Genetic Analysis of Yield Components in Cucumber at Low Plant Density

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ABSTRACT. Plant architecture can be manipulated in cucumber (*Cucumis sativus* L.) to provide an array of phenotypes. Determinate, multiple-lateral plants are unique because they afford an opportunity to increase fruit yield per plant. Estimates of genetic variances, numbers of genetic factors, and genotypic and phenotypic correlations between traits were made in a population, segregating for sex expression, leaf size, and plant habit at low plant density ($\approx 19,000$ plants/ha). Replicated evaluation of 100 F_3 families derived from an initial mating between a gynoecious, determinate, moderately branched line (G421) and a monoecious, indeterminate, multiple lateral branching line ('H-19') indicated that mainstem length and multiple lateral branching exhibit mostly additive genetic variance. For sex expression, additive and dominant genetic variances were important. The minimum number of genetic factors controlling sex expression, number of lateral branches, and mainstem length were estimated at five, four, and eight, respectively. Phenotypic and genotypic correlations between traits indicated that relative leaf size may influence fruit mass while having only limited influence on the number of fruit produced per plant. The amount and type of genetic variation suggests that the development of an array of determinate, multiple-lateral branching plant types with varying sex expression and plant stature is possible.

Average yield in processing cucumber (*Cucumis sativus*) has increased from ≈ 4076 kg·ha⁻¹ in 1920 to 12,550 kg·ha⁻¹ in 1980 [U.S. Dept. of Agriculture (USDA), 1940, 1981]. This increase in yield was primarily due to improved cultural practices, incorporation of disease resistance genes, and the accumulation of yield genes in elite breeding lines (Peterson, 1978; Wehner, 1989; Wehner and Cramer, 1996). Although newly released hybrids under replicated trials have shown steady increases in yield in some locations (Wehner, 1989), the average commercial yield has remained relatively constant in the last 15 years [$\approx 13,200$ kg·ha⁻¹ in 1991; USDA, 1992].

Standard cucumber processing cultivars are monoecious (bearing staminate and pistillate flowers) and indeterminate (*De*). Although such genotypes typically produce at least 20 nodes before first harvest, they seldom produce more than two fruit per harvest (Miller and Hughes, 1969). Most cucumber cultivars possess one to two primary lateral branches originating from the mainstem. A few cultivars produce secondary lateral branches (originating from primary lateral branches) under some growing conditions. In addition to such traits, which are under polygenic control, a wide range of plant characters exist in cucumber that are conditioned by single genes. These genes can be combined to produce an array of phenotypes (Pierce and Wehner, 1990). For example, the breeding lines AR 79-75 and the related cultivar H-19 have the little leaf (*ll*) trait as well as an indeterminate habit, multiple lateral branches, and simultaneous fruiting not present in standard commercial processing cucumber types (Goode et al., 1989; Plant Variety Protection Certificate, 1993).

About 35% of the total cucumber production areas in the United States is devoted to machine harvest (personal communication, R. Hentschel). For once-over mechanical harvesting, plants should possess uniform, early flowering characteristics. Determinate (*de*) plant types have a concentrated time span for fruit set, and fruit are typically borne close to the center of the row, thus allowing for precision in determining optimal harvest time and easiest harvest (George, 1970; Kaufman and Lower, 1976). Gynoecious (bearing all pistillate flowers), determinate types can provide for a uniform, early, concentrated fruit set (Lower et al., 1983; Nienhuis et al., 1984; Prend and John, 1976).

Determinate and indeterminate gynoecious and monoecious cucumber lines that possess multiple lateral branching are being developed for use in hybrid production and population development (Staub and Crubaugh, 1995a). Gain from selection during population improvement depends on the magnitude of heritability and the selection differential imposed (Falconer, 1989). A knowledge of genetic characteristics for quantitatively inherited traits, along with their genotypic and phenotypic trait correlations, is critical for the development of gynoecious, determinate, multiple-lateral plant types. Therefore, a cucumber population segregating for sex expression, leaf size, and plant habit was developed 1) to estimate the kinds and amounts of genetic variances of traits potentially important for once-over harvest, 2) to estimate the minimum number of genetic factors involved in controlling these traits, and 3) to define genotypic and phenotypic correlations among the traits examined. Such information would provide genetic information for the tactical assessment of populations containing unique cucumber genotypes.

Materials and Methods

GERMPLASM. The gynoecious, determinate cucumber line G421, possessing normal-sized leaves, was crossed with the monoecious, indeterminate, little-leaf line 'H-19'. G421 was received from R. L. Lower, Univ. of Wisconsin, and 'H-19' is a line released by the Univ. of Arkansas, Fayetteville. G421 typically produces one to two fruit per harvest on one or two lateral branches originating

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from the mainstem. In contrast, 'H-19' produces five to 20 branches, depending on growing environment, and possesses a simultaneous sequential fruiting habit (i.e., several fruit enlarge on a lateral branch). The F_1 subsequently was self-pollinated to produce F_2 progeny and 100 F_3 families.

