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Increasing the probability of success in restored forested wetlands

Final Report to the United States Environmental Protection Agency Wetlands Protection State Development Project Period: April 28, 1997 to December 31, 1998

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Introduction

An estimated 1.4 million hectares of palustrine forested wetlands were lost in the continental United States during the mid-1970's to mid-1980's with a majority of the loss occurring in the southeast (Dahl and Johnson 1991).

Forested wetlands are some of the most difficult wetland community types to restore or construct. Not only is obtaining or restoring the proper hydrologic regime to the site extremely difficult, but also these systems require a significant amount of time to mature (Niswander and Mitsch 1995). In addition to creation due to compensatory mitigation, the restoration of riparian forested buffers has become a priority for stream restoration (Winger 1986, Prichard et al. 1993, Lowrance et al. 1997).

Planting the proper woody species for the desired hydrologic regime is an essential component before the constructed forested wetland or restored riparian forest buffer can mature as planned. Certain woody species are more tolerant of wetland conditions while some can be found growing in both wetland and upland situations (Hook 1984, Tiner 1991). While different species have developed different mechanisms for adapting to waterlogged conditions (Pereira and Kozlowski 1977, Hook and Scholtens 1980, Ernst 1990, Havens 1997), it has been demonstrated that genetic differentiation among populations within species may exist. Keeley (1979) working with *Nyssa sylvatica* Marsh. demonstrated that differences in seedling survival are linked to the hydrologic regime of the parents. Lessman and others (1997) working with marsh species demonstrated that the existence of more flood-tolerant populations of *Spartina alterniflora* Loisel, *Spartina patens* L., and *Panicum hemitomon* Schultes.

This study investigated survival and growth of two distinct ecotypic populations, with varying tolerance to waterlogging, of four species, *Taxodium distichum* (L.) Richard, *Carpinus caroliniana* Walt., *Quercus michauxii* Nutt. and *Quercus pagoda* Raf. (Syn. *Q. falcata* var. *pagodifolia* Ell.).

T. distichum is a deciduous conifer of southern bottomland forests which develops pneumatophores ("knees") in flooded conditions. *T. distichum* has short (1-1.5 cm) flat, narrow leaves which are pale green above and yellowish to whitish beneath. The mature, 2.5 cm, seed bearing cones are globose, green and turn black after falling. The fruits are winged. *T. distichum* is considered highly tolerant to waterlogging but grows well under drained conditions and intermittently flooded sites (Wilhite and Toliver). *T. distichum* is considered an obligate wetland plant that occurs almost always in wetlands (estimated probability >99%) (Reed 1988).

Carpinus caroliniana is an understory tree with relatively grayish-blue bark. The trunk often has longitudinal bulges that appear as tensioned muscle, hence the common name "muscle wood". The leaves are deciduous, alternate, 2-6 cm long with double serrated margins. The fruits are pendulous, with several bracts. Each bract subtends a ribbed nutlet. Young branches are very slender and usually reddish-brown. *C. caroliniana* grows well on saturated hardwood swamp mineral soil sites (Barnes 1976, Silberhorn 1997) as long as the sites are not inundated more than

25% of the time (Metzger 1990). Frequent flooding has been shown to reduce survivability (Streng et al. 1989). *C. caroliniana* is considered a facultative plant that occurs an equal percentage of time in both wetlands and uplands (estimated probability 34-66%) (Reed 1988).

Quercus michauxii is a deciduous oak with shallowly lobed leaves ranging from 10 to 20 cm long and 5 to 15 cm wide. Leave size is highly variable even on the same tree. The number of lobes range from 5 to 15 per side. The upper surface is smooth contrasting to a whitish, pubescent underside. Young twigs are also pubescent, becoming glabrous and reddish-brown as they mature. Q. michauxii is generally found on well-drained silty clay and loamy terraces and colluvial sites in the bottom lands of streams (Edwards 1990). Q. michauxii is considered a facultative wetland plant that usually occurs in wetland systems (estimated probability 67-99%) (Reed 1988).

