Theor Appl Genet (1989) 78:143–151

Inheritance of seed dormancy in *Cummis sativus* var. *hardwickii* (Royle) Alef.

J.E. Staub [1], **D. Globerson** [2] **and A. Genizi** [2]

[1] USDA, Agricultural Research Service, Department of Horticulture, University of Wisconsin, Madison, WI 53706, USA
[2] Agricultural Research Organization, The Volcani Center, Bet Dagan 50 250, Israel

Received October 16, 1989; Accepted March 17, 1989
Communicated by A.R. Hallauer

Summary. Reciprocal matings were made between two *Cucumis sativus* var. *sativus* L. inbred lines (WI 1606 and WI 2808) and two var. *hardwickii* (Royle) Alef. accessions (PI 215589 and PI 183967). Each case produced a series of reciprocal F_1, F_2, and BC_1 and BC_2 progenies which were used to evaluate seed dormancy in var. *hardwickii.* Under controlled conditions (25° ± 1 °C and 85% ± 5% RH; 12 h fluorescent light, 30 μmol s^{-1} m^{-2}), no seed dormancy was observed in the var. *sativus* inbred lines 36 days following seed extraction from fruit. With rare exception, var. *hardwickii* accessions were dormant for at least 60 days. Seed dormancy in the F_1 was absent 36 days post extraction, indicating that dormancy in var. *hardwickii* is conditioned by recessive genes present. Seed of some F_1 progeny germinated between 36 and 50 days post-extraction, indicating the presence of transient dormancy or the more variable expression of the dormancy of var. *hardwickii.* No significant reciprocal differences in either germination rate or percentage were detected in either of the F_1 and F_2 progeny sets, suggesting lack of cytoplasmic or maternal control over these traits. It was estimated that three to seven factors or loci are involved with the expression of this trait depending on the method of calculation, and that a complex interaction between embryonic and non-embryonic tissue exists. Least square estimates indicate that both additive and dominance effects were important in the expression of dormancy. Comparison of theoretical geometric and arithmetic F_2 means to observed F_2 means also suggests that non-additive gene action contributes substantially to the observed variation. Broad-sense heritability ranged between 78 and 95%.

Key words: Cucumber – Seed ecology – Quantitative genetics – Vegetable breeding

Introduction

The plasticity of many wild plant species enables them to respond to fluctuating environmental conditions and is an important factor in their survival. Some characteristics that influence species survival include time of flowering, sufficient perennation to permit adequate seed production during extended suboptimal periods, and sufficient seed dormancy to enable re-establishment at the end of suboptimal episodes (Hacker 1984). The entry into or loss of dormancy which is mediated by the environment has a genetic component and is often a reflection of interactions between these factors (Roberts 1981; Levin 1983). Although both hormonal and genetic regulation of seed dormancy in monocots have been investigated (Adkins et al. 1984; Powell et al. 1984; De Klerk and Smulders 1984; Upadhyaya et al. 1981), little information is available with regard to the inheritance of seed dormancy in dicot species.

Seed dormancy in cucumber (*Cucumis sativus* var. *sativus* L., hereafter referred to as *sativus*) dissipates within 12–30 days from seed extraction. Two notable exceptions are cultivars 'Black Diamond' and 'Baroda' (PI 212896), which have dormancy periods ranging from 40–50 days (Watts 1938) and 180–270 days (Shifriss and George 1965), respectively. Whereas the breaking of dormancy of 'Black Diamond' can be accomplished by removal of the seed coat or hastened by high relative humidity and high temperatures after extraction (Watts 1938), such is not the case with 'Baroda'. Dormancy of 'Baroda' is reduced by high temperatures (50 °C) and high humidities (90%) after extraction, but not by seed coat removal, red or far-red light, oxidizing agents, or gibberellic acid (Shifriss and George 1965).

Cucumis sativus var. *hardwickii* (Royle) Alef. (hereafter referred to as *hardwickii*), a progenitor or a feral form of the cultivated cucumber (Horst 1977), possesses a multiple fruiting habit not found in *sativus*. It is, therefore, a potential germplasm source for increasing fruit yield in cucumber (Lower et al. 1982). *Hardwickii* accessions differ in their combining ability for economically important traits (Kupper and Staub 1988). Seed dormancy has been observed to dissipate within 60 (PI 215589) to 270 (PI 183967) days after seed extraction from mature fruit (Staub and Globerson 1984). Unlike 'Baroda', dormancy in *hardwickii* can usually be overcome by removal of the seed coat, as well as by extended exposure to high temperature and high humidity (unpublished data). In view of the potential usefulness of *hardwickii* germplasm for cucumber improvement, a series of experiments was undertaken to estimate heritability of the difference in dormancy between *hardwickii* and *sativus*.

