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I am submitting herewith a dissertation written by Allan Edward Houston entitled "Beaver Control and Reforestation of Drained Beaver Impoundments." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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BEAVER CONTROL AND REFORESTATION  
OF DRAINED BEAVER IMPOUNDMENTS

A Dissertation  
Presented for the  
Doctor of Philosophy  
Degree  
The University of Tennessee, Knoxville

Allan Edward Houston

May 1991



## ACKNOWLEDGMENTS

The author is grateful to Dr. Edward R. Buckner, Chairman of the Graduate Committee, for his guidance, wisdom, and support throughout the course of the study. Appreciation is also expressed to Drs. Dewey L. Bunting, Michael R. Pelton, and John C. Rennie as members of the Graduate Committee for their counsel throughout the study and review of this manuscript.

Special appreciation is expressed to Dr. James M. Anderson, Superintendent, Ames Plantation, for supporting the study and allowing the author to return to graduate school. Appreciation is also expressed to Dr. Ricky J. Carlisle, Assistant Superintendent, Ames Plantation, for his moral support and sound advice.

Sincere appreciation is expressed to the Trustees of the Hobart Ames Foundation: Mr. Richard Harte, Jr., Mr. Waldo E. Dodge, and Mr. Robert Frey. Without their support and the financial support of the Hobart Ames Foundation the study was not possible.

The author is sincerely appreciative of Dr. D. M. "Pete" Gossett, Vice President for Agriculture, and Dr. Don O. Richardson, Dean, Agricultural Experiment Station, for their support throughout the course of the study. The author is deeply appreciative of the support of the Tennessee Agricultural Experiment Station.

The author is indebted to Mr. Ray Henry who first envisioned the study's feasibility and who caught most of the beaver. Appreciation is extended to Dr. James L. Byford for his help in the initial stages of the project and to Mr. John A. Mullins, Jr., for producing and planting seedlings and for his statistical expertise.

Appreciation is extended to Dr. William L. Sanders for his help with statistical analysis. Drs. George M. Hopper and James B. McLaren were a source of encouragement and wise counsel.

The author is grateful to the following landowners and agents for access to their property for beaver control: Mr. F. H. Boswell, Mrs. H. Johnson, Mr. J. P. Matthews, Mr. L. Meadows, Mr. and Mrs. C. W. Middlecoff, Mr. W. Middlecoff, Mr. I. W. Pursell, Dr. J. W. Smith, Dr. W. Sparks, Mr. R. Rucker, Mr. G. P. Walker.

Great appreciation is extended to the author's parents, Lawton and Ella Mae Houston for their constant support and love. The author wishes to extend appreciation to his parents-in-law, Miles and Ann Hudson, for their support.

The author wishes to extend his deepest appreciation to two women, one whom he has never met, and the other to whom he is married. Mrs. Julia Colony Ames passed away before the author was born. The Hobart Ames Foundation is the result of her great wisdom and altruism. The author's work



is a only a small part of her legacy; however, it is a direct result of her vision.

Mrs. Becky Houston is the author's wife and best friend. She was a source of good advice, love, and support throughout the duration of the project. Her constancy and devotion provided the foundations upon which the success of this project was built. This dissertation is dedicated to her.

The author's children, Brian and Laura, were a constant source of love; and their cheerful faces made even the grim times less onerous.



## ABSTRACT

In November, 1984, the Hobart Ames Foundation in cooperation with the University of Tennessee Agricultural Experiment Station began a beaver (Castor canadensis) control project on approximately 4000 acres of the North Fork Wolf River bottom in west Tennessee.

Resident populations (169 beaver) were removed from the study area from 1 November 1984, to 31 May 1985. From June, 1985, through September, 1988, 162 immigrants were removed. Immigration October through May averaged 46.4 beaver. From June through September average immigration dropped significantly to 5.5. More immigrating males (86) were identified than females (55). More than 89% of all immigrants were in the 3-4 year age class or younger.

In the spring of 1986 two drained beaver impoundments were planted with 1-0 bare-root stock of green ash (Fraxinus pennsylvanica Marsh.), sycamore (Platanus occidentalis L.), baldcypress (Taxodium distichum L., Rich.) and containerized seedlings of swamp white oak (Quercus michauxii Nutt.) and willow oak (Quercus phellos L.). A grass herbicide was sprayed over 1/2 of each plot in May and July of the first growing season.

At the end of the first growing season herbaceous competition on untreated subplots averaged 8185 kg dry

weight per ha of which 53.8% was primarily swamp cut grass (Leersia oryzoides). On treated plots herbaceous competition averaged 6823 kg dry weight per ha with 15.2% grass species.

First year survival of green ash, sycamore, baldcypress and swamp white oak was significantly greater in herbicide treatments (92% versus 85%). Herbicide treatments had no effect on third year heights or survival. Third year mean height for cypress (15 dm) was significantly less than green ash (25 dm) while sycamore was significantly taller than both (32 dm). Willow oak and swamp white oak failed due to poor quality seedlings.

Results suggest that well stocked stands of desirable species can be established on drained beaver impoundments; however beaver control likely will be required to prevent recolonization.



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## CHAPTER I

## INTRODUCTION

The Beaver

The beaver (Castor canadensis) historically has been an important player on the American stage. Prior to European colonization of North America beaver populations were estimated between 60 and 400 million individuals (Naiman et al. 1986). The value of beaver pelts provided a powerful incentive to trappers and explorers who expanded the early frontier. For example, from 1620 to 1630 more than 10,000 beaver were taken annually from Connecticut and Massachusetts; and in the following decade (1630-1640) an estimated 800,000 were trapped from the Hudson River in western New York (Naiman et al. 1986). As eastern beaver populations declined, many early 19th century expeditions were sent westward with the primary purpose of opening new trapping territory. During this era goods often were often purchased on the "beaver standard"; and in many places the beaver pelt became the basic unit of exchange (Wesley 1978).

Uncontrolled trapping in the 1800s and early 1900s largely extirpated beaver populations from many parts of their native range (Wesley 1978; Jenkins and Busher 1979). However, land use patterns associated with an increasing rural population also contributed to the beaver's demise.

For example, open range grazing along numerous watercourses destroyed small tree seedlings along with herbs and grasses that beaver populations depended on for food supplies (Milne 1960). In addition, since 1834 an estimated 195,000 to 260,000 square kilometers of prime beaver and wetland habitat have been converted to dry land (Naiman et al. 1986).

Beaver populations were virtually nonexistent in South Carolina (Penny 1949), Virginia and West Virginia (Swank 1949), Alabama (Moore and Martin 1949), and Mississippi (Cook 1965) by the late 1800s. Beaver populations were rare in Tennessee during the early 1900s (Shultz 1954). For example, Barkalow (1949) reported only 41 known beaver dams in Alabama in 1929. However, isolated populations continued to exist over most of the beaver's native range in the South (Shultz 1954).

Restocking programs were initiated in many states by the mid 1900s (Saylor 1956; Cook 1965; Beshears 1967; Wigley 1986). Stocking programs were carried out in Tennessee by both the Tennessee Game and Fish Commission and U.S. Fish and Wildlife Service (Shultz 1954). Low pelt prices and a decrease in trapping pressure along with an increasingly urban society enabled the rapid expansion of native and reintroduced beaver populations across much of the historical southern range.



### Beaver Damage

Beaver populations across the Southeastern United States have increased dramatically since the late 1950s (Arner and Dubose 1979; Bullock and Arner 1985). On many watersheds within the region, the beaver has become a nuisance species through dam-building activities which inundate valuable forest and farm land. In addition, in nonimpounded forested areas adjacent to active colonies, substantial damage results from girdling activities associated with the beaver's search for food and building materials (Bullock and Arner 1985).

A report (Bullock and Arner 1985) on the amount of beaver damage in Mississippi occurring from 1975 to 1985 estimated that the loss to Mississippi's economy approached 2.4 billion dollars and suggested similar damage for the neighboring states of Arkansas, Alabama, Tennessee, and Georgia. Hill (1976) estimated that beavers had flooded at least 162,000 ha in the Southeast.

A recent survey (Miller 1985) of the extent of damage caused by principal wildlife species concluded: "without question the beaver is the vertebrate animal causing the most damage to Southern forests at the present time." The survey noted that monetary estimates of damage caused by beaver were 10 times greater than damage caused by all other vertebrate species combined.

A report compiled by the Tennessee Division of Forestry (1980) identified approximately 327,556 ha of bottomland forest in west Tennessee (Appendix A). In that report timber on 38,051 ha was classified as dead or fading due to beaver, altered stream drainage patterns, or sedimentation, with each category expected to increase over time. However, beaver were directly implicated in nearly two thirds of the problem areas. These figures represent an initial loss in standing timber conservatively estimated at 50 million dollars in today's stumpage prices. Without adequately developed beaver control measures and proper silvicultural techniques to reforest these sites, this acreage also represents a continuing loss in terms of future forest productivity.

A report to the Georgia Forestry Commission (Godbee and Price 1975) estimated the total value of beaver damaged timber in Georgia at more than 45 million dollars, and increasing yearly. Damage reports from landowners increased from 519 in 1960 to 2,632 in 1967 and to 9,988 in 1975. There were 6,357 ha affected in 1960, 51,178 ha in 1967, and 116,478 ha in 1975. Over 91 percent of all inundated acres in 1975 were timbered lands. Woodward et al. (1976) reported 4,444 ha lost to beaver in South Carolina with 25% of surveyed landowners reporting beaver populations on their lands. Woodward et al. (1985) reported that 43% of the



landowners surveyed in North Carolina indicated beaver were present on their land.

A survey (Wigley 1986) of 3,369 rural, noncorporate landowners owning more than 2 ha of land in Arkansas was conducted to estimate the impact of beaver populations on the resources of that State. Useable responses from 1,716 individuals holding 312,006 ha, or 2.3% of the land base, projected that beaver activity had negatively impacted 342,105 ha statewide. In that study some form of beaver damage was reported by 32% of all respondents. One-half of those with beaver activity described damage as being substantial or severe. Seventy-two percent of these described damages exceeding \$1000. Twenty-five percent of the landowners reporting damage stated they would be willing to pay for beaver removal. Landowners who had tried controlling beavers were more likely to pay for beaver control than those who had not attempted control. Control measures reported successful elsewhere (Hill 1976) were largely perceived as being ineffectual by many respondents, an attitude which probably represents frustration and unfamiliarity with successful control techniques, along with a basic failure to understand the biology of the animal.

The principal loss from beaver damage in most watersheds is the value of impounded timber. Because these bottomland sites are potentially the most productive in the

region, damage assessments should consider not only the loss of on-site timber, but the impact on future productivity as well. Even if a colony is successfully removed or should naturally abandon an impounded site, natural succession is slow and is comprised mainly of commercially undesirable species such as various maples (Acer spp.), elms (Ulmus spp.), boxelder (Acer negundo L.), river birch (Betula nigra L.), and black willow (Salix nigra Marsh.) (Waldrop et al. 1982; Seifert et al. 1984).

The detrimental economic impact of nuisance beaver in the Southeastern region has stimulated widespread interest in the development of effective control programs. The impetus for such programs comes primarily from concern over the loss of present and future forest productivity. Successful programs will be those based on a thorough understanding of beaver habits and biology.

A great deal has been written about the northern and western subspecies of Castor canadensis (Jenkins and Busher 1979; Hill 1982); however, relatively little work has been done with the southern beaver (Castor canadensis carolinensis). Therefore, managers and researchers alike have been forced to extrapolate preexisting, nonempirical research conclusions to situations involving the southern beaver. The validity of such extrapolations is questionable.



### Reforestation

Although approximately 40,000 to 60,000 ha are in hardwood plantations in the United States, natural stands still account for more than 99% of hardwood production in this country (Kennedy 1981). There are approximately 8.9 million ha of bottomland hardwoods in the South alone (Kennedy 1981) and these sites are potentially the most productive in the region. Much of the bottomland timber acreage has already been lost to agricultural interests, lakes, and development while demand for hardwood products has increased. Better forest and plantation management of desirable species will be necessary to meet those demands (Kennedy 1981). However, so little information is available on growth and yield or response to cultural treatments for bottomland hardwoods that foresters and landowners have difficulty evaluating the effects of cultural alternatives (Langdon et al. 1981).

In some areas, hardwood companies have found it uneconomical to manage particular hardwood tracts due to the risk imposed by beaver (Jim Baer, Westvaco Corporation, personal communication, 1987). Successful hardwood management in these areas is dependent on the development of reliable beaver management programs.

Beaver control programs may be categorized at three basic levels (Houston et al. 1987). At the most intense

level, involving population removal and effective suppression of recolonization attempts, justification for the control program should be based on realistic predictions of land productivity. If beaver-kill sites can be reforested using artificial regeneration methods, then added flexibility is given to land managers forced to make choices regarding beaver control investments and land use alternatives. The two problems are entwined. Without effective beaver control, hardwood management in these areas is generally not feasible. Without reliable estimates of forest productivity on reclaimed sites, cost benefit analysis of beaver control and reforestation of drained beaver impoundments cannot be made.



## CHAPTER II

## OBJECTIVES

Beaver Control

The first phase of this study reported the influence of dispersal patterns on an isolated beaver control program in west Tennessee. Specifically the study examined the following objectives:

1. Is immigration into the study area seasonal (as characterized by 4-month intervals)?
2. Are immigration patterns into the study area generally tied to age groups?
3. Is immigration into the study area sex-biased?

These findings could prove important in the formation of realistic philosophical and management options.

Reforestation

The second phase of this study investigated the feasibility of reclaiming drained beaver impoundments by planting green ash (Fraxinus pennsylvanica Marsh.), sycamore (Platanus occidentalis L.), baldcypress (Taxodium distichum L., Rich.), swamp white oak (Quercus michauxii Nutt.), and willow oak (Quercus phellos L.). The need to control the dense cover of swamp cut grass (Leersia oryzoides) that typically invades these sites was evaluated by controlling

early successional grasses with Fusilade 2000. The study also quantified early natural forest succession on these sites. Specifically, this phase of the study reported:

1. Comparison of survival at the end of the first and third growing seasons and total height growth at the end of the third growing season of 5 planted bottomland tree species.
2. Effect of herbicide application on survival at the end of the first and third growing seasons and total height growth at the end of the third growing season for 5 planted bottomland tree species.
3. Comparison of artificial versus natural regeneration at the end of the first growing season.



## CHAPTER III

## LITERATURE REVIEW

Beaver

The American beaver (Castor canadensis) is one of two living species in the genus Castor. The other member, Castor fiber, is native to portions of Europe and Asia. Fossil records indicate that the family dates back to the Oligocene period (Cahn 1932; Garrison 1967). During the Pleistocene a giant beaver (Castoroides ohioensis), estimated to have weighed in excess of 202 kg, ranged from Alaska to Florida (Parmalee et al. 1976).

Although 24 subspecies of the American beaver have been described (Hall and Kelson 1959), local population declines due to intense trapping pressures or destruction of beaver habitat followed by reintroduction of beaver transported long distances by various state agencies (Schultz 1954) has made it unlikely that all 24 subspecies remain distinct (James L. Byford, University of Tennessee, personal communication, 1986). However, the southern beaver (Castor canadensis carolinensis) remains distinct and appears to be the major component of current populations in the Southeast (Edward Hill, Mississippi State University, personal communication, 1986).

Bradt (1938) defined a beaver colony as a group of beavers occupying a pond or stretch of stream, utilizing a common food supply, and maintaining a common dam or dams. A number of studies have described the typical colony as consisting of 5 to 8 beavers with two adults (parents), the kits of the current year, and yearlings from the previous year (Busher et al. 1983).

Beavers are generally monogamous (Kleiman 1977; Svendsen 1989) and produce one litter each year. Pair bonds can be formed throughout the year but most commonly occur in late summer and fall (Svendsen 1989). In an Ohio beaver population age discrepancy at time of mating and death of the older mate was the primary cause of mate turnover; however, desertion was shown to be a factor in 4% of the cases studied (Svendsen 1989).

The breeding season generally occurs from January to March in colder climes (Svendson 1980), but may occur in December or January in the South (Hill 1982). Gestation is approximately 100 days (Bergerud and Miller 1977; Woodward 1977). Kits weight approximately 0.5 kg and average 38 cm long including a 9 cm tail. Kits will begin to ingest solid food as early as 1 month but will not be fully weaned until 2 months old (Burton and Burton 1969; Wilsson 1971, in Hill 1982; Zurowski et al. 1974).



Litter size ranges from 1 to 9 and varies with several factors, especially age of the female. A review of the literature (Svendsen 1980) indicated an average of 3.7 kits per litter. Females from 4 to 6 years of age typically have the largest litters. Restricted food intake can depress litter size (Brenner 1964).

First parturition in beavers normally occurs at age 3, but may occur as early as age 2 depending on habitat or social structure of the colony. Hill (1982) concluded from a review of the literature that sexual maturity may occur as early as 1.5 or 2 years of age in middle latitudes provided food conditions are favorable. Reproduction in yearlings may discontinue if more than 40% of potential sites are being utilized (Parsons and Brown 1979). Although breeding activity is generally confined to the adult pair, sexually mature male and female progeny within the colony may reproduce if either or both adults are removed (Brooks et al. 1980). Therefore, trapping within a population may tend to stimulate yearling reproduction.

Most studies of sex ratios in beaver show slightly more males than females at young ages, but the reverse at older ages (Hammond 1943; Osborn 1955). In a Wyoming study (Osborn 1955) the sex ratio in fetuses was 1.29 males:female. For juveniles the ratio was 1.33 males:female, subadults 0.91 males:female, and adults 0.88 male:female.

For all age classes it was 1.01 males:female. The oldest ages documented for wild beavers include individuals 19 (Larson 1967) and 21 years (Brown 1979) old.

For a beaver colony to thrive two major site requirements must be met: (1) some form of surface water, and (2) an adequate food supply (Byford 1981). Beavers appear to do best where forest development is in the early successional stages (Patric and Webb 1954). One study in Wisconsin (Barnes and Dibble 1986) found that foraging activities were confined to a 60 m band paralleling the bank. Foraging is usually confined to vegetation within 100 m of water habitat (Erickson 1939).

Beaver are powerful swimmers; however, their ambulatory movements on land are awkward, leaving them vulnerable to predation (Hill 1982). Jenkins (1980) reporting foraging activity of beaver in central Massachusetts characterized a size-distance relationship in food selection. Beavers cut all sizes of vegetation near the pond but progressively smaller trees further from the water. Jenkins postulated that increasing selectivity with increasing distance from the water, made the beaver a "time-minimizer," an adaptation to predation pressures. Beavers have been characterized as "choosy generalists" (Jenkins 1979), showing marked seasonal and year to year preference for certain tree genera. These preferences correlated strongly with increasing nutritional



values of certain trees and suggest that beaver can assess temporal variation in relation to nutrition (Jenkins 1979).

Other studies have shown that beavers regularly supplement their diet with nonwoody aquatic and shoreline vegetation during spring and summer months (Townsend 1953; Chabreck 1958; Brenner 1962; Hilfiker 1968; Northcott 1972; Barnes and Dibble 1986). One study in Ohio (Svendson 1980) reported that nonwoody vegetation comprised 90% of the beaver's diet during summer and up to 50% percent in early fall and spring. For the most part dietary shifts in types of vegetation utilized were similar among age classes. The ability to subsist on nonwoody vegetation during spring and summer is probably an aid in dispersal from natal sites. As a time minimizer, use of nonwoody vegetation affords the beaver a risk-reducing foraging strategy helpful in the search for mates and new colony sites.

Beaver could not persist over a large part of their native range without adequate supplies of woody vegetation to support them during fall and winter months. Although beavers have been known to fell trees in excess of 1.2 m in diameter (Hatt 1944), they prefer smaller diameter trees and generally confine their feeding activities to tree stems or limbs that are 2.5 to 12.5 cm in diameter. A New York Study (Shadle et al. 1943) showed that only 7.6% of all cuttings

were in excess of 15 cm. A study in Wisconsin (Barnes and Dibble 1988) concluded that beaver tended to select stems in the 4 to 6 cm diameter class and generally ignored stems greater than 8 cm in diameter.

A study of 57 colonies in Michigan (Bradt 1938), produced a simplified model to provide a measure of resource limitations in beaver populations. In this study beavers typically utilized small trees averaging 5 cm inches and would require about 216 trees per year. Based on previous forest surveys for the area, 0.4 ha could support 1 beaver for 7 years or 7 beaver for 1 year.

A study in Saskatchewan (Gunson 1970, in Hill 1982) suggested greater numbers of beaver were maintained in colonies that were located in higher quality habitats. In marginal habitats there appeared to be more rapid dispersal of immature animals from parent colonies.

Over time a beaver colony will significantly decrease the amount of woody vegetation around their impoundment. Depletion of forage increases risk to the beaver. Beavers can react to these circumstances by moving to another colony site (Svendsen 1989) or adding to preexisting dams thereby backing water closer to new food supplies. However, topography within each colony system allows only so much expansion.



Beavers are capable of building large dams. One dam in Montana was 650 m long, another in New Hampshire 1,213 m long (Rue 1969). A dam in Wyoming was 5.4 m feet high (Rue, 1969). However, they seldom attempt damming a stream carrying more than 2.8 cubic meters of water per second (Cox 1940).

Beaver density within a region can be determined as the percentage of potential sites that are actually being used by beaver (Parsons and Brown 1978, Brown and Parsons 1979). Generally the best sites within a watershed are utilized first with marginal sites being utilized as population pressures increase.

#### Beaver Movements

Four types of beaver movements have been listed (Bergerud and Miller 1977): (1) movement of an entire colony, (2) wandering of yearlings, (3) dispersal of 2-year-olds away from the natal territory, and (4) movement of adults who have lost a mate. The longest and most dependable movement is dispersal of 2-year olds away from the natal territory (Bradt 1947; Townsend 1953; Beer 1955).

Young beaver generally disperse from the natal colony during the season of their second birthday, coinciding with parturition of the adult female (Bradt 1947; Townsend 1953; Beer 1955; Libby 1957; Brooks 1980). Hodgdon (1978, in Brooks et al. 1980) reported spring dispersal of 90% of all

2-year-olds in several colonies in Massachusetts. Studies have shown that young adult beavers are most likely to move among all age classes (Beer 1955; Leege 1968).

Two-year-old beaver apparently spend much of their first summer away from the natal colony in search of mates and acceptable colony sites. Two-year-olds consistently showed the longest movements, with males showing a greater tendency to roam than females (Beer 1955; Townsend 1953). However, Townsend (1953) found that September was the month of greatest dam building activity and surmised that this was the primary month when 2-year-olds "settled down" into their new home. One study reported that adult males were driven from the lodge at parturition and may live alone for some portion of the summer, often traveling extensively (Townsend 1953).

Although there seems to be an inherent tendency to leave, there is also indirect evidence that 2-year-olds are driven from the colony by dominant adults (Hodgson and Larson 1973). Most trappers and fur buyers in west Tennessee are aware of dispersal timing due to a significant increase in bite wounds in pelts during late winter and early spring (Ray Henry, Tennessee Wildlife Resources Agency, retired, personal communication, 1988). Barring adult mortality or abandonment by either mate (Svendsen 1989), social structure in the colony remains constant (Cook



1943). Food demand appears to play an integral part in dispersal. Even though several individuals may be required to maintain dams, dispersal acts to stabilize density, and therefore, food demand within the colony.

