FUNDAMENTAL RESEARCH

For. Sci. 65(5):556–561
doi: 10.1093/forsci/fxz028
Published by Oxford University Press on behalf of the Society of American Foresters 2019.

forest ecology

The Influence of Dormancy Break Requirements on Germination and Viability Responses to Winter Submergence in Acorns of Three Bottomland Red Oak (Sect. Lobatae) Species

Tracy S. Hawkins

The objective of this study was to examine the relation of dormancy break requirements to winter submergence effects on germination and viability in cherrybark, willow, and Nuttall oak acorns. Acorns were submerged in a greentree reservoir and received 0, 21, 42, 63, or 84 days of winter submergence, followed by 8 weeks of incubation in four temperature regimes (15/6°, 20/10°, 25/15°, and 30/20° C). Winter submergence substituted for cold stratification requirements of cherrybark oak acorns, and dormancy break was achieved with 63 days of submergence. Although winter submergence exerted a positive effect on germination in Nuttall and willow oak acorns, dormancy break was not achieved in acorns of either species. Germination percentages were highest in the 30/20° C incubation temperature—cherrybark oak acorns (75–83 percent), followed by Nuttall oak (33–55 percent) and willow oak (14–52 percent). Among treatment combinations, all willow oak nongerminants were viable. Viability loss in cherrybark and Nuttall oak acorns was greatest in the 63- and 84-day treatments. The dynamics of acorn germination in response to winter hydrologic regime is influenced by submergence duration that may, or may not, satisfy dormancy break requirements in acorns of these red oak species.

Keywords: acorn germination, acorn submergence, bottomland forests, *Quercus*, red oak acorns

Flooding regime is one of the most important environmental factors affecting plant species distribution in bottomland forests in the southeastern United States (Hodges 1997, Gardiner 2001). Red oaks (*Quercus* spp.) of section *Lobatae* are often a major component of these forests; therefore, much research has focused on tree morphological and physiological responses to flooding frequency and duration. In turn, these research efforts have identified species-specific adaptations that direct plant distribution throughout the forest and allow for persistence in this type of habitat (Pezeshki and Anderson 1996, Gravatt and Kirby 1998, Anderson and Pezeshki 1999, Gardiner and Krauss 2001, and others). Far fewer studies have examined the effect of hydrologic regime on bottomland oak acorn germination and viability loss, and intra- and interspecific comparisons have varied dependent upon research protocol. Prior research has shown that acorn germination may be influenced by submergence duration (Briscoe 1961, Larsen 1963, Guo et al. 2002), water temperature (Guo et al. 1998), and whether submergence is static or intermittent (Walls et al. 2005). However, the fate of acorns that fail to germinate (i.e., remain viable or are nonviable) is severely underreported in the literature (but see Guo et al. 1998), and knowledge gaps regarding causative effects for interspecific differences in acorn germination success or failure continue to exist. Additionally, post-submergence acorn fate has not been investigated relative to seed dormancy.

Seed dormancy is defined as a failure of seeds to germinate, although environmental conditions (e.g., water, temperature, light availability) are favorable for germination (Baskin and Baskin 2004, 2014). In turn, this ecological adaptation delays seed germination until conditions are conducive for seedling establishment and survival. The underlying cause of seed dormancy may be anatomical, such as an impermeable barrier (e.g., seed-coat) that prevents water uptake (imbibition; Baskin et al. 2000) or an underdeveloped embryo that must grow and develop prior to seed germination (Baskin and Baskin 2005). Alternatively, if seeds possess a developed embryo and readily imbibe water, dormancy break occurs when environmental cues, such as a period of warm or cold stratification,

Manuscript received July 24, 2018; accepted April 17, 2019; published online June 5, 2019.

Affiliation: *Tracy S. Hawkins (tracyhawkins@fs.fed.us), USDA Forest Service, Center for Bottomland Hardwoods Research, Box 9681, Mississippi State, MS 39762.*

Acknowledgments: *The author thanks Rory Thornton for help with data collection, the Mississippi Forestry Commission for permitting acorn collection at Winona Seed Orchard, and Dr. Charles Sabatia for contributions to data analyses and review of an earlier draft of this manuscript.*

initiate physiological changes (biosynthesis of gibberellic acids, decreased abscisic acid levels) in the seed (Obroucheva 2010). In temperate forests, stratification generally occurs on a moist substrate such as soil or in leaf litter following dispersal.

