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Responses of Stokes Aster Achenes to Chilling

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Abstract. **Stokes aster [*Stokesia laevis* Hill (Greene)] is a perennial ornamental; achenes are a prospective source of vernolic acid for the chemical industry. Responses of achenes of 6 Stokes aster accessions to temperatures of 0° to 20°C were studied. There was no germination below 11°; germination was near 0 at 11° and reached a maximum at 20°. Achenes equilibrated at 15% moisture generally germinated more rapidly than those at 5% moisture. In hydration-chilling experiments, more than one day of exposure to chilling prior to germination decreased germination and increased the frequency of abnormal seedlings in some entries. Equilibration at 15% moisture prior to chilling reduced damage slightly compared to 5% moisture. There seemed to be a direct relationship between early imbibition rate and susceptibility to chilling damage. Gradual chilling and warming of germinated achenes resulted in a significant reduction in damage compared to abrupt chilling and warming.**

Stokes aster (*Stokesia laevis*) is a perennial composite native to the southeastern United States. Plants are normally 10 to 70 cm tall, and flowers are bluish violet to white. The species is of some ornamental importance and several cultivars have been released (5). Achenes are about 0.5 cm long and are a prospective source of vernolic acid (*cis*-12, 13-epoxy-*cis*-9-octadecenoic acid) for the chemical industry. Epoxidized products are used as stabilizers for vinyl plastics and as binders for coatings and adhesives. They constitute an annual market of 57 million kg (2, 5).

Propagation generally is done by plantlets because of poor seedling vigor (2, 5). Since vernalization often is necessary to induce flowering, Stokes aster established in the spring may not flower until the summer of the following year (2). A breeding program designed to develop lines which can be direct seeded is underway (2). If Stokes aster were tolerant to chilling, early spring seeding might provide sufficient vernalization to induce seeding-year flowering. Alternatively, the species could be seeded in the fall and vernalized during the winter. An ideal germination temperature is 20°C, and light seems to have no effect on germination (G.A. White and T.A. Campbell, unpublished data).

The temperature at which seeds will germinate varies widely among species, and the transition from temperatures which allow germination to temperatures at which few seeds will germinate often is quite abrupt (7). Several factors recognized as mediating a seed's response to low temperatures are species or cultivar, temperature and duration of exposure, stage of germination, and initial seed moisture content (11). Generally, warm season species are less tolerant to low temperatures than cool season species, and increasing exposure to chilling temperatures increases damage (11). Most important crop species of tropical or subtropical origin are sensitive to low temperatures in the range of 0° to 20°C (6). Several species tolerate chilling temperatures if the embryo moisture is above 12% and are progressively less tolerant as the embryo moisture is reduced to 6% (4). The rate of water entry also is important, and seeds that are hydrated slowly in a water saturated atmosphere at low temperatures generally are not injured (4), whereas seeds that are hydrated rapidly at low temperatures often are damaged (11). Abortion of the radicle tip is a commonly reported symptom of imbibitional chilling injury (3). Tully et al. (8) concluded that rapidity of imbibition was directly related to permeability of the seed coat. A 2nd period of chilling sensitivity that occurs 1 to 4 days past the period of imbibition also has been reported (11).

Seedlings of some species may be conditioned or "hardened" by exposure to temperatures slightly above the chilling range. Seedlings conditioned in this manner are more resistant to subsequent chilling than seedlings exposed abruptly to chilling temperatures (9, 10). This study was designed to investigate the effects of chilling on germination of Stokes aster achenes.