EXPERIMENTAL DESIGN. Parental lines and F_1 and F_3 progeny were evaluated in Hancock, Wis., in Plainfield loamy sand (Typic Udipsament; sandy mixed, mesic) and in Tifton, Ga., in loamy sand (Ultisol Plintic Paleoedults: fine loamy silicious, thermic). Genotypes were arranged in a randomized complete-block design with three replications at each location. Each replication consisted of 15 plants spaced 0.7 m apart in rows positioned on 1.5-m centers. This plant density was chosen because it provided a manageable and unbiased appraisal of the traits measured. This data set also is being used for genetic map construction and quantitative and qualitative trait analysis using molecular marker loci (Serquen et al., 1997).

DATA COLLECTION. Data were collected on days to anthesis, sex expression, leaf size, number of lateral branches originating from the mainstem, length of the mainstem, fruit number and mass, fruit length and diameter, and fruit length : diameter ratio (L:D) was calculated. While the classification of sex expression, number of lateral branches, and mainstem length were made on individual plants, data of other traits were taken collectively per replication. Plants were harvested once when $\approx 10\%$ of the fruit on plants within a replication were ≥ 40 mm in diameter (75 and 71 d after planting in Wisconsin and Georgia, respectively).

The number of days to anthesis was taken as the days from planting to the stage when at least three plants per plot had reached anthesis. Sex expression was recorded as the fraction of pistillate nodes in the first 10 flower-bearing nodes. Data were collected on the first 10 plants of each replication. A node was considered pistillate if it had at least one pistillate flower.

The number of laterals on the mainstem and the mainstem length were recorded on the first 10 plants in each plot. The first node was taken as that node above the cotyledonary node. Lateral count was taken 2 d before harvest, and mainstem length was taken at harvest.

Fruit length, diameter, and L:D were determined at harvest by measuring five randomly selected fruit from each plot that were > 35 mm in diameter.

One week before harvest, plants were classified as little, standard, or intermediate leaf types by visual examination. Extreme

parental leaf types were easily separated by general inspection (little-leaf area of the first fully expanded leaf = 30 to 40 cm² and standard-leaf area = 80 to 100 cm²; Staub et al., 1992). If a family was homogeneous for one leaf type it was considered homozygous [class 1 (little) or 3 (standard)] for the genetic analyses. Where there were intermediate-leaf size phenotypes (leaf area of first fully expanded leaf = about 50 to 70 cm²) in a plot along with parental phenotypes, the family was considered segregating (heterozygous; class 2).

ANALYSIS OF VARIANCE (ANOVA). To improve normality for the analysis of variance, sex expression data (x) were transformed using $(x + 0.5)^{1/2}$ due to small numbers that included zero values. The ANOVA was performed according to the following linear model: $Y_{ijk} = \mu + G_i + L_j + R_{k(j)} + (GL)_{ij} + e_{ijk}$, where μ is the common effect, G_i the genotypic effect, L_j the location effect, $R_{k(j)}$ the k th replication effect within j th location, $(GL)_{ij}$ the genotype by location interaction effect, and e_{ijk} the residual effect (Table 1). All effects were considered random. The G_i effect was subdivided into "among and within entries" genotypic effects. The among entries effect was partitioned into 1) generation effects, which included the parental (P1 and P2), hybrid (F_1) and F_3 generations and 2) the F_3 family effect (f_n), with their respective location interactions (Table 1). The within entries effects were divided into that due to heterogeneous (F_3 family) and homogeneous (P1, P2, and F_1) generation effects. Partitioning among and within entries, as previously described, allowed for the estimation of genetic variances and narrow-sense heritabilities. For those traits where individual progeny values were not recorded, the within sources of variation (Table 1) could not be evaluated, and, therefore, this source of variation was not considered in the ANOVA. ANOVA as well as mean comparisons were performed using PROC GLM (Type III; all effects considered random) of SAS/STAT (SAS Institute, 1988). Mean comparisons among generations for all traits were performed using least significant difference (LSD) tests.

GENETIC ANALYSES The F_3 population was derived by crossing two homozygous and homogeneous inbred lines (less than F_{10}). Gene frequencies at a locus were considered to be equal in the F_2 generation from which F_3 families were derived ($p = q = 0.5$). Expected genetic components of variances for the different types of generations produced by crossing two inbred lines were applied to this analysis (Mather and Jinks, 1977). The estimation of genetic characteristics involved comparisons of variances among parental lines and F_1 and F_3 progeny (Table 1). Family data allowed for the

estimation of two sources of genetic variation present in the F_3 generation: 1) variation among F_3 progeny means ($\sigma_g^2 F_3$) and 2) mean variation of F_3 progenies ($\sigma^2 F_3$). The variance among F_3 progeny means ($\sigma_g^2 F_3$) can be calculated and is equivalent to $\sigma_g^2 F_3 = \sigma_A^2 + 1/4 \sigma_D^2$, where σ_A^2 and σ_D^2 denote additive and dominance variances, respectively. The mean variance of F_3 families ($\sigma^2 F_3$) was calculated as the variation within progenies and has an expectation of $\sigma^2 F_3 = 1/2 \sigma_A^2 + 1/2 \sigma_D^2$. The values for the estimation of these variances were obtained from the ANOVA (see Table 1) as follows: $\sigma_g^2 F_3 = (M_{42} - M_{32})/RL = \sigma_A^2 + 1/4 \sigma_D^2$ and

