correlated with the multiple-harvest test to be substituted completely. Also, the rapid tests do not necessarily provide adequate measure of earliness, quality, and stress resistance. The small-plot, once-over harvest test provides an excellent method for evaluation of families from recurrent selection, and for development of lines for use as hybrid cultivars.

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Estimates of Heritabilities and Variance Components for Low-temperature Germination Ability in Cucumber

Todd C. Wehner[1]

Department of Horticultural Science, North Carolina State University, Raleigh, NC 27695-7609

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Abstract. **Variance components for low-temperature germination ability in cucumber (*Cucumus sativus*) were estimated for 3 germination variables (actual days to germination, days to 50% germination, and percentage of germination) at 17°C using a North Carolina Design I analysis. The estimates were made using the North Carolina Medium Base Pickle (NCMBP) population, which was developed by intercrossing adapted pickling cucumber cultivars with diverse lines for 3 cycles without selection. Estimates of additive and dominance variance for the percentage of germination and days to 50% germination were equal, but additive variance was predominant for actual days to germination. Heritabilities based on half-sib families tested in 2 replications ranged from 0.44 to 0.61 for the 3 germination variables. There were large significant genetic correlations among the 3 germination variables, ranging from 0.61 to 1.03 in absolute value. Selection for either the percentage of germination or for actual days to germination at 17° should result in significant progress in improving low-temperature germination ability of cucumbers in the NCMBP population.**

Low-temperature germination ability has been studied in vegetable crops for several decades using seed sprouting response in cold chambers, and has been found to be both heritable and a useful predictor of field emergence under adverse conditions. Narrow sense heritability for low-temperature germination ability in 2 different tomato (*Lycopersicon esculentum* Mill.) populations was 0.25 (5) and 0.66 (13), respectively.

Cold tests are valuable tests of seed vigor, but have been used with varying degrees of success. Cold test results were not correlated with field emergence in tomato (1), but were positively correlated for maize (*Zea mays* L.) (12). Cold tests for germination of carrot (*Daucus carota* L.) seeds had a high correlation with field emergence and provided better prediction of field emergence than the standard germination tests run at optimum temperature conditions (7). In cotton (*Gossypium hirsutum* L.), high (25°C) and low (15°) temperature germination results were not correlated (2). The best tomato lines germinating at cold temperatures were not necessarily the best ones for low temperature seedling growth, plant growth, or fruit setting (8). The mechanism of cold tolerance has been studied. For example, failure of low-temperature germination in cucumber (*Cucumis sativus* L.) was not due to damage from imbibing cold water, to loss of membrane integrity, or to failure of mitosis, but was most likely due to denaturing of proteins (16).

Incorporation of low-temperature germination ability into cucumber cultivars should be useful for establishing early uniform stands in spring plantings. If combined with cold tolerance at the seedling stage, it also may be possible to extend the growing

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[1] Assistant Professor.

season by allowing early planting in the spring. Dutch slicing cucumbers that are tolerant to cooler greenhouse production temperatures at posttransplant growth stage recently have been released (15), suggesting that cold tolerant seedlings might be developed through similar techniques. Lower (9) showed that there were differences among 11 cultivars for germination speed at temperatures between 14° and 17°C. Cultivars developed in the northern United States (SMR-58, Wisconsin SMR-18) were better cold germinators than those developed in the southern United States (Palomar, Chipper, and Ashley). The exception was 'Pixie', which had good cold germination ability, but was developed in the south.

Nienhuis and Lower (14) estimated the narrow sense heritability of the percentage of germination at 13°C to be 0.17 among half-sib families. Furthermore, good progress was made for germination ability using half-sib family selection in a broad based population selected for 3 cycles at 15° (10). Germination speed of 203 cucumber lines and cultivars was found to vary widely (3.5 to 17.3 days to germination) at 15°, but not at 20° (18, 19). Heritability was estimated to be 0.15 to 0.20 using parent-progeny regression (19).

The objective of this study was to determine the heritabilities, variance, and covariance components for 3 germination variables (actual days to germination, days to 50% germination, and percentage of germination) in a cucumber population tested at 17°C.

