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THE INHERITANCE OF SEVERAL CHARACTERISTICS
IN PEPPER

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William M. Randle

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Shigemi Honma
Major professor

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THE INHERITANCE OF SEVERAL CHARACTERISTICS IN PEPPER

By

William M. Randle

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for the degree of

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ABSTRACT

THE INHERITANCE OF SEVERAL CHARACTERISTICS IN PEPPER

By

William M. Randle

Studies were conducted on 19 cultivars representing four species of *Capsicum* to determine the expression of dormancy in seed germination and emergence, and to investigate the inheritance of this character.

Differences in dormancy were found among cultivars. Fruit age was shown to affect dormancy. Warm dry storage also affected the length of dormancy while still maintaining a high level of emergence.

Data from reciprocal progeny crosses in three families of *C. annuum* suggested partial dominance for non-dormancy. Ratios obtained by partitioning segregating generations suggested that 3 major genes (*A*,*B*,*C*)influenced the expression of dormancy. A (3:1)(15:1) factorial gene model best explained the observed ratios. *C* in the homozygous recessive condition was necessary for the expression of dormancy.

Studies on one hundred thirty-seven cultivars of *C. baccatum* var. pendulum were conducted to determine low temperature emergence response and to investivate the inheritance of the trait. Significant differences (5% level) were found between temperatures (10 and 13°C) and between cultivars at 13°C suggesting genetic variability at low temperature emergence.

Data from reciprocal progeny crosses generated from four families of *C. baccatum* var. pendulum suggested partial dominance for slow emergence at low temperatures with additive and dominance gene action playing a role in trait expression.

ACKNOWLEDGMENTS

The author wishes to express his sincere appreciation to Professors Shigemi Honma, M.W. Adams, Hugh Price, and Charles Cress for their guidance as this work was being conducted and for their suggestions and review in the preparation of this manuscript.

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I

THE INHERITANCE OF DORMANCY IN PEPPERS

INTRODUCTION

Pepper (*Capsicum*) seeds have often shown variable rates in germination and emergence resulting in uneven growth, poor stands, and non-uniform maturity. Environmental factors such as poor soil, inadequate moisture, or improper temperatures are all known causes for irregular germination and emergence. However, dormancy was never considered. Seed dormancy is an established mechanism for survival in a large number of plant species, but has not been reported in the genus *Capsicum*.

Dormancy may be thought of as any phase in the life cycle of a plant where active growth is temporarily suspended. Active growth halted by adverse environments such as low or high temperatures, is classified as imposed dormancy or quiescence, whereas growth stopped when all conditions are favorable for growth appear to be caused by conditions within the dormant organ itself, and is said to show innate dormancy or rest. There can be relative dormancy as opposed to true dormancy. Dormant organs induced to grow under rather specific conditions, i.e. a narrow temperature range or photoperiod, are said to exhibit relative dormancy while growth which can not be induced under any environmental conditions is referred to as true dormancy. Crocker (1916) has suggested that dormancy in seeds may occur by several different mechanisms: rudimentary embryos that must mature before germination can begin, complete inhibition of water absorption, mechanical resistance to the expansion of the embryo and seed contents by enclosing structures, encasing structures interferring with oxygen absorption by the embryo and perhaps CO_2 elimination from it, a state of dormancy in the embryo itself, and combinations of any of the former.

Freshly harvested pepper seed was observed to exhibit an alleged dormancy resulting in a delay in time to germination. This delay alluded to an after-ripening nature of the seed; the after-ripening being the process by which dormancy is overcome. Researchers anxious to grow as many generations in as short a time period as possible need to recognize dormancy in freshly harvested seed and know the methods to overcome it. The objectives of this study were:

1. To determine if dormancy is exhibited in pepper seeds.
2. Analyse the nature and characteristics of the dormancy.
3. Determine the genetic control of the dormancy.

LITERATURE REVIEW

Peppers were traditionally thought of as a non-dormant crop, their seeds known to germinate soon after extraction from ripe fruits. Studies on seeds of Solanaceous plants (peppers and tomatoes) revealed no indication of a dormant period (Odland, 1938). These seeds germinated equally well at all intervals after harvest with germination percentages of pepper seed being 73.8, 76.7, 69.0, and 71.0 at one, four, twelve, and twenty weeks post harvest respectively.

Mahideem, _et al_. (1973) observed a case of viviparous germination in chillies, showing various degrees of germination _in situ_. Lateral roots were observed on some seedlings. Location in the fruit had an effect on the precocious germination with most germinated seeds being found in the top and mid regions of the fruit. Moreover, climatic factors seemed to be involved with the phenomena exhibited. High humidity and warm temperatures (maximum temperature, 26.3°C; minimum temperature, 17.8°C; relative humidity, 93%) were needed to stimulate germination. The authors summarized the results as "an indication of the non-dormant nature of chilli seeds."

Lack of germination and non-uniformity in germination of pepper seeds has been attributed to a number of different causes. Storage temperature and moisture content of the seed previous to planting was shown to have an effect on the germinability of peppers (Barton, 1935). Air dried pepper seeds stored at room temperature for one, two, and three years had germination percentages of 67, 64, and 45 respectively while seed stored at -5°C showed germination percentages of 80, 86, and 73. In addition, seeds containing 66% moisture stored at room temperature and -5°C had germination percentages of 74, 74, 65 and 70, 81, 81 respectively.

Fruit maturity expressed as days following anthesis and degree of fruit color was observed to affect germination in peppers (Cochran, 1934). Mature green fruit thirty days post anthesis had a germination percentage of 61, while fruit 40 days post anthesis with red-green fruit had 68.5% germination. Superior germination existed at 60 days post anthesis. Fruit that was dark red and shriveled had a germination percentage of 96.

Gikalo (1966) demonstrated that location of the fruit on the pepper plant influenced the quality of the seed and its subsequent germination. Mainstem, first, and second order branches showed good germination while seeds from third, forth and fifth order branches had a reduced germination.

Temperature has had an effect on a pepper seeds ability to germinate quickly and uniformly. Germination rate was found to increase as temperatures rose from 11°C to 30°C (Kotowski, 1926).

A reduction in uniformity and germinability in pepper seeds due to coat bounding has been reported by Baker (1948). Coat bounding was a condition where pepper seeds emerged from the soil before the cotyledons and plumules could be freed from the seed coats. This condition resulted from the combined effects of the seed structure, the epigeal type of germination, and an unfavorable environment. Injury to the seedling resulted from the rapid drying of the testa after emergence of the radicle and elongation of the hypocotyl, but before the cotyledons were freed. In addition, the endosperm cuticle was thought to have a slight confining effect while the arched character of the cotyledons increased the binding by the inflexible dry coat.

Numerous species of plants have been found to contain substances which inhibit or delay the germination of seeds. Such inhibitors were brought about by environmental conditions, but more often by conditions within the plant itself (Evenari, 1949). Groups of substances which were found in different organs of the plant body and acted as germination inhibitors were: alkaloids, essential oils, glycosides, organic acids, pectins, tannins, and sugars.

Konis (1947) demonstrated that among the vegetables a comparatively weak inhibitor was found in the garden sorrel, bean, cucumber, maize, sweet potato and eggplant, whereas parsley, turnip-rooted parsley, beetroot, carrot, and spinach had strong inhibitors. Within peppers, the germination inhibitors were found in the fruit, fruit juice, and leaf sap. The intensity of their suppression varied depending on the location of the substances (Konis, 1947; Evenari, 1949). Konis (1947) showed the inhibitory effect of the leaf sap exceeded that of the fruit juice. Inhibitors isolated from the leaf sap were thermostable, water soluble, and non-specific with their degree of activity depending on the concentration of the inhibitor. Moreover, the inhibitory action of a given plant depended, to a certain extent, on the age of the leaves as well as on the season.

Since dormancy has been shown to occur in a number of different ways, only dormancy as affected by the embryo will be reviewed. Delayed germination in hawthorne was the first observation of dormancy secured by the embryo and not the seed coat (Crocker, 1906). Freshly harvested seed failed to germinate even with the seed coats removed, under high temperature treatments, and with increased oxygen. Since that study a number of economical plants have been studied showing embryo controlled dormancy.

Dormancy in Trifolium subterraneum L. was orginally attributed to the morphological basis of hardness in seeds (Aitken, 1938). Here the development of hard seeds depended on the continuity of the suberin layer over the distal end of the malpighian cells in the testa. Quality of the hardness was controlled by the tension of the stiophiole cell walls and the toughness of the suberin. Similar results were found in other members of Leguminosae (Rees, 1911).

A subsequent study by Loftus Hill (1944a) indicated that embryo dormancy concurrent with the morphological basis of hard seeds in T. subterraneum resulted in a delay in time to germination and was a varietal character influenced by the temperatures in which it was germinated. Depending on the variety, the dormant period ranged from five to twelve months at 22°C. In addition, a later study showed that lower temperatures (10°C opposed to 20°C) accelerated the after-ripening process. But as the seed matured, the speed of germination at 10°C and 20°C approached equality (Loftus Hills, 1944b). Quinlivan (1971) later refuted Loftus Hills' results by showing that high summer temperatures were the causative agent in the subsequent breakdown of embryo dormancy; the germination inhibitors in the seed were apparently susceptible to heat.

Morely (1958) found higher levels of dormancy in _T_. _subterraneum_ associated with varieties developed in cooler climates. Seed dormancy was shown to be highly heritable and dependent, at least in part, on the genotype of the embryo as distinct from that of the testa. The fact that dormancy was affected by environmental factors acting on the mother plant suggested a substance was produced by the plant and stored in the developing seed.

With the absence of any mechanical resistance to dormancy in cereals, dormancy appeared to be a function of the embryo or those tissues immediately surrounding it (Vines, 1947). Barley was tested for relative dormancy and duration of an after-ripening period. When very immature, the grain was able to germinate. But with progressive ripening, it entered a dormant stage through which it had to pass in order to again germinate.

The loss of dormancy in oats (_Avena_ spp.) was illustrated in a number of different ways. Germination of freshly harvested _Avena fatua_ seeds was increased by the breaking of the seed coat (Atwood, 1914). He observed that the restriction of oxygen by the seed coat was a limiting factor in germination and searing them with a hot needle increased the percentage of germination. This was later confirmed by Johnson (1935a) who inferred that delayed germination was due to post-fertilization changes related either to tissue absorption or development. He also found that exposure to light appeared to slightly stimulate germination in the early stages of after-ripening, but was harmful to mature seeds. In addition, location of the panicle on the plant influenced the after-ripening period; secondary grains required a much longer period than primary grains. Paterson (1976) found only a limited influence of storage temperature on the loss of dormancy. He indicated that a series of changes in the tissues of the seed coat resulted in an increased permeability to oxygen.

Genetic control of delayed germination in oats was reported to behave as a recessive character in crosses between _A. fatua_ and _A. sativa_ (Barber, 1923). This was confirmed by Johnson (1935b) and a model was proposed. The germinative potentialities of the genotypes varied with the time elapsing between harvesting and testing. He hypothesized that very shortly after harvest, only embryos with six dominant allelomorphs (AAAAAA) were germinable and as time passed, embryos with a progressively smaller number of dominant allelomorphs became germinable. Considerable overlapping was noted.

Variability in germination due to after-ripening has been observed in peanut (_Arachis hypogaea_) (Hull, 1937). Hull observed in some peanut seeds that a rest period of at least several weeks after maturity was required before germination could occur under average field conditions. In addition, storage temperatures had a pronounced effect on the after-ripening process. Peanuts stored at 20°C to 25°C reduced the rest requirements while at 3°C, progress of after-ripening was greatly retarded. Subsequent storage tests indicated that after-ripening may have continued beyond the germination threshold when a cold treatment was applied. Genetic control of the rest period behavior in peanuts was reported to be multigenic.

Stier (1937) reported potato seeds which exhibited delayed germination up to five months with the duration of the delayed period dependent upon seasonal differences. In addition, Simmonds (1964) observed a high correlation between seed and tuber dormancy suggesting the two dormancies were under a common biochemical control. Futher investigation by Simmonds indicated that the embryo was not in a state of rest, but that the delayed germination was caused by some tissue or agency exterior to the embryo. He therefore suggested selection of dormancy operated at the tuber level and seed dormancy followed.

MATERIALS AND METHODS

Section 1

The effect of dry storage on the loss of dormancy

Seed from nineteen cultivars representing four species (*C*. *annuum*, *C*. *frutescence*, *C*. *chacoense*, and *C*. *microcarpum*) were used in determining and evaluating the dormancy period in peppers. Sixteen cultivars were obtained from Dr. Paul Smith, University of California, Davis, two from the Southern Regional Plant Introduction Station, Experiment, Georgia, and one from Shigemi Honma, Michigan State University, East Lansing, Michigan (Table 1).

