Theor Appl Genet (1987) 74:522-526

Inheritance of seed weight in *Cucumis sativus* (L.) var. *sativus* and var. *hardwickii* (Royle) Kitamura

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

[1] Volcani Center, Agricultural Research Organization, Ministry of Agriculture, P.O. Box 6, Bet Dagan 50-250, Israel
[2] USDA/ARS, Department of Horticulture, University of Wisconsin, Madison, WI 53706, USA

Received February 23, 1987; Accepted March 12, 1987
Communicated by A. R. Hallauer

Summary. A series of experiments was conducted to determine the inheritance of seed weight in cucumber. Matings between a *Cucumis sativus* var. *sativus* (Cs) L. inbred line (USDA WI 1606; P_1) and a *C. sativus* var. *hardwickii* (Royle) Kitamura (Ch) collection (PI 215589; P_2) were made to produce seed of reciprocal F_1, F_2, and BC_1 families. Families were grown under field and greenhouse conditions, and seeds were extracted from fruit 55 to 60 days post-pollination. Seed of F_1 and F_2 families was obtained using the Cs inbred WI 2808 (P_{12}) and the Ch collection LJ 90430 (P_{10}), and seed of F_1 families were produced using a North Carolina Design II mating scheme in which three Cs (P_3 = GY-14; P_4 = WI 1379; P_5 = WI 1909) inbreds were used as maternal parents and seven Ch collections (P_2; P_6 = PI462369; P_7=486336; P_8=LJ91176; P_9=273469; P_{10}= 2590430; P_{11}=PI187367) were used as paternal parents. Mean seed weights of F_1 progeny reflected the dominance of genes of the *C. sativus* var. *sativus* parent. Transformation to number of seeds per unit weight resulted in increased variance homogeneity within generations and a broad-sense heritability ranging between 26% to 56%. Additive and dominance effects were important in the expression of seed weight in $P_1 \times P_2$ progeny produced in the greenhouse and additive effects were important in field grown progeny resulting from $P_1 \times P_2$ and $P_{10} \times P_{12}$ matings. The estimated number of factors or loci involved ranged between 10 to 13, depending on the method of calculation.

Key words: *Cucumis sativus* – *Cucumis hardwickii* – Quantitative genetics

Introduction

In vegetable crops, where dry seeds may not be of primary economic importance, seed weight and morphology may affect germination and stand establishment (Dickson 1980). In cucumber (*Cucumis sativus* var. *sativus;* hereafter referred to as *sativus*), the compact plant type (cpcp) is of interest for high-density, mechanically harvested production systems. Although the cp locus conditions a reduction in mainstem length, cpcp genotypes exhibit a number of pleiotropic effects (Edwards 1983). Typically the cp locus is associated with poor seed quality which often results in erratic stands.

Cucumis sativus var. *hardwickii* (Royle) Kitamura (hereafter referred to as *hardwickii*), which is either a progenitor or feral form of *sativus*, commonly has 50 to 75 mature fruits per plant (Horst 1977). The *hardwickii* may provide a source for increasing yields of *sativus* (Della Vecchia 1982; Nienhuis 1982). We have observed that there is dormancy associated with *hardwickii* seed (Staub and Globerson 1984) and that the seed size and weight of various *hardwickii* accessions are noticeably less than those of *sativus* lines used in our breeding program (unpublished data).

In view of the potential significance of *hardwickii* germplasm to plant improvement, a study was initiated to determine the inheritance and heritability of seed weight among *hardwickii* and *sativus* lines. This information would from the basis of subsequent studies investigating correlated responses to selection for seed weight.

