Cranberry Germination and Emergence Response to Environmental Factors and Seeding Depth

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Abstract. Cranberry (*Vaccinium macrocarpon* Ait.) cultivars are clonally propagated. Germination of cranberry seeds produces off-type varieties that are generally characterized by lower fruit productivity and higher vegetative vigor. Over time, the productivity of cranberry beds decreases as off-type frequency increases over time. Improved knowledge of cranberry germination biology would facilitate the use of targeted agronomic practices to reduce the emergence and growth of less productive off-types. The influences of light, temperature regime, pH, and water potential on cranberry seed germination were assessed in a growth chamber, whereas the effect of seeding depth on seedling emergence was evaluated in a greenhouse. Seeds stratified for 6 months at 3 °C were used for these experiments. Cranberry germination was influenced by light quality, with maximum germination reaching 95% after 15 minutes of exposure to red light but decreasing to 89% under far-red light. However, light was not required for inducing germination. Cranberry seeds germinated over a range of alternating diurnal/nocturnal temperatures between 5 and 30 °C, with an average maximum germination of 97% occurring for diurnal temperatures of 20 to 25 °C. The length of emerged seedlings was reduced by an average of 75% for pH 6 to 8 compared with pH 3 to 5. Seedlings that emerged at pH greater than 5 showed increasing chlorotic and necrotic injuries and were not considered viable at pH 7 or 8. Germination at 15 °C was reduced when seeds were subjected to water stress as low as –0.2 MPa, and no germination occurred below –0.4 MPa. Seeds incubated at 25 °C were more tolerant to water stress, with at least 70% maximum germination for osmotic potential (ψ_s) –0.6 MPa or greater. The average seedling emergence was 91% for seeds left on the soil surface or buried at a maximum depth of 1 cm; however, it was null at a burying depth of 4 cm. These results indicate that germination of cranberry seeds in cultivated beds in the northeastern United States likely occurs during the summer months, when temperatures are optimal and the moisture requirement is supported by irrigation. However, timely application of residual herbicide or sanding (a traditional cranberry agronomic practice) of open areas in cranberry beds could help prevent seed germination and reduce minimizing the onset of off-type varieties.

Cranberry (*Vaccinium macrocarpon* Ait.) is a low-growing, woody, perennial vine native to eastern North America that grows in moist acidic soils with variable organic matter content. In New Jersey, large-fruited

cranberry is a common native species in wet, sandy, peaty bogs, and along the edges of streams in the Pine Barrens (Beckwith, 1922). Cranberry distribution ranges from Newfoundland to Minnesota in the west and Delaware in the south, with populations also present at higher elevations in the Appalachian Mountains of North Carolina and Tennessee (Vander Kloet, 1988). Cranberry domestication from selected wild plants and cultivation began in the early 1800s in Massachusetts and New Jersey (Eck, 1990). Cranberry is now commercially cultivated in the United States, Canada, and Chile, which produced 53% (359,110 t), 26% (172,440 t), and 21% (141,338 t) of the global cranberry production, respectively, in 2019 (FAOSTAT, 2019). In 2019, Wisconsin was the highest cranberry-producing state in the United States (202,791 t) followed by Massachusetts (90,839 t), Oregon (23,854 t), New Jersey (20,279 t), and Washington (6433 t) (Cranberry Marketing Committee, 2019).

Cranberry propagates asexually from stolons that spread over the ground and rapidly form a dense mat, and sexually by seed (Eck,

1990). Seeds are produced through outcrossing by native pollinators or European honeybee (*Apis mellifera* L.), or through self-pollination (Marucci and Filmer, 1964; Sarracino and Vorsa, 1991). Historically, growers cultivated cranberries from wild selections that were clonally maintained and propagated (Eck, 1990). Genetic improvement since the 1950s has been conducted either by crossing wild selections to produce first-generation hybrids or by crossing first-generation hybrids with elite wild selections (Eck, 1990; Fajardo et al., 2013). Hybrid cultivars currently grown by growers are considered to have higher levels of heterozygosity than cultivars selected from wild populations (Bruederle et al., 1996). Maintaining heterozygosity may be advantageous for improving cranberry tolerance to abiotic stresses, therefore contributing to a higher fruit yielding capacity (Davenport and Vorsa, 1999; Ortiz and Vorsa, 1998). Commercial cranberry beds are generally maintained for long periods of time, often surpassing 20 years. This longevity provides opportunities for seeds contained in rotten or unharvested fruit to germinate and become established, thereby increasing the genetic heterogeneity of cranberry plantings over time. Using random amplified polymorphic DNA (RAPD) markers, Novy et al. (1996) observed high genetic heterogeneity and identified 15 genetic profiles in 12 Washington ‘McFarlin’ beds, including four associated with low-producing cranberry beds and not corresponding to the true ‘McFarlin’ profile. Reduced pollen viability, mean seed/berry, and fruit set indicated that these divergent genotypes were less fertile. It was hypothesized that genotypes with reduced fertility would be more vegetatively competitive and preferentially selected when stolons were collected for establishing new cranberry beds, thus contributing to yield reduction in beds contaminated with these genotypes (Novy et al., 1996; Polashock and Vorsa, 2002; Vorsa and Johnson-Cicalese, 2012).

