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Breeding for Improved Yield in Cucumber

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I. INTRODUCTION

A. Cucumber Types

Cucumber (*Cucumis sativus* L.) is thought to have originated in India or China (Harlan 1975), with domestication occurring later throughout Europe. It was used for food in ancient Egypt, and by the Greeks and Romans 3000 to 4000 years ago (Whitaker and Jagger 1937). It was used in

England as early as the 1300s, and was brought to the Americas by Christopher Columbus. It is now grown throughout the world in a number of distinct forms for use as either a fresh or processed vegetable.

The accepted commercial types include American pickling (processing), European pickling, American slicing (fresh-market), European greenhouse (parthenocarpic), outdoor trellis (burpless), Middle Eastern, and schälgurken (Table 8.1). There are also Armenian or Chinese cucumbers which can be considered a type of cucumber. They belong to *C. melo*, but have long, green-skinned, white-fleshed fruits like *C. sativus*. American pickling cucumbers are used in many processed products, including wholes, halves, strips, chips, cubes, and relish. There are three main methods of processing the cucumbers: brining (fermenting), fresh-pack (pasteurizing), and cold-pack (refrigerating). In the United States, pickling cucumbers are grown on a larger area than slicing cucumbers (53,000 vs. 20,000 ha in 1979). The major producing states are Michigan, North Carolina, Ohio, Wisconsin, and Texas.

Table 8.1. Major Cucumber Types for Fresh-Market or Processing[a].

				Fruit skin characteristics			
Type	Major use	Length (mm)	Length diameter ratio	Shade green	Color uniformity	Skin thickness	Skin surface
American pickle	Proc	150	3.0	Medium	Mottled	Medium	Warts
European pickle	Proc	150	3.0	Medium	Uniform	Medium	Hairs
Middle Eastern	Fresh	180	3.5	Light	Uniform	Thin	Hairs
American slicer	Fresh	200	4.0	Dark	Uniform	Thick	Warts
Schälgurken	Proc	250	4.0	Medium	Uniform	Thick	Hairs
Outdoor trellis	Fresh	300	6.0	Medium	Uniform	Thin	Ridges
European greenhouse	Fresh	400	7.0	Medium	Uniform	Thin	Ridges
Armenian cucumber	Fresh	480	8.0	Medium	Mottled	Medium	Ridges

[a] All types are *Cucumis sativus* L. except Armenian cucumber, which is *C. melo*. Data taken partly from Wehner and Horton 1986b.

The European pickling industry is small compared to that of the United States, and deals with fewer types of products, mostly fresh-packed wholes and chips. The schälgurken is a little-used German cucumber type for pickled products such as large cubes.

Fresh-market cucumber types include the American slicer which is grown throughout the United States (mainly Florida, California, Texas, North Carolina, and South Carolina), the outdoor trellis type which is mainly used in home gardens, and the European greenhouse type. The greenhouse cucumber is grown on a very small scale in the United States, but is widely grown in Europe. The plants are parthenocarpic, producing seedless fruits without pollination. The Middle Eastern cucumbers are popular in Europe and the Middle East. The fruits are smaller and lighter green than the American slicers, usually with larger seed cell and smoother skin. They are often eaten whole, as opposed to the American slicer which is often peeled and sliced before eating. The last type, Armenian cucumbers, are not well known and are mainly grown as a novelty in home gardens. They have promise for use as a commercial crop, offering improved resistance to drought and some diseases compared to *Cucumis sativus* types.

B. Breeding for Yield

Cultivars for use in the United States have been listed in catalogs published as early as 1806, and have increased in number continuously since then (Tapley et al. 1937). Most of the cultivars used in the United States in the 1800s were European derived. Since then, the important breeding objectives in most United States programs have been earliness, yield, fruit type, disease resistance, fruit quality, sex expression, plant type, and environmental stress resistance (cold, drought). Other characteristics, such as adaptation to machine harvest and insect resistance, have received emphasis at various times. Incorporation of disease resistance into cultivars (Peterson 1975), and use of improved cultural practices (Cargill et al. 1975) have increased the yield of pickling cucumbers. Improvements made in disease resistance, plant habit, and sex expression in U.S. cultivars over the past 5 decades are shown in Table 8.2.

Yield is no more important than the other traits listed above, but it is a subject of interest to me, receiving much emphasis in my breeding program for the past 8 years. Thus, I have chosen to review that subject for cucumber. Many of the research findings that relate to yield have been studied in the cucumber breeding program in North Carolina, and some examples will be given that are taken from this program. The objective of the North Carolina program is the improvement of American pickling and slicing types for yield, earliness, plant type, quality, disease resistance, and stress resistance for the southeastern United States. There is a small emphasis on new and different cucumber types, such as Middle Eastern, outdoor trellis, and Armenian, for possible adaptation to the U.S. market.

