Lifting Dates, Chilling Hours, and Storage Duration on Slash Pine Seedling Root Growth Potential, Growth, and Survival

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Abstract

Annually, the Southern United States produces over 1 billion forest tree seedlings, the majority of which are conifers (pine) produced as bareroot seedlings. Typically grown for less than a year, seedlings are then lifted from the soil, packed in boxes, bags or bundles, and placed in cold storage before being transported to sites for reforestation. Lifting operations typically occur from late November to early March each year. On occasion, however, circumstances require seedlings to be lifted later or stored longer than recommended. Over three lifting seasons, we investigated pine seedling storability based on a series of delayed lift dates (January through March) and varying storage durations (0 to 14 weeks). Data patterns varied among the three seasons. In general, later lift dates and longer storage durations resulted in reduced seedling growth and survival. This paper was presented at the 2019 Joint Annual Meeting of the Northeast and Southern Forest Conservation Nursery Associations (Atlantic City, NJ, July 23–25, 2019).

Introduction

The United States annually produces more than 1.2 billion seedlings for reforestation, of which 80 to 90 percent is produced in the 13 Southern States (Haase et al. 2019). The majority of seedlings produced in the South are conifers, produced as bareroot seedlings and grown in a similar manner to that of regular agricultural crops (Haase et al. 2019, Starkey et al. 2015). Seedlings are typically grown in native soils within open fields for approximately 9 months before they are removed from the soil during harvesting, or what is called lifting (Starkey et al. 2015).

Lifting usually occurs between late November and late February, the optimum time when seedlings are dormant. These seedlings are packed in boxes, bags, or bundles and placed in cold storage for a 2- to 3-week period before being shipped to the field, where they are planted in areas that have recently been harvested and prepared for reforestation (Carlson 1991, Johnson and Cline 1991, Starkey et al. 2015), or into fields for converting land back to forests. Seedling storage avoids issues of mold and decay, which can decrease seedling survival after outplanting (Grossnickle and South 2014, Landis and Haase 2008). Weather conditions, however, are not always favorable and may delay outplanting, thus requiring longer storage durations than recommended. With fluctuating freezing and above-normal temperatures occurring more often across the Southern United States during the winter months of December, January, and February, there are concerns regarding optimum lifting time, seedling storability, and seedling growth and survival after outplanting (Harrington and Gould 2015).

Environmental conditions during seedling growth in the nursery impact seedling quality and physiological readiness for storage and outplanting (Carlson 1991). Seedling quality can be defined as a seedling that can survive periods of environmental stress and produce vigorous growth following outplanting (Grossnickle and MacDonald 2018, Grossnickle and South 2017). Seedlings must be physiologically ready to grow. Photoperiod and environmental cues during the growing season within the nursery are fundamental to this physiological readiness (Haase et al. 2016). Seedling dormancy, cold hardiness, and the accumulation of carbohydrate reserves (Deligöz 2013) are the main physiological processes that ensure seedlings are physiologically ready to withstand the stresses of lifting, handling, and planting such that optimal root and shoot growth can occur after outplanting (Burdett and Simpson 1984).

Bud dormancy commences in mid-fall (October–November) and the development of cold hardiness in all seedling tissues follows in early winter (December–January) (Burr 1990, Haase 2011). Note that the physiological processes of dormancy and cold hardiness are complex and not well understood for southern pine species (Johnson and Cline 1991).

Dormancy

Physiologically, bud dormancy can arise whenever stressful environmental conditions occur, even during the phenological phase of active growth. For example, drought, temperature extremes, or nutrition limitations can cause bud dormancy (Ritchie and Dunlap 1980). Bud dormancy during the active growth stage is, however, reversible with the removal of the environmental stress (Ritchie and Landis 2004). Typically, active growth of conifer seedlings slows in summer and bud formation occurs with the initiation of quiescence (ectodormancy) (Burr 1990). For northern provenances, photoperiod also plays an important role (Cooke et al. 2012, Haase 2011). If favorable conditions occur for seedling growth, ectodormancy is reversible. Beginning late fall (October/ November), true internal dormancy (endodormancy) starts and continues into December. During endodormancy, seedlings will not resume growth even when favorable conditions for growth are present. Growth resumes after seedlings experience a certain period of low temperatures (chilling requirement). Once the chilling requirement is met, the seedling re-enters ectodormancy and will resume growth if favorable conditions (primarily warmer temperatures) are present (Ritchie and Landis 2004).

For southern pine species, little is known about the dormancy cycle and its relation to photoperiod and temperature. Both nutrition and water availability can influence bud development timing (Cooke et al. 2012, Harrington and Gould 2015, Larsen et al. 1986, Ritchie and Dunlap 1980). Decreased photoperiod was found to partially substitute for chilling temperatures (Cooke et al. 2012). While southern pine species have chilling requirements, the quantity is still unclear when compared with that of northern pine species (Cooke et al. 2012, Hallgren and Tauer 1989, Johnson and Cline 1991, Kolb et al. 1985, Larsen et al. 1986). Exposure to low (but above-freezing) temperatures has been observed to enhance bud break and root growth potential (RGP) (Cooke et al. 2012, Ritchie and Dunlap 1980).