The importance of off-types as an endogenous source of genetic diversity has been emphasized by studies investigating the impact of cranberry fairy ring (*Thanatophyllum* sp.) disease on crop losses and cultivar homogeneity (Oudemans et al., 2008; Polashock and Oudemans, 2006). Higher fruit morphological diversity was noted in areas recovering from fairy ring disease than in healthy areas with ‘Ben Lear’ cranberry beds. This was correlated with greater genotypic diversity within areas affected by fairy ring, with an average of seven haplotypes compared to an average of two haplotypes in healthy areas (Oudemans et al., 2008). Cranberry seedlings recolonizing open areas where vines were killed by fairy ring disease may originate from a soil seed bank. The proportion of off-types with more vigorous vegetative development and reduced yield potential will increase and contribute to long-term decline of the productivity of cranberry beds (Oudemans et al., 2008).

Because cranberry cultivars are traditionally propagated vegetatively to ensure the preservation of genetic characteristics and

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rapid fruit set (Vorsa and Johnson-Cicalese, 2012), few studies have investigated the effects of biotic and abiotic factors on seed germination. Devlin and Karczmarczyk (1977) assessed the influence of light intensity, abscisic acid (ABA), and gibberellic acid (GA) on cranberry seed dormancy; they demonstrated that cranberry seeds are photoblastic and will germinate if exposed to sufficient light, whereas GA will promote seed germination under dark conditions. Paglietta (1977) indicated that premoistened seeds germinate 2 to 3 d quicker than dry seeds, whereas Demoranville (1974) reported that a temperature of at least 22 °C was required for >90% cranberry seed germination.

We hypothesize that openings in the cranberry canopy may induce changes in the local environmental conditions that may be favorable to the germination of cranberry seeds from the seedbank. A better understanding of cranberry germination in relation to environmental conditions may help provide cranberry growers with practical information about minimizing the onset of off-type varieties in renovated cranberry beds or in open areas that result from damage to the cranberry canopy. Therefore, the objectives of this research were to explore the effects of light, temperature regime, solution pH, water stress, and seeding depth under controlled conditions on cranberry seed germination.

Materials and Methods

Growth chamber and greenhouse studies were conducted at the Rutgers University P.E. Marucci Center for Blueberry and Cranberry Research in Chatsworth, NJ, in 2019 and 2020. Ripe berries were collected from the ground after harvest in a commercial 'Ben Lear' bed (Chatsworth, NJ) on 25 and 26 Oct. 2018. Seeds for the different experiments were obtained after gently crushing the berries. Seeds were washed and sieved under tap water flow for 10 min to remove remaining fragments of the endocarp and dried in open air at room temperature (24 °C) for 5 d. Then, seeds were placed in paper bags and stratified at 3 °C for 6 months under complete darkness in a controlled environmental chamber. Cranberry seed viability was $95 \pm 3\%$ based on the results of a 1% (weight/volume) tetrazolium chloride test conducted for 150 seeds before performing experiments (Association of Official Seed Analysts, 2010). Seed surface disinfection was conducted in a laminar flow hood by rinsing seeds in a 70% (v/v) ethanol solution for 1 min, dipping them in a mixed solution of sodium hypochlorite (1.06%) and a nonionic surfactant (Tween 20 at 0.1%) for 10 min, and rinsing them three consecutive times with sterilized distilled water. Germination of stratified cranberry seeds in response to light quality, temperature, pH, and water potential was evaluated in 10-cm diameter petri dishes with 25 seeds per replication. Seeds were placed on two sheets of filter paper (Whatman #1) moistened with 8 mL of treatment solution. Then, petri dishes were wrapped with a single layer of parafilm

(Bemis Company, Neenah, WI) around the circumference to reduce evaporation. The number of germinated seeds was monitored daily for 21 d, and then every 3 d until there were no newly germinated seeds for 7 d. Cumulative germination for each rating date was calculated as the total number of germinated seeds divided by the total number of seeds in the treatment.

Lighting conditions. The light requirement and effect of light quality on cranberry seed germination were assessed using a growth chamber fitted with red (R) (650- to 670-nm waveband) and far-red (FR) (720- to 740-nm waveband) light-emitting diode (LED) lamps. Artificial light treatments included 15 min of R light, FR light, R light immediately followed by 15 min of FR light, and FR light immediately followed by 15 min of R light. Light irradiance values to which the seeds were exposed during the treatment were 2 $\text{W}\cdot\text{m}^{-2}$ and 13 $\text{W}\cdot\text{m}^{-2}$ for R and FR light, respectively. After artificial light treatments, petri dishes were wrapped in two layers of aluminum foil to prevent further exposure to light and incubated at 25 °C. Other treatments

included seeds maintained in full darkness as well as exposure to natural light. Seed exposed to natural light were placed on a bench in a greenhouse maintained at 24 °C.