Quercus pagoda is deciduous with sharp-pointed, bristle-tipped lobes. Principle veins extend beyond the lobe tip. Lobes vary from 5 to 9 per leaf. Leaf shape and size is variable. The upper side of the leaf is usually dark green and shinny, whereas the bottom is gray to brownish pubescent. Bark on mature trees is furrowed longitudinally, dark gray and somewhat resembles the bark of wild black cherry, *Prunus serotina* Ehrh. The saucer-like acorn cups cover about 1/4 of the brown acorn. *Q. pagoda* can be found in wetland sites but is generally associated with hummocks and well-drained soils (Krinard 1990). *Q. pagoda* is considered a facultative wetland plant that usually occurs in wetlands (estimated probability 67-99%) (Reed 1988).

The goal of this project was to investigate whether seedlings from parent populations adapted to waterlogged sites have a higher probability of survival than seedlings from upland sites when grown under waterlogged conditions. This was investigated using reciprocal transplantation and seedling transplantation methods. Reciprocal transplantation between field sites subjects transplants to natural selection pressures and is considered a powerful method for measurement of relative fitness (Davy and Smith 1988, Davy et al. 1990). Seedling transplantation subjects newly germinated seedlings to specific, regulated hydrologic conditions and is of value in following the seasonal progression of plant growth (Davy and Smith 1985).

Materials and Methods

Reciprocal Transplantation Investigation

First year seedlings of ironwood (*Carpinus caroliniana*) and one year old seedlings of swamp basket oak (*Quercus michauxii*.) were selected for the reciprocal transplant experiment. Seedlings of each species were collected from both upland and wetland areas. Upland and wetland areas were identified by an examination of the soils, associated vegetation and evidence (or lack thereof) of a hydrologic regime (Table 1).

Species	Soils	Associated vegetation	Evidence of hydrologic regime
Upland <i>Q. michauxii</i> Upland <i>C. caroliniana</i>	Catpoint loamy sand - nonhydric	Sweetgum- Liquidambar styraciflua L. Tulip poplar- Liriodendron tulipifera L. Beech- Fagus grandifolia Ehrh	none
Wetland <i>Q. michauxii</i> Wetland <i>C. caroliniana</i>	Bibb- hydric	River birch- <i>Betula nigra</i> L. Red maple- <i>Acer rubrum</i> L. Bald cypress- <i>T. distichum</i>	Saturated soils wrack line crayfish burrows gage station records

Table 1. Soils, vegetation, and hydrologic regime of seedling collection sites.

Seedlings were washed, dried with paper towels, and immediately measured for height and mass. Height was measured in centimeters from the first lateral root to the terminal bud. Mass was measured on a Scientech 3350 balance to the nearest 0.1 gram. Fresh weight was used in order to utilize the more powerful statistical comparative power of the paired t-test. Seedling height and mass were tested statistically (Student's T-test) to examine the variance of the population. There was a significant difference in stem height and mass between upland and wetland seedlings from both species. To correct for this, seedlings with similar height and mass were collected from each ecotone and relative growth was tested after treatment. Ten upland seedlings and ten wetlands seedlings of each species were transplanted randomly along a transect in both the upland and wetland area (Table 2).

Table 2. Mass and stem height of initial sample of *Carpinus caroliniana* (Cc) and *Quercus michauxii* (Qm). Upland1 and upland2 seedlings were removed from an upland ecotone. Wetland1 and wetland2 seedlings were removed from a wetland ecotone.

		Ι	nitial Sample		
		Mass	S	Stem Height	
Species	⊼ (g)	SD	⊼ (cm)	SD	N
Cc (upland1)	0.312	0.239	8.58	2.22	10
Cc (upland2)	0.214	0.155	8.19	2.11	10
Cc (wetland1)	0.186	0.155	7.67	2.31	10
Cc (wetland2)	0.121	0.091	7.04	1.75	10
Qm (upland1)	10.00	4.02	33.87	8.82	10

Qm (upland2)	7.51	6.81	27.20	12.4	10
Qm (wetland1)	5.34	2.80	23.70	6.24	10
Qm (wetland2)	5.31	1.04	24.96	3.46	10

Data from a United States Geologic Survey stream gage station, located 15 m downstream of the wetland transplant area, was used to confirm site hydroperiod.

All seedlings were removed on November 12, 1998. Seedlings were washed, dried with paper towels, and immediately measured for height and mass.