Cold Hardiness

Cold hardiness develops with physiological changes throughout all seedling tissues following the suspension of rapid cell expansion. For southern pine species, cold temperature acclimation in response to decreasing air temperatures is referred to as hardening initiating. Thus, cold hardiness initiates after bud dormancy initiation (Johnson and Cline 1991). Although the two are often referred to synonymously, they are completely separate processes (Haase 2011). For southern pines species, tissues within the seedling acclimate differently (Hallgren and Tauer 1989, Kolb et al. 1985). Once a sufficient amount of chilling hours are met (maximum usually achieved in winter), we assume there is a corresponding increase in seedling freeze tolerance (Burr 1990, Grossnickle and South 2017, Haase 2011). The level of cold hardiness for a species is genotype-specific (Grossnickle and South 2014). In contrast to bud endodormancy, cold hardiness can decrease or "be lost" if seedlings are exposed to increasing temperatures. Seedlings have been shown to de-acclimate with as little as 3 to 7 warm nights (South et al. 2008, 2009).

Chilling Hours and Seedling Storage

Seedling chilling hours are quantified based on the cumulative number of hours of exposure to a specified range of cold temperatures. The accepted temperature range to define a chilling hour is often species- and nursery-dependent (Burdett and Simpson 1984, Carlson 1991, Johnson and Cline 1991). In the Southeastern United States, chilling hours are usually quantified in the range of 32 to 46 °F (0 to 8 °C), and temperatures below 32 °F do not count (Grossnickle and South 2014, South 2012). Using this preferred method of chilling hour calculation, nurseries target 200 to 400 chilling hours for loblolly pine (*Pinus taeda* L.) to overcome rest (internal dormancy) depen ding on geographic origin (Johnson and Cline 1991, Ritchie and Dunlap 1980). For the Southeastern States, this chilling hour target is usually met in early to mid-December, after which point seedlings can be lifted for long- or short-term storage.

Successful long-term storage (1 to 3 months) of seedlings requires that they be able to tolerate extended periods in cool, dark conditions while maintaining physiological quality (Grossnickle and South 2014). Short-term storage (1 to 3 weeks) is often used for keeping a supply of seedlings available in the cooler but does not necessarily require chilling hours (Grossnickle and South 2014). Studies have shown that container loblolly pine seedlings could be stored successfully for a month without exposure to any chilling hours prior to storage (Grossnickle and South 2014, Larsen et al. 1986, Boyer and South 1985). In two studies, bareroot seedlings exposed to 113 or 223 chilling hours tolerated 4 weeks or 11 weeks of storage, respectively (South 2013, South and Donald 2002). Inadequate number of chilling hours has occasionally been used to explain low outplanting survival following a hard freeze (Larsen et al. 1986). Cold storage can partially satisfy chilling requirements for several northern species, but this is unlikely to occur for southern pine species due to their likely short chilling requirements (Harrington and Gould 2015, Ritchie and Dunlap 1980).

Although chilling hours is known to be beneficial to pine seedlings, the impact of chilling hours on seedling storability and their subsequent growth is poorly understood, as evidenced by several popularly held myths (South 2012). Thus, this area of seedling quality needs further research. The objective of our 3-year study was to better understand the relationships between chilling hours and seedling storability, as well as seedling growth and survival after outplanting.

Materials and Methods

Seedlings, Chilling Hours, and Outplanting

For this study, a single seedlot (genotype) of slash pine (*Pinus elliottii* Engelm.) was used over three seedling production and lifting seasons (2016–2017; 2017–2018; and 2018–2019). Seedlings were grown and lifted from a commercial bareroot forest tree nursery in Georgia using standard operational procedures (figure 1a). Seedlings were lifted and stored (figure 1b and c) at varying intervals (see description in subsequent sections). Chilling hours were calculated using the Utah chill-hour model from 1 November until each lifting date (table 1). The Utah chill hour model is a weighted function assigning different chilling efficiencies to different temperature ranges, including negative contributions for higher temperatures (Anderson and Seeley 1992).

Figure 1. Slash seedlings were (a) grown under operational conditions in a nursery bed. After lifting on a range of dates, seedlings were stored for varying durations in (b) boxes within (c) a cooler. (Photos by Ryan Nadel, 2017)

Table 1. Chilling hours calculated for each seedling-lifting period over three lifting seasons.