Yield is usually measured as a function of weight per unit area, but its measurement is complicated by the fact that it involves immature fruits. Since the fruits are removed before they reach physiological maturity, weight is dependent on the time of harvest as well as the productivity of the plant. High yielding ability of cucumber cultivars, experimental lines, hybrids or inbreds (hereafter referred to as lines) is useful to

Table 8.2. Important Steps in the Genetic Improvement of Cucumber in the U.S.

Cultivar or breeding line	Developer or seed source	Year introduced	Economically important trait(s)[a]
	Improvement of disease resistance		
Shamrock	Iowa State College, Ames	1937	CMV
Maine No. 2	Maine Agr. Expt. Sta.	1939	Scab
P.R. 39	Puerto Rico Agr. Expt. Sta.	1944	DM
Wis. SMR 12	Wis. Agr. Expt. Sta.	1955	Scab,CMV
Ashe	N. C. Agr. Expt. Sta.	1959	Scab,DM
Tablegreen	N. Y. Agr. Expt. Sta.	1960	CMV,PM,late maturity
Polaris	S. C. Agr. Expt. Sta.	1961	DM,PM,Anth
Poinsett	S. C. Agr. Expt. Sta.	1966	DM,PM,Anth,ALS
Chipper	S. C. Agr. Expt. Sta.	1968	DM,PM,Anth,ALS,CMV
Sumter	S. C. Agr. Expt. Sta.	1973	DM,PM,Anth,ALS,CMV, Scab,WMV
Wis. 2757	U.S.D.A., Univ. Wis.	1982	DM,PM,Anth,ALS,CMV, Scab,TLS,BW FW
	Improvement of other traits		
Midget	Minnesota Agr. Expt. Sta.	1940	Dwarf-determinate habit
Burpee Hybrid	W. Atlee Burpee Co.	1945	Mon-Hyb,CMV,DM
MSU 713-5	Mich. Agr. Expt. Sta.	1960	Gyn
Spartan Dawn	Mich. Agr. Expt. Sta.	1962	Gyn-Hyb,CMV,Scab
Gy 3	S. C. Agr. Expt. Sta.	1969	Gyn,DM,PM,Anth,ALS
Gy 14	S. C. Agr. Expt. Sta.	1973	Gyn,DM,PM,Anth,ALS, Scab,CMV,WMV
M 21	N. C. Agr. Expt. Sta.	1979	Dwarf-determinate, DM,PM,Anth,ALS
Little-leaf	Univ. Arkansas	1980	Small leaf,Multibranched habit
Marketmore 80F	N. Y. Agr. Expt. Sta.	1980	Gyn,Fruit quality, DM,PM,Scab,CMV
Castlepik	A. L. Castle (SunSeeds)	1983	Dwarf-determinate,Gyn-Hyb

[a] CMV=cucumber mosaic virus resistance, DM=downy mildew resistance, Anth=anthracnose resistance, ALS=angular leafspot resistance, WMV=watermelon mosaic race 2 resistance, TLS=target leafspot resistance, BW=bacterial wilt resistance, FW=fusarium wilt resistance, Mon=monoecious sex expression, Gyn=gynoecious sex expression, Hyb=hybrid.

growers only if the fruits are of the proper horticultural type. Therefore, yield trials must be run using lines that are of similar type in order to be of value to the growers and plant breeders who are making the evaluations.

Although comparable data on yield improvement over time as a result of breeding are not available, it can be measured crudely from yield trial results. Some of the more popular gynoecious cultivars of pickling cucumber in the southeastern United States tested in my breeding program for the years 1981 through 1985 demonstrate the improvement for yield over time (Table 8.3). For example, in a span of 20 years, the cultivars 'Explorer', 'Carolina', 'Calypso', 'Regal', and 'Raleigh' represent an average yield improvement of 0.4 Mg/ha per year. The improvement might have been greater if it were not for the fact that breeders were improving numerous other traits simultaneously with, or instead of, yield.

Table 8.3. Yield Data from Spring (Sp) and Summer (Sm) Yield Trials at Clinton, North Carolina, run in 1981 through 1985 using 5 cultivars[a].

		Fresh weight in 8 trials (Mg/ha)								
	Release[b]	1981		1982	1983	1984		1985		
Cultivar	date	Spr	Sum	Spr	Sum	Spr	Sum	Spr	Sum	Mean
Explorer	1969	19	20	29	34	31	22	38	37	28.8
Carolina	1973	20	10	28	33	41	21	45	38	29.6
Calypso	1975	21	21	32	34	42	30	41	41	32.7
Regal	1979	24	18	40	38	41	27	48	41	34.6
Raleigh	1987	26	26	37	34	33	27	52	48	35.5
Mean		22.0	19.0	33.2	34.6	37.6	25.4	44.8	44.8	32.2

[a] Data are from 3 replications and 6 harvests in yield trials run by the North Carolina Agr. Expt. Sta. cucumber breeding program.

[b] Cultivars released from the North and South Carolina cucumber breeding programs.