Materials and methods

Parents and progeny

Experiment 1. To determine the inheritance of dormancy, matings among individual plants were made between the USDA *sativus* processing cucumber inbred line WI 1606 (P_1) and *hardwickii* PI 215589 (P_2), to produce reciprocal F_1, F_2 and F_3 progenies and the following BC_1 and BC_2 families: $(P_1 \times P_2) \times P_1$, $(P_1 \times P_2) \times P_2$, $(P_2 \times P_1) \times P_2$, $[(P_2 \times P_1) \times P_2] S_1$ and $[(P_1 \times P_2) \times P_2] \times P_2$.

Seed of F_1, F_2, F_3, and BC_1 from P_1 and P_2 were produced in a greenhouse (May 3 and August 11, 1983 plantings). After extraction, seeds were air-dried at 25 °C and stored under laboratory conditions ($21° \pm 3$ °C and about 70% RH) until evaluation. In preliminary tests, the seed lots were classified as either dormant or non-dormant at 30 and 60 days post-extraction. Their germination was compared and tested under controlled conditions ($25° \pm 1$ °C, and about 85% RH). Seeds were considered to have germinated when a radicle length of ≥ 3 mm was observed (non-dormant).

Subsequently, dormant and non-dormant BC_1S_1 and BC_2 families were produced in the greenhouse (November 15, 1983 and February 23, 1984 plantings). Each plant was grown in 20-cm diameter pots, individually staked, and pruned to the mainstem. Cool-white fluorescent lights, providing 600–700 lx (approximately 100 $\mu mol\ s^{-1}\ m^{-2}$ at shoot apices), extended the photoperiod to 16 h. Growing temperatures ranged between 17° and 35 °C. Hand pollinations produced seed which were extracted from fruits at 55–60 days post pollination and soaked in their mesocarp tissue for 24 h at $28° \pm 3$ °C. The seed were then dried for 3–4 days at $28° \pm 2$ °C and held at $24° \pm 1$ °C with 50%–60% relative humidity until evaluation for germination. Bulked seeds from each fruit (seed lot) were used in this and in Experiment 2.

Preliminary studies indicated that 30 days was the minimum number of days to germination of cross progeny seeds. At 30 and 60 days after extraction, 25–30 seeds of each progeny seed lot were evaluated for germinability in 9-cm petri plates containing two filter paper discs (Whatman No. 2). Five ml of distilled water was added to each plate, and plates were placed in a controlled environment at $25° \pm 1$ °C and about 85% RH under a 12-h photoperiod (cool-white fluorescent lighting at approximately 30 $\mu mol\ s^{-1}\ m^{-2}$). Percentage and rate of germination, measured as cumulative percent differences between days, were observed over 12 days at 72-h intervals.

Both dormant and non-dormant BC_1S_1 and BC_2 families resulted from BC_1 individuals which were classified as dormant or non-dormant at 60 days. This second round of selection was accomplished by selecting both dormant and non-dormant individuals from BC_1 families segregating for dormancy. After the 60 days, the dormancy of BC_1 seeds which had not germinated was broken by removal of the seed coat. Thereby, both dormant and non-dormant individuals from the same BC_1 family were transplanted to the greenhouse for self-pollination or cross-pollination with the recurrent parent. Dormant and non-dormant F_3 and BC_1 progenies were also generated from F_2 families.

Experiment 2. Seeds of *hardwickii* PI 183967 held unter $20° \pm 5$ °C, 70% RH remain dormant up to 270 days post-extraction from mature fruit (unpublished data). This is considerably longer than the 60-day dormancy period of *hardwickii* PI 215589. This germplasm should provide additional information regarding the inheritance of dormancy in *hardwickii*. Therefore, F_1, F_2, F_3, and BC_1 families were also developed using the *sativus* USDA inbred line WI 2808 (P_3) × *hardwickii* PI 183967 (P_4). Seeds of F_1 and F_2 progeny obtained in the greenhouse (as in Experiment 1) were used in the production of F_2 and F_3 seeds in an isolation cage in the field (June 15 and August 26, 1983). Plants were transplanted approximately 24 cm apart in rows which were on 92-cm centers, and bees (*Apis mellifera* L.) were introduced into each cage during flowering to ensure adequate pollination. Uniform fruits were selected at seed maturity (white or yellow epidermis) for evaluation, and seeds were processed from these as described above. Dormant and non-dormant individuals were indentified as described above to produce segregating generations for genetic analysis.