Year	Number of chilling hours at the time of lifting					
	$Time_0$	$Time_1$	$Time_2$	$Time_3$	$Time_4$	$Time_5$
2017	-302	-426	-428	-637	-820	-1016
2018	97	142	121	-103	-91	-152
2019	118	135	-6	-67	-142	-262

Following storage, seedlings were planted at the Auburn University trophotron (deep plastic-lined beds filled with sand) (figure 2), where they grew without supplemental water, weed control, or fertilization for 12 months before being harvested and measured.

Lift Dates and Storage Durations

For each lifting season, 1,000 seedlings (equivalent to a full box of seedlings) were hand lifted from the bareroot nursery bed at the start of the study period (January) (figure 1). Every 2 weeks thereafter, for a total of 6 lift dates ending in late April/early May each year ($Time_0$, $Time_1$, $Time_2$, $Time_3$, $Time_4$, $Time_5$).

At each lift date, 15 seedlings were randomly selected for measurement and outplanting (storage duration = 0); the rest were placed into cooler storage (33 to 37 °F [0.6 to 2.8 °C]) in standard shipping boxes. Over a 14-week period, 15 seedlings from each lift date were randomly removed from the cooler, measured, and outplanted for a maximum of eight storage durations (table 2). A total

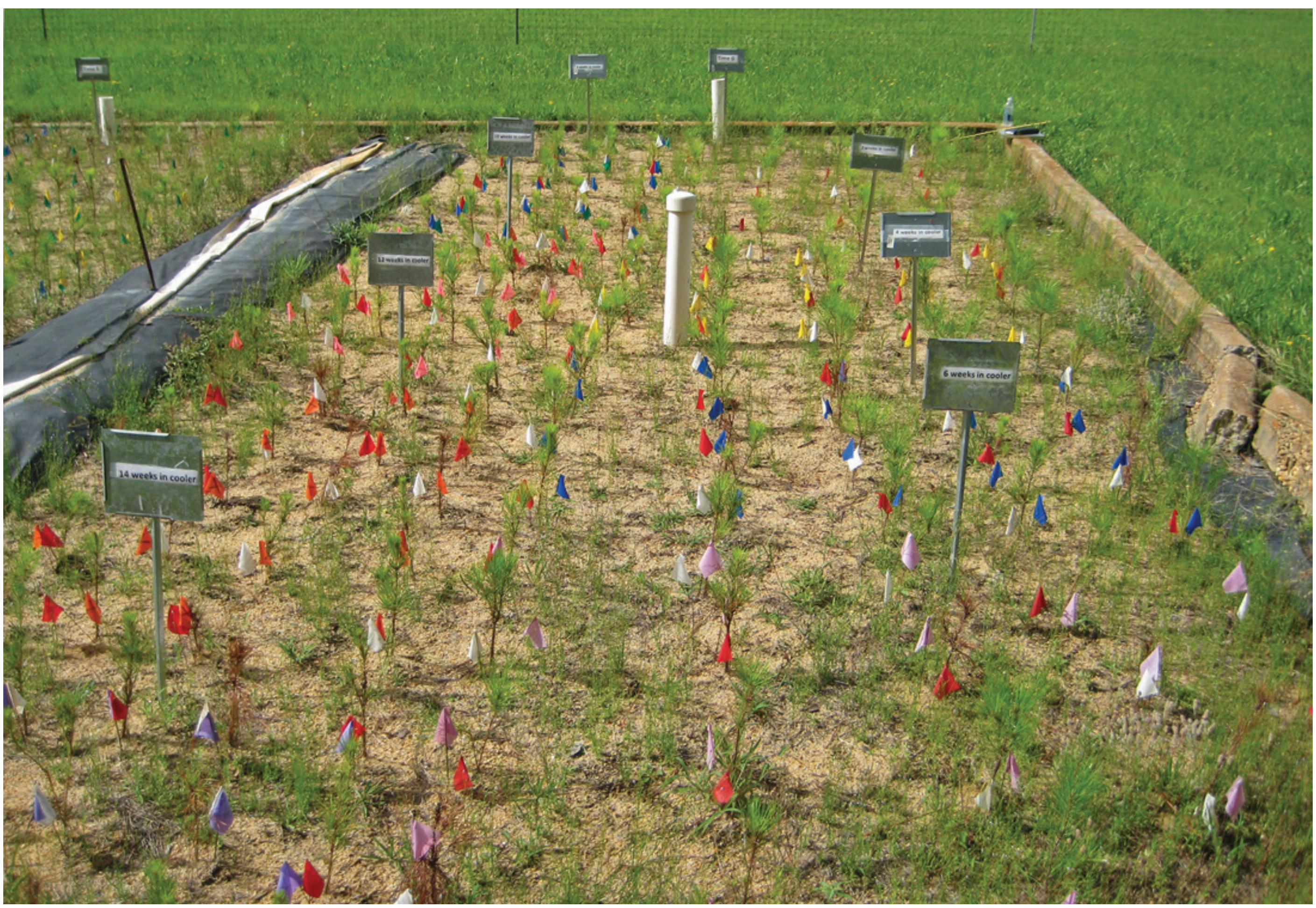

Figure 2. Seedlings from varying lift dates and storage durations were outplanted in the trophotron at Auburn University to evaluate first season shoot and root development. (Photo by Ryan Nadel, 2017)

Table 2. Sample groups of seedlings (indicated by X) each year for the different combinations of lift date and storage duration.