Bonner and Vozzo (1987) describe acorns of red oaks of *Lobatae* as having the ability to imbibe water and possessing fully developed embryos that do not grow during cold stratification. Interspecifically, red oak acorns require varying lengths of cold stratification to "enhance germination rate" (Bonner and Vozzo 1987). Thus, we can infer from these descriptions that red oak acorn germination is delayed by a physiological inhibiting mechanism, and these acorns possess what is termed physiological dormancy (PD; Baskin and Baskin 2004, 2014). Seeds that possess PD are further categorized as displaying nondeep, intermediate, or deep PD. Nondeep PD is broken by ≤12 weeks of stratification (warm or cold), and application of gibberellic acid (GA_3) substitutes for stratification. A stratification period of greater than 12 weeks is required for dormancy break in seeds with deep PD, and GA_3 does not satisfy the stratification requirement. Seeds with intermediate PD fall somewhere between those with nondeep and deep PD, and require 8–12 weeks of stratification, and GA_3 promotes germination in seeds of some, but not all, species (Baskin and Baskin 2014). Additionally, dry storage may shorten the stratification period normally required. Relative to red oaks, Hawkins (2018) recently identified the presence of nondeep physiological dormancy in acorns of cherrybark oak (*Q. pagoda* Raf.).

Seed stratification often occurs in an aerobic environment and on a moist substrate such as soil, sand, or leaf litter. However, in habitats prone to flooding, seeds may be subject to submergence and anaerobic conditions, although it has been found that submergence may partially, or fully, replace stratification requirements in seeds of some species (Insausti et al. 1995, Moravková et al. 2002, Hawkins et al. 2011). Therefore, if cold water submergence of red oak acorns substitutes for cold stratification, then the role of seed dormancy should be factored into the interpretation of submergence effect on germination and viability in these acorns. For example, if, following submergence, acorn germination percentages are low, and remaining ungerminated acorns are viable, potential explanations are (1) submergence time or temperature did not satisfy dormancy break requirements, (2) post-submergence temperature(s) did not meet germination temperature requirements, or 3) an interaction of submergence time (or temperature) and post-drop down temperatures did not satisfy dormancy break and germination requirements.

This research was designed to simulate winter submergence durations and post-drop down temperatures that may occur in bottomland forests in the southeastern United States. The focus of the study are three sympatric red oak species—cherrybark oak, willow oak (*Q. phellos* L.), and Nuttall oak (*Q. texana* Buckley). These species are commonly found in bottomland hardwood forest canopies. Mature Nuttall oak and willow oak trees are described as moderately flood tolerant and may be found growing along a continuum from ridges to low flats (Tanner 1986, Gardiner 2001). Cherrybark oak is moderately flood intolerant and typically grows on well-drained sites and ridges (Gardiner 2001).

The objectives of this study were to examine the effects of winter submergence on cherrybark, Nuttall, and willow oak acorn germination and viability, determine whether these two parameters are affected by post-submergence temperatures, and interpret responses (or lack of) to winter submergence as they may relate to seed dormancy break and germination requirements.

Methods

Winter Submergence Treatments

On November 9, 2010, mature acorns were harvested directly from randomly chosen cherrybark and Nuttall oak trees growing at Winona Seed Orchard, Winona, Mississippi, and from willow oak trees growing on the Mississippi State University campus, Mississippi State, Mississippi. The rationale for harvesting mature acorns directly from trees was to ensure that they had not received stratification and were in equivalent states of dormancy.

Acorns were immediately taken to the laboratory, placed in 5-gallon buckets containing distilled water and labeled by oak species. Acorns remained in the distilled water for approximately 1 hour. Acorns that floated were considered nonviable and discarded. Water was then removed, and acorns (nonfloaters) remained in the bucket overnight at ambient room temperature (~20° C).