To circumvent the reported seasonal and environmental effects imposed on the after-ripening character in other species (Johnson, 1935; Loftus Hills, 1944a; Morely, 1958), all material was grown in greenhouses at Michigan State University from April, 1977 to July, 1977 to obtain seed of approximately the same age and stage of development. During this period, normal cultural practices were followed.

Each cultivar was selfed once before the study. All seeds were harvested by hand from fully ripe fruit approximately 55 days ± 5 days after anthesis depending on the cultivar. Freshly harvested seeds were air dried for 48 hours, treated with 50 Arasan Red, and stored at 24°C ± 1°C until needed.

To characterize the length of the dormancy period and its progression, two replicates of 20 seeds from each cultivar were planted

Table 1. List of dormant pepper cultivars

Line	Species	Accession No.	Origin
1	_Capsicum microcarpum_	PI 281398	Mexico*
2	_C. chacoense_	PI 260431	Bolivia*
3	_C. frutescens_	CMV SA-8	Columbia**
4	_C. frutescens_	CMV SA-374	Peru**
5	_C. frutescens_	CMV SA-218	Brazil**
6	_C. frutescens_	CMV SA-217A	Columbia**
7	_C. frutescens_	CMV SA-91	Brazil**
8	_C. annuum_	CMV 971	Mexico**
9	_C. annuum_	CMV 972	Mexico**
10	_C. annuum_#	CMV 1534	Mexico**
11	_C. annuum_	CMV 1535	Mexico**
12	_C. annuum_	CMV 1615	Guatelamala**
13	_C. annuum_	CMV	Puerto Rico**
14	_C. annuum_	CMV Resist. 1	****
15	_C. annuum_#	CMV Resist. 2	****
16	_C. annuum_#	CMV Resist. 3	****
17 C.	_C. frutescens_	CMV 2062	Brazil**
18	_C. frutescens_	CMV 2063	Guatelmala**
19	_C. annuum_#	Big Boy	****

*Southern Regional Plant Introduction Station, Experiment, Georgia

**Paul Smith, University of California, Davis

***Shigemi Honma, Michigan State University, East Lansing, Michigan

#Used in genetic study

at 7 day intervals for a period of 56 days. The first planting was sown between July 31, 1977 and August 12, 1977 (the actual day was dependent on the harvest date of each cultivar) and placed in two temperature controlled chambers - one replicate per chamber. Temperatures were held at 22.5°C ± 1°C for seedling emergence and each chamber was illuminated with two ITT F 40/cv Coolwhite fluorescent bulbs.

Seeds were planted in wooden flats containing Wedron White Silica (Wedron Silica Division, Del Monte Properties Co.) using a randomized complete block design. Rows were 15cm long and 2cm apart with a planting depth of 8mm. Twenty seeds were planted per row. The seeded flats were irrigated daily using water of the same temperature as that of the chamber. Seedlings were considered emerged when the cotyledons were freed from the growing medium. In instances where the seedlings emerged from the medium with the seed coat still attached, seedlings were considered emerged when the seed coat cleared the medium surface. Emergence was recorded daily and all emerged seedlings cut off at the medium surface. Dormancy was considered broken when 50% of the seeds had emerged.

MATERIALS AND METHODS

Section II

The effect of fruit age on the dormancy of the seed of peppers

The effect of fruit age on the dormancy of pepper seeds was determined using seed from cultivars CMV 1534, CMV, CMV Resistant 2, and CMV Resistant 3 harvested from fruit at various stages of maturity. All plants were grown in the greenhouse from July, 1978 to October, 1978. Seeds were classified into three catagories depending on the stage of fruit maturity and color: Immature - the fruits were half green and half colored, approximately 48 days post anthesis; mature - color full, approximately 55 days post anthesis; overmature - full color with the initiation of fruit desication, approximately 65 days post anthesis. Two replicates of 30 seeds each were sown in a flat containing Wedron White Silica on October 10, 1978. Row dimensions, planting depth, temperature, irrigation, and emergence criteria followed that previously outlined. Emergence was recorded daily and the experiment terminated when emergence became asymptotic.

MATERIALS AND METHODS

Section III

The genetic control of dormancy in peppers

The following C. annuum cultivars were classified and used in this study: CMV 1534, CMV Resistant 2, and CMV Resistant 3 were classified as dormant while Big Boy was classified as non-dormant. All material was grown in the greenhouse from May, 1978 to September, 1978. Each cultivar was selfed one generation prior to hybridization.

The one non-dormant parent and three dormant parents were hybridized reciprocally to obtain the various populations for the study. Three separate families were generated: Family I (Big Boy x CMV 1534), Family II (Big Boy x CMV Resistant 2), and Family III (Big Boy x CMV Resistant 3). P_1, P_2, F_1, F_2, and backcross populations were produced by hand pollination in a greenhouse. Seed was hand harvested from the fruit and air dried for 48 hours and then planted. All material was treated with 50 Arasan Red prior to planting.

Three replications were used for each family with 20 seeds per replicate for the parental lines, 30 seeds per replicate for the F_1 generation, and 60 seeds per replicate in the F_2 and backcross generations. Seeds were sown in wooden flats containing Wedron White Silica using a randomized complete block design with 15cm rows, 2cm apart. A planting depth of 8mm was used. Temperatures were held at 22.5°C ± 1°C and irrigated daily with water of identical temperature. Emergence criteria followed that previously outlined.

Means, variances, and standard deviations were calculated from individual plant data. Population means were statistically compared by the use of the 2-tailed t-test. Population data was analyzed by applying a chi-square goodness of fit. Since no significant differences (5% level) were found between reciprocal F_1's or between F_2's, the data were pooled for the genetic analysis (Table 2).

Table 2. Difference (d) between reciprocal F_1 and F_2 means and their corresponding standard errors for expressing dormancy in three pepper families

	Family I[x]		Family II[y]		Family III[z]	
Generation	d	SE	d	SE	d	SE
F_1	0.73	2.59	2.27	2.54	1.17	2.54
F_2	3.28	3.00	0.19	2.77	1.04	2.42

[x] Big Boy x CMV 1534

[y] Big Boy x CMV Resistant 2

[z] Big Boy x CMV Resistant 3

RESULTS AND DISCUSSION

Section I

The effect of dry storage on the loss of dormancy

The period of after-ripening of the pepper seeds following extraction and storage varied with each cultivar. PI 260431 had the longest after-ripening period with 61 days to reach 50% emergence while Big Boy had the least with a 14 day period to 50% emergence. All other cultivars were intermediate (Table 3). Holding the seeds in dry storage at 24°C decreased dormancy for all cultivars except Big Boy, PI 281398, and CMV SA-218. These three cultivars had similar emergence patterns from the initial planting interval to the last planting interval (Table 3). A threshold for overcoming dormancy was noted at week six where time to 50% emergence leveled off for all cultivars. Since most of the environmental factors were kept constant, the variations observed in the length of dormancy and the subsequent loss of it suggested genetic differences for this character within the genus *Capsicum*.

Initial rest requirements and the germination pattern of cultivars CMV 1534, CMV, CMV Resistant 2, CMV Resistant 3, and Big Boy suggested genetic variation for dormancy in *C. annuum* (Figure 1). The cultivar Big Boy exhibited no dormancy and after-ripening while cultivars CMV 1534, CMV, CMV Resistant 2, and CMV Resistant 3 showed different levels of dormancy and after-ripening. Since the cultivars showing lower emergence percentages were cultivars with a long after-ripening

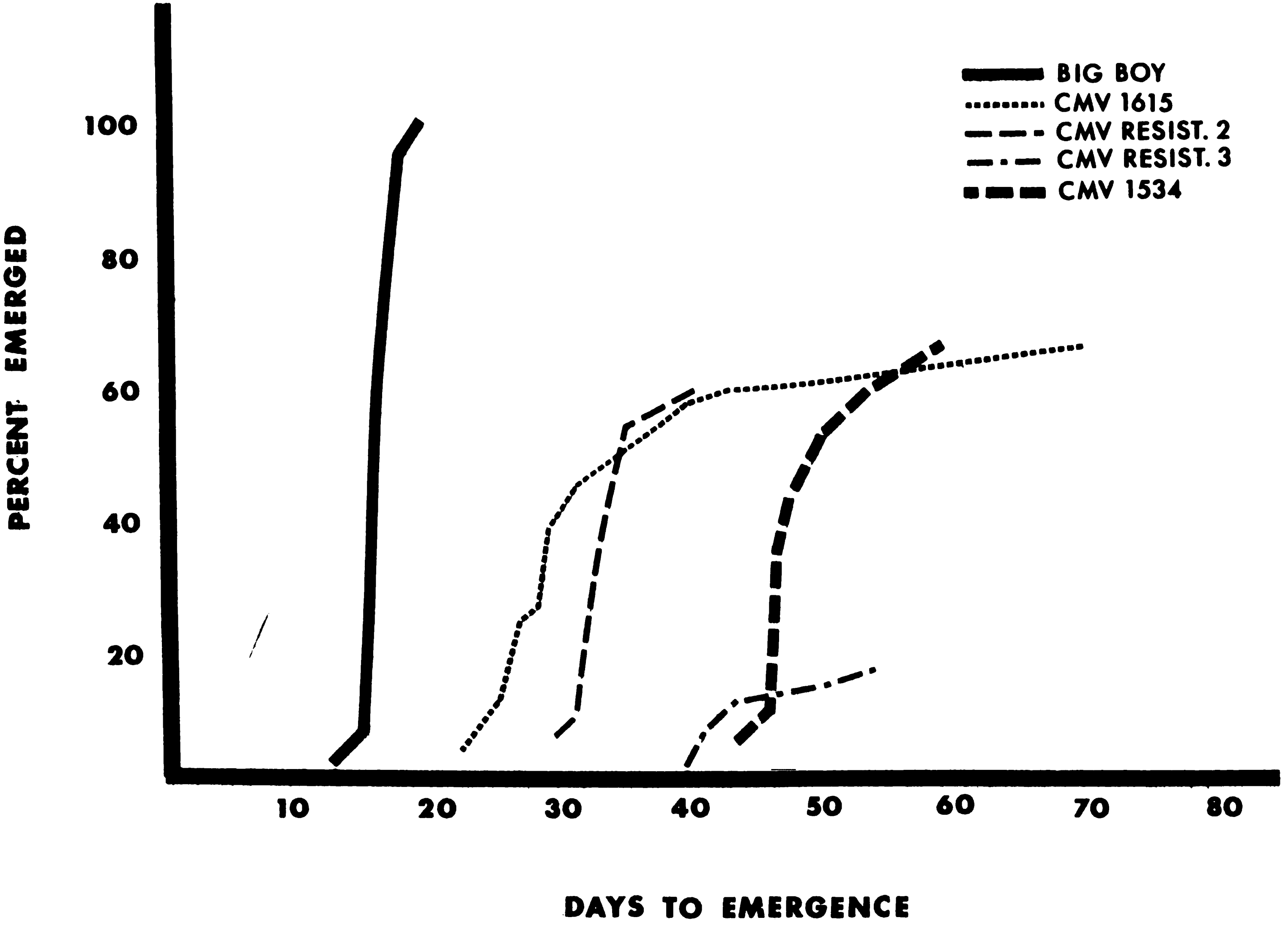
Table 3. The effect of after-ripening in pepper seeds on days to 50% emergence

	Length of storage at 24°C prior to planting (in weeks)						
Cultivar	0	1	2	3	4	5	6
PI 281398	16	16	14	15	18	16	16
PI 260431	61	56	45	38	28	23	23
CMV SA-8*							
CMV SA-374*							
CMV SA-218	19	18	15	15	14	15	15
CMV SA-91*							
CMV SA-217A	54	42	36	20	16	17	16
CMV 971	26	20	21	13	13	15	14
CMV 972	24	22	19	18	13	15	15
CMV 1534	50	42	28	23	20	19	18
CMV 1535*							
CMV 1615*							
CMV	30	25	22	15	17	16	15
CMV Resist. 1	27	21	20	19	16	15	15
CMV Resist. 2	33	24	20	19	16	15	15
CMV Resist. 3	40	31	25	20	19	15	15
CMV 2063*							
Big Boy	14	16	15	16	12	14	14

*Denotes cultivars having less than 50% emergence.