Kleiman (1977) suggested that monogamy may have evolved through one or more causative factors that would render group living advantageous: (1) lower susceptibility to predation, (2) improved food acquisition, and (3) localization or limitation of some necessary resource. Aggressive behavior by adults (usually the parental male) toward 2-year-olds might be explained in two ways: (1) the male's territorial defense prevents over utilization of necessary resources, and (2) sexually maturing individuals within the colony are viewed as competitors in a monogamous situation and are driven away. Wigley et al. (1983) reported that the social structure in a beaver colony generally permits only the dominant female to breed. However, progeny or immigrating individuals can mate with the remaining adult if his or her mate is removed (Payne 1975, Wilsson 1971, in Brooks et al. 1980).

Studies in Minnesota, Idaho, and Alaska (Beer 1955; Libby 1957; Leege 1968) involved capture and release of a total of 229 beaver. Seventy-seven percent of these animals moved less than 1.6 km. Mean distance moved was approximately 9.6 km; however, a few individuals moved in excess of

160 km. Transplanted beaver can move great distances. Knudsen and Hale (1965) caught and marked 2,200 beaver in Wisconsin. Of 472 recaptures 90% moved less than 12.8 km with an individual maximum of 48 km. In a study in North Dakota (Hibbard 1958) one beaver moved 237 km in 7 months. Denney (1952, in Hibbard 1958) studied 26 beaver in Colorado reporting mean movement for all animals at 16.6 km and an individual maximum of 48 km. In addition, entire colonies may move from one site to another (Brooks et al. 1980; Svendsen 1989).

Beavers are territorial (Bradt 1939; Aleksuik 1968; Bergerud and Miller 1977) and resource defense has been postulated as a driving mechanism in mating systems and pair bond (Greenwood 1980). Bergerud and Miller (1977) reported that 2-year-old beaver failed to disperse from natal colonies if new colony sites were lacking. Beaver have effective dispersal methods as can be inferred from the rapid expansion of populations across the Southeastern United States during the past 25 years (Arner and Dubose 1979; Bullock and Arner 1985).

#### Beaver Control

Hill (1976) reported that strychnine was an effective poison for beaver. Hill (1976) also reported sodium monofluoroacetate at a dosage of 0.2mg/kg body weight and administered intramuscularly to be lethal for beaver.



However, these chemicals are not registered for use on beaver. The use of toxicants in beaver populations is apt to be contrary to public acceptance (Wesley 1978).

Chemosterilants have been suggested as a means to control rodent populations (Davis 1961) including beaver (Arner 1964). Hill (1977) examined the effectiveness of quinestrol (17-alpha-ethynyl-estradiol-3-cyclopentyl ether) but found no feasible method to get the chemosterilant into wild populations.

Surgical sterilization was performed on either adult in 14 colonies in Massachusetts, effectively inhibiting colony reproduction (Brooks et al. 1980). Practical methods to induce sterility in wild populations have not been developed.

Biological controls such as introducing alligators (Alligator mississippiensis) have been used to attempt to control beaver but with little documented success (Hill 1976). Biological controls are controversial and are difficult to direct and evaluate with any degree of certainty.

After following its effectiveness on several Alabama watersheds, Hill (1976) concluded that trapping could be successful. He expressed concern that trapping was reducing beaver populations dramatically in 6 counties in southeast Alabama where high populations had existed previously

(Wesley 1978). However, Wigley (1986) indicated that many landowners with problem beaver believe trapping to be ineffective despite the fact that trapping was largely responsible for population declines prior to the turn of the century.

### Reforestation

#### Beaver Impoundments in the Bottomlands

Within the bottomland hardwood forest, distinct floral mosaics can be identified that reflect increasingly subtle substrate differences. Generally, the floral distribution in the floodplain is tied directly to the selective power of hydrologically generated anaerobic gradients (Wharton et al. 1982). Wharton (1977) and Fredrickson (1979) pointed out that beavers play a prominent role in bottomland ecosystems. Their activities create new subsystems within the bottomland ecosystem by inundating previously dry land. Their activity in southeastern Missouri was apparently important in baldcypress distribution (Wharton et al. 1981). Ruedmann and Schoomaker (1938) concluded that beavers were able to aggrade smaller valleys and silt gathering behind their impoundments thereby greatly affecting the substrate pattern of the northern half of North America.

The presence of an active beaver population in a riparian area can alter natural water, nutrient, and energy



flows within the colony site. Naiman et al. (1986) listed a number of stream alterations that can result from beaver activity: (1) modification of channel geomorphology and hydrology, (2) greater retention of sediment and organic materials, (3) creation of wetlands, (4) modification of nutrient cycling, (5) modification of the riparian zone, (6) modification of water quality, and (7) modification of habitat, influencing community composition and diversity. A study in Wisconsin (Barnes and Dibble 1988) suggested that the beaver's foraging activities might have a significant effect on the composition of future generations of trees.

Inundation transforms a structurally complex riparian floral system to a somewhat simpler semiaquatic system (Brinson et al. 1981). Broadfoot and Williston (1973) stated that the majority of bottomland tree species cannot survive 2 years of constant flooding. Within a bottomland, the hardwoods that persist are well adapted to the stresses imposed by the natural hydroperiod. These trees are a fundamental and integral part of the dynamics of the system (Wharton et al. 1982). Inundation results in a number of specific chemical and physical changes:

1. Depletion of available oxygen in soil water,
2. Shift in soil pH—generally a convergence toward neutrality,

3. Accumulation of toxic compounds in plants growing in a saturated substrate,
4. Shifts in redox states—generally from more oxidized to more reduced,
5. A general lessening in nutrient availability (Teskey and Hinckley 1977).

As a result of these factors, transpiration and photosynthesis rates are generally slowed and overall plant growth is impeded (Teskey and Hinckley 1977). In standing water, plants literally die of dehydration (Wharton et al. 1982). System productivity suffers if flooding duration and intensity are severe.

Suspended sediments and dissolved nutrients are transported from upstream portions of the watershed into the floodplain where reduced water velocity causes deposition of some of the suspended material. Seasonal decomposition of detritus releases nutrients for plant uptake. Transpiration lowers water table levels. Therefore, riparian systems have a relatively high capacity to recycle nutrients compared to the relatively low rates they are transported in from outside systems (Brinson et al. 1981).

The major factor contributing to the high productivity in a floodplain forest is the regular pulse of wet and dry cycles (Brinson et al. 1981). Within a beaver impoundment, the natural pulse is prevented by year-round water



retention. With the loss of a highly structured forest ecosystem and associated transpiration, retention time for water and detrital material increase.

A study of a beaver pond ecosystem in Canada (Hodkinson 1975a) concluded that total energy input was distributed as follows: 18% exported, 26% respired, and 56% accumulated in the sediments. In that study a beaver pond was considered to be a highly accretive heterotrophic system. Litter breakdown is slow in systems where water movement is slow (Hodkinson 1975b; Post and de la Cruz 1977).

Even in drained or abandoned beaver impoundments the water table may remain high due to loss of transpirational drawdown during the growing season. Natural reforestation of these areas in west Tennessee is a slow process with early seral stages comprised of low-value, wet-site tree species which often capture the site at the expense of later developing, commercially valuable species (Waldrop et al. 1982; Rushton 1983; Houston et al. 1987).

#### Artificial Hardwood Regeneration

Bottomland hardwood sites have long been recognized as potentially among the most productive in the temperate forest region of North America (Barrett 1980). Yet, without management, natural regeneration on these sites following agricultural abandonment or timber harvest usually consists of low value species (Waldrop et al. 1982; Seifert et al.

1984). Although most naturally existing hardwood stands can be managed to produce significantly greater volumes, an alternative method of management on these highly productive sites may be through artificial regeneration (Hunt 1976). Also, artificial regeneration may be necessary on some sites to ensure the perpetuation of species which, for one reason or another, fail to reproduce naturally (Sternitzke 1972; Toliver and Jackson 1989; Conner and Toliver 1990).

Research on artificial establishment of bottomland hardwoods has been focused primarily on sweetgum (Liquidambar styraciflua L.), sycamore, green ash, and cottonwood (Populus deltoides Bartr.) because these species have been shown to generally produce high biomass yields and have historically maintained relatively high market values (Waldrop et al. 1982; Gilmore and Rolfe 1984; Seifert et al. 1984; Houston and Buckner 1988).

Without adverse factors, such as flooding or animal damage, survival of planted hardwoods has generally proved to be adequate (Krinard and Johnson 1981). Silker (1948) reported success planting bottomland tree species along the margins of fluctuating-level reservoirs. In that study baldcypress, water oak (Quercus nigra L.), willow oak, green ash, and sweetgum showed satisfactory to excellent survival and growth five years after planting on sites supporting



only hydrophytic weeds previously. Green ash and sycamore were recommended for wetter sites. At the end of five growing seasons sycamore was 4.4 m tall, green ash 2.0 m tall, and baldcypress 1.5 m tall. Growth in nine- to twelve-year-old hardwood plantations was as good or better than that of upland plantations of pine or hardwood. He concluded that periodically flooded sites hold considerable promise for plantation timber production.

One study (Haynes and Moore 1987) examined examples of bottomland hardwood reestablishment on 12 National Wildlife Refuges in the Southeast. Limiting factors governing the success of these plantings were listed to include (1) drought or late freeze following planting, (2) standing water and elevated temperatures in the initial growing season, (3) flooding on sites where species were not tolerant to prolonged periods of saturated soils, (4) animal damage to seedlings, and (5) poor quality seedlings. Although efforts to control competing vegetation were seldom employed in these plantings, the authors suggested that reestablishment of bottomland forests by planting desirable species was possible.

Mechanical damage to young seedlings during flooding is an often overlooked aspect of planting trees in the bottomlands (Loucks 1987). Floating debris along with strong currents can destroy or displace young seedlings.

Baker (1977) listed green ash and sycamore as being tolerant to spring flooding with 90% survival after 4 weeks of inundation. Loucks and Keen (1973) listed seedling tolerance to submersion for 10 bottomland species and determined that only green ash and baldcypress could withstand 4 weeks of submersion and retain 100% survival. In a report (Hosner and Boyce 1961) on the impact of water saturated soils on the performance of 17 bottomland hardwood species there were 9 species, including green ash, which actually gave greater height growth in soils that were saturated for the maximum 60 day period. Cherrybark oak had the highest mortality of all species tested. Sycamore lost height but survived satisfactorily. If sycamore plantation management is to be successful, sites must be chosen carefully (Rich 1989). Briscoe (1973) suggested that sycamore could be planted successfully all year if available moisture exceeded transpiration. Artificial regeneration of bottomland oak species has rarely been successful (Wigley et al. 1984, Seifert et al. 1984). However, Seifert et al. (1984) reported satisfactory growth of five-year-old swamp chestnut oak planted on poorly drained sites in southeastern Indiana. Chemicals were used to control herbaceous competition on control, disked, and disked/bedded plots. Growth in disked plots was significantly greater than on control plots, but no difference was noted between disked



and disked/bedded plots. Results suggested that planting swamp chestnut oak may be a feasible land use alternative for these sites. Shumard oak (Quercus shumardii Buckl.) was successfully planted on high pH, Mississippi alluvium soils where other oaks had failed (Kennedy and Krinard 1985). In that study survival and growth at ages 10, 11, and 25 years in three separate plantings were consistent with expectations for good timber and wildlife production.

Cottonwood, sycamore, green ash sweetgum, swamp chestnut oak, Shumard oak, sugarberry (Celtis laevigata Willd.), and sweet pecan (Carya illinoensis Wangenh., K. Koch) were planted for three successive years on clay-capped soils in the Mississippi batture (Krinard and Johnson 1981). The first year there was no flooding while in the second and third year there was flooding. The study concluded that a flood-free initial growing season was desirable in the establishment of hardwood plantations. However, species planted in the years with flooding had better than 70% survival except Shumard oak, swamp chestnut oak, and sweetgum. Height after 3 years in these plantings ranged from 0.7 m for sweet pecan to 12.3 m for cottonwood. Sycamore averaged 6.7 m tall. Survival for sycamore, sweetgum, and green ash was greater than 80%, but only 20% for cottonwood on Sharkey clay soils with ponded water. Beaver damage was noted in this study with long rows of

seedlings pulled up. Sycamore was less damaged than other species.

A study of cultural treatments for establishment of bottomland hardwoods in west Tennessee (Waldrop 1982) reported third year heights of sycamore and green ash planted on abandoned agricultural fields to be 2.0 m and 1.3 m respectively. Krinard and Johnson (1983) reported fifth year height for sycamore and green ash on Sharkey clay soils to be 4.0 m and 4.5 m respectively in mowed plantations. A study in South Carolina (Klawitter 1961) reported successful baldcypress plantings on wetland sites. The fastest growing treatments had produced trees averaging 1.1 m tall at the end of the second growing season.

A study in west Tennessee (Houston et al. 1987) reported first year survival for cottonwood, green ash, sweetgum, sycamore, and baldcypress planted on drained beaver impoundments. Seedling survival on sites where the water table was below ground surface was greater than 50% for all species except cottonwood (20% survival). However, on sites where the water table was exposed on approximately 1/3 or more of the site, survival dropped below 50% for all species except baldcypress (88% survival). The authors suggested that successful establishment of desirable bottomland tree species is possible only if topography



within impounded areas allows sufficient lowering of the water table after removal of the beaver dam.

A study (Conner and Toliver 1990) examining 4-year-old baldcypress plantings in Louisiana swamps concluded that such plantings could be successful even in partial shade, if nutria (Myocastor coypus Molina) girdling damage could be controlled. Survival averaged 90% in plots escaping nutria damage. Height growth averaged 29 and 48 cm inches per year.

Hardwood plantations have been shown to derive growth and survival benefits from intensive control of competing vegetation (Malac and Heeren 1979; McCormack 1981; Bowersox and McCormack 1987; Ponder 1987). The need for control of herbaceous vegetation at planting and for at least 3 years following establishment has been stressed (Wright and Holt 1985). Hardwood species showing improved survival and increased early growth with herbaceous control include black walnut (Juglans nigra L.), yellow-poplar (Liriodendron tulipifera L.), white ash (Fraxinus americana L.) green ash, sweetgum, sycamore, cottonwood, cherrybark oak (Quercus falcata pagodaefolia Ell.), Nuttall oak (Quercus nuttalli Palmer), and sweet pecan (Krinard and Kennedy 1983, Miller 1987). Briscoe (1969) suggested that clean cultivation in sycamore plantings might significantly shorten rotation or increase final yield by 1000 to 2000 board feet per acre.

One study (Krinard and Kennedy 1987) examined 15-year growth of cottonwood, sycamore, green ash, sweetgum, Nuttall oak, and sweet pecan planted on Sharkey clay soils. Trees disked for the first five years were significantly taller at age 5 when compared to mowed sites. By age 15 there were no significant differences in height growth between treatments for all species except sweet pecan.

Height growth of 5-year-old green ash, sycamore, and sweetgum plantings on abandoned bottomland agricultural fields in west Tennessee exhibited significant gains with disking over mowing or control plots (Houston and Buckner 1988). Height gains from disking over control plots were 81% for green ash, 73% for sycamore, and 50% for sweetgum. Among cultural treatments survival was best in disked plots (97.0%), but no significant difference was found between mowing (91.0%) and control (93.5%) plots.

Early efforts to control herbaceous vegetation relied on the use of mechanical control because no satisfactory chemicals were available (Malac and Heeren 1979). However, with introduction of a number of herbicides effective in hardwood plantation establishment there is a growing body of evidence to suggest that mechanical control may be less desirable than chemical control (e.g., less soil compaction, erosion, and crop tree damage) (Zutter et al. 1986). Byrnes et al. (1973) showed that for black walnut and yellow-poplar



chemical treatments were better than cultivation and both treatments were superior to the control.

Hansen et al. (1984) demonstrated improved tree survival and height growth of 2-year-old hybrid polars (Populus spp.) using chemical control of competition. Their study concluded that an array of weed control strategies will work, with the most promising being a mixture of chemical and mechanical control.

On drained beaver impoundments in west Tennessee increased first year survival of planted green ash, sycamore, cottonwood, and baldcypress was noted in plots treated with a grass herbicide (Houston et al. 1987). This study concluded that plantation management might be successful on sites created by draining beaver impoundments if topography within the impoundment allowed sufficient lowering of the water table.

Artificial establishment of bottomland hardwoods is not well documented. Much research has been done by large timber companies, but this information is not generally available to the public. Although research is currently in progress, much is on abandoned agricultural fields or nonswamp areas (Conner and Toliver 1990). Unfortunately, results from these studies cannot be extrapolated with confidence to drained beaver impoundments. For the most part, mechanical control of competing vegetation will prove

to be impractical on drained beaver-kill sites where high soil moisture conditions prevail.



## CHAPTER IV

## METHODS

Study Area

This study was conducted on the Ames Plantation, cooperatively administered by the Hobart Ames Foundation and Agricultural Experiment Station of the University of Tennessee. Ames Plantation is an 7527 ha landholding in the headwater basin of the North Fork of the Wolf River, a tributary of the Mississippi River. The watershed is located in the Mississippi Embayment section of the Gulf Coastal Plain physiographic province, 80 km east of Memphis, Tennessee, and 80 km southwest of Jackson, Tennessee. It encompasses 31,842 ha with approximately 23,562 ha in Fayette County and the remaining 8,279 ha in Hardeman County (USDA 1987).

Topography is characterized by rolling hills with broad flat floodplains. A layer of Pleistocene loess overlies Tertiary Coastal Plain sediments of Grenada and Holly Springs formations (Flowers 1960). On many upland areas erosion has removed much of the loess, exposing fluvial deposits that are composed primarily of highly erodible sands. Recent alluvial deposits of sand, silt, clay, and fine gravel from uplands are found in the floodplain areas of the watershed (USDA 1987).

Mean annual precipitation is 155 cm with 61 cm occurring in the April-September growing season. The wettest month is January (mean precipitation: 15.5 cm) and the driest month is October (mean precipitation: 7.1 cm). Mean annual temperature is 16.3 degrees C, ranging from a mean of 5.9 degrees C in January to 26.8 degrees C in July. The growing season lasts approximately 210 days with first and last killing frost in October and April, respectively (USDA 1987).

Soils within the watershed are generally good for agriculture but are highly erodible. Croplands comprise 9,498 ha of the watershed of which 6,534 ha are identified as eroding at a rate of more than 1,800 kg per ha per year. Approximately 2,176,110 metric tons of soil are removed yearly from these croplands. An additional 1,964 ha are now comprised of large gullies, degrading ditches, and eroding roadbanks (USDA 1987).

Within the watershed the most significant water quality problems are associated with stream sediment loads. Soil washed from the uplands increases sediment concentrations, both suspended and as bedloads. Bottomland timberlands are constantly threatened by sand deposition, acting to "smother" existing stands or create water flow obstructions which result in standing water (USDA 1987). In an investigation (TDF 1980) of the causal agents in dead and



fading forest conditions in mainstream and tributary forest lands for west Tennessee bottomland hardwood forests, sedimentation was implicated in over 60% of the sites examined. In that same investigation beaver activity was usually associated with sedimentation because of their tendency to take advantage of altered or restricted stream flow patterns to locate dams.

#### Beaver Control

The 1619 hectare study area (Fig. 1; USDA 1987) was located in the floodplain of the North Fork Wolf River beginning at the downstream departure of the river from Ames Plantation property and continuing upstream approximately 12.8 kilometers until the river became intermittent. Downstream, at the point of departure from the study area, the North Fork Wolf River averages 1 to 2 m deep and 7 m feet in width. Flood waters rarely stay above the banks more than 48 hours.

Written permission was gained from adjacent ownerships within the bounds of the study area to access their property for the purpose of beaver control. Upland farm ponds also were monitored.

From November 1984 to November 1989 the Hobart Ames Foundation, in cooperation with the University of Tennessee Agricultural Experiment Station, conducted an intensive

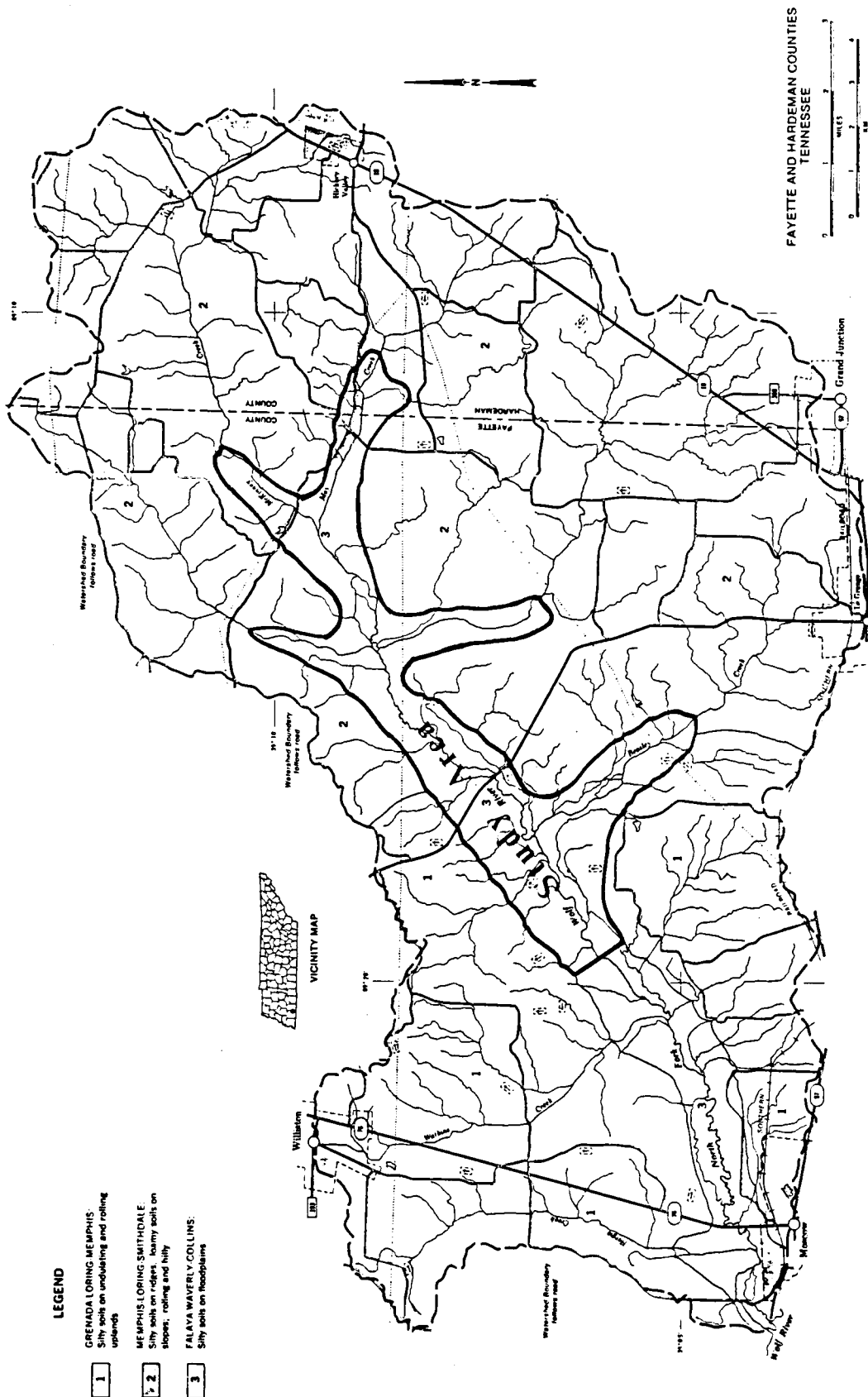


Figure 1. Study area, general soil map, North Wolf River watershed.



year-round beaver control program, designed to eliminate all beavers in the study area and prevent successful recolonization by catching "pioneer" beaver as they attempt to recolonize. Trapping was initiated in all known colonies more or less simultaneously. An experienced trapper was hired year-round to accomplish the goals of the project. He was regularly assisted by Ames Plantation personnel.