For each species, 25 acorns each were placed in 64 mesh bags. Bags were connected to a rope with plastic cable ties at a distance of approximately 6 cm between bags. On November 10, 2010, each group of bags was secured between two steel t-posts and submerged to a depth of 45 cm in a greentree reservoir (GTR) at Sam D. Hamilton Noxubee National Wildlife Refuge (33°17′39.76″N, 88°46′43.68″W), which is located in the Interior Flatwoods of east-central Mississippi, USA. The mean temperature for this area during winter is 7° C (Brent 1986).

Water temperature at submerged acorn depth was recorded at approximately 10 day intervals from November 10, 2010 to February 14, 2011.

Post-Winter Submergence Temperature Treatments

Four incubators were set at 12-hour/12-hour daily alternating temperature regimes to simulate seasonal air temperatures in the range of the three oak species: 15/6°, 20/10°, 25/15°, and 30/20° C. The light regime in the incubators was set for 12 hours of light (50 μmol/m^2/s) diurnally during the high-temperature period and 12 hours of uninterrupted dark during the low-temperature period. For the control (0 days winter submergence), acorns were placed in

Management and Policy Implications

This research has shown that the impact of winter submergence on acorn germination for three bottomland red oak species is species-specific and influenced by flood duration, acorn dormancy break requirements, and post-drop down temperatures. Although short-duration winter flooding (~3 weeks) may enhance post-drop down germination in cherrybark oak acorns, the same effect may not be observed in acorns of willow oak and Nuttall oak. Winter flooding of longer duration (≥6 weeks) may further increase the percentage of germinating cherrybark acorns, exert a neutral effect on willow oak acorns, and render a large percentage of Nuttall oak acorns nonviable. Regardless of whether winter flooding occurs naturally, or is anthropogenically controlled, red oak acorn germination, and the synchrony of germination, may be somewhat equivalent among species following short-duration winter flooding, but vary significantly in years with longer winter flood duration.

16 cm × 16 cm × 2 cm clear plastic dishes and on moistened river sand purchased from a local hardware store. Four replicates of 25 acorns of each oak species were placed in each of the incubation temperature regimes on November 10, 2010.

Sixteen bags of acorns for each species were removed from the GTR and returned to the laboratory at 21, 42, 63, and 84 days of winter submergence. Acorns were removed from the bags, washed gently, and placed on moist sand in clear plastic dishes. Four replicates of 25 acorns for each of the species were placed in each of the four incubators.

Acorn germination was recorded at 1-week intervals for 8 weeks. Emergence of the radicle (≤2 mm) was the criterion for germination. At 8 weeks of incubation, all acorns that did not germinate were checked for viability. Firm, white embryos were considered viable. Acorns with soft, brown to gray embryos, or those partially or fully decayed were considered nonviable.

Statistical Analysis

Means and standard errors were calculated for germination and nonviability percentages. A binomial distribution generalized linear model with partitioned analysis of least significant means was used to test for fixed effects and interaction of winter submergence duration and incubation temperature on acorn germination and viability. An overdispersion parameter was included for fitting the model. A post-hoc Tukey's HSD (P = .05) procedure was used to adjust P-values for simple effect comparisons of the levels of temperature at a given level of winter submergence treatment and vice versa. The SAS procedure GLIMMIX was used to perform all analyses (SAS Institute Inc. 2007).

Results

The water temperature in the GTR at the depth of submerged acorns (45 cm) was 13.0° C at the beginning of the study (November 10, 2010). Thereafter, water temperatures steadily declined, showed minimal fluctuation over the course of winter submergence treatments, and remained below 8° C (Figure 1). Acorns did not germinate during submergence.

The interaction of winter submergence duration and incubation temperature had a significant effect on germination percentages of cherrybark oak acorns (df = 12, F = 10.00, P < .0001). Germination percentages increased with increasing winter submergence duration when incubated at 15/6° (df = 4, F = 137.18, P < .0001) and 20/10° C (df = 4, F = 102.81, P < .0001) through the 63-day treatment, and at 25/15° C (df = 4, F = 29.95, P < .0001) through the 42-day treatment (Table 1). In the 63- and 84-day treatments, mean total germination percentages across all incubation temperatures were ≥75 ± 5 percent (Table 1), and in these treatments, maximum germination percentages were reached within 4 weeks at the 25/15° and 30/20° C incubation temperatures (data not shown).