Figure 1. The effect of dormancy and after-ripening on the emergence pattern for cultivars CMV 1534, CMV, CMV Resistant 2, CMV Resistant 3, and Big Boy sown immediately after harvest

FIGURE 1


PERCENT EMERGED
100
80
60
40
20
10
20
30
40
50
60
70
80
DAYS TO EMERGENCE
BIG BOY
CMV 1615
CMV RESIST. 2
CMV RESIST. 3
CMV 1534

period, it is possible that a loss in vigor and/or seed decay could have decreased emergence due to the warm, moist environment encountered during after-ripening. High respiration rates have been equated with decreased seed vigor while seed decay could be caused by microbial attack under extended warm, moist periods (Copeland, 1976). Therefore, it is possible that these environmental conditions may have effected the emergence percentage. A high susceptibility to seed decay and/or vigor loss was evident for CMV Resistant 3. It appears that warm dry storage is necessary to overcome dormancy and still retain high emergence percentages. Tokumasu (1971) reported similar findings showing freshly harvested seed held in a saturated atmosphere delayed germination.

RESULTS AND DISCUSSION

Section II

The effect of fruit age on the dormancy of pepper seeds

Fruit age effected the dormancy period for the cultivars CMV 1534, CMV, CMV Resistant 2, and CMV Resistant 3 (Figures 2-5). Seed harvested from the overmature fruit emerged sooner for these cultivars although not always at a higher percentage than seeds harvested from mature fruit. Similarly, seed from mature fruit emerged earlier than those from immature fruit. This pattern suggested that after-ripening took place while still in the fruits and on the plant. Similar results were reported by Odland (1938) in Cucurbits. Failure of cultivars CMV Resistant 2 and CMV Resistant 3 to emerge at the immature stage may have been a result of lower vigor and susceptibility to seed decay or immature embryos. Similar findings were reported by Cochran showing seed germination was affected by pepper fruit maturity (1934). Conversely, cultivars CMV 1534 and CMV had a moderately high emergence rate at the immature fruit stage suggesting a higher resistance to a loss of vigor or seed decay. Or these two cultivars could have matured morphologically at a different rate than those of CMV Resistant 2 and 3. As a result, the higher germination percentages may have been due to a more advanced stage of development.

Figures 2-5. The effect of fruit age on the dormancy and seedling emergence for four pepper cultivars

FIGURE 2

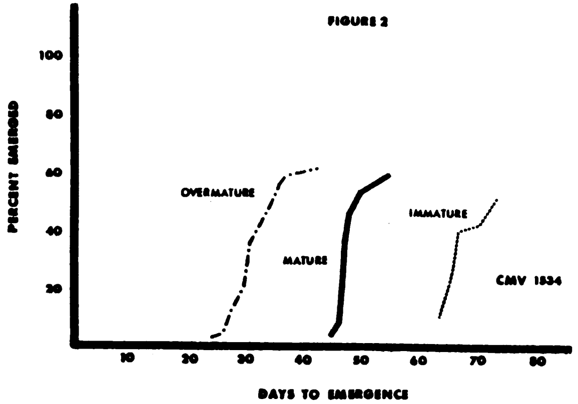


FIGURE 3

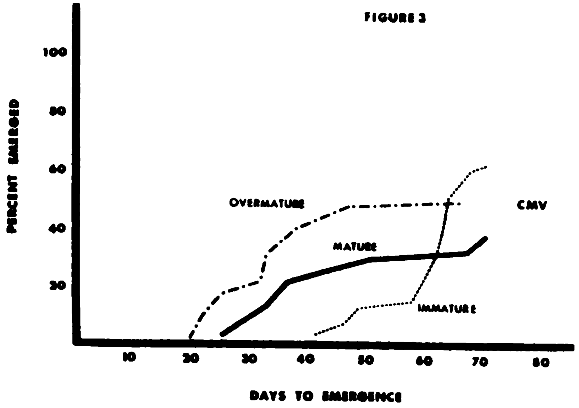


FIGURE 4

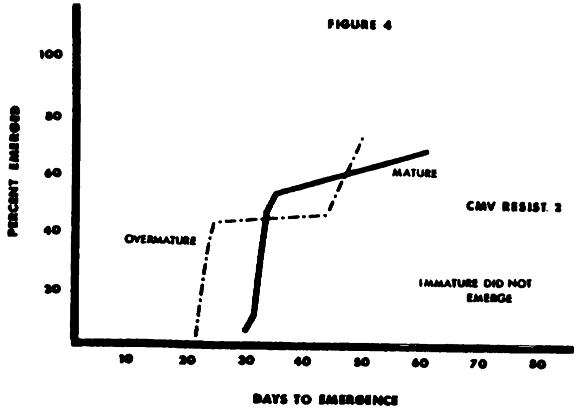
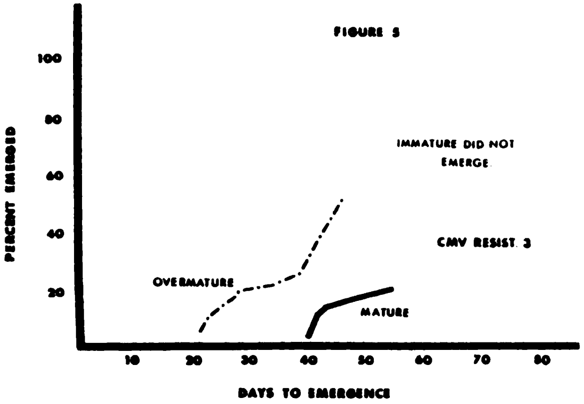


FIGURE 5



RESULTS AND DISCUSSION

Section III

The genetic control of dormancy in peppers

Due to a similarity in the results of the genetic control, discussion of all three families will take place simultaneously. The modality expressed in the F_2 frequency distribution of progeny from the crosses Big Boy x CMV 1534, CMV Resistant 2, and CMV Resistant 3 suggested that differences in dormancy between Big Boy and the other cultivars were controlled by a relatively few number of genes (Figures 6-8). Due to the absence of P_2 type individuals, however, a true estimate of the number or quantity of genes can not be ascertained. The F_1 mean was skewed toward the non-dormant parent with partial dominance for non-dormancy indicated (Table 4). No significant deviations from zero were found between F_1, F_2, and backcross generation means. In addition, the F_2 and backcross generation means were located between the F_1 mean and the dormant parental mean.

The large variance recorded for the F_1 generation may be due to heterozygosity of one or both of the parents. Comparing the distribution and variation of both parents, greater heterozygosity is noted for the P_2 parent for Families I and III, but not Family II. The lower variance in Family II may be accounted for by a loss of 34 individuals (38% of the population). A greater number of individuals may have led to a higher variance since those not recovered probably had deeper dormancy than those recovered. The heterozygous condition

Figure 6. The emergence frequency distribution for parents, F_1, F_2, BC_1, and BC_2 progeny from the cross Big Boy x CMV 1534

FIGURE 6

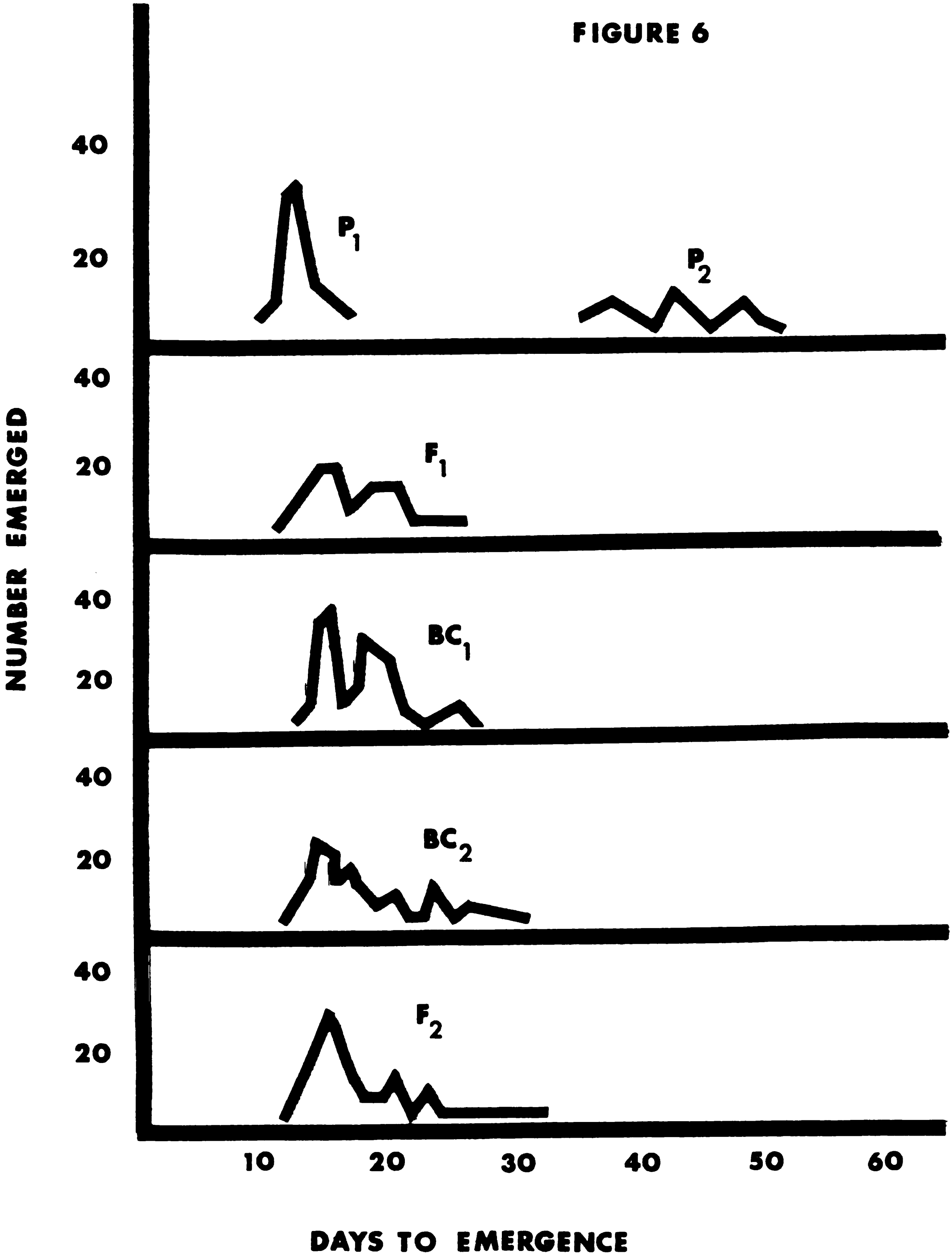

40
20
P1
P2
40
20
F1
40
20
BC1
40
20
BC2
40
20
F2
NUMBER EMERGED
10
20
30
40
50
60
DAYS TO EMERGENCE

Figure 7. The emergence frequency distribution for parents, F_1, F_2, BC_1, and BC_2 progeny from the cross Big Boy x CMV Resistant 2