Data analysis. The dormant versus nondormant status of each seed lot was determined and the frequency of dormant and non-dormant progeny was tabulated. Contingency Chi-square analysis of reciprocal F_2 and F_3 progeny sets was employed to determine the influence of cytoplasmic and maternal factors on rate and percentage of germination.

Inspection of F_2, F_3, and BC segregations suggested that the inheritance of dormancy was complex. Hence, data analyses were conducted according to Kotechan and Zimmerman (1978), to estimate broad sense heritability (h^2), and provide two measures (h_1 and h_2) of the degree of dominance. Linear relationships did not exist between generation means and standard deviations. Various transformations were applied to increase variance homogeneity within generations. No transformations substantially improved homogeneity, therefore analyses of untransformed data are presented.

Two methods of analysis were used to study the nature of gene action. The method of Burton (1951) was used to calculate arithmetic, geometric and observed F_2 means, and a Mather-Hayman analysis (Mather and Jinks 1977) was used to estimate the base population mean (m) and additive (a) and dominance (d) variance effects. Employing this analysis, one can compare observed and calculated F_2 means, thus obtaining estimates of gene action. An agreement between observed and theoretical arithmetic F_2 values indicates additive gene action, agreement between calculated theoretical geometric and observed F_2 values indicates nonadditive gene action. The number of factors or loci involved was estimated using the methods of Castle and Wright (1921) and Burton (1951; according to Wright).

Least squares estimates of the variances of base population mean, additive, and dominance effects were calculated from all available progenies in each experiment based on F_2 data. Lack-of-fit to the genetic model was tested on data obtained from several repetitions of F_1, F_2, and BC progeny seed lots resulting from initial parental matings of $P_1 \times P_2$ by an F-test comparing the linear model based on m, d, and h against the model corresponding to six populations (two parents, F_1, F_2 and two backcrosses). Lack of fit to the model using F_2 progenies from $P_3 \times P_4$ matings could not be tested, since an inadequate number of degrees of freedom remained for Chi-square analysis.

Segregation of cross progeny families derived from either dormant or non-dormant individuals can provide additional information about the expression of dormancy. If segregations in some families are adequately explained by fit to Mendelian ratios, then a provisionary genetic hypothesis could be developed to help describe major gene action. After closer inspection of segregating non-dormant families, it appeared that the expression of dormancy in many cross progeny seed lots might be explained by the action of few genes, perhaps two. Therefore, cross progeny families derived from both dormant or non-dormant individuals were tested for goodness-of-fit to hypothesized ratios for two-factor segregation (Steel and Torrie 1980).

Results

Dominance relationships and cytoplasmic/maternal influence

Comparison of the *hardwickii* (P_2 and P_4) and *sativus* (P_1 and P_3) genotypes confirmed preliminary observations regarding dormancy of seeds at 30 days after extraction (Tables 1–3). Seeds of some *sativus* seed lots had not germinated 9 days after imbibition, but all seed of most lots were germinated by 12 days (Table 1). A few seeds of *sativus* remained dormant for 30 days (Tables 2 and 3), but all germinated after 36 days. Both *hardwickii* PI's remained dormant at least 60 days. In most instances, *hardwickii* seedcoat removal before testing resulted in 50% germination within 2–18 days (data not presented).

With the exception of one progeny lot (Experiment 1), germination of F_1 populations was influenced by dominant genetic effects conferred by either *sativus* parent (Table 1). The rates of germination of all BC_1 progeny possessing *sativus* cytoplasmic backgrounds [$(P_1 \times P_2) \times P_1$ and $(P_1 \times P_2) \times P_2$] were similar, and percentage germination was 100% at 3 days after imbibition (data not presented). Percent germination of seeds of $(P_2 \times P_1) \times P_2$ progeny lots was 45% after 12 days (data not presented).

Progeny segregations of F_2 and F_3 families provide information regarding cytoplasmic and/or maternal influences by the maternal F_1 and F_2 tissues, respectively. No significant reciprocal differences among F_2 progeny sets (Experiment 1) in either germination rate or percentage were apparent ($P > 0.05$), but reciprocal differences were detected among F_3 families.