Besides yield, improvement has occurred for darker green fruit exocarp (skin) color, improved resistance of fruit to balloon bloating (carpel separation) in brine tanks, slower seed development and smaller seed cell, and added resistance to diseases such as scab (*Cladosporium cucumerinum* Ellis & Arthur), cucumber mosaic virus and anthracnose (*Colletotrichum lagenarium* (Ross.) Ellis & Halst). Although some of the increase in yield over the years was due to improvement in related traits such as disease resistance and gynoecious expression, some direct improvement in productivity through genetic manipulation has undoubtedly occurred. That improved cultural practices are responsible for yield improvement can be seen from the increase in the North Carolina trial mean from 1981 to 1985 (Table 8.3).

The literature on cucumber breeding has been reviewed recently (through 1983) by Lower and Edwards (1986). A review by Whitaker and Davis (1962) covered cucumber breeding through the 1950s. Therefore, I will restrict this review to the more recent literature on cucumber yield. Methods for improving the efficiency of vegetable trials have also been reviewed (Wehner 1987b). Those methods could be applied to such areas as the improvement of efficiency of cucumber yield trials and will, therefore, not be covered in depth.

I have observed that yield is extremely variable over years and locations. Even so, it would be appropriate to mention the lines that have high yield (based on data from several years of North Carolina trials; not shown). Representative examples of each cucumber type are 'Raleigh' from NCSU and 'Royal' from Harris-Moran (pickles), 'Colet' and 'Marbel' from Royal Sluis (Dutch pickles), 'Sprint 440' from Asgrow and 'Raider' from Harris-Moran (slicers), 'Amra' from Nickerson and 'Celebrity' from Ferry-Morse (Middle Eastern), and 'Tasty Time' from Sakata (outdoor trellis).

II. YIELD TRIALS

A. Test Method

Yield of cucumber lines is of interest at three stages of cultivar development: the early stage where single plants or segregating families are being evaluated in the early generations of a cross, the intermediate stage where stabilized lines (inbred for 5 or more generations) are evaluated for possible use as inbreds or hybrids, and the final stage where promising inbreds and hybrids are evaluated in many locations, season, and years to confirm their performance in the intermediate stage.

Early stage testing for yield should provide only general information (e.g., whether the plant produces many or few fruits), and emphasis should be on other economically important characteristics (e.g., fruit quality, disease resistance). This strategy is followed because yield of single plants is poorly correlated with either once-over or multiple-harvest yield in replicated field trials (Wehner 1986b; Wehner and Miller 1984). Likewise it is not useful to make yield selections to improve field performance based on single plants in the greenhouse for similar reasons. A preliminary test indicated that yield (fruits per plant) of greenhouse-grown plants was poorly correlated ($r = 0.09$–0.15) with yield in two field locations in a test run in Israel (Nerson et al. 1987).

The major emphasis on yield selection should be in the intermediate stage, where inbred lines are evaluated for possible use as new cultivars, or as parents of hybrids, and where hybrids are evaluated for suitability and advancement to final-stage testing. At the intermediate stage, yield is correlated with yield in final-stage trials. Eighteen diverse lines of pickling cucumbers harvested once-over for yield (fruit number per plot) from three replications of 1.5 × 3 m plots had a correlation of 0.58 with the same lines harvested six times for yield ($/ha) from three replications of 1.5 × 6 m plots (Wehner 1986). A similar study with fresh-market cucumbers (except that yield for the multiple-harvest method was measured as kg/ha) had a correlation of 0.83 between the two test methods (Wehner and Miller 1984). Thus, it is efficient to use small-plot, single-harvest trials at the intermediate stage instead of the large-plot, multiple-harvest trials which require much time and labor. Those labor-intensive methods should be used in final-stage trials to assure accurate testing before release of the new cultivars.

Previously, I have summarized the general methodology for determining the most efficient design of trials to run when testing the performance of new lines (Wehner 1987b). Efficient trials for intermediate-stage testing make use of a single harvest rather than multiple harvests (Wehner 1986b; Wehner and Miller 1984) and small, single-row plots (Wehner and Miller 1983) without end borders (Wehner 1987a) rather than large, multiple-row, bordered plots. Also, intermediate-stage tests should have two or three different seasons or locations with one replication (Wehner and Swallow 1986; Wehner 1987d), rather than many replications in one season, location, or year. For example, an efficient intermediate-stage test might have three locations planted in the spring, each with one replication. That would require three plots per line and, under North Carolina conditions, would take about 60 days from the planting to harvest.

In my program, multiple-harvest trials are run using only six harvests (two harvests per week for 3 weeks), instead of the nine harvests used by growers. A relatively high correlation ($r > 0.9$) for yield between cumulative early harvests and total yield (nine harvests), permits us to stop yield evaluations after the sixth, or even the fourth harvest (unpublished data). Part of the reason for using six harvests is the requirement we have for fruits to use in the measurement of traits other than yield. For example, harvest 1 is made early to identify the earliest lines, harvests 2, 4 and 6 are for fruit-quality measurements, and harvests 3 and 5 are for brinestock evaluation.