Materials and methods

Parents and progeny

Experiment 1. Matings were made between the USDA *sativus* inbred line WI 1606 (P_1) and the *hardwickii* PI 215589 (P_2) to produce reciprocal F_1 and F_2 progenies and the following

BC_1 families: $P_1 \times (P_1 \times P_2)$, $(P_1 \times P_2) \times P_1$, $(P_2 \times P_1) \times P_1$, $(P_2 \times P_1) \times P_2$. Families were grown under field (June 15 to August 26, 1983) and greenhouse (May 3–August 11, 1983) conditions. In the greenhouse, at least 12 plants from each family were grown individually in 20 cm pots and staked and pruned to the mainstem. Cool-white fluorescent lights, providing 600 to 700 lux (approximately 100 μmol s^{-1} m^{-2}) at shoot apex height, were used to extend the photoperiod to 16 h. Minimum and maximum temperatures during the entire period ranged from 17° to 35 °C. Hand pollinations were made and seeds were extracted from fruit 55 to 60 days post-pollination. Seed from each fruit was bulked in this and subsequent experiments, and these bulks were designated as progeny seed lots. Correlations between seed weight and seed length and width were examined by weighing and measuring seeds from randomly selected progeny lots.

In the field, plants were arranged in a randomized complete block design with four replications under field nursery conditions where treatment rows 6.1 m long were spaced 1.5 m apart, and between plant spacing in each plot was approximately 0.12 m. Plants were allowed to random mate and supplemental irrigation was used along with standard cultural practices. Mature fruits from the innermost plants of each treatment plot were randomly selected for seed extraction. Uniform fruit with a white or yellow epidermis was selected for evaluation. Greenhouse and field derived seed was extracted and allowed to soak in their mesocarp tissue for 24 h. The seed was then dried for 3 to 4 days at 28 °C and held at 24 °C until seed weight measurements were taken. For each treatment 20 to 50 seeds were weighed and data expressed as a function of g per 1,000 seeds.

Experiment 2. Since the seed size of the *hardwickii* collection LJ 90430 (P_{10}) is significantly smaller than PI 215589 (P_2) (Globerson et al. 1985), LJ 90430 was mated with the *sativus* inbred line WI 2808 (P_{12}) to produce F_1 and F_2 families. The seed-size variation found in these families provides genetic information on *hardwickii* collections with smaller seed sizes.

Seed of P_{10}, P_{12} and their F_1 progenies was planted in an isolation cage approximately 0.24 m apart in rows which were on 0.92 m centers to produce F_1 and F_2 families. Bees were placed in each cage during flowering to assure adequate pollination and seed was harvested as described above.

Experiment 3. Introductions of *hardwickii* differ in their growth habits, and leaf and stem anatomy (Schuman et al. 1985), and combining ability for several horticulturally important characters (Kupper 1984). Therefore, progenies of F_1 families developed from crosses between *hardwickii* germplasm having a wide range of seed sizes and several *sativus* lines were used to provide additional information regarding the inheritance, dominance relationships, and the range of seed weight in the accessions used. The *hardwickii* lines used had been maintained by self pollination for several generations. A North Carolina Design II mating scheme was used to produce F_1 families in which three *sativus* cucumber inbreds (P_3 = GY-14; P_4 = WI 1379; P_5 = WI 1909) and seven *hardwickii* collections (P_2, P_6 = PI 462369; P_7 = 486336; P_8 = LJ 91176; P_9 = 273469; P_{10} = LJ 90430; P_{11} = PI 187367) were used as maternal and paternal parents, respectively. Seeds of F_1 resulting from the design II mating scheme were planted at Hancock, Wisconsin, in a randomized complete block design with six replications. In each block, nine individuals of each cross were spaced 1.5 m within a row (plot), and parallel rows were on 1.5 m centers. The outermost plants in a row were designated as plot borders and mature fruits from random mated plants were collected from the seven innermost plants of a plot or row. Fruits were collected and seed extracted as described above.

Data analysis

Analysis of the standard deviations of all generations indicated that a quadratic relationship existed between means and standard deviations. Therefore an inverse transformation of the data (x to 1/x) was performed. Since transformations of data resulted in an increase in variance homogeneity within generations, analyses of transformed data are presented. The transformed seed weights have biological meaning since they represent the number of seed in unit weight (seeds/g).