Seedling Transplantation Investigation

Seeds were collected in the fall of 1997 from both upland and wetland bald cypress, *Taxodium distichum*, and cherrybark oak, *Quercus pagoda*. Upland and wetland areas were identified by an examination of the soils, associated vegetation and evidence (or lack thereof) of a hydrologic regime (Table 3).

Species	Soils	Associated vegetation	Evidence of hydrologic regime
Upland T. distichum	Catpoint fine sand - nonhydric	All T. distichum	None
Wetland T. distichum	Nawney silt loam - hydric	All T. distichum	Flooded
Upland <i>Q.</i> pagoda	Tetotum silt loam- nonhydric	Loblolly pine - <i>Pinus taeda</i> L.	None
Wetland Q. pagoda	Not mapped but profile similar to Kinston. 0-10cm 10YR 4/2 10-23cm 10YR 4/2 rmf 3/6 23-51cm 2.5Y 5/2 rmf 5YR 4/4 51-76cm 10YR 3/2 76-91cm 2.5Y 5/2 91- 122cm YR 4/2 rmf 5/8 122-152cm 10YR 5/1 hydric	Green ash - Fraxinus pennsylvanica Marsh. Willow oak - Quercus phellos L. Water gum - Nyssa aquatica L. Bald cypress -T. distichum	Saturated soil wrack lines Oxidized rhizosphere

Table 3. Soils, associated vegetation, and hydrologic regime of seed collection sites. Rmf = redoximorphic features.

T. distichum seeds were submerged in water for 60 days and sown in beds in the spring. *Q. pagoda* seeds were tested for viability by flotation and visual inspection (Burns and Honkala 1990) and were planted in beds in the fall of 1997. In the spring *T. distichum* and *Q. pagoda* seedlings from upland and wetland parents were removed from the beds, weighed and measured.

Seedling measurements were statistically tested (Student T-test) to determine population variance. Outliers were rejected and 80 *T. distichum* and 40 *Q. pagoda* seedlings that were not significantly different (p < 0.05) in height and mass were selected (Table 4).

]	nitial Sample		
Species \bar{x} (g)	Mass Stem Height		Stem Height		
	⊼ (g)	SD	⊼ (cm)	SD	Ν
Qp (upland)	1.86	0.95	14.11	3.38	20
Qp (wetland)	2.37	0.96	15.91	3.67	20
Td (upland)	1.69	0.35	20.25	2.01	40
Td (wetland)	1.52	0.36	19.04	3.24	40

Table 4. Mass and stem height of initial sample of Quercus pagoda (Qp) and Taxidium distichum (Td).

The field experimentation area consists of a 12 m by 6 m grid of sandy loam soil with a 45 mm EPDM liner at a 30 cm depth. Water depth was maintained at the soil surface for one half of the system and the other half received 2.5 cm of water per week (except for a 5 day period of inundation in August due to Hurricane Bonnie). Twenty *T. distichum* seedlings from upland parents and 20 seedlings from wetland parents were randomly planted in both the saturated and drained area. Ten *Q. pagoda* seedlings from upland parents and 10 seedlings from wetland parents were randomly planted in both the saturated and drained area. All seedlings were numbered, tagged and transplanted to the field experimentation area in a randomized block design. After 6 months all seedlings were removed, washed, dried with paper towels and measured for height and mass.

Statistical Analysis

Sample populations were tested for normal distribution using probit plots. Student's t-test was used to compare mass and stem height of normally distributed data. Relative mass and stem height was tested using the Mann Whitney U-test. Welch's t-test was used for small sample sizes and for samples with unequal variances. The paired t-test was used to compare pre and post treatments.

Results

Reciprocal Transplantation Investigation

The wetland site was saturated (water within 30 cm of the soil surface) 32% of the time and inundated 17% of the time. Twenty five percent of the saturation and 17% of the inundation took place between March 1, 1997 and July 1, 1997.

C. caroliniana seedlings from both parent types had complete survival (100%) and had

significant (p < 0.02) growth from pre to post treatment in both the saturated and drained plots (except for the mass of seedlings from upland parents grown under saturated conditions). *C. caroliniana* seedlings from wetland parents had significantly (p < 0.03) higher relative growth than seedlings from upland parents (Table 5).

