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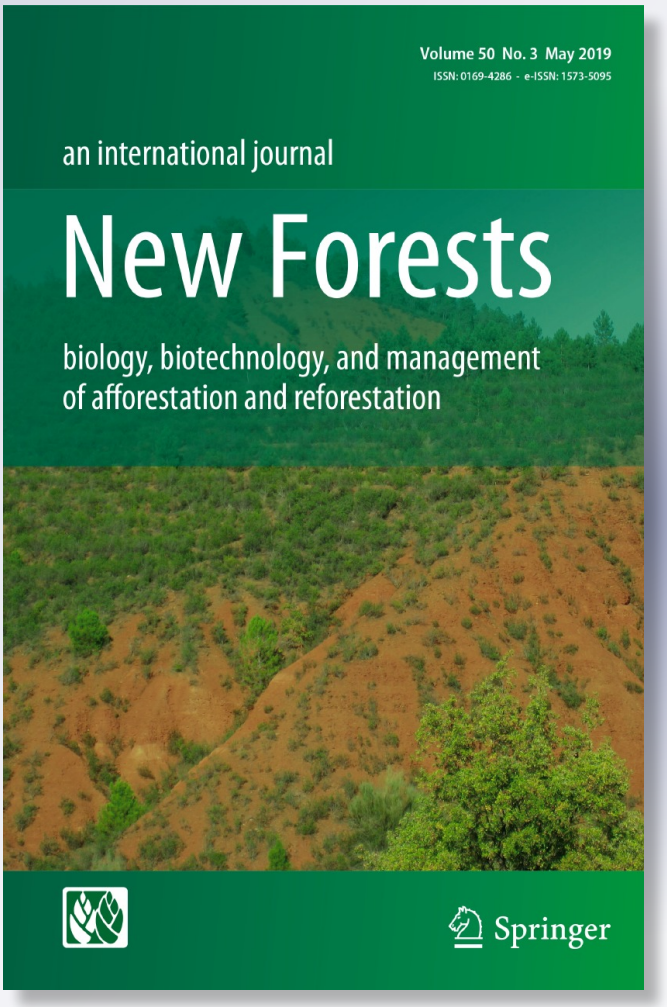

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Regulating acorn germination and seedling emergence in *Quercus pagoda* (Raf.) as it relates to natural and artificial regeneration

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Abstract

Dormancy break and germination requirements for *Quercus pagoda* (Raf.) acorns were determined, as well as the effects of acorn pretreatment and post-germination temperatures on epicotyl emergence, seedling development, and seedling biomass accumulation. There was an inverse linear relationship between length of cold stratification (5/1 °C for 0–12 weeks) and cumulative germination percentages in all incubation temperatures (15/6, 20/10, 25/15, 30/20 °C). Acorns required 12 weeks of cold stratification to break dormancy. Gibberellic acid substituted for cold stratification; although, it was not as effective as 12 weeks cold stratification. At 16 weeks of cold stratification, 20% of acorns had germinated, and the remaining 80% of ungerminated acorns reached $\geq 97 \pm 1\%$ cumulative germination within 4 days in all incubation temperatures. Post-germination time to epicotyl emergence and to leaf flush was a function of temperature, and time decreased with increased temperatures. With light held constant (50 µmol m^{-2} s^{-1}), seedlings accumulated greater biomass in temperatures >20/10 °C. *Q. pagoda* acorns possess Type 2 nondeep physiological dormancy, and this allows for artificial manipulation of timing and duration of germination. Extending cold stratification 4 weeks beyond dormancy break (i.e., 16 weeks) yields more uniform germination across a range of temperatures. Epicotyl emergence, seedling development, and biomass accumulation may be regulated by manipulating growing temperature. In this study, the most uniform seedling cohort with the greatest total biomass was produced when acorns received 16 weeks of cold stratification, followed by transfer of germinants to 30/20 °C.