Table 1. Analysis of variance of two inbred cucumber parents, their F_1 hybrid, and 100 F_3 families tested in two environments.

Source	Statistical parameters ^a		
	DF	MS	EMS
Locations (L)	L-1		
Replications (R)/L	L(R-1)		
Entries	N-1	M_4	
Among generations (G)	G-1	M_{41}	$\sigma^2 + r\sigma_{LG}^2 + rl\sigma_g^2$
Among F_3 families (F)	F-1	M_{42}	$\sigma^2 + r\sigma_{LF}^2 + rl\sigma_g^2 F_3$
Loc $\times$ entries	(L-1)(N-1)	M_3	
Among generations	(L-1)(G-1)	M_{31}	$\sigma^2 + r\sigma_{LG}^2$
Among F_3 families	(L-1)(F-1)	M_{32}	$\sigma^2 + r\sigma_{LF}^2$
Error	L(R-1)(N-1)	M_2	σ^2
Total	LRN-1		
Within	LRN(K-1)	M_1	
F_3 families	LRF(K-1)	M_{12}	$\sigma^2 we + \sigma^2 F_3$
Homogeneous entries	LRH(K-1)	M_{11}	$\sigma^2 we$

^aDF = degrees of freedom, MS = mean square, EMS = error mean square.

Table 2. Analysis of variance for mainstem length, sex expression, and number of lateral branches per plant in cucumber (recorded in two locations).

Source	Mainstem length ²			Sex expression ²			No. lateral branches ²		
	DF	SS	MS	DF	SS	MS	DF	SS	MS
Location (Loc)	1	80.5587	80.5587**	1	3.8334	3.8334**	1	0.5355	0.5355
Replication (Loc)	4	10.8539	2.7135**	4	0.2653	0.0663**	4	30.012	7.503**
Entries	102	1384.453	13.5731**	102	23.3584	0.2584**	102	326.849	3.2044**
Among generations	3	63.0603	21.0201**	3	17.4709	5.8236**	3	43.592	14.531**
Among F ₃	99	1321.393	13.3474**	99	5.8839	0.0594**	99	283.257	2.8612**
Loc × entries	96	256.9448	2.6765	96	1.2796	0.0133*	96	49.6687	0.5174
Among generations	3	35.0737	11.6912	3	0.1018	0.0339*	3	13.6994	4.5665
Among F ₃	93	221.8711	2.3857	93	1.1778	0.0127	93	35.9693	0.3868
Error	378	809.2199	2.1408	381	3.9373	0.0103	377	211.234	0.5603
Within entries	4163	2743.177	0.6589	4804	34.1531	0.0071	4821	763.855	0.1584
Homogeneous	142	65.0915	0.4584	154	0.0646	0.0004	154	18.1212	0.1177
F ₃	4021	2678.085	0.66602	4650	34.0885	0.0073	4667	745.734	0.1598
CV (%)		13.7			10.5			21.6	

²DF = degrees of freedom, MS = mean square, EMS = error mean square.

*,** Significant at $P \leq 0.05$ and 0.01 , respectively.

$\sigma^2 F_3 = M_{12} - M_{11} = 1/2 \sigma^2_A + 1/2 \sigma^2_D$. These two equations permitted the estimation of additive (σ^2_A) and dominance (σ^2_D) genetic variances (Hallauer and Miranda, 1988).

The variance (Var) of these genetic parameters were obtained using the formulae: $\text{Var}(\sigma^2_A) = (128/324) [M^2_{42}/F + 1 + M^2_{32}/(L - 1)(F - 1) + 2] + 32/36 [M^2_{12}/LRF(K - 1) + 2 + M^2_{11}/LRH(K - 1) + 2]$ and $\text{Var}(\sigma^2_D) = 2048/144 [M^2_{12}/LRF(K - 1) + 2 + M^2_{11}/LRH(K - 1) + 2] + 512/1296 [M^2_{42}/F + 1 + M^2_{32}/(R - 1)(F - 1) + 2]$, where L = number of locations, R = number of replications, F = number of F_3 progenies; and K = number of individuals per plot. The ses of each genetic variance were estimated as the square root of the respective variances.