Temperature regime. Four temperature regimes were selected to represent typical seasonal variations in New Jersey. Regimes of 5 and 15 °C, 10 and 20 °C, 15 and 25 °C, and 20 and 30 °C corresponded to mean daily low and high temperatures for the months of April, May, June, and July, respectively, in Indian Mills, NJ (Robinson, 2020). Low temperatures were maintained for 8 h under complete darkness, whereas high temperatures were maintained for 16 h under multicolor LED lights set to deliver irradiance of 15 $\text{W}\cdot\text{m}^{-2}$.

Solution pH. Cranberry seed germination was evaluated for pH values ranging from 3 to 8. Buffer solutions were prepared using the procedure described for hairy beggarticks (*Bidens pilosa* L.) (Reddy and Singh, 1992). A 0.1-M potassium hydrogen phthalate buffer solution was adjusted to pH 3 and 4 with 0.1 N hydrochloric acid (HCl) and to pH 5 with 0.1 N sodium hydroxide (NaOH). A 0.1-M solution of potassium phosphate monobasic

Table 1. Effect of lighting conditions on the maximum germination ($G_{\max}$), daily germination rate (R_s), time of germination onset (LAG), and time required for 50% of viable cranberry seeds to germinate (t_{50}).

Light	$G_{\max}$ (%)	R_s (seed/day)	LAG (d)	t_{50} (d)
Natural	95 a ^y	17.4 ab	5.8	8.3 bc
Dark	94 ab	14.6 b	5.2	9.4 a
15 min FR ^z	89 b	15.2 b	5.3	8.7 ab
15 min FR + 15 min R	94 ab	18.9 a	5.4	7.7 c
15 min R	95 a	18.9 a	5.1	7.9 bc
15 min R + 15 min FR	89 b	15.5 b	5.1	8.6 abc
Significance	*	*	NS	*

^zR = red light; FR = far-red light.

^yMeans ($n = 8$) were pooled across runs separated by Tukey's honestly significant difference test at $P \leq 0.05$. Means within a column followed by the same letters are not significantly different from each other. NS, *Nonsignificant or significant at $P < 0.01$, respectively.

Table 2. Effects of day/night temperature regime (TR) on maximum germination ($G_{\max}$), daily germination rate (R_s), time of germination onset (LAG), and time required for 50% of viable cranberry seeds to germinate (t_{50}).

Day/night TR	$G_{\max}$ (%)	R_s (seed/day)	LAG (d)	t_{50} (d)
15 °C/5 °C	63 c ^z	1.4 c	13.8 a	18.5 a
20 °C/10 °C	96 a	5.1 bc	12.4 a	19.3 a
25 °C/15 °C	98 a	13.8 b	6.8 b	10.9 b
30 °C/20 °C	81 b	24.6 a	3.3 c	5.9 c
Significance	*	*	**	**

^zMeans ($n = 8$) were pooled across runs separated by Tukey's honestly significant difference test at $P \leq 0.05$. Means within a column followed by the same letters are not significantly different from each other. *, **Significant at $P < 0.01$ or 0.001, respectively.

Table 3. Effects of solution pH on maximum germination ($G_{\max}$), daily germination rate (R_s), time of germination onset (LAG), and time required for 50% of viable cranberry seeds to germinate (t_{50}).

pH	$G_{\max}$ (%)	R_s (seed/day)	LAG (d)	t_{50} (d)
3	96	30.6 a ^z	5.6 c	8.6 e
4	94	28.2 a	6.2 bc	9.3 d
5	95	26.6 a	6.9 abc	10.1 c
6	88	21.7 b	6.7 abc	11.5 b
7	90	20.5 b	7.9 ab	12.6 a
8	90	20.2 b	8.2 a	12.3 a
Significance	NS	**	*	**

^zMeans ($n = 8$) were pooled across runs separated by Tukey's honestly significant difference test at $P \leq 0.05$. Means within a column followed by the same letters are not significantly different from each other. NS, *, **Nonsignificant or significant at $P < 0.01$ or 0.001, respectively.

was adjusted with 0.1 N NaOH to obtain solution pH values of 6 and 7. A 25-mM solution of sodium tetraborate anhydrous was adjusted with 0.1 N HCl to obtain buffer solution with a pH value of 8. The pH value of the solutions was tested with a pH meter calibrated with standardized buffers before the filter paper (Whatman #1) was moistened with the prepared solutions. Seeds were incubated at 25 °C and subjected to an 8-h dark/16-h light photoperiod with multicolor LEDs set to deliver a photosynthetically active radiation (PAR) flux density of 70 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Seed germination was evaluated daily until no new germination occurred for 7 d. Additionally, measurements of the seedling radicle and shoot length as well as ratings of the shoot coloration and development of rootlets along the radicle were collected from all emerged seedlings at the end of the incubation period. Shoot coloration was rated using the following scale of 0 to 4: 0 = healthy green epicotyl and reddish radicle; 1 = muddy green epicotyl and brown radicle; 2 = yellow-green epicotyl and yellow-brown radicle; 3 = white epicotyl and yellow radicle; and 4 = brown epicotyl and black radicle.