Materials and Methods

Six Stokes aster entries were taken at random: Plant Introduction numbers 347645, 383887, 383889, 383885, 354065, 383888 were designated entries 1 through 6, respectively. The origins of entries 1 and 5 are unknown, the remainder came from Mississippi. All achenes were from field increases conducted the same year in isolation plots at Beltsville, Md. Achenes which would pass through a 0.30 × 2 cm rectangular-mesh screen but were stopped by a 0.22 × 2 cm rectangular-mesh screen were used. All achenes were surface sterilized by exposure to chlorine gas in a desiccator for 24 hr. Achenes were equilibrated to 15% moisture (SE = 0.7%) by hydrating in a moisture saturated atmosphere at 5°C for 48 hr or to 5% moisture (SE = 0.2%) by equilibrating for 48 hr at 27° over a 40% solution of H_2SO_4. The 40% H_2SO_4 solution was selected based on replicated experiments with several concentrations of H_2SO_4. All percentage data were arcsin transformed for analyses of variance except for those from the imbibition rate study where the CV was only 0.12. Regression analysis was performed on untransformed response data. Except for postgermination chilling studies where orthogonal polynomials were fitted, quantitative data were analyzed using a stepwise regression procedure. Levels to enter and stay were set at 0.05; all terms retained in the models were significant at ≤ the 0.05 level.

Thermogradient plate studies. Achenes were placed on 2 adjacent thermogradient plates at temperatures of 2°, 5°, 8°, 11°, 14°, 17°, and 20°C. Each plate was randomly assigned achenes at 1 moisture level. No light was supplied. An experimental unit was a seed line 10 cm long containing 30 achenes. Germination counts were taken daily for 21 days (D) (an achene was con-

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sidered germinated if the radicle tip had cleared the seed coat). Experimental design was a split-split plot with 3 replications. Whole plots were a 2 (achene moisture level) × 21 (days) complete factorial. Subplots were temperatures and sub-subplots were entries.

There was no germination below 11°C. The cumulative percentage of germinations were computed for temperatures (T) of 11° and above, and regressed on T, T^2, T^3, D, D^2, D^3, and all cross products. Since there were many interaction terms, terms which did not contribute at least 3% to the R^2 were deleted. Models were derived for each moisture level and entry combination.

Hydration chilling studies. Achenes were imbibed at 0°, 5°, 10°, or 20°C temperatures in rolled standard germination paper for 1, 3, or 6 days. There were 30 achenes per experimental unit (seed roll). Imbibition was in the dark for 0°, 5°, and 10°C and under continuous fluorescent light (30 μmol s^{-1} m^{-2}) for 20°. Watering was by capillary action, and experimental designs within each time period were randomized complete blocks with 4 replications. Treatments were arranged in 2 (achene moisture level) × 4 (temperatures) × 6 (entries) complete factorials. After imbibition, achenes were maintained at 20° for one week under continuous fluorescent light (30 μmol s^{-1} m^{-2}), at 27° for 1 week under fluorescent light (18 hr daylength; 140 μmol s^{-1} m^{-2}), then evaluated. The percentage of germination and the percentage of abnormal seedlings (germinated achenes that were weak with poor radicle development) were calculated.

Imbibition rate study. Achenes (10 per experimental unit) were imbibed in 3 cm (diameter) × 0.7 cm (height) round vented plastic cases (experimental units) by immersion in 20°C distilled water for 0, 1, 2, 3, 4, 5, 6, 7, 24, 48, 72, or 144 hr. They then were surface dried in a force-draft oven for 10 min on filter paper at 30°, weighed, oven dried (105°) 24 hrs, and then reweighed. The experimental design was a randomized complete block with 3 replications. Treatments were arranged in a 2 (achene moisture levels) × 12 (imbibition time) complete factorial.

Postgermination chilling study. The effects of 15 temperature regimes (Table 1) applied during the early stages of germination (few radicles had emerged) on entries 4, 5, and 6 were evaluated. Treatments were selected so that the effects of temperature, duration of chilling (1, 3, or 6 days), and type of chilling (gradual vs. abrupt) could be evaluated. For analysis, treatments were divided into 5 groups (G) (G1 = treatments 1 to 3, G2 = treatments 4 to 6, G3 = treatments 7 to 9, G4 = treatments 10 to 12, and G5 = treatments 13 to 15). Orthogonal polynomials were fitted to the duration of chilling for all groups and to temperature for G3 to G5.

Achenes were treated in standard germination paper rolls (experimental units) and kept moist by capillary action; there were 30 achenes per roll. A continuous fluorescent light was supplied, and the intensity for the 0°, 5°, 10°, and 20°C temperatures was 10, 130, 130, and 30 μmol s^{-1} m^{-2}, respectively. Experimental design was a randomized complete block with 3 replications. Treatments were arranged in a 15 (treatments) × 3 (entries) factorial. The percentage of germination and abnormal seedlings were calculated.