Storage duration (weeks)	2017						2018						2019			
	Lift date						Lift date						Lift date			
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3
0	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
2	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
4	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
6	X	X	X	X	X		X	X	X	X			X	X	X	X
8	X	X	X	X			X	X	X				X	X	X	
10	X	X	X				X	X					X	X		
12	X	X					X						X			
14	X															

of 1,230 seedlings (820 outplanted) over the study's three seasons represented a total of 82 lift date/storage duration sample groups (table 2).

Measurements

Root growth potential (RGP) was determined on five seedlings for all $Time_0$/storage duration combinations and for all lift date/storage duration = 0 combinations. RGP is a measure of a seedling's ability to rapidly produce new root growth (Ritchie and Dunlap 1980). To measure RGP, seedlings were placed in aquarium tanks filled with continuously aerated water. After 30 days, the number of new white root tips greater than 0.2 inches (0.5 cm) for each seedling was recorded.

Root collar diameter (RCD) and height (Ht) were measured on all 15 seedlings for each sample group. Additionally, the 10 outplanted seedlings for each sample group were re-measured for RCD and Ht as well as percent survival in June and December. At the conclusion of the study each year (December 2017, 2018, and 2019), seedlings were harvested. Shoots and roots of harvested seedlings were separated and pooled by sample group, then placed in a drying oven until constant mass was achieved. Mean shoot and root mass were calculated from the total mass of pooled seedlings divided by the number of living seedlings. The ratio of shoot-to-root was calculated by simple division. In addition, root weight ratios (RWR) were calculated as follows:

$$RWR\,(\%) = \frac{dry\,root\,weight}{(dry\,root\,weight\,+\,dry\,shoot\,weight)} \times 100$$

Experimental Design and Data Analyses

The study design was an incomplete factorial (lift date by storage duration) with limited replication. It was not possible to apply valid statistical analyses without a replicated, full factorial design. We elected not to include all combinations because later lift dates with longer storage durations are too far beyond operational procedures and the seedling phenological cycle. Nonetheless, the data generated from this study represent a logistical feat for demonstrating seedling responses to a wide range of lift dates and storage durations. Despite the inability to apply statistics to the data, we calculated the means for each sample groups and noted several trends, discussed below.

Results

Root Growth Potential and Morphology at the Time of Outplanting

The relationship between seedling RGP and storage duration (lift date = $Time_0$) varied by season with a decreasing, neutral, and increasing relationship with increasing storage duration for the 2017, 2018, and 2019 seasons, respectively (figure 3a). Similarly, RGP response to lift date (storage = 0 weeks) varied by season with decreasing RGP at later lift dates in 2017 but the opposite in 2018 and 2019 (figure 3b).

RCD tended to increase with later lift dates but was not affected by storage duration (table 3). Seedling height did not follow any consistent pattern with regard to lift date or storage duration (table 3).