B. Yield Measurement

Cucumber growers generally measure yield by volume or weight. However, they are most interested in market value, which is a function of quality, weight, and size. Fresh-market cucumbers must meet certain criteria for shape and color, and have a diameter of 38 to 60 mm to be marketable. Pickling cucumbers are graded according to diameter, with the small fruits having the greatest value. In North Carolina, there are three grades with diameters as follows: less than 27 mm, 27 to 38 mm and 39 to 50 mm for grades 1, 2, and 3, respectively. In that scheme, oversized fruits are classified as grade 4, and have no commercial value. The 1987 prices for pickling cucumbers in North Carolina were $330, $154, and $88/Mg for grades 1, 2, and 3, respectively.

Measurement of yield among lines in a trial presents a difficult problem for the researcher. The question arises as to the best way to measure yield: volume, weight, number, or value. Generally, it is easiest to measure yield as weight or number, since value requires that the fruits be graded before weighing. Volume, weight, and value are unstable measures, especially in once-over harvest trials, since all change rapidly from one day to the next as the fruits increase in size on the plants. In addition, value is difficult to standardize over years, because the prices change with market demand and under the effect of inflation.

Many researchers use fruit number as the measure of yield in the intermediate-stage trials, especially for once-over harvest. In once-over harvest trials of pickling cucumbers, fruit number was more stable over several harvest dates than weight or value if all fruit sizes, including oversize, were counted (Ells and McSay 1981). If only the marketable sizes (up to 50 mm diameter) were considered, all three yield measurements were dependent on maturity. However, total fruit number is stable for a 2–3 week period, at least under Colorado conditions. Therefore, yield evaluation for once-over harvest of cucumbers should be measured as fruit number per plot, assuming that all lines being evaluated have the same fruit type (resulting in little difference in weight per fruit).

The determination of when to harvest can be made using a harvest index that records the number or weight of oversized fruits. Miller and Hughes (1969) determined that 14–31% (by weight) oversized fruits was the optimum stage to maximize $/ha for 'Piccadilly' and 'Southern Cross' gynoecious hybrids in North Carolina. That system maximizes fruit value using a pricing scheme (per 100 lbs.) of $7 for grade 1, $3.50 for grade 2, and $1.50 for grade 3. In a computer simulation, Chen et al. (1975) found that once-over harvest at 10% oversized fruits provided optimum yield ($/ha) of 'Picadilly' hybrid under North Carolina conditions. Optimum harvest stage to maximize yield ($/ha) for 'Femcap' and 'Greenstar' gynoecious hybrids in Ontario occurred at 5–15% oversized fruits by weight, or 1–6% by number (Colwell and O'Sullivan 1981).

Under different pricing systems, and with different lines, the optimum harvest stage may be different. However, those indices provide a convenient method for standardizing comparisons among lines. In my program, we usually harvest all plots in a test when the check plots have 10% oversized fruits, by number. We have defined oversize as > 51 mm diameter for pickling and > 60 mm diameter for fresh-market cucumbers. The system for fresh-market cucumbers was adapted directly from the one used in pickling cucumbers since there is no commercial use of once-over harvest for fresh-market cucumbers, and since they are salable at a single price (under U.S.D.A. standards) if they have a diameter of 38–60 mm, and meet other grade requirements. Check lines should be chosen carefully, having the same maturity and fruit type as the other lines being tested. The system I use penalizes the late-maturing as well as the low-yielding lines.

Preliminary results indicate that it may be possible to estimate the time from planting to harvest of pickling and fresh-market cucumbers using heat units with better accuracy than using average number of days to harvest (Perry et al. 1986). The best prediction formula for heat-unit calculation used a base temperature of 15.5°C and a ceiling of 32°C, but replacing the maximum temperature with a maximum of 32 if it was above 32°C. That system makes it possible to predict harvest times for a given location and planting date for trials planted at several different dates using 10-year means for temperature at the trial location. Current temperatures recorded at a particular trial location can be substituted for 10-year means as the data become available. Thus, as the season proceeds, harvest dates are predicted with increasing accuracy. The system assumes no damage from excessively high or low temperatures, or from drought.

C. Mechanization

For yield improvement in cucumber, it is important to evaluate as many lines in as many environments as possible. Planting and harvesting (including data collection and analysis) expend most of the resources involved in running a yield test of cucumber lines, taking 28% and 46% of the worker hours respectively, regardless of whether for once-over or multiple harvest (Swallow and Wehner 1986). The remainder of the labor (26%) is spent planning the trial, packeting the seeds and checking the stand after seedling emergence. Planting can be mechanized using small-plot planters, although some uniformity of spacing is lost.