Results and Discussion

Thermogradient plate studies. Entries equilibrated to 15% moisture generally germinated more rapidly than those at 5% moisture. Differential responses to temperatures were evident among entries with, presumably, the vigorous entries germinating at low temperatures. Extended period of ≥ 18°C seem necessary for adequate germination in Stokes aster. Response surfaces for entries 3 and 5 (Fig. 1) depict the range of responses observed. The slight decrease in germination between 15 and 21 days in Fig. 1B is probably an artifact produced by the modeling procedure.

Table 1. Treatments applied in a study of the effects of postgermination chilling on Stokes aster achenes.

Group[y]	Treatment code	Temperature[z] Days of exposure 20°C	10°	5°	0°	5°	10°	20°
		Begin						End
1	1	6	3	3	6	3	3	6
	2	6	3	3	3	3	3	6
	3	6	3	3	1	3	3	6
2	4	6	3	6	---	---	3	6
	5	6	3	3	---	---	3	6
	6	6	3	1	---	---	3	6
3	7	6	---	---	6	---	---	6
	8	6	---	---	3	---	---	6
	9	6	---	---	1	---	---	6
4	10	6	---	6	---	---	---	6
	11	6	---	3	---	---	---	6
	12	6	---	1	---	---	---	6
5	13	6	6	---	---	---	---	6
	14	6	3	---	---	---	---	6
	15	6	1	---	---	---	---	6

[z]Treatments applied to unimbibed achenes.
[y]Treatments were clustered into 5 groups for statistical analysis.

Table 2. Mean square values (each with 1 df) from analysis of variance of response of germinated Stokes aster achenes to 15 temperature regimes (Table 1).[z]

Effect	Mean square: Germination (%)[x]	Abnormal seedlings (%)[x]
Duration of chilling:		
Linear (DL)	2.59	48.64
Quadratic (DQ)	0.17	20.96
Temperature[w]		
Linear (TL)	0.65	8.38
Quadratic (TQ)	174.97	352.23*
DL × TL	257.56*	3.39
DL × TQ	1.53	93.62
DQ × TL	31.87	75.03
DQ × TQ	7.56	2.58
G1 vs. G3	344.03*	367.03*
G2 vs. G4	1121.42**	1987.78**
DL × (G1 vs. G3)	413.57**	25.30
DL × (G2 vs. G4)	0.09	12.87
DQ × (G1 vs. G3)	8.58	25.10
DQ × (G2 vs. G4)	62.22	336.93*

[z]Treatments were divided into 5 groups (G): G1 = treatments 1 to 3, G2 = treatments 4 to 6, G3 = treatments 7 to 9, G4 = treatments 10 to 12, and G5 = treatments 13 to 15.
*, **Significant at the 5% or 1% level, respectively.
[x]Arcsin transformed.
[w]Computed for G3 to G5 only.