Keywords Oak regeneration · Acorn dormancy · Acorn germination · Oak seedling growth

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Introduction

Knowledge of the seed ecology of *Quercus* (oak) species is fundamental to our understanding of natural regeneration, and to developing efficient nursery practices for production of seedlings for afforestation (Dey 2014). Several studies have addressed factors affecting acorn viability, such as recalcitrance (e.g., Poulsen and Eriksen 1992; Bonner 1996; Connor and Sowa 2003; Oliet et al. 2015; and others) and storage techniques (Bonner and Vozzo 1987; Bonner 1993; Connor 2004). Other studies have reported pretreatment conditions needed to promote germination or epicotyl emergence. For example, in some white oaks (subgenus *Lepidobalanus*), acorns germinate prior to, or at the time of dispersal; therefore, the radicle is considered nondormant. However, emergence of the epicotyl occurs only after a period of cold stratification (i.e., epicotyl dormancy; Farmer 1977; Bonner and Vozzo 1987). Acorns of many of the red and black oak species (subgenus *Erythrobalanus*) require a period of cold stratification to promote rapid and uniform germination (Peterson 1983; Hopper et al. 1985; Bonner and Vozzo 1987).

Seed dormancy is an evolutionary adaptation that delays germination until conditions are favorable for seedling establishment and survival. In order to standardize comparison of various dormancy types exhibited among species throughout the plant kingdom, Baskin and Baskin (2004) developed a classification system for seed dormancy, which currently is used by seed scientists throughout the world (Baskin and Baskin 2014). Five classes of seed dormancy are recognized—physical (PY), physiological (PD), morphological (MD), morphophysiological (MPD), and combined (PY + PD). Criteria for placement within a dormancy class is dependent on several factors such as embryo development, length of stratification (warm and/or cold) required to break seed dormancy, and water-permeability of the seed coat (Baskin and Baskin 2004, 2014). Further, dormancy break is defined as the ability for a high percentage of seeds to germinate across a range of temperatures within 2–4 weeks of exposure to germination temperatures (Baskin and Baskin 2014).

In temperate deciduous forests, PD is prevalent in seeds of canopy, subcanopy, and successional tree species (Baskin and Baskin 2014). At maturity, seeds with PD have fully developed embryos (i.e., embryo is differentiated into radicle and shoot), and seeds may require up to 4 months of cold stratification to break dormancy. Three levels of PD are recognized—nondeep, intermediate, and deep—and are defined primarily by the length of stratification required for dormancy break, and whether treatment of seeds with gibberellic acid acts as a replacement for stratification (Baskin and Baskin 2004, 2014). Additionally, in seeds with nondeep physiological dormancy (NDPD), as seeds progress from dormancy to nondormancy, the range of temperatures in which seeds will germinate may gradually increase. For example, in seeds with Type 1 NDPD, the maximum temperature at which seeds will germinate increases from low to high during dormancy loss. In contrast, the minimum temperature for germination decreases in seeds with Type 2 NDPD. In species with Type 3 NDPD, seed germination may occur at a mid-range temperature, and with decreasing dormancy, extend to higher and lower temperatures (Baskin and Baskin 2004, 2014).

Although dormancy type in acorns of red and black oaks has not been identified, and hence classified, it can be inferred that some level of PD exists, based on reports of germination response to cold stratification treatments (Peterson 1983; Hopper et al. 1985; Bonner and Vozzo 1987), as well as acorn anatomical features and physiological processes outlined by Bonner and Vozzo (1987). However, published research regarding germination response of cold stratified acorns has been limited to testing at a single incubation

temperature. This protocol is an excellent method for determining seed viability percentages within or among samples or cohorts. However, to elucidate ecological implications of seed dormancy break and germination requirements, and to identify seed dormancy class, it is necessary for seeds to be tested across a range of germination temperatures, and preferably those that simulate seasonal temperature variation (sensu Baskin and Baskin 2014). By having insight into the effects of variable lengths of stratification and a range of germination temperatures on acorn germination, it is possible to (1) determine the dormancy class of acorns of various *Quercus* species, (2) understand the dynamics of acorn germination and seedling emergence in naturally occurring forest stands, and (3) artificially manipulate natural processes within controlled environments.

The focus of this study is *Q. pagoda* Raf. (cherrybark oak), an economically and ecologically important red oak species that grows in mixed hardwood bottomland forests in the southern United States (Putnam et al. 1960; Krinard 1990). The primary objectives of this study were to identify dormancy class by determining dormancy break and germination requirements for acorns of this species, as well as, to test the effect of temperature on epicotyl emergence. Although epicotyl dormancy is characteristic of acorns of some white oak species, Allen and Farmer (1977) reported epicotyl dormancy in *Q. ilicifolia* Wangenh. (bear oak; subgenera *Erythrobalanus*). Therefore, progression beyond radicle emergence in *Q. pagoda* acorns should not be overlooked in the event that epicotyl dormancy in *Erythrobalanus* is not limited to *Q. ilicifolia*.