Table 5. Pre and Post treatment measurements and survival rates for saturated and drained seedlings of *Carpinus caroliniana* (Cc). * = significant difference (p < 0.05) between pre and post treatments. Like letters indicate a significant difference (p < 0.05) between seedling ecotone types.

Saturated Treatmen	t							
	Pre	-treatmer	nt	Post-treatment				
Species	x	SD	N	x	SD	N	% increase (median)	% survival
Cc upl stem	8.58*	2.22	10	9.30*	2.39	10	8 (a)	100
Cc wet stem	7.67*	2.31	10	9.19*	2.87	10	19 (a)	100
Cc upl mass	0.31	0.24	10	0.35	0.24	10	13 (b)	100
Cc wet mass	0.19*	0.16	10	0.49*	0.30	10	200 (b)	100
Drained Treatment								
	Pre	-treatmer	it	Post-	-treatmen	t		
Species	×	SD	N	x	SD	N	% increase (median)	% survival
Cc upl stem	8.19*	2.11	10	10.60*	3.45	10	26	100
Cc wet stem	7.04*	1.75	10	9.00*	2.83	10	35	100
Cc upl mass	0.21*	0.16	10	0.73*	0.33	10	333	100
Cc wet mass	0.12*	0.09	10	0.50*	0.23	10	500	100

Q. michauxii seedlings from wetland parents had a higher survival rate (80%) than seedlings from upland parents (50%) and a significant difference (p < 0.02) in growth between treatments in the saturated plot. *Q. michauxii* seedlings of both parent types grown in the drained plot had significant (p < 0.01) growth between pre and post treatments but no significant difference (p = 0.43) in relative growth between seedling type (Table 6).

Table 6. Pre and Post treatment measurements and survival rates for saturated and drained seedlings of *Quercus* michauxii (Qm). * = significant difference (p < 0.05) between pre and post treatments. Like letters indicate a significant difference (p < 0.05) between seedling ecotone types.

Saturated Treatm	nent							
	Pre	treatmen	t	Post-treatment \bar{x} SD N				
Species	×	SD	N				% increase (median)	% survival
Qm upl stem	28.68	15.01	5	29.00	17.05	5	0 (a)	50
Qm wet stem	24.96*	3.46	8	28.01*	5.61	8	10 (a)	80
Qm upl mass	7.88	8.13	5	7.82	9.46	5	2 (b)	50
Qm wet mass	5.16*	1.13	8	5.44*	1.23	8	7 (b)	80
Drained Treatme	ent							
	Pre	treatmen	t	Pos	Post-treatment			
Species	×	SD	N	×	SD	N	% increase (median)	% survival
Qm upl stem	33.87	8.82	10	43.40	9.29	10	32	100
Qm wet stem	23.07	6.24	10	31.58	7.84	10	32	100
Qm upl mass	10.00	4.02	10	12.16	4.72	10	23	100
Qm wet mass	5.34	2.80	10	6.98	3.91	10	28	100

Seedling Transplantation Investigation

Survival rates of *Q. pagoda* were poor (40%) for seedlings of both parent types grown under saturated conditions. There was no significant difference (p < 0.11) in growth between seedling type. *Q. pagoda* seedlings grown under drained conditions had high (90%) survival and significant (p < 0.001) growth between pre and post treatment. There was no significant difference (p < 0.50) in growth between seedling types (Table 7).

Table 7. Pre and Post treatment measurements and survival rates for saturated and drained seedlings of *Quercus* pagoda (Qp). * = significant difference (p < 0.05) between pre and post treatments. No significant difference (p < 0.05) between seedling ecotone types.

Saturated Treatme	ent						
		Pre-treatmen	ıt		Post-treatment		
Species	x	SD	N	×	SD	N	% survival
Qp upl stem	15.00	2.25	4	14.90	2.25	4	40
Qp wet stem	15.60	2.42	4	15.28	2.59	4	40
Qp upl mass	2.43	0.60	4	2.33	0.56	4	40
Qp wet mass	1.90	0.73	4	1.68	0.65	4	40
Drained Treatmen	it						
		Pre-treatmen	ıt		Post-treatment		
Species	x	SD	N	×	SD	N	% survival
Qp upl stem	14.23*	4.08	9	22.41*	4.59	9	90
Qp wet stem	16.61*	4.14	9	24.23*	3.80	9	90
Qp upl mass	2.09*	0.95	9	3.91*	1.17	9	90
Qp wet mass	1.90*	0.73	9	1.68*	0.65	9	90

T. distichum seedlings of both parent types had high survival rates under both drained and saturated treatments. There was no significant difference (p < 0.11) in growth between pre and post treatment under saturated conditions for either seedling type. There was a significant (p < 0.013) increase in mass for seedlings from both parent types between pre and post treatment under drained conditions however, there was no significant difference (p = 0.908) in mass between seedling types (Table 8).

