GENOTYPIC VARIATION IN FLOOD TOLERANCE OF BLACK WALNUT AND THREE SOUTHERN BOTTOMLAND OAKS

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Abstract—Open-pollinated bare-root seedlings from six families of cherrybark oak (*Quercus pagoda* Raf.), seven families of water oak (*Q. nigra* L.), six families of willow oak (*Q. phellos* L.), and eight families of black walnut (*Juglans nigra* L.) were planted in spring 2003 in nine channels of the University of Missouri Center for Agroforestry Flood Tolerance Laboratory. At onset of budburst, seedlings were left non-flooded or flooded for 5 weeks with 15 cm deep flowing water or stagnant water. A species by flood treatment interaction existed for seedling survival, new shoot growth, and basal sprouting. Based on seedling response, black walnut exhibited the least flood tolerance followed by cherrybark oak, water oak, and willow oak. No significant differences were found for any oak species by partial inundation between flowing or stagnant water flooding. Significant family differences in survival, growth, and basal spouting were found within all three oak species. A strong opportunity exists to make significant genetic gains in field survival and growth on flood-prone sites through selection of flood tolerant seedling families for all three oak species.

INTRODUCTION

In the Central Hardwood region, there is considerable interest in restoring native ecosystems on former bottomland forests that are now used for agriculture (Kruse and Groninger 2003). The suitability of a particular tree species in a bottomland hardwood forest depends on soil moisture, stream deposition patterns, flooding season and duration, and disturbance history (Hodges 1997). Planted oak acorns and seedlings are a major component of these restoration efforts. However, with the exception of overcup oak (*Q. lyrata* Walt.), the published flood tolerance of oak species is rated no higher than "moderately tolerant" (Hook 1984), and even this classification is open to some debate (Kabrick and Dey 2001).

Results of past restoration efforts have been mixed. Stanturf and others (2001) observed major (90 percent) regeneration failures in tree plantings established under the 1992 Wetland Reserve Program in Mississippi. While some of the regeneration failures may be attributable to planting species that are not adapted to the hydrological conditions that are common in floodplain soils, these poor planting results maybe due to the use of maladapted planting stock (Connor and others 1998). Battaglia and others (2004) suggested that many oak species have the capacity to grow on both upland and lowland sites. In Missouri, nine of the twenty native oak species can be found growing on bottomland sites (Kurz 2003, Steyermark 1974). Bottomland forest restoration programs in both the Missouri and Mississippi River floodplains have yet to focus on the role of non-adapted seed sources in contributing to planting failures.

A few studies exist that have looked at intraspecific patterns of genetic variation within woody species in response to flooding. Hook (1984) suggested that the ability of a bottomland tree species to survive flooded conditions is dependent on a number of factors including age, microclimate, soil type and internal drainage, topography, and its inherent genetic makeup. Keeley (1979) found significant levels of genetic variation in flood adaptations among three seedling populations of blackgum (*Nyssa sylvatica* Marsh.). Topa and McLeod (1986a, 1986b) likewise noted significant growth differences in response to flooding for two distinct loblolly pine (*Pinus taeda* L.) seed sources. Recently, Bauerle and others (2003) reported intraspecific variation in red maple (*Acer rubrum* L.) as mesic-origin seedlings suffered greater growth

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losses due to flooding than seedlings from more flood prone (hydric) provenances. Nielsen and Jorgensen (2003) also found significant variation in growth rates among provenances of European beech (*Fagus sylvatica* L.) that had been exposed to three different levels of soil moisture.

The goals of our project were (1) to determine if significant levels of genetic variation for flood tolerance exists within hardwood species, especially those that are capable of growing from frequently flooded bottomlands to dry uplands, (2) to ascertain if nursery environment affected flood tolerance for large, high quality bare-root seedlings, and (3) to evaluate field performance of high-quality nursery seedlings grown under protocols described by Kormanik and others (1994) and Schlarbaum and others (1997). This study represents the first attempt to quantify intraspecific genetic responses to flooding for any North American oak species.