Additionally, the relationship of stratification duration on early seedling growth in *Quercus* spp. of *Erythrobalanus* is unclear. In 14 and 28 day old *Q. rubra* L. (northern red oak) seedlings, Hopper et al. (1985) found that the length of acorn cold stratification had a significant effect on subsequent seedling height and total dry weight. In contrast, Allen and Farmer (1977) found no relationship between stratification or germination temperatures and shoot length in *Q. ilicifolia*. In light of this, a secondary objective of this study was to determine if lengths of acorn cold stratification and germination temperatures affected early *Q. pagoda* seedling growth and seedling total mass.

Materials and methods

On 9 Nov 2010, mature acorns were harvested directly from *Quercus pagoda* trees growing at Winona Seed Orchard, Winona, Mississippi (33°29′33″N, 89°43′40″W). Trees represented a cross-section of genotypes ranging from Texas to Kentucky, USA. Acorns were immediately taken to the laboratory, and remained in collection buckets overnight, at laboratory ambient temperature.

Four incubators were set at 12/12 h daily alternating temperature regimes to simulate seasonal air temperatures in the range of *Q. pagoda*—15/6 °C (early spring/late fall), 20/10 °C (late spring/early fall), 25/15 °C (early/late summer), and 30/20 °C (summer). One incubator was set at 5/1 °C (winter) for cold stratification of acorns. The incubators were set to provide 12 h of light (50 μmol m^{-2} s^{-1}) diurnally during the high-temperature period and 12 h of uninterrupted dark during the low-temperature period.

In each experiment, acorns were placed in 16 cm (length)×16 cm (width)×5 cm (depth) clear plastic dishes on sand moistened with either distilled water or gibberellic acid, as described in each experiment. Plastic lids were placed on the dishes to retard water loss.

Acorn dormancy break and germination

Three replicates of 50 acorns per dish were used in each treatment and control. Acorns were placed on sand moistened with distilled water, and cold stratified at 5/1 °C for 0, 2, 4, 6, 8, 12, or 16 weeks, after which they were incubated at each of the test temperature regimes (15/6, 20/10, 25/15, and 30/20 °C). Acorns used as controls (0 weeks stratification) were placed directly at test temperatures (and 5/1 °C), where they remained for the duration of the study. Acorns were monitored at 1-week intervals for 22 weeks, with the exception of those cold stratified for 16 weeks which, after being moved to incubation temperatures, were monitored daily. Emergence of the radicle (≤ 2 mm) was the criterion for germination. Upon completion of the study, ungerminated acorns were checked for embryo viability. Firm, white embryos were considered viable, and soft, brown to gray embryos were considered nonviable.

Effects of gibberellic acid (GA_3)

Germination response to GA_3 is one criterion for identifying a level of PD (nondeep, intermediate, or deep). To determine if GA_3 would substitute for cold stratification, acorns were placed on sand moistened with either distilled water (control), or a solution of 10, 100, or 1000 mg L^{-1} GA_3. Three replicates of 25 acorns per dish were used in the control and in each treatment. Acorns were incubated at 25/15 °C because this temperature regime is considered too high to be effective for cold stratification (Stokes 1965). Germination was monitored at 1-week intervals.

Epicotyl emergence and seedling growth

Three replicates of 25 acorns per dish were used in each treatment. Acorns were cold stratified at 5/1 °C for 0, 8 or 16 weeks, after which they were incubated at each of the test temperature regimes (15/6, 20/10, 25/15, and 30/20 °C). Germination was monitored at 3-day intervals. When acorns in each test temperature germinated (radicle emergence), 15 germinants from each replicate were removed gently from the dish and placed on the surface of moist potting soil in a plastic seedling starter tray (5 cm × 5 cm × 9 cm cells). All starter trays remained in their assigned temperature regime with one exception. Additional trays with 15 germinants from each replicate in the 15/6 °C temperature regime were moved to the 30/20 °C temperature regime. Germination date was recorded and thereafter germinants were monitored daily. Number of days post-germination date to epicotyl emergence was recorded. Once the epicotyl was visible outside the pericarp, epicotyl emergence was considered to have occurred.

Number of days post-epicotyl emergence to leaf flush (fully expanded leaves) was recorded. Seedlings were harvested 14 days after leaf flush and placed in paper bags labeled with the respective length of cold stratification and incubation temperature. Seedlings were dried at 70 °C until desiccated, and then weighed to the nearest 0.001 grams.