Materials and Methods

The research was conducted in germination chambers in the Phytotron at North Carolina State Univ. with one chamber for each of the 2 temperatures (17° and 21°C). The cold test was run at 17° because previous studies have shown that lines can be distinguished best for cold tolerance at 14° to 17° (9), and because preliminary research (unpublished) showed that many families in the reference population were not cold tolerant.

The reference population was the North Carolina Medium Base Pickle (NCMBP) population which was formed by intercrossing adapted pickling cucumber cultivars and breeding lines, large-fruiting lines, compact lines, multiple-fruiting *Cucumis sativus* var. hardwickii lines, determinate lines, and several hundred lines from the USDA plant introduction collection held at Ames, Iowa. The initial lines were crossed in various combinations for different experiments before compositing and intercrossing in 1977, 1978, and 1980 to form the NCMBP population. The NCMBP population was chosen because it has a wide genetic base with useful levels of variability for yield, fruit quality, disease resistance, and low-temperature germination ability. It was anticipated that the genetic estimates obtained would, therefore, be somewhat applicable for half- or full-sib family selection in other populations not developed specifically for cold tolerance studies.

The mating design used to estimate the variance components in this reference population was a North Carolina Design I. Construction and analysis of this design were given by Comstock and Robinson (3, 4). In this study, 70 S_o plants were chosen at random from the population and designated as males. Each male was mated to 3 S_o plants chosen at random, which were designated as females. The pollinations were made in the greenhouse with 1 cross being made on each plant to produce about 100 seeds per full-sib family. Seeds were extracted from the fruit 6 weeks after pollination, treated with a fungicide, and stored for about one month at room temperature before testing.

The experimental design was a randomized complete block with 2 replications, 70 males (half-sib families), and 3 females (full-sib families) nested within males. The 2 blocks were placed in the upper and lower sections of the germination chamber to control any vertical gradients in temperature. Seeds of each of the 210 families were tested in 60 mm-diameter petri plates into which 2 pieces of filter paper, 1.5 ml of distilled water, and 20 seeds were added. Two replications of 20 seeds each were used for each of the 2 test temperatures because this number has been adequate to distinguish test materials in previous studies (9, 19), and because it would be practically impossible to obtain more seeds per full-sib family in this mating design for additional replications. A similar situation would exist for seed production in most recurrent selection schemes that might make use of the heritability estimates generated by this study.

Seeds and water were allowed to equilibrate to chamber temperature for one day before the start of the experiment. The number of seeds germinating were counted each day for 30 days from the start of the test. Seeds were considered germinated when the radicle reached 6 mm in length. The 3 germination variables used for genetic analysis of the NCMBP population (actual days to germination, days to 50% germination, and percentage of germination) were then calculated. All treatment units with less than 70% germination at 21°C were removed from the analysis (15 full-sib families), although the results were not significantly changed by including them. Actual days to germination was calculated as mean days to germination of those seeds that germinated. Where less than 50% of the seeds germinated, days to 50% germination was calculated by giving ungerminated seeds a value of 30 days to germination, as done by Lower (9). This procedure provided a more conservative estimate for ungerminated seeds than if missing values were calculated using least squares estimates from those seeds that did germinate. Thus, days to 50% germination was actually a germination index, weighted by the percentage of germination if germination was lower than 50%.

Genetic expectations of the experiment design variance components were derived using the following assumptions: A) regular diploid behaviour, B) no maternal effects, C) linkage equilibrium, and D) no epistasis. Assumption B seems reasonable since no maternal effects were found in a preliminary study of the NCMBP population using parent-progeny regression (19). Heritabilities (h^2) for use in selecting among half-sib and full-sib families tested in 2 replications were calculated as follows: A) $h^2(hs) = \frac{1}{4}\, s^2_A/s^2_{p(hs)}$, and B) $h^2(fs) = \frac{1}{2}\, s^2_A/s^2_{p(fs)}$ where s^2_A was the estimate of additive genetic variance, and $s^2_{p(hs)}$ and $s^2_{p(fs)}$ were the phenotypic variances among half-sib and full-sib family means, respectively. The term s^2_A was estimated as $4s^2_m$. The term s^2_m was the estimate of the variance among males and has been shown to estimate the covariance among half-sibs, which is $\frac{1}{4}s^2_A$, given the above assumptions.