FIGURE 7

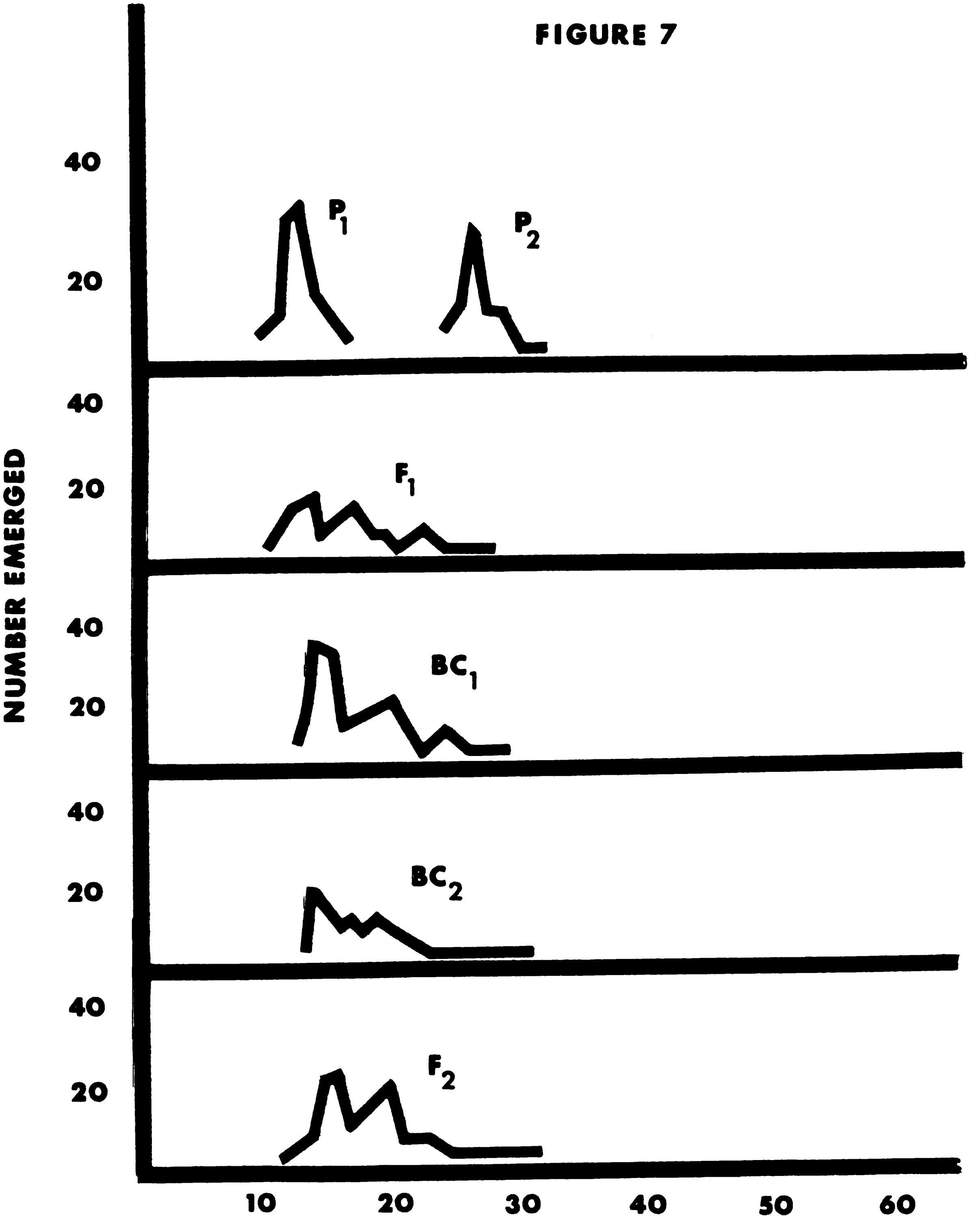

NUMBER EMERGED
40
20
P_1
P_2
40
20
F_1
40
20
BC_1
40
20
BC_2
40
20
F_2
10
20
30
40
50
60
DAYS TO EMERGENCE

Figure 8. The emergence frequency distribution for parents, F_1, F_2, BC_1, and BC_2 progeny from the cross Big Boy x CMV Resistant 3

FIGURE 8

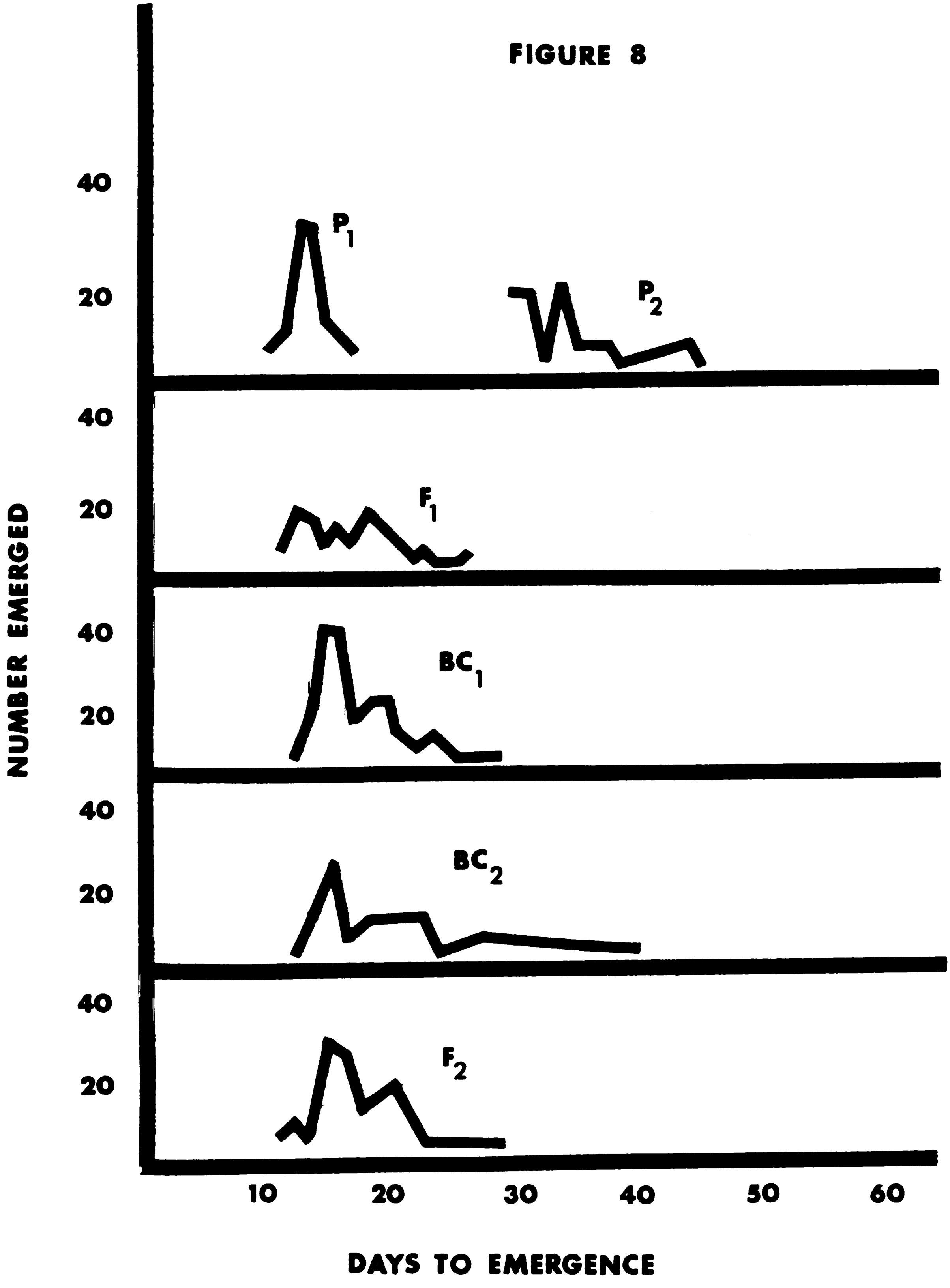

NUMBER EMERGED
40
20
P1
P2
40
20
F1
40
20
BC1
40
20
BC2
40
20
F2
10
20
30
40
50
60
DAYS TO EMERGENCE

Table 4. Population size, means, standard errors, parental range, and mid-parent values for the germination period in three *Capsicum* families

	Family I[x]			Family II[y]			Family III[z]		
Population	N	Mean	SE	N	Mean	SE	N	Mean	SE
P_1	90	12.64	1.02	90	12.64	1.02	90	12.64	1.02
P_2	78	43.40	4.19	54	27.56	1.58	79	34.69	3.76
F_1	115	17.52	3.38	112	16.52	3.29	116	15.79	3.15
F_2	158	18.23	3.97	126	18.23	3.35	127	17.22	2.99
BC_1	172	18.03	3.28	171	17.78	3.32	167	17.32	2.91
BC_2	105	19.35	4.89	83	17.73	3.14	92	19.59	4.64
P_1-P_2, range		43			23			35	
Mid-parent		28.02			20.10			23.67	

[x] Big Boy x CMV 1534

[y] Big Boy x CMV Resistant 2

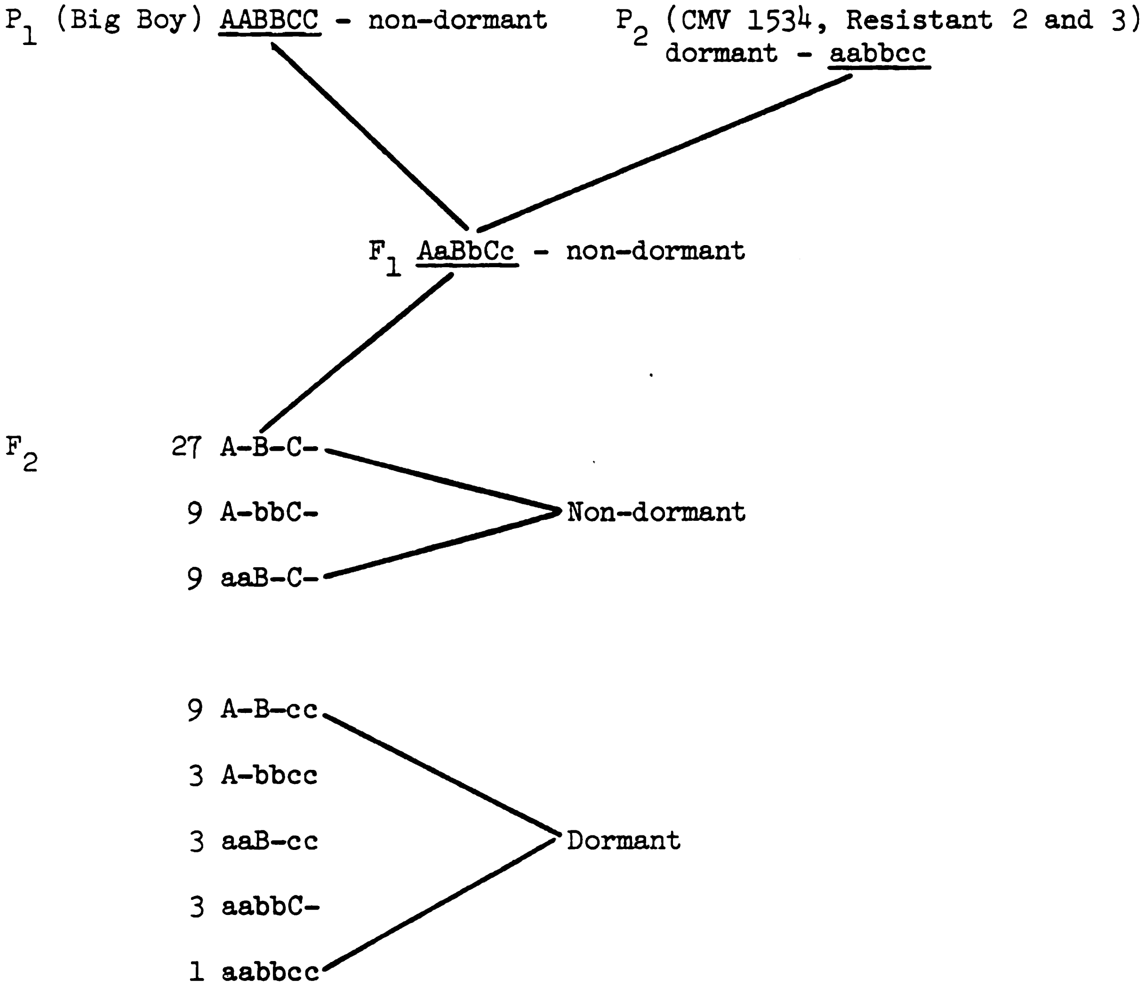
[z] Big Boy x CMV Resistant 3

of the P_2 parent could affect skewness of the BC_2 and F_2 population means as noted. It is also possible that skewness may have been a result of the loss of a high number of individuals in the BC_2 and F_2 generations with the P_2 type expression.

The heterozygosity and reduced germination percentages in the parental generation and the F_2 and BC_2 generations may be explained by the presence of semilethal genotypes. The genotype which expresses delayed germination phenotypically may also give the seed the disadvantage of extended exposure to warm, moist conditions, hence reducing the chances of the seed to germinate by succumbing to disease or reduced vigor. This is evident by the percentages observed in this study and the study in Section I where the P_2 emergence percentages were 86% and 66% (CMV 1534), 60% and 60% (CMV Resistant 2), and 86% and 22% (CMV Resistant 3) respectively.