Saturated Treatme	ent						
		Pre-treatment Post-treatment					
Species	x	SD	N	x	SD	N	% survival
Td upl stem	21.25	2.37	13	25.18	5.40	13	65
Td wet stem	18.85	3.27	14	22.57	8.91	14	70
Td upl mass	1.77	0.22	13	4.60	2.88	13	65
Td wet mass	1.58	0.42	14	3.33	1.98	14	70
Drained Treatmen	it						
		Pre-treatment Post-treatment					
Species	×	SD	N	×	SD	N	% survival
Td upl stem	20.70	1.92	15	18.97	3.69	15	75
Td wet stem	19.36	1.79	18	21.63	5.85	18	90
Td upl mass	1.71*	0.35	15	3.49*	2.11	15	75
Td wet mass	1.35*	0.25	18	3.39*	1.89	18	90

Table 8. Pre and Post treatment measurements and survival rates for saturated and drained seedlings of *Taxodium* distichum (Td). * = significant difference (p < 0.05) between pre and post treatments. No significant difference (p < 0.05) between seedling ecotone types.

Discussion

C. caroliniana seedlings from both parent ecotones had complete survival however, relative growth (both mass and stem height) under saturated conditions was greater in seedlings from wetland parents. There was no difference in growth between seedlings of both parent types grown under drained conditions. This suggests that parent type may play a role in plant vigor and ultimately in survivability when planted in saturated sites.

Q. michauxii showed a distinct difference in survivability of seedlings of wetland parents as compared to seedlings of upland parents when grown under saturated conditions (80% and 50%, respectively). Growth, measured as a relative increase in mass and stem height, was also greater in seedlings from wetland parents under saturated conditions. Burke and Chambers (1999) found survival rates of *Q. michauxii* seedlings of 22-66%, depending on flooding time, while Denslow and Battaglia (1999) showed survival rates of 40-80% for seedlings transplanted to inundated tree blow-down pits. Data from this study suggests that differences between different parent ecotypes may be reflected in seedling tolerance to waterlogging.

Q. pagoda seedlings from both parent types had poor survivability (40%) under saturated condition. Necrotic roots were evident on seedlings of both parent types which may be reflective of its habitat preference. Even though *Q. pagoda* is considered a facultative wetland plant, found more often than not growing in wetlands, it is considered a flood-sensitive species that suffers high mortality under inundated conditions (Hook 1984). Nix and Cox (1986) documented survival rates of 40% for two-year-old nursery-grown seedlings transplanted to a red river bottomland site. Both height growth and biomass have been shown to be reduced in *Q. pagoda* seedlings subjected to flooding (Pezeshki and Anderson 1997). It has been suggested that *Q. pagoda* occurrence in wetlands is due to its colonization of hummocks which are raised above the surrounding terrain and are usually well-drained (Krinard 1990). Data from this study suggest that seedlings from both parent ecotypes have equally poor survivorship and growth when subjected to continuous saturation, though a study by Dicke and Toliver (1987) found a difference in survivorship between 'families' (not defined) of *Q. pagoda* grown on poorly drained soils.

T. distichum seedlings of upland and wetland parents did not differ in survivorship or growth. Seedlings from both parent types developed adventitious roots. *T. distichum* is highly flood-tolerant (Pezeshki et al. 1996) and can grow well under a variety of flooding regimes (Conner et al. 1997) though short-term reduced growth has been observed in seedlings grown under flooded conditions (Shanklin and Kozlowski 1985, Megonigal and Day 1992). Data from this study suggests that parent type does not affect survivorship or growth of seedlings. It must be noted that our seedling sampling technique may have biased this data. A documented, long-term natural population of upland *T. distichum* could not be verified so seeds were collected from a stand of approximately 50 year-old trees. It was not possible to rule out the possibility that these upland parent trees had not been transplanted from a wetland area.