Statistical analyses

In the acorn dormancy break and germination experiment, and the GA_3 experiment, means and standard errors were calculated for germination percentages. The square root of percentages was arcsine transformed before analyses, but actual values are used for presentation. In the dormancy break and germination experiment, a two-way analysis of variance (ANOVA, $P=0.05$) was used to test for effects and interaction of length of stratification and incubation temperature on germination. A one-way ANOVA was used to compare germination percentages at a given incubation time, and regression analysis was used to evaluate the relationship between cumulative germination percentages ($\geq 90\%$) and length of cold stratification.

In the GA_3 experiment, a one-way ANOVA was used to test for effects of GA_3 at a given incubation time.

A two-way ANOVA was used in the epicotyl emergence and seedling growth experiment to test for the effects and interaction of length of acorn stratification and incubation temperature on post-germination days to epicotyl emergence, post-epicotyl emergence days to leaf flush, and seedling total dry weight. The control of 0 weeks stratification was monitored for epicotyl emergence but was not used in statistical analyses due to extreme variation in time among incubation temperatures to acquire the desired number of germinants per replicate for valid statistical comparison.

Tukey's HSD test ($P=0.05$) was used as the multiple comparison procedure. The SAS procedures GLM and REG were used to perform all statistical analyses (SAS Institute, Inc. 2007; $\alpha=0.05$).

Results

Acorn dormancy break and germination

The interaction of length of stratification and incubation temperature had a significant effect on germination ($P\leq 0.0029$). In the absence of cold stratification (controls), acorns achieved germination percentages $>60\%$ over a time period of 12 weeks in the 25/15 and 30/20 °C incubation temperatures (Fig. 1a). Germination percentages at 12 weeks incubation for acorns in 15/6 and 20/10 °C temperature regimes were significantly less than those in the two highest incubation temperatures ($df=3$, $F=8.12$, $P=0.0082$; Fig. 1a).

Following 8 weeks of cold stratification, germination percentages $>80\%$ were recorded at 6 weeks of incubation in the three highest test temperatures (Fig. 1b). However, following 12 weeks of cold stratification, acorns reached 75 ± 1, 87 ± 7, 99 ± 1, and $96\pm2\%$ within 4 weeks of incubation at 15/6, 20/10, 25/15, and 30/20 °C, respectively (Fig. 1c). Germination percentages for acorns incubated at 15/6 °C were consistently lower than germination percentages in the three higher test temperatures through 12 weeks of stratification ($P\leq 0.0123$; Fig. 1a–c). Regression analysis revealed a strong inverse linear relationship between length of cold stratification (2–12 weeks) and time to $\geq 90\%$ cumulative germination among all incubation temperatures, with germination time decreasing with increasing cold stratification time (Fig. 2). However, acorns began to germinate at 16 weeks of cold stratification and when moved to incubation, the remaining ungerminated acorns reached $\geq 97\pm1\%$ germination within 4 days at all temperature regimes (Fig. 3).