The narrow sense heritability (h^2_N) was estimated as: $h^2_N = \sigma^2_A/\sigma^2_P$, where σ^2_P = the phenotypic variance, and is estimated as $\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2_{GL} + \sigma^2$ (over locations), where $\sigma^2_{GL} = (M_{32} - M_2)/R$, $\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2$ (for each location), and σ^2 = error variance.

The SE of the heritability estimates were calculated as $\text{SE}(h^2_N) = \text{SE}(\sigma^2_A)/\sigma^2_P$.

Broad sense heritabilities (h^2_B) were estimated for days to flowering, leaf size, number of fruit per plant, mass of fruit per plant, fruit length, fruit diameter, and L:D. Since data for these traits were recorded as F_3 progeny means, only total genotypic and phenotypic variances were calculated, using the formulae $\sigma^2_G = \sigma^2_F = M_{42} - M_2/RL$, (from Table 1), where R = number of replications, and L = number of locations, such that $\sigma^2_P = \sigma^2_G + \sigma^2_{GL} + \sigma^2_E$, and $h^2_B = \sigma^2_G/\sigma^2_P$.

When a family × location interaction was significant for a trait, the ANOVA and estimation of h^2_B was performed separately for each location.

Phenotypic correlations were calculated from F_3 family trait means. Genotypic correlations (r) were calculated using the formulae: $r = \sigma_{xy}/(\sigma^2_x \times \sigma^2_y)^{1/2}$ and $\sigma_{xy} = 1/2[\sigma(x+y) - (\sigma^2_x + \sigma^2_y)]$, where σ^2_x , σ^2_y , and σ_{xy} are the total genetic variances (σ^2_G) and covariances for the traits x and y , respectively. For those traits that exhibited significant genotype × environment interaction, phenotypic and genotypic correlations were performed separately by location.

ESTIMATION OF MINIMUM NUMBER OF FACTORS. The minimum number or least number of effective factors (n) (Lande, 1981) influencing sex expression, the number of laterals per plant, and stem length was estimated according to Wright (1968) using the

correction factor suggested by Cockerham (1986) as $n = [(P_1 - P_2)^2 - (\sigma^2_{P1} + \sigma^2_{P2})] \div 8 \sigma^2_A$, where P_1 and P_2 are estimates of the mean phenotypic trait value of the parents, σ^2_{P1} and σ^2_{P2} are the estimated error variances of these means, and σ^2_A is the additive genetic variance for the trait.

Results and Discussion

ANOVA. Significant variation ($P \leq 0.01$) between locations was detected for all traits, except number of laterals per plant. The means for number of pistillate nodes in 10 nodes, days to anthesis, mainstem length, number and mass of fruit, and fruit length and mass were all higher in Georgia than in Wisconsin. Significant differences also were recorded among families for all traits (Table 2).

The coefficients of variation (cv) for sex expression (Georgia = 12.3%, Wisconsin = 8.8%), days to anthesis (Georgia = 1.4%, Wisconsin = 3.6%), mainstem length (Georgia = 15.2%, Wisconsin = 12.5%), and fruit length (Georgia = 5.8%, Wisconsin = 8.2%) and diameter (Georgia = 4.6%, Wisconsin = 7.1%) were relatively low. The cv for number of lateral branches (Georgia = 22.6%, Wisconsin = 20.7%), leaf size (Georgia = 12.8%, Wisconsin = 24.4%), and fruit number (Georgia = 18.3%, Wisconsin = 17.6%) and mass (Georgia = 17.6%, Wisconsin = 19.1%) was comparatively larger.

There were location × entry interactions for most traits examined, except leaf size, number of laterals per plant, mainstem length, and fruit count per plant. However, most of these interactions were due to differences in magnitude and not to change in rank. Thus, data are presented as averages across locations.

GENERATION MEANS. Plants of G421 were more gynoeious, slightly later flowering, less branching, shorter, and produced more and heavier fruit than 'H-19' plants (Table 3). Although no differences between G421 and 'H-19' were detected in fruit length, the fruit diameter of 'H-19' was smaller, and thus the L:D of 'H-19' fruits was larger than those of G421.

If sowing occurs during the first 2 weeks of June in Wisconsin, 'H-19' flowers ≈ 10 to 14 d later than G421 (unpublished data). The delayed flowering in other *C. sativus* cultivars, plant accessions, and lines (but not necessarily in 'H-19') is due to a photoperiodic (short day) response (Della Vecchia and Peterson, 1984; Shiffriss and George, 1965). The similarity in flowering date between 'H-

Table 3. Means of locations and generations for traits in cucumber evaluated in two environments.