Conclusion and State Wetland Management Considerations

It has been shown that for monocots a one-gene change at a single locus can be sufficient to favor survival under waterlogged conditions (Marshall et al. 1973). In a study of upper and lower marsh populations of *Salicornia europaea* L., Jefferies and Gottlieb (1982) found genetic differences between the two populations. In a more recent study, Lessman and others (1997) identified more flood-tolerant genotypes of *P. hemitomon*, *S. patens*, and *S. alterniflora*. In woody species, differences in flood tolerance have been shown for *N. sylvatica* (Keeley 1979) and for clones of *Populus* (Hallgren 1989).

This study demonstrated that for woody species considered moderately flood-tolerant, Q. *michauxii* and *C. caroliniana*, genetic differences to flood tolerance may exist between upland and wetland populations, while highly flood-sensitive and highly flood-tolerant species, such as Q. *pagoda* and *T. distichum*, may not exhibit a difference in survivorship. This is an important factor when restoration of forest riparian buffers or the creation of forested wetland systems is considered. Resource managers may be able to increase forested wetland restoration or creation success rates by selecting seedling stock from wetland parents in order to enhance flood tolerance traits.

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Literature Cited

- Barnes, B.V. 1976. Succession in deciduous swamp communities of southeastern Michigan formerly dominated by American elm. Canadian Journal of Botany 54:19-24.
- Burke, M. And J. Chambers. 1999. Root dynamics of bottomland hardwood trees under different hydrologic regimes: implications for winter water management and ecological restoration. Ecology and Management of Bottomland Hardwood Systems: the State of our Understanding, March 11-13, 1999, Memphis, Tn.
- Burns, R.M. and B.H. Honkala. 1990. Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C. vol. 2, 877 pp.
- Conner, W.H., K.W. McLeod and J.K. McCarron. 1997. Flooding and salinity effects on growth and survival of four common forested wetland species. Wetlands Ecology and Management 5:99-109.
- Dahl, M. And C.E. Johnson. 1991. Status and trends of wetlands in the coterminous United States, mid-1970's to mid-1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., 28pp.
- Davy, A.J., S.M. Noble, R.P. Oliver. 1990. Genetic variation and adaptation to flooding in plants. Aquatic Botany 38:91-108.
- Davy, A.J. and H. Smith. 1985. Population differentiation in the life-history characteristics of salt-marsh annuals. Vegetatio 61:117-125.
- Davy, A.J. and H. Smith. 1988. Life-history variation and environment. In: A.J. Davy, M.J. Hutchings, and A.R. Watkinson (Editors), Plant Population Ecology. Blackwell Scientific, Oxford, pp 1-22.
- Denslow, J.S. and L.L. Battaglia. 1999. Variation in stand composition and population structure across a changing hydrologic gradient. Ecology and Management of Bottomland Hardwood Systems: the State of our Understanding, March 11-13, 1999, Memphis, Tn.
- Dicke, S.G. and J.R. Toliver. 1987. Response of cherrybark oak families to different soil-site conditions. In: Proceedings of the Fourth Biennial Southern Silvicultural Research Conference, D.R. Phillips (Editor), November 4-6, 1986, Atlanta, Georgia, Southeastern Forest Experiment Station, Asheville, North Carolina, p. 260-263.
- Edwards, M.B. 1990. *Quercus michauxii* Nutt: Swamp chestnut oak. In: Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C. vol. 2, 877 pp.