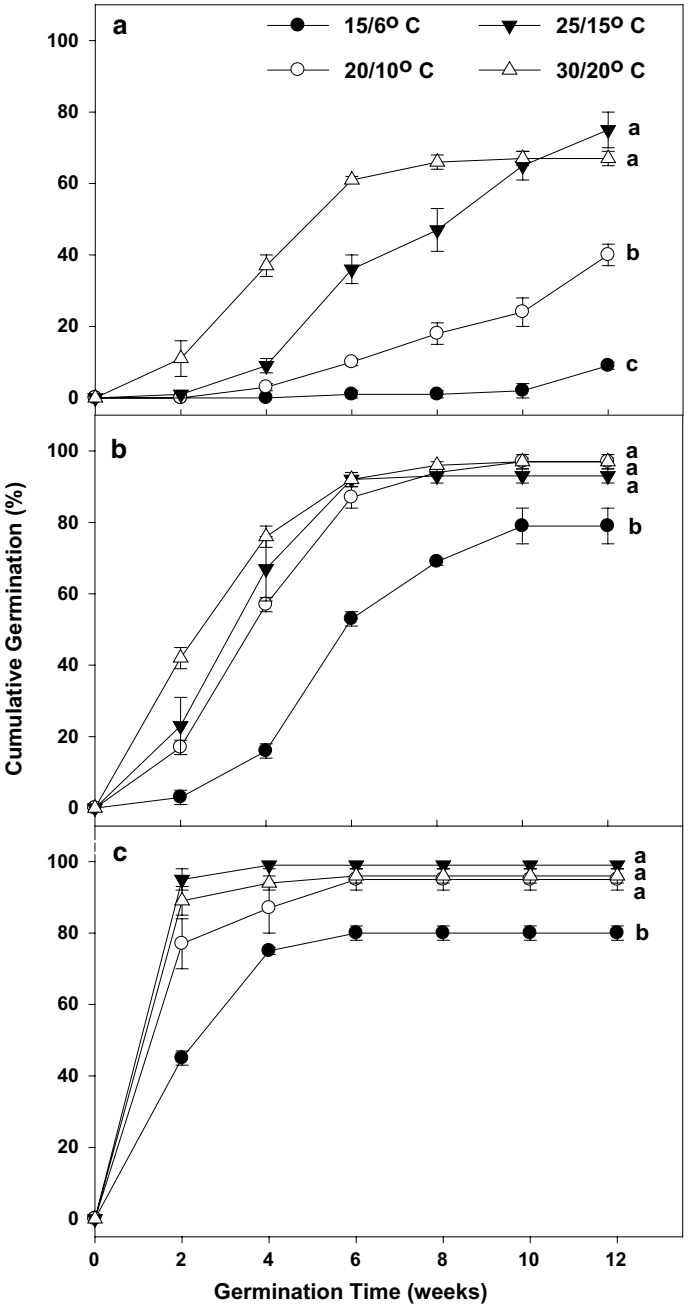

Fig. 1 Mean (±SE) germination percentages for *Quercus pagoda* acorns incubated for 12 weeks in four alternating temperature regimes following **a** 0 weeks, **b** 8 weeks, and **c** 12 weeks of cold stratification at 5/1 °C. Means at 12 weeks with dissimilar letters are significantly different (Tukey's HSD, $P = 0.05$)

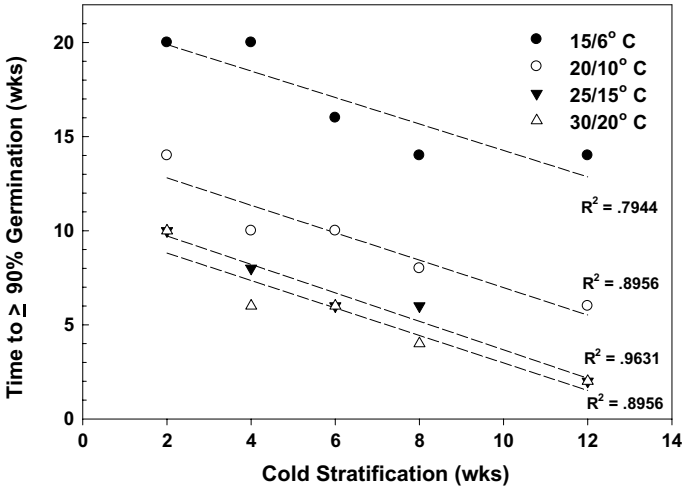

Fig. 2 The relationship between varying lengths of cold stratification (5/1 °C) and time to ≥ 90% cumulative germination for *Quercus pagoda* acorns in four alternating temperature regimes

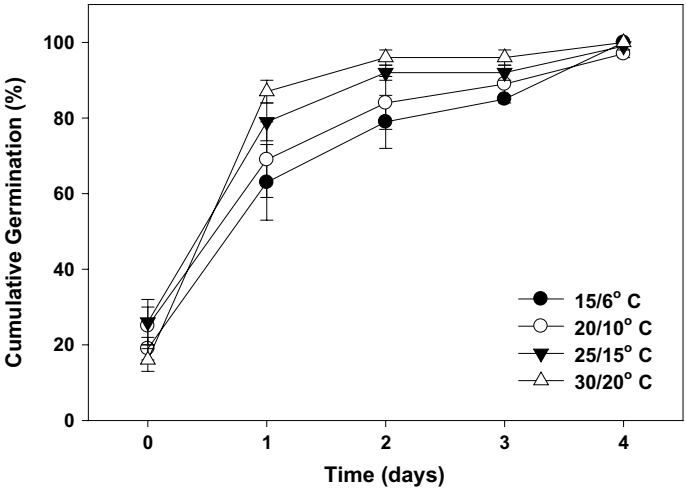

Fig. 3 Mean (± SE) germination percentages for *Quercus pagoda* acorns in four alternating temperature regimes following 16 weeks of cold stratification at 5/1 °C