Cross products were computed for all pairs of characters using analogus procedures for variance components. Mode and Robinson (11) showed that covariance components could be used in a manner similar to the way variance components were used. The additive genetic correlation (r_{Aij}) for a pair of characters, i and j, was estimated as $r_{Aij} = s_{Aij}/(s^2_{Ai} \cdot s^2_{Aj})^{1/2}$ where s_{Aij} was the estimated additive covariance component, and s^2_{Ai} and s^2_{Aj} were the estimated additive variance components for characters i and j, respectively. The phenotypic correlation (r_{pij}) for unrelated full-sib family means grown in 2 replications was estimated as $r_{pij} = s_{p\ (fs)ij}/(s^2_{p(fs)i} \cdot s^2_{(fs)j})^{1/2}$ where $s_{p(fs)ij}$ is the phenotypic estimate of covariance and $s^2_{(fs)i}$ and $s^2_{p(fs)j}$ were phenotypic estimates of components of variance for traits i and j, respectively.

Table 1. Analysis of variance and expected mean squares for cucumber seed germination at 17°C with full-sib families nested in half-sib families in a North Carolina Design I analysis.[z]

Source of variation	Degrees of freedom	Expected mean squares	Mean squares: Actual days to germination	Mean squares: Days to 50% germination	Mean squares: Percentage of germination
Blocks	1	$s^2 + 210s^2_b$	233.63*	841.00**	3887.84**
Males	69	$s^2 + 2s^2_{f/m} + 6s^2_m$	76.94**	207.75**	2039.48**
Females/Males	125	$s^2 + 2s^2_{f/m}$	29.70	116.64**	1059.34**
Error	194	s^2	35.97	34.22	212.08

[z]Families having germination rates below 70% at 21°C were removed from the analysis (15 full-sib families were removed out of 210 tested).

*,**Mean squares significantly greater than the error mean square at the 5% (*) and 1% (**) levels.

Results and Discussion

Of the 210 full-sib familes tested, 15 had germination below 70% at 21°C. The remaining 195 families had a mean percentage of germination that ranged from 0% to 100%, and a mean days to actual germination that ranged from 3.8 to 24.0 days. There was a large block effect (Table 1) due to vertical temperature gradient in the chamber which may have been caused by warm air replacing cold air in the top of the chamber when the door was opened each day to count germinated seeds.

Mean squares for the 3 germination variables measured (actual days to germination, days to 50% germination, and percentage of germination) were all significant for the effect of males and for females in males, with one exception (Table 1). The females in males mean square for actual days to germination was slightly smaller than the error mean square. Thus, the estimate of that design component ($s^2_{f/m}$) was not significant and negative (Table 2), which resulted in a negative estimate for dominance variance. The dominance variance was larger than additive variance for days to 50% germination and for the percentage of germination. The degree of dominance ($\bar{d}$) for those 2 traits was greater than 1, indicating the present of overdominance, or of linkage disequilibrium. Although the NCMBP population had been intercrossed 3 times before running this study, linkage disequilibrium was probably the cause of the overdominance readings. Linkage disequilibrium has been shown to be the major cause of overdominance in maize populations (6).

Heritabilities based on half-sib family means were moderate for all germination variables, and similar in value to full-sib family heritabilities. Actual days to germination at 17°C had the highest heritability (0.61), and the percentage of germination at 17°C was less heritable (0.48). These heritabilities are similar to those measured for fruit quality traits in a monoecious pickling cucumber population by Smith et al. (17). Previous heritability estimates of low-temperature germination ability in cucumber were considerably lower than those obtained in this study, possibly because of lower temperatures used in those studies. Heritability was 0.17 for the germination percentage at 13°C (14), and was 0.15 to 0.20 for days to germination at 15° (18, 19).

Strong correlations, both genetic and phenotypic, existed among the 3 germination variables (Table 3). The percentage of germination had a large negative genetic correlation with both actual days to germination (−0.61) and days to 50% germintion (−1.03). Thus, selection for a high percentage of germination also should reduce the number of days to germination. Since it is easier to measure the percentage of germintion than days to germination of a seed lot, progress could be made by taking advantage of the significant genetic correlation. Since the correlation was not complete, however, and since the heritability for actual days to germination was higher than the percentage of germination, it may be more efficient to select for days to germination when improving low-temperature germination ability in cucumber.