Initial populations were removed during the first 7 months of trapping (November 1984 through May 1985) (Fig. 2). During that interval 169 individuals were removed from 22 active colony sites which ranged in size from approximately 0.4 to 24.3 ha. Individual locations were considered trapped-out if beaver activity (e.g., dam repair, tracks, cuttings) was not observed during repeated visits (spanning several days) to the site (Peterson and Payne 1986). No attempt was made during this period to distinguish initial populations from immigrants. From 1 June 1985, through 30 September 1988, all colony sites were kept under strict surveillance and beaver attempting to recolonize were removed within 1 month of immigration. Transient beaver or those residing in the North Fork of the Wolf River were ignored unless attempting to dam the river. It was impracticable to quantify or regulate the river population. Therefore, a small number of beaver could be found within the bounds of the study area at any given time.

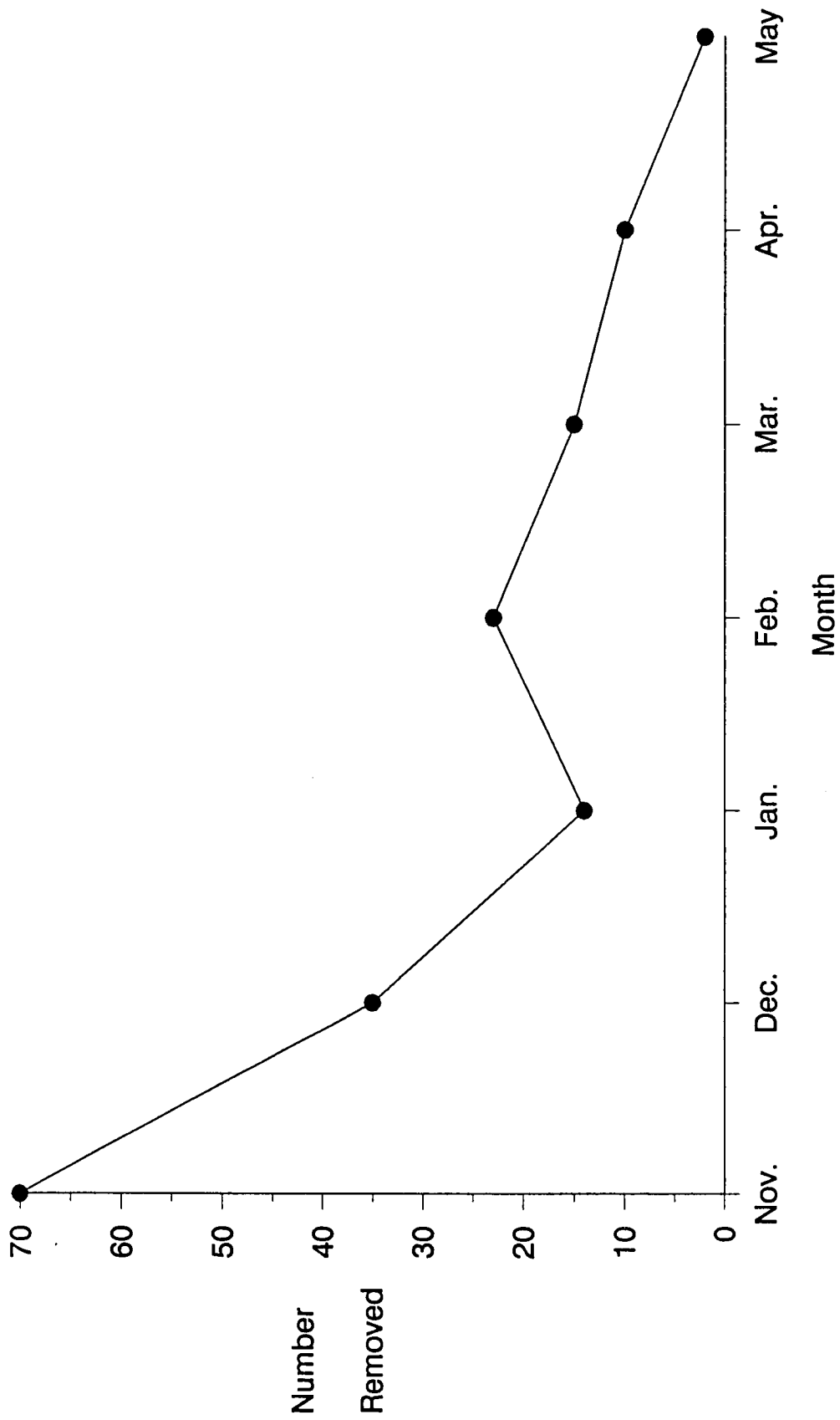


Figure 2. Removal of initial beaver populations from the Ames Plantation Study Area, Fayette County, West Tennessee, November 1984 through May 1985.



Dispersal is commonly measured in 3 ways: (1) recording emigrants, immigrants, and transients from one area to another, (2) recording natal-to-breeding or breeding to breeding movements, or (3) by recording movements from one group of individuals to another (Dobson 1982). Lidicker (1975) defined a dispersal sink as a place into which dispersers move. Generally it is some empty or unfilled habitat where survival is possible. Dispersal sinks may be created by removing resident populations from an area. Artificial sinks can be designed to mimic natural sinks (Dobson 1981); and dispersal of several species has been evaluated using them (Davis et al. 1964; Myers and Krebs 1971; Joule and Cameron 1975; Windberg and Keith 1976; Gaines et al. 1979).

In this study only those beaver attempting to colonize or "homestead" a previous or new colony site were considered as immigrants. The aggregate of all colony sites within the study area represents the dispersal sink. Using this definition, from 1 June 1985, to 30 September 1988, 162 immigrating beaver were removed from the study area.

Transient and river populations remained low and did not seem to fluctuate during the course of the study. It is probable that some beavers residing in the river attempted colonization and were caught. It is possible that some

individuals included in final totals were part of the river population or transients that were caught while exploring.

Trapping techniques used were those outlined by Hill (1976 and 1982) and Weaver et al. (1985), employing primarily the Conibear 330 with limited use of the wire snare. Conibear traps accounted for approximately 95% of all beaver caught during the study. The most productive technique was to make a small break or series of breaks in the major dam and place one or several Conibears near the breach. Escaping water stimulated colony members to attempt repair (Hartman 1975). Other common sets included those on runways across the top of dams or sets in association with well worn feeding runs.

Trapping in a given colony site was directly related to beaver activity: dam building or repair, feeding activity, tracks, and droppings. Although it was difficult to determine the number of beaver in a colony site from these indications alone (Easter-Pitcher 1990), beaver activity associated with colonization can be readily detected by frequent surveillance (Hill 1977). Trapping was conducted at each colony site until indications of beaver activity ceased.

Based on aerial surveillance (Swank and Glover 1948, Hay 1958) of active colony sites by Tennessee Division of Forestry personnel, beaver populations were high from the



study area downstream to the confluence of the Wolf and Mississippi Rivers (Charles Riddell, Tennessee Division of Forestry, personal communication, 1987). Colonies upstream from the study area were generally associated with farm ponds.

Where possible, the lower mandible of each specimen was extracted for age determination. Age determinations were assigned using the van Nostrand-Stephenson technique (van Nostrand and Stephenson 1964; Larson and van Nostrand 1968) based on tooth eruption, degree of closure of basal openings, and annual cementum layers visible at the bases of molars and premolars. Beaver do not form cementum annuli until their third summer (Larson and van Nostrand 1968; van Nostrand and Stephenson 1964) and until that age the first two criteria are sufficient for reliable age determinations.

All specimens were tagged. Teeth were extracted by cracking the jaw with a steel punch. A knife was used to lightly scrape excess flesh and dried blood from the base of each tooth. If basal openings were closed or atypical, age determinations were made by grinding the lingual surfaces of molars or premolars to achieve a longitudinal cross-section through the center of each tooth. A 120-grit stone mounted on an ordinary bench grinder proved satisfactory for grinding. Ground surfaces were polished with 400-grit emery cloth. Cementum layers were observed and estimated using low magnification (van Nostrand and Larson 1964).

Sex of each specimen was determined by probing for the baculum (Osborn 1955), the presence of nipples on lactating females (Hodgdon and Larson 1973), or, when in doubt, incising the abdomen to locate reproductive organs. Date and location within the study area was recorded for each capture.

### Statistical Analysis

Data on beaver caught during the period from 1 June 1985, to 30 September 1988, were summed by 4-month periods. The periods were chosen based on documented facets of beaver biology and behavior.

Original populations were removed by 30 May 1985, making 1 June 1985, a convenient beginning point. However, the 4 months beginning in June (June–September) also mark the portion of the year in the South when beaver are not solely dependent on woody materials for their diet, but subsist largely on herbaceous vegetation. The absence of harsh environmental extremes combined with relative abundance of food would seem to indicate this as being the least stressful part of the year. In the fall and winter (October–January) frost kills herbaceous vegetation, forcing beaver to revert to woody material for food. Pair bonding is most common at this time of the year (Svendsen 1989). Mating may occur as early as November and is generally concluded by January (Jenkins and Busher 1979;



Hill 1982). During the months February through May gestation, parturition, and dispersal of 2-year-olds typically occurs (Jenkins and Busher 1979; Hogdon 1978, in Brooks et al. 1980; Svendsen 1989).

To maintain the assumptions necessary for analysis of variance, total number caught by individual 4-month periods were transformed to  $\log(\text{sum} + 1)$  (Sokal and Rohlf 1980). Analysis of variance was conducted on transformed data to determine if colonization attempts were significantly related to season (4-month time period) or sex (General Linear Models Procedure; SAS 1985). Trappability was assumed equal for each time period. Sexes were combined if no significant differences were noted. Mean separation was accomplished using Least Square Means Procedure (SAS, 1985). Statistical significance was evaluated at the 95% confidence level unless otherwise reported.

#### Plantation Establishment

Two former beaver impoundments were chosen for plantation establishment. Both sites were characterized by having no living overstory and were inundated prior to control efforts. Dead timber on both sites indicated previously well stocked, young sawtimber stands consisting primarily of green ash, cow oak, sycamore, sweetgum, and other indigenous bottomland associates. Soils on both sites

belonged to the Waverly-Falaya-Collins association (USDA 1964) and were suitable for the species selected for planting (Broadfoot 1976). Drainage was accomplished by breaching the beaver dam with hand tools and maintained by preventing recolonization. For safety reasons dead snags on each site were felled prior to planting. The logs were left in place, or cut into manageable pieces and moved slightly to facilitate planting.

Two years after drainage, green ash, sycamore, cypress, willow oak, and swamp chestnut oak were planted on a 1.22 x 1.22 m spacing in 4 replications of 120 trees per species per replication. Initial herbaceous cover consisted mainly of a thick mat of swamp cut grass, with woody vegetation comprised primarily of scattered black willow clumps and boxelder seedlings.

At the time of planting the water table on both sites was beneath ground level during the growing season except for periods of partial inundation associated with recolonization attempts or flooding. Green ash, sycamore, and swamp chestnut oak are rated as moderately tolerant to flooding, being able to survive saturated or flooded soils for several months during the growing season (Fowells 1965; McKnight et al. 1981). Baldcypress is tolerant to flooding and is able to survive long periods during the growing season in saturated or flooded soils. Willow oak is

considered moderately tolerant, able to survive saturated soils a few days or weeks during the growing season (Fowells 1965; McKnight et al. 1981).

Species blocks were split and one-half of each block was sprayed over-the-top with fluazifopbutyl (trade name: fusilade 2000), a grass herbicide, in a mixture of 4.4 cl fusilade and 1.5 cl nonionic surfactant per 3.8 l of water in mid May and late June of the first growing season. All species subplots and herbicide treatments were randomly assigned. Nonplanted control plots were also included in each replication and herbicide was also applied to one-half of each (Appendix B).

Green ash and sycamore seedlings were 1-0 bareroot stock obtained from local corporate nurseries. Baldcypress seedlings were obtained from the Tennessee Division of Forestry nursery also as 1-0 bareroot stock. Willow oak and swamp chestnut oak acorns were collected from Ames Plantation in the fall of 1986, then germinated and grown in containers in the greenhouse for spring planting (Mullins and Buckner 1987), because commercial seedlings for these species were unavailable. Seed source in all cases was judged satisfactory for Ames Plantation. Tree survival was measured at the end of the first growing season. Survival and total height were measured at the end of the third growing season. Heights were obtained by placing an



inscribed pole beside each stem and reading to the nearest centimeter.

At the end of the first growing season nonplanted subplots were divided into 3 equal sections and a 4.05 ca plot was randomly located in each, providing a 13.6% sample by area. Above ground vegetation in each mil-acre plot was destructively sampled and oven dried until no additional weight loss occurred. Vegetation was separated according to 3 broad categories: (1) grasses, primarily Leersia oryzoides, (2) broadleaf herbaceous competition, and (3) woody vegetation. The three 4.05 ca samples from each subplot were combined per vegetation category and weighed to the nearest 5 g. Woody stems were tallied by species. Black willow clumps, generally resulting from trees cut by beaver, were counted as single stems.

The major herbaceous materials were identified at the species level, but were not weighed separately. Rather, predominant herbaceous competitors in each subplot were noted (Appendix C). Principal herbaceous competitors at each location were generally obvious. No biomass data were collected at the end of the third growing season.

#### Statistical Analysis

Preliminary analysis of survival data indicated nonconformity to the normal distribution. To maintain the

assumptions necessary for analysis of variance, angular transformation of the data was employed (Sokal and Rohlf 1981).

All tree survival and height data were analyzed using a standard split plot analysis of variance; mean separation was determined using orthogonal contrasts (General Linear Models Procedure; SAS 1985). Statistical significance was evaluated at the 95% confidence level unless otherwise reported.

Biomass data from nonplanted subplots were treated as individual observations per mil-acre plot. Dry weight data were analyzed to determine if herbicide treatments significantly reduced the grass component (General Linear Models Procedure; SAS 1985).

Correlation analysis of grass and broadleaf weed dry weights was conducted. Polynomial regressions were fitted to determine the relationship between grass and broadleaves (General Linear Models Procedure; SAS 1985). Mean separation was determined using orthogonal contrasts and statistical significance evaluated at 95% confidence level unless otherwise reported.

## CHAPTER V

## RESULTS

Beaver Control

During the study period 162 beaver attempting to recolonize original or new sites were removed (Table 1). Of these, sex was determined on 141 individuals and age data were obtained from 154 individuals.

Scavengers prevented acquisition of data from some individuals trapped. Dominant scavengers were the black vulture (Coragyps atratus), turkey vulture (Cathartes aura), and coyote (Canis latrans). Completely or partially devoured carcasses usually made sex identification impossible. However, if the lower mandible was salvaged, reliable age determinations could be made. Scavengers seemed to become more proficient as the study progressed.

Analysis of variance revealed highly significant differences in recolonization among the three time periods. Recolonization attempts were relatively low during the period June–September with approximately 5.5 attempts. Recolonization during this period was significantly less than the periods October–January (22.7) and February–May (23.7). The periods October–January and February–May did not differ significantly (Fig. 3).



Table 1. Total number of beaver immigrating into the Ames Plantation study area, Fayette County, west Tennessee, 1 June 1985 through 30 September 1988 by 4-month period.

| Month                  | ----- Number Caught by Year ----- |      |      |      |             |
|------------------------|-----------------------------------|------|------|------|-------------|
|                        | 1985                              | 1986 | 1987 | 1988 |             |
| <u>February-May</u>    |                                   |      |      |      | <u>MEAN</u> |
| February               | -                                 | 4    | 2    | 9    | 5.0         |
| March                  | -                                 | 14   | 6    | 1    | 7.0         |
| April                  | -                                 | 13   | 9    | 2    | 8.0         |
| May                    | -                                 | 4    | 1    | 6    | 3.7         |
| TOTALS                 |                                   | 35   | 18   | 18   | 23.7        |
| <u>June-September</u>  |                                   |      |      |      | <u>MEAN</u> |
| June                   | 1                                 | 3    | 3    | 1    | 2.0         |
| July                   | 2                                 | 3    | 1    | 1    | 1.8         |
| August                 | 0                                 | 1    | 0    | 1    | 0.5         |
| September              | 3                                 | 0    | 2    | 0    | 1.2         |
| TOTALS                 | 6                                 | 7    | 6    | 3    | 5.5         |
| <u>October-January</u> |                                   |      |      |      | <u>Mean</u> |
| October                | 4                                 | 2    | 8    | -    | 4.7         |
| November               | 5                                 | 5    | 13   | -    | 7.7         |
| December               | 5                                 | 10   | 3    | -    | 6.0         |
| January                | -                                 | 4    | 3    | 6    | 4.3         |
| TOTALS                 | 14                                | 21   | 27   | 6    | 22.7        |

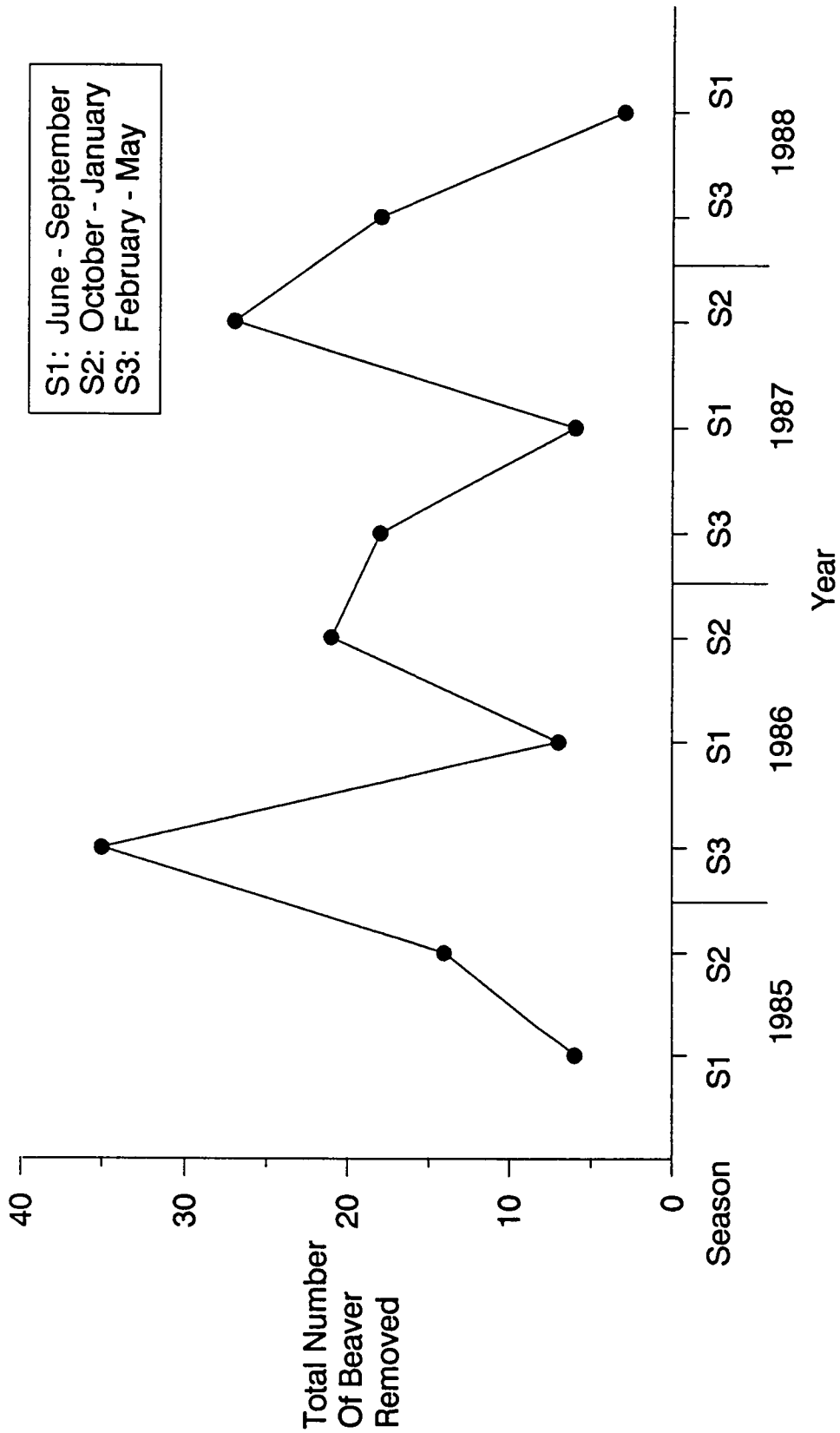


Figure 3. Total number of immigrating beaver removed from Ames Plantation Study Area, Fayette County, West Tennessee, 1 June 1985 through 31 September 1988, by 4-month trapping period.

On the average only 10.4% of all recolonization activity occurred in the summer period, with the bulk of this activity generally confined to June and July. The interval from the first of October through the end of May accounted for 89.6% of average yearly immigration.

Although more males than females were caught (86 versus 55, respectively), the difference was not significant. Therefore, males and females were combined (Table 2).

Colonization attempts were difficult to predict on a monthly basis. Colonization attempts, particularly February-May, seemed to be positively correlated with flooding. Frequency of girdling damage to trees along the river bank also increased during high water episodes.

In this study 89.4% of all beaver on which age could be determined were in the 3-4 year age class or less. Only 3 individuals were estimated older than 8 years of age. Immigrants in the 1-2 year age class were prominent throughout the year. This age class made up 46.3% of all immigrants during the months February through May, which is the time generally thought to encompass dispersal of 2-year-olds. Beaver in the 0-1 age class made up 22.5% of all captures, being especially prevalent in the October-January period (34.8%).

The oldest individual, a 12 year-old female, also was the largest, weighing 34.2 kg while carrying four near term



Table 2. Total number of beaver immigrating into the Ames Plantation study area, Fayette County, west Tennessee, 1 June 1985, through 30 September 1988, by month and age class.

| Month                | 0-1 | 1-2 | 2-3 | 3-4 | 4-5 | 5-6 | 6-7 | 7-8 | 8+ |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|----|
| <u>Winter/Spring</u> |     |     |     |     |     |     |     |     |    |
| February             | 4   | 3   | 2   | 3   | -   | -   | -   | -   | 1  |
| March                | 2   | 13  | 4   | -   | -   | -   | -   | -   | 1  |
| April                | 2   | 13  | 4   | 3   | -   | -   | -   | 2   | -  |
| May                  | 2   | 2   | 3   | 2   | 1   | -   | -   | -   | -  |
| Total                | 10  | 31  | 13  | 8   | 1   | -   | -   | 2   | 2  |
| <u>Summer</u>        |     |     |     |     |     |     |     |     |    |
| June                 | 1   | 3   | 3   | -   | 1   | -   | -   | -   | -  |
| July                 | -   | 3   | 1   | 2   | -   | -   | -   | -   | -  |
| August               | 1   | 1   | 1   | -   | -   | -   | -   | -   | -  |
| September            | 1   | -   | 2   | 1   | -   | -   | -   | -   | 1  |
| Total                | 3   | 7   | 7   | 3   | 1   | -   | -   | -   | 1  |
| <u>Fall/Winter</u>   |     |     |     |     |     |     |     |     |    |
| October              | 7   | 2   | 2   | 2   | -   | -   | -   | -   | -  |
| November             | 10  | 3   | 8   | -   | -   | 1   | 1   | -   | -  |
| December             | 3   | 4   | 4   | 8   | 1   | -   | -   | -   | -  |
| January              | 3   | 2   | -   | 3   | -   | -   | -   | -   | -  |
| Total                | 23  | 11  | 14  | 13  | 1   | 1   | 1   | -   | -  |
| Grand Total          | 36  | 49  | 34  | 24  | 3   | 1   | 1   | 2   | 4  |

fetuses. She was difficult to catch. Although occasional individuals proved difficult to catch, these incidents seemed to be associated with circumstances other than trap recognition. For example, a very large individual might naturally avoid openings as small as that afforded by a Conibear 330. Young beaver were difficult to catch due to the trapper's inability to reliably predict their behavior patterns versus those of adults.