MATERIALS AND METHODS

In the fall of 2001, seed from open-pollinated mother trees from western Tennessee and northern Mississippi were collected from the following species: cherrybark oak (*Q. pagoda* Raf.) (n=6), water oak (*Q. nigra* L.) (n=7), willow oak (*Q. phellos* L.) (n=6), and black walnut (*Juglans nigra* L.) (n=8). The University of Tennessee Tree Improvement Program grew the seedlings in replicated nursery plots at the Georgia Forestry Commission's Flint River Nursery. In the fall, seedlings were lifted, individually numbered, and evaluated for number of first-order lateral roots (FOLR), root collar diameter (RCD), and stem length before shipping to Missouri. In the spring of 2003, 1706 seedlings were planted in the Flood Tolerance Laboratory (FTL) at the University of Missouri Horticulture and Agroforestry Research Center (HARC) in New Franklin, MO.

The 1-0 bare-root seedlings were planted in early April 2003 using a split-plot design replicated three times with three flooding treatment as main plots and species as subplots. The nine channels with predominantly Nodaway silt loam soils were planted with a tree-spacing of 0.75 x 1.00 m as described by Van Sambeek and others (2007). Each species was represented by a total of 6 to 8 families within each flood channel and each family was represented by a total of 2 to 14 individual trees randomly distributed within each species plot.

The flooding treatments commenced at the onset of seedling budbreak in mid May. The flooding treatments were 15 cm deep flowing water for five weeks, 15 cm deep stagnant water for five weeks, and a non-flooded control. As described by Van Sambeek and others (2007), soils in the non-flooded channels developed a high water table and remained saturated for five weeks in response to seepage from adjacent flooded channels and frequent spring rains. In addition, the entire facility was under water for three days midway during the treatment period due to a heavy rain event. Based on twice weekly sampling for gravimetric soil water content, soils remained at or above field capacity in all channels for an additional two weeks as a result of two post-flooding rain events.

Approximately 10 months after flooding, we evaluated all seedlings for survival, stem basal diameter (mm) and live height (cm), total number of new shoots with > 0.5 cm growth including basal sprouts, total new shoot length (cm), and total number of basal sprouts originating within 20 cm of the root collar (cm). Family means by species and channel were determined for percent survival, total number of new shoots, total length of new shoots, and percent of surviving seedlings producing basal sprouts. Because of unbalanced seedling numbers, a general linear model (PROC GLM) was used to determine sums of squares and examined for differences (alpha = 0.05) among treatments, species, families within species, and their interactions (SAS, Cary, NC). Least significant difference values were calculated to determine differences among specific treatments and families.

RESULTS AND DISCUSSION

Overall survival across all flood treatments ranged from 12.5 percent for black walnut, 61.4 percent for water oak, 66.4 percent for cherrybark oak, and 82.5 percent for willow oak. The low survival of black walnut seedlings (33 percent) within the non-flooded channels is likely a response to prolonged exposure to saturated soils and a high water table and not low quality planting stock. Other studies have shown that mishandling of black walnut planting stock leads to extensive stem dieback and basal sprouting but not high mortality (Rietveld and Van Sambeek 1989, von Althen and Webb 1982). Because survival within the treatments with flowing or stagnant water was less than 1 percent, black walnut was not included in any further analyses.

To evaluate genetic variation for flood tolerance, we chose to examine survival, total number and length of new shoots, and sprouting. Due to variable seedling planting depth and shoot dieback on most seedlings, we could not use the original stem diameter and length measurements to determine net height and diameter growth. In addition, Rink and Van Sambeek (1987) had previously shown that total length of new shoots produced during the first growing season in the field for planted walnut was a better indicator of future tree height than was net height and diameter growth. Analysis of variance on all measured variables for the three oak species using family means frequently showed a significant interaction for species by flooding treatment and highly significant responses among species and families within species (table 1). The lack of an interaction between flood treatment and family indicates that each family within a species had a similar response to flooding treatment while maintaining genetic differences in overall growth and survival.

The interaction between species and flood treatment was significant for two of the three oak species. Willow oak seedlings had greater than 80 percent survival across all flood treatments, while seedlings of cherrybark and water oak had lower survival rates when exposed to partial inundations in both flowing and standing water than did seedlings in the water-saturated control treatments (table 2). The flood duration was probably too brief for the more flood-tolerant willow oaks to reveal treatment differences in this study although we did find differences in survival among the six willow oak families across all three flood treatments (table 3). Differences in survival among families for cherrybark and water oak tended to be larger than for willow oak.