Genetic analyses and estimates

The estimated number of factors or loci involved in the expression of dormancy ranged from three to seven, depending on the accession and method of calculation (Table 4). The range of segregation in F_2 families was narrow and, as a consequence, broad-sense heritability estimates for this trait were high (78% and 95% for $P_1 \times P_2$ and $P_3 \times P_4$, respectively). Least square estimates of the contribution of additive and dominance effects indicate that both were important in the expression of dormancy (Table 4). However, comparison of theoretical geometric and arithmetic F_2 means to observed F_2 means suggests that non-additive gene action contributes substantially to the observed variation.

Families resulting from matings involving non-dormant and dormant progenies derived from seeds which had been selected from lots classified as dormant in Experiments 1 (Table 2) and 2 (Table 3) were evaluated. Segregations of F_3, BC_1, BC_1S_1 and BC_2 families, originating from seed classified as non-dormant and dormant, provided additional information on the nature of dormancy. If at least one dominant allele, Ds_1, was hypothesized at a locus which conditioned germination 30 days post seed extraction, and a second allele (ds_2) at another locus possessed variable expressivity and was epistatic to ds_1, then segregations in several progeny seed lots would fit those predicted by a two-gene model (Tables 2 and 3). In such a case, individuals genotypically $ds_1ds_1Ds_2$ would possess a transient type of dormancy lasting between 36 and 50 days. For example, in experiment 1 (Table 1), the appearance of a dormant F_1 family ($P_1 \times P_2$) would have been predicted if P_1 was genotypically $Ds_1ds_1Ds_2ds_2$, and P_2 was $ds_1ds_1Ds_2ds_2$, and the expressivity of Ds_2 was incomplete producing $ds_1ds_1Ds_2ds_2$ dormant progeny (transient). Germination (no dormancy) is conditioned by dominance at both loci; hence, individuals genotypically Ds_1Ds_2 (i.e., P_1 and P_3) germinate.

Such a hypothesis could be used to explain the presence of dormant individuals in the F_1 (Experiment 1, Table 1). However, all backcross and many F_3 families derived from seed classified as dormant did not segregate to adequately fit predicted ratios.

Discussion

Delayed germination in cucumber has been observed in several wild races of Indian origin (Shifriss and George 1965). *Hardwickii*, a feral form or wild progenitor of *sativus*, possesses delayed flowering characteristics (Della Vecchia and Peterson 1984) and dormancy. Both are conditioned by recessive genes, which lends support to the hypothesis presented by Shifriss and George (1965) that, "the wide range of adaptation of world cultivars, under domestication, was brought about in part by dominant gene mutations which accelerate the speed of ger-

Table 1. Distribution, mean, SD and Chi-square analysis of germination 30 days post-seed extraction for parents and cross progenies resulting from matings between *C. sativus* var. *sativus* and *C. sativus* var. *hardwickii* (R) Alef

Parent or progeny generation	Pedigree	No. of seed lots tested	Germination (%) of seed lot 30 days post-seed extraction											$\bar{X}$	SD	Hypothesized parental genotypes[c]	Test ratio[d]	Chi-square analysis ($P \geq$)
			0	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100					
			Dormant								Non-dormant							
		Experiment 1																
P_1	WI 1606[a]	12											12	98	2.6	$Ds_1\_\_Ds_2\_\_$		
P_2	PI 215589[b]	12	12											0	0	$ds_1ds_1ds_2ds_2/ds_1ds_1Ds_2ds_2$		
F_1	$P_1 \times P_2$	12					1						11	90	17.3	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1Ds_2ds_2$	4:7	0.75
F_1	$P_2 \times P_1$	10											10	97	3.6	$ds_1ds_1Ds_2ds_2 \times Ds_1ds_1Ds_2ds_2$	1:7	0.10
F_2	$(P_1 \times P_2)\otimes$				1	1		1	3		1	3	7	73	26.5	$(Ds_1ds_1Ds_2ds_2)^2$	1:3	0.60
F_2	$(P_2 \times P_1)\otimes$								2	2		3	11	86	14.7	$(Ds_1ds_1Ds_2ds_2)^2$	1:3	0.90
F_3	$[(P_1 \times P_2)\otimes]\otimes$			2	1	1	2				3	4	6	66	33.6			
F_3	$[(P_2 \times P_1)\otimes]\otimes$										3		12	91	8.3			
BC_1	$(P_1 \times P_2) \times P_1$	3									1		2	88	11.5	$Ds_1ds_1Ds_2ds_2 \times Ds_1Ds_1Ds_2Ds_2$	0:1	1.0
BC_1	$(P_1 \times P_2) \times P_2$	8		2	1	1	1	1	1			1		34	27.5	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	1:1	0.05
		Experiment 2																
P_3	WI 2808[a]	10											10	100	0	$Ds_1\_\_Ds_2\_\_$		
P_4	PI 183967[b]	8	8											0	0	$ds_1ds_1ds_2ds_2/ds_1ds_1Ds_2ds_2$		
F_1	$P_3 \times P_4$	10											10	100	0	$Ds_1ds_1Ds_2Ds_2 \times ds_1ds_1ds_2ds_2$	0:1	1.0
F_2	$(P_3 \times P_4)\otimes$	30				1		1	6	7	4	9	2	73	16.1	$(Ds_1ds_1Ds_2ds_2)^2$	1:3	0.001