Water potential and temperature. Solutions of water potentials of -0.1, -0.2, -0.4, -0.6, -0.8, and -1.0 MPa were prepared by dissolving 7.6 to 28.7 g of polyethylene glycol (PEG-8000) in 100 mL of deionized water (Michel, 1983). The PEG concentrations were corrected for incubation temperature. A control treatment with deionized water alone (0.0 MPa) was also included. Seeds were incubated at either 15 or 25 °C and subjected to an 8-h dark/16-h light photoperiod with multicolor LEDs set to provide a PAR flux density of 70 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Seeds not germinated after 50 d were removed, rinsed for 3 min with tap water, and placed for 2 min in deionized water. Then, seeds were placed in petri dishes containing two layers of filter paper (Whatman #1) and moistened with 8 mL of distilled water. Seed germination was assessed daily over a 30-d period.

Seeding depth. The effect of seeding depth on cranberry seedling emergence was determined on a greenhouse bench and using 0.3-L plastic containers. Depths of 0, 0.5, 1, 2, 3, and 4 cm from the base of the pot ring were marked inside. Then, pots were filled to the mark with a sterilized 1:1 (v/v) mix of sphagnum peatmoss (Sun Gro Horticulture Distribution Inc., Agawam, MA) and pre-sieved Woodmansi sand (coarse-loamy, siliceous, semiactive, mesic Typic Hapludults) obtained from a local gravel pit. The organic matter content (3.9%) and pH (4.4) of the potting mix were adjusted to be representative of typical New Jersey cranberry soils based on a soil analysis conducted over multiple years in local commercial cranberry beds by Ocean Spray (Middleborough, MA). Then, 25 seeds were equidistantly placed on the soil surface at the required depth before being covered with the same soil mix. Two high-pressure sodium 2000 K lamps were equidistantly placed above the bench to provide a 16-h light period with a PAR flux density of 640

Fig. 1. Effects of the solution pH on cranberry seedling (radicle + shoot) length 30 d after seeding in petri dishes. Seeds were incubated at 25 °C and subjected to an 8-h dark/16-h light photoperiod in a growth chamber. Means ($n = 8$) are provided as the seedling length (mm) $\pm$ SE. Means with the same letters are not significantly different according to Tukey's honestly significant difference test at $P \leq 0.05$.

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ followed by an 8-h dark period. Greenhouse temperature was maintained at 24 °C during the duration of the experiments. All pots were initially sub-irrigated to bring soil to field capacity and later surface-irrigated twice per day with a garden spray hose to provide adequate soil moisture for emerging seedlings. Seed germination was evaluated daily until no new germination occurred for 7 d.

Statistical analysis. Two experimental runs were conducted for each study between Jan. and May 2020. The statistical design was a randomized complete block with four replications. Each petri dish or plastic pot was

considered a single replication unit. Cumulative germination data for each replication were described by a four-parameter Hill function (Eq. [1]) and plotted with SigmaPlot 12.0 software (Systat Software, San Jose, CA) (El-Kasaby et al., 2008; Nin et al., 2017).

$$y = y_0 + \frac{ax^b}{c^b + x^b} \quad [1]$$

In Eq. [1], y is considered the percentage of cumulative germination after x days after planting (DAP), y_0 is the intercept on the y axis (≤ 0), a is the maximum cumulative germination or emergence percentage, b is a

Fig. 2. Development of cranberry seedlings 30 d after seeding when grown in solution at pH 3 (A), pH 4 (B), pH 5 (C), pH 6 (D), pH 7 (E), and pH 8 (F). Seeds were incubated at 25 °C and subjected to an 8-h dark/16-h light photoperiod in a growth chamber.

mathematical parameter controlling the shape and steepness of the germination or emergence curve, and c represents the time (DAP) required to reach 50% of the final cumulative germination or emergence (t_{50}). As recommended by Soltani et al. (2015), t_{50} was used instead of the mean germination time (MGT) for the postmodeling analysis of variance (ANOVA).

Parameters a , b , c , and y_0 were used to compute the time of germination or emergence onset (LAG) in Eq. [2] and the final germination or emergence percentage ($G_{\max}$) in Eq. [3].

$$\text{LAG} = b \sqrt{\frac{-y_0 c^b}{a + y_0}} \quad [2]$$

$$G_{\max} = y_0 + a \quad [3]$$

The average daily rate of seed germination or emergence (R_s) was computed using Eq. [4] (Maguire, 1962; Asgarpour et al., 2015).

$$R_s = \sum_{i=1}^n (S_i / D_i) \quad [4]$$

where R_s is the daily germination or emergence rate (germinated seeds per day or emerged seedling per day), S_i is the number of germinated seeds or emerged seedling on d_i , and D_i is the number of days after the start of the experiment.