Table 1—Analysis of variance results for three oak species exposed to three flooding treatments in spring 2003 (expressed as percent contribution to total sums of squares)

Source	df	Seedling survival	New shoots	Length of new shoots	Basal sprouting
		(percent)	*(number)*	*(cm)*	*(percent)*
Block	2	5.04	3.95	0.05	0.18
Treatment	2	8.24	3.39	0.13	1.90
Error A	4	4.11	6.14	2.77	1.16
Species	2	12.45 [a]	12.77 [a]	46.03 [a]	47.06 [a]
S X T	4	3.72 [a]	5.13 [b]	0.59	3.83 [a]
Family (species)	16	26.96 [a]	16.45 [a]	14.01 [a]	11.45 [a]
T X F(S)	32	10.61	10.59	7.01	13.00 [a]
Error B	103	39.24	27.64	26.98	21.53

[a] = statistical differences at p = 0.01.
[b] = statistical differences at p = 0.05.

Table 2—Effects of three flooding treatments on percent survival, total number of new shoots, total length of new shoot growth, and percent with basal sprouts for cherrybark, water, and willow oak species

Treatment[a]	CBO	WAO	WLO
	Percent survival fall 2003		
	- - - - - - - - - - *percent* - - - - - - - - - -		
DRY	79.9	77.5	83.1
FLOW	52.9	52.1	83.2
STAG	66.2	54.1	81.4
Mean	66.4	61.4	82.5
$LSD_{0.05}$ = 11.0 percent			
	Total number of new shoots		
	- - - - - - - - - - *number* - - - - - - - - - -		
DRY	3.8	2.9	3.8
FLOW	2.5	2.5	3.9
STAG	2.4	3.2	3.8
Mean	2.9	2.9	3.8
$LSD_{0.05}$ = 0.7 percent			
	Total length new shoots/seedling		
	- - - - - - - - - - - - *cm* - - - - - - - - - - - -		
DRY	25.0	52.6	67.1
FLOW	16.5	49.3	72.2
STAG	18.6	54.5	69.1
Mean	20.0	52.2	69.5
$LSD_{0.05}$ = 12.9 percent			
	Percent seedling w/basal sprouts		
	- - - - - - - - - - *percent* - - - - - - - - - -		
DRY	15.4	92.5	66.5
FLOW	32.1	76.9	73.8
STAG	25.8	66.1	57.5
Mean	24.4	65.8	79.0
$LSD_{0.05}$ = 13.4 percent			

CBO = cherrybark oak; WAO = water oak; WLO = willow oak.
[a] Flooding treatments were a water-saturated, nonflooded control (DRY), 15 cm deep flowing water for 5 weeks (FLOW), and 15 cm deep stagnant water for 5 weeks (STAG).

Table 3—Percent seedling survival, total number of new shoots, total length of new shoots, percent basal sprouting, and flood tolerance index values for six to seven families of cherrybark oak, water oak, and willow oak

Species[a]	Family	Seedling survival	New shoots	Length of new shoots	Basal sprouting	Flood tolerance index
		percent	*number*	*cm*	*- - - - - - percent*	*- - - - - -*
CBO	CBO6	54.8	3.4	31.1	28.0	0.65
	PHC4	78.6	3.4	20.6	7.8	0.61
	MS57	71.8	2.9	19.4	30.4	0.45
	MS56	56.4	2.4	19.9	25.5	0.34
	PHC1	84.8	2.4	11.0	22.2	0.28
	CBO1	50.0	2.7	18.0	33.8	0.27
WAO	MS2	73.7	3.6	61.0	71.3	0.90
	PH2	80.0	2.8	62.3	89.3	0.78
	PHWA4	70.6	3.0	53.3	51.5	0.63
	MS54	59.0	3.0	54.4	81.7	0.53
	MS51	63.9	2.6	45.8	73.9	0.43
	WTR26	54.2	2.3	37.6	92.9	0.26
	PHWA1	26.6	2.7	46.1	99.9	0.18
WLO	PH17	87.3	6.9	82.8	54.4	0.93
	PH18	93.1	4.1	79.5	63.7	0.56
	PHWL1	86.7	4.0	79.2	57.4	0.51
	MS25	79.9	3.4	83.8	80.2	0.42
	PH8	75.1	3.3	46.0	67.1	0.21
	PH13	71.0	2.8	48.1	72.5	0.16
$LSD_{0.05}$		15.6	1.0	18.3	18.9	NA

CBO = cherrybark oak; WAO = water oak; WLO = willow oak; NA = non-applicable.
[a] Flood tolerance index is the product of ratio of family mean divided by mean for the best family within each species for survival, number, and length of new shoots.