[a] *C. sativus* var. *sativus*

[b] *C. sativus* var. *hardwickii*

[c] Allele 'Ds_1' is hypothesized to condition germination and is dominant to 'ds_1' conditioning dormancy. Individuals genotypically $ds_1ds_1Ds_2ds_2$ have transient dormancy lasting 36–50 days

[d] Dormant:non-dormant

Table 2. Seed dormancy relationships and Chi-square analyses of parents and cross progenies resulting from matings between a *C. sativus* var. *sativus* L. inbred line (USDA WI 1606) and a *C. sativus* var. *hardwickii* (R) Alef. accession (PI 215589) 30 days post-seed extraction in Experiment 1

Generation	Pedigree	Seed lot designation of parent[c]	Mean germination of parental seed lot (%)	Dormancy status of parent									
				Nondormant					Dormant				
				Classification of offspring (no. of seeds)									
				Non-dormant families	Dormant segregating families	Hypothesized parental genotype	Test ratio	Chi-square analysis ($P \geq$)	Non-dormant families	Dormant segregating families	Hyothesized parental genotypes[e]	Test ratio	Chi-square analysis ($P \geq$)
P_1	WI 16061[a]	–	100	124	6	$ds_1ds_1Ds_2\_\_$ $Ds_1\_\_Ds_2\_\_$	15:1	0.50	–	–	–	–	–
P_2	PI 215589[b]	–	0	0	130	$ds_1ds_1ds_2ds_2$ or $ds_1ds_1Ds_2ds_2$	0:1	1.00	0	80	$ds_1ds_1ds_2ds_2$	0:1	1.00
F_3	$[(P_1 \times P_2)\otimes]\otimes$	84	60	185	0	$Ds_1ds_1\_\_\ \_\_$	1:0	1.00	–	–	–	–	–
BC_1	$[(P_2 \times P_1) \times P_2]$	84	60	84	36	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	3:1	0.25	21	59	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1Ds_2ds_2$	3:5	0.03
BC_1S_1	$[(P_2 \times P_1) \times P_2]\otimes$	75	45	75	105	$ds_1ds_1Ds_2ds_2$	1:1	0.03	17	58	$ds_1ds_1Ds_2ds_2$	1:3	0.90
		76	70	67	67	$ds_1ds_1Ds_2ds_2$	1:1	1.00	0	240	$ds_1ds_1ds_2ds_2$	0:1	1.00
		77	70	110	35	$Ds_1ds_1ds_2ds_2$	3:1	0.75	–	–	–	–	–
		78	70	191	9	$Ds_1ds_1Ds_2ds_2$	15:1	0.25	35	133	$ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	1:1/ 0:1	0.001[d]
BC_2	$[(P_1 \times P_2) \times P_2] \times P_2$	75	45	42	168	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	3:1/ 1:1	0.001	1	159	$ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	0:1	0.001[f]
		76	70	110	99	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	1:1	0.50	2	89	$ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	0:1	0.001[f]
		77	70	92	91	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	1:1	0.90	106	194	$ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	1:3	0.001
		78	70	126	64	$Ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	3:1	0.06	11	239	$ds_1ds_1Ds_2ds_2 \times ds_1ds_1ds_2ds_2$	0:1	0.001[f]

[a] *C. sativus* var. *sativus*; bulk of six seed lots

[b] *C. sativus* var. *hardwickii*; bulk of six seed lots

[c] Identifies parental seed lot from which dormant and non-dormant individuals were selected