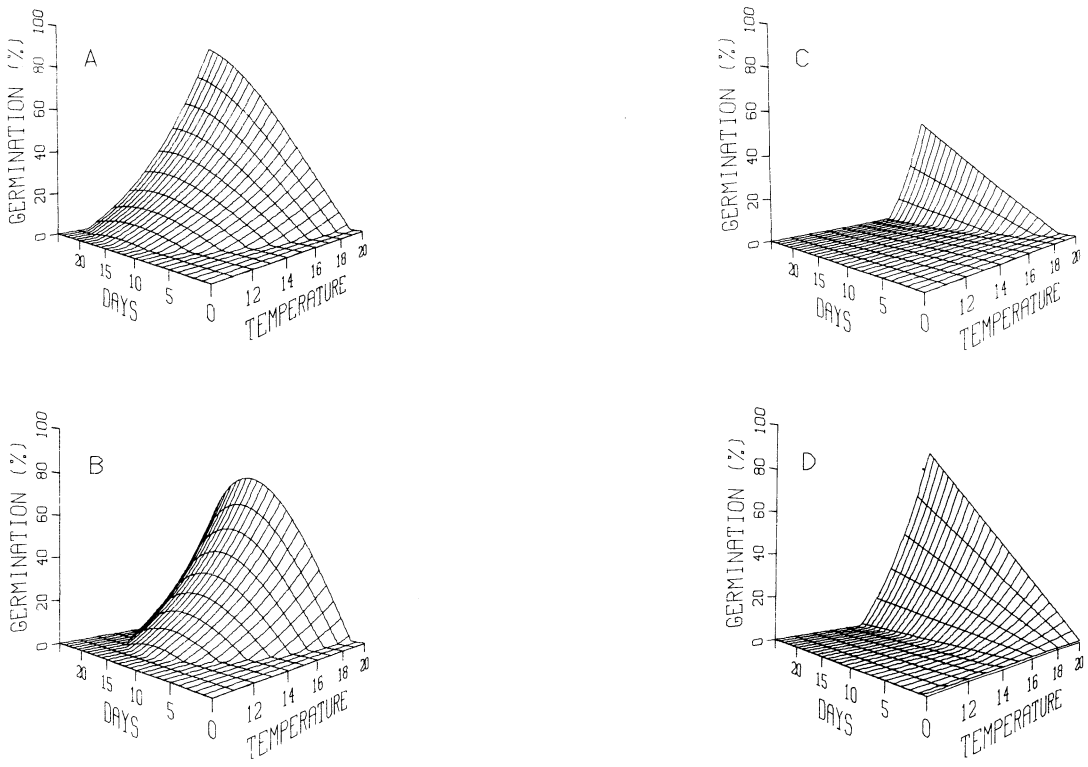

Fig. 1. The relationship of the cumulative percentage of germination of achenes (PG) from 2 Stokes aster entries (E3 and E5) equilibrated at 2 moisture levels (5% or 15%) to temperature (T = 0° to 20°C) over time (D = 0 to 21 days). Predicted values <0 were set to 0, those > 100 were set to 100. **A**. For E3 at 5% moisture: $PG = -8.89 - 0.0001\ TD^3 + 0.0007\ T^3D$ $R^2 = 0.68$. **B**. For E3 at 15% moisture: $PG = -13.52 - 0.00002\ T^2D^3 + 0.001\ T^3D$ $r^2 = 0.91$. **C**. For E5 at 5% moisture: $PG = -5.45 + 0.72\ TD - 0.11\ T^2D + 0.004\ T^3D$ $R^2 = 0.90$. **D**. For E5 at 15% moisture: $PG = 0.89 - 0.03\ T^2D + 0.002\ T^3D$ $R^2 = 0.84$.

Hydration chilling studies. After one day of exposure to the temperature regimes, entry effects were significant for the percentage of germination, and entry and moisture effects for the percentage of abnormal seedlings. No interactions were significant. Germination ranged from 78% (entry 5) to 90% (entry 2). The percentage of abnormal seedlings ranged from 6.3% (entry 4) to 13.6% (entry 5), and was 8.6% at 15% moisture and 11.7% at 5% moisture.

After 3 days exposure, entry and temperature (T) × moisture (M) effects were significant for the percentage of germination; and temperature, temperature × moisture, and temperature × moisture × entry effects were significant for the percentage of abnormal seedlings. Germination ranged from 76% (entry 1) to 84% (entry 5). The percentage of germination was regressed on TM, T^2M, and T^3M. No terms were selected. For each entry, the percentage of abnormal seedlings was regressed on T, T^2, T^3, M, TM, T^2M, and T^3M. Regression was significant only for entries 1 and 4, and only temperature terms were selected. In both cases, there was an essentially linear, inverse relationship between the percentage of abnormal seedlings and temperatures of 0° to 10°C (Fig. 2, A and B). Entry 4 seemed more sensitive to marginal (10° to 20°) chilling temperatures.