### Plantation Establishment

#### First Year Results

Because oak seedlings of acceptable species were not available at commercial nurseries, an attempt was made to grow containerized willow and swamp white oak seedlings in the Department of Forestry, Wildlife, and Fisheries research greenhouse in Knoxville, Tennessee. Due to propagation problems, willow oak seedlings were very small at time of establishment. Root collar diameters averaged less than 3 mm. Willow oak survival at the end of the first growing season did not appear to exceed 20%; therefore, the species was dropped from consideration.

There were no significant differences between locations in first year survival for the remaining species. Locations were combined and the following results obtained on the basis of 8 replications.

Mean survival for all species at the end of the first growing season was 89%. Mean survival for swamp white oak at 74% was significantly lower than average survival of the other three species. The majority of swamp white oak seedlings appeared to be under stress and many showed signs of dieback. Mean survival for green ash (98%) was significantly higher than the average survival of cypress and sycamore. Mean survival for cypress and sycamore were not significantly different—92% (Fig. 4).

Seedling survival in herbicide treatments was significantly increased. Across all species mean survival was 92% in treated subplots and 86% in untreated subplots.

Herbaceous competition across both locations in the herbicide treatments averaged 6,823 kg per ha while untreated areas carried 8,328 kg per ha. The difference was not statistically significant.

Herbicide treatments appeared to be responsible for a significant reduction in grass competition. Across both locations oven dry weight of grasses in untreated areas averaged 4,478 kg per ha. In treated areas the grass component averaged 1,035 kg per ha, a statistically significant difference. Location 2 (the wetter site) had a significantly larger grass component overall than location 1: 4,093 kg per ha versus 1,421 kg per ha, respectively. Dry weights of broadleaf weeds were not significantly



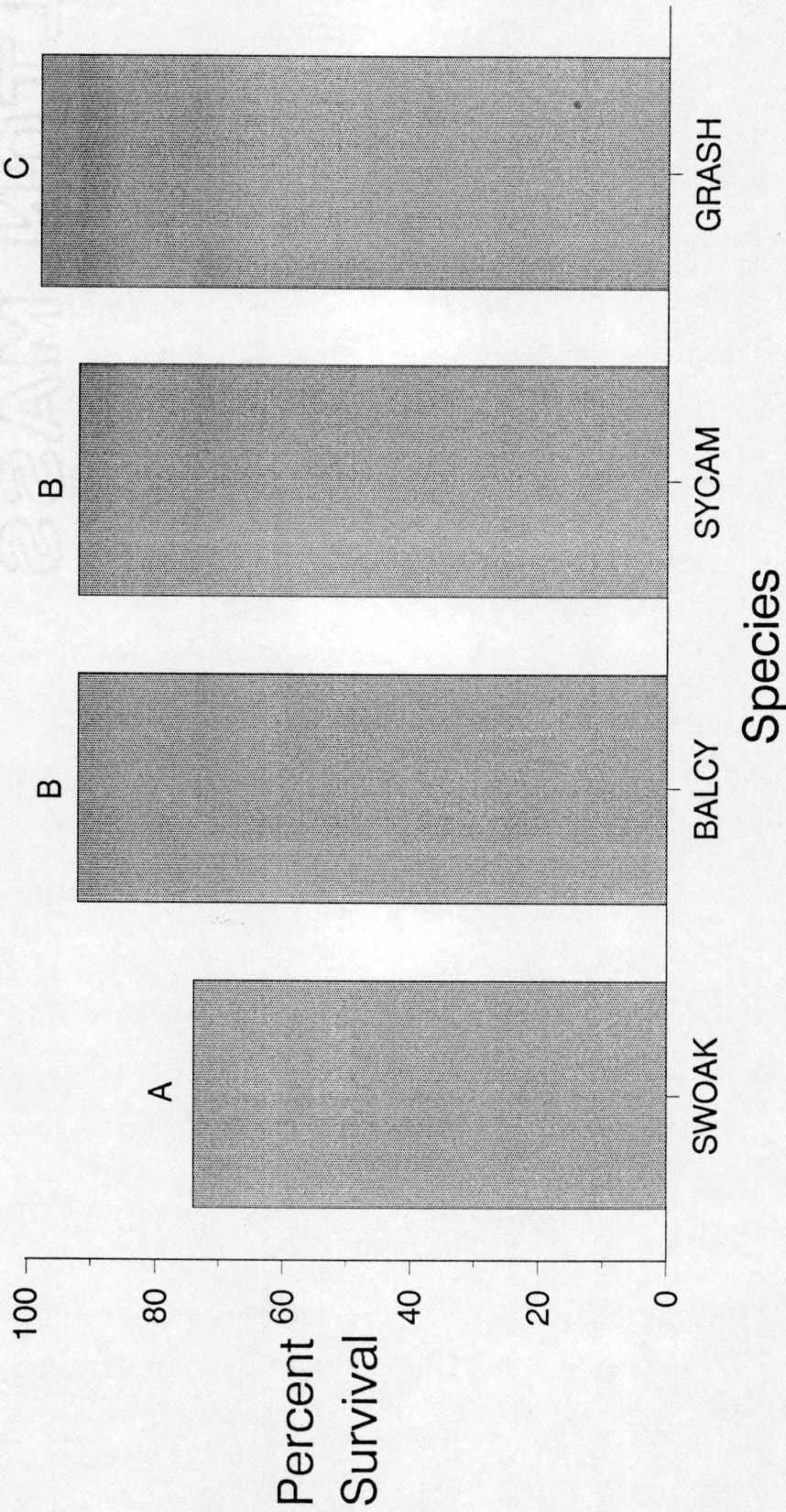


Figure 4. Percent survival of Swamp Oak (SWOAK), Bald Cypress (BALCY), Sycamore (SYCAM), and Green Ash (GRASH) planted on drained beaver impoundments on Ames Plantation, Fayette County, West Tennessee, after one growing season.

Bars with the same letter are not significantly different.

different across locations ( $p = .096$ ). Location 1 had an average broadleaf component of 5,633 kg per ha while location 2 averaged 4,006 kg per ha.

Although herbicide treatments did not significantly affect the dry weight of broadleaved components ( $p = .130$ ), there was a tendency for an increase on treated subplots. Treated areas averaged 5,788 kg per ha and untreated areas averaged 3,851 kg per ha. The dry weight of broadleaf weeds was strongly and negatively correlated with grass across both locations (correlation coefficient =  $-0.69$ ,  $p < .0001$ ). Within locations the trend was repeated (location 1, correlation coefficient =  $-0.65$ ,  $p = .0006$  and location 2, correlation coefficient =  $-0.77$ ,  $p < .0001$ ). The relationship was curvilinear with a slight but significant increase in dry weight of grass at the extreme high range of the broadleaved component (Fig. 5).

Dominant broadleaf weed species at the two locations were markedly different, due to differences in water regimes and available seed source. The predominant broadleaf herbaceous species on location 1 was Spanish nettles (Bidens bipinnata) followed by water hemlock (Cicuta maculata). On location 2 the most common broadleaf competitor was the sharp winged monkey flower (Mimulus alatus). See Appendix C for a listing of major herbaceous competitors on both sites.

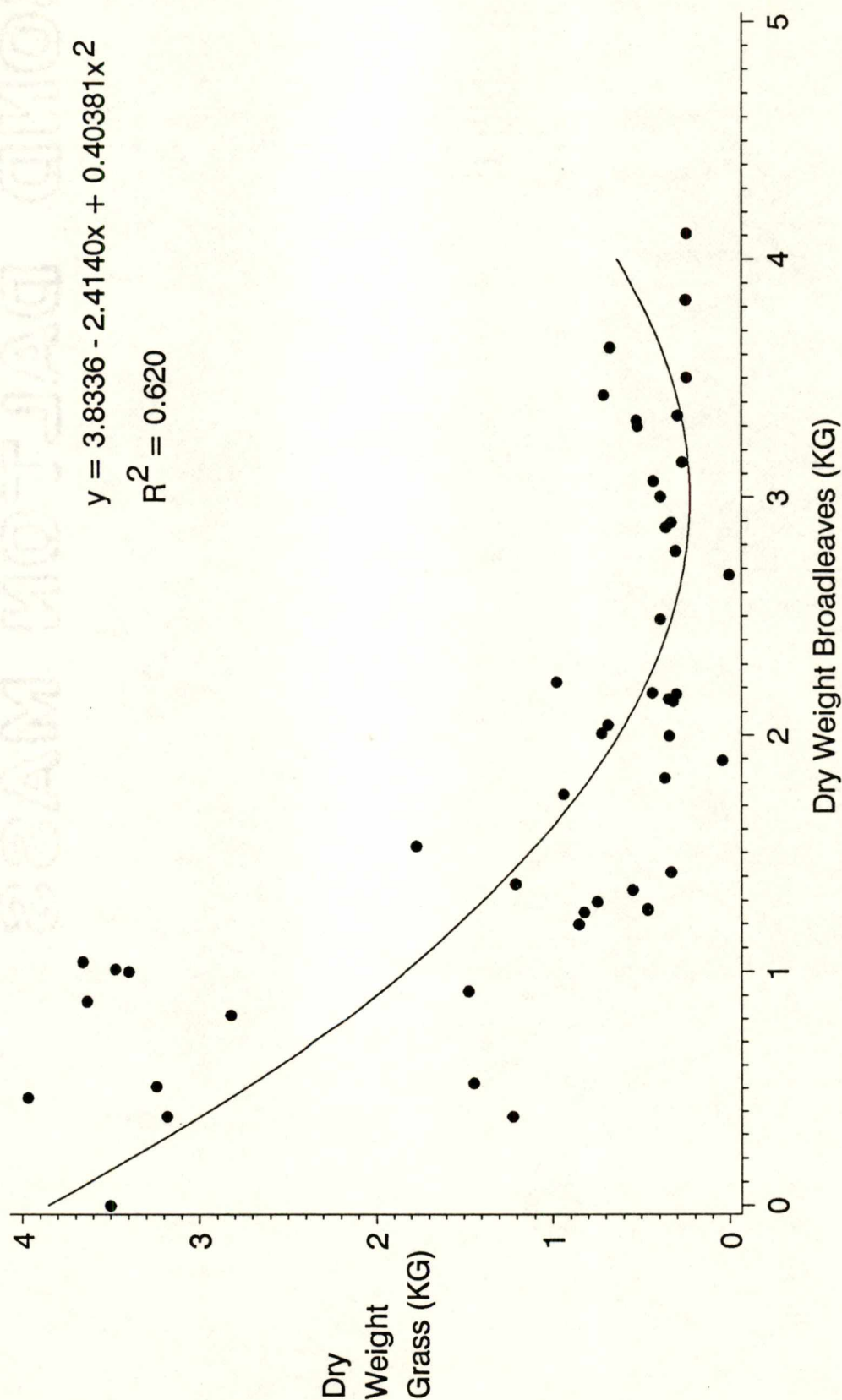


Figure 5. Polynomial regression showing relationship of dry weight grasses versus broadleaves in the herbaceous component on two drained beaver impoundments on Ames Plantation, Fayette County, West Tennessee.



Dry weights of naturally occurring woody vegetation were not significantly different between locations, although there was some indication of increased woody vegetation on herbicide plots. Treated areas averaged 834 kg per ha and untreated areas averaged 486 kg per ha. Biomass of naturally occurring tree seedlings was low overall, averaging only 661 kg dry weight per ha. Three growing seasons after drainage average stocking per hectare was 823 boxelder stems, 103 black willow clumps, and 51 cherrybark red oak (Quercus falcata pagodaefolia Ell.) stems.

### Third Year Results

By the end of the third growing season it was apparent that willow oak and swamp white oak plantings had failed. Fewer than 20% of swamp white oak seedlings had survived to the end of the third growing season. Only green ash, sycamore, and cypress are included in the following analysis.

No significant differences in third year survival were noted between locations. Location was dropped from the model and the following results assume 8 replications.

Mean survival for all species at the end of the third growing season was 85%. Green ash retained a significant advantage in survival (94%) over both sycamore (84%) and cypress (77%). Cypress survival was significantly less than mean survival for sycamore (Fig. 6). Although there was

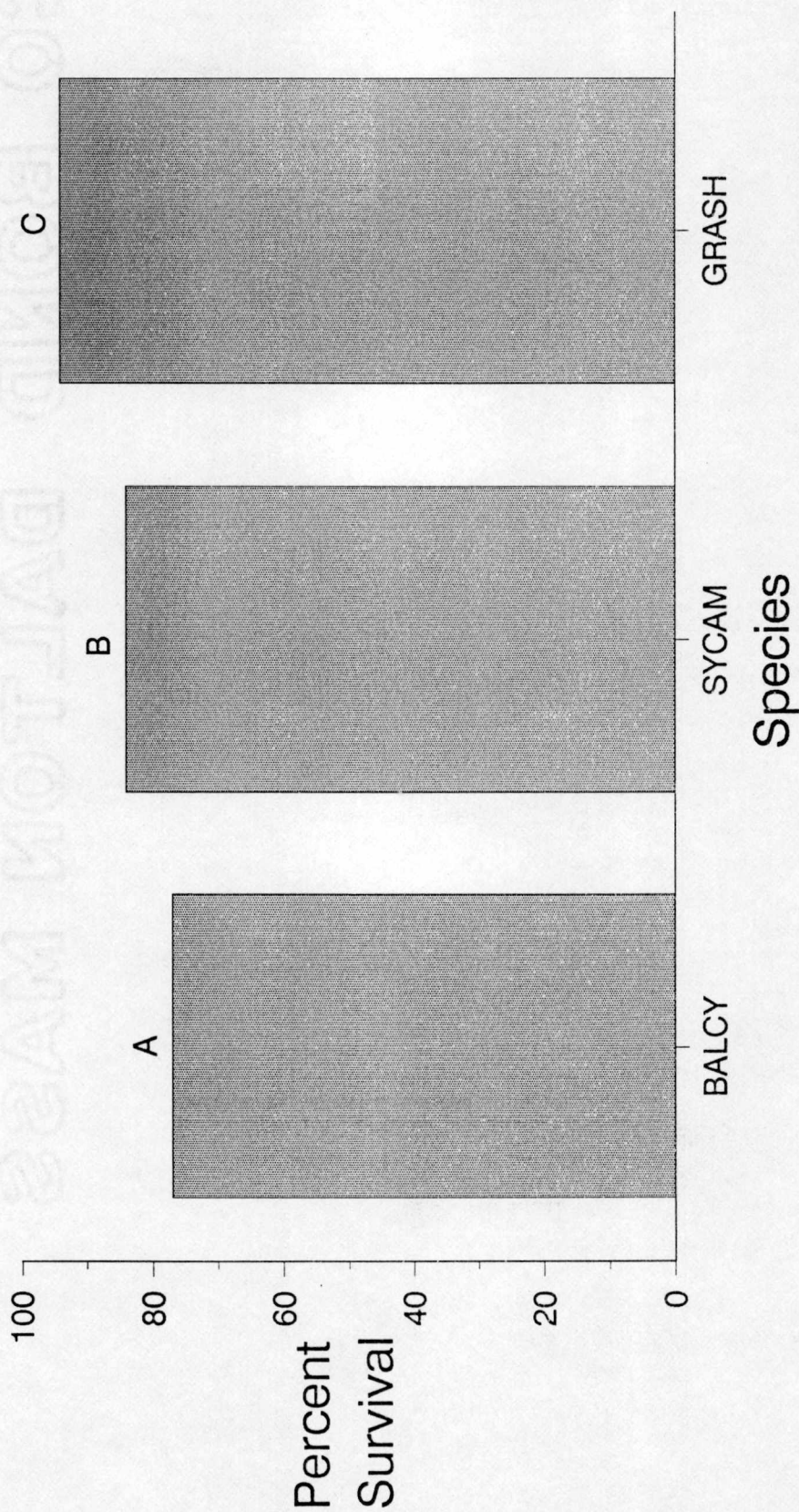


Figure 6. Percent survival of Bald Cypress (BALCY), Sycamore (SYCAM), and Green Ash (GRASH) planted on drained beaver impoundments on Ames Plantation, Fayette County, West Tennessee, after three growing seasons.  
 Bars with the same letter are not significantly different.



better survival in herbicide subplots (88%) than nonherbicide subplots (82%), these values were not significantly different.

There were highly significant differences among species for total height at the end of the third growing season (Fig. 7). Cypress (15 dm) was significantly shorter than the average for the other two species. Green ash (25 dm) was significantly shorter than sycamore (32 dm).

Location had no appreciable influence on mean heights, nor did herbicide treatment. Average height across all species were 25 dm in treated areas and 24 dm in untreated areas.

No quantitative measurements were made of herbaceous competition in year three. However, visual examination could identify residual effects of herbicide treatments. Although some grass species had reestablished in treated subplots where broadleaves did not produce heavy shade, grass components remained generally lower in treated as opposed to untreated subplots. This was particularly true on location 2 where grass components had been higher initially, and was most noticeable in plots containing baldcypress. Sycamore and green ash had produced some degree of crown closure, significantly impeding all herbaceous competition.

During the spring of 1989 several episodes of high water transported logs which had been felled at the



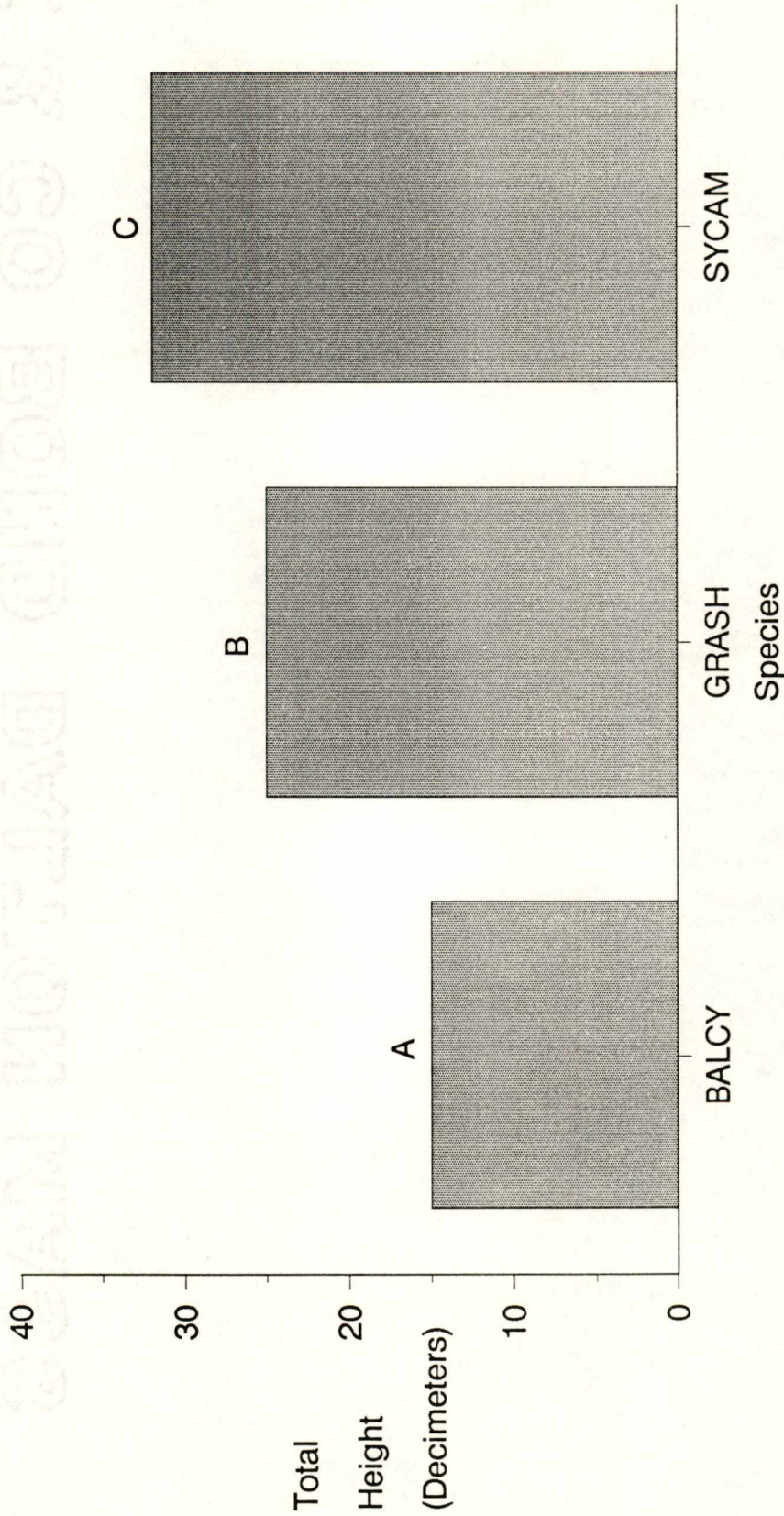


Figure 7. Total height of Bald Cypress (BALCY), Sycamore (SYCAM), and Green Ash (GRASH) planted on drained beaver impoundments on Ames Plantation, Fayette County, West Tennessee, after three growing seasons.  
Bars with the same letter are not significantly different.

beginning of the study. On some subplots otherwise healthy trees were buried beneath logjams. This phenomenon rendered survival and height measurements impractical. Subplots with good survival and larger stems were generally more severely impacted by providing greater initial obstacle to the flow of debris.

Beaver cut approximately 35 planted stems scattered over a number of subplots. This damage likely occurred in the initial stages of recolonization or during episodes of high water when noncolonizing individuals would leave the river and feed in flooded bottoms. Damage was predominately in plots nearest the water. Beaver rarely utilized sycamore in this study.

Overall, beaver damage was minimal. However, without rigorous surveillance and trapping, losses would have been excessive. Recolonization of these locations was attempted several times during the course of the study. Prolonged inundation during the growing season and girdling damage would have led to the loss of essentially all plantings.



## CHAPTER VI

## DISCUSSION

Beaver Control

The underlying objective of this phase of the Ames Plantation study was to quantify beaver immigration into a portion of a watershed where initial populations had been removed. Seasonal differences in immigration patterns were clearly demonstrated.

Because February through May is the period when young adult beaver are believed to disperse from natal territories in search of mates and suitable habitat, most immigration should be expected in this period. However, in this study immigration totals from October through January were equally high and were not statistically different from February through May. This result was not expected.

Townsend (1953), working in Montana, determined that September was the month of greatest dam building and was the time when 2-year-olds "settled down" into their new home. Another study (Svendsen 1989), conducted in Ohio, determined that pair bonds are formed predominately in the late summer and early fall. However, observations at Ames Plantation suggest that the period of greatest dam building and "settling down" occurs later in the year, from late October to early December.



First frost usually occurs in mid October at Ames Plantation, forcing beaver to abandon herbaceous food sources and begin to utilize woody species. Needing a dependable food source, young adult beaver apparently attempt to "settle down" before the onset of harsh weather. Also, during this time of the year deciduous leaves are in greatest abundance in west Tennessee streams and are heavily utilized for dam building.

Where beaver populations are high, suitable colony sites are difficult to locate. The beaver's ability to take advantage of relatively abundant food sources occurring during spring and summer may delay the urgency of finding a suitable permanent home. Therefore, two populations of dispersers may exist, those which "settle down" immediately following dispersal, and those which delay "settling down" until herbaceous food sources decline or available habitat is found. Individuals remaining "at large" throughout the summer represent a surplus population available to fill suitable habitat or replace lost mates in established colonies (Beer 1955; Peterson and Payne 1986; Svendsen 1989). Some beaver may remain "at large" for more than one year.