$G_{\max}$, LAG, R_s , and t_{50} data computed for each experiment were subjected to an ANOVA using SAS software (version 9.4; SAS Institute, Cary, NC) and PROC GLIMMIX. A similar analysis was also conducted using seedling measurement data collected for the solution pH experiment. Before the analysis, the percent values were arcsine-transformed and seedling growth data were subjected to a logarithm transformation to achieve normality assumptions. All data were subsequently back-transformed for presentation purposes. Lighting conditions, temperature regime, water potential, pH, and seeding depth were considered fixed variables, and replications, experimental runs, and their interaction were considered random effects (Grafen and Hails, 2002). The treatment $\times$ run interaction was not significant; therefore, data were pooled across experimental runs. Mean comparisons were performed using Tukey's honestly significant difference test at a 5% level of significance.

A regression analysis was used to analyze the effects of solution ψ_s and incubation temperature as well as seeding depth on final seed germination or seedling emergence. Data were fitted to a three-parameter sigmoidal model, as shown in Eq. [5] (Asgarpour et al., 2015):

$$G = a / \{1 + \exp[-(x - x_{50})/b]\} \quad [5]$$

where G is the total germination (%) at different water potential and temperature, a is the maximum germination (%), x_{50} is the ψ_s required for 50% inhibition of maximum germination, and b indicates the slope.

Table 4. Effects of the interaction between temperature (T) and osmotic pressure (OP) on maximum germination ($G_{\max}$), daily germination rate (R_s), time of germination onset (LAG), and time required for 50% of viable cranberry seeds to germinate (t_{50}).

T	OP	$G_{\max}$ (%)	R_s (seed/day)	LAG (d)	t_{50} (d)
15 °C	0.0 MPa	94 ab ^z	16.7 c	16.2 bc	24.5 b
15 °C	-0.2 MPa	74 c	8.6 d	18.9 ab	31.4 ab
15 °C	-0.4 MPa	40 d	1.1 e	28.3 a	37.4 a
15 °C	-0.6 MPa	0 f	0.0 e	—	—
15 °C	-0.8 MPa	0 f	0.0 e	—	—
15 °C	-1.0 MPa	0 f	0.0 e	—	—
25 °C	0.0 MPa	96 a	47.3 a	3.9 d	7.0 d
25 °C	-0.2 MPa	95 ab	43.6 ab	5.2 cd	8.1 d
25 °C	-0.4 MPa	91 abc	37.5 b	6.1 cd	9.4 cd
25 °C	-0.6 MPa	75 bc	24.3 c	7.9 bcd	14.1 c
25 °C	-0.8 MPa	15 e	5.1 de	11.1 bcd	13.7 c
25 °C	-1.0 MPa	0 f	0.0 e	—	—
Significance		**	***	*	***

^zMeans ($n = 8$) were pooled across runs separated by Tukey's honestly significant difference test at $P \leq 0.05$.

Means within a column followed by the same letters are not significantly different from each other.

*, **, ***Significant at $P < 0.05$, 0.01, or 0.001, respectively.

Results and Discussion

Lighting conditions. The light treatment significantly affected cranberry germination, with an average $G_{\max}$ of 95% under natural light or when seeds were exposed to R light, but it decreased to 89% for seeds exposed to FR light (Table 1). However, $G_{\max}$ and R_s remained statistically comparable for seeds incubated under continuous darkness or exposed to natural light. Germination occurred faster for seeds exposed to R light (18.9 seeds per day) than for seeds exposed to FR light (15.2 seeds per day). LAG was not significantly affected by light treatments, whereas t_{50} occurred significantly earlier for seeds exposed to FR light followed by R light (7.7 d) compared with darkness (9.4 d). Overall, these results suggest that FR light may partially inhibit cranberry seed germination, whereas natural light or dark conditions only affect the rapidity of seed germination.

In agreement with observations of other species (Benvenuti et al., 2001; Leon and Owen, 2003), the stratification of cranberry seeds in this study for 6 months at 3 °C may have contributed to the loss of dormancy, with 94% germination recorded in darkness. Previous work demonstrated that seeds from freshly harvested cranberries remained dormant under dark conditions at 25 °C, but that 69% germinated 20 d after being treated with 500 ppm GA (Devlin and Karczmarczyk, 1977). Therefore, in the absence of treatments enhancing seed germination, cranberry seeds are photoblastic (i.e., require light to germinate) (Devlin and Karczmarczyk, 1975). R light promotes the germination of photoblastic seeds (Benech-Arnold et al., 2000), and nonstratified seeds of European blueberry (*Vaccinium myrtillus* L.) incubated at 25 °C have been shown to require at least 18 h of R light irradiation daily for 9 d to reach 90% germination (Giba et al., 1995).