After 6 days, temperature, entry, and temperature × entry effects were significant for the percentage of germination; and temperature, moisture, entry, and temperature × moisture effects were significant for the percentage of abnormal seedlings. The percentage of germination was regressed on T, T^2, and T^3 for each entry. Regression was significant only for entries 3 and 6. Analyses indicate a direct, linear relationship between germination and temperature for these entries (Fig. 2, C and D); however, temperature effects were quite mild. The percentage of abnormal seedlings was regressed on T, T^2, T^3, M, TM, T^2M, and T^3M. The response surface (Fig. 2E) indicates a linear, inverse relationship between the percentage of abnormal seedlings and temperature, and that a small degree of protection from chilling was afforded by 15% achene moisture.

Results indicate that exposure to chilling for one day would have little effect on Stokes aster embryos, indicating at least a moderate degree of tolerance. The 5% moisture treatment seemed to damage seedlings slightly. Three days of exposure to chilling probably would not reduce germination substantially in the field but could reduce emergence substantially even at marginal chilling temperatures. Six days of exposure could have a mild effect on germination and a pronounced effect on emergence. High moisture content probably would not protect embryos to any great extent, and the most important factor in embryo damage would be duration of exposure to chilling. Differential responses of entries indicates that some entries are more tolerant to chilling than others, probably due to the variations in achene quality and/or to genetic factors.

Imbibition rate studies. Moisture, entry, hours of imbibition (H), moisture × H and entry × H effects were significant (0.01 level). Considering H = 0 and 1 only, moisture × H effects were highly significant based on orthogonal contrasts. Imbibition in the 1st hour was much faster for achenes at 5% (28% moisture at H = 1) compared to those at 15% (32% moisture at H = 1). Differences in imbibition rates did not seem great enough, however, to cause a substantial increase in protection from chilling injury at 15% moisture (Fig. 2E).

For each entry, the percentage of achene moisture was regressed on H, H^2, H^3, M, HM, H^2M, and H^3M, after transforming H and M using the formula Log (x + 1). Only variables