	Sex expression	Leaf size	Days to flower	No. laterals/plant	Main stem length	No. fruit/plant	Mass fruit/plant	Fruit length (L)	Fruit diam. (D)	Fruit L : D
Location										
Georgia	0.19 a ^z	1.70 a	34.21 a	3.10 a	38.02 a	2.78 a	1.69 a	5.47 a	2.15 a	2.59 a
Wisconsin	0.11 b	1.90 b	29.80 b	3.21 a	33.60 b	2.18 b	0.61 b	4.74 b	1.74 b	2.62 a
LSD _{0.05}	0.01	0.11	0.09	0.06	0.12	0.05	0.04	0.03	0.02	0.02
CV (%)	10.5	19.5	2.65	21.6	13.7	18.04	19.0	6.97	5.8	4.8
Generation										
P1 (G421)	0.96 a	1.0 c	34.33 a	0.96 c	22.67 b	2.1 b	0.95 b	4.8 b	2.18 a	2.26 b
P2 (H19)	0.04 c	3.0 a	31.68 b	6.30 a	43.22 a	1.8 b	0.41 c	4.9 b	1.79 c	2.60 a
F ₁	0.96 a	1.1 c	30.03 c	2.89 b	41.52 a	4.0 a	2.05 a	5.5 a	2.07 ab	2.67 a
F ₃	0.14 b	1.8 b	31.98 b	3.12 b	35.83 a	2.5 b	1.14 b	5.1 ab	1.94 bc	2.61 a
LSD _{0.05}	0.04	0.6	0.396	0.25	0.54	0.41	0.18	0.4	0.07	0.27

^zMean separation within columns by least significant difference test at $P \leq 0.05$.

Table 4. Narrow-sense heritability (h^2_N), additive and dominance genetic variances, and minimum number of factors for mainstem length, number of laterals per plant, and sex expression in cucumber.

Parameter ^z	Mainstem length	No. lateral branches	Sex expression	
			Georgia	Wisconsin
σ^2_A	2.297 ± 0.426	0.522 ± 0.286	0.0046 ± 0.0025	0.0049 ± 0.002
σ^2_D	-1.88 ± 0.42	-0.437 ± 0.009	0.0136 ± 0.0026	0.0184 ± 0.002
h^2_N	0.52 ± 0.04	0.48 ± 0.08	0.14 ± 0.01	0.16 ± 0.04
n	8	4	5	5

^z σ^2_A = additive genetic variance; σ^2_D = dominance genetic variance; n = minimum number of factors.

19' and G421 in our study may be due to the relatively late planting (July), which resulted in a flowering response during a shortened photoperiod (e.g., late August in Wisconsin).

The percentage of pistillate flowers in the first 10 nodes was 96% in gynoeious G421 and 4% in monoecious 'H-19'. While there was dominance of the *F* locus for gynoeicy (96%) in the *F*₁ generation, *F*₃ progeny segregated to produce plants with a high proportion of staminate flowers in the first 10 nodes (86%). The lack of fully pistillate nodes in G421 can be explained by the presence of modifying genes, environmental factors affecting the formation of bud primordia, or both (Galun, 1961). The difference in the frequency of pistillate flowers in monoecious and predominately gynoeious line can be explained by a lack of complete dominance at the *F* locus (Shifriss, 1961) or the proposed existence of multiple *F* alleles (Kubicki, 1969).

The relatively long mainstem and L:D typical of 'H-19' was observed in *F*₁ progeny, indicating dominance for these traits in 'H-19'. Although no differences were detected between the parents in number and mass of fruit per plant, hybrid progeny (*F*₁) means were higher than parental means in both locations, thus suggesting a heterotic response. Heterosis for fruit mass and count has been reported in populations developed from North American-adapted cucumber germplasm (Ghaderi and Lower, 1979a, 1979b). Likewise, heterosis for fruit mass also has been detected in cucumber populations derived from unadapted (i.e., exotic) sources (Lower et al., 1982). Although such heterotic effects were not observed by Rubino and Wehner (1986) in lines derived from an open-pollinated pickling cucumber population, the heterotic effects using adapted germplasm in this study (Table 3) agree with those reported by Ghaderi and Lower (1979a, 1979b).

Lower et al. (1982) attributed the heterotic effects observed in their experiments to the diverse parentage used. Mapped randomly amplified polymorphic DNA (RAPD) markers have been used to analyze genetic distances (GD) between G421 and 'H-19' (Staub

et al., 1997). Results using 43 RAPD markers indicate that G421 is more closely related to 'H-19' (GD = 0.65) than to the exotic germplasm *C. sativus* var. *hardwickii* (R) Alef. (hereafter referred to as *C. hardwickii*) [GD_(G421 vs. C. hardwickii) = 0.47]. Therefore, the heterosis observed in this cucumber population may not be solely a function

of the divergence of parental material. In part, heterosis may be due to chromosomal regions present in adapted cucumber that interact (i.e., epistatically) when intercrossed to produce extreme phenotypes. If this is the case, then the identification and characterization of quantitative trait loci (QTLs) responsible for yield heterosis may be worthwhile for continued selection in this population.