[d] Dormancy classified at 30 days post-seed extraction (<71% germination was taken as dormant segregating families)

[e] Allele 'Ds_1' is hypothesized to condition germination and is dominant to 'ds_1', conditioning dormancy. Individuals genotypically $ds_1ds_1Ds_2ds_2$ have transient dormancy lasting 36–50 days

[f] Variable expressivity of 'Ds_2' allele in genotypically $ds_1ds_1Ds_2ds_2$ individuals could produce non-dormant individuals and therefore provide an explanation for lack-of-fit to genetic model

Table 3. Seed dormancy relationships and Chi-square analyses of parents and cross progenies resulting from matings between a *C. sativus* var. *sativus* L. inbred line (USDA WI 2808) and a *C. sativus* var. *hardwickii* (R) Alef. accession (PI 183967) 30 days post-seed extraction in Experiment 2

Generation	Pedigree	Seed lot designation of parent[c]	Mean germination of parental seed lot (%)	Dormancy status of parent									
				Nondormant					Dormant				
				Classification of offspring (no. of seeds)									
				Non-dormant families	Dormant segregating families	Hypothesized parental genotypes	Test ratio	Chi-square analysis ($P \geq$)	Non-dormant families	Dormant segregating families	Hyothesized parental genotypes[e]	Test ratio	Chi-square analysis ($P \geq$)
P_3	WI 2808[a]	–	100	127	3	$ds_1ds_1Ds_2\_\_/$ $Ds_1\_\_Ds_2$	15:1	0.50	–	–	–	–	–
P_4	PI 183967[b]	–	0	0	120	$ds_1ds_1Ds_2ds_2/$ $ds_1ds_1Ds_2ds_2$	0:1	1.0	0	205	$ds_1ds_1ds_2ds_2$	0:1	1.0
F_3	$[(P_3 \times P_4)\otimes]\otimes$	30	70	60	5	$Ds_1ds_1Ds_2ds_2$	15:1	0.75	183	72	$ds_1ds_1Ds_2ds_2$	1:3	0.001
		34	70	181	59	$Ds_1ds_1Ds_2ds_2$	3:1	0.75	288	182	$ds_1ds_1Ds_2ds_2$	1:3	0.001
		43	65	117	22	$Ds_1ds_1Ds_2ds_2$	15:1	0.10	75	110	$ds_1ds_1Ds_2ds_2$	1:3	0.001
		47	60	197	3	$Ds_1ds_1Ds_2ds_2$	15:1	0.001	148	147	$ds_1ds_1Ds_2ds_2$	1:3	0.001
		50	70	40	0	$Ds_1ds_1Ds_2ds_2$	1:0	1.0	201	200	$ds_1ds_1Ds_2ds_2$	1:3	0.001
		51	60	–	–	–	–	–	93	157	$ds_1ds_1Ds_2ds_2$	1:3	0.001
BC_1	$(P_3 \times P_4) \times P_4$	30	70	69	31	$Ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	3:1	0.10	11	19	$ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	1:3	0.001[d]
		34	70	7	17	$Ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	3:1	0.001	2	48	$ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	0:1	0.001[f]
		43	65	44	31	$Ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	1:1	0.10	24	96	$ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	1:3	0.100[f]
		47	60	80	30	$Ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	3:1	0.50	62	88	$ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	1:3	0.001[f]
		50	70	36	34	$Ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	1:1	0.90	–	–	–	–	–
		51	60	–	–	–	–	–	1	39	$ds_1ds_1Ds_2ds_2 \times$ $ds_1ds_1ds_2ds_2$	1:3	0.001[f]

[a] *C. sativus* var. *sativus*; bulk of six seed lots

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[d] Dormancy classified at 30 days post-seed extraction (<71% germination was taken as dormant segregating families)

[e] Allele 'Ds_1' is hypothesized to condition germination and is dominant to 'ds_1', conditioning dormancy. Individuals genotypically $ds_1ds_1Ds_2ds_2$ have transient dormancy lasting 36–50 days

[f] Variable expressivity of 'Ds_2' allele in genotypically $ds_1ds_1Ds_2ds_2$ individuals could produce non-dormant individuals and therefore provide an explanation for lack-of-fit to genetic model

Table 4. Estimates of the genetic behavior of seed dormancy observed in progenies resulting from *Cucumis sativus* var. *sativus* and var. *hardwickii* matings