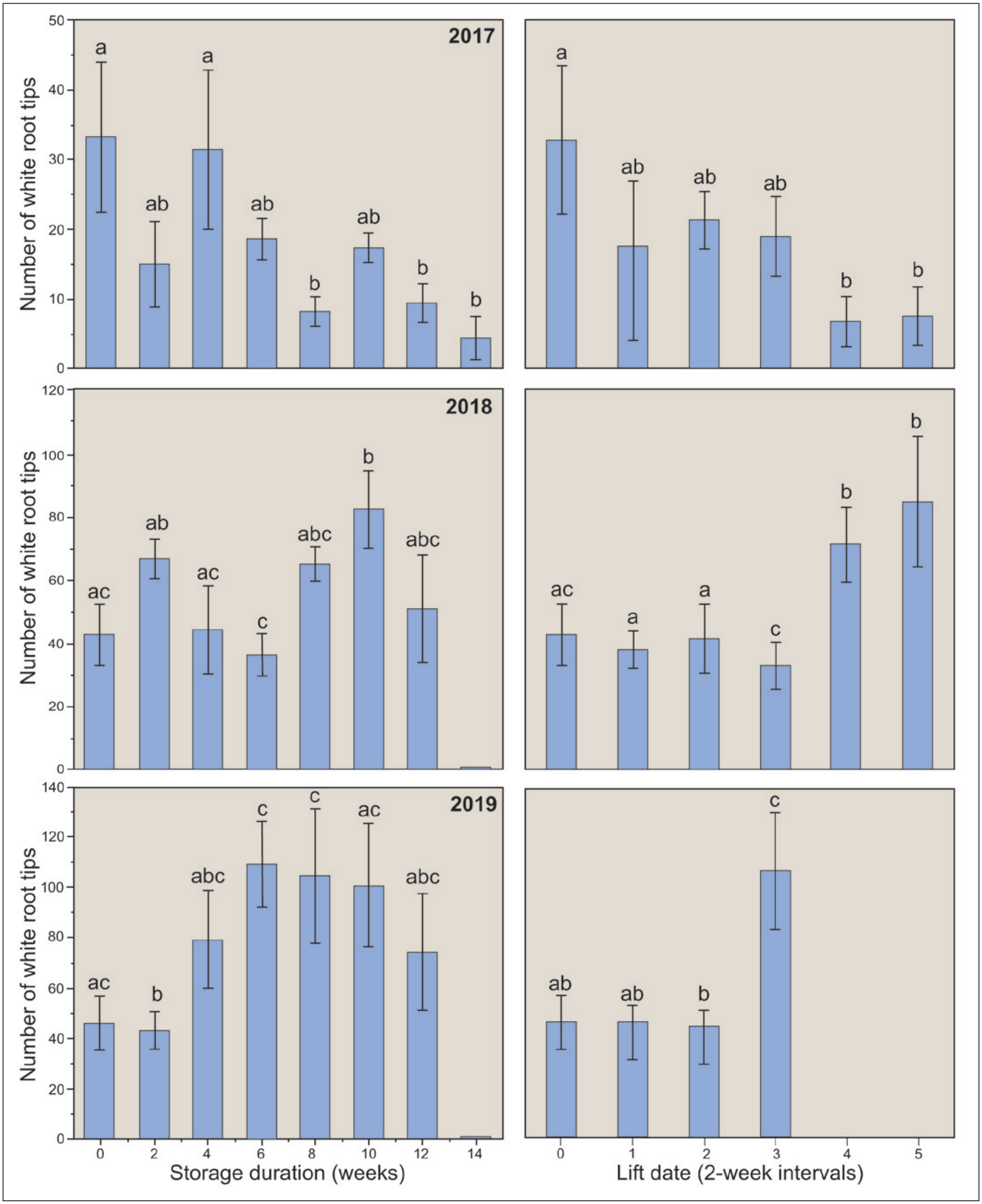

Figure 3. Mean root growth potential (number of white root tips) of tree seedlings based on (a) storage duration or (b) lift date over three seasons. Within each graph, bars with different letters are significantly different ($\alpha < 0.05$).

Table 3. Morphology at the time of outplanting for seedlings with varying combinations of lift date and storage duration.

Storage duration (weeks)	Initial RCD (mm)						Initial Height (cm)					
	Year 2017											
	Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5
0	4.42	4.36	5.20	5.22	5.59	5.63	33.5	32.3	33.4	30.8	35.3	34.2
2	4.70	5.54	5.66	6.46	4.82	5.51	32.6	32.0	31.4	34.6	32.9	33.6
4	5.69	4.92	5.31	5.19	5.76	4.69	32.5	31.0	30.5	32.2	34.9	32.6
6	5.49	5.73	6.43	6.43	7.04	.	32.3	30.8	33.1	31.0	34.3	.
8	4.79	6.21	6.13	5.47	.	.	30.6	32.3	31.8	31.6	.	.
10	6.10	5.58	4.81	.	.	.	33.9	33.1	30.7	.	.	.
12	5.29	5.15	.	.	.	.	31.5	32.9	.	.	.	.
14	5.01	.	.	.	.	.	31.5	.	.	.	.	.

Storage duration (weeks)	Year 2018											
	Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5
0	5.13	6.41	5.75	6.05	5.82	5.78	26.3	28.6	26.6	28.9	28.9	28.6
2	5.88	5.43	5.78	5.61	6.08	6.01	27.2	27.8	29.3	27.6	27.7	30.3
4	5.16	5.37	6.10	6.14	6.13	.	25.9	30.3	26.4	29.3	26.7	.
6	5.22	6.02	6.00	6.18	.	.	27.9	26.1	26.9	27.3	.	.
8	5.56	5.35	5.74	.	.	.	25.5	26.9	25.0	.	.	.
10	5.58	5.77	.	.	.	.	27.2	27.9	.	.	.	.
12	5.59		.	.	.	.	25.7	.	.	.	.	.

Storage duration (weeks)	Year 2019											
	Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5
0	5.52	5.43	6.13	6.00	.	.	30.2	30.3	33.9	34.2	.	.
2	5.68	5.91	6.06	6.41	.	.	27.2	31.7	32.5	34.1	.	.
4	5.98	6.43	6.08	6.23	.	.	29.9	30.7	31.4	35.9	.	.
6	5.31	5.74	5.78	6.05	.	.	28.5	29.9	32.9	34.7	.	.
8	5.00	6.12	5.98	.	.	.	28.0	29.9	33.2	.	.	.
10	5.17	5.95	.	.	.	.	28.0	29.6	.	.	.	.
12	6.16	.	.	.	.	.	28.5	.	.	.	.	.