GENETIC PARAMETERS. Since data on sex expression, mainstem length, and number of laterals per plant were taken on individual plants, genetic variances and narrow sense heritability (h^2_N) were estimated. As significant variation for genotype $\times$ environment interaction was found for sex expression, variance components were estimated by location. Variance component analysis of sex expression indicated that, in both locations, dominance was the main component of the total genetic variance (Table 4). The magnitude of the dominance variance was ≈ 2.9 and 3.8 times higher than the additive genetic variance in Georgia and Wisconsin, respectively. Evaluation of cross-progeny resulting from matings between elite gynoeious and hermaphroditic lines indicate that additive and nonadditive gene action affected sex expression (El-Shawaf and Baker, 1981). Likewise, sex expression also was found to be conditioned by additive and non-additive genetic effects in wide cucumber crosses (Kupper and Staub, 1988).

Gynoeious sex expression has proven to be unstable even in breeding lines that have been subjected to rigorous selection for gynoeicy (Lower et al., 1983). In our study, narrow sense heritability for gynoeicy was also low in both locations (Georgia = 0.25; Wisconsin = 0.20). The relatively small additive genetic variance associated with this trait combined with potential influence of environment suggest that gain from selection may be slow during population improvement (e.g., mass selection). Rigorous family selection performed under diverse environmental conditions (replications, environments) may allow for a more effective selection of genotypes suitable for mechanized harvesting.

Cucumis hardwickii is cross compatible with *C. sativus* and also

is a potential source of multiple branching and sequential fruiting genes (Horst and Lower, 1978). In a broad-based cucumber population (*C. sativus* × *C. hardwickii*), Lower et al. (1982) found that additive effects were important for producing lateral branches, and dominance effects conditioned mainstem growth. In our study, additive genetic variation was the most important variance component for expressing the number of lateral branches and stem length, and the estimation of the dominance component resulted in negative values (Table 4). Likewise, narrow sense heritability for these traits was high (0.48 and 0.52 for number of lateral branches and stem length, respectively; Table 4). Thus, rapid response to single plant selection for multiple lateral determinate phenotypes might be expected in this population.

Total genetic variance was estimated for days to flowering, number of fruit per plant, mass of fruit per plant, fruit length, fruit diameter, and L:D. These variances were used to estimate broad sense heritabilities (Table 5) and to calculate genotypic correlations (Table 6). Broad sense heritability estimates were relatively low for most traits in both locations. In Georgia, heritabilities ranged from zero (number of fruit per plant) to 0.26 (mass of fruit per plant), while in Wisconsin values ranged from 0.08 (fruit diameter) to 0.40 (fruit length) (Table 5). The low broad-sense heritabilities for fruit yield obtained in our study may be due to the population's narrow genetic base or the influence of environmental factors that may have negated progeny differences. The response to direct selection for traits with low heritability (e.g., fruit number) in this population will likely be slow.

ESTIMATION OF MINIMUM NUMBER OF FACTORS. Minimum number of genetic factors (n) were estimated for sex expression ($n = 5$ in Georgia and Wisconsin), number of laterals per plant ($n = 4$), and mainstem length ($n = 8$). Although the genetic control of lateral branches and mainstem length is not understood, sex expression clearly has been determined by the epistatic interaction of three genes (Galun, 1961). This simplistic model is confounded by genetic background and environmental influences, both of which exert a significant influence on sex expression. In our study, there was a significant genotype × location interaction detected for sex expression, demonstrating a complex relationship with environment. Data from Galun (1961) suggest the existence of a gene(s) that influences sex expression by exerting a quantitative influence on the intensity of gynoecey as manifested in the number of flowers with pistils. The genetic analysis presented in our study identifies the potential existence of at least two genetic factors in addition to the three major genes postulated to control sex expression in cucumber.

Source-sink relationships and hormonal regulation play a role in determining the number and length of lateral branches (Staub, 1989; Widders and Price, 1989). The phenotypic distribution of segregating families in our study indicates that mainstem length and the number of laterals are under polygenic control (data not presented). Hutchins (1940) observed that lateral branch length was under polygenic control. It is not known whether genes for mainstem length are the same as or epistatic to the genes that control the number and length of lateral branches. The manipulation of these traits might be enhanced if factors for their genetic control [i.e., quantitative trait loci (QTLs)] could be mapped.

GENOTYPIC AND PHENOTYPIC CORRELATIONS. Genotypic and phenotypic correlations were calculated among all characters evaluated, and their correlations combined over locations are presented (Table 6). Correlation values that exceed 1.0 are the result of differences in the magnitude of the variables involved in the calculation of genetic covariance (σ_{xy}). These data provide information regarding potential linkage and pleiotropic relation-

Table 5. Heritability (h^2_B) and SEs for traits in cucumber evaluated in two locations.