At Ames Plantation two distinct and predictable periods of immigration seemed apparent. Relatively high immigration began in October and continued through May, while a less

intense period of immigration began in June and concluded at the end of September. Therefore, a model of expected immigration into an isolated control area would predict relatively high immigration October through May and significantly reduced levels of immigration during June through September (Fig. 8). However, control efforts must be rigidly maintained year round to protect hardwood plantations, standing timber, or other resources unable to withstand prolonged periods of inundation. Because immigration cannot be predicted on a monthly basis, regular surveillance of sites that need protection is required. Control measures that are not focused on specific resources, as opposed to being "aimed at all beaver" in a watershed or region, are likely to be prohibitively expensive and are unlikely to protect resources.

Although the difference failed to be statistically significant, more males than females were caught during the course of this study. There has been much interest in the causes of sex-biased philopatry and dispersal patterns in mammals (Greenwood 1980; Dobson 1981; Dobson 1982; Waser and Jones 1983; Johnson 1986). Greenwood (1980) suggested that the preponderance of male dispersal in mammals can be contrasted with primarily female dispersal in most bird species. The importance of genetic (Howard 1960; Whitney

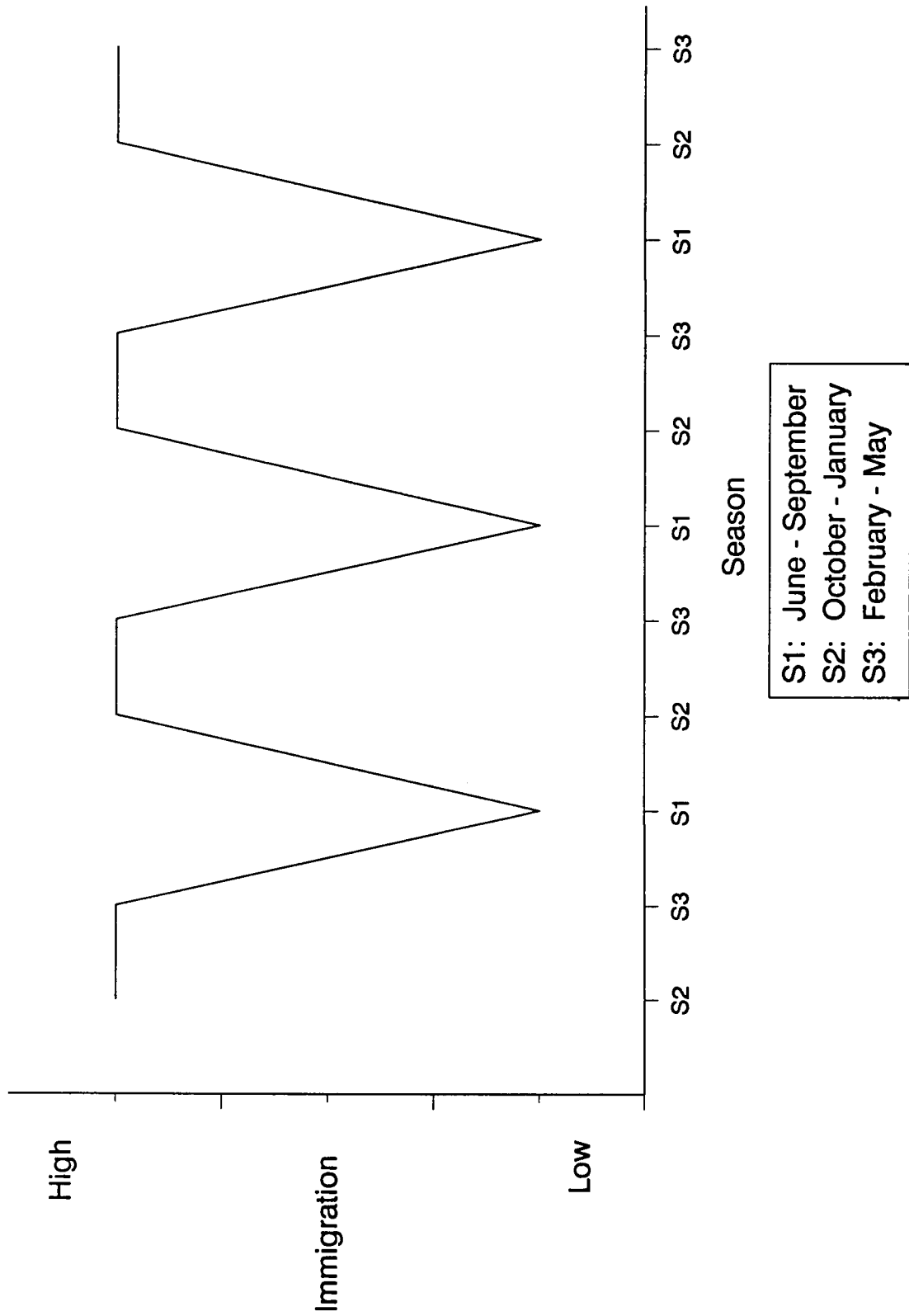


Figure 8. Expected seasonal immigration of beaver into an isolated control area.



1976; Greenwood et al. 1978; Packer 1978), behavioral (Gauthreaux 1978), and environmental (Greenwood and Harvey 1978) mechanisms leading to observed differences in dispersal patterns of mammals versus birds have been documented. Greenwood (1980) suggests that these factors fail to account for the direction of sex bias between taxa. Noting that the majority of mammals are polygamous and the majority of birds monogamous, Greenwood argued that sex differences in dispersal and the nature of the pair bond are a consequence of "mating system." Mating systems are defined as the cast of behaviors and physical adaptations specific to mating (Vehrencamp and Bradbury 1984). In a mate defense system where one sex (usually the male) must locate and defend members of the opposite sex, it should be to the defender's advantage to disperse in search of the opposite sex, thus favoring polygamy and male-biased dispersal. Alternately, resource defense by one sex (usually the male) to attract the opposite sex should favor monogamy and promote female-biased dispersal. In this system, the male attempts to partition the resource prior to attracting a mate. Therefore, it should be advantageous for him to set up and defend a territory in familiar natal surroundings.

Johnson (1986) theorized that differences in dispersive tendencies of the sexes will be slight or inconsistent in

species where both sexes begin reproduction at similar ages, and where members of each sex have potential for breeding over more than one season. Sex bias in dispersal and philopatry will be greatest when energy demands involved with dispersal across suboptimal habitat are severe. Johnson also argued that male territoriality and monogamy also contributes greatly to dispersal patterns.

Waser and Jones (1983) defined natal philopatry as "continued residence on the natal home range past the age of independence from parents." They further pointed out that many mammalian social systems have some component that is dependent on natal philopatry: cooperative raising of kin, delayed reproduction by progeny in the presence of parents, competition of among sibs for parental prerogatives, and cooperation in resource defense.

Dobson (1982) concluded that competition among males for mates may be partially responsible for male-biased dispersal of juvenile California ground squirrels (Spermophilus beechyi). Dobson tested the validity of this hypothesis against published studies of dispersal patterns of 69 mammalian species. In 46 of 57 polygamous or promiscuous species, juvenile males were the predominant dispersers. In monogamous species, competition for mates should be shared equally between sexes. Juveniles should disperse without sex bias. Of 12 mammalian species



examined, 11 were listed as having no sex bias in dispersal. Beaver were included among the monogamous species in which sexes were thought to disperse equally.

Dobson's (1982) analysis listed the beaver as being likely to exhibit no sex bias in dispersal, and the study on Ames Plantation seemed to support this hypothesis. Yet, it is surprising that actual numbers of males and females removed during the course of the study were not more closely aligned. One reason for the observed difference may be that there are more males than females at young ages (Hammond 1943; Osborn 1953; Bergerud and Miller 1977). Also, studies have shown that males are more prone to move than females and males spend more time away from the home colony (Leege 1968; Townsend 1953).

Greenwood's (1980) hypothesis predicts male-biased dispersal for a resource defender like the beaver. In the Ames Plantation study "pioneer" males were removed soon after settling in. By removing the resource defender and freeing available habitat, a sex biased trap may have been "baited."

Dispersal phenomena as they relate to isolated control programs are likely to be related to the genetic and behavioral factors which influence the evolution of mating systems. Mating systems can also be correlated with environmental factors (Emlen and Oring 1977). A complete



understanding of the driving forces and population interactions which drive these mechanisms may prove critical in the conception of effective management strategies. Beaver control is possible. However, immigration into an isolated control area will be likely and will vary over the course of a year in agreement with evolutionary mechanisms tied to environmental and population stresses as well as mating systems.

Over 89% of all immigrants into the study area were in the 3-4 age class or less (Fig. 9). Most wildlife populations are heavily skewed toward younger classes. Also, young adult beaver are more likely to move (Leege 1969; Beer 1955); however, the fact that 22.5% of all immigrants had not reached their first birthday was unexpected. It was presumed that individuals less than 1 year of age would stay close to familiar natal surroundings.

In this study, kits were often removed from colony sites where adults, presumably the parents, were also present. Such instances may have been the result of immigrating, pregnant females which gave birth on site. In other cases adults may have arrived with kits in tow (Bergerud and Miller 1977). In an Ohio study (Svendsen 1989) stream-living beaver were much more likely to disperse to a new site than were those living in more stable habitats, such as a lake. Therefore, the Ames Plantation

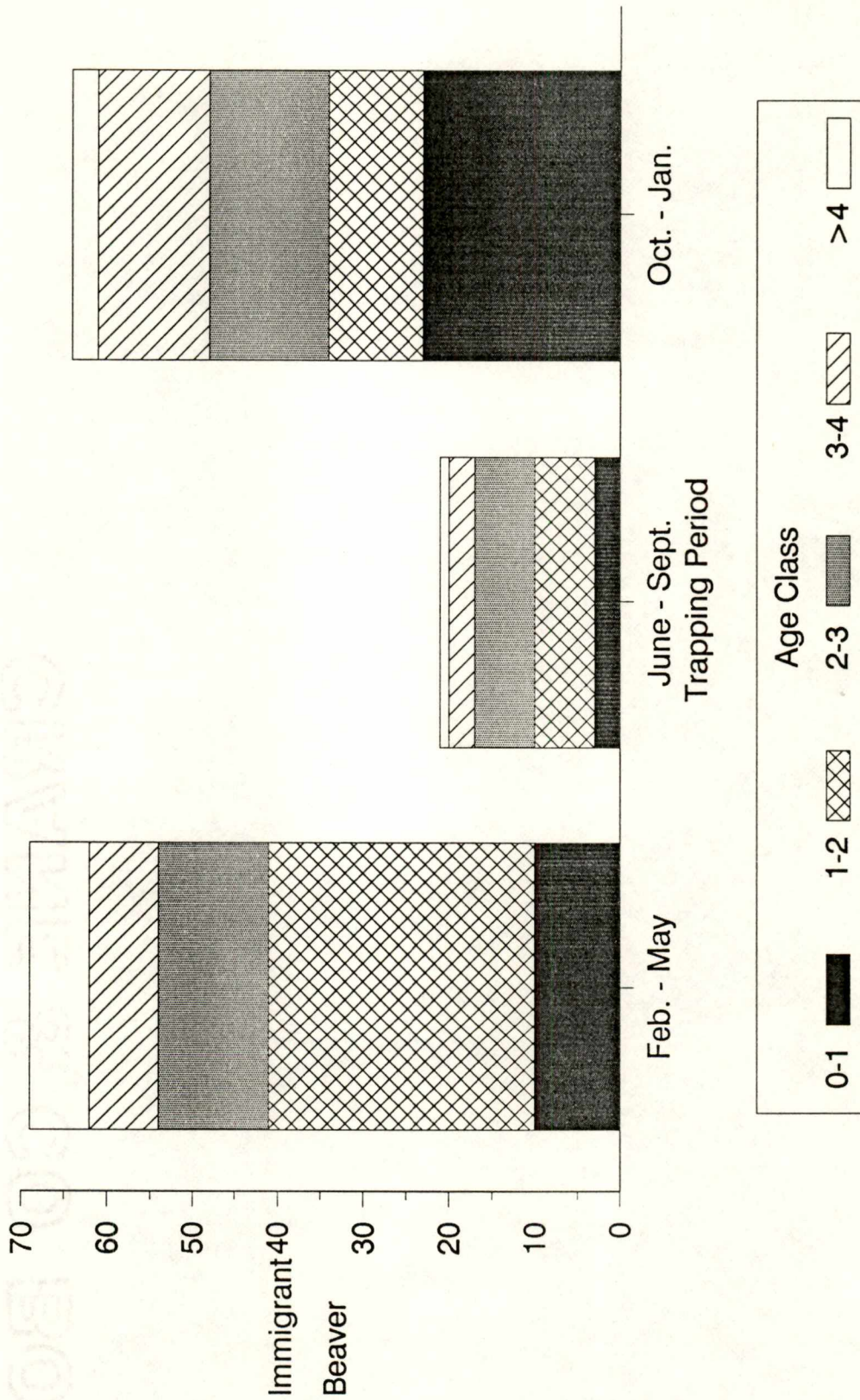


Figure 9. Total number of beaver immigrating into the Ames Plantation Study Area, Fayette County, West Tennessee, by age class and 4-month trapping period from 1 June 1985 through 30 September 1988.

river population probably contributed mated pairs and related juveniles on occasion.

Kits caught from July to December were often unaccompanied by adults and attempted to colonize in rudimentary fashion. Although dams were often partially repaired, residence at the colony site tended to be erratic, giving the impression these individuals were simply "exploring" (Bergerud and Miller 1977). It is probable that these individuals were offspring of the transient river population or downriver colonies not included in the study. It is doubtful that such episodes represented true recolonization attempts, although where dam repair was successful the impact on growing timber was detrimental.

The results of the study on Ames Plantation argue against the use of a "bounty system" to control beaver on a small watershed. From November 1984 through May 1985 beaver populations were removed from the study area. During the first month 70 beaver were removed. Under a bounty system, this would probably represent an adequate economic reward to a bounty trapper. However, catch totals were halved during the following month. During the third month the catch total was only 14 beaver. Quickly diminishing returns would force a bounty trapper to abandon control efforts.

Also, in the Ames study older individuals at each colony site tended to be caught first (Hogdon 1978).



Removal of either or both adult has been shown to stimulate sexual activity in remaining yearlings (Brooks et al. 1980). Recruitment within the residual population, along with immigration, would replenish beaver populations by the following year. Therefore, even if the trapper had persisted through the second month, little in the way of effective control would have been accomplished, particularly as relates to the protection of specific resources. Residual populations would have repaired and maintained dams; therefore, the land would have remained inundated and timber resources would have remained in jeopardy.

The Ames Plantation study also demonstrated that persistent trapping can extirpate beaver populations. In the face of sustained and sufficient economic pressures applied over large regions (e.g., greatly inflated pelt prices) beaver populations may require careful management to prevent over exploitation.

#### Plantation Establishment

Land clearing often represents the single most expensive aspect of planting hardwoods. Where lands have already been cleared, such as on abandoned agricultural fields, artificial regeneration gains certain advantages over natural regeneration. These include better control of species, stocking, and genetic composition of the ensuing

stand. Beaver impoundments represent highly productive, naturally cleared land where inundation has removed competing hardwoods; however, this is counterbalanced by costs associated with beaver control.

Based on third year growth and survival data, this study suggests that adequately stocked stands of sycamore, green ash, and baldcypress can be successfully established on drained beaver impoundments. Several studies have documented the ability of these species to tolerate flooding and saturated soils (Hosner and Boyce 1962; Fowells 1965; Loucks 1973; McKnight et al. 1981) Height growth after three growing seasons for green ash (25 dm), sycamore (31 dm), and baldcypress (15 dm) was encouraging when compared to other documented plantings. (Silker 1948; Klawitter 1961; Krinard and Johnson 1981; Waldrop et al. 1982; Kennedy 1983; Krinard and Kennedy 1983; Conner and Toliver 1990).

Examination of natural regeneration 3 years after draining beaver impoundments at Ames Plantation suggests that early successional stages are likely to develop slowly and be composed primarily of low commercial value hardwoods. The major early successional species in this study were willow and boxelder, with a very small component of cherrybark oak. Boxelder represented more stems per acre than black willow; however, black willow clumps tended to be relatively large and predominated where they occurred.



Stocking was about 978 stems per ha, with only 5.3% of the total comprised of desirable species.

It is probable that early successional tree species that are generally of low commercial value will impede establishment of later successional stages which tend to be comprised of higher value species. Initial stocking will tend to be erratic. Some sites may stagnate in an arrested willow stage for significant intervals (Rushton 1983). The results of this study suggest that reforestation of beaver killed sites with planted bottomland hardwoods seems to be a more attractive alternative.

Because beaver control costs must be considered a necessary part of timber management on these sites, it is important to produce high value stands in the shortest possible time. In turn, a developing resource provides incentive and focus for control programs.

The loss of swamp white oak and willow oak in this study does not preclude their potential on these sites. Their loss can better be explained by the use of poor seedlings developed in a single winter in the greenhouse. Mullins and Buckner (1987) reported that white and red oak seedlings produced over winter in the greenhouse can produce a plantable seedling, but additional time must be allowed to improve handling characteristics and survival. A dictum of large companies experienced in hardwood plantation



establishment is the need for large planting stock to insure success (Malac and Hereen 1979). Large bare root or containerized bottomland oak seedlings should perform well on these sites.

The significantly higher survival of green ash, sycamore, baldcypress, and swamp white oak at the end of the first growing season in herbicide treatments may be related to the interval after the grass had died and before broadleaf weeds were firmly established. In this short and critical time period the young seedlings grew essentially competition free. Also, by preventing development of the grass component, "matting" (discussed below) was avoided in the critical first year. The failure of green ash, sycamore, and cypress to maintain a survival advantage in herbicide treatments after three growing seasons may be related to several factors.

The ability of cut grass to affect growth and survival of planted seedlings is twofold. First, cut grass can draw critical moisture and nutrients away from the seedling or produce intolerable shade. Second, cut grass can physically drag a seedling down by forming a "mat" over it.

Moisture and nutrients were not severely limiting factors for survival and growth of firmly established seedlings on the study area. Thriving forest stands adjacent to drained impoundments illustrated the rich

potential of these sites prior to inundation; and accumulation of detrital materials during inundation provided an additional source of nutrients (Hodkinson 1975a). Following drainage, the water table remained near the surface and moisture was readily available throughout the growing season.

After first frost swamp cut grass died back and matted over smaller seedlings. The effect was exacerbated by periods of high water and associated floating debris that pushed the mat down more firmly. Some seedlings were buried and unable to escape this matting effect. The slender, slow growing oaks and baldcypress were particularly vulnerable, although baldcypress seemed better able to survive under the mat. Baldcypress can survive moderate amounts of shade (Conner and Toliver 1990). Willow oak is intolerant to shading (Fowells 1965; McKnight et al. 1981). Therefore, grass control early in the life of the stand might prove beneficial to small or slow growing seedlings.

Swamp cut grass proved to be very intolerant to shade. Once partial crown closure within the plantation was accomplished, it quickly began to disappear. Therefore, if a seedling could withstand matting, its chances of survival may not have been unduly compromised by having to compete with swamp cut grass in an otherwise rich environment.

Decrease in the grass component on herbicide treatments was accompanied by an associated invasion of broadleaf weeds. At the end of the first growing season broadleaf herbaceous species averaged nearly 2 meters tall whereas grass species on untreated areas averaged only about 1 meter tall. Therefore, seedlings freed from swamp cut grass competition were eventually forced to compete in the shade of aggressively invading broadleaves that quickly outgrew them in height. This shading effect would be greater in the second and third growing seasons after broadleaf weeds were well established.

The significant increase in dry weight of grasses where broadleaf weeds were most abundant is largely attributable to areas containing broadleaved species such as pokeberry (Phytolacca americana), which had massive stems, but produced insufficient shade to prevent grasses from reestablishing.

A real potential for damage to seedlings on these sites is mechanical injury during episodes of high water (Loucks 1987). Flooding during the spring of 1989 transported onsite materials at both locations, producing logjams in what appeared to be a nonrandom manner. Logs were often piled on better stocked subplots due to the ability of these areas to produce significant initial resistance to the movement of debris. As a result survival figures may be somewhat biased



against species and treatments exhibiting superior growth and survival. However, flooding is to be expected on these sites; and the general success of the plantations on Ames Plantation speaks well for the ability of artificial regeneration to tolerate this factor.

The close spacing of seedlings established in this study was chosen mainly to conserve space, but in retrospect may prove to be a desirable management option. Moisture is commonly over abundant on these sites. Increasing the number of stems increases transpiration. It is possible that stands established at a relatively close spacing may actually benefit from competition for moisture. Also, a close spacing produces early crown closure, inhibiting herbaceous competitors.

Although the results of the Ames Plantation study suggest that well stocked stands can be established without herbaceous weed control, this may not always prove true for specific species and site combinations. Many herbicides will prove impractical or illegal on these sites due to the constraints imposed by an exposed water table. However, a close initial spacing and may insure the eventual success of a stand where herbicides cannot be used. Thinnings could be conducted to achieve proper stocking once crown closure is accomplished.

Beaver seemed to avoid sycamore, choosing instead to cut adjacent green ash plantings (Krinard and Johnson 1981). Although traditionally less valuable than many bottomland hardwoods, sycamore may become a more attractive alternative if proven to be less at risk to beaver damage.

Reforestation of beaver-kill sites is apparently feasible with planted hardwoods. However, the process will necessarily be limited to landowners with long term commitments to timber growing. Successful establishment of a plantation will be insufficient to insure success. Beaver control must be part of the process.

#### In Summary

A survey of landowner attitudes toward beaver damage and control in Arkansas reported that respondents often perceived control measures such as trapping to be largely ineffective (Wigley 1986), despite having been demonstrated successfully elsewhere (Hill 1976). Such responses probably represent unfamiliarity with successful techniques. Also, the average landowner generally can't differentiate between "initial populations" and "immigrants." The rapid return of immigrant beaver may explain the perception that trapping programs do not work. The landowner is left with unrealistic ideas that there must be "something better."

Effective beaver control will rarely prove to be a "one shot deal." Beaver move back.

Successful control programs must first pinpoint the resource they are designed to protect. The focus of the Ames Plantation study was not solely on the nuisance species. It was "focused on," and was "judged by" the protection afforded specific resources. By capturing beaver attempting to recolonize sites containing vigorous young plantations, control efforts were largely successful.

Wholesale trapping "aimed at all beaver," which lacks sustained economic incentive to greatly reduce or extirpate populations over large regions is, at best, a temporary solution (Peterson and Payne 1986) and will generally fail to protect specific timber resources. In addition, extirpation of any species from major portions of its range is socially unacceptable, which is as it should be. In the Ames Plantation study transients or beaver living in the main river system were generally not molested. Adjacent beaver populations remained high.

Beaver control and associated surveillance is labor intensive, expensive, and in the South where the cottonmouth moccasin (Agkistrodon pisivorous) is likely to be encountered, sometimes dangerous. However, costs of control should be borne largely by the party owning the land affected. This places the burden of decision for or against



control in the hands of those most likely to benefit. The landowner must make a decision based on objectives and anticipated marketplace conditions. Otherwise, local governments may be placed into a position of paying perpetual subsidies for timber management and beaver control in the bottomlands. The major role of government should be in educational efforts.

Control cooperatives are a possibility where affected landholdings are contiguous. This scheme would make control efforts generally more efficient and proportionally less expensive. As the Ames Plantation study demonstrated, practical control within any portion of a watershed could not be accomplished without the cooperation of all landowners impacted. Beavers do not recognize property boundaries.