RCD = Root collar diameter.

Morphology and Survival After One Growing Season

Shoot and root mass tended to decrease with increasing storage duration for each lifting date, especially in 2017 and 2019 (table 4). Shoot:root was highest (greater than 3) during the 2017 season and lowest (less than 2) during the 2018 season, but did not vary notably due to lift date or storage duration (table 4). RWR at the end of one growing season tended to increase with increasing storage duration (table 4).

Both RCD and height growth at the end of each growing season tended to decrease with later lift dates and with longer storage durations (table 5). Seedling survival varied by season but tended to decrease with increasing storage duration, especially for later lift dates (table 5).

Discussion

Root Growth Potential and Morphology at the Time of Outplanting

The relationship between RGP and increasing storage duration differed among years (figure 3a). Studies on other southern pine species have also shown annual variations in RGP in response to storage and attributed these variations to lifting date, storage temperature, and storage duration (Deligöz 2013, Grossnickle and South 2014, Haase et al. 2016, Hallgren and Tauer 1989, Ritchie and Dunlap 1980). Root growth potential is linked to the bud dormancy cycle and peaks in mid- to late winter, just before bud break when seedling shoots are ectodormant (Carlson 1991, Deligöz 2013, Ritchie and Dunlap 1980). With increasing temperatures, seedling RGP

Table 4. Morphology after one growing season for outplanted seedlings following different lift dates and storage durations.

Storage duration (weeks)	Shoot Mass (g)						Root Mass (g)						shoot: root						Root weight ratio					
	Year 2017																							
	Lift date						Lift date						Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
0	36.32	26.31	.	36.92	10.77	9.66	8.83	8.15	.	10.27	2.38	3.07	4.1	3.2	.	3.6	4.5	3.1	19.6	23.7	.	21.8	18.1	24.1
2	26.42	22.65	22.72	28.35	10.59	4.65	8.34	7.63	7.45	9.37	2.32	0.36	3.2	3.0	3.0	3.0	4.6	12.9	24.0	25.2	24.7	24.8	18.0	7.2
4	15.48	20.12	17.66	19.05	10.65	5.07	4.64	7.34	5.60	6.49	2.42	1.01	3.3	2.7	3.2	2.9	4.4	5.0	23.1	26.7	24.1	25.4	18.5	16.6
6	13.85	19.82	30.01	21.02	12.52	.	5.31	6.70	12.64	6.40	3.36	.	2.6	3.0	2.4	3.3	3.7	.	27.7	25.3	29.6	23.3	21.2	.
8	12.45	32.33	13.14	13.85	.	.	3.24	12.17	5.31	3.23	.	.	3.8	2.7	2.5	4.3	.	.	20.7	27.4	28.8	18.9	.	.
10	16.98	19.34	7.37	.	.	.	4.01	6.91	2.62	.	.	.	4.2	2.8	2.8	.	.	.	19.1	26.3	26.2	.	.	.
12	8.70	12.95	.	.	.	.	1.69	6.10	.	.	.	.	5.1	2.1	.	.	.	.	16.3	32.0	.	.	.	.
14	7.93	.	.	.	.	.	2.26	.	.	.	.	.	3.5	.	.	.	.	.	22.2	.	.	.	.	.

Storage duration (weeks)	Year 2018																							
	Lift date						Lift date						Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
0	6.35	10.80	9.54	3.92	5.85	6.86	3.63	4.72	5.06	1.92	2.89	2.85	1.7	2.3	1.9	2.0	2.0	2.4	36.37	30.41	34.66	32.85	33.07	29.35
2	6.47	13.98	9.22	6.25	5.20	7.96	4.12	7.68	5.67	3.46	2.32	3.22	1.6	1.8	1.6	1.8	2.2	2.5	38.90	35.46	38.08	35.63	30.85	28.81
4	8.50	9.43	10.49	7.13	4.83	.	4.88	5.18	6.45	4.27	1.87	.	1.7	1.8	1.6	1.7	2.6	.	36.47	35.46	38.08	37.46	27.91	.
6	4.61	9.53	7.50	5.52	.	.	3.09	5.51	5.31	2.95	.	.	1.5	1.7	1.4	1.9	.	.	40.13	36.64	41.45	34.83	.	.
8	7.01	5.08	8.00	.	.	.	3.82	4.71	4.19	.	.	.	1.8	1.1	1.9	.	.	.	35.27	48.11	34.37	.	.	.
10	5.36	7.66	.	.	.	.	3.25	3.86	.	.	.	.	1.6	2.0	.	.	.	.	37.75	33.51	.	.	.	.
12	5.79	.	.	.	.	.	4.96	.	.	.	.	.	1.2	.	.	.	.	.	46.14	.	.	.	.	.