The interaction of winter submergence duration and incubation temperature affected nonviability percentages of cherrybark oak acorns (df = 12, F = 5.06, P < .0001). In the control and 21-day treatment, all cherrybark oak acorns that did not germinate were viable (Table 1). However, in the 42-day treatment, 40 ± 4 percent and 21 ± 6 percent of acorns were nonviable in the 15/6° and 20/10° C temperatures, respectively. All nongerminants in the 63- and 84-day treatments were nonviable in all temperature regimes (Table 1).

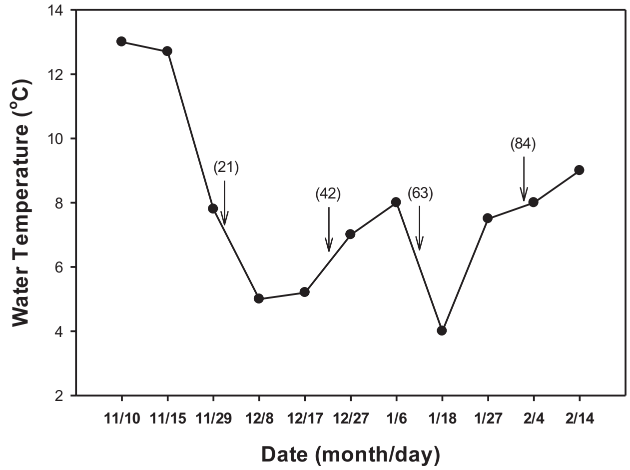

Figure 1. Water temperatures (° C; depth = 45 cm) received by cherrybark (*Quercus pagoda*), Nuttall (*Q. texana*), and willow oak (*Q. phellos*) acorns during a gradient of winter submergence treatments in a greentree reservoir at Sam D. Hamilton Noxubee Wildlife Refuge, Noxubee County, Mississippi. Arrows indicate time (date) of acorn removal from the GTR, and numbers represent the total number of days of the winter submergence treatment.

Mean total germination in willow oak acorns was affected independently by winter submergence duration (df = 4, F = 10.22, P < .0001) and incubation temperature (df = 3, F = 10.91, P < .0001). At 30/20° C, total germination was ≥46 percent among winter submergence treatments, with the exception of the 42-day treatment, where mean total germination was 14 ± 4 percent (Table 2). Mean total germination percentages were greatest in the 84-day treatment for acorns incubated at 15/6° (25 ± 7 percent), 20/10° (23 ± 3 percent), and 25/15° C (43 ± 3 percent) incubation temperatures. All ungerminated acorns in all treatments were viable (Table 2).

Nuttall oak acorn germination was affected by the interaction of winter submergence duration and incubation temperature (df = 12, F = 3.58, P = .0005). Mean total germination percentages for acorns in the 30/20° C temperature regime increased with 42 days of winter submergence and were consistently highest among incubation temperatures in all submergence treatments (Table 3). At the 20/10° and 25/15° C incubation temperatures, germination percentages increased with 63 days (df = 4, F = 17.47.96, P < .0001) and 84 days (df = 4, F = 70.07, P < .0001) of winter submergence, respectively. Some acorns at the 15/6° C incubation temperature germinated in the 63- and 84-day treatments; however, percentages were ≤10 ± 2 percent (Table 3).

The interaction of winter submergence duration and incubation temperature (df = 12, F = 3.04, P = .0021) affected nonviability percentages in Nuttall oak acorns. All nongerminants in the control were viable. However, in the 21-day treatment, 51 ± 4 percent of all acorns in the 30/20° C incubation temperature were nonviable (Table 3). Among incubation temperatures in the 42-day treatment, nonviability percentages ranged from 3 ± 2 percent (25/15° C) to 39 ± 4 percent (30/20° C). All ungerminated acorns in all incubation temperatures in the 63- and 84-day treatments were nonviable (Table 3).

Discussion

Seed dormancy break is a dynamic process, and in the vast majority of species with seeds that possess physiological dormancy

Table 1. Mean (±SE) total germination, viability, and nonviability percentages for cherrybark oak (*Quercus pagoda*) acorns receiving 0, 21, 42, 63, and 84 days of winter submergence in a greentree reservoir, followed by 8 weeks of incubation at 15/6°, 20/10°, 25/15°, and 30/20° C.