Statistical analyses were conducted according to Kotecha and Zimmerman (1978) resulting in estimates of broad sense heritability (h^2), degree of dominance h_1 and h_2. These estimates were obtained using the following formulae:

$$h^2 = \frac{S^2_{F_2} - 1/3\,(S^2_{P_1} + S^2_{P_2} + S^2_{F_1})}{S^2_{F^2}},$$

where $S^2_{F_2}$, $S^2_{P_1}$, $S^2_{P_2}$, and $S^2_{F_1}$ are the estimates of variability among plants within each generation.

Except in $P_1 \times P_2$ field experiment where large $S^2_{F_2}$ values were obtained, parameters were estimated as:

$$h^2 = \frac{S^2_{F_2} - 1/2\,(S^2_{P_1} + S^2_{P_2})}{S^2_{F_2}},$$

$$h_1 = \frac{\bar{F}_1 - \overline{MP}}{\overline{HP} - \overline{MP}} \quad \text{and,}$$

$$h_2 = \frac{2\,(\bar{F}_2 - \overline{MP})}{\overline{HP} - \overline{MP}},$$

where MP = midparent and HP = high parent.

Two methods of analysis were used to study the nature of gene action. One method calculates arithmetic, geometric and observed F_2 means (Burton 1951) while the other estimates of the base population mean (m) and additive (a) and dominance (d) effects from variances using a Mather-Hayman analysis (Mather and Jinks 1977). The theoretical arithmetic and geometric F_2 means were calculated as follows:

$$\text{Theoretical Arithmetic } \bar{F}_2 = \frac{\bar{P}_1 + 2\,\bar{F}_1 + \bar{P}_2}{4};$$

$$\text{Theoretical Geometric } \bar{F}_2 = \text{Antilogarithm of log } \frac{\bar{P}_1 + 2\log \bar{F}_1 + \log \bar{P}_2}{4}.$$

Employing this analysis, one can compare observed and calculated F_2 means, thus obtaining estimates of gene action. While 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.

Least squares estimates weighted by the inverse 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 based on three parameters was tested on data obtained from field grown populations resulting from initial parental matings of $P_{12} \times P_{10}$, by chi-square analysis with 1 degree of freedom. Where several replicates of F_1, F_2, and BC progenies (i.e., from P_1 and P_2 matings) were available, fit to the genetic model was evaluated 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).

Table 1. Mean ($\bar{X}$), standard deviation (SD) and range of seed weights (g/1,000 seeds) of a *Cucumis sativus* var. *sativus* line (WI 1606) and a *C. sativus* var. *hardwickii* collection (PI 215589) and progeny derived from matings between these varieties. Analyses of transformed (1/x) data presented

Generation	Pedigree[c]	No. of[b] seed lots tested		Seed wt (g/1,000 seeds)[a]					
				Greenhouse			Field		
		GH	FLD	$\bar{X}$	SD	Range	$\bar{X}$	SD	Range
P_1	WI 1606 (Cs)	18	20	44.4	6.9	34 – 59	37.0	5.3	30 – 47
P_2	PI 215589 (Ch)	36	12	77.8	4.4	67 – 91	96.0	9.0	91 – 111
F_1	$P_1 \times P_2$	27	27	49.2	7.3	40 – 67	56.4	11.3	43 – 91
F_1	$P_2 \times P_1$	22	33	45.9	4.6	37 – 53	55.8	11.7	43 – 91
F_2	$(P_1 \times P_2)^2$	23	27	53.0	10.4	40 – 91	53.2	8.8	40 – 67
F_2	$(P_2 \times P_1)^2$	15	29	49.3	6.7	40 – 67	55.4	8.4	40 – 77
BC_1	$P_1 \times (P_1 \times P_2)$	24	28	46.4	8.3	37 – 67	41.1	3.9	34 – 48
BC_1	$(P_1 \times P_2) \times P_1$	8	30	49.0	7.0	37 – 59	40.9	4.3	34 – 53
BC_1	$(P_2 \times P_1) \times P_1$	15	33	44.4	7.1	34 – 59	45.5	1.1	37 – 51
BC_1	$(P_2 \times P_1) \times P_2$	7	22	59.9	3.0	59 – 67	73.2	1.2	53 – 91