Although the results of this study are highly encouraging, final judgement of the suitability of plantation management on sites created by draining beaver impoundments must await testing across a wide range of conditions. Even so, the information derived from this study is pertinent where timber management is the primary objective; and these principles are generally applicable to the reforestation of many thousands of acres currently impounded across the Southeast.

## CHAPTER VII

## CONCLUSIONS

Beaver Control

Three conclusions regarding immigration into the study area may be inferred:

1. Immigration, as measured by attempted recolonization, was seasonal. Immigration dropped significantly during the period June through September as opposed to the period October through May.
2. More than 89% of all immigrants were in the 3-4 year age class or younger. Average immigration from January through May tended to be largely comprised of individuals in the 2 year age class, which is consistent with assumptions of literature on the American beaver.
3. Although more males than females immigrated into the study area, the difference was not statistically significant.

Therefore, an isolated control program under similar circumstances might expect relatively large numbers immigrating from October through January and a decrease, but not cessation, of immigration June through September. Immigrants will be comprised largely of individuals in the

younger age classes with a preponderance in the 2 year age class. Although this study failed to establish statistical significance, more males than females might be expected in a vigorous control program where immigrants are removed within 1 month of recolonization.

#### Plantation Establishment

Three conclusions can be supported by this study:

1. Artificial regeneration of the sites created by draining beaver impoundments looks promising based on the growth and survival of baldcypress, green ash, and sycamore at three years of age. Good quality planting stock is necessary as was evidenced by the failure of poor containerized swamp white oak and willow oak seedlings.
2. Application of Fusilade 2000 during mid-May and late June of the first growing season effectively decreased grass competition and positively impacted survival of planted seedlings. The decrease in grass competition tended to be compensated by an associated increase in broadleaf herbaceous competition. Herbicide effects on planted seedlings were lost by the third year.
3. Natural hardwood regeneration was poorly stocked at the end of the first growing season and was largely



comprised of low value species. Artificial regeneration was more promising than natural succession.

Reforestation of drained beaver impoundments with planted hardwoods seems to be practical. Resultant stands will most likely be economically superior to those which establish naturally. Herbaceous competition control to establish successful stands may be unnecessary on these rich sites, although more work needs to be done in this area.

Perhaps the most important observation of the study is that isolated beaver control programs are likely to be perpetual so long as the control area lies near significant beaver populations. Immigration should be expected. Therefore, plantation establishment and subsequent management should consider beaver control as an integral and continuing part of the reclamation process.

## CHAPTER VIII

## RECOMMENDATIONS

Beaver Control

Recommendation 1. Future research on the beaver should examine dispersal in relatively undisturbed populations. Because beaver colonies are socially stable and geographically stationary through time, they provide excellent opportunities for observation. Also, this animal is tied to the waterways, and dispersal routes can be easily inferred. Specific attention should be focused on parental-offspring interactions as relates to dispersal (Hogdon 1978). Also, the role of territoriality and competition for mates as relates to dispersal should be examined (Johnson 1986).

Recommendation 2. Using the broad framework of "mating system" as a foundation, it would be important to document the existence or absence of a sex bias in dispersal patterns for the beaver, a social and monogamous mammal known to defend a resource.

These two objectives could be attained by live-trapping and marking all beaver in several relatively undisturbed colonies. Marking could be accomplished using 2 cm colored plastic ribbons for individual sight recognition (Hogdon and Larson 1973; Miller 1964). Miller (1964) reported that

these ribbons were carried by Newfoundland and Manitoba beaver for two full seasons. Parental-offspring interactions would be observed prior to and during dispersal from the natal colony. Radio telemetry would track dispersing individuals.

The underlying mechanisms that determine the evolution of mating systems have drawn much attention in recent years. Several broad-based models have been developed which suggest that dispersal patterns and nature of the pair bond are a consequence of the type of mating system. In a review of philopatry and dispersal of 69 mammalian species (Dobson 1982), only 42% of the studies were characterized as having quantitative data.

This research would not only shed light on the broad based theories regarding mating systems, but would have practical implications as well. Identification of the mechanisms which lead to predictable immigration into an isolated control program, would be useful in the formation of management programs that are effective. For example, if territoriality is a prime force in dispersal and resource partitioning then a better understanding of its role might aid control programs.



### Plantation Establishment

Recommendation 3. The plantings reported in this study should be reevaluated periodically to document their development. Eventually a thinning will need to be conducted in the plantings to maintain their development.

Recommendation 4. Other similar sites across the Southeast should be evaluated with planted hardwoods. Bottomland oaks should be included where possible.

Recommendation 5. Of particular interest would be to direct seed appropriate oak species on similar sites (Johnson 1981). If this technology is applicable to drained beaver-kill sites, then the potential to enrich subsequent regeneration with highly desirable oak species might prove attractive.

Recommendation 6. Exotics such as dawn redwood (Metasequoia glyptostroboides) may also have potential on these sites and should be tested.

Any discussion regarding successful artificial reforestation of bottomland tree species on these potentially wet sites must consider soil moisture regimes. Sites that cannot be adequately drained due to topography within the impoundment might prove unsuitable for the establishment of most indigenous bottomland species.

### Ecological Implications

Recommendation 7. The positive ecological aspects of beaver colony sites need to be quantified.

Unless unforeseeable circumstances deem otherwise, beaver populations in the Southeast are permanent. On many ownerships timber resources have been replaced by thriving beaver colonies. What may be construed as a short term economic bane in many circumstances may also be a long term ecologic boon. The return of the beaver represents one of the greatest natural impacts in the bottomland ecosystem of this century, providing a host of recreational, wildlife, and ecologic effects that are often positive.

Dispersion of beaver colonies across the landscape seems to be under partial control of behavioral traits tied directly to mating system and nature of the pair bond. The scientific community has become increasingly aware of the need for larger measures of organization, allowing comparison of communities (Kikkawa 1986) or insight into the conception of communities. Study of the beaver and the beaver's impact on the bottomland system (Naiman et al. 1986) may provide insight to these questions.

LITERATURE CITED



## LITERATURE CITED

- Aleksiuk, M. 1969. Scent-mound communication, territoriality, and population regulation in beaver (Castor canadensis Kuhl.). J. Mammal. 49:759-762.
- Arner, D. H. 1964. Research and practical approach needed in management of beaver and beaver habitat in the Southeastern United States. Trans. North Am. Wildl. Conf. 29:150-158.
- \_\_\_\_\_, J. S. Dubose. 1979. The impact of the beaver on the environment and economics in the Southeastern United States. pp. 241-247. Proc. XIV International Wildl. Congress
- Baker, J. B. 1977. Tolerance of planted hardwoods to spring flooding. S. J. Appl. For. (3):23-25.
- Barkalow, F. S. 1949. A game inventory of Alabama. Bull. No. 18. La. Dept. Of Conserv., New Orleans, LA. 444 pp.
- Barnes, W. J., and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Can. J. Bot. 66:40-44.
- Barret, J. W. 1980. The Southern Hardwood Region. pp. 145-230. In: J. W. Barrett (ed.), Regional silviculture of the United States, 2nd ed. John Wiley and Sons, New York.
- Beer, J. R. 1955. Movements of tagged beaver. J. Wildl. Manage. 19: 492-493.
- Bergerud, A. T., and Miller, D. R. 1977. Population dynamics of Newfoundland beaver. Can. J. Zool. 55:1480-1492.
- Beshears, W. W. 1967. Status of the beaver in Alabama, pp. 2-6. In: Proc. First Alabama Beaver Symposium. p. 2-6. Game and Fish Div., Ala. Dept. of Conserv.
- Bowersox, T. W., and L. H. McCormick. 1987. Herbaceous communities reduce juvenile growth of northern red oak, white ash, yellow poplar, but not white pine. Proc. Sixth Cent. Hardwood For. Conf. pp. 39-44. Knoxville, TN, February 24-26, 1987.
- Bradt, G. W. 1938. A study of beaver colonies in Michigan. J. Mammal. 19:139-162.

- \_\_\_\_\_. 1947. Michigan beaver management. Michigan Dept. Conser. Game Div. 56 pp.
- Brenner, F. J. 1962. Foods consumed by beavers in Crawford County, Pennsylvania. J. Wildl. Manage. (26)1:104-107.
- Brinson, M. M., B. L. Swift, R. C. Plantico, and J. C. Barclay. 1981. Riparian ecosystems: their ecology and status. FWS/OBS-81/17.
- Briscoe, C. B. 1969. Establishment and early care of sycamore plantations. Res. Note SO-50. New Orleans, LA: U.S. Dept. of Agric., For. Serv., Sou. For. Exp. Sta. 1969. 18 pp.
- \_\_\_\_\_. 1973. Extended planting seasons for sycamore and cottonwood. USDA For. Serv. Res. Note SO-160. Sou. For. Exp. Sta., New Orleans, LA. 3 pp.
- Broadfoot, W. M., and H. L. Williston. 1973. Flooding effects on southern forests. J. Forestry 71(9):584-587.
- \_\_\_\_\_. 1976. Hardwood suitability for and properties of important Midsouth soils. U.S. Dept. Agric., For. Ser., Res. Paper SO-127, Sou. For. Exp. Stn., New Orleans, LA. 84 pp.
- Brooks, R. P., M. W. Fleming, and J. K. Kennelly. 1980. Beaver colony response to fertility control: Evaluating a concept. J. Wildl. Manage. 44(3):568-575.
- Brown, M. K., and Parson, G. 1979. Reliability of fall aerial censuses in locating active beaver colonies in northern New York. Proc. Northeast Fish and Wildl. Conf.
- Bullock, J. F., and D. H. Arner. 1985. Beaver damage to nonimpounded timber in Mississippi. S. J. Appl. For. 9(3):137-140.
- Burton, M., and R. Burton (eds.). 1969. Beavers. In: International Wildlife Encyclopedia, Marshall Cavendish Corp., New York 2:175-179.
- Busher, P. E., R. J. Warner, and S. H. Jenkins. 1983. Population density, colony composition, and local movements in two Sierra Nevadan beaver populations. J. Mammal. (64)2:226-241.



- Byford, J. L. 1981. Beaver management in North America. University of Tennessee. Department of Forestry, Wildlife, and Fisheries. Report to Southern Forest Experiment Station. 170 pp.
- Byrnes, W. R., J. E. Krajicek, and J. R. Wichman. 1973. Weed control, pp. 42-48. In: Black walnut as a crop. U.S. Dept. of Agric., For. Ser., Gen Tech. Rep. NC-4. St. Paul, MN.
- Cahn, A. R. 1932. Records and distribution of the fossil beaver, Castoroides ohioensis. J. Mammal. 13:229-241.
- Cook, D. B. 1943. History of a beaver colony. J. Mammal. 24(1):12-18.
- Cook, F. A. 1965. Fur resources of Mississippi. Bull. Miss. State Game and Fish Comm. 100 pp.
- Chabreck, R. H. 1959. Beaver-forest relationship in St. Tammany Parish, Louisiana. J. Wildl. Manage. 22:179-183.
- Conner, W. H., and J. R. Toliver. 1990. Observations on the Regeneration of Baldcypress (Taxodium distichum L. Rich.) in Louisiana Swamps. S. J. Appl. For. 14(3):115-118.
- Cox, W. T. 1940. The beaver-friend of the forest. Am. For. 46(10):448-450.
- Davis, D. E. 1961. Principles for population control by gametocides. Trans. North Am. Wildl. Conf. 26:160-167.
- Davis, D. E., J. J. Christian, and F. Bronson. 1964. Effect of exploitation on birth, mortality, and movement rates in a woodchuck population. J. Wildl. Manage. 28:1-9.
- Denny, R. N. 1952. A summary of North American beaver management, 1946-1948. Colo. Game and Fish Dept., Current Report No. 28. 58 pp.
- Dobson, F. S. 1981. An experimental examination of an artifical dispersal sink. J. Mammal. 62(1):74-81.
- \_\_\_\_\_. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Anim. Behav. 30:1183-1193.



- Easter-Pilcher, A. 1990. Cache size as an index to beaver colony size in northwestern Montana. *Wildl. Soc. Bull.* 18:110-113.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215.
- Erickson, A. B. 1939. Beaver populations in Pine County, Minnesota. *J. Mammal.* 20(2):195-201.
- Flowers, R. L. 1960. Soil Survey of Fayette County, Tennessee. U.S. Dept of Agric., Soil Cons. Ser. Series 1960 No. 13.
- Fowells, H. A. (ed.). 1965. Silvics of forest trees of the United States. U.S. Dept. Agric. Handbook No. 271. Washington, DC. 762 pp.
- Fredrickson, L. H. 1979. Floral and faunal changes in lowland hardwood forests in Missouri resulting from channelization, drainage, and impoundment. U.S. Fish and Wildl. Serv. FWS/OBS-78/91. 130 pp.
- Gaines, M. S., A. M. Vivias, and C. L. Baker. 1979. An experimental analysis of dispersal in fluctuating vole populations: demographic parameters. *Ecology* 60:814-828.
- Garrison, G. C. 1967. Pollen stratigraphy and age of an early post-glacier beaver site near Columbus, Ohio. *Ohio Journal of Science* 67:96-105.
- Gilmore, A. R., and G. L. Rolfe. 1984. Effects of past agriculture practice on height growth of planted sweetgum after twenty-one years. University of Illinois Forestry Report No. 84-3. 3 pp.
- Godbee, J., and T. Price. 1975. Beaver damage survey. Georgia Forestry Commission. 24 pp.
- Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Anim. Behav.* 28:1140-1162.
- Gunson, G. C. 1967. Pollen stratigraphy and age of an early post-glacial beaver site near Columbus, Ohio. *Ohio J. Sci.* 67:96-105.

- Hall R., and K. R. Kelson. 1959. The mammals of North America. pp. 547-551. The Ronald Press Company. New York.
- Hartman, A. M. 1975. Analysis of conditions leading to the regulation of water flow by a beaver. Psychol. Rec. 25(3): 427-432.
- Hammond, M. C. 1943. Beaver on the Lower Souris Refuge. J. Wildl. Manage. 7(3):316-321.
- Hatt, R. T. 1944. A large beaver-felled tree. J. Mammal. 25(3): 315.
- Hay, K. G. 1958. Beaver census methods in the Rocky Mountain region. J. Wildl. Manage. 22:395-401.
- Haynes, R. J., and L. Moore. 1987. Reestablishment of bottomland hardwoods within national wildlife refuges in the southwest, pp. 95-103. In: Increasing our Wetland Resources, Proc.: Nat. Wildl. Fed.-Corp. Conser. Coun., Washington, DC.
- Hibbard, E. A. 1958. Movements of beaver transplanted in North Dakota. J. Wildl. Manage. 22(2):209-221.
- Hilfiker, E. L. 1968. Did you ever wonder-what do beavers eat? Pa. Game News 39(8):12-15.
- Hill, E. P. 1976. Control methods for nuisance beaver in the southeastern United States. Vert. Pest Control Conf. 7:86-98.
- Hill, E. P. 1982. Beaver, pp. 256-281. In: J. A. Chapman and G. A. Foldhammer (eds.), Wild animals of North America, biology, management, and economics. Johns Hopkins Press, Baltimore, MD.
- Hill, E. P., D. N. Lasher, and R. B. Roper. 1977. A review of techniques for minimizing beaver and white-tailed deer damage in southern hardwoods. Proc. Second Symp. Southern Hardwood, pp. 79-93. U.S. For. Ser. Southeast Region.
- Hodkinson, I. D. 1975a. Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem. J. Ecol. 63(1):131-142.



- \_\_\_\_\_. 1975b. Energy flow and organic matter decomposition in a beaver pond ecosystem. *Oecologia* 21(2):131-139.
- Hogdon, H. E. 1978. Social dynamics and behavior within an unexploited beaver (Castor canadensis) population. Ph.D. Dissertation, Univ. Massachusetts, Amherst. 292 pp.
- Hogdon, H. E., and J. S. Larson. 1973. Some sexual differences in behavior with a colony of marked beavers (Castor canadensis). *Anim. Behav.* 21:147-152.
- Hosner, J. F., and S. G. Boyce. 1962. Tolerance to water saturated soil of various bottomland hardwoods. *For. Science* 8(2):187-186.
- Houston, A. E., and E. R. Buckner. 1989. Cultural treatments for the establishment of bottomland hardwoods in West Tennessee. In: Proc. Fifth Biennial Sou. Silvi. Res. Conf. 1988 Nov. 1-3; Memphis, TN. Gen. Tech. Rep. SO-74. New Orleans, LA, U.S. Dept. of Agric., For. Ser., Sou. For. Exp. Sta. 618 pp.
- Houston, A. E., R. Henry, and E. R. Buckner. 1987. Reforestation of beaver-kill sites with planted hardwoods. Proc. Central Hardwood For. Conf. VI., February 24-26, 1987. Univ. Tenn., Knoxville, TN. 526 pp.
- Hunt, R. 1976. Commercial hardwood planting. Hardwood Short Course. pp. 63-67. School of Forest Resources, NC. State Univ., Raleigh, NC.
- Jenkins, S. H. 1975. Food selection by beavers: A multi-dimensional contingency table analysis. *Oecologia* 21:157-173.
- \_\_\_\_\_. 1979. Seasonal and year to year differences in food selection by beavers (Castor canadensis). *Oecologia* 44(1): 112-116.
- \_\_\_\_\_. 1980. A size distance relationship in food selection by beavers (Castor canadensis). *Ecology* 61(4):740-746.
- Jenkins, S. H., and P. E. Busher. 1979 Castor canadensis. *Mammal. Species* 120:8.
- Johnson, C. N. 1986. Sex-biased philoptry and dispersal in mammals. *Oecologia* 69:626-627.



- Johnson, R. L. 1981. Oak seeding—it can work. S. J. Appl. For. 5(1):28-33.
- Joule, J. J., and G. N. Cameron. 1975. Species removal studies. In: Dispersal strategies of sympatric Sigmodon hispidus and Reithrodontomys fulvescens populations. J. Mammal. 56:378-396.
- Kennedy, H. E., Jr. 1981. Bottomland hardwoods research on site preparation, plantation establishment, and cultural treatments at the southern hardwoods laboratory. For. Ser., Gen. Tech. Rep. SO-34, pp. 75-78. Sou. For. Exp. Sta.
- Kennedy, H. E., Jr., and R. M. Krinard. 1985. Shumard oaks successfully planted on high pH soils. Res. Note SO-321. New Orleans, LA: U.S. Dept. of Agric., For. Ser., Sou. For. Exp. Sta. 3 pp.
- Kikkawa, J. 1986. Complexity, diversity, and stability, pp. 19-29. In: J. Kikkawa and D. J. Anderson (eds.), Community ecology: Pattern and process. Blackwell Scientific Publications, Palo Alto, CA.
- Kleiman, D. G. 1977. Monogamy in mammals. Q. Rev. Bio. 52: 39-69.
- Knudsen, G. J., and J. B. Hale. 1965. Movements of transplanted beavers in Wisconsin. J. Wildl. Manage. 29(4):685-688.
- Krinard, R. M., and R. L. Johnson. 1981. Flooding, beavers, and hardwood seedling survival. Res. Note SO-270. New Orleans, LA: U.S. Dept. of Agric., For. Ser., Sou. For. Exp. Sta. 6 pp.
- Krinard, R. M., and H. E. Kennedy. 1983. Ten-year growth of five planted hardwood species with mechanical weed control on Sharkey clay soil. Res. Note SO-303. New Orleans, LA: U.S. Dept. of Agric., For. Ser., Sou. For. Exp. Sta. 4 pp.
- \_\_\_\_\_. 1987. Fifteen-year growth of six planted hardwood species on Sharkey Clay Soil. Res. Note SO-336. New Orleans, LA: U.S. Dept. of Agric., For. Ser., Sou. For. Exp. Sta. 4 pp.

- Langdon, O. G., J. P. McClure, D. D. Hook, J. M. Crocket, and R. Hunt. 1981. Extent, condition, management, and research needs of bottomland hardwood-cypress forests in the Southeast, pp. 225-273. In: J. K. Clark and J. Benforado, eds.), Wetlands of bottomland hardwood forests. Elsevier Scientific Publ. Co., New York.
- Larson, J. S. 1967. Age structure and sexual maturity within a western Maryland beaver (Castor canadensis) population. J. Mammal. 48:408-413.
- Larson, J. S., and F. C. van Nostrand. 1968. An evaluation of beaver aging techniques. J. Wildl. Manage. 29(4):685-688.
- Leege, T. A. 1968. Natural movements of beavers in southeastern Idaho. J. Wildl. Manage. 32(4):973-976.
- Libby, W. L. 1957. Observations on beaver in Alaska. J. Mammal. 38(2):269.
- Liddicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals, pp. 103-128. In: F. B. Golley, K. Petrusewicz, and L. Ryszkowski (eds.), Small mammals: Their productivity and population dynamics. Cambridge Univ. Press, London. 451 pp.
- Loucks, W. L. 1987. Flood-tolerant trees. J. For. 85:37-40.
- Loucks, W. L., and R. A. Keen. 1973. Submersion tolerance of selected seedling trees. J. For. 71:496-497.
- Malac, B. F., and R. D. Heeren. 1979. Hardwood plantation management. S. J. Appl. For. 3(1):3-6.
- McCormack, M. C. 1981. Chemical weed control in northeastern forests, pp. 108-115. In: Proc. John S. Wright For. Conf., Forest Weed Control, p. 108-115. Purdue Univ., West Lafayette, IN.
- McKnight, J. S., D. D. Hook, O. G. Langdon, and R. S. Johnson. 1981. Occurrence, shade and flood tolerance, and reproductive characteristics of the principle species of the southern bottomland forest, pp. 45-69. In: J. R. Clark and J. Benfordo (eds.), Wetlands of bottmland forests. Elsevier Publ. Co., New York.
- Miller, D. R. 1964. Colored plastic ear tags for beavers. J. Wildl. Manage. 28(4):859-861.



- Miller, J. E. 1986. Assessment of wildlife damage on southern forests. Paper presented at the Soc. of Am. For. Annual Meet., Wildl. and Fish Ecol. Work. Group, Tech. Session, Birmingham, Alabama, October 5-9, 1986.
- Miller, J. H. 1987. The use of herbicides in hardwood forestry, pp. 31-50. In: Proceedings Fifteenth Annual Hardwood Symposium, Memphis, TN.
- Milne, L., and M. Milne. 1960. The Balance of Nature. Alfred A. Knopf Inc., New York.
- Moore, G. C., and E. C. Martin. 1949. Status of beaver in Alabama. Alabama Dept. of Conserv. 30 pp.
- Myers, J. H., and C. J. Jrebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles Microtus pennsylvanicus and Microtus ochrogaster. Ecol. Monogr. 41:53-76.
- Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (Castor canadensis). Ecology 67(5):1254-1269.
- Northcott, T. H. A. 1964. An investigation of the factors affecting carrying capacity of selected areas in Newfoundland for beaver (Castor canadensis caecator Bangs.). M.S. thesis, Memorial University, St. Johns, Newfoundland. 133 pp.
- Osborn D. J. 1953. Age classes, reproduction and sex ratios of Wyoming beaver. J. Mammal. 34:27-44.
- Parmalee, P. W., A. E. Gogan, and J. E. Guilday. 1976. First records of the giant beavers Castoroides ohioensis. New record from eastern Tennessee. J. Tenn. Acad. Sci. 51(3):87-88.
- Parson, G. R., and M. K. Brown. 1978. An assessment of aerial photography interpretation for recognizing potential beaver colony sites. Tran. Northeast Fish and Wildl. Conf. 35:181-184.
- Patrick, E., and W. L. Webb. 1954. A preliminary report on intensive beaver management. J. For. 52:31-32.
- Payne, N. F. 1975. Trapline management and population biology of Newfoundland beaver. Ph.D. Dissertation, Utah State Univ., Logan. 178 pp.