	Winter submergence (days)	Incubation alternating temperature regime (° C)			
		15/6	20/10	25/15	30/20
Germination (percent)	0	5 ± 3^{Aa}	23 ± 4^{Ba}	62 ± 7^{Ca}	80 ± 4Da
	21	5 ± 2^{Ab}	49 ± 4^{Bb}	64 ± 4^{Ca}	83 ± 3Da
	42	42 ± 3^{Ac}	68 ± 5^{Bc}	85 ± 4^{Bb}	83 ± 5^{Ba}
	63	82 ± 1^{Ad}	88 ± 5^{Ad}	82 ± 3^{Ab}	81 ± 4^{Aa}
	84	84 ± 6^{Ad}	85 ± 2^{Ad}	87 ± 3^{Ab}	75 ± 5^{Aa}
Viable (percent)	0	95 ± 3^{Aa}	77 ± 4^{Ba}	38 ± 7^{Ca}	20 ± 4Da
	21	75 ± 2^{Ab}	51 ± 4^{Bb}	36 ± 4^{Ca}	17 ± 2Da
	42	18 ± 3^{Ac}	11 ± 3^{Ac}	15 ± 4^{Ab}	17 ± 5^{Aa}
	63	0^{Ad}	0^{Ad}	0^{Ac}	0^{Ab}
	84	3 ± 2^{Ad}	0^{Ad}	1 ± 1^{Ac}	1 ± 1^{Ab}
Nonviable (percent)	0	0^{Aa}	0^{Aa}	0^{Aa}	0^{Aa}
	21	0^{Aa}	0^{Aa}	0^{Aa}	0^{Aa}
	42	40 ± 4^{Ab}	21 ± 6^{Bb}	0^{Ca}	0^{Ca}
	63	18 ± 1^{Ac}	12 ± 5^{Ac}	18 ± 3^{Ab}	19 ± 4^{Ab}
	84	13 ± 6^{Ac}	15 ± 2^{Ac}	12 ± 3^{Ab}	24 ± 5^{Bb}

Note: Means with dissimilar uppercase letters are significantly different within a submergence duration, and means with dissimilar lowercase letters are significantly different within a given incubation temperature and acorn fate (Tukey's HSD, $P = .05$).

Table 2. Mean (±SE) total germination and viability percentages for willow oak (*Quercus phellos*) acorns receiving 0, 21, 42, 63, and 84 days of winter submergence in a greentree reservoir, followed by 8 weeks of incubation at 15/6°, 20/10°, 25/15°, and 30/20° C.

	Winter submergence (days)	Incubation alternating temperature regime (° C)			
		15/6	20/10	25/15	30/20
Germination (percent)	0	0^{Aa}	0^{Aa}	6 ± 3^{Aa}	50 ± 8^{Ba}
	21	0^{Aa}	4 ± 2^{Aa}	20 ± 5^{Bb}	46 ± 12^{Ca}
	42	3 ± 2^{Aa}	6 ± 3^{Aa}	11 ± 6^{Aa}	14 ± 4^{Ab}
	63	0^{Aa}	6 ± 1^{Aa}	22 ± 9^{Bb}	52 ± 5^{Ca}
	84	25 ± 7^{Ab}	23 ± 3^{Ab}	43 ± 3^{Bc}	52 ± 2^{Ba}
Viable (percent)	0	100 ± 0^{Aa}	100 ± 0^{Aa}	94 ± 3^{Aa}	50 ± 8^{Ba}
	21	100 ± 0^{Aa}	96 ± 2^{Aa}	80 ± 5^{Bb}	54 ± 12^{Ca}
	42	97 ± 2^{Aa}	94 ± 3^{Aa}	89 ± 6^{Aa}	86 ± 4^{Ab}
	63	100 ± 0^{Aa}	94 ± 1^{Aa}	78 ± 9^{Bb}	48 ± 5^{Ca}
	84	75 ± 7^{Ab}	77 ± 3^{Ab}	57 ± 3^{Bc}	48 ± 2^{Ba}

Note: Means with dissimilar uppercase letters are significantly different within a submergence duration, and means with dissimilar lowercase letters are significantly different within a given incubation temperature and acorn fate (Tukey's HSD, $P = .05$).