The total number of new shoots per seedling reflected both a significant species by treatment and family response (table 1). While seedlings of water oak and willow oak showed no differences in the number of elongating shoots in response to flooding, both flowing and stagnant flooding reduced the number of elongating shoots on cherrybark oak seedlings (table 2). There were no significant differences in the total number of new shoots among families of cherrybark oak, in contrast to water oak and willow oak (table 3). For water and willow oak, better surviving families tended to have the highest number of new shoots. This trend was particularly noticeable among willow oak families where the best surviving families, PH17, PH18 and PHWL1, had the greatest number of actively elongating shoots during the first growing season.

There was a significant species effect but not a significant species by treatment effect on total length of new shoots (table 1). Willow oak appeared to be the most flood tolerant species and showed the greatest cumulative new shoot growth across all flood treatments followed by water oak and cherrybark oak (table 2). Differences were found in cumulative shoot growth among families within all three oak species (table 3). As expected, the families with the highest number of elongating shoots had the greatest cumulative shoot growth.

The expected pattern of extensive dieback followed by basal sprouting observed with black walnut was not observed among the three oak species. For the least flood tolerant species, cherrybark oak, increased flooding stress in response to flowing or stagnant flooded increased the percent basal sprouting (table 2). In contrast, over 90 percent of the water oak seedlings in the non-flooded control channels produced basal sprouts compared to approximately 70 percent of the seedlings in the channels flooded with flowing or stagnant water. There was also a significant family within species effect for percent sprouting. For cherrybark oak, one of the best surviving families, PHC4, had the lowest basal sprouting percentage (table 3). In contrast, family CB001 had the poorest survival and highest basal sprouting percentage. Similarly, water oak family PHWA1 had only 26.8 percent survival and 100 percent sprouting compared to family PH2 that had 80.0 percent survival and an 89 percent sprouting rate. For willow oak, however, the best surviving families, PH17, PH18, and PHWL1, had fewer seedlings producing basal sprouts than did the families with the poorest survival.

Significant family within species variation occurred for FOLR number (first order lateral roots > than 1 mm in diameter), root collar diameter, and stem height (table 4). To determine whether family differences associated with size of planting stock out of the nursery impacted flood tolerance, we created an index to rank families within species as to their flood tolerance. Index values were determined by multiplying the ratios of observed divided by maximum values for survival and total number and length of new shoots, i.e. flood tolerance index for water oak MS2 equals 0.89 or (73.7/80.8) x (3.6/3.6) x (61.0/62.3), which allowed us to rank families from most to least tolerant. Using Spearman's rank correlations, we found strong concordance between flood tolerance and outplanting root collar diameter and FOLR number for willow oak. In contrast, no concordance was found between initial seedling size and the family flood tolerance index rankings for black walnut, cherrybark oak, or water oak. Kormanik and others (2005) have indicated that under stress newly planted upland oak seedlings can rapidly shed lateral roots including the first order lateral roots. The lack of significant correlation between seedling FOLR and flood response may in part be due to root loss and differences among families within the less flood tolerant species to recover from stress.

In summary, all four hardwood species tested responded differently to the flooding treatments used in this study. The low survival for black walnut confirms previously published results that indicate black walnut is a flood-intolerant species as reported by Kabrick and Dey (2001). There was a definite trend towards the greatest shoot growth, highest numbers of shoots, and lowest percent sprouting among the best surviving willow oak families (e.g., PH17, PH18, and PHWL1). These relationships were less apparent among the water oak families, in which the best surviving families tended to also have the greatest shoot growth (e.g., MS2, PH2, and PHWA4), but not necessarily the fewest number of new shoots or lowest percent sprouting. Similarly, the best surviving cherrybark oak families did not always have the greatest shoot length and lowest sprouting percentage. The highly significant differences among families within oak species for all variables would lead us to conclude that there is a strong opportunity to make significant genetic gains in field survival through selection of more flood tolerant seedling families.