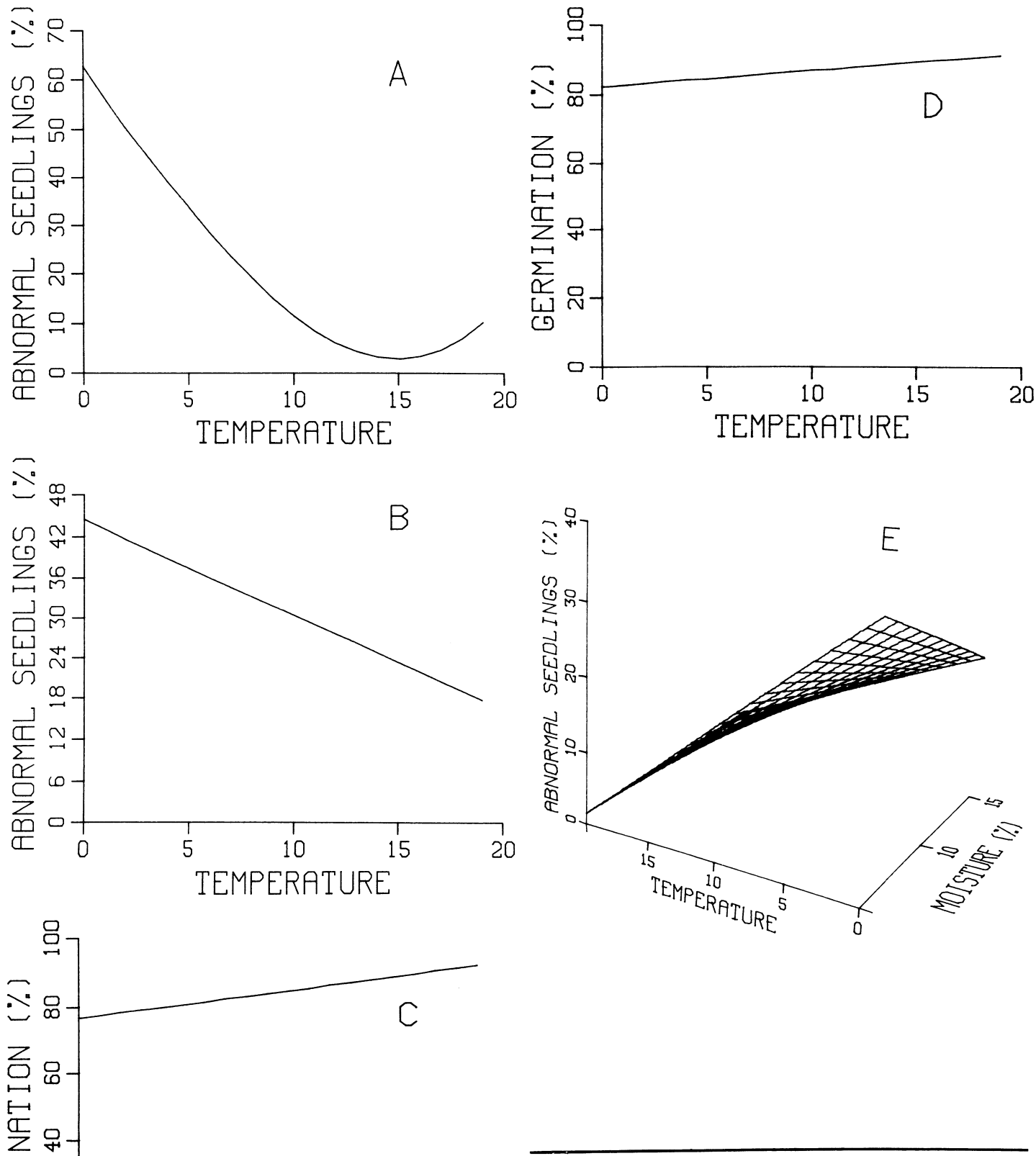

Fig. 2. The relationship of the percentage of germination (PG) and the percentage of abnormal seedlings (PA) to temperature (T) (exposed 3 or 6 days) and moisture (M) for selected Stokes aster entries. **A**. E1 after 3 days: PA = 62.55 − 6.004 T + 0.009 T^3 R^2 = 0.40. **B**. E4 after 3 days: PA = 44.43 − 1.41T R^2 = 0.22. **C**. E3 after 6 days: PG = 76.67 + 0.82 T R^2 = 0.39. **D**. E6 after 6 days: PG = 82.33 + 0.47 T R^2 = 0.22. **E**. Mean response over all entries after 6 days: PA = 41.58 − 2.06 T − 1.36 M + 0.08 TM R^2 = 0.38.

representing hour effects were selected. Generally, imbibition rate in seeds is rapid during initial stages, becomes quiescent, then increases rapidly again at germination (1). Responses of entries 1, 3, 4, and 6 (Fig. 3B) reflected this imbibition pattern. The response of entry 2 (Fig. 3A) was quadratic and that of entry 5 (Fig. 3C) was linear. Partial regression coefficients for the linear terms (H) of the models reflect initial imbibition rates and were 42.5, 27.7, 43.1, 62.5, 13.1, and 56.9 for entries 1 to 6, respectively. Imbibition rate leveled off to nearly 0 at about 10 hr in those entries with relatively rapid initial imbibition rates (entries 1, 3, 4, and 6) and continued to increase at a relatively even rate throughout the experiment in those with slow initial rates (entries 2 and 5).

The moderate chilling tolerance observed in the species may be, at least partially, a function of imbibition rate. It is interesting to note, for example, that in the hydration chilling studies, chilling was more deleterious to entries 1, 3, 4, and 6 than to entries 2 and 5. The former entries may have sustained more damage due to rapid hydration caused by high seed coat permeability (4, 8, 11). It would probably be desirable to develop lines with slow imbibition rates through breeding.

Postgermination chilling study. Entry and treatment effects were significant for the percentage of germination and the percentage of abnormal seedlings; the entry × treatment interactions were nonsignificant. G1 vs. G3 and G2 vs. G4 effects were significant for both response variables based on orthogonal contrasts (Table 2). Duration × (G1 vs. G3) and duration × temperature effects were significant for the percentage of germination. $(\text{Duration})^2$ × (G2 vs. G4) and $(\text{temperature})^2$ effects were significant for the percentage of abnormal seedlings. Regression of the percentage of germination on duration was nonsignificant for G1 ($P = 0.14$) and G3 ($P = 0.11$) as was the regression of the percentage of germination on duration × temperature ($P = 0.59$). The regression of the percentage of abnormal seedlings on $(\text{duration})^2$ was also nonsignificant for G2 ($P = 0.69$) and G4 ($P = 0.27$) as was regression of the percentage of abnormal seedlings on $(\text{temperature})^2$ ($P = 0.75$). High P values indicate very weak responses; thus interpretations of regression models could be spurious.