Storage duration (weeks)	Year 2019																							
	Lift date						Lift date						Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
0	7.51	7.83	6.99	5.94	.	.	2.35	2.36	1.87	1.86	.	.	3.2	3.3	3.7	3.2	.	.	23.8	23.2	21.1	23.8	.	.
2	3.65	6.67	5.01	5.33	.	.	1.31	1.52	1.65	1.57	.	.	2.8	4.4	3.0	3.4	.	.	26.4	18.6	24.8	22.8	.	.
4	4.84	7.41	3.79	3.22	.	.	1.56	1.92	0.64	1.02	.	.	3.1	3.9	5.9	3.2	.	.	24.4	20.6	14.4	24.1	.	.
6	4.35	3.69	2.31	.	.	.	1.27	1.11	0.9	.	.	.	3.4	3.3	2.6	.	.	.	22.6	23.1	28.0	.	.	.
8	2.08	2.93	1.82	.	.	.	0.93	0.85	0.91	.	.	.	2.2	3.4	2.0	.	.	.	30.9	22.5	33.3	.	.	.
10	3.08	7.34	.	.	.	.	1.02	1.98	.	.	.	.	3.0	3.7	.	.	.	.	24.9	21.2	.	.	.	.
12	2.7	.	.	.	.	.	1.22	.	.	.	.	.	2.2	.	.	.	.	.	31.1	.	.	.	.	.

usually decreases as competition for resources (water and nutrients) transitions from root growth to bud elongation (Deligöz 2013, Ritchie and Dunlap 1980). Studies with loblolly pine found RGP increased with increasing chilling hours, and seedlings with a high proportion of ectodormant buds at planting had higher RGP (Carlson 1991, Larsen et al. 1986, Ritchie and Dunlap 1980). This relationship was also observed in our study with nearly twice the RGP values occurring in 2019 and 2018 as compared with those for 2017, when chilling hours were very low (table 1; figure 3). Our 2018 and 2019 data also show that RGP increased with later lift dates and longer storage times, likely due to a further increase in chilling hours (figure 3).

As would be expected, initial RCD tended to increase with later lift dates because root growth and RCD growth continue after budset as long as soils are warm enough. Height, on the other hand, did not show a pattern with regard to lift date (table 3). Any height variations can be attributed to normal sampling error, since seedlings had already set bud by the onset of the study each season.

Morphology and Survival After One Growing Season

After outplanting, the most notable differences were among seasons. Those planted in 2017 received no chilling at the time of lifting (table 1) and shoots were already starting to grow inside the storage boxes. This early growth is evident in the higher initial values for height (table 3) and likely resulted in a growth advantage after planting as evidenced by the higher values for shoot and root biomass (table 4) and for RCD and

Table 5. Growth (RCD and Ht) and survival after one growing season for outplanted seedlings following different storage and lifting periods.

Storage duration (weeks)	RCD growth (mm)						Height growth (cm)						Survival (%)					
	Year 2017																	
	Lift date						Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
0	6.09	5.57	.	6.68	1.84	1.61	12.5	15.0	.	21.5	3.2	5.8	90	70	0	80	60	50
2	4.85	3.34	3.07	4.04	1.91	0.00	13.2	11.9	9.5	17.3	5.8	5.4	100	80	70	100	70	10
4	1.98	3.42	3.02	3.34	1.92	0.19	8.9	13.5	11.5	13.2	5.8	2.4	80	100	90	100	60	30
6	1.90	2.89	4.49	2.92	0.76	.	4.3	12.2	13.0	10.3	8.5	.	70	100	100	90	80	.
8	1.14	4.42	1.52	2.04	.	.	12.0	14.9	6.7	8.1	.	.	90	100	100	100	.	.
10	2.24	3.04	0.82	.	.	.	9.9	5.9	3.3	.	.	.	90	40	100	.	.	.
12	0.61	2.75	.	.	.	.	3.5	5.7	.	.	.	.	60	90	.	.	.	.
14	0.62	.	.	.	.	.	6.5	.	.	.	.	.	60	.	.	.	.	.

Storage duration (weeks)	Year 2018																	
	Lift date						Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
0	0.57	0.29	0.28	0.00	0.00	0.00	0.6	5.6	2.6	0.0	0.0	0.0	100	90	100	20	90	100
2	0.16	1.38	0.32	0.14	0.00	0.00	2.0	6.4	1.7	0.5	0.0	1.7	100	100	100	80	70	100
4	0.78	0.44	0.43	0.00	0.00	.	4.9	0.5	4.5	0.0	0.4	.	100	90	90	80	60	.
6	0.00	0.22	0.00	0.00	.	.	0.0	4.8	1.3	0.0	.	.	70	100	30	60	.	.
8	0.00	0.00	0.01	.	.	.	4.0	0.2	2.4	.	.	.	70	30	60	.	.	.
10	0.00	0.00	.	.	.	.	0.0	1.9	.	.	.	.	80	100	.	.	.	.
12	0.00	.	.	.	.	.	0.9	.	.	.	.	.	100	.	.	.	.	.