Trait	Georgia		Wisconsin	
	h^2_B	SE	h^2_B	SE
Sex expression	0.14 ^z	0.01	0.16 ^z	0.04
Days to anthesis	0.09	0.064	0.13	0.032
Leaf size	0.50	0.11	0.24	0.13
No. lateral branches	0.33 ^z	0.01	0.60 ^z	0.01
Mainstem length	0.40 ^z	0.06	0.73 ^z	0.06
No. fruit/plant	0.00	0.089	0.27	0.081
Mass fruit/plant	0.26	0.079	0.31	0.083
Fruit length (L)	0.08	0.066	0.40	0.09
Fruit diameter (D)	0.11	0.068	0.08	0.07
Fruit L:D	0.09	0.068	0.11	0.071

^zNarrow sense heritability (h^2_N) designated by superscript and other values represent broad sense heritability (h^2_B).

ships. In general, there was good agreement between locations with regard to the value of these coefficients (data not presented). There were moderate positive phenotypic correlations between leaf size and mass of fruit per plant ($r = 0.57$), leaf size and fruit length ($r = 0.59$), fruit length and fruit width ($r = 0.78$), fruit length and fruit mass ($r = 0.57$), fruit mass and fruit count ($r = 0.68$), gynoecey and mainstem length ($r = 0.56$), and mainstem length and number of lateral branches ($r = 0.51$). Moderate to large, positive genotypic correlations were detected between leaf size and mass of fruit per plant ($r = 0.88$); leaf size and fruit length ($r = 0.92$); leaf size and fruit diameter ($r = 0.84$); and mainstem length and fruit length ($r = 0.80$), fruit diameter ($r = 0.60$), and mean fruit mass ($r = 0.52$) and between mean fruit mass and fruit length ($r = 0.49$), fruit diameter ($r = 0.60$), and L:D ($r = 0.86$). Moderate to large negative genotypic correlations were detected between fruit number and L:D ($r = -0.98$), days to flower and fruit count ($r = -0.62$), gynoecey and mainstem length ($r = -0.57$), and gynoecey and lateral branch number ($r = -0.56$).

As with previous studies (Fredrick and Staub, 1989; Kupper and Staub, 1988), we did not detect a phenotypic correlation between fruit count and degree of gynoeceous sex expression or early flowering in this study. However, low to moderate genotypic correlations were detected between gynoecey and fruit count, mainstem length, and number of lateral branches (Table 6). This result suggests that phenotypes that have staminate or barren nodes at their base may be useful in developing multiple-lateral determinate types. Some early flowering multiple-lateral determinate plants in this population supported the enlargement of long fruit. The mainstem length of these plants varied (37 to 175 cm), and, therefore, the possibility exists for selecting determinate multiple-lateral phenotypes that possess a flowering habit and plant stature that optimizes yield in once-over mechanical harvesting operations. Nevertheless, plant measurements in this study were taken at relatively wide spacings ($\approx 19,000$ plants/ha). Any genotype considered to have potential for once-over mechanical harvesting must be evaluated at higher plant populations (150,000 to 200,000 plants/ha) in standard commercial spacings (i.e., three or four row beds). The plant types having potential use for once-over machine harvesting operations at low plant densities may change when they are subjected to reduced intra-row spacings. Genotypes have been identified that retain gynoeceous sex expression, a multiple branching habit, and relatively small size when placed at high densities ($\approx 120,000$ plants/ha) (Staub et al., 1995b; unpublished data).

The positive relationship between fruit count and number of lateral branches previously reported in indeterminate, multiple-

Table 6. Genotypic (above diagonal) and phenotypic (below diagonal) correlations among traits in cucumber evaluated under two environments.

	Sex expression	Leaf size	Days to flower	No. laterals/ plant	Main stem length	No. fruit/ plant	Mass fruit/ plant	Fruit length (L)	Fruit diam. (D)	Fruit L:D
Sex expression		-0.13	-0.23	-0.56	-0.57	-0.34	-0.17	-0.23	0.24	-0.61
Leaf size	0.19		-0.21	-0.4	0.07	0.23	0.88	0.92	0.84	0.08
Days for flower	-0.24*	0.02		-1.26	0.26	-0.62	-0.57	-0.67	-1.3	-0.11
Laterals/plant (no.)	-0.27*	-0.01	-0.15		0.63	0.39	0.02	-0.04	-0.23	0.63
Mainstem length	-0.56**	0.20*	0.01	0.57**		0.68	0.52	0.8	0.6	1.05
Fruit/plant (no.)	-0.27*	0.16	-0.23*	0.03	0.39**		1.08	-0.03	0.17	-0.98
Mass fruit/plant	-0.21*	0.57**	-0.24*	-0.11	0.42**	0.68**		0.49	0.6	0.88
L	-0.14	0.59**	-0.26*	0.02	0.35**	0.28**	0.57**		0.88	0.93
D	0.07	0.41**	-0.26*	-0.31*	-0.06	0.25*	0.41**	0.78**		0.17
L:D	-0.30**	0.35**	0.07	0.13	0.44**	0.10	0.32**	0.41**	-0.06	