Days to 50% germination does not, however, seem to be a useful measure of germination at low temperature. When germination of a seed lot is below 50%, the variable was weighted by the percentage of germination (since ungerminated seeds are given a value of 30 days to germination). Therefore, since the average full-sib family had 34.2% germination (Table 1), days to 50% germination was weighted by the percentage of germination for many of the families. Genetic correlation of the percentage of germination and days to 50% germination was −1.03,

Table 2. Means, estimates of design components, genetic variances, degree of dominance and heritabilities for cucumber seed germination at 17°C with full-sib families nested in half-sib families in a North Carolina Design I analysis.[z]

Component	Actual days to germination	Days to 50% germination	Percentage of germination
$\bar{x}$	7.5	16.4	34.2
s^2_m	7.87 ± 2.24	15.18 ± 6.30	163.36 ± 61.20
$s^2_{f/m}$	− 3.13 ± 2.60	41.21 ± 7.52	423.63 ± 67.33
s^2_e	35.97	34.22	212.08
s^2_A	31.49 ± 8.96	60.74 ± 25.21	653.43 ± 244.80
s^2_D	−44.03 ± 13.74	104.11 ± 39.25	1041.09 ± 363.94
$\bar{d}$	(0)	1.85	1.78
h^2(hs)	0.61	0.44	0.48
h^2(fs)	0.69	0.41	0.47

[z]Families having germination rates below 70% at 21°C were removed from the analysis (15 full-sib families were removed out of 210 tested). SE are shown for variance components.

Table 3. Genotypic and phenotypic correlations for cucumber seed germination at 17°C in a North Carolina Design I analysis.[z]

Germination variable	Actual days to germination	Days to 50% germination	Percentage of germination
Actual day to germination	---	0.48**	−0.40**
Days to 50% germination	0.72**	---	−0.91**
Percentage of germination	−0.61**	− 1.03**	---

[z]Phenotypic correlations above, additive genetic correlations below the diagonal.

**Correlation coefficient significant at the 1% level of probability.

indicating that the percentage of germination would be an excellent measure of days to 50% germination (Table 3). In addition, the percentage of germination was easily measured and had a higher heritability than days to 50% germination.

There seems to be sufficient genetic variability in the NCMBP population, and a high enough heritability that rapid progress should be possible in a selection program for percentage of germination and days to germination at 17°C. It seems from previous studies that selection progress would be slowed if seeds were tested at colder temperatures. Dominance variance played an important role in the percentage of germination, so the germination ability of selected lines also should be checked in hybrid combinations. Recurrent selection for specific combining ability would therefore seem to be useful in the development of lines with cold germination ability.

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Variation in Calcium Efficiency among Strains of Cauliflower

G.J. Hochmuth[1]

Department of Plant and Soil Sciences, University of Massachusetts, Amherst, MA 01003

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Abstract. **Using a nutrient solution providing 375 µmol calcium (Ca) to each plant, 40 cauliflower (*Brassica oleracea*, Botrytis) strains were evaluated for growth under low-Ca stress. The most efficient strain produced 14 times the dry matter as the least efficient. Calcium efficiency ratios (mg plant dry matter produced per mg Ca in tissue) differed by a factor of 3 between Ca-efficient and Ca-inefficient strains. Increased Ca accumulation and increased Ca utilization contributed to the increased growth by cauliflower strains under Ca deficiency.**

The recognition of genetic variability in plant species for response to environmental stress has prompted the search for strains having the capacity to grow under suboptimal conditions. An area which has received considerable attention is that of tolerance to nutrient stress. Large intraspecific variation has been found for uptake and efficiency in utilization of macronutrients (2, 6, 12, 14, 17) and micronutrients (1, 11). In numerous cases, the genetic and physiological bases of efficiency have been described (5, 7, 8, 12, 14, 17). Two recent reviews summarized research on physiological and genetic factors contributing to plant mineral nutrition (3, 16).

Isolation of nutrient-efficient strains might help control serious disorders relating to mineral deficiencies in plants. For example, isolation of Ca-efficient tomato germplasm might further the breeding of cultivars tolerant of blossom-end rot (7, 9). Progress in breeding cultivars tolerant of mineral-element stress should accelerate as nutrient-efficient germplasm is isolated. The re-

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[1] Assistant Professor. Present address: Vegetable Crops Dept., IFAS, University of Florida, Gainesville, FL 32611.