In light of this evidence, the F_2 and backcross populations were partitioned into non-dormant and dormant types based on the observed modality in Figures 6, 7, and 8 assuming a normal distribution of P_1 and P_2 phenotypes and all individuals not recovered were of the dormant genotype. The following genetic model is proposed: Three major genes (designated <u>A</u>, <u>B</u>, <u>C</u>) constitute P_1 (Big Boy) and P_2 (CMV 1534, CMV Resistant 2 and 3) for expressing either non-dormancy or dormancy. The proposed genotype for Big Boy is <u>AABBCC</u> and is non-dormant while the genotype for CMV 1534, CMV Resistant 2 and 3 is <u>aabbcc</u>. The F_1 genotype is <u>AaBbCc</u> and is non-dormant (Figure 9). A (3:1)(15:1) factorial gene model is suggested by the observed F_2 and backcross ratios assuming all non-recovered individuals to be dormant. <u>C-</u> conditions the non-dormant expression when at least one

Figure 9. Gene model for dormancy in peppers



Ratio 45:19

dominant gene is present either at the *A*, *B*, or both loci. *C-* shows partial dominance. Recessive homozygosity at the *C* locus expresses dormancy although *A* and *B* may modify its expression. Moreover, the homozygous recessive *A* and *B* loci are epistatic to a dominant *C* and express dormancy. The F_2 generation genotypes *A-B-C-*, *A-bbC-*, and *aaB-C-* are non-dormant, while *A-B-cc*, *A-bbcc*, *aaB-cc*, *aabbC-*, and *aabbcc* are dormant. The ratios expected (non-dormant:dormant) from the (3:1)(15:1) factorial gene model are 45:19 and 1:1 for the F_2 and BC_2 generations respectively. An acceptable fit was obtained for both the F_2 (P= 0.5-0.1 Family I, P= 0.5-0.1 Family II, P= 0.9-0.5 Family III) and BC_2 (P= 0.9-0.5 Family I, P= 0.5-0.1 Family II, P= 0.5-0.1 Family III) generations (Table 5). The BC_1 generation was not testable because 0 was the expected frequency in one of the classes. However, the observed ratios recorded do not approximate the expected phenotypes. A modifier may be influencing this generation, delaying the emergence of some of the progeny.

Table 5. Distribution and chi-square analysis of F_2 and backcross progenies of crosses between dormant and non-dormant plant types for three different pepper families.

Population	Total	No. of Seedlings Dormant	 Non-dormant	Ratio	P
Family I					
Big Boy	90	0	90	-	-
CMV 1534	72	72	0	-	-
F_1	120	12	108	-	-
F_2	180	48	132	19:45	0.5-0.1
BC_1	180	22	158	0:1	-
BC_2	180	87	93	1:1	0.9-0.5
Family II					
Big Boy	90	0	90	-	-
CMV Resist.2	54	54	0	-	-
F_1	120	15	105	-	-
F_2	180	61	119	19:45	0.5-0.1
BC_1	180	23	157	0:1	-
BC_2	180	100	80	1:1	0.5-0.1
Family III					
Big Boy	90	0	90	-	-
CMV Resist.3	79	79	0	-	-
F_1	120	7	113	-	-
F_2	180	57	123	19:45	0.9-0.5
BC_1	180	25	155	0:1	-
BC_2	180	101	79	1:1	0.5-0.1

SUMMARY AND CONCLUSION

Genetic variation was found for the expression of dormancy in seed germination and emergence in four species of Capsicum. Cultivar response to fifty percent emergence ranged from 14 days to 61 days when planted immediately after harvest from mature fruit. Fruit age was also shown to affect dormancy; dormancy increased with decreased fruit age. This would support the idea that after-ripening of the pepper seeds was occurring while still attached to the mother plant. Gutterman (1978) reported the maternal environment had a pronounced effect on the germinability of seeds as a result of internal changes in hormonal levels. From this it would seem that the after-ripening of the seeds was independent of the maternal plant since after-ripening occurred both attached to and removed from the mother plant.

Reduced germination was associated with increased dormancy suggesting a loss of vigor or seed decay encountered during after-ripening when planted immediately after harvest from mature fruits. Warm dry storage was shown to be effective in overcoming rest while still maintaining a high level of germination. The seeds appeared to develop the capacity to break down the inhibitory activity under such conditions. Hull (1937) reported similar results in peanuts with storage at 25°C much more effective in overcoming dormancy than at 3°C.

The progenies of reciprocal crosses between three families of C. annuum were evaluated to determine the mode of inheritance of dormancy. Partial dominance for the non-dormant parent was noted. Progeny mortality in segregating generations made quantitative analysis invalid for all families. Lack of P_2 individuals in all families may have been the result of an interaction of Big Boy with the dormancy parents. The penetrance and recovery of a dormant phenotype may have been decreased by a dominant factor in Big Boy. Heterozygosity and reduced germination found in the dormant parental generation and the F_1, F_2, and BC_2 generations was explained by the presence of semilethal genotypes. Extended exposure to warm, moist environmental conditions resulted in a decline in germination. Chavagnat (1978) reported heterogeneity to be important in the germination of Lavandula L. seeds. Heterogeneity was said to be due to the quality of the seed, the percent of seed that was dormant and the depth of dormancy. Since dormancy has been reported as a survival mechanism (Harper and McNaughton, 1960), survival may be enhanced by the presence of heterozygous genotypes, extending the chances of a species' seed to germinate and survive under a favorable environment. Such may be the case for Capsicum.

Ratios obtained by partitioning segregating generations into phenotypic classes suggested a three gene system (designated A, B, C) for the expression of dormancy. A (3:1)(15:1) factorial model of the three genes best explained the observed ratios with the P_1 parental line designated AABBCC and the P_2 parental lines designated aabbcc. A modifier appeared to influence the expression of the trait. This model is tentative, however, due to the assumptions made and further investigation is needed to verify the genetic control of dormancy in peppers.

THE INHERITANCE OF SEVERAL CHARACTERISTICS IN PEPPER

II

THE INHERITANCE OF COLD EMERGENCE IN PEPPERS

INTRODUCTION

Currently peppers grown in Michigan and other areas of similar climate are established through the use of transplants. Although transplanting peppers is effective in decreasing the length of the growing season while still obtaining a quality product, there are problems and uncertainties such as poor initial growth, disease, and limited choice associated with this method. Establishing peppers by direct seeding would have the advantages of lower cost per acre, lower labor costs, flexability in varietal choice, and disease control (Johnson and Wilcox, 1972). Being a warm season crop, the temperatures for optimum germination in peppers are between 20 - 30°C. Under these conditions seeds should germinate quickly and uniformly. Unfortunately, soil temperatures range from 10 - 18°C at the time when direct seeding should be made. At this temperature, however, germination and growth of the pepper seeds would be retarded.

Genetic variation in the ability of peppers to withstand moderately cold temperatures has been reported by Gerson and Honma (1978). In the study it was shown that several cultivars were able to germinate and emerge at temperatures of 13 - 15°C. However, most of the cultivars that expressed quick emergence under the suboptimal conditions were of non-commercial types. To insure improved crop stands at low soil temperatures by direct seeding, it would be necessary to incorporate this trait into commercial cultivars. The purpose of this study was to identify the genetic control in the ability of peppers to germinate and emerge at low soil temperatures.

LITERATURE REVIEW

During cold wet conditions encountered during early spring plantings, a major problem in direct seeding is the failure to attain a uniform stand with rapid emergence (Robinson and Mayberry, 1976). Several methods have been used for hastening emergence for uniform stands under such conditions. Hardening of seeds was shown to improve germination in several crops. By soaking seeds for twenty-four hours and then drying them for twenty-four hours, carrot seeds which were hardened had a higher rate of germination than those that were untreated (Austin, 1969). Similar results were reported in two cultivars of corn (Hegarty, 1970). In addition, seed soaked in water and sown in a moist condition also germinated sooner than dry seed (Kid and West, 1918).

Germination has been accelarated by the method of osmotic pretreatment (Heydecker, 1973). With this method seeds are allowed partial imbibition and the initial processes of germination without radicle emergence via an osmotic potential. An increase in rate and earliness of germination was shown in onions (Heydecker, 1975) while uniformity of germination was noted with celery (Salter and Darby, 1976).

Inorganic salts have been used to improve seed germination. Ells (1963) reported the germination of tomato seeds at 10°C night temperatures were stimulated following K_3PO_4 and KNO_3 treatments. Similarly, methods of treating tomato seeds with aerated nutrient solutions to increase germination rates was shown by Oyer and Koehler (1966).

Pregerminated seed has been used to increase germination rate and uniformity. Biddington, *et al*. (1975) reported that pre-germinated celery seed sown in a fluid gel germinated earlier with increased emergence as compared to dry seed. Taylor (1977) has indicated seed that germinates slow, especially at low temperatures, benefited most from pregermination.

Genetic variability in the ability to germinate under sub-optimal conditions has been reported in a number of different crops. Varietal response to growth rate and germination in tomato at low temperatures was reported by Kemp (1967) and Smith and Millet (1973). Similarly, Pinnell (1949) has shown wide differences between corn inbreds in the ability to germinate at low temperatures which appeared heritable in crosses as did Jones and Peterson (1976) in rice. Selection produced a 20 - 30% improvement in the rate of germination in sugar beets indicating that the character was heritable (Wood, 1952). Littlejohns, *et al*. (1976) reported differences in emergence among soybean cultivars at 10°C but not at 20°C and 30°C. Moreover, Gerson and Honma (1978) showed genetic variability in emergence within species and between species in *Capsicum* at low temperatures.

Heritability estimates were obtained for the control of time to germination in tomato (Whittington and Fierlinger, 1972). The inheritance was largely additive and closely related to seed size. El Sayed and John (1973) found the inheritance of tomato emergence at different temperatures to be quantitative with an estimated 24 gene pairs. There was strong evidence for additive gene action. Cannon, *et al*. (1973) reported the germination of the tomato at 10°C to be inherited by a single gene. Similarly the emergence of tomato seedlings at low temperatures was highly heritable and suggested to be controlled by 3 - 5 genes (Ng and Tichelaar, 1972).

MATERIALS AND METHODS

Section I

Evaluating the emergence response of the pepper at low soil temperatures

One hundred thirty-seven accessions of *Capsicum baccatum* var. pendulum were used in evaluating emergence response at low soil temperatures, hereafter referred to as cold emergence. Two accessions were obtained from Dr. Paul Smith, University of California, Davis and one hundred thirty-five accessions from the Southern Regional Plant Introduction Station, Experiment, Georgia. All of the seed used in this study was grown in greenhouses at Michigan State University from May, 1977 to September, 1977. During this period, normal cultural practices were followed. All seed was harvested by hand from fully ripe fruit approximately 55 ± 5 days after anthesis depending on the accession and air dried for 48 hours. Prior to sowing, all seeds were treated with 50 Arasan Red.

Two replicates of 25 seeds from each accession were planted on October 20, 1977 and placed in four temperature controlled chambers; one replicate per chamber. Temperatures were held at 13°C ± 1°C in two chambers and 10°C ± 1°C in two chambers for seedling emergence and each chamber was illuminated with two ITT F 40/cv Coolwhite fluorescent bulbs.

Seeds were planted in wooden flats containing Wedron White Silica (Wedron Silica Division, Del Monte Properties Co.) using a randomized complete block design. Rows were 15cm long and 2cm apart with a planting depth of 8mm. Twenty-five seeds were planted per row. The flats were irrigated every other day with water of the same temperature as that of the chamber.

Seedlings were considered emerged when the cotyledons were freed from the growing medium. In instances where the seedlings emerged from the medium with the seed coat still attached, seedlings were considered emerged when the seed coat cleared the medium surface. Emergence was recorded daily and all emerged seedlings were cut off at the medium surface to facilitate counting. Sampling continued for seventy-five days.

An emergence index (EI) for each accession was calculated using the formula:

$$\mathrm{EI} = \frac{\mathrm{Sum(Days\ To\ Emergence)(Number\ Emerged)}}{\mathrm{Total\ Number\ Emerged}}$$

This index was adopted from that used to measure low temperature sprouting of tomatoes (Smith and Millet, 1973). The formula provides an average for emergence that favors early emergence. The lower the value calculated, the better the response to cold emergence.

MATERIALS AND METHODS

Section II

The genetic control of the emergence response of the pepper at low temperatures

Four accessions of C. baccatum var. pendulum were used in determining the genetic control of cold emergence: 2033 and PI 257185 were classified as early emerging lines while PI 260593 and PI 281310 were classified as late emerging lines. All material was grown in the greenhouse from May,1978 to September, 1978. Each cultivar was selfed one generation prior to hybridization.

The two early emerging parents and the two late emerging parents were hybridized reciprocally. Four separate families were generated: Family I (2033 x PI 260593), Family II (2033 x PI 281310), Family III (PI 257185 x PI 260593), and Family IV (PI 257185 x PI 281310). P_1, P_2, F_1, F_2, BC_1, and BC_2 populations were produced by hand pollination in a greenhouse. Seed was hand harvested from the fruit and air dried for 48 hours. All material was treated with 50 Arasan Red prior to planting.