Fig. 3. Effects of water potential on cranberry germination after 50 d of incubation at 15 °C or 25 °C. Seeds were grown in petri dishes and subjected to an 8-h dark/16-h light photoperiod in a growth chamber. Bars represent the SEM ($n = 8$) of the germination rate.

Although stratification before the experiment probably broke cranberry seed dormancy, a higher germination rate was still noted for seeds exposed to R light. Conversely, FR light treatment for 15 min caused lower germination when applied alone or after irradiation with R light, indicating that phytochrome is involved in the germination process of cranberry seeds. Similarly, a gradual decrease in European blueberry germination was noted with increasing FR irradiation time, and germination of European blueberry seeds exposed to R light for 3 d decreased by 50% when irradiated with 5 min of FR light, thus supporting the view that phytochrome is responsible for the light-induced germination of European blueberry seeds (Giba et al., 1995). The results of FR light on cranberry seed germination imply that the germination of cranberry seeds could be partially inhibited in cranberry beds characterized by dense vine canopy, as noted for various sedge (*Carex* spp.) species for which germination was inhibited in wetlands with a dense leaf canopy and a low R:FR ratio (Kettenring, 2006; Schütz, 1997). This supports the hypothesis that areas of cranberry beds where the crop canopy is thin or has disappeared (e.g., caused by fairy ring disease) may provide light conditions that will stimulate the germination of cranberry seeds from the soil seed bank. However, this may also depend on how long cranberry seeds can remain viable until environment conditions become suitable for inducing germination.

Temperature regime. The G_{max} was statistically similar for the 20/10 °C and 25/15 °C day/night temperature regimes, with an average germination rate of 97% (Table 2). The G_{max} declined to 63% and 81% with 5/15 °C and 30/20 °C day/night temperature regimes, respectively. R_s was not statistically different for the 20/10 °C and 25/15 °C day/night temperature regimes, with an average of 9.5 germinating seeds per day, but it increased to 24.6 seeds per day with the 30/20 °C regime. LAG was delayed by 10.5 d, 9 d, and 3.5 d for the 15/5 °C, 20/10 °C, and 25/15 °C regimes, respectively, in comparison with the 30/20 °C regime, for which seed germination was initiated 3.3 d after the start of the experiment. Time to 50% germination (t_{50}) was 5.9 d for the 30/20 °C regime, and it significantly increased by 5 d for the 25/15 °C regime and by an average of 13 d for the 15/5 °C and 20/10 °C regimes.

The reduced G_{max} at 15 or 30 °C indicated that the optimal temperature range for cranberry seed germination is 20 to 25 °C, which is in agreement with previous research reporting a temperature of 22 °C to obtain a minimum of 90% cranberry germination (Demoranville, 1974). The lower G_{max} at low temperatures suggests that cranberry germination occurs during the spring and summer months of the growing season, but it may slow in July and August, when daily air and soil surface maximum temperatures frequently exceed 30 °C (Robinson, 2020). These results may also suggest that cranberry seed germination is more likely to occur at or near the soil surface, where

temperature fluctuates more than it does at deeper depths. Similar optimal seed germination temperatures have been reported for other *Vaccinium* spp. Baskin et al. (2000) reported 82% and 73% average germination rates for nonstratified seeds of European blueberry and lingonberry (*Vaccinium vitis-idaea* L.), respectively, with a 25/15 °C alternating temperature regime, whereas the maximum germination was only 12% for both species with a 15/5 °C regime. Nin et al. (2017) obtained 82% and 83% germination of European blueberry seeds at constant temperatures of 22.5 and 25 °C, but only 10% at 15 °C. Ranwala and Naylor (2004) suggested that germination of European blueberry occurs above the threshold of 15 °C but sharply decreases beyond 23 °C. Cranberry may have a similar range of optimal germination temperatures because the data indicate reduced germination when the day temperature

exceeds 25 °C. However, the decrease is not sharp, suggesting that cranberry germination will likely occur at higher temperatures. European blueberry and lingonberry grow at higher latitudes or elevations than American cranberry (Tirmenstein, 1990, 1991), and they may have lower tolerance to high temperature. Further evaluations of germination at higher temperature regimes are warranted to provide valuable information regarding the upper temperature germination threshold for cranberry.