Effects of gibberellic acid (GA_3)

Concentration of GA_3 exerted a significant effect on acorn germination. Acorns began germinating at 2 weeks of incubation in the 1000 mg L^{-1} GA_3 solution, and cumulative germination was greater than in other solutions and the control (distilled water) at 4 weeks ($df = 3$, $F = 6.63$, $P = 0.0170$) and 6 weeks ($df = 3$, $F = 11.93$, $P = 0.0020$) of incubation (Fig. 4). At 12 weeks of incubation, cumulative germination was greater in all three GA_3 solutions than in the control ($df = 3$, $F = 4.96$, $P = 0.0312$; Fig. 4).

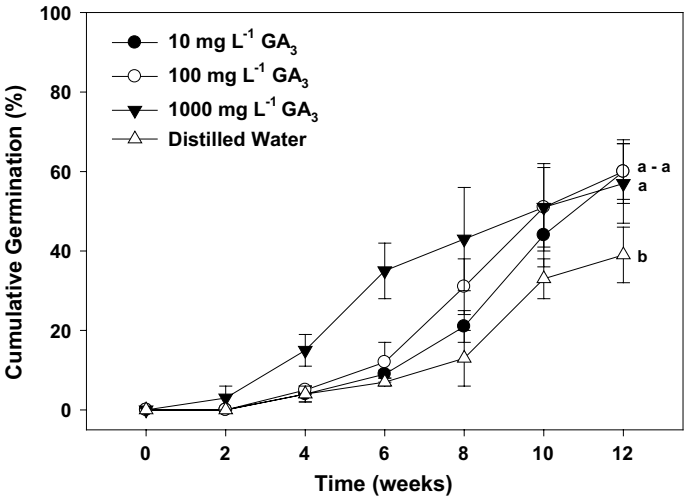

Fig. 4 Mean (±SE) germination percentages for *Quercus pagoda* acorns receiving 0 weeks cold stratification and incubated for 12 weeks at 25/15 °C in distilled water (control) or a solution of 10, 100, and 1000 mg L^{-1} gibberellic acid (GA_3). Means at 12 weeks with dissimilar letters are significantly different (Tukey's HSD, $P=0.05$)

Epicotyl emergence and seedling growth

For acorns that received no cold stratification, epicotyl emergence occurred at the three highest test temperatures. However, at the lowest temperature (15/6 °C) only 50% of germinants experienced epicotyl emergence, while the remaining germinants rotted in the potting soil (data not shown).

Number of days (post-germination) to epicotyl emergence was affected by the interaction of acorn stratification time and temperature ($df=4$, $F=8.88$, $P=0.0003$). In temperatures ≥20/10 °C, time to epicotyl emergence decreased with increased temperature (Fig. 5). However, for germinants that remained in the lowest temperature (15/6 °C), time to epicotyl emergence was dependent on acorn stratification time (Fig. 5), and emergence time was greater for acorns that received 16 weeks stratification than those that received 8 weeks stratification (Fig. 5). There was no difference in time to epicotyl emergence between germinants that were transferred from 15/6 to 30/20 °C and those that remained in the 30/20 °C temperature regime (Fig. 5).

Time (post-epicotyl emergence) to leaf flush was affected by temperature ($df=4$, $F=254.87$, $P<0.001$), and time decreased with increasing temperature to 25/15 °C (Fig. 5). There was no difference in time to leaf flush between the 25/15, 30/20 °C, and 15/6° → 30/20 °C temperature regimes (Fig. 5).

At 14 days post-leaf flush, seedling total dry mass was affected by temperature ($df=4$, $F=166.27$, $P<0.0001$). Total dry mass was greatest for seedlings that remained in 25/15 and 30/20 °C, as well as for those that were moved from 15/6 to 30/20 °C (Fig. 6).