Five replications were used for each family with 20 seeds per replicate for the parental lines, 30 seeds per replicate in the F_1 generation, and 60 seeds per replicate in the F_2 and backcross generations. Seeds were sown in wooden flats containing Wedron White Silica using a randomized complete block design with 15cm rows, 2cm apart. A planting depth of 8mm was used. Temperatures were held at

$13^{\circ}C \pm 1^{\circ}C$ in a temperature controlled chamber and irrigated every other day with water of identical temperature. Emergence criteria followed that previously outlined.

Means, variances, and standard deviations were calculated from individual plant data. Population means were statistically compared by the use of the 2-tailed t-test. The conformity of the data to the additive-dominance model by Mather's A,B,C scaling test was used (Mather and Jinks, 1971). The equations used for this test were: $A = 2\overline{BC}_1 - \overline{F}_1 - \overline{P}_1$, $B = 2\overline{BC}_2 - \overline{F}_1 - \overline{P}_2$, $C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$. Significance was obtained by computing the standard error of the corresponding population means and applying a 2-tailed t-test. Significance suggested the existence of non-allelic interactions.

Estimates of additive (D), dominance (H), and environmental (E) variances were obtained by the equations: $E = V_{F_1}$, $H = 4[(V_{BC_1} + V_{BC_2} - V_{F_2}) - V_{F_1}]$, and $D = 2[V_{F_2} - (1/4H + E)]$ (Mather and Jinks, 1971). Narrow and broad sense heritability estimates were computed as the ratio of additive genetic variance to phenotypic variance $(\frac{D}{D+H+E})$ and the ratio of total genetic variance to phenotypic variance $(\frac{D+H}{D+H+E})$ respectively. The genetic advance of the trait was calculate using methods described by Allard (1961).

Since no significant differences (5% level) were found between reciprocal F_1's and between F_2's, the data were pooled for the genetic analysis (Table 6).

Table 6. Difference (d) between reciprocal F_1 and F_2 means and their corresponding standard errors in four pepper families for the ability to emerge at cold soil temperatures

Generation	Family I[w] d	Family I[w] SE	Family II[x] d	Family II[x] SE	Family III[y] d	Family III[y] SE	Family IV[z] d	Family IV[z] SE
F_1	6.51	11.82	3.69	12.47	8.95	9.90	8.29	10.36
F_2	5.89	11.52	10.62	10.21	0.93	7.16	5.75	9.51

[w] 2033 x PI 260593

[x] 2033 x PI 281310

[y] PI 257185 x PI 260593

[z] PI 257185 x PI 281310

RESULTS AND DISCUSSION

Section I

Evaluating emergence response of the pepper at low soil temperatures

Table 7 shows the means and range in days to emergence of 119 pepper cultivars at 13°C and 10°C. Mean emergence differences between temperatures were significant (5% level) showing a much slower rate at 10°C opposed to 13°C.

Table 8 shows the preformance of 137 cultivars at 10°C and 13°C. Of the total number of cultivars screened, eighteen cultivars failed to germinate at either temperature. Also a lower number of cultivars were able to germinate and emerge at 10°C than at 13°C suggesting a threshold for some cultivars in the ability to germinate between these two temperatures. In general, cultivars exhibiting superior emergence at 13°C did so at 10°C. The emergence index for among cultivars was significantly different (5% level) at 13°C but not at 10°C. Cultivar 2033 had the lowest mean emergence index of 22.10 which was significantly different (5% level) than 107 other cultivars at 13°C. 2033 also had the lowest mean emergence index of 40.57 at 10°C. Differences in emergence rate of the cultivars at 13°C suggested wide genetic variability for this character. Cultivar PI 281310, on the other hand, had the highest mean emergence index of 43.08 at 13°C. However, cultivars PI 213915, PI 257183, and PI 260545 had the highest mean emergence index of 71.00 at 10°C. Moreover, cotyledons of seedlings emerging at 10°C were yellow to virescent in color suggesting a threshold

Table 7. Mean emergence indices, ranges, variances, and standard errors for 119 cultivars of pepper as affected by low soil temperatures

Temperature	N	Mean	Range	s^2	SE
°C		——days——			
13	119	31.68*	22.10 - 43.08	10.18	3.14
10	99	54.32*	40.57 - 71.00	329.27	18.14

*Significant at the 5% level

Table 8. Origin and performance of 137 pepper cultivars at low soil temperatures

Cultivar	Origin	Emergence Index 13°C	 10°C
2033	Paul Smith	22.10	40.57
PI 257185	Peru	24.01	60.92
PI 159244	Georgia	26.00	57.85
PI 241658	Peru	26.00	50.43
PI 215700	Peru	26.80	51.67
PI 241664	Peru	27.33	54.99
PI 199506	B. Guiana	27.66	58.78
PI 257184	Peru	27.74	57.80
PI 281406	Peru	27.82	52.94
PI 260580	Bolivia	27.95	53.44
PI 257149	Peru	28.15	64.33
PI 257154	Columbia	28.19	50.66
PI 241679	Chile	28.33	62.33
PI 257163	Peru	28.35	49.00
PI 238063	Peru	28.41	56.09
PI 159235	Georgia	28.57	55.00
PI 260551	Peru	28.80	55.00
PI 257157	Peru	29.00	68.00
PI 257161	Peru	29.14	63.66
PI 260488	Bolivia	29.25	-
PI 241662	Peru	29.28	66.00
PI 257173	Peru	29.30	65.00
PI 241659	Peru	29.35	54.99
PI 260560	Bolivia	29.39	53.08
PI 241674	Ecuador	29.40	59.99
PI 159245	Georgia	29.42	-
PI 260570	Bolivia	29.42	64.50
PI 260583	Bolivia	29.44	61.81
PI 188803	Philippines	29.47	65.67
PI 281436	Hawaii	29.49	47.73
PI 260590	Bolivia	29.53	-
PI 257164	Peru	29.54	61.00
PI 290983	Peru	29.58	57.28
PI 260589	Bolivia	29.59	62.60
PI 257122	Columbia	29.67	58.86
PI 224440	Costa Rica	29.78	59.00
PI 257169	Peru	29.95	59.80
PI 241656	Peru	29.99	63.00
PI 260561	Bolivia	29.99	-
PI 159272	Georgia	30.10	60.70
PI 257177	Peru	30.16	-
PI 260559	Bolivia	30.18	57.82
	LSD	6.29 (5% level)	

Table 8.(continued)

Cultivar	Origin	Emergence Index 13°C	Emergence Index 10°C
PI 260587	Bolivia	30.20	62.56
PI 257174	Peru	30.37	65.67
PI 281308	Bolivia	30.40	-
PI 257135	Ecuador	30.49	62.99
PI 315025	Peru	30.53	51.50
PI 260545	Brazil	30.62	71.00
PI 159279	Georgia	30.64	62.50
PI 260541	Brazil	30.79	59.00
PI 260592	Brazil	30.90	62.80
PI 260539	Argentina	31.00	63.67
PI 281300	Argentina	31.05	62.82
PI 257134	Ecuador	31.06	-
PI 260506	Peru	31.07	63.00
PI 159267	Georgia	31.11	65.67
PI 260540	Argentina	31.17	66.25
PI 241648	Peru	31.28	63.33
PI 257153	Peru	31.31	67.11
PI 257183	Peru	31.35	71.00
PI 260579	Bolivia	31.42	62.67
PI 260542	Brazil	31.47	53.50
PI 260581	Bolivia	31.47	61.80
PI 370010	India	31.47	53.53
PI 257133	Ecuador	31.56	65.49
PI 188481	Peru	31.73	63.99
PI 260549	Peru	31.80	52.50
PI 257179	Peru	31.88	60.50
PI 260584	Bolivia	31.88	62.70
PI 281340	Ecuador	31.88	64.25
PI 260571	Bolivia	31.90	63.67
PI 257130	Columbia	31.92	64.28
PI 260543	Brazil	31.99	-
PI 152234	Peru	32.12	58.33
PI 260536	Argentina	32.30	59.17
PI 159249	Georgia	32.35	57.33
PI 159260	Georgia	32.40	63.00
PI 260538	Argentina	32.42	63.00
PI 260552	Peru	32.46	-
PI 355814	Ecuador	32.47	-
PI 266042	Mexico	32.50	-
PI 257186	Peru	32.67	68.00
PI 260598	Peru	32.73	-
PI 159270	Georgia	32.91	-
PI 281321	Chile	32.99	52.50
	LSD	6.29 (5% level)	

Table 8.(continued)

Cultivar	Origin	Emergence Index	
		13°C	10°C
PI 159259	Georgia	33.06	45.50
PI 281311	Brazil	33.08	60.00
PI 238062	Brazil	33.12	-
PI 260460	Peru	33.20	-
PI 257152	Peru	33.28	-
PI 281307	Bolivia	33.33	-
PI 260550	Peru	33.49	-
PI 260574	Bolivia	33.67	-
PI 290982	Peru	34.08	-
PI 281313	Brazil	34.32	60.00
PI 241662	Peru	34.35	66.00
PI 260591	Brazil	34.62	-
PI 260562	Bolivia	34.83	-
PI 260566	Bolivia	34.86	-
PI 337522	Argentina	34.93	60.88
PI 293349	Peru	34.99	55.71
PI 257143	Peru	35.25	-
PI 260569	Bolivia	35.33	-
PI 281437	USA	35.38	63.00
PI 260576	Bolivia	35.57	-
PI 213915	Bolivia	35.83	71.00
PI 281408	Peru	36.23	-
PI 257180	Peru	36.33	-
PI 215741	Peru	36.38	-
PI 215727	Peru	36.44	60.00
PI 260563	Bolivia	36.88	-
PI 215739	Peru	36.89	66.00
PI 281414	Peru	36.92	-
PI 281407	Peru	37.22	-
PI 260572	Bolivia	37.50	-
PI 273420	Netherlands	37.50	-
PI 260565	Bolivia	37.91	-
PI 260593	Brazil	40.25	-
PI 281310	Brazil	43.08	-
	LSD	6.29 (5% level)	

Cultivars which failed to germinate

2034	**	PI 260564	Bolivia
PI 257141	Peru	PI 260575	Bolivia
PI 257150	Peru	PI 260578	Bolivia
PI 257151	Peru	PI 260585	Bolivia
PI 260458	Brazil	PI 266041	Mexico
PI 260535	Argentina	PI 267729	Guatemala
PI 260546	Brazil	PI 281309	Brazil

for chlorophyll formation may be between 10°C and 13°C. Seedlings with yellow cotyledons when placed in the greenhouse became green within five days or failed to turn green. It appears that seedlings which failed to turn green were susceptible to the cold temperatures. The secondary leaves which emerged in the greenhouse from plants with green and yellow cotyledons were green suggesting no permanent damage to the plant as a whole.

RESULTS AND DISCUSSION

Section II

<u>The genetic control of the emergence response of the pepper at low temperatures</u>

Results of Mather's A,B,C scaling test are shown in Table 9. Non-significant deviations from zero (1% level) were found in all four families suggesting that epistasis was not involved in the inheritance of cold emergence. Hence the additive-dominance model was determined adequate for the analysis of the data. In addition, data was grouped into three day classes for frequency distribution analysis.

Family I (2033 x PI 260593): The F_2 frequency distribution of progeny from the cross 2033 x PI 260593 suggested that differences in cold emergence between these two cultivars were controlled by a few number of genes (Figure 10). The F_1 mean was slightly skewed toward the P_2 mean (Table 10) with partial dominance for slower germination at low temperatures. In addition, the F_2 and BC_1 means fell between the F_1 mean and the P_2 mean. The BC_2 mean exceeded that of the P_2 mean suggesting a preponderance of genetic effects expressing a slower emergence at low temperatures for the population. Transgressive variation was noted in the F_2, BC_1, and BC_2 generations showing individuals which exceeded those of the P_2. The F_1 did not deviate significantly (5% level) from the mid-parental value, suggesting that non-additive gene action is not a major contributor in the expression of the character (Ketata, <u>et al</u>., 1976). However, the F_1 also did not deviate

Table 9. Estimation for the adequacy of using the additive-dominance model for Families I, II, III, IV by Mather's A,B,C scaling test.