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Table 4—Initial seedling size measurements (standard deviation) for first-order lateral roots, root collar diameter, and stem height on six to eight families of black walnut, cherrybark oak, water oak, and willow oak from the University of Tennessee Tree Improvement Program planted in 2003 in the Flood Tolerance Laboratory

Species	Family[a]	Number	FOLR	RCD	Stem height
			number	*mm*	*cm*
BLW	BW14	72	—	15.2 (2.6)	90.2 (24.0)
	BW17	65	—	13.6 (2.2)	83.2 (19.1)
	BW21	29	—	14.2 (1.9)	63.7 (14.7)
	BW02	36	—	13.0 (2.4)	73.4 (17.7)
	BW21	29	—	14.2 (1.9)	63.7 (14.7)
	BW35	37	—	12.6 (2.1)	69.0 (15.0)
	BW36	72	—	13.3 (2.7)	81.3 (13.8)
	BW45	34	—	14.3 (5.0)	78.6 (22.9)
	BW49	34	—	13.3 (2.8)	85.6 (20.8)
CBO	CBO6	93	7.6 (5.3)	9.4 (1.3)	112.9 (13.7)
	PHC4	52	7.8 (4.2)	10.4 (1.8)	106.9 (16.9)
	MS57	90	5.6 (3.6)	9.0 (1.1)	108.1 (13.0)
	MS56	88	6.8 (4.3)	9.4 (1.2)	120.6 (12.6)
	PHC1	91	8.7 (6.3)	9.3 (1.4)	106.9 (15.0)
	CBO1	40	7.4 (3.4)	9.9 (1.8)	108.3 (26.5)
WAO	MS2	62	5.6 (3.9)	10.0 (1.9)	107.9 (12.3)
	PH2	63	4.3 (2.8)	9.9 (1.4)	99.4 (14.4)
	PHWA4	80	5.8 (3.1)	9.6 (1.5)	101.9 (13.2)
	MS54	53	5.2 (4.1)	9.3 (1.6)	112.3 (14.6)
	MS51	60	5.9 (2.7)	10.2 (1.3)	103.5 (16.3)
	PHWA1	92	2.5 (2.0)	8.8 (1.6)	98.2 (16.4)
	WTR26	24	4.0 (2.0)	8.8 (0.9)	100.2 (8.7)
WLO	PH17	37	6.6 (2.9)	11.0 (1.8)	92.7 (11.6)
	PH18	76	4.8 (2.5)	10.2 (1.4)	101.1 (13.2)
	PHWL1	84	5.2 (2.8)	9.9 (1.3)	97.4 (12.9)
	MS25	89	5.0 (3.0)	9.9 (1.6)	105.6 (12.8)
	PH8	52	3.1 (2.4)	9.5 (1.3)	103.2 (15.2)
	PH13	93	2.9 (1.9)	9.4 (1.3)	106.4 (12.7)

— = data not measured.
FOLR = first-order lateral roots; RCD = root-cellar diameter; BLW = black walnut; CBO = cherrybark oak; WAO = water oak; WLO = willow oak.
[a] Families within species are ranked from most to least flood tolerant according to flood tolerance index values shown in table 3.

LITERATURE CITED

Battaglia, L.L.; Collins, B.S.; Sharitz, R.R. 2004. Do published tolerance ratings and dispersal factors predict species distributions in bottomland forests? Forest Ecology and Management. 198(1-3):15-30.

Bauerle, W.L.; Whitlow, T.H.; Setter, T.L. [and others]. 2003. Ecophysiology of *Acer rubrum* seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. Tree Physiology. 23:841-850.

Connor, W.H.; McLeod, K.W.; McCarron, J.K. 1998. Survival and growth of seedlings of four bottomland hardwood oak species in response to increases in flooding and salinity. Forest Science. 44(4):618-624.

Hodges, J.D. 1997. Development and ecology of bottomland hardwood sites. Forest Ecology and Management. 90:117-125.