With the exception of seed extraction (Wehner et al. 1983) and seed cleaning (Steiner and Letizia 1986) from increase plots, harvesting is difficult to mechanize if the fruits are to be saved for other uses, such as tests of quality. However, paraquat (1,1′-dimethyl-4,4′-bipyridinium ion) can be sprayed on the plants in a trial on the day they would normally be evaluated in a once-over harvest trial (Wehner et al. 1984). The plots will be defoliated in 1 or 2 days depending on temperature and chemical concentration. That permits counts of fruits per plot to be made with fewer resources than for the conventional system in which the plants in each plot were pulled from the soil and the fruits removed for counting. Other general herbicides, such as glyphosate (n-phosphonomethyl glycine), do not work as well on cucumbers as paraquat.

Portable microcomputers used in data collection from field plots can decrease time and labor requirements for data summarization (Wehner 1986a). The savings allow more lines to be evaluated, and theoretically, should improve gain in yield from the research program. In some cases, use of computers makes it possible to accomplish tasks which were not possible before. For example, in my breeding program, each line is tested in three locations during intermediate-stage testing. Data collected at harvest is analyzed immediately in order to generate a list of the best lines. Remnant seeds of the best lines are then planted the day after harvesting in order to produce the next generation increase or population intercross. Time and labor were too limiting to consider doing that before computerization.

Computerization of data collection does not prevent researchers from making non-numeric observations during evaluation of cucumber lines. Computerized collection of yield data is compatible with the use of comments regarding the lines being tested. This is made more efficient if comments are abbreviated to a single letter, such as the system used for fruit-quality evaluation (Wehner 1985).

III. FIELD PLOTS

A. Plot Size

Optimum plot size can be determined by running uniformity trials using small plots or by reanalysing data from yield trials, where the replication and line effects are removed. Using those methods, Swallow and Wehner (1986) determined the optimum plot size under North Carolina conditions for pickling cucumbers harvested once-over to be 1.0 to 3.8 m^2 for conventional hand-harvest, or 1.5–5.6 m^2 (depending on year) for harvest using paraquat. The study was done with a basic unit of 15 plants in 1.5-m-long plots (61,750 plants/ha). For fresh-market cucumbers, the plot sizes were 0.7–1.5 m^2 for conventional hand-harvest, or 1.0–2.2 m^2 for harvest using paraquat to defoliate plants for fruit counting. Plot sizes were all based on rows 1.5 m apart.

A similar estimate for optimum plot size of 3.6 m^2 was obtained by Smith and Lower (1978) for once-over harvest of pickling cucumbers with a basic unit of 25 plants in 3.6-m-long plots (54,700 plants/ha). They suggested 25 plants be used as a minimum plot size in order to have sufficient fruits to make the necessary measurements for traits other than yield. Optimum plot size for multiple-harvest of pickling cucumbers was 6.4–10.3 m^2, depending on the year and the method of yield measurement (Swallow and Wehner 1986). For fresh-market cucumbers, plot sizes were 8.8–9.8 m^2.

A reduction in experimental error can be obtained using rectangular-shaped plots (Christidis 1931; Federer 1955). In peas (*Pisum sativum* L.), plots of 1 × 9 units were more uniform than those made up of 3 × 3 units (Zuhlke and Gritton 1969). However, appropriate studies on cucumbers have not been carried out.

B. Plot Borders

In final-stage testing, it may be useful to evaluate lines in multiple-row plots where the side rows (borders) are not harvested, but are used only to provide competition to simulate monoculture conditions. Side borders are not necessary in multiple-harvest trials of cucumbers if the lines are all of the same plant type (Wehner and Miller 1983; Wehner and Miller 1988). Therefore, single-row plots can be used for final-stage testing if indeterminate and determinate lines are tested in separate trials. If controlled environment chambers are used for yield evaluations, cucumbers should be bordered with at least one row around each treatment to remove biasing factors due to unequal competition among different treatments (Schapendonk and Spitters 1984).

The question of whether to use plot end-borders is similar to the one for side borders. Studies are often conducted with 0.9 m^2 end-borders on plots to prevent bias due to reduced competition where the plot meets the alley (Smith and Lower 1978). However, in intermediate-stage trials, as in most trials, differences among lines are important but actual yields are not. In intermediate-stage testing, plot end-borders were not needed to prevent interaction for yield in plots 1.5 m long separated by 1.5 m alleys (Wehner 1984a, 1988). However, yields were inflated by approximately 7% if end-borders were not used. Thus, if an unbiased estimate of yield is required (e.g., to determine potential yield for growers under ideal conditions), end-borders and side borders should be used on all plots, planting them with the same line, but not measuring yield from them.

An alternative to the use of end-borders is to plant a different species at the ends of each plot. They should be easy to identify and to separate from the harvest area, but still provide competition for the lines tested. R. L. Lower (personal communication 1984) has used squash (*Cucurbita pepo* L.) end-borders for cucumber plots being tested for yield in the eastern United States.

Regardless of whether bordered plots are used, guard rows and plots should be used to surround all trials to provide competition for plants in the outside plots. Guard rows on the sides and guard plots at the ends of the test rows in a field will increase the uniformity of the trial by taking any accidental abuse by those working nearby. Guards also help avoid uneven application of irrigation, fertilizer, and pesticides.