- Penny, J. T. 1949. Distribution and bibliography of mammals of South Carolina. *J. Mammal.* 31(1):81-89.
- Petersen, R. P., and N. F. Payne. 1986. Productivity, size, age, and sex structure of nuisance colonies in Wisconsin. *J. Wildl. Manage.* 50(2):265-268.
- Ponder, F., Jr. 1987. Effect of weed control on early growth and survival of planted black walnut in a forest clearcut, pp. 63-68. *Proc. Sixth Central Hardwood Forest Conference, Knoxville, TN, February 24-26, 1987.*
- Post, H. A., and A. A. de la Cruz. 1977. Litterfall, litter composition, and flux of particulate organic material in a Coastal Plain stream. *Hydrobiologia* 55(3):201-208.
- Rich, M. F. 1989. Planting loblolly pine and sycamore vs. natural regeneration on a bottomland site. *S. J. Appl. For.* 13:22-24.
- Rue, L. L., III. 1969. Beaver, pp. 586-593. *In: Hall Borland (ed.), Our natural world.* J. B. Lippincott Company, Philadelphia and New York.
- Ruedemann, R., and W. J. Schoonmaker. 1938. Beaver dams as geologic agents. *Science* 88(2292):523-525.
- Rushton, B. 1983. Examples of natural wetland succession as a reclamation alternative, pp. 148-189. *In: D. J. Robertson (ed.), Reclamation and the phosphate industry.* *Proc. of a symposium; 26-28 January, 1983, Clearwater Beach, Fl., Florida Institute of Phosphate Research, Bartow.*
- SAS. 1985. *SAS User's Guide: Statistics.* SAS Institute, Inc., Box 8000, Cary, NC. 955 pp.
- Saylor, J. C. 1946. The Carolina beaver: A vanishing species. *J. Mammal.* 27(4):331-335.
- Seifert, J. R., P. E. Pope, and B. C. Fisher. 1984. The effects of three levels of site preparation on planted swamp chestnut oak on a poorly drained site. *Southern Silvicultural Research Conference, Atlanta, Georgia, November 7-8, 1984.*
- Shadle, A. R., A. M. Nauth, E. E. Gese, and T. S. Austin. 1943. Comparison of tree cuttings of six beaver colonies in Allegany State Park, New York. *J. Mammal.* 24(1): 32-39.

- Shultz, V. 1954. Status of beaver and otter in Tennessee. J. Tenn. Acad. Sci. 29(1):73-81.
- Silker, T. H. 1948. Planting of water-tolerant trees along margins of fluctuating-level reservoirs. Iowa State College J. of Sci. 22(4):431-448.
- Smith, K. C. 1958. Beaver in Louisiana. Louisiana Wildl. and Fish. Commision, Fish and Game Division. 12 pp.
- Sternitzke, H. S. 1972. Bald cypress: Endangered or expanding species? Econ. Bot. 26:130-134.
- Svendson, G. E. 1980. Seasonal change in feeding patterns of beaver (Castor canadensis) in southeastern Ohio. J. Wildl. Manage. 44(1):285-290.
- \_\_\_\_\_. 1989. Pair formation, duration of pair bonds, and mate replacement in a population of beavers (Castor canadensis). Can. J. Zool. 67:336-340.
- Swank, W. G. 1949. Beaver ecology and management in West Virginia. Bull. No. 1. Div. of Game, Conserv. Comm. West Virginia. 65 pp.
- Tennessee Department of Conservation. 1980. West Tennessee bottomland hardwood impact survey. Tennessee Division of Forestry, Department Natural Resources, Nashville, TN. 62 pp.
- Teskey, R. O., and T. M. Hincley. 1977. Impact of water level changes on woody riparian and wetland communities. Vol. II: Southern forest region. FWS/OBS-77/59.
- Toliver, J. R., and B. D. Jackson. 1989. Recommended silvicultural practices in Southern wetland forests. Proc., The forested wetlands of the Southern United States; 1988 July 12-14: Orlando, Fl. Gen. Tech. Rep. SE-50. Asheville, NC: U.S. Dept. of Agric., For. Ser. 168 pp.
- Townsend, J. E. 1953. Beaver ecology in Western Montana with special refence to movements. J. Mammal. 34:459-479.
- U.S. Dep. of Agric., Soil Survey. Soil Conser. Ser. 1964. Fayette County Tennessee. Series 1960, No. 13. Washington, DC: U.S. Dept. of Agric.



- \_\_\_\_\_. For. Ser., Soil Conser. Ser. 1987. Watershed plan-environmental assessment North Fork Wolf river, Fayette and Hardeman counties, Tennessee. Interagency Draft, Nashville, TN., U.S. Dept. of Agric.
- van Nostrand, F. C., and A. B. Stephenson. 1964. Age determination for beavers by tooth development. J. Wildl. Manage. 28(3):430-434.
- Vehrencamp, S. L., and J. W. Bradbury. 1984. Mating systems and ecology. In: J. R. Krebs and N. B. Davies, (eds.), Behavioral ecology: An evolutionary approach. Sinauer, Sunderland, MA.
- Waldrop, T. A., E. R. Buckner, and A. E. Houston. 1982. Suitable trees for the bottomlands of West Tennessee. Proc. Second Biennial Southern Silvicultural Research Conference. November 4-5, 1982, Atlanta, GA, U.S. Dept. of Agric., For. Ser., Southeast. For. Exp. Sta., Asheville, NC. Gen. Tech. Rep. SE-24. 514 pp.
- Waser, P. M., and W. J. Jones. 1983. Natal philoptry among solitary mammals. Q. Rev. Biol. 58:355-390.
- Weaver, K. M., D. H. Arner, C. Mason, and J. Hartley. 1985. A guide to using snares for beaver capture. S. J. Appl. For. 9(3): 141-146.
- Wesley, D. E. 1978. Beaver control in the southeast United States, pp. 84-91. In: Proc. Sixth Annual Hardwood Symposium of the Hardwood Research Council, May 1978. Hardwood Research Council, Memphis, Tennessee.
- Wharton, C. H. 1977. The natural environments of Georgia. Georgia Geological Survey, Dept. of Natural Resources, Atlanta. 227 pp.
- Wharton, C. H., W. M. Kitchens, E. C. Pendleton, and T. W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: A community profile. FWS/OBS-81/37. March 1982.
- Wharton, C. H., V. W. Lambour, J. Newsom, P. V. Winger, L. L. Gaddy, and R. Mancke. 1981. The fauna of bottomland hardwoods in Southeastern United States, pp. 87-160. In: J. R. Clark and J. Benforado (eds.), Wetlands of bottomland hardwood forests. Elsevier Scientific Publishing Company, New York.
- Wigley, T. B., T. H. Roberts, and D. H. Arner. 1983. Reproductive characteristics of beaver in Mississippi. J. Wildl. Manage. 47(4):1172-1176.



- \_\_\_\_\_. 1986. Landowner estimates of and attitudes toward beaver damage in Arkansas. Project PR-W56-26. Study No. I-B-1. Ark. Agric. Exp. Sta. University of Arkansas, Monticello, AR. 22 pp.
- Wilsson, R. K. 1971. Observations and experiments on ethology of the European beaver (Castor fiber L.). Swedish Sportsmen's Assoc. 8:266.
- Windberg, L. A., and L. B. Keith. 1976. Experimental analysis of dispersal on snowshoe hare populations. Canadian J. Zool. 55: 2061-2081.
- Woodward, D. K. 1977. Status and ecology of the beaver (Castor canadensis carolinensis) in South Carolina with emphasis on the Piedmont. M.S. Thesis, Clemson Univ., Clemson, SC. 208 pp.
- Woodward, D. K., J. D. Hair, and B. P. Gaffney. 1976. Status of beaver in South Carolina as determined by a postal survey of landowners. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 30:448-454.
- Woodward, D. K., R. B. Hazel, and B. P. Gaffney. 1985. Economic and environmental impacts of beavers in North Carolina, pp. 89-96. Proc., Second Eastern Wildlife Damage Control Conf., Raleigh, NC.
- Wright, G. M., P. E. Pope, B. C. Fisher, H. A. Holt, and W. R. Byrnes. 1974. Chemical control to establish natural and artificial oak regeneration in a mechanically thinned upland hardwood stand, pp. 266-272. Proc. Southern Silvicultural Res. Conf., November, 1984, Atlanta, GA, U.S. Dept. of Agric., For. Ser., Southeast For. Exp. Sta., Asheville, NC.
- Wright, G. M., and H. A. Holt. 1985. Effects of chemical weed control on hardwood plantation establishment. Proc. North Central Weed Control Conf. 40:28.
- Zurowski, W., J. Kiza, Al Kruk, and A. Roskosz. 1974. Lactation and chemical composition of milk of the European beaver (Castor fiber L.). J. Mammal. 55:847-850.
- Zutter, B. R., L. R. Nelson, P. J. Minogue, and D. H. Gjerstad. 1986. Hardwood plantation growth following weed control using herbicides and cultivation. Auburn Univ. Silv. Herbicide Cooperative Res. Note No. 86-9. 10 pp.

APPENDIXES



## APPENDIX A

Acreage and percentage of live, dead, fading, and regenerated forestland in the west Tennessee bottomland hardwood forest and western portion of the Tennessee River basin bottomland hardwood forest in 1980 (Source: TDF 1980).

## West Tennessee Bottomland Forest

|       | Live    | Dead   | Fading | Total   |
|-------|---------|--------|--------|---------|
| Acres | 586,589 | 53,220 | 27,992 | 678,124 |

## Western Portion Tennessee River Basin

|       | Live    | Dead  | Fading | Total   |
|-------|---------|-------|--------|---------|
| Acres | 116,179 | 6,589 | 6,184  | 130,940 |

|       |         |        |        |         |
|-------|---------|--------|--------|---------|
| Total | 702,668 | 68,809 | 34,176 | 809,064 |
|-------|---------|--------|--------|---------|



## APPENDIX B

Sample plot design, artificial regeneration of baldcypress, green ash, swamp white oak, sycamore, and willow oak, on drained beaver impoundments, Ames Plantation, west Tennessee.

|               |               |                 |               |               |                 |
|---------------|---------------|-----------------|---------------|---------------|-----------------|
| 96 feet       |               |                 |               |               |                 |
| Green Ash     | Sycamore      | Control         | Willow Oak    | Cypress       | Swamp White Oak |
| Herbicide     | Herbicide     | Herbicide       | Herbicide     | Herbicide     | Herbicide       |
| 120 feet      |               |                 |               |               |                 |
| Non Herbicide | Non Herbicide | Non Herbicide   | Non Herbicide | Non Herbicide | Non Herbicide   |
| Cypress       | Control       | Swamp White Oak | Green Ash     | Sycamore      | Willow Oak      |

## APPENDIX C

List of major herbaceous vegetation on Location 1 and Location 2, drained beaver impoundments, Ames Plantation, west Tennessee, 3 years after drainage. Plants arranged in alphabetical order.

Agrostis sp.  
Ambrosia artemisiifolia  
Ambrosia trifida  
Aster sp.  
Bidens bipinnata  
Cicuta maculata  
Cuscuta gronovii  
Cyperus retrofractus  
Eupatorium coelestinum  
Hypernicum sp.  
Impatiens capensis  
Juncus effusus  
Leersia oryzoides  
Lonicera japonica  
Lycopus sp.  
Microstegium vimineum  
Mikania scandens  
Mimulus alatus  
Onoclea sensibilis  
Phytolacca americana  
Polygonum hydropiperoides  
Polygonum pennsylvanicum  
Polygonum punctatum  
Rosa palustris  
Rubellus sp.  
Sambucus canadensis  
Scirpus cyperinus  
Solidago rugosa  
Triandenum walterii

## APPENDIX D

Dry weight of grass and broadleaf herbaceous competition samples per location, replication, and herbicide treatment on drained beaver impoundments on Ames Plantation, west Tennessee.

| Location | Replication | Herbicide | Mil-Acre | -- Kilograms -- |           |
|----------|-------------|-----------|----------|-----------------|-----------|
|          |             |           |          | Grass           | Broadleaf |
| 1        | 1           | no        | 1        | 1.205           | 1.370     |
| 1        | 1           | no        | 2        | 0.725           | 2.010     |
| 1        | 1           | no        | 3        | 0.820           | 1.250     |
| 1        | 1           | yes       | 1        | 0.365           | 1.820     |
| 1        | 1           | yes       | 2        | 0.245           | 3.505     |
| 1        | 1           | yes       | 3        | 0.430           | 3.070     |
| 1        | 2           | no        | 1        | 0.975           | 2.225     |
| 1        | 2           | no        | 2        | 0.520           | 3.300     |
| 1        | 2           | no        | 3        | 0.305           | 2.775     |
| 1        | 2           | yes       | 1        | 0.525           | 3.325     |
| 1        | 2           | yes       | 2        | 0.270           | 3.150     |
| 1        | 2           | yes       | 3        | 0.320           | 2.145     |
| 1        | 3           | no        | 1        | 1.220           | 0.380     |
| 1        | 3           | no        | 2        | 1.440           | 0.525     |
| 1        | 3           | no        | 3        | 0.935           | 1.750     |
| 1        | 3           | yes       | 1        | 0.710           | 3.430     |
| 1        | 3           | yes       | 2        | 0.295           | 3.345     |
| 1        | 3           | yes       | 3        | 0.040           | 1.895     |
| 1        | 4           | no        | 1        | 0.245           | 4.110     |
| 1        | 4           | no        | 2        | 0.000           | 2.625     |
| 1        | 4           | no        | 3        | 0.360           | 2.875     |
| 1        | 4           | yes       | 1        | 0.850           | 1.200     |
| 1        | 4           | yes       | 2        | 0.545           | 1.345     |
| 1        | 4           | yes       | 3        | 0.460           | 1.260     |
| 2        | 1           | no        | 1        | 3.965           | 0.460     |
| 2        | 1           | no        | 2        | 3.240           | 0.510     |
| 2        | 1           | no        | 3        | 1.770           | 1.530     |
| 2        | 1           | yes       | 1        | 0.250           | 3.830     |
| 2        | 1           | yes       | 2        | 0.345           | 2.155     |
| 2        | 1           | yes       | 3        | 0.330           | 2.895     |
| 2        | 2           | no        | 1        | 3.655           | 1.040     |
| 2        | 2           | no        | 2        | 3.470           | 1.010     |
| 2        | 2           | no        | 3        | 2.820           | 0.820     |
| 2        | 2           | yes       | 1        | 0.390           | 2.490     |
| 2        | 2           | yes       | 2        | 0.340           | 2.000     |
| 2        | 2           | yes       | 3        | 0.300           | 2.175     |
| 2        | 3           | no        | 1        | 3.395           | 1.000     |
| 2        | 3           | no        | 2        | 0.675           | 3.630     |



| Location | Replication | Herbicide | Mil-Acre | -- Kilograms -- |           |
|----------|-------------|-----------|----------|-----------------|-----------|
|          |             |           |          | Grass           | Broadleaf |
| 2        | 3           | no        | 3        | 3.360           | 0.875     |
| 2        | 3           | yes       | 1        | 0.435           | 2.180     |
| 2        | 3           | yes       | 2        | 0.685           | 2.045     |
| 2        | 3           | yes       | 3        | 0.390           | 3.005     |
| 2        | 4           | no        | 1        | 1.470           | 0.920     |
| 2        | 4           | no        | 2        | 3.500           | 0.000     |
| 2        | 4           | no        | 3        | 3.180           | 0.380     |
| 2        | 4           | yes       | 1        | 0.330           | 1.420     |
| 2        | 4           | yes       | 2        | 0.745           | 1.295     |
| 2        | 4           | yes       | 3        | 0.460           | 1.265     |

## APPENDIX E

First Year Survival Means for Swamp White Oak(SWO), Baldcypress (CY), Sycamore (SY), and Green Ash (GA) per Location, Replication, and Herbicide Treatment (Herbicide = 1; No Herbicide = 0) on Drained Beaver Impoundments on the Ames Plantation Study Area.

| Loc. | Rep. | Herbicide | Species | % Survival |
|------|------|-----------|---------|------------|
| 1    | 1    | 0         | SWO     | 0.7667     |
| 1    | 1    | 0         | SY      | 0.7333     |
| 1    | 1    | 0         | CY      | 0.9167     |
| 1    | 1    | 0         | GA      | 0.9833     |
| 1    | 1    | 1         | SWO     | 0.7368     |
| 1    | 1    | 1         | SY      | 0.8936     |
| 1    | 1    | 1         | CY      | 0.9348     |
| 1    | 1    | 1         | GA      | 0.9821     |
| 1    | 2    | 0         | SWO     | 0.8000     |
| 1    | 2    | 0         | SY      | 0.9500     |
| 1    | 2    | 0         | CY      | 0.9167     |
| 1    | 2    | 0         | GA      | 0.9667     |
| 1    | 2    | 1         | SWO     | 0.7333     |
| 1    | 2    | 1         | SY      | 1.0000     |
| 1    | 2    | 1         | CY      | 0.9667     |
| 1    | 2    | 1         | GA      | 0.9500     |
| 1    | 3    | 0         | SWO     | 0.7167     |
| 1    | 3    | 0         | SY      | 1.0000     |
| 1    | 3    | 0         | CY      | 0.9167     |
| 1    | 3    | 0         | GA      | 0.9833     |
| 1    | 3    | 1         | SWO     | 0.8667     |
| 1    | 3    | 1         | SY      | 1.0000     |
| 1    | 3    | 1         | CY      | 0.9667     |
| 1    | 3    | 1         | GA      | 0.9500     |
| 1    | 4    | 0         | SWO     | 0.7833     |
| 1    | 4    | 0         | SY      | 1.0000     |
| 1    | 4    | 0         | CY      | 0.8500     |
| 1    | 4    | 0         | GA      | 0.9333     |
| 1    | 4    | 1         | SWO     | 0.9333     |
| 1    | 4    | 1         | SY      | 0.8667     |
| 1    | 4    | 1         | CY      | 0.9333     |
| 1    | 4    | 1         | GA      | 0.9500     |
| 2    | 1    | 0         | SWO     | 0.8000     |
| 2    | 1    | 0         | SY      | 0.9333     |
| 2    | 1    | 0         | CY      | 0.8667     |
| 2    | 1    | 0         | GA      | 1.0000     |
| 2    | 1    | 1         | SWO     | 0.8333     |
| 2    | 1    | 1         | SY      | 0.9833     |
| 2    | 1    | 1         | CY      | 1.0000     |

| Loc. | Rep. | Herbicide | Species | % Survival |
|------|------|-----------|---------|------------|
| 2    | 1    | 1         | GA      | 1.0000     |
| 2    | 2    | 0         | SWO     | 0.5833     |
| 2    | 2    | 0         | SY      | 0.9500     |
| 2    | 2    | 0         | CY      | 0.9833     |
| 2    | 2    | 0         | GA      | 1.0000     |
| 2    | 2    | 1         | SWO     | 0.7500     |
| 2    | 2    | 1         | SY      | 0.9833     |
| 2    | 2    | 1         | CY      | 1.0000     |
| 2    | 2    | 1         | GA      | 0.9833     |
| 2    | 3    | 0         | SWO     | 0.5500     |
| 2    | 3    | 0         | SY      | 0.9667     |
| 2    | 3    | 0         | CY      | 0.8500     |
| 2    | 3    | 0         | GA      | 1.0000     |
| 2    | 3    | 1         | SWO     | 0.7500     |
| 2    | 3    | 1         | SY      | 1.0000     |
| 2    | 3    | 1         | CY      | 0.9833     |
| 2    | 3    | 1         | GA      | 0.9833     |
| 2    | 4    | 0         | SWO     | 0.5333     |
| 2    | 4    | 0         | SY      | 0.5000     |
| 2    | 4    | 0         | CY      | 0.7000     |
| 2    | 4    | 0         | GA      | 1.0000     |
| 2    | 4    | 1         | SWO     | 0.7333     |
| 2    | 4    | 1         | SY      | 0.9333     |
| 2    | 4    | 1         | CY      | 0.9333     |
| 2    | 4    | 1         | GA      | 1.0000     |



## APPENDIX F

Third Year Total Height and Survival Means for Cypress (CY), Green Ash (GA), and Sycamore (SY) per Location, Replication, and Herbicide Treatment (Herbicide = 1; No Herbicide = 0) on Drained Beaver Impoundments on the Ames Plantation Study Area. Heights reported in centimeters. Survival Data Reported as Percent and with Angular Transformation (Sokal and Rohlf 1981).

| Loc. | Rep. | Herbicide | Species | Height | % Survival | Trans.Survival |
|------|------|-----------|---------|--------|------------|----------------|
| 1    | 1    | 0         | CY      | 157.08 | 0.8833     | 1.22221        |
| 1    | 1    | 0         | GA      | 219.02 | 0.9500     | 1.34528        |
| 1    | 1    | 0         | SY      | 331.45 | 0.7000     | 0.99116        |
| 1    | 1    | 1         | CY      | 136.03 | 0.6500     | 0.93774        |
| 1    | 1    | 1         | GA      | 229.28 | 0.8500     | 1.17310        |
| 1    | 1    | 1         | SY      | 239.07 | 0.6833     | 0.97311        |
| 1    | 2    | 0         | CY      | 150.78 | 0.9000     | 1.24905        |
| 1    | 2    | 0         | GA      | 265.44 | 0.9500     | 1.34528        |
| 1    | 2    | 0         | SY      | 307.06 | 0.9167     | 1.27795        |
| 1    | 2    | 1         | CY      | 140.04 | 0.8333     | 1.15026        |
| 1    | 2    | 1         | GA      | 242.30 | 0.8833     | 1.22221        |
| 1    | 2    | 1         | SY      | 324.81 | 0.8833     | 1.22221        |
| 1    | 3    | 0         | CY      | 128.21 | 0.7833     | 1.08993        |
| 1    | 3    | 0         | GA      | 249.83 | 0.9833     | 1.44134        |
| 1    | 3    | 0         | SY      | 336.41 | 0.8500     | 1.17310        |
| 1    | 3    | 1         | CY      | 132.88 | 0.8500     | 1.17310        |
| 1    | 3    | 1         | GA      | 224.94 | 0.9000     | 1.24905        |
| 1    | 3    | 1         | SY      | 384.00 | 0.9333     | 1.30964        |
| 1    | 4    | 0         | CY      | 108.33 | 0.6500     | 0.93774        |
| 1    | 4    | 0         | GA      | 199.96 | 0.7333     | 1.02816        |
| 1    | 4    | 0         | SY      | 313.67 | 0.9833     | 1.17310        |
| 1    | 4    | 1         | CY      | 133.00 | 0.7667     | 1.06667        |
| 1    | 4    | 1         | GA      | 263.78 | 0.9000     | 1.24905        |
| 1    | 4    | 1         | SY      | 288.34 | 0.7333     | 1.02816        |
|      |      |           |         |        |            |                |
| 2    | 1    | 0         | CY      | 151.31 | 0.5833     | 0.86912        |
| 2    | 1    | 0         | GA      | 302.17 | 0.9667     | 1.38719        |
| 2    | 1    | 0         | SY      | 429.11 | 0.9000     | 1.24905        |
| 2    | 1    | 1         | CY      | 218.15 | 0.9833     | 1.44134        |
| 2    | 1    | 1         | GA      | 319.18 | 1.0000     | 1.57080        |
| 2    | 1    | 1         | SY      | 390.77 | 0.9500     | 1.34528        |
| 2    | 2    | 0         | CY      | 183.96 | 0.8833     | 1.22221        |
| 2    | 2    | 0         | GA      | 273.13 | 1.0000     | 1.57080        |
| 2    | 2    | 0         | SY      | 295.26 | 0.9167     | 1.27795        |
| 2    | 2    | 1         | CY      | 157.66 | 0.9333     | 1.30964        |
| 2    | 2    | 1         | GA      | 247.93 | 0.9167     | 1.27795        |
| 2    | 2    | 1         | SY      | 357.27 | 0.9333     | 1.30964        |
| 2    | 3    | 0         | CY      | 145.08 | 0.7833     | 1.08663        |
| 2    | 3    | 0         | GA      | 267.47 | 1.0000     | 1.57080        |

| Loc. | Rep. | Herbicide | Species | Height | % Survival | Trans.Survival |
|------|------|-----------|---------|--------|------------|----------------|
| 2    | 3    | 0         | SY      | 307.77 | 0.8833     | 1.22221        |
| 2    | 3    | 1         | CY      | 137.88 | 0.8333     | 1.15026        |
| 2    | 3    | 1         | GA      | 221.71 | 0.9833     | 1.44134        |
| 2    | 3    | 1         | SY      | 285.76 | 0.9833     | 1.44134        |
| 2    | 4    | 0         | CY      | 125.36 | 0.2333     | 0.50413        |
| 2    | 4    | 0         | GA      | 252.97 | 0.9833     | 1.44134        |
| 2    | 4    | 0         | SY      | 126.68 | 0.4167     | 0.70167        |
| 2    | 4    | 1         | CY      | 131.89 | 0.7833     | 1.08663        |
| 2    | 4    | 1         | GA      | 278.75 | 0.9833     | 1.44134        |
| 2    | 4    | 1         | SY      | 302.14 | 0.9167     | 1.27795        |



## APPENDIX G

## STATISTICAL ANALYSIS

ANOVA: Immigration into the Ames Plantation Study Area by 4-Month Trapping Period June 1, 1985 through September 30, 1988. Data Transformed: log (sum +1).