Table 3. Mean (±SE) total germination, viability, and nonviability percentages for Nuttall oak (*Quercus texana*) acorns receiving 0, 21, 42, 63, and 84 days of winter submergence in a greentree reservoir, followed by 8 weeks of incubation at 15/6°, 20/10°, 25/15°, and 30/20° C.

	Winter submergence (days)	Incubation alternating temperature regime (° C)			
		15/6	20/10	25/15	30/20
Germination (percent)	0	0^{Aa}	0^{Aa}	4 ± 2^{Aa}	33 ± 4^{Ba}
	21	1 ± 1^{Aa}	4 ± 2^{Aa}	14 ± 4^{Ba}	39 ± 6^{Ca}
	42	0^{Aa}	6 ± 3^{Ba}	9 ± 2^{Ba}	55 ± 2^{Ca}
	63	7 ± 2^{Aa}	15 ± 4^{Ab}	15 ± 7^{Aa}	43 ± 5^{Ba}
	84	10 ± 2^{Ab}	21 ± 1^{Bb}	46 ± 5^{Cb}	51 ± 8^{Ca}
Viable (percent)	0	100 ± 0^{Aa}	100 ± 0^{Aa}	96 ± 2^{Aa}	66 ± 4^{Ba}
	21	99 ± 1^{Aa}	96 ± 2^{Aa}	86 ± 4^{Aa}	9 ± 3^{Bb}
	42	93 ± 3^{Aa}	74 ± 7^{Bb}	82 ± 1^{Bb}	6 ± 2^{Cb}
	63	0^{Ab}	0^{Ac}	0^{Ac}	0^{Ab}
	84	0^{Ab}	0^{Ac}	0^{Ac}	0^{Ab}
Nonviable (percent)	0	0^{Aa}	0^{Aa}	0^{Aa}	0^{Aa}
	21	0^{Aa}	0^{Aa}	0^{Aa}	51 ± 4^{Bb}
	42	6 ± 3^{Aa}	14 ± 7^{Ab}	3 ± 2^{Aa}	39 ± 4^{Bb}
	63	93 ± 2^{Ab}	85 ± 4^{Ac}	85 ± 7^{Ab}	57 ± 5^{Bb}
	84	90 ± 2^{Ab}	79 ± 1^{Bc}	54 ± 5^{Cc}	49 ± 8^{Cb}

Note: Means with dissimilar uppercase letters are significantly different within a submergence duration, and means with dissimilar lowercase letters are significantly different within a given incubation temperature and acorn fate (Tukey's HSD, $P = .05$).

(PD), dormancy break is characterized by germination occurring in an expanding range of temperatures following increasing stratification time. Additionally, increasing germination percentages within these respective temperatures are observed (Baskin and Baskin 2004, 2014). In the laboratory, these parameters are most often evaluated at 4 weeks of incubation; however, in this study, incubation time was extended to 8 weeks to allow more time to investigate the fate of nongerminants.

Among the three red oak species, dormancy break was achieved only in cherrybark oak acorns. Following 63 days of winter submergence, germination percentages were ≥80 percent in all incubation temperatures and did not increase with 84 days of submergence. These germination percentages are consistent with those reported for cherrybark oak acorns following the same period of cold stratification on moist medium (Hawkins 2018). In other words, winter submergence of at least 63 days may substitute for cold stratification in breaking dormancy in cherrybark oak acorns. Guo et al. (2002) reported 81–97 percent germination (at approximately 20° C post-submergence) for cherrybark oak acorns following only 0–30 days of winter submergence. However, acorns received 45 days of cold stratification prior to the treatments (Guo et al. 2002). Prior cold stratification for the control (0 days) and the additive effect of cold stratification plus winter submergence would be expected to yield higher germination percentages relative to treatments of comparable submergence duration in this study. Additionally, in the Guo et al. (2002) study, acorns were collected from the ground during late autumn (November) and thus had received some stratification prior to collection.