Entry means for entries 4, 5, and 6 were 76.6%, 67.8%, and 63.5% for the percentage of germination and 22.2%, 29.9%, and 32.0% for the percentage of abnormal seedlings, respectively. Differences in entries are attributed to variations in achene quality and/or genetic factors. At 0° and 5°C, germination for hardened vs. nonhardened seedlings was 75.8% vs. 67.9%, and 77.0% vs. 62.5%, respectively. The percentage of abnormal seedlings was 20.9% vs. 28.8% and 18.0% vs. 36.7%, respectively. Results indicate that sudden chilling and warming in the field could have more serious effects on germinated Stokes aster achenes than the effects of gradual chilling and warming. The difference in damage between hardened and nonhardened seedlings was more pronounced at 5° compared to 0°C, perhaps because seedlings remained physiologically active during chilling at 5° and thus susceptible to damage. Duration of chilling and temperature had little effect on responses, indicating that the species is considerably more susceptible to chilling damage during hydration than after.

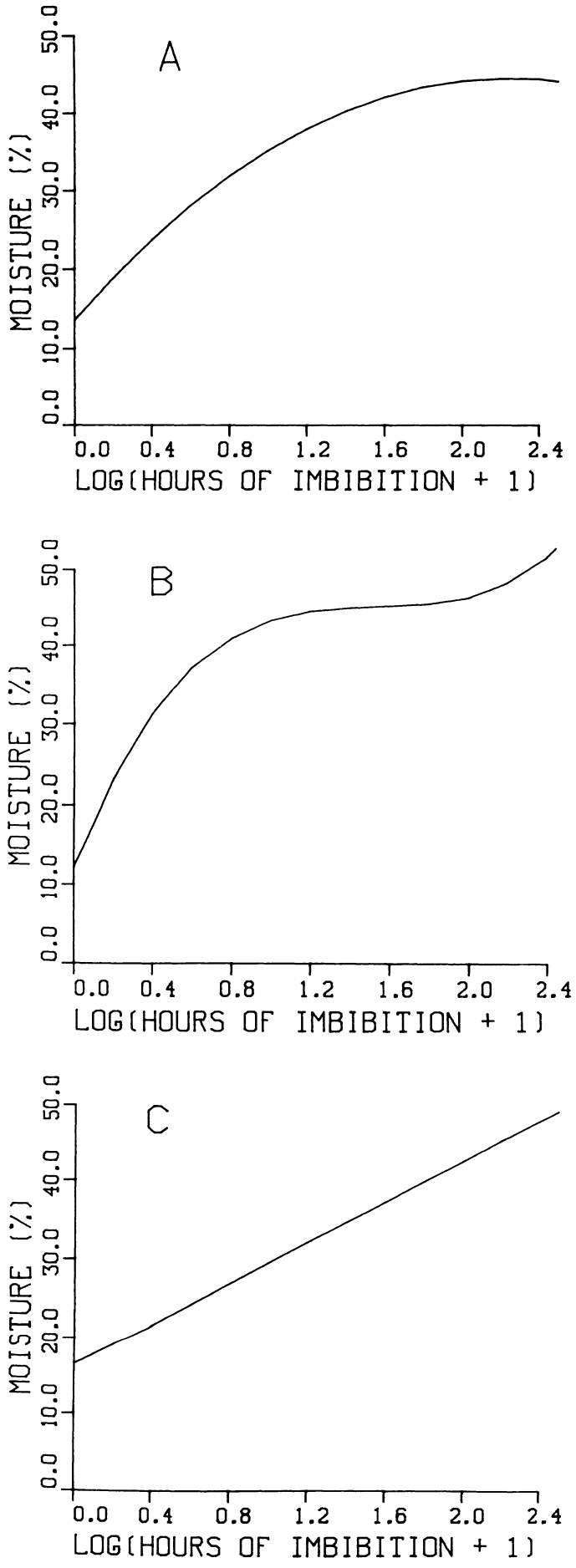

Fig. 3. The regression of the percentage of moisture (PM) in Stokes aster achenes on Log(hours of imbibition + 1) (H). **A**. For E2: $PM = 13.64 + 27.75\ H - 6.22\ H^2\ R^2 = 0.079$. **B**. For E4: $PM = 12.23 + 62.49\ H - 40.09\ H^2 + 8.68\ H^3\ R^2 = 0.82$. **C**. For E5: $Pm = 16.53 + 13.09\ H\ R^2 = 0.65$.

Conclusions

It seems that Stokes aster could tolerate early spring or fall seeding. Equilibration at 15% moisture would reduce germination time as well as chances of hydration chilling damage; however, extended periods of 18°C or above would be necessary for adequate germination. Development of breeding lines with slow imbibition rates also would enhance chances of success. Once germinated, tolerance to chilling in achenes would probably increase; however, the effects of chilling on seedlings at an advanced stage of growth requires further study.

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Inheritance and Characterization of the Fruit Ripening Mutation in 'Alcobaca' Tomato

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Abstract. **A single recessive gene was found to be responsible for the abnormal fruit ripening of 'Alcobaca' tomato (*Lycopersicon esculentum* Mill.). This gene causes a ripening syndrome characterized by attenuated respiratory activity and ethylene production, delayed softening of the fruit, low polygalacturonase (PG) activity, and extended shelf life. Allelism tests showed that the mutant gene of 'Alcobaca' is allelic to *nor*. It is proposed that the symbol *nor*^{A} be used to refer to this mutant. The *nor*^{A} allele is dominant to the *nor* allele.**