Statistic	Mating series[a]	
	$P_1 \times P_2$	$P_3 \times P_4$
Broad sense heritability %	77.5	95.0
Degree of dominance (h_1)	0.90	1.00
Degree of dominance (h_2)	1.00	0.92
Theoretical arithmetic ($F_2\bar{X}$)	71.1 ± 2.5	75.0 ± 0
Theoretical geometric ($F_2\bar{X}$)	30.4 ± 0.6	37.6 ± 0
Observed ($F_2\bar{X}$)	79.6 ± 3.8	73.0 ± 2.9
Minimum number (n) of genetic factors[b]	2.98	4.81
Minimum number (n) of genetic factors	4.13	7.21
Base population mean (m)	49.3 ± 1.3	50.0 ± 0.2
Additive effect (d)	49.1 ± 1.3	50.0 ± 0.2
Dominance effect (h)	49.3 ± 3.5	50.0 ± 0.4
Significance of F or χ^2 due to model (P)	0.0001	0.007
Lack-of-fit significance	n.s.	–[c]

[a] P_1 = WI 1606, P_2 = PI 215589, P_3 = PI 2808, P_4 = PI 183967

[b] First and second estimations according to Castle and Wright (1921) and Burton (1951), respectively

[c] No *df* remained for lack-of-fit test

mination and the speed of flowering in long days.“ The genetic control of dormancy found in the *sativus* cultivar 'Baroda' appears to be different from that found in *hardwickii.* Moreover, there are differences in recovery from dormancy among *hardwickii* accessions. Therefore, although specialized types of adaptation which are associated with recessive genes may be present in several cultivars in tropical India (Shifriss and George 1965), it appears that their mechanism of expression differs by the source from which they acquired such genes.

A trait such as seed dormancy, which might be hypothesized to be conditioned by two major loci that exhibit low penetrance and variable expressivity and are subject to the action of other modifying genes, is difficult to characterize. Factors such as time of data collection and framing of the dormancy criterion can affect the frequency of individuals classified as dormant and, consequently, the resulting genetic hypothesis. What is considered a dormant individual under one criterion may not be if that individual were evaluated at a different time or grouped using another set of parameters.

Our data indicate that strict utilization of the hypothesized two-factor model leading to a comprehensive interpretation of gene action is not possible. Since the distribution of progeny in the F_2 was continuous and a deficiency of non-dormant individuals was observed in some cross progeny seed lots, it is likely that more than two genetic factors contribute to the expression of this trait. The speed of germination in progeny from 'Marketer' and 'Baroda' matings was hypothesized to be under the control of relatively few genes, perhaps three (Shifress and George 1965). In *hardwickii,* depending on the accession, as few as three to seven genes may operate to control dormancy.

The *sativus* lines used were processing types, but were derived from different sources. The fact that some *sativus* seeds (1%) were dormant after 30 days (Tables 2 and 3), but germinated between 36 and 50 days (data not presented), indicates that these *sativus* lines possess a complex recessive transient type of dormancy ($ds_1ds_1Ds_2$ or Ds_1 Ds_2). The heterozygous nature of the *sativus* parent is supported by the fact that dormant individuals were observed (Tables 2 and 3).

Segregation for transient dormancy is possible since selection against transient dormancy has not been practiced in this germplasm. Frequently, seeds are treated with acetone immediately after extraction. This procedure allows for rapid germination and, hence, for individuals possessing transient dormancy to be carried along in the inbred line. Furthermore, fruit maturity (i.e., stage of seed development) may be a factor in a seed's recovery from dormancy. Although seeds evaluated in Experiment 2 were extracted from mature fruit, no effort was made to control time of pollination. Therefore, seed maturity differences may have contributed to the observed variation in this experiment. These facts indicate the need for extreme care in seed handling procedures and for conducting germination tests in cucumber.

Since seed dormancy in *hardwickii* can be broken by removal of the seed coat, it is likely that an interaction between embryonic and non-embryonic tissue exists. The fact that seed coat removal either occasionally does not result in germination or results in a rate to 50% germination ranging between 2 and 18 days suggests that the expression of this interaction is complex. Since the F_1 embryo is encapsulated in maternal tissue (nucellus, integuments, and seed coat), these genotypically different tissues may interact to regulate seed dormancy. In most instances, seedcoat removal breaks dormancy in *hardwickii* within 10–30 days. Given this fact and the observed germination response in F_1 progenies suggests that germination of F_1 seed is a reflection of the embryo and the dominant P_1 character.