Scaling Test Parameter	Family I[w]		Family II[x]	
	Mean	SE	Mean	SE
A	50.14	25.63	52.57	27.29
B	39.21	24.79	25.69	26.48
C	77.41	63.38	57.84	61.06

	Family III[y]		Family IV[z]	
	Mean	SE	Mean	SE
A	24.98	23.18	42.70	28.37
B	2.82	21.86	10.19	22.86
C	28.30	48.59	38.51	66.49

[w] 2033 x PI 260593

[x] 2033 x PI 281310

[y] PI 257185 x PI 260593

[z] PI 257185 x PI 281310

Figure 10. The emergence frequency distribution for parents, F_1, F_2, BC_1, and BC_2 from the cross 2033 x PI 260593

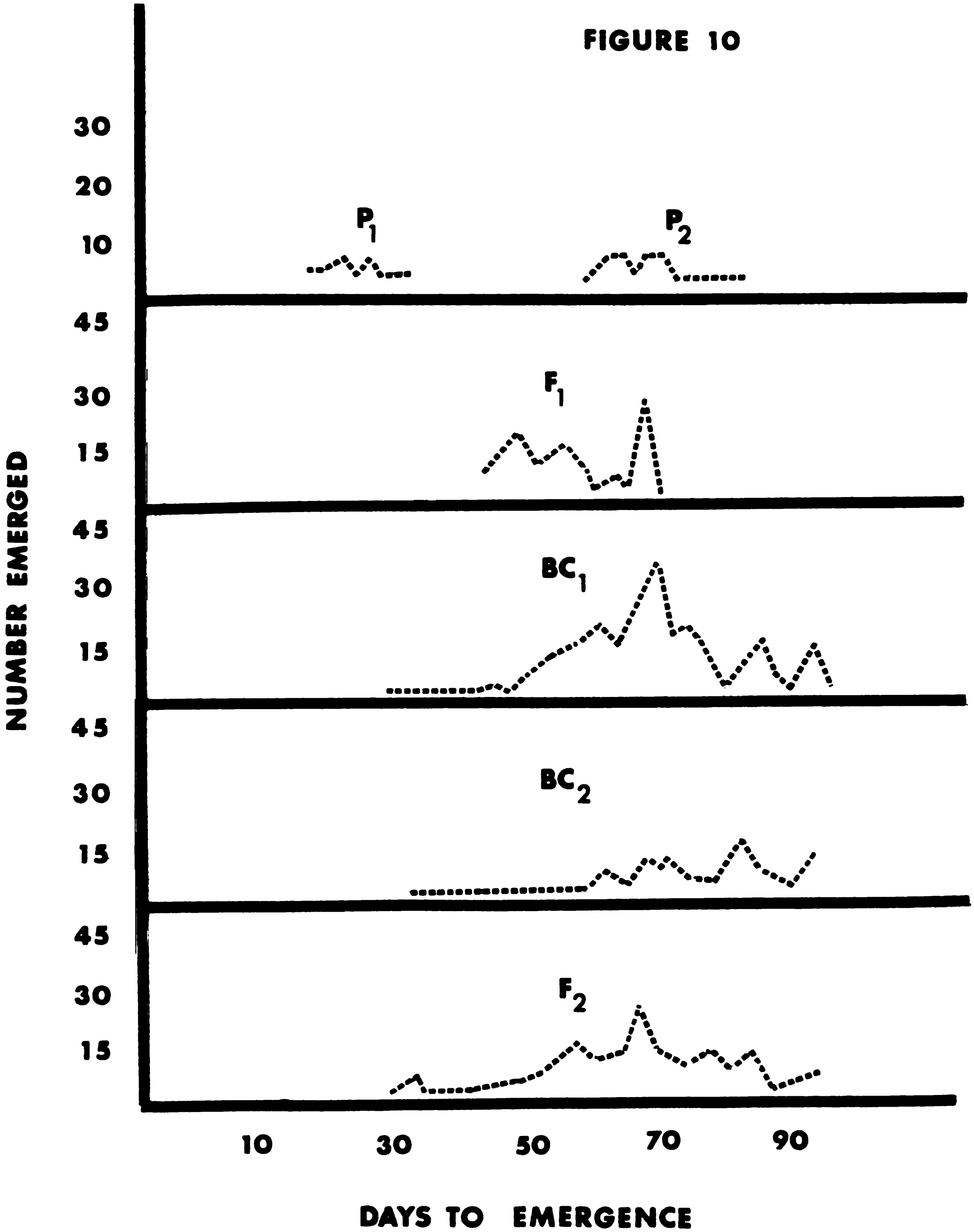


FIGURE 10
NUMBER EMERGED
30
20
10
P1
P2
45
30
15
F1
45
30
15
BC1
45
30
15
BC2
45
30
15
F2
10
30
50
70
90
DAYS TO EMERGENCE

Table 10. Population size, means, standard errors, parental range, mid-parent values and F_1 deviation from mid-parent values in four *Capsicum* families for ability to emerge at low soil temperatures

	Family I[w]			Family II[x]			Family III[y]			Family IV[z]		
Population	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE
P_1	80	24.30	3.44	80	24.30	3.44	76	27.05	3.45	76	27.05	3.45
P_2	56	69.28	5.25	64	65.56	3.97	56	69.28	5.25	64	65.56	3.97
F_1	114	57.35	8.40	127	53.24	6.22	103	48.87	10.23	147	59.38	7.79
F_2	188	65.78	14.59	290	55.91	11.67	179	67.12	14.91	216	62.22	16.11
BC_1	255	67.08	12.87	289	51.26	11.03	240	63.53	11.62	212	64.57	13.53
BC_2	128	74.92	12.28	218	60.31	10.29	79	77.18	10.98	169	67.06	10.56
P_1-P_2, range		61			60			56			55	
Mid-parent		46.79			44.93			48.16			46.31	
F_1 - mid-parent		10.56			8.31			0.71			13.07	

[w] 2033 x PI 260593

[x] 2033 x PI 281310

[y] PI 257185 x PI 260593

[z] PI 257185 x PI 281310

significantly (5% level) from the P_2 mean which also suggests that non-additive gene action does contribute to the expression of the trait. The contradiction of these results may be due to low progeny recovery in the F_2 and backcross generations skewing population means.

Additive variance (D) appeared to be the most important factor (52% of the total phenotypic variance) contributing to the genetic control of cold germination and emergence (Table 11). Dominance variance was positive and smaller than the additive (D) variance in determining cold emergence. Heritability estimates were moderate to high for the trait with narrow and broad sense heritability estimates of 0.52 and 0.82 respectively.

The value for expected genetic advance (G.S.) is reported in Table 11 as 15.63. Expected genetic advance shows the possible gain from selection as percent increase in the F_3 over the F_2 mean when the most desirable 5% (K = 2.06) of the F_2 plants are selected. Heritability and genetic advance generally agreed in showing characters for which selection in the F_2 would lead to substantial improvement. Therefore, reporting genetic advance and heritability estimates should be more informative in genetic and breeding studies than showing either of them alone. These estimates may again, however, be biased due to the low number of individuals recovered in the P_2, F_2, and backcross generations.

Family II (2033 x PI 281310): The F_2 frequency distribution of progeny from the cross 2033 x PI 281310 suggested that differences in cold emergence between these two cultivars were also controlled by a low number of genes (Figure 11). The F_1 mean was skewed toward the P_2 mean (Table 10) with dominance for slower germination at reduced

Table 11. Estimates of components of variation; environmental (E), additive (D), dominance (H), and total phenotypic (T) variances, heritability, and genetic advance for cold emergence in four pepper families

Component	Families			
	I^{w*}	II^{x}	III^{y*}	IV^{z*}
E	70.65	38.66	104.74	60.69
D	218.86	89.49	378.42	448.26
H	131.36	211.16	-286.12**	-101.53**
T	420.87	339.31	483.16	508.95
Heritability for F_2				
Narrow	0.52	0.26	0.78	0.88
Broad	0.83	0.89	0.78	0.88
Genetic advance	15.63	6.25	29.20	23.90

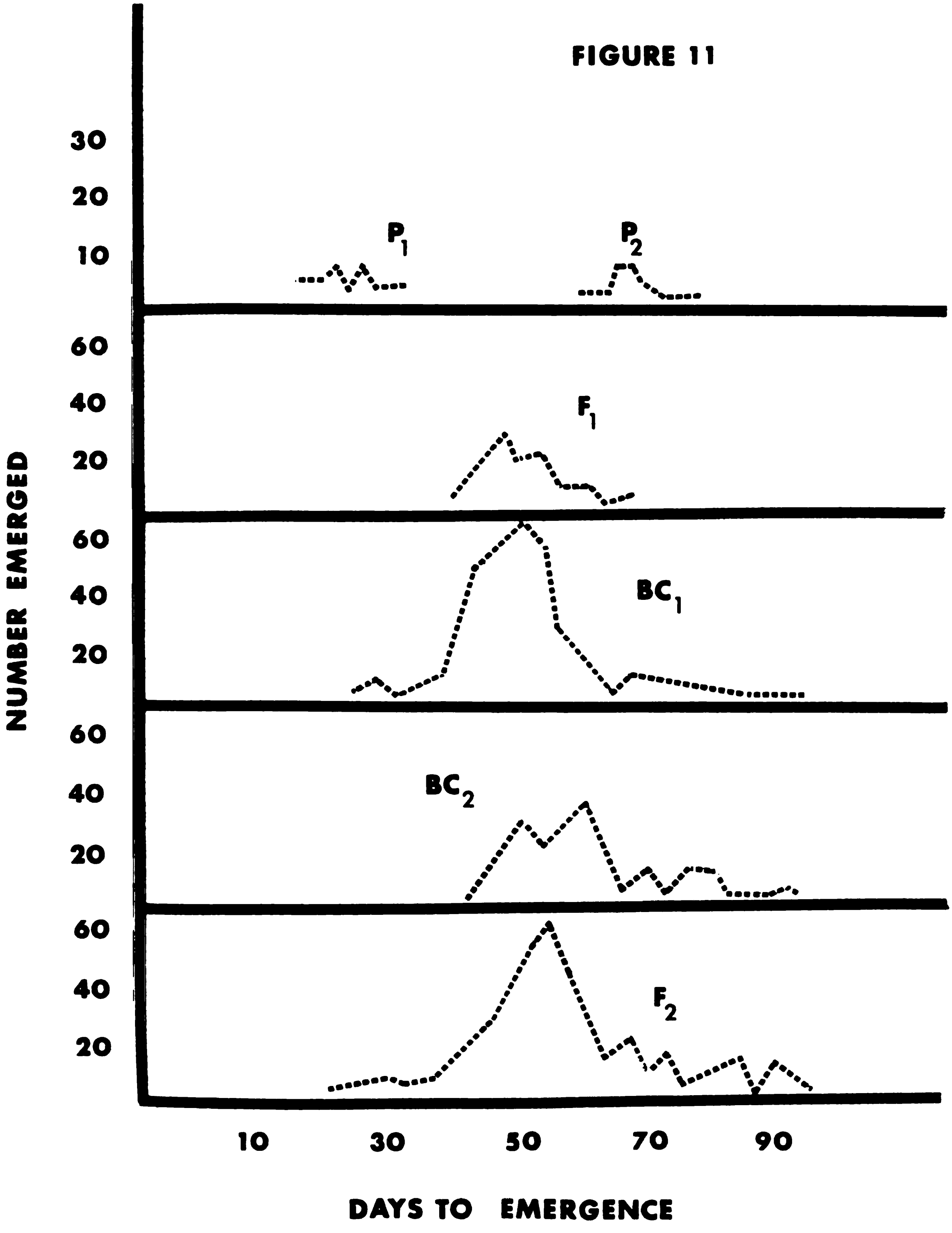
[w] 2033 x PI 260593
[x] 2033 x PI 281310
[y] PI 257185 x PI 260593
[z] PI 257185 x PI 281310

[*] Estimates may be biased due to the low number of individuals recovered in the various populations

[**] Negative values can be interpreted as zero

Figure 11. The emergence frequency distribution for parents, F_1, F_2, BC_1, and BC_2 progeny from the cross 2033 x PI 281310

FIGURE 11


30
20
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P1
P2
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40
20
F1
60
40
20
BC1
60
40
20
BC2
60
40
20
F2
NUMBER EMERGED
10
30
50
70
90
DAYS TO EMERGENCE

temperatures also indicated. The F_2 and BC_2 generation means fell between the F_1 mean and the P_2 mean while the BC_1 generation mean was slightly skewed toward the P_1 mean. Transgressive variation was noted in the F_2 and backcross generations showing individuals which exceeded those of the P_2 population.

Dominance variance (H) appeared to be the most important factor (62% of the total phenotypic variance) contributing to the genetic control of cold emergence. Additive variance (D) was positive and smaller than the dominance variance (H) (Table 11). Heritability estimates were moderate to low for the trait with narrow and broad sense heritability estimates being 0.26 and 0.89 respectively. The value for expected genetic advance (G.S.) is reported in Table 11 as 6.25 and shows the possible gain from selection as a percent increase in the F_3 over the F_2 mean when the most desirable 5% (K = 2.06) of the F_2 plants are selected. A preponderance of dominance effects along with moderate heritability and genetic advance obtained in this family suggests that selection for this character would be moderate to low.