'Alcobaca' was first described by Almeida (1) as a tomato (*Lycopersicon esculentum*) with prolonged fruit storage life. A long shelf life was subsequently confirmed by a number of other researchers (7, 9, 10, 11, 12). Leal and Mitzubuti (9) produced a series of reciprocal crosses between 'Alcobaca' and normal ripening materials. Differences in storage life between reciprocal crosses were not found. The authors also suggested that the long fruit storage life was quantitative in nature. Kopeliovitch et al. (8) have established that the ripening mutation in 'Alcobaca' is controlled by a single recessive gene. Tigchelaar et al. (22) noted that 'Alcobaca' is an aberrant ripening cultivar, phenotypically distinct from both *rin* and *nor* and suggested, based on unpublished allelism tests, that 'Alcobaca' may carry a 3rd allele at the *nor* locus. Kopeliovitch et al. (7) questioned this allelism relationship, although no data were presented to support their argument. Mutschler (13) has reported that the 'Alcobaca' ripening mutant is not allelic to *nor*, but is linked to *nor* (18 map units). Lobo (12) reported that hybrids between 'Alcobaca' and normal ripening tomatoes exhibited normal fruit phenotype but prolonged fruit shelf life. The *rin* x 'Alcobaca' hybrid had a normal fruit phenotype and extended fruit shelf life. The *nor* x 'Alcobaca' hybrid, however, had the mutant fruit phenotype and a very long shelf life.

The current study was carried out to clarify the inheritance of the abnormal ripening behavior of 'Alcobaca' and the genetic relationship between this mutant and the ripening mutants *rin* and *nor*.

Materials and Methods

All materials were grown under full-bed plastic mulch without stakes at the Horticultural Unit of the Univ. of Florida, Gainesville, during the spring of 1980. The 1st experimental planting included the normal ripening parent 'Florida 1C', 'Alcobaca', and 'Florida 1C' x 'Alcobaca'. A randomized complete block design with 5 blocks was used (originally part of an inheritance study not reported here). There were 10 plants per block or 50 plants per genotype. Two harvests were made of fruit from these materials. For measurements of ripening parameters (respiration, ethylene evolution, and fruit firmness), fruits were harvested at the mature-green stage and stored at 20°C. For studies of storage life, fruit were harvested at the breaker stage, rinsed with running water, air dried, and stored at 20°.

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