

	Weeks of Submersion					Mean
	0	1	2	3	4	
	(Centimeters)					
Green ash	33.0	24.9	22.3	19.5	17.2	23.4
Baldcypress	29.8	28.0	34.3	26.1	23.4	28.3
Boxelder	33.5	27.2	20.0	10.4	12.2	20.7
Bur oak	7.0	7.1	4.8	4.3	5.0	5.6
Eastern cottonwood	119.2	119.4	89.9	63.4	59.3	90.2
Siberian elm	87.5	91.9	88.5	66.1	15.1	69.8
Honeylocust	35.9	36.3	30.4	33.4	11.7	29.5
Silver maple	63.7	53.7	38.7	27.0	22.9	41.2
Pecan	7.4	6.6	7.2	8.5	5.6	7.1
Black walnut	7.7	14.8	3.7	4.0	0.0	6.1
Mean	42.5	41.0	33.9	26.3	17.2	

*Means based on surviving seedlings.

Analysis of Variance

Source	df	Mean Squared
Treatment	4	3,337.92*
Error (a)	10	43.30
Species	9	11,863.09*
Species x Treatment	36	453.49*
Error (b)	90	90.91

LSD_{.05} = 15.5

*Indicates significance at 0.01 level.

Table 20. Survival following submersion.

	Weeks of Submersion				
	1	2	3	4	
	(Percent)				
Green ash	100.0	100.0	100.0	100.0	100.0
Baldcypress	100.0	100.0	100.0	100.0	100.0
Boxelder	100.0	100.0	88.9	44.4	83.3
Bur oak	100.0	88.9	66.7	66.7	80.6
Eastern cottonwood	100.0	100.0	100.0	77.8	94.4
Siberian elm	100.0	100.0	55.6	77.8	83.3
Honeylocust	100.0	100.0	66.7	100.0	91.7
Silver maple	100.0	100.0	100.0	100.0	100.0
Pecan	100.0	100.0	100.0	100.0	100.0
Black walnut	100.0	100.0	77.8	0.0	69.4
Mean	100.0	98.9	85.6	76.7	

Analysis of Variance

Source	df	Mean Squared
Treatment	3	3,762.35*
Error (a)	8	46.17
Species	9	1,363.17*
Species x Treatment	27	943.41*
Error (b)	72	252.05

LSD_{.05} = 25.8

*Indicates significance at 0.01 level.

Table 21. Survival in October, 1970.

	Weeks of Submersion					Mean
	0	1	2	3	4	
	(Percent)					
Green ash	100.0	100.0	100.0	100.0	100.0	100.0
Baldcypress	100.0	100.0	100.0	100.0	100.0	100.0
Boxelder	100.0	100.0	100.0	77.8	33.3	82.2
Bur oak	88.9	100.0	88.9	66.7	55.6	80.0
Eastern cottonwood	100.0	100.0	100.0	100.0	66.7	93.3
Siberian elm	100.0	100.0	100.0	44.4	11.1	71.1
Honeylocust	100.0	100.0	100.0	55.6	66.7	84.4
Silver maple	100.0	100.0	100.0	100.0	100.0	100.0
Pecan	100.0	100.0	100.0	66.7	88.9	91.1
Black walnut	100.0	100.0	100.0	66.7	0.0	73.3
Mean	98.9	100.0	98.9	77.8	62.2	

Analysis of Variance

Source	df	Mean Squared
Treatment	4	8,618.53*
Error (a)	10	118.52
Species	9	1,797.53*
Species x Treatment	36	931.27*
Error (b)	90	176.10

LSD_{.05} = 21.5

*Indicates significance at 0.01 level.

Table 22. Survival in May, 1971.

	Weeks of Submersion					Mean
	0	1	2	3	4	
	(Percent)					
Green ash	100.0	100.0	100.0	100.0	100.0	100.0
Baldcypress	100.0	100.0	100.0	100.0	100.0	100.0
Boxelder	100.0	100.0	100.0	66.7	33.3	80.0
Bur oak	88.9	77.8	88.9	55.6	55.6	73.3
Eastern cottonwood	100.0	100.0	100.0	100.0	66.7	93.3
Siberian elm	100.0	100.0	100.0	44.4	11.1	71.1
Honeylocust	100.0	100.0	100.0	55.6	66.7	84.4
Silver maple	100.0	100.0	100.0	100.0	88.9	97.8
Pecan	100.0	77.8	77.8	55.6	77.8	77.8
Black walnut	100.0	100.0	100.0	55.6	0.0	71.1
Mean	98.9	95.6	96.7	73.3	60.0	

Analysis of Variance

Source	df	Mean Squared
Treatment	4	9,011.11*
Error (a)	10	59.26
Species	9	2,136.63*
Species x Treatment	36	928.80*
Error (b)	90	207.37

LSD_{.05} = 23.4

*Indicates significance at 0.01 level.

SUBMERSION TOLERANCE OF SELECTED SEEDLING TREES

by

WILLIAM LEROY LOUCKS

B. S., The Colorado State University, 1963

AN ABSTRACT OF A MASTER'S THESIS

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The relative tolerance to submersion of selected seedling trees was determined by covering one year old seedlings with two feet of water for periods of one, two, three and four weeks.

There was no significant decrease in the rate of survival of any species in the one and two week treatments. In the three week treatment, the most tolerant group included green ash, baldcypress, eastern cottonwood and silver maple; and the least tolerant group consisted of boxelder, bur oak, Siberian elm, honeylocust, pecan and black walnut.

In the four week treatment, the most tolerant species were green ash, baldcypress and silver maple. The intermediate group included pecan, eastern cottonwood, honeylocust and bur oak. The least tolerant species were boxelder, Siberian elm and black walnut.

Although the rate of growth of the seedlings decreased with an increase in the duration of submersion, the comparative amount of terminal growth by species generally corresponded to the comparative amount in the control. Eastern cottonwood had the highest rate of growth. The intermediate group included silver maple, Siberian elm, baldcypress, green ash, boxelder and honeylocust. The group with the lowest rate of growth included bur oak, pecan and black walnut.