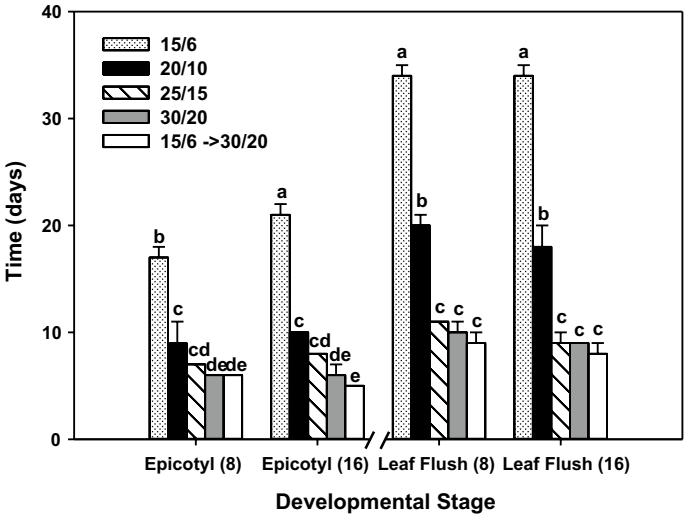

Fig. 5 Mean (±SE) number of days post-germination to epicotyl emergence, and days post-epicotyl emergence to leaf flush for *Quercus pagoda* germinants receiving 12 h light (50 µmol m^{-2} s^{-1}) diurnally and grown in four alternating temperature regimes. Germinants were produced from acorns receiving 8 weeks or 16 weeks cold stratification (5/1 °C). 15/6→30/20 represents acorns that germinated in 15/6 °C, and were then moved to 30/20 °C. Means with dissimilar letters are significantly different within a given developmental stage (Tukey's HSD, $P=0.05$)

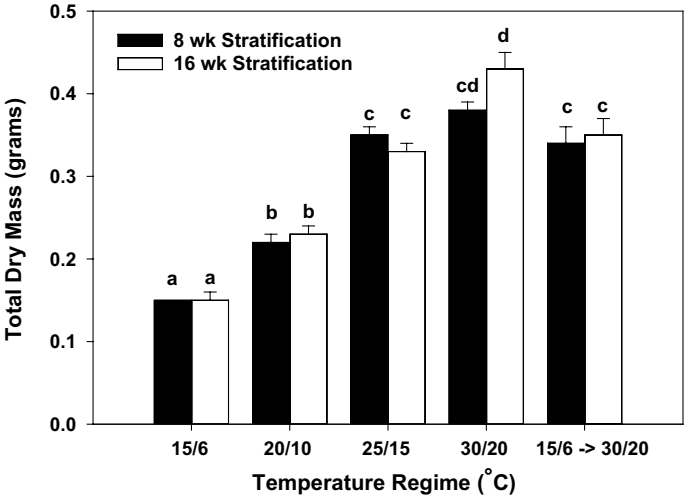

Fig. 6 Mean (±SE) total dry mass for *Quercus pagoda* seedlings receiving 12 h light (50 µmol m^{-2} s^{-1}) diurnally and grown in four alternating temperature regimes. Seedlings were produced from acorns receiving 8 weeks or 16 weeks cold stratification (5/1 °C). 15/6→30/20 represents acorns that germinated in 15/6 °C, and were then moved to 30/20 °C. Means with dissimilar letters are significantly different (Tukey's HSD, $P=0.05$)

Discussion

At the time of dispersal, *Quercus pagoda* oak acorns have fully developed embryos, and they do not grow during cold stratification. There was an inverse linear relationship between length of cold stratification (5/1 °C for 0–12 weeks) and cumulative germination percentages in all incubation temperatures (15/6, 20/10, 25/15, and 30/20 °C). However, at least 12 weeks of cold stratification was effective in overcoming dormancy over the broadest range of temperatures, with cumulative germination percentages ≥ 87% at the three highest incubation temperatures, and 75% at 15/6 °C within 4 weeks of being placed in incubation test temperatures. Gibberellic acid (GA_3) substituted for cold stratification; although, it was not as effective in overcoming dormancy as 12 weeks of cold stratification. These findings indicate that dormancy in *Q. pagoda* acorns is consistent with Type 2 nondeep physiological dormancy (NDPD) as described by Baskin and Baskin (2004, 2014).