***Significant at $P \leq 0.05$ and 0.01 , respectively.

lateral *C. hardwickii* types (Fredrick and Staub, 1989; Kupper and Staub, 1988) was not clearly evident in this study using *C. sativus* germplasm (Table 6; $r = 0.03$ phenotypic; $r = 0.39$ genotypic). Moreover, Kupper and Staub (1988) reported that, although the multiple-lateral branching plants of *C. hardwickii*-derived lines produced many fruit, these fruit were relatively short. In contrast to *C. hardwickii*-derived types, some moderately branching determinate plants in our study produced fruit that were relatively long (L:D = 2.7 to 3.7). However, because of the positive genotypic correlations detected between mainstem length and fruit length and diameter, small determinate genotypes (mainstem ≈ 30 to 40 cm) that bore commercially acceptable fruit (i.e., L:D ≈ 2.9 to 3.3) may be difficult to recover in this population.

High correlations between leaf size and yield components (e.g., fruit count and mass) may indicate the presence of potential source-sink relationships. If such correlations are consistent over years and locations, they may have value for developing plant improvement strategies. Like *C. hardwickii*, line 'H-19' is a small-leaved, multiple-branching phenotype. Nienhuis and Lower (1980) suggested that *C. s. var. hardwickii* provides a large photosynthetic area, which in turn can support higher numbers of fruit. Ramirez et al. (1988a), however, found that, although *C. hardwickii* produced more fruit than the *C. sativus* 'Calypso', it flowered later and its fruit were smaller (less mass). Moreover, growth rates of the whole plant followed similar trends in the *C. sativus* and *C. hardwickii* lines examined. Similar conclusions were reached by Kupper and Staub (1988) during an examination of an array of *C. hardwickii* accessions.

Positive phenotypic and genotypic correlations between leaf type and yield-related traits (e.g., fruit mass and fruit count) indicate that leaf size may influence source-sink relationships in this population (Table 6). The hypothesis that unique cucumber genotypes (i.e., determinate, multiple lateral branching) in this population may differ in net photosynthetic capacity depending on leaf size and plant habit is testable. The CO_2 exchange rate may influence fruit mass while having only a limited influence on the number of fruit produced per plant. The fact that the correlation between leaf size and number of fruit per plant was relatively low (phenotypic: $r = 0.16$, and genotypic: $r = 0.23$) lends support to this hypothesis.

Since fruit count is influenced by plant spacing and environmental conditions (Staub et al., 1992), manipulation of plant architecture (e.g., plant habit and sex expression) with concomitant adjustments in plant density might be used to increase the yield potential of cucumber. Our breeding objective is to develop multiple-lateral, determinate genotypes suitable for once-over

mechanical harvest. Genetic estimates (e.g., high heritability and additivity) indicate that adequate variation (branch number and mainstem length) exists in the population evaluated to select for multiple-lateral branching types differing in plant stature. In contrast, the genetic variance and heritability (h^2_B) for days to flower and fruit count, mass, and size are relatively low. Therefore, breeding strategies in this population should be developed that try to fix the number of lateral branches while maintaining an array of sex types in a determinate background. The dominance of genes affecting gynoecy (*F*) and leaf size (*ll*) can be used effectively to produce an array of phenotypes.

Source-sink relationships among architecturally different cucumber plant types are complex (Ramirez et al., 1988a, 1988b) and have not been completely defined. Most commercial cucumber cultivars are monoecious, indeterminate, and produce one to two lateral branches. Source-sink relationships differ among multiple-lateral *C. hardwickii* genotypes with simultaneous fruiting habits (Kupper and Staub, 1988; Staub, 1989). When compared to the standard-branching, indeterminate 'Calypso' and the determinate *C. sativus* line M 21, *C. hardwickii* line LJ 90430 has strong vegetative sinks and weak reproductive sinks (Ramirez et al., 1988a). The strong source-sink relationships observed in *C. hardwickii* may not be present in germplasm derived from the multiple-lateral branching line 'H-19'. The time to anthesis of 'H-19' is less than that of *C. hardwickii*. Moreover, while *C. hardwickii* fruit are relatively small in size and mass (L:D ≈ 1.9 to 2.2) (Staub and Kupper, 1988), fruit of 'H-19' are of commercial size (L:D ≈ 3.0 to 3.2).

Adding the multiple-lateral characteristic to breeding objectives adds complexity to selection for determinate types in a segregating population since differences in vine length are mitigated by the removal of apical dominance (Staub et al., 1995b). Biochemical genetic markers closely linked to *de* could be effective selection tools for identifying potentially useful determinate types. Likewise, markers linked to QTLs that are conditioned by additive genetic factors, such as number of laterals and mainstem length, might be used to increase gain from selection for multiple-lateral plant types (Serquen et al., 1997). Thus, breeding strategies for the development of multiple-lateral determinate types might use genetic markers, appropriate index selection procedures, and multiple-location testing to increase gain from selection.

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