- Ernst, W.H.O. 1990. Ecophysiology of plants in waterlogged and flooded environments. Aquatic Botany 38:73-90.
- Hallgren, S.W. 1989. Growth response of *Populus* hybrids to flooding. Ann. Sci. For. 46:361-372.
- Havens, K.J. 1997. The effect of vegetation on soil redox within a seasonally flooded forested system. Wetlands 17:237-242.
- Hook, D.D. 1984. Waterlogging tolerance of lowland tree species of the south. Southern Journal of Applied Forestry 8:136-149.
- Hook, D.D. and J.R. Scholtens. 1980. Adaptations and flood tolerance of tree species, p. 299-331. IN D.D. Hook and R.M.M. Crawford (eds.) Plant Life in Anaerobic Environments. Ann Arbor Science, Ann Arbor, MI, USA.
- Jefferies, R.L. and L.D. Gottlieb. 1982. Genetic differentiation of the microspecies Salicornia europaea L. (Sensu stricto) and S. ramosissima J. Woods. New Phytologist 92:123-129.
- Krinard, R.M. 1990. Quercus falcata var. pagodifolia Ell. Cherrybark oak. In: Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C. vol. 2, 877 pp.
- Lowrance, R., L.S. Altier, J.D. Newbold, R.S. Schnabel, P.M. Groffman, J.M. Denver, D.L. Correll, J.W. Gilliam, J.L. Robinson, R.B. Brinsfield, K.W. Staver, W. Lucas, and A.H. Todd. 1997. Environmental Management 21:687-712.
- Marshall, D.R., P. Broue', and A.J. Pryor. 1973. Adaptive significance of alcohol dehydrogenase isoenzymes in maize. Nature (London) New Biology 244:16-17.
- Megonigal, J.P. and F.P. Day. 1992. Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. Ecology 73:1182-1193.
- Metzger, F.T. 1990. *Carpinus caroliniana* Walt. American Hornbeam. In: Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C. vol. 2, 877 pp.
- Niswander, S.F. and W.J. Mitsch. 1995. Functional analysis of a two-year-old created in-stream wetland: Hydrology, phosphorus retention, and vegetation survival and growth. Wetlands 15:212-225.
- Nix, L.E. and S.K. Cox. 1987. Cherrybark oak enrichment plantings appear successful after seven years in South Carolina bottomlands. In: Proceedings of the Fourth Biennial

Southern Silvicultural Research Conference, D.R. Phillips (Editor), November 4-6, 1986, Atlanta, Georgia, Southeastern Forest Experiment Station, Asheville, North Carolina, p. 129-132.

- Pereira, J.S. and T.T. Kozlowski. 1977. Variation among woody angiosperms in response to flooding. Physiologia Plantarum 41:184-192.
- Pezeshki, S.R. and P.H. Anderson. 1997. Responses of three bottomland species with different flood tolerance capabilities to various flooding regimes. Wetlands Ecology and Management 4:245-256.
- Pezeshki, S.R., J.H. Pardue, and R.D. DeLaune. 1996. Leaf gas exchange and growth of floodtolerant and flood-sensitive tree species under low soil redox conditions. Tree Physiology 16:453-458.
- Prichard, D., H. Barrett, J. Cagney, R. Clark, J. Fogg, K. Gebhardt, P. Hansen, B. Mitchell, and D. Tippy. 1993. Riparian Areas Management: Process for assessing proper functioning condition. TR-1737-9. Bureau of Land Management, BLM/SC/ST-93/003+1737, Service Center, CO, 60 pp.
- Reed, P.B. 1988. National list of plant species that occur in wetlands: 1988 national summary. U.S. Fish and Wildlife Service, Washington, D.C., U.S.A. Biological Report 88 (24).
- Shanklin, J. N and T.T. Kozlowski. 1985. Effect of flooding of soil on growth and subsequent responses of *Taxodium distichum* seedlings to SO₂. Environmental Pollution 38:199-212.
- Silberhorn, G.M. 1997. Ironwood/Blue beech/American hornbeam/Muscle wood: *Carpinus caroliniana* Walter. Technical Report Wetland flora 97-2. College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, Va. 2 p.
- Streng, D.R., J.S. Glitzenstein, and P.A. Harcome. 1989. Woody seedling dynamics in an east Texas floodplain forest. Ecological Monographs 59:177-204.
- Tiner, R.W. 1991. The concept of a hydrophyte for wetlands identification. Bioscience 41:236-247.
- Wilhite, L.P. and J.R. Toliver. 1990. T. distichum (L.) Rich. var. distichum: Baldcypress. In: Silvics of North America: 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, D.C. vol. 1, 675 pp.
- Winger, P.V. 1986. Forested wetlands of the southeast: Review of major characteristics and role in maintaining water quality. U.S. Fish and Wildlife Service, Washington, D.C., USA, Resource Publication 163.