In common wheat (*Triticum aestivum* L.), the germination of F_1 seeds of reciprocal crosses between dormant and less-dormant cultivars were observed to be different (Noll et al. 1982), indicating that the maternal parent, the seed coat, and/or the endosperm or otherwise have a significant influence on seed dormancy. Reciprocal differences in the speed of germination were observed among cucumber BC_1 progeny derived from matings between 'Marketer' and 'Baroda' (Shifriss and George 1965). Reciprocal differences observed in F_3 progeny in our study provide further evidence that, in *hardwickii,* the interaction between the seed coat and the embryonic tissue is complex. Since reciprocal differences were not seen in the F_1 and F_2 these were interpreted as embryonic effects. The lack of reciprocal differences among F_2 progeny (lack of cytoplasmic or maternal control over this character) and the hypothesized polygenic nature of dormancy may provide a partial explanation for the reciprocal differences observed among F_3 progeny. However, a comprehensive explanation of reciprocal differences in later generations is not possible and awaits further experimentation.

Families derived from seed classified as dormant provide information about embryonic and non-embryonic interactions. The appearance of a high frequency of non-dormant individuals among many F_3 (Tables 2 and 3) and BC progeny derived from dormant F_2 individuals (Table 2) can be explained by the hypothesized two-factor model. Two of three BC_1S_1 families, derived from parents classified as dormant in Experiment 1 (Table 2), segregated to fit the predicted ratios. Although segregations of BC_1 and BC_2 to P_2 families derived from dormant individuals did not adequately fit predicted ratios, the dormant progeny recorded in lots 84, 75, 76, and 78 (Table 2) could be explained by a lack of germination in $ds_1ds_1Ds_2ds_2$ individuals possessing transient dormancy. Likewise, the excess of non-dormant progeny in family 77 derived from a dormant individual could be due to germination of $ds_1ds_1ds_2ds_2$ individuals, which would comprise 25% of the population under the hypothesized model. In Experiment 2, excess numbers of non-dormant progeny in F_3 families and in four of five BC_1 families (lots 30, 34, 47, and 51) led to lack-of-fit to predicted ratios (Table 3). Lack-of-fit to these ratios was due to an excess of non-dormant individuals in families 30 and 47 and to a deficiency of non-dormant types in families 34 and 51. Although it was not possible to directly test whether non-germinating seeds were dormant or dead, seed lots of families tested 36 months after extraction germinated within a range of 92%–100%, indicating seed viability.

The observed lack-of-fit could be due to the presence of inhibitors or to the lack of stimulating factors contributing to germination. The hypothesized two-factor model does not directly account for possible interactions between the embryo and seed coat. It is attractive to speculate that gene "messages" (interactions) may be operating to regulate metabolic pathways as the dormancy period progresses. The presence of a germination inhibitor in the fruit juice of 'Baroda' was suggested as a possible explanation for the observed differences between 'Marketer' and 'Baroda' (Shifriss and George 1965). In muskmelon (*C. melo* L.), seed coat removal significantly increases uptake of oxygen, resulting in lowered respiratory quotient values after imbibition (Pesis and Ng 1986). It is likely that the seed coat inhibits germination by promoting anaerobiosis in this species. We have observed that endogenous inhibitors are not present in dormant *hardwickii* seed extracted with water, methanol, chloroform, or hexane; however, infusion of acetone enhances germination. The growth potential of excised embryos in osmotic PEG solutions increased with increasing after-ripening period, suggesting an osmotic regulation of germination (Weston et al. 1988). Populations derived from this study provide the genetic stocks necessary to investigate more precisely the physiological mechanisms of dormancy in cucumber.

We have observed seed dormancy in populations with high yielding plants derived from *hardwickii* germplasm. Although frequencies of dormant seed are low in advanced material obtained by recurrent selection for fruit yield, the elimination of dormancy in these populations may be difficult due to the contribution of non-additive effects and the apparent interaction between embryonic and non-embryonic tissue. High yielding lines can be extracted from these populations and concurrently selected through single-seed descent for the ability to germinate, thereby providing potentially useful germplasm.

Acknowledgements. Research supported by Agricultural Research Service, U.S. Department of Agriculture, and the College of Agriculture and Life Sciences, University of Wisconsin, Madison. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of the other products or vendors that may also be suitable. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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