Seed dormancy class tends to be phylogenetically constrained (Baskin and Baskin 2014; Hawkins 2003); therefore, one can hypothesize that acorns of other *Quercus* spp. of *Erythrobalanus* possess some level of PD. Further support of this hypothesis is that cold stratification was found to have a positive effect on acorn germination in *Q. nigra* (Peterson 1983), and *Q. rubra* (Hopper et al. 1985). Indeed, Bonner and Vozzo (1987) describe "variable dormancy" among several *Quercus* species of *Erythrobalanus* and found positive effects on germination following varying periods of cold stratification. However, past research has utilized a single incubation test temperature (25/15 or 30/20 °C) which makes it impossible to speculate on germination response to a range of naturally occurring or artificially induced conditions. Additionally, acorns were often collected from the ground, which affects germination responses through post-dispersal time and reception of some stratification conditions. Regarding the former, PD will wear off with time (Baskin and Baskin 2014), and regarding the latter, stratification is incurred at temperatures below 15–20 °C (Stokes 1965).

The greatest uniformity in germination was achieved following 16 weeks cold stratification, which was 4 weeks beyond the time required for dormancy break (12 weeks). *Quercus pagoda* acorns began germinating (~ 20%) at 16 weeks cold stratification, and upon transfer to incubation temperatures, the remaining acorns germinated within 96 h in all test temperatures. Germination during cold stratification has also been observed in *Q. shumardii* (Bonner and Vozzo 1987), and this "presprouting" was shown to have no adverse effect on direct-seeded germinants for this species, as well as for seedlings of *Q. pagoda* (Bonner 1982).

Time to epicotyl emergence and to leaf flush in *Q. pagoda* is largely a function of temperature. The trend is that the amount of time to complete both life cycle phases decreases with increasing temperatures; although, interaction of variables (stratification time × incubation temperature) did occur in the 15/6 °C temperature regime. However, there was no difference in times recorded between germinants that remained at 30/20 °C, and those transferred from 15/6 to 30/20 °C, which is further evidence of post-germination temperature effect (within the scope of this study). These data suggest that as a function of time, suboptimal and optimal temperatures may influence the rate of tissue changes and metabolic processes required for epicotyl emergence and leaf flush in *Q. pagoda*. Temperature effect on these processes is consistent with findings for *Quercus* species in both *Erythrobalanus* and *Lepidobalanus* as represented by *Q. ilicifolia*, *Q. petraea*, and *Q. robur* (Allen and Farmer 1977; Corbineau et al. 2001; McCartan et al. 2015).

Light availability is one of the most important factors influencing oak seedling growth and morphology (Crow 1992; Gardiner and Hodges 1998; Dey et al. 2012). For example, in field plantings, light availability exerted a positive influence on seedling growth in *Q. rubra* (Crow 1992) and *Q. pagoda* (Gardiner and Hodges 1998). Furthermore, this response increased with time and into the second growing season. However, in this study with light held constant (50 µmol m^{-2} s^{-1}), seedlings responded to temperature and accumulated significantly more biomass at temperatures greater than 20/10 °C. It is unknown whether differences in biomass among test temperatures would continue beyond the time period used in this study; although, these results do suggest the potential for a light availability and temperature interaction effect on early seedling biomass accumulation.

Conclusions

In natural environments, dormancy break requirements associated with nondeep physiological dormancy in *Q. pagoda* acorns delay germination until conditions are favorable for seedling establishment. Additionally, the cold stratification requirement in tandem with spring temperatures dictate germination uniformity. Acorns that receive longer periods of fall and winter stratification will exhibit greater synchrony in germination, particularly over a range of springtime temperatures. Subsequently, ambient temperature influences the time required for epicotyl and seedling emergence, as well as early seedling development and accumulation of biomass. Collectively, synchrony, or lack thereof, in *Q. pagoda* seedling emergence is dependent upon seasonal temperature variation both pre- and post germination. Further, while low temperatures delay epicotyl emergence in germinants, remaining acorns will continue to germinate. Therefore, upon increased ambient temperature, uniformity in seedling emergence occurs in germinants, regardless of time of acorn germination.

The relationship of cold stratification time and incubation temperature on acorn germination allows for manipulation of timing and duration of germination for purposes of acorn outplanting or nursery generation of seedlings. Dormancy break in *Q. pagoda* acorns occurs with 12 weeks of cold stratification, and a high percentage of acorns will germinate at temperatures > 20/10 °C within a time period of 2–4 weeks. However, extending cold stratification to 16 weeks, diminishes germination time of the cohort to a few days and this occurs across a wide range of temperatures. Subsequent epicotyl emergence and seedling growth may be regulated by manipulating growing temperature. In this study, the most uniform seedling cohort with the greatest total biomass was produced by cold stratification of acorns for 16 weeks, followed by transfer of germinants to 30/20 °C.

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