Solution pH. Rapidity of cranberry seed germination was affected by the solution pH, with LAG indicating that the first seeds germinated an average of 2.5 d earlier at pH 3 than at pH 7 or 8, and t_{50} occurring 4 d later at pH 7 than at pH 3 (Table 3). However, the average G_{max} was 92% and unaffected by solution pH, whereas the R_s was 28.5 germinating seeds per day for pH 3 to 5 and declined to 20.8

Fig. 4. Cranberry germination after 50 d of incubation at various water potentials (stressed) and after an additional 30-d period at a water potential of 0 MPa (stress removed). Seeds were incubated in a growth chamber at constant 15 °C (A) or 25 °C (B) temperatures and subjected to an 8-h dark/16-h light photoperiod. Bars represent the SEM of total germination rate. Means ($n = 8$) in Fig. 1A with the same letters are not significantly different according to Tukey's honestly significant difference test at $P \leq 0.05$. Means ($n = 8$) in Fig. 1B were not significantly different according to the aforementioned test.

germinating seeds per day for pH 6 to 8. Based on these results, cranberry germinates faster under acidic conditions, but it can also germinate near neutral or basic pH. The development of new shoots and roots following germination was investigated to assess the viability of the seedlings under different pH conditions. The radicle plus shoot length significantly increased as pH decreased, ranging from 2.5 mm at pH 8 to 16.4 mm at pH 4 (Fig. 1). At pH 6 to 8, the radicle plus shoot length was less than 4 mm, and none of the seedlings produced leaves or rootlets; however, at pH 3 to 5, the leaf and rootlet production rates ranged from 62% to 80% and 78% to 96%, respectively (data not shown). Seedlings grown at pH 3 to 5 had green to dark green epicotyl and reddish radicle and were considered healthy (Fig. 2A–C). Conversely, at pH higher than 6, seedlings were not considered viable, with white to brown epicotyl and brown to black radicle (Fig. 2D–F). These results suggest that cranberry germination may occur over a broad pH range, but that elongation of the seedlings only occurs under acidic conditions, corresponding to the soil pH deemed optimal for adequate growth of this crop (Eck, 1990). Similarly, Stanienė and Stanytė (2007) reported that clonally propagated and hydroponically grown cranberry can tolerate alkaline pH when grown in vitro, but that the plants will die or show very weak growth when transferred to soils with pH higher than 6.45.

Water potential and temperature. The two-way interaction of water potential $\times$ temperature was significant for $G_{\max}$, t_{50} , and R_s ($P < 0.0001$), as well as for LAG ($P < 0.05$). After incubation for 50 d at 0 MPa ψ_s , the $G_{\max}$ averaged 95% and was not significantly different for 15 and 25 °C (Table 4). No germination occurred at incubation temperatures at -1.0 MPa. For seeds incubated at 15 °C, germination declined rapidly with decreasing water potential, and no germination occurred at water potential lower than -0.4 MPa (Fig. 3). Compared with 0 MPa, $G_{\max}$ and R_s were reduced at -0.2 MPa by 21% and 8.1 seeds per day, respectively, and by 54% and 15.6 seeds per day, respectively, at -0.4 MPa. Reduced germination with increased water stress was also noted at 25 °C, but it occurred at lower potential than at 15 °C. For example, and compared with the absence of water stress, decreases in $G_{\max}$ and R_s were noted at -0.6 MPa and -0.4 MPa water potential, respectively. Germination onset was not delayed by decreasing the water potential at 25 °C, whereas t_{50} increased by an average of 7 d at -0.6 and -0.8 MPa compared with 0 MPa. These results suggest that the spread of cranberry through seeds may be restricted to moist soils when the temperature is lower than the optimal range of 20 to 25 °C, but it may occur in drier soil when exposed to temperatures within the optimal range. Reduced germination at 15 °C compared with 25 °C under equivalent water potential is possibly the result of concurrent environmental stresses that may reduce water imbibition of the seeds and decrease the germination rate. Similar to cranberry, germination of slender amaranth (*Amaranthus*

Fig. 5. Effects of seeding depth on cranberry seedling emergence 60 d after seeding. Seeds were grown in pots filled with a 1:1 mix of sphagnum peatmoss and sand and subjected to an 8-h dark/16-h light photoperiod in a greenhouse maintained at 24 °C. Bars represent the SEM ($n = 8$) of the emergence rate.

viridis L.) and sicklepod [*Senna obtusifolia* (L.) H.S. Irwin & Barneby] decreased as water stress increased and temperature decreased (Norsworthy and Oliveira, 2006; Thomas et al., 2006). Oberbauer and Miller (1982) reported no germination from lingonberry seeds collected in Alaska at temperatures fluctuating between 20 and 25 °C and at water potential lower than -0.2 MPa.

Removing the water stress increased total germination at 15 °C (Fig. 4A) and 25 °C (Fig. 4B). The total germination rate at 25 °C after 30 d without water stress was an average of 92%, and it was unaffected by the previous ψ_s . However, only 20% to 43% of the seeds that had been subjected to water potential between -0.4 and -1.0 MPa germinated at 15 °C after water stress was removed, indicating that the adverse residual effect of water stress may persist when environmental conditions are not adequate for optimal germination. These results confirm that cranberry germination will preferentially occur at temperatures recorded during the summer months (25 °C) rather than during early spring (15 °C) in the northeastern United States. They also suggest that cranberry may

continue to germinate when exposed to moisture after a period of water stress, as long as temperatures are within the optimal range for germination. Cranberry beds are usually irrigated when the soil water potential decreases to between -4.5 and -6.5 KPa (Jeranyama, 2021), and cranberry can tolerate water potential as low as -8.0 KPa without yield loss (Pelletier et al., 2013). These values are adapted to tensiometers usually installed at a depth of 10 cm below the soil surface, whereas cranberry seeds essentially remain at or near the soil surface, where the water potential can be lower. However, recurring irrigation of cranberry beds during the summer months may provide sufficient soil moisture in the subsurface soil layer for cranberry seeds to germinate.