IV. ENVIRONMENT

A. Test Environment

As discussed in Section II, a good estimate of yield in a large-plot (6-m long), multiple-harvest, final-stage test will be provided by a test using a single harvest with 2 or 3 replications per line (Wehner 1986b; Wehner and Miller 1984). That intermediate-stage test is most efficient if the 2 or 3 plots are not planted in the same environment, however. Greatest information (1/variance) is gained by allocating test plots of each line to 2 or 3 years or seasons (Swallow and Wehner 1987; Wehner and Swallow 1986). Less information is gained when using different locations, and the least using replications within environments. Unfortunately, although more information can be gained using different years and seasons, it is much more costly in time and resources than locations and replications. A reasonable compromise is to conduct intermediate-stage trials with 3 locations of 1 replication each separated by 1 or 2 weeks in planting date. Uniform fields should be chosen for selection trials to maximize the number of detectable differences among plots.

Environments for evaluation of yield in once-over harvest trials were examined to determine the best season-location combinations in North Carolina (Wehner 1987a). Three seasons (spring, summer, and fall) and 4 locations (Clayton, Clinton, Castle Hayne, and a stressed field at Clinton) were studied. The stressed field received less fertilizer, irrigation, and pesticides than the other locations. Good environments were defined as those that produced large differences among lines and a good correlation with line means over all environments. The best ones in North Carolina were the spring and summer seasons at both the stressed and nonstressed Clinton locations. As a result, we have begun using a stressed environment as one of the 3 test environments in our trials. Since our trials are all planted in the spring, they are completed in time to make a summer crossing block using the best performing lines from spring trials (Fig. 8.1). This procedure requires 150 days (60 days for the trials and 90 days for the pollinations) per cycle under North Carolina conditions.

B. Yield Stability

We have determined that genotype and environment are important sources of variation for yield in once-over harvest trials in 24 North Carolina environments (Wehner 1987c). However, the mean square for the genotype × environment interaction effect provided by analysis of variance was generally not as large as for the main effects, but was significant for 44 diverse pickling and fresh-market cucumber lines tested (22 of each type). The component for genotype × environment interac-

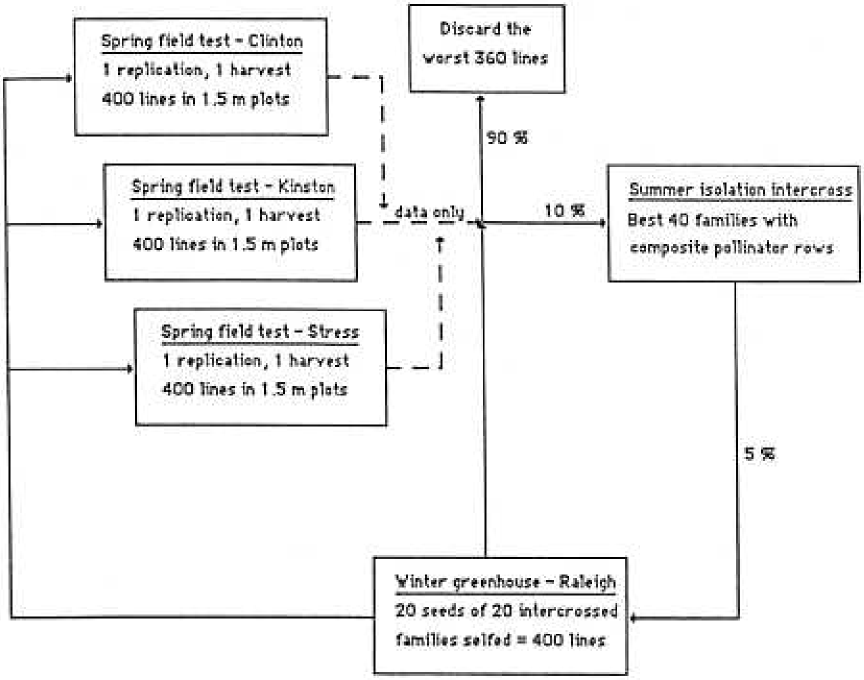

Fig. 8.1. The North Carolina State University breeding program to improve yield in cucumber using S_1 line selection with 3 seasons (spring, summer, winter) per year, 4 field plantings, and 1 greenhouse planting. The 'Stress' location is at Clinton, NC, but with half the recommended applications of fertilizer and irrigation. The 20 fruits with the best fruit quality and disease resistance are harvested from the summer isolation, and 20 seeds from each are planted in the greenhouse to make 400 lines for the next year. See text for discussion.

tion (σ^2_{GE}) was only 52 and 32% as large as the component for genotype (σ^2_G) for pickling and fresh-market types, respectively.