[a] $\bar{X}$ = mean, SD = standard deviation

[b] GH = greenhouse grown; FLD = field grown, where between 20 to 50 seeds of each lot were tested. Bulked seed from individual fruits are regarded as a seed lot

[c] CS = *C. sativus* var. *sativus*; Ch = *C. sativus* var. *hardwickii*

The number of factors or loci involved was estimated using the methods of Castle and Wright (1921) and Burton (1951; according to Wright) which involve the following formulae, respectively:

$$n = \frac{(P_1 - P_2)^2}{8\,(S^2_{F_2} - S^2_{F_1})},$$

where $S^2_{F_2}$ and $S^2_{F_1}$ are variances among respective F_2 and F_1 progenies.

$$n = \frac{0.25\,(0.75 - h + h^2)\,D^2}{S^2_{F_2} - S^2_{F_1}},$$

where

$$h = \frac{\bar{F}_1 - \bar{P}_1}{\bar{P}_2 - \bar{P}_1}, \quad \text{and } D = \bar{P}_2 - \bar{P}_1$$

in which $P_1 = \bar{X}$ of smaller parent and $P_2 = \bar{X}$ of larger parent (Kotecha and Zimmerman 1978).

Results and discussion

Relationships among seed characteristics

Data obtained from greenhouse grown progeny lots of P_1 and P_2 matings were used to measure the correlated response of seed weight with seed width and length. Correlations between these parameters were relatively high (r = 0.73 to 0.79, where *n* = 68). It seems that any one of these parameters could be a useful descriptor in identifying differences among progeny lots.

Dominance relationships and cytoplasmic maternal influence

Experiment 1. The transformed (1/x) seed weights of P_1, P_2, and their F_1, F_2, and BC progenies produced under greenhouse and field conditions are given in Table 1. Seed weights of the *hardwickii* parent (PI 215589; 67–111 g/1,000 seeds) were less than that of the *sativus* parent (WI 1606; 30–59 g/1,000 seeds). The mean weight of greenhouse produced seed of the *hardwickii* parent (PI 215589) was greater than mean seed weights obtained from field grown plants. The converse was true of the *sativus* parent.

Mean seed weights of reciprocal F_1 progenies of $P_1 \times P_2$ grown under greenhouse and field conditions were similar to the *sativus* parent. Mean seed weights of BC_1 progeny derived when *sativus* was used as the recurrent parent approximated parental *sativus* values. Mean seed weights of those BC_1 progeny obtained using the *hardwickii* recurrent parent approached but did not attain seed weights expressed by the *hardwickii* parent.

Although significant differences between reciprocals occurred among some F_1 seed lots (frequency data not presented), the overall lack of differences was more striking than was their presence (Table 1). Seed weight differences were not evident in reciprocal F_2 progeny seed lots.

Experiment 2. The mean seed weight of 28 F_1 progeny lots (83 g/1,000 seeds) resulting from $P_{12} \times P_{10}$ matings was closer to the mean of P_{12} (WI 2808; 42 g/1,000 seeds) than to P_{10} (LJ 90430; 155 g/1,000 seeds). The mean seed weight of 31 F_2 progeny lots was 80.0, ranging from 59 to 111 g/1,000 seeds.

Table 2. Mean ($\bar{X}$) and standard deviation (SD) of seed weight (g/1,000 seeds) of F_1 progenies between three cultivars of *Cucumis sativus* var. *sativus*, and seven *C. sativus* var. *hardwickii* collections at Hancock, WI, 1983. Analysis of transformed (1/x) data presented