Viability loss in cherrybark oak acorns began with 42 days of winter submergence and only at the two lowest incubation temperatures. This indicates that viability loss was temperature-dependent following winter submergence and occurred prior to dormancy break in the acorn cohort. On the other hand, the percentage of nonviable acorns in the 63- and 84-day treatments was relatively low (12–24 percent) and existed in all incubation temperatures. These data suggest that acorn viability loss with longer flood durations is not dependent upon post-drop down temperatures. However, it is not possible to determine whether acorn loss occurred during or after winter submergence.

Larsen (1963) and Guo et al. (2002) reported 45–55 percent total germination for willow oak acorns when incubated at a single temperature (20–27° C) following varying submergence durations at water temperatures ranging from 8 to 22° C. Similarly, germination percentages for willow oak acorns (≤52 percent) in this study were low, particularly relative to those of cherrybark oak. A significant increase in total germination percentages among the three lower incubation temperatures occurred only with 84 days of winter submergence, which suggests a further increase in germination percentages was possible with increased winter submergence. This pattern of germination response for acorns cold stratified on moist medium would indicate a failure of stratification time in satisfying dormancy break requirements. Therefore, either dormancy break in willow oak acorns requires a period of cold stratification (or winter submergence) longer than that of cherrybark oak, or presuming acorns require less than 84 days of cold stratification for dormancy break, winter submergence does not substitute for cold stratification.

Of note is the significant decrease in willow oak acorn total germination in the 25/15° and 30/20° C temperature regimes following the 42-day treatment. A reduction in total germination at these incubation temperatures has not been observed in acorns of this species following a gradient of cold stratification treatments of the same duration (Hawkins, unpublished results); nor was it observed in the cherrybark or Nuttall oak acorns in this study. Therefore, this occurrence presents two possibilities. The depression in germination percentages is an artifact of this study, or this is a species-specific response to this length of flood duration, water temperature, incubation temperature, or an interaction of these variables. Effective cold stratification temperatures of seeds on a moist substrate are within the range of 0–10° C (Stokes 1965), and water temperatures during the 42-day treatment were ≤10° C for the latter 32 days of the treatment. Therefore, it is unlikely that the decrease in germination percentages for this treatment is solely the result of water temperature.

Germination percentages (≤62 percent) in Nuttall oak acorns were similar to that of willow oak and thus were low relative to those of cherrybark oak acorns. Although increasing winter submergence durations resulted in increasing germination percentages across a wider range of temperatures, nongerminants were nonviable in the 63- and 84-day winter submergence treatments without respect to incubation temperature. These results are in contrast to those of Briscoe (1961), who found that submergence at water temperatures of 3–4° C had no effect on Nuttall oak acorn germination. The discrepancy is most likely related to submergence time, which was terminated at 34 days in Briscoe's (1961) study.

Mature Nuttall oak trees are moderately flood-tolerant and may withstand up to 3 years of inundation (Gardiner 2001). This level of flood tolerance was not exhibited in acorns of this species. In winter flood durations of 21 and 42 days, the percentage of acorns found to be nonviable was dependent on incubation temperature, indicating acorn loss occurred post-submergence. However, with 63 and 84 days of winter submergence, all nongerminants (49–93 percent of total) were nonviable, regardless of incubation temperature. Within the methodology of this study, it is impossible to determine whether acorns in these two winter submergence treatments were rendered nonviable during or after submergence. Regardless of the time of occurrence, Nuttall oak acorns appear to be more susceptible to viability loss than those of cherrybark and willow oak when subject to winter submergence.

Conclusions

The dynamics of red oak acorn germination in response to hydrologic regime is influenced by dormancy break requirements, which vary among species of *Lobatae*. In bottomland forests, and within the constraints of the variables in this research, if winter submergence is of sufficient length for dormancy break in cherrybark oak acorns, a high percentage of acorns will readily germinate post-drop down across a range of ambient temperatures. Concurrently, the percentage of germinants in a cohort of willow acorns may be less than that of cherrybark oak because of dormancy break requirements not being met, and immediate germination post-drop down would be strongly dependent on ambient temperature. However, retention of viability in willow oak nongerminants allows for further stratification post-drop down, and acorns may continue to germinate as the cohort approaches dormancy break. Similarly, germination in Nuttall oak acorns would be expected to be low relative to cherrybark oak acorns. However, the potential for post-drop down germination in Nuttall oak acorns may be offset because of viability loss during winter submergence durations greater than 42 days.

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