Ghaderi and Lower (1979b) reported significant additive genetic × environment interaction for yield (fruit number or weight) in 3 of the 6 crosses of pickling cucumbers they tested. Others have reported significant interaction for genetic (or additive genetic) × environmental (years, seasons, location or a combination) effects in pickling and fresh-market cucumbers (Owens et al. 1985a; Smith et al. 1978; Strefeler and Wehner 1986).

Although there were a few cases where genotype × environment interactions were not significant in yield tests, that interaction has been shown to be important in several studies which sampled diverse genotypes and environments (Table 8.4). Therefore, yield of a line in a

Table 8.4. Genotype-Environment Interaction for Yield in Cucumber.

Reference population[a]	Yield measure -ment[b]	Fruit harvest stage[c]	GxE		Reference
			Variance component[d]	Signif-icance[e]	
M 20 × Tiny Dill	Number	Green	VarA × Loc	*	Ghaderi & Lower 1979b
Addis × M 20	Number	Green	VarA × Loc	ns	Ghaderi & Lower 1979b
PG × SMR 18	Number	Green	VarA × Loc	*	Ghaderi & Lower 1979b
M 21 × PG	Number	Green	VarA × Loc	*	Ghaderi & Lower 1979b
Addis × SMR 18	Number	Green	VarA × Loc	ns	Ghaderi & Lower 1979b
8A × M 21	Number	Green	VarA × Loc	ns	Ghaderi & Lower 1979b
M 20 × Tiny Dill	Weight	Green	VarA × Loc	*	Ghaderi & Lower 1979b
Addis × M 20	Weight	Green	VarA × Loc	ns	Ghaderi & Lower 1979b
PG × SMR 18	Weight	Green	VarA × Loc	*	Ghaderi & Lower 1979b
M 21 × PG	Weight	Green	VarA × Loc	*	Ghaderi & Lower 1979b
Addis × SMR 18	Weight	Green	VarA × Loc	ns	Ghaderi & Lower 1979b
8A × M 21	Weight	Green	VarA × Loc	ns	Ghaderi & Lower 1979b
W 1540 × W 1925	Wt./fruit	Mature	VarG × Year	*	Owens et al. 1985a
W 1540 × W 1928	Wt./fruit	Mature	VarG × Year	*	Owens et al. 1985a
Mon. Pickle	Number	Green	VarA × Ssn	*	Smith et al. 1978
Mon. Pickle	Weight	Green	VarA × Ssn	ns	Smith et al. 1978
Mon. Pickle	Value	Green	VarA × Ssn	ns	Smith et al. 1978
NCES1	Number	Green	VarA × Ssn	*	Strefeler & Wehner 1986
NCES1	Number	Green	VarA × Ssn	*	Strefeler & Wehner 1986
NCMBS	Number	Green	VarA × Ssn	*	Strefeler & Wehner 1986
NCMBS	Number	Green	VarA × Ssn	*	Strefeler & Wehner 1986
NCWBS	Number	Green	VarA × Ssn	*	Strefeler & Wehner 1986
NCWBS	Number	Green	VarA × Ssn	*	Strefeler & Wehner 1986
Pickles	Number	Green	VarG × Env	*	Wehner 1987c
Slicers	Number	Green	VarG × Env	*	Wehner 1987c

particular region can best be improved by sampling several environments in intermediate-stage testing, and many environments in final-stage testing. In tobacco (*Nicotiana tabacum* L.), it has been recommended that cultivars destined for release be tested in 2 years at 5 locations before making the release decision (Jones et al. 1960). In cucumber, it is important to test lines in several different seasons (or planting dates) and years to gain maximum information on yield (Swallow and Wehner 1988).

Certain yield characteristics can be measured faster and easier than others. As mentioned previously, total (marketable plus oversized) fruit number in once-over harvest trials is stable for a longer time than total fruit weight or value, so is less dependent on the harvest date. Fruit number also had a higher heritability (0.17) than fruit weight (0.02), yet was highly correlated (genetic correlation = 0.87) with weight (Smith et al. 1978). Therefore, fruit number is an excellent substitute for weight or value, being highly correlated with the other measures, easier to measure in some cases, and having a higher heritability.

However, it may be necessary to consider fruit weight in addition to fruit number during selection. In one study, greater additive variance existed for fruit weight per plant and for average weight per fruit than for fruit number per plant (Ghaderi and Lower 1981). Data on the three yield components were collected in a single-environment test of 20 F_3 families from each of 6 crosses (involving 8 monoecious pickling cucumber inbreds) in North Carolina. Estimates of additive variance for fruit number per plant were near zero for most crosses, and dominance variance was larger than additive variance in several crosses for all three of the yield components measured.

The stability of several traits that all estimate the same thing can be checked to determine which is best using measures such as the coefficient of variability (CV). The trait with the lowest CV in a series of trials should be used in place of other similar traits. Another estimator of the usefulness of a trait is to calculate Fisher's least significant difference (LSD) and the range over line means in a trial. The best trait to use will have the largest range/LSD for line means, since it provides the greatest number of statistically significant differences among the lines.