Hook, D.D. 1984. Waterlogging tolerance of lowland tree species in the South. Southern Journal of Applied Forestry. 8:136-148.

Kabrick, J.M.; Dey, D.C. 2001. Silvics of Missouri bottomland tree species. Notes for forest managers report #5. Jefferson City, MO: Missouri Department of Conservation. 8 p.

Keeley, J.E. 1979. Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica*. Ecological Monographs. 49(1):89-108.

Kormanik, P.P.; Sung, S.S.; Kormanik, T.L. 1994. Toward a single nursery protocol for oak seedlings. In: Proceedings of northeast and intermountain forest and conservation nursery associations. Gen. Tech. Rep. RM-243. Fort Collins, CO: U.S. Department of Agriculture, Rocky Mountain Forest Experiment Station:115-121.

Kormanik, P.P.; Sung, S.S.; Zarnoch, S.J. 2005. Is seedling grading beneficial to artificial regeneration of northern red oaks? In: Weigel, D.R.; Van Sambeek, J.W.; Michler, C.H., editors. Ninth workshop on seedling physiology and growth problems in oak plantings (abstracts); Gen. Tech. Rep. NC-262. St. Paul, MN: U.S. Department of Agriculture, Forest Service. North Central Research Station. 8 p.

Kruse, B.S.; Groninger, J.W. 2003. Vegetative characteristics of recently reforested bottomlands in the Lower Cache River watershed, Illinois, U.S.A. Restoration Ecology. 11(3):273-280.

Kurz, D. 2003. Trees of Missouri. Jefferson City, MO: Missouri Department of Conservation. 399 p.

Nielsen, C.N.; Jorgensen, F.V. 2003. Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and among provenances. Forest Ecology and Management. 174(1-3):233-249.

Rietveld, W.R.; Van Sambeek, J.W. 1989. Relating black walnut planting stock quality to field performance. In: Rink, G.; Budelsky, C.A., editors. Proceedings, seventh central hardwood forest conference. Gen. Tech. Rep. NC-132. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station:162-169.

Rink, G.; Van Sambeek, J.W. 1987. Seedling-sapling growth variation in a southern Illinois black walnut provenance/progeny test. In: Guries, R.P., editor. Proceedings, fifth north central tree improvement conference. Madison, WI: University of Wisconsin:156-162.

Schlarbaum, S.E.; Kormanik, P.P.; Tibbs, T.; Barber, L.R. 1997. Oak seedlings: quality improved available now- genetically improved available soon. In: Myer, D.A., editor. Twenty-five years of hardwood silviculture: a look back and a look ahead (Proceedings, twenty-fifth annual hardwood symposium). Memphis, TN: National Hardwood Lumber Association:123-130.

Stanturf, J.A.; Schoenholtz, S.H.; Schweitzer, C.J.; Shepard, J.P. 2001. Achieving restoration success: myths in bottomland hardwood forests. Restoration Ecology. 9(2):189-200.

Steyermark, J.A. 1974. Flora of Missouri. 4th edition. Ames, IA: Iowa State University Press. 1728 p.

Topa, M.A.; McLeod, K.W. 1986a. Responses of *Pinus clausa*, *Pinus serotina* and *Pinus taeda* to anaerobic solution culture. I. Changes in growth and root morphology. Physiologia Plantarum. 68:523-531.

Topa, M.A.; McLeod, K.W. 1986b. Responses of *Pinus clausa*, *Pinus serotina* and *Pinus taeda* to anaerobic solution culture. II. Changes in tissue nutrient concentration and net acquisition. Physiologia Plantarum. 68:532-539.

Van Sambeek, J.W.; McGraw, R.L.; Kabrick, J.M. [and others]. 2007. Developing a field facility for evaluating flood tolerance of hardwood seedlings and understory ground covers. In: Buckley, David S.; Clatterbuck, Wayne K., eds. Proceedings, 15th central hardwood forest conference. e-Gen. Tech. Rep. SRS–101. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 642-648.

Von Althen, F.W.; Webb, D.P. 1982. Effects of packaging methods on the survival and growth of cold-stored hardwood planting stock. In: Proceedings, northeastern area nurseryman's conference: 74-79.