Storage duration (weeks)	Year 2019																	
	Lift date						Lift date						Lift date					
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5
0	0.68	0.61	0.08	0.00	.	.	2.8	5.1	0.0	0.0	.	.	100	100	90	80	.	.
2	0.00	0.01	0.00	0.00	.	.	2.6	1.3	0.0	0.0	.	.	100	100	80	100	.	.
4	0.00	0.00	0.00	0.00	.	.	1.9	5.6	0.0	0.0	.	.	100	100	40	90	.	.
6	0.00	0.00	0.00	0.00	.	.	1.0	0.8	0.0	0.0	.	.	100	100	40	0	.	.
8	0.00	0.00	0.00	.	.	.	0.8	0.3	0.0	.	.	.	100	80	70	.	.	.
10	0.00	0.07	.	.	.	.	0.0	2.2	.	.	.	.	100	100	.	.	.	.
12	0.00	.	.	.	.	.	0.0	.	.	.	.	.	100	.	.	.	.	.

RCD = Root Collar Diameter

height growth (table 5) at the end of the 2017 growing season compared with the other two seasons, in spite of relatively dry and warm growing conditions in 2017. On the other hand, seedlings planted in 2018 and 2019 were exposed to chilling hours and were likely still ectodormant at the time of outplanting. In those seasons, seedlings lifted in $Time_0$, $Time_1$, and $Time_2$ (2018 only) had approximately 100 or more chilling hours at the time of lift, while those lifted at later dates had negative chilling hours as temperatures increased (table 1). Interestingly, 2018 and 2019 seedlings lifted during those later dates with negative chilling had little or no growth after outplanting. They broke bud but did not elongate. Because we used the Utah chill hour model to calculate chilling (Anderson and Seeley 1992), we were able to show this interactive effect of warming before lifting and subsequent field performance. Similarly, Haase et al. (2016) demonstrated differences in chilling hour accumulation using two calculation methods, though that study did not have notable negative values. For regions prone to warm temperatures after bud set, a weighted chilling model can provide vital information.

Within each growing season, seedling morphology and survival tended to decrease with increasing storage duration and later lift dates (tables 4 and 5). Studies have shown a significant effect of lift date on subsequent root and shoot growth (Deligöz 2013, Haase et al. 2016). Furthermore, as cold storage duration increases, a corresponding reduction in growth after outplanting can occur (Deligöz 2013, South and Donald 2002). For other conifer species, reduction in growth was related to total seedling carbohydrate content at planting affecting early root growth (Deligöz 2013). Roots and shoots compete within the plant for carbohydrates. Lifting into late winter or early spring usually means seedlings have been exposed to higher temperatures, which stimulate bud elongation and reduce root growth (Ritchie and Dunlap 1980). The ability of seedlings to grow roots shortly after planting is positively correlated to improved seeding survival after outplanting (Grossnickle 2005, Mena-Petite et al. 2001). Our results reflect these phenological cycles, with those from earlier lift dates and shorter storage durations likely having the advantage to grow roots and establish on the outplanting site before bud break.

Shoot:root is commonly used as an indicator of drought avoidance potential (Grossnickle 2012). The ratio indicates the balance between transpiring shoot tissues and moisture-absorbing root tissues. Loblolly pine seedling survival after outplanting is negatively correlated with increasing shoot:root (Larsen et al. 1986). Sufficient root growth is important for seedling survival and successful establishment (Carlson 1986, Grossnickle and South 2017, Larsen et al. 1986, Mena-Petite et al. 2001). Greater root mass indicates there is a greater absorptive surface for water and nutrient uptake (Grossnickle 2012, Mena-Petite et al. 2001). Thus, seedlings with shoot:root greater than 3 have lower survival potential compared with seedlings that have shoot:root between 1 and 3 (Grossnickle 2012). Similarly, lower RWR (which follows shoot:root patterns) will have lower survival potential. In our study, shoot:root in 2017 was greater than 3 for nearly every lift date/storage duration group, which is likely linked to the low initial RGP coupled with immediate height growth following planting during that season. In turn, the high shoot:root likely contributed to the lower survival of those lifted later in the 2017 growing season (table 4).

Our study shows potential effects of lift date and storage duration on subsequent seedling quality and performance. These effects, however, were strongly influenced by seasonal variations in chilling hour accumulation (and de-accumulation). This variation demonstrates the importance of multi-year assessments. Conclusions based on just 1 year would not have captured the range of seasonal variability. The interactive effect of seasonal weather patterns and lift date makes it challenging to offer management recommendations, though it is clear that late lift dates and long storage durations can reduce field growth and survival after outplanting.

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