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[a] Population abbreviations are: NCES1=North Carolina Elite Slicer 1, NCMBS=North Carolina Medium Base Slicer, NCWBS=North Carolina Wide Base Slicer, Pickles=22 diverse pickling cucumber lines, Slicers=22 diverse slicing cucumber lines.

[b] Yield is either fruit number, weight, or dollar value per plot (or per fruit if specifically stated).

[c] Harvest is once-over at edible green stage, or at mature seed stage.

[d] VarA=additive genetic variance component, VarG=genetic variance component, Loc=location, Ssn=season, Env=environment (year-season-location combinations).

[e] NS=nonsignificant, *=significant at the 5% level, or larger than its standard error.

V. CONSIDERATIONS IN SELECTION

A. Heterosis and Inbreeding Depression

Cucumber, like other species of the Cucurbitaceae, expresses little inbreeding depression (Allard 1960). When a random sample of plants from an open-pollinated pickling cucumber population were self-pollinated for 6 generations, the yield of the resulting lines was unaffected in either of the seasons tested (Rubino and Wehner 1986b).

In spite of the lack of inbreeding depression in families from random-mated populations, heterosis for yield has been observed in a number of cases (Table 8.5). Hayes and Jones (1916) reported that first-generation crosses in cucumber frequently exhibit high-parent heterosis due to increased fruit size and number per plant. Heterosis did not occur, however, if lines with similar vine and fruit phenotype were crossed. In order

Table 8.5. Heterosis for Yield in Cucumber.

Hybrid or population[a]	Test environ-ment	Yield measure-ment	Fruit harvest stage[b]	% heter-osis[c]	Reference
Pickle × slicer	—	Weight	Green	32	Hutchins 1938
6 Mon. pickles	Clinton	Number	Green	14	Ghaderi & Lower 1979a
6 Mon. pickles	Method	Number	Green	35	Ghaderi & Lower 1979a
6 Mon. pickles	Clinton	Weight	Green	59	Ghaderi & Lower 1979a
6 Mon. pickles	Method	Weight	Green	70	Ghaderi & Lower 1979a
Gy 14 × LJ 90430	—	Number	Mature	8	Nienhuis et al. 1980
Gy 14 × LJ 90430	—	Weight	Mature	204	Nienhuis et al. 1980
Gy 14 × LJ 90430	—	Number	Mature	8	Lower et al. 1982
Gy 14 × LJ 90430	—	Weight	Mature	204	Lower et al. 1982
NCMBP	Spring	Number	Green	5	Rubino & Wehner 1986b
NCMBP	Summer	Number	Green	7	Rubino & Wehner 1986b

[a] Hybrids or populations were: 6 Mon. Pickles=8 inbreds crossed in 6 pairs; Pickle × slicer='Mincu' pickle crossed with 9 fresh-market inbreds; NCMBP=45 inbreds developed at random from the North Carolina Medium Base Pickle population.

[b] Harvest stage is once-over at edible green harvest stage or mature seed stage.

[c] Percent heterosis is the percentage increase of the hybrid over the average of the 2 parents (midparent).

to test the effect of diverse lines on heterosis, Hutchins (1938) crossed 'Mincu' pickling cucumber with 9 different fresh-market cucumbers and measured fruit yield (weight) in a 6-harvest test. Eight of 9 hybrids had more fruits per plant than the high-parent, and the hybrids yielded an average of 32% more than the parental inbreds.

Heterosis was significant (14–70% above midparent, depending on environment) for 8 elite inbreds of pickling cucumbers crossed in 6 pairs to make monoecious hybrids (Ghaderi and Lower 1979a). In contrast to the above reports, Rubino and Wehner (1986b) measured only a small amount of heterosis (5–7% above the midparent, depending on environment) in crosses of Gy 14, a gynoecious inbred, with 45 S_6 lines developed at random from a population.

A large amount of heterosis was measured for fruit weight at the mature seed stage with 1.5 × 1.5 m plant spacing in the cross of Gy 14 × LJ 90430 (Lower et al. 1982). However, yield of LJ 90430 had to be estimated from other data since photoperiod sensitivity prevented fruit set. LJ 90430 belongs to *Cucumis sativus* var. *hardwickii* (R.) Alef. (Horst and Lower 1978). It is an inbred line selected from PI 183967 (Staub 1985), and has been used in breeding programs because of its ability to set many fruits simultaneously.

Significant estimates of heterosis in particular combinations of elite inbred lines indicate that heterosis, linkage, or epistasis is important in yield of cucumber. Since heterosis and inbreeding depression were small in lines taken at random from an open-pollinated population, that indicates either little genetic variance existed, or that linkage and/or epistasis were responsible for much of the heterosis found in particular crosses of elite inbred lines. The latter seems more likely, which means that hybrids are not essential to the production of a cultivar with high yield. Hybrids are often used to take advantage of dominant genes present in the parental inbreds, and to protect parental lines from usage by growers or competing seed companies without the developer's permission.

B