Family III (PI 257185 x PI 260593) and Family IV (PI 257185 x PI 281310): The F_2 frequency distribution of progeny from these two families suggested that differences in cold emergence between the two parents were controlled by a small number of genes (Figure 12 and 13). The F_1 mean was slightly skewed toward the P_2 mean (Table 10) with partial dominance for slower germination at low temperatures also suggested. In addition, the F_2 and BC_1 means were located between the F_1 mean and the P_2 mean. The BC_2 mean exceeded that of the P_2 mean suggesting a preponderance of genetic effects in this population expressing a slower emergence at low temperatures. Transgressive

Figure 12. The emergence frequency distribution for parents, F_1, F_2, BC_1, BC_2 progeny from the cross PI 257185 x PI 260593

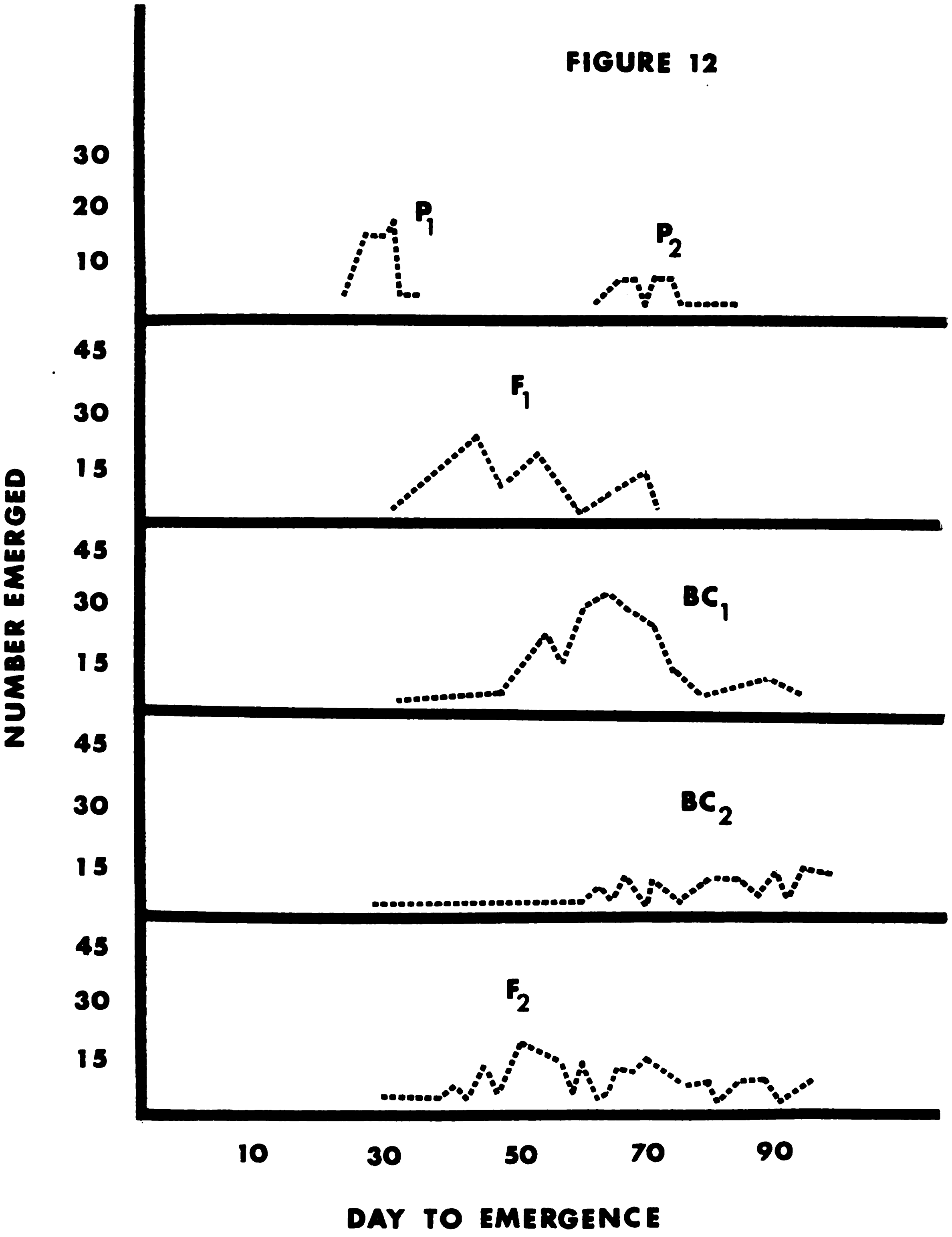
FIGURE 12
NUMBER EMERGED
30
20
10
45
30
15
45
30
15
45
30
15
45
30
15
P_1
P_2
F_1
BC_1
BC_2
F_2
10
30
50
70
90
DAY TO EMERGENCE

Figure 13. The emergence frequency distribution for parents, F_1, F_2, BC_1, and BC_2 progeny from the cross PI 257185 x PI 281310

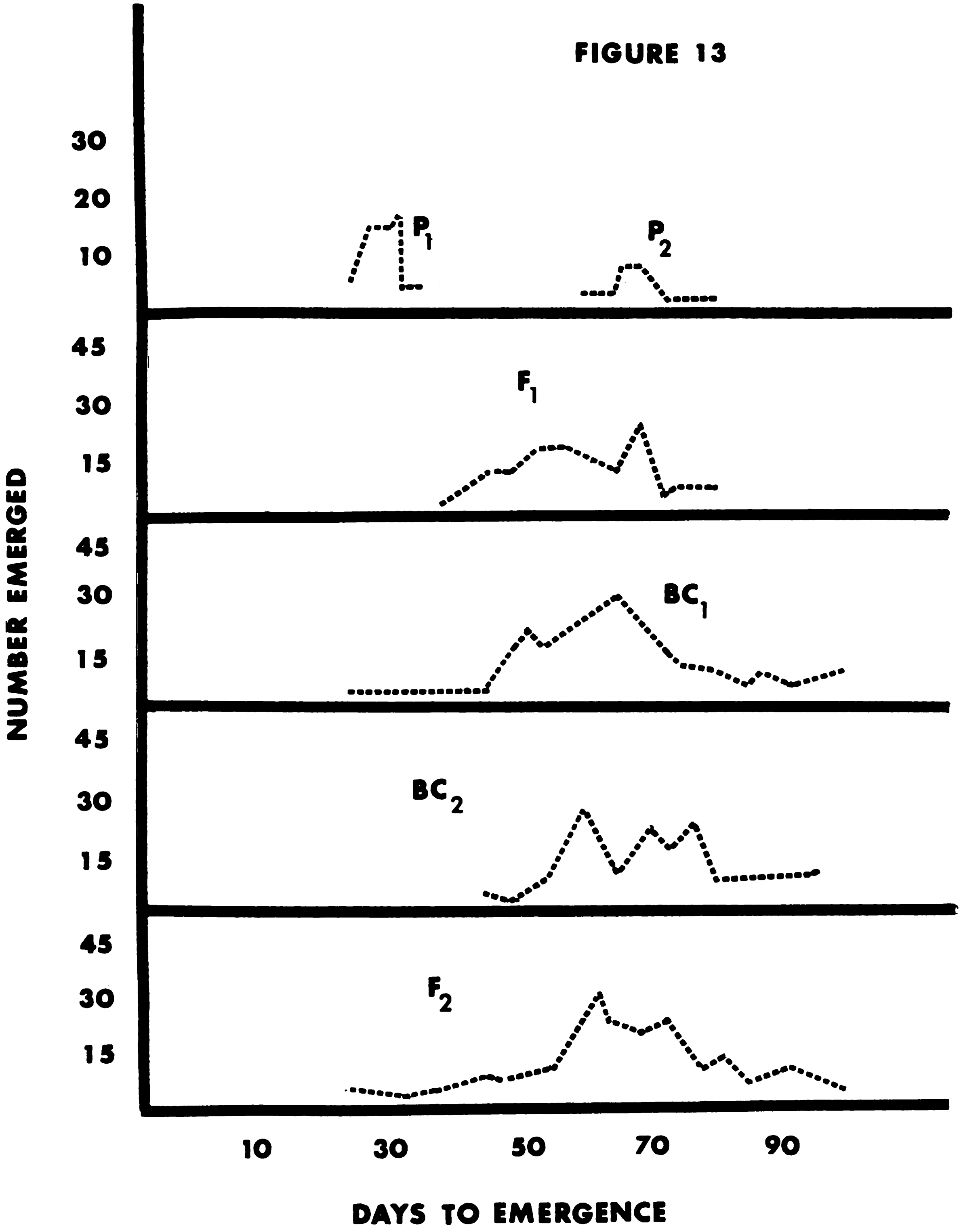
FIGURE 13
30
20
10
P1
P2
45
30
15
F1
45
30
15
BC1
45
30
15
BC2
45
30
15
F2
NUMBER EMERGED
10
30
50
70
90
DAYS TO EMERGENCE

variation was noted in the F_2 and backcross generations showing individuals which exceeded those of the P_2.

Additive variance (D) appeared to be the most important factor (78% in Family III and 88% in Family IV of the total phenotypic variance) contributing to the genetic control of cold emergence (Table 11). Dominance variance (H) was negative which may have been the result of a sampling error, or large environmental variance (E), a large F_2 variance along with a lower than normal variance in the backcross generations along with low progeny recovery. The heritability estimates were high (0.78 in Family III and 0.88 in Family IV). However, these estimates may have been biased due to the negative value for the dominance variance.

The value for expected genetic advance (G.S.) is reported in Table 11 as 29.20 (Family III) and 23.90 (Family IV). Expected genetic advance shows the possible gain from selection as percent increase in the F_3 over the F_2 mean when the most desirable 5% ($K = 2.06$) of the F_2 plants are selected.

SUMMARY AND CONCLUSION

Genetic variation was found for the expression of cold germination and emergence in _C_. baccatum var. pendulum. Cultivar response to emergence at 13°C ranged from an emergence index of 22.10 (cultivar 2033) to 43.08 (cultivar PI 281310) while an emergence index range of 40.57 (cultivar 2033) to 71.00 (cultivar PI 213915) was found at 10°C (Table 8). Mean emergence differences between temperatures were significant (5% level) showing a much slower rate at 10°C opposed to 13°C (Table 7). In general, cultivars exhibiting superior emergence at 13°C did so at 10°C. Similar findings have been reported in tomatoes (El Sayed and John, 1973), maize (Pinnell, 1949) and cucumber (Lower, 1974) for germination at suboptimal temperatures.

Seedlings which emerged at 10°C were found to be yellow to virescent in color suggesting a threshold for chloroplast development between 10 and 13°C. Apparently temperatures at 10°C were too low for normal chloroplast development resulting in the lack of chlorophyll in the cotyledons.

The progenies of reciprocal crosses between four families of _C_. baccatum var. pendulum were evaluated to determine the mode of inheritance of cold emergence. Partial dominance for slow emergence at low temperatures was noted. Additive and dominance gene action played a role in trait expression with additive gene action most important in families I, III, and IV while dominance gene action was greatest in Family II (Table 11). Low progeny recovery in families

I, III, and IV, however, may have biased those estimates. In addition, frequency distributions in all families generally agreed with the results in Family II for dominance gene action. In Family III and IV, with PI 257185 as a common parent, dominance variance was negative. This was accounted for by the genetic interaction of PI 257185 with the other parents producing a large environmental variance, a large F_2 variance, or an unusually small backcross variance in addition to low progeny recovery. Narrow sense heritability estimates ranged from 26% to 88%, while estimated genetic advance was calculated to be 6.25 to 29.20. Heritability and genetic advance generally agreed in showing characters for which selection in the F_2 would lead to substantial improvement. Excluding Families I, III, and IV because of possible biased results from low progeny recovery, a preponderance of dominance gene effects coupled with low heritability estimates and genetic advance obtained in Family II, suggest that selection for this character should be slow.

Because today's agriculture dictates the efficient production of crops, direct seeding would be an important practice to increase efficiency for the grower (Taylor, 1977). It would therefore be advantageous for the development of cold emerging cultivars to aid in direct seeding northern areas. Through earlier planting dates, cultivars tolerant to cool spring conditions during emergence and early seedling growth may allow for better utilization of a longer growing season resulting in increased production and yield.

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