Seeding depth. Cranberry emergence occurred at all seeding depths except 4 cm (Fig. 5). $G_{\max}$, R_s , LAG, and t_{50} were not significantly different at shallow seeding depths ranging from soil surface to 1 cm, with averages of 91%, 4.4 seedlings per day, 13.7 d, and 24.2 d, respectively (Table 5). $G_{\max}$ and R_s decreased to 38% and 1.4 seedlings per day, respectively, for the seeding depth of

Table 5. Effects of seeding depth on maximum emergence ($G_{\max}$), daily emergence rate (R_s), time of emergence onset (LAG), and time required for 50% of viable cranberry seeds to emerge (t_{50}).

Depth ^z	$G_{\max}$ (%)	R_s (seed/day)	LAG (d)	t_{50} (d)
Soil surface	92 a ^y	4.6 a	12.4 c	25.8 b
0.5 cm	94 a	4.2 a	14.0 c	22.4 b
1 cm	86 a	4.4 a	14.8 c	24.5 b
2 cm	38 b	1.4 b	20.8 b	33.6 a
3 cm	12 c	0.3 bc	26.0 a	37.2 a
4 cm	0 d	0.0 c	—	—
Significance	**	**	**	*

^zSeeds were grown in pots filled with a 1:1 mix of sphagnum peatmoss and sand.

^yMeans ($n = 8$) were pooled across runs separated by Tukey's honestly significant difference test at $P \leq 0.05$. Means within a column followed by the same letters are not significantly different from each other.

*, **Significant at $P < 0.01$ or 0.001, respectively.

2 cm, whereas the onset of seedling emergence increased to 20.8 d. Minimal emergence occurred at a depth of 3 cm, with G_{max} and R_s not exceeding 12% and 0.3 seedling per day, respectively. Therefore, cranberry emergence is substantially reduced at seeding depths exceeding 1 cm in a medium reproducing the soil characteristics of New Jersey cranberry beds, indicating that cranberry germination may mainly occur at the surface of the soil. Cranberry seeds used for this experiment were small, with an average length of 2.01 mm, and had limited carbohydrate reserves, with a 100 seeds weight of 0.11 g. Therefore, seedling emergence from a burial depth more than 1 cm may be limited because larger seeds are usually able to emerge from greater burial depths because of their larger capacity to store carbohydrates (Baskin and Baskin, 2014). Weed species in the pigweed (*Amaranthus* spp.) family have seeds similar in size to cranberry and have been shown to preferentially emerge from shallow burial depths. For example, Thomas et al. (2006) reported that a burial depth of 1 cm was optimal for the emergence of slender amaranth, whereas Ghorbani et al. (1999) noted that the optimal burial depth of redroot pigweed (*Amaranthus retroflexus* L.) was between 0.5 and 3 cm.

Because the soil depth at which seeds are buried may limit seedling emergence, sanding could be an option for reducing the development of off-type varieties in areas of cranberry beds where bare ground is exposed. A 1- to 5-cm layer of sand is periodically applied over cranberry vines during the dormant season to promote new shoot development and rooting (Demoranville and Sandler, 2008). This technique has reduced the emergence of swamp dodder (*Cuscuta groenovii* Willd. ex Schult.) seedlings by at least 67% when a 2.5-cm layer of sand was applied over dodder seeds (Sandler et al., 1997).

Overall, these results suggest that light quality influences cranberry germination. When seeds were exposed to an environment enriched with R light, which is a condition that occurs in areas of cranberry beds where the crop canopy is damaged or absent and bare soil is exposed, germination was stimulated. Similar to other *Vaccinium* species, increased germination has been noted with diurnal temperatures ranging from 20 to 25 °C and acidic soil conditions. Cranberry may germinate from shallow soil depths under moist and warm conditions encountered from July to August in the northeastern United States, especially because cranberry beds are frequently irrigated. The sensitivity of cranberry seed to burial could be exploited by specifically sanding open areas of cranberry beds to prevent germination and further emergence of off-type cranberry varieties. Residual herbicides that effectively prevent cranberry seed germination and are labeled for use on this crop, such as sulfentrazone, have been identified (Besançon, 2019; Colquhoun and Rittmeyer, 2017) and could be spot-applied in areas of beds where cranberry seed germination is more likely to occur.

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