S. sativus var. *hardwickii* collections	*C. sativus* var. *sativus* – Inbred parents						Grand mean [a]
	F_1 seed wt (g/1,000 seeds)						
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	
	GY-14 (P_3; 32.5)		WI 1379 (P_4; 32.5)		WI 1909 (P_5; 33.8)		
PI 462369 (P_6; 83.3) [b]	52.1	4.3	51.5	9.0	45.5	3.3	49.5 A
PI 215589 (P_2; 98.0)	49.8	6.2	48.8	2.9	49.3	2.4	49.3 A
PI 486336 (P_7; 98.0)	52.0	4.1	59.9	3.2	55.6	5.6	55.9 B
LJ 91176 (P_8; 113.6)	69.4	10.6	61.7	4.2	62.9	6.3	64.5 C, D
PI 273469 (P_9; 125.0)	69.9	7.3	60.6	2.9	58.5	7.2	62.5 C
LJ 90430 (P_{10}; 178.6)	82.0	8.7	71.4	7.1	69.9	7.8	74.1 E
PI 187367 (P_{11}; 166.7)	71.4	8.2	74.6	7.2	70.4	3.5	72.5 D, E
Grand mean	61.7 A		59.9 A		57.5 A		59.9

[a] Mean separation within column or row by Waller-Duncan's K-ratio *t*-test, K = 100

[b] Parental designation and mean seed weight (g/1,000 seeds); means represent values obtained from six, seven plant replications in which bulked seed from individual fruits are regarded as a seed lot

Experiment 3. Data of F_1 progenies indicate the variable nature of *hardwickii* accessions for seed weight. Mean seed weights of F_1 progenies resulting from matings between P_2 and three other *sativus* lines (P_3, P_4, and P_5) were closer to the mean weights of the *sativus* parents (Table 2). Similar results were recorded for mean seed weight in F_1 progenies resulting from crosses between *hardwickii* P_6 through P_{11} and the above three *sativus* lines. These data and those of experiments 1 and 2 reflect the dominance of genes of the *sativus* parent for seed weight.

Genetic estimates

Seed weights like those of the *hardwickii* parent were not observed in F_2 progeny lots or in BC_1 families using *sativus* as the recurrent parent. Moreover, when considering all matings and growing environments the range of F_2 progeny classes was considerably narrower than would have been predicted based on individual plant. Only in BC_1 families where *hardwickii* was used as the recurrent parent were progeny obtained with *hardwickii*-like seed weight characteristics. As a consequence, broad-sense heritability estimates for this complex trait were relatively high (Table 3): 54%, 26%, and 56% for greenhouse grown $P_1 \times P_2$ and field grown $P_1 \times P_2$ (experiment 1) and $P_{10} \times P_{12}$ (experiment 2), respectively. These estimates reflect the seed size differences among parents.

The estimated number of factors or loci involved in the expression of this trait ranged from 10 to 13, depending on the method of calculation. Negative values for the number of factors were obtained using data from $P_1 \times P_2$ cross progenies grown in the field, indicating that seed weight is a complex trait not amenable to the simplifying assumptions needed for factor number calculations.

Least square estimates of the contribution of additive and dominance effects indicate that both were important in the expression of seed weight in $P_1 \times P_2$ and $P_{10} \times P_{12}$ progeny produced in the greenhouse and field, respectively. The similarity in seed weights of the F_2 progeny means from initial $P_1 \times P_2$ matings and mean values that are close to the calculated arithmetic means (Table 3) of seed produced in the greenhouse and the field indicate that additive effects contribute to the observed variation. In contrast, the observation that the F_2 progeny seed weights of $P_{10} \times P_{12}$ were close to the calculated geometric mean, suggests nonadditive factors may also be important in the expression of this trait. This may be due either to parental genotypic differences conditioning seed weight or to pleiotropic effects.