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>MEAN SQUARE</u> | <u>F VALUE</u> |
|---------------|-----------|-----------------------|--------------------|----------------|
| Model         | 2         | 9.77154121            | 4.88577061         | 16.28          |
| Error         | 37        | 11.10454833           | 0.30012293         | pr > F         |
| Total         | 39        | 20.87608955           |                    | 0.0001         |

|          |         |            |            |
|----------|---------|------------|------------|
| R-Square | CV      | Root MSE   | Y Mean     |
| 0.468073 | 41.9863 | 0.54783476 | 1.30479509 |

|        |    |             |         |        |
|--------|----|-------------|---------|--------|
| Source | DF | Type III SS | F Value | Pr > F |
| Season | 2  | 9.77154121  | 16.28   | 0.0001 |

LEAST SQUARE MEANS: Seasonal Immigration into the Ames Plantation Study Area June 1, 1985 through September 30, 1988.

| <u>SEASON</u>      | <u>LS MEAN</u> | Pr > T LSMEAN(I)=LSMEAN(J) |        |        |
|--------------------|----------------|----------------------------|--------|--------|
|                    |                | 1                          | 2      | 3      |
| 1. February-May    | 1.67007832     | -                          | 0.0001 | 0.7388 |
| 2. June-September  | 0.70050862     | 0.0001                     | -      | 0.0001 |
| 3. October-January | 1.74522716     | 0.7388                     | 0.0001 | -      |



ANOVA: Immigration into the Ames Plantation Study Area by 4-Month Trapping Period and Sex June 1, 1985 through September 30, 1988. Data Transformed: log (sum +1).

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>MEAN SQUARE</u> | <u>F VALUE</u> |
|---------------|-----------|-----------------------|--------------------|----------------|
| Model         | 5         | 5.60738792            | 1.12147758         | 2.27           |
| Error         | 13        | 6.42479455            | 0.49421497         | Pr > F         |
| Total         | 18        | 12.03218246           |                    | 0.1086         |

|          |         |            |            |
|----------|---------|------------|------------|
| R-Square | CV      | Root MSE   | Y Mean     |
| 0.466032 | 37.6262 | 0.70300424 | 1.86839127 |

| <u>Source</u> | <u>DF</u> | <u>Type III SS</u> | <u>F Value</u> | <u>Pr &gt; F</u> |
|---------------|-----------|--------------------|----------------|------------------|
| Season        | 2         | 4.42846293         | 4.48           | 0.0343           |
| Sex           | 1         | 0.24453507         | 0.49           | 0.4942           |
| Season*Sex    | 2         | 1.04795543         | 1.06           | 0.3745           |

LEAST SQUARE MEANS: Seasonal Immigration into the Ames Plantation Study Area By Sex June 1, 1985 through September 30, 1988.

| <u>SEX</u> | <u>LSMEAN</u> | <u>Pr &gt; T</u> | <u>LSMEAN(M)=LSMEAN(F)</u> |
|------------|---------------|------------------|----------------------------|
| Male       | 1.75514323    |                  | 0.4942                     |
| Female     | 1.98334690    |                  |                            |

ANOVA: First Year Survival and Herbicide Treatments of Baldcypress, Green Ash, Swamp White Oak, and Sycamore Planted on Drained Beaver Impoundments on the Ames Plantation in West Tennessee. Includes "location" in the model. Angular Transformation of Data (Sokal and Rohlf 1981).

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 42        | 2.68867421            | 5.43           | 5. E-05          |
| Error         | 21        | 0.24767173            |                |                  |
| Total         | 63        | 2.93634594            |                |                  |

|          |          |                  |
|----------|----------|------------------|
| R-Square | CV       | Transformed Mean |
| 0.915653 | 8.386064 | 1.29500192       |

| Source        | DF | Type III SS | F Value | Pr > F  |
|---------------|----|-------------|---------|---------|
| Loc           | 1  | 0.00019252  | 0.02    | .89955  |
| Rep(Loc)      | 6  | 0.23618013  | 3.34    | .01812  |
| Herb          | 1  | 0.14535411  | 12.32   | .00208  |
| Loc*Herb      | 1  | 0.04875197  | 4.13    | .05487  |
| Rep*Herb(Loc) | 6  | 0.04292911  | 0.61    | .72218  |
| Sp            | 3  | 1.49214337  | 42.17   | 5. E-09 |
| Sp*Herb       | 3  | 0.11712037  | 3.31    | .03993  |
| Loc*Sp        | 3  | 0.17383217  | 4.91    | .00968  |
| Rep*Sp(Loc)   | 18 | 0.43217045  | 2.04    | .06001  |

Tests of hypothesis using Type III MS for Rep(Loc) as error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Loc    | 1  | 0.00019252  | 0.00    | .94652 |

Tests of hypothesis using Type III MS for Rep\*Herb(Loc) as error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 0.14535411  | 20.32   | .00407 |

Tests of hypothesis using Type III MS for Rep\*Herb(Loc) as error term:

| Source   | DF | Type III SS | F Value | Pr > F |
|----------|----|-------------|---------|--------|
| Loc*Herb | 1  | 0.04875197  | 6.81    | .04010 |

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 21        | 2.08267158            | 4.88           | 6. E-06          |
| Error         | 42        | 0.85367436            |                |                  |
| Total         | 63        | 2.93634594            |                |                  |

|          |          |                  |
|----------|----------|------------------|
| R-Square | CV       | Transformed Mean |
| 0.709273 | 11.00908 | 1.29500192       |

| Source       | DF | Type III SS | F Value | Pr > F  |
|--------------|----|-------------|---------|---------|
| Rep          | 7  | 0.23637266  | 1.66    | .14511  |
| Herb         | 1  | 0.14535411  | 7.15    | .01063  |
| Rep*Herb     | 7  | 0.09168108  | 0.64    | .71674  |
| Species      | 3  | 1.49214337  | 24.47   | 3. E-09 |
| Species*Herb | 3  | 0.11712037  | 1.92    | .14089  |

Tests of hypothesis using Type III MS for Rep(Loc) as error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 0.14535411  | 11.10   | .01257 |



ORTHOGONAL CONTRASTS: First Year Survival and Herbicide Treatments of Baldcypress, Green Ash, Swamp White Oak, and Sycamore Planted on Drained Beaver Impoundments on the Ames Plantation in West Tennessee. Angular Transformation of Data (Sokal and Rohlf 1981).

| <u>CONTRAST</u>   | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-------------------|-----------|--------------------|----------------|------------------|
| SWO vs SYC,CYP,GA | 1         | 1.32007210         | 64.95          | 5. E-10          |
| GA vs SYC,CYP     | 1         | 0.16142322         | 0.61           | .00733           |
| SYC vs CYP        | 1         | 0.01064805         | 7.85           | .47321           |

Tests of hypothesis using Type III MS for Rep\*Herb as an error term:

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| Herb vs No Herb | 1         | 0.14535411         | 11.10          | .01257           |

ANOVA: Dry Weights of Grasses Sampled on Two Beaver Impoundments on the Ames Plantation Study Area Three Years After Drainage.

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 15        | 54427631.25           | 9.89           | 4. E-08          |
| Error         | 32        | 11741766.67           |                |                  |
| Total         | 47        | 66169397.92           |                |                  |

|          |          |          |            |
|----------|----------|----------|------------|
| R-Square | CV       | Root MSE | Grass Mean |
| 0.822550 | 54.27644 | 605.7476 | 1116.04167 |

| Source        | DF | Type III SS | F Value | Pr > F  |
|---------------|----|-------------|---------|---------|
| Loc           | 1  | 14050852.08 | 38.29   | 6. E-07 |
| Rep(Loc)      | 6  | 744229.17   | 0.34    | .91158  |
| Herb          | 1  | 23324408.33 | 63.57   | 4. E-09 |
| Loc*Herb      | 1  | 14170133.33 | 38.62   | 6. E-07 |
| Rep*Herb(Loc) | 6  | 2138008.33  | 0.97    | .46041  |

Tests of hypothesis using Type III MS for Rep(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F  |
|--------|----|-------------|---------|---------|
| Loc    | 1  | 14050852.08 | 113.28  | 4. E-05 |

Test of hypothesis using Type III MS for Rep\*Herb(Loc) as an error term:

| Source | DF | Type III SS | F value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 23324408.33 | 65.46   | .00019 |

ANOVA: Dry Weights of Broadleaf Herbaceous Vegetation Sampled on Two Beaver Impoundments on the Ames Plantation Study Area Three Years After Drainage.

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 15        | 38223320.31           | 5.36           | 3. E-05          |
| Error         | 32        | 15205566.67           |                |                  |
| Total         | 47        | 53428886.98           |                |                  |

|          |          |          |            |
|----------|----------|----------|------------|
| R-Square | CV       | Root MSE | Grass Mean |
| 0.715406 | 35.32565 | 689.3286 | 1951.35417 |

| Source        | DF | Type III SS | F Value | Pr > F |
|---------------|----|-------------|---------|--------|
| Loc           | 1  | 5204125.52  | 10.95   | .00232 |
| Rep(Loc)      | 6  | 8018640.63  | 2.81    | .02953 |
| Herb          | 1  | 7382929.69  | 15.54   | .00041 |
| Loc*Herb      | 1  | 2225254.69  | 4.68    | .03803 |
| Rep*Herb(Loc) | 6  | 15392369.79 | 5.40    | .00060 |

Tests of hypothesis using Type III MS for Rep(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Loc    | 1  | 5204125.521 | 3.89    | .09591 |

Test of hypothesis using Type III MS for Rep\*Herb(Loc) as an error term:

| Source | DF | Type III SS | F value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 7382929.687 | 2.88    | .14073 |



ANOVA: Dry Weights of Natural Tree Regeneration Sampled on Two Beaver Impoundments on the Ames Plantation Study Area Three Years After Drainage.

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 15        | 12745495.31           | 0.85           | .61650           |
| Error         | 32        | 31850900.00           |                |                  |
| Total         | 47        | 44596395.31           |                |                  |
| R-Square      | CV        | Root MSE              | Grass Mean     |                  |
| 0.285787      | 373.3961  | 997.6676              | 267.18757      |                  |

| Source        | DF | Type III SS | F Value | Pr > F |
|---------------|----|-------------|---------|--------|
| Loc           | 1  | 32813.021   | 0.03    | .85707 |
| Rep(Loc)      | 6  | 5028528.125 | 0.84    | .54707 |
| Herb          | 1  | 237304.687  | 0.24    | .62868 |
| Loc*Herb      | 1  | 1898063.021 | 1.91    | .17687 |
| Rep*Herb(Loc) | 6  | 5548786.458 | 0.93    | .48756 |

Tests of hypothesis using Type III MS for Rep(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Loc    | 1  | 32813.02083 | 0.04    | .84968 |

Test of hypothesis using Type III MS for Rep\*Herb(Loc) as an error term:

| Source | DF | Type III SS | F value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 237304.6875 | 0.26    | .63054 |

ORTHOGONAL CONTRASTS: Effect of Herbicide Treatment on Dry Weight of Grasses, Broadleaf Herbaceous Vegetation, and Natural Tree Regeneration Sampled on Two Beaver Impoundments on the Ames Plantation Study Area Three Years After Drainage.

#### Grasses

Tests of Hypothesis using the Type III Rep\*Herb as an error term:

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| Herb vs Noherb  | 1         | 23324408.33        | 10.01          | .01584           |

#### Broadleaf Herbaceous Vegetation

Tests of Hypothesis using the Type III Rep\*Herb as an error term:

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| Herb vs Noherb  | 1         | 7382929.687        | 2.93           | .13049           |

#### Natural Tree Regeneration

Tests of Hypothesis using the Type III Rep\*Herb as an error term:

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| Herb vs NoHerb  | 1         | 237304.6875        | 0.22           | .65108           |

ANOVA: Polynomial Regression: Grass = Dependent Variable and Broadleaf Weeds = Independent Variable.

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>MEAN SQUARE</u> | <u>F VALUE</u> |
|---------------|-----------|-----------------------|--------------------|----------------|
| Model         | 2         | 40738045.2690         | 36.04              | Pr > F         |
| Error         | 45        | 25431352.6476         |                    | 5. E- 10       |
| Total         | 47        | 66169397.9167         |                    |                |

|          |          |             |
|----------|----------|-------------|
| R-Square | CV       | Grass Mean  |
| 0.615663 | 67.35938 | 1116.041667 |

| Source      | DF | Type III SS   | F Value | Pr > F |
|-------------|----|---------------|---------|--------|
| Weeds       | 1  | 18826730.4396 | 33.31   | 7 E-07 |
| Weeds*Weeds | 1  | 9361524.4227  | 16.56   | .00019 |

| Parameter   | Estimate    | T for Ho:<br>Parameter=0 | Pr > T  | STD Error of<br>Estimate |
|-------------|-------------|--------------------------|---------|--------------------------|
| Intercept   | 3852.493128 | 10.12                    | 4. E-13 | 380.83338438             |
| Weeds       | -2.422468   | -5.77                    | 7. E-07 | 0.41970979               |
| Weeds*Weeds | 0.000405    | 4.07                     | .00019  | 0.00009939               |



ANOVA: Third Year Survival of Baldcypress, Green Ash, and Sycamore Planted on Drained Beaver Impoundments on the Ames Plantation in West Tennessee. Includes "location" in the model. Angular transformation of Data (Sokal and Rohlf 1981).

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 21        | 1.69350872            | 4.89           | .0001            |
| Error         | 26        | 0.42911829            |                |                  |
| Model         | 47        | 2.12262701            |                |                  |
| R-Square      |           | CV                    | Transurv Mean  |                  |
| 0.797836      |           | 10.581485             | 1.21295587     |                  |

| Source        | DF | Type III SS | F Value | Pr > F |
|---------------|----|-------------|---------|--------|
| Loc           | 1  | 0.09822041  | 5.95    | 0.0218 |
| Rep(Loc)      | 6  | 0.40131182  | 4.05    | 0.0053 |
| Herb          | 1  | 0.04524552  | 2.74    | 0.1098 |
| Loc*Herb      | 1  | 0.13094813  | 7.93    | 0.0091 |
| Rep*Herb(Loc) | 6  | 0.23509904  | 2.37    | 0.0581 |
| Species       | 2  | 0.58519123  | 17.73   | 0.0001 |
| Herb*Species  | 2  | 0.09586322  | 2.90    | 0.0727 |
| Loc*Species   | 2  | 0.10162962  | 3.08    | 0.0631 |

Tests of hypothesis using the Type III MS for Rep(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Loc    | 1  | 0.09822041  | 1.47    | 0.2711 |

Tests of hypothesis using the Type III MS for Rep\*Herb(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 0.04524525  | 1.15    | 0.3239 |

Tests of hypothesis using the Type III MS for Rep\*Herb(Loc) as an error term:

| Source   | DF | Type III S | F Value | Pr > F |
|----------|----|------------|---------|--------|
| Loc*Herb | 1  | 0.13094813 | 3.34    | 0.1173 |

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 19        | 1.59187910            | 4.42           | .0002            |
| Error         | 28        | 0.53074791            |                |                  |
| Model         | 47        | 2.12262701            |                |                  |

|          |           |               |
|----------|-----------|---------------|
| R-Square | CV        | Transurv Mean |
| 0.749957 | 11.350634 | 1.21295587    |

| Source       | DF | Type III SS | F Value | Pr > F |
|--------------|----|-------------|---------|--------|
| Rep          | 7  | 0.49953223  | 3.76    | 0.0054 |
| Herb         | 1  | 0.04524525  | 2.39    | 0.1336 |
| Rep*Herb     | 7  | 0.36604717  | 2.76    | 0.0260 |
| Species      | 2  | 0.58519123  | 15.44   | 0.0978 |
| Herb*Species | 2  | 0.09586322  | 2.53    | 0.0978 |

Tests of hypothesis using the Type III MS for Rep\*Herb as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Rep    | 7  | 0.49953223  | 1.36    | 0.3460 |

Tests of hypothesis using the Type III MS for Rep\*Herb as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 0.04524525  | 0.87    | 0.3832 |

ORTHOGONAL CONTRASTS: Third Year Survival and Herbicide Treatments of Baldcypress, Green Ash, and Sycamore Planted on Drained Beaver Impoundments on the Ames Plantation in West Tennessee. Angular Transformation of Data (Sokal and Rohlf 1981).

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| CYP VS SG&SYC   | 1         | 0.34342162         | 18.12          | 0.0002           |
| SG VS SYC       | 1         | 0.24176961         | 12.75          | 0.0013           |

Tests of hypothesis using the Type III MS for Rep\*Herb as an error term:

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| HERB VS NOHERB  | 1         | 0.04524525         | 0.87           | 0.3832           |



ANOVA: Third Year Total Height of Baldcypress, Green Ash, and Sycamore Planted on Drained Beaver Impoundments on the Ames Plantation in West Tennessee. Includes "location" in the model. Angular Transformation of Data (Sokal and Rohlf 1981).

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 21        | 283782.7299068        | 8.52           | .0001            |
| Error         | 26        | 41214.1930910         |                |                  |
| Model         | 47        | 324996.9229978        |                |                  |

|          |           |             |
|----------|-----------|-------------|
| R-Square | CV        | Mean Height |
| 0.873186 | 16.741627 | 237.81      |

| Source        | DF | Type III SS   | F Value | Pr > F |
|---------------|----|---------------|---------|--------|
| Loc           | 1  | 3394.947983   | 2.14    | 0.1553 |
| Rep(Loc)      | 6  | 35110.669702  | 3.69    | 0.0087 |
| Herb          | 1  | 533.805878    | 0.34    | 0.5667 |
| Loc*Herb      | 1  | 986.615240    | 0.62    | 0.4373 |
| Rep*Herb(Loc) | 6  | 9582.314718   | 1.01    | 0.4418 |
| Species       | 2  | 230770.572898 | 72.79   | 0.0001 |
| Herb*Species  | 2  | 526.899145    | 0.17    | 0.8478 |
| Loc*Species   | 2  | 2876.904343   | 0.91    | 0.4160 |

Tests of hypothesis using the Type III MS for Rep(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Loc    | 1  | 3394.947983 | 0.58    | 0.4751 |

Tests of hypothesis using the Type III MS for Rep\*Herb(Loc) as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 533.805878  | 0.33    | 0.5842 |

Tests of hypothesis using the Type III MS for Rep\*Herb(Loc) as an error term:

| Source   | DF | Type III SS | F Value | Pr > F |
|----------|----|-------------|---------|--------|
| Loc*Herb | 1  | 986.615240  | 0.62    | 0.4618 |

| <u>SOURCE</u> | <u>DF</u> | <u>SUM OF SQUARES</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|---------------|-----------|-----------------------|----------------|------------------|
| Model         | 19        | 280905.8255637        | 9.39           | 0.0001           |
| Error         | 28        | 44091.0974341         |                |                  |
| Model         | 47        | 324996.9229978        |                |                  |

|          |           |             |
|----------|-----------|-------------|
| R-Square | CV        | Mean Height |
| 0.864334 | 16.686198 | 237.81      |

| Source       | DF | Type III SS   | F Value | Pr > F |
|--------------|----|---------------|---------|--------|
| Rep          | 7  | 38505.617684  | 3.49    | 0.0081 |
| Herb         | 1  | 533.805878    | 0.34    | 0.5651 |
| Rep*Herb     | 7  | 10568.929958  | 0.96    | 0.4793 |
| Species      | 2  | 230770.572898 | 73.28   | 0.0001 |
| Herb*Species | 2  | 526.899145    | 0.17    | 0.8468 |

Tests of hypothesis using the Type III MS for Rep\*Herb as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Rep    | 7  | 38505.61768 | 3.64    | 0.0548 |

Tests of hypothesis using the Type III MS for Rep\*Herb as an error term:

| Source | DF | Type III SS | F Value | Pr > F |
|--------|----|-------------|---------|--------|
| Herb   | 1  | 533.8058780 | 0.35    | 0.5708 |

ORTHOGONAL CONTRASTS: Third Year Total Height and Herbicide Treatments of Baldcypress, Green Ash, and Sycamore Planted on Drained Beaver Impoundments on the Ames Plantation in West Tennessee. Angular Transformation of Data (Sokal and Rohlf 1981).

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| CYP VS SG&SYC   | 1         | 201864.3437        | 128.19         | 0.0001           |
| SG VS SYC       | 1         | 28906.2292         | 18.36          | 0.0002           |

Tests of hypothesis using the Type III MS for Rep\*Herb as an error term:

| <u>CONTRAST</u> | <u>DF</u> | <u>CONTRAST SS</u> | <u>F VALUE</u> | <u>Pr &gt; F</u> |
|-----------------|-----------|--------------------|----------------|------------------|
| HERB VS NOHERB  | 1         | 533.805878         | 0.35           | 0.5708           |



## VITA

Allan Edward Houston was born October 31, 1952, in Clayton, Georgia, to Mr. and Mrs. Lawton Edward Houston. He was reared in Brevard, North Carolina, and attended Brevard High School, graduating in 1971.

In August 1971, he enrolled at Brevard Junior College and completed requirements for the Associate Arts degree in spring of 1973. He attended North Carolina State University beginning in August 1973 and completed Bachelor of Science degrees in Forestry and Biology in 1976. He was accepted into the Graduate Program at North Carolina State University and completed requirements for the Master of Science degree in Forestry in spring of 1979.

In February 1979, he accepted the position of Research Assistant with the University of Tennessee Agricultural Experiment Station, Ames Plantation, in west Tennessee. In the summer of 1986 he was accepted into the Graduate Program at the University of Tennessee, Knoxville, and began pursuit of the Doctor of Philosophy degree in Ecology.

The author is a member of Xi Sigma Xi, Phi Kappa Phi, and Society of American Foresters.

He has been married to the former Rebecca Louise Hudson since June 1977 and currently resides at Ames Plantation in the position of Research Associate with his wife and two children, Brian and Laura.