Data from this study suggests that heritable seed weight differences exist between *sativus* and *hardwickii* and that these differences are conditioned at least in part by multigenic additive factors. The presence of additive gene effects suggests that selection for seed weight may be effective in populations derived during early cycles. Breeding strategies could be devised in later generations which would utilize the observed nonadditive components. Furthermore, since seed weight differences among and between these botanical varieties were characterized, studies could be directed towards identifying potential associations between this

Table 3. Various genetic estimates which explain the variation in seed weight observed in progenies resulting from *Cucumis sativus* var. *sativus* and *C. sativus* var. *hardwickii* matings. Analysis of transformed (1/x) data presented

	Mating series[a] and production location		
	$P_1 \times P_2$ (Greenhouse)	$P_1 \times P_2$ (Field)	$P_{10} \times P_{12}$ (Field)
Broad-sense heritability % (h^2)[b]	54	26	56
Degree of dominance (h_1)	− 0.81	− 0.32	− 0.28
Degree of dominance (h_2)	− 1.27	− 0.83	− 0.59
Arithmetic mean F_2	54.3 ± 0.6	61.2 ± 1.0	90.8 ± 1.4
Geometric mean F_2	57.8 ± 0.9	57.7 ± 1.3	81.9 ± 1.4
Observed mean F_2	51.0 ± 1.4	54.3 ± 1.1	82.0 ± 2.6
Minimum no. (*n*) of genetic factors[c]	11	− 18.0	12
Minimum no. (*n*) of genetic factors	10	− 18.1	13
Base population mean (m)	60.9 ± 1.2	63.4 ± 2.4	96.1 ± 6.4
Additive effect (d)	16.4 ± 1.2	30.5 ± 2.2	54.7 ± 6.6
Dominance effect (h)	14.6 ± 1.8	12.4 ± 4.2	14.2 ± 8.1
Lack-of-fit (significance)	n. s.	n. s.	n. s.

[a] P_1 = WI1606, P_2 = PI215589, P_{10} = LJ90430, P_{12} = WI2808

[b] After inverse transformation

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

and other traits of horticultural significance. If a positive genetic correlation exists between progeny lots with *hardwickii*-like seed weights and the potentially useful traits of *hardwickii*, such as multiple branches and fruit production, then selection among segregating populations might be effective. In this way there might be an opportunity to use seed weight as a selection parameter in plant improvement programs.

References

Burton GW (1951) Quantitative inheritance in pearl millet (*Pennisetum glacum*). Agron J 43:409–417

Castle WE, Wright SA (1921) An improved method of estimating the number of blending inheritance. Science 54:223

Della Vecchia P (1982) Inheritance of short-day responses to flowering and of some fruit characteristics in crosses between *Cucumis sativus* var. *hardwickii* (R.) Alef. and *Cucumis sativus* L. lines. PhD Thesis, University of Wisconsin, Madison

Dickson MH (1980) Genetic aspects of seed quality. Hort Science 15:771–773

Edwards MD (1983) Evaluations of genetic control, selection procedures and responses to selection for improved emergence of compact cucumbers. PhD Dissertation, University of Wisconsin, Madison

Globerson D, Genizi A, Staub JE (1985) Inheritance of seed weight in cucumber. Hort Science 20:28

Horst EK (1977) Vegetative and reproductive behavior of *Cucumis hardwickii* and *Cucumis sativus* as influenced by photoperiod, temperature and planting density. MS Thesis, North Carolina State University, Raleigh

Kotecha A, Zimmerman LH (1978) Inheritance of seed weight pappus and striped hull in safflower species. Crop Sci 18: 999–1002

Kupper RS (1984) Evaluation of combining ability between lines of *Cucumis sativus* L. and *Cucumis hardwickii* (R.) Alef. MS Thesis, University of Wisconsin, Madison

Mather K, Jinks JL (1977) Introduction to biometrical genetics. Cornell University Press, Ithaca, New York

Niehuis J (1982) Response to different selection procedures for increased fruit yield in two pickling cucumber populations. PhD Thesis, University of Wisconsin, Madison

Schuman DA, Staub JE, Struckmeyer BE (1985) Morphological and anatomical comparisons between two botanical varieties of *Cucumis sativus: Hardwickii* and *sativus*. Cucurbit Genet Coop Rep 8:15–17

Staub JE, Globerson D (1984) The inheritance of seed dormancy in the *C. sativus* var. *hardwickii* (Royle) Kitamura, PI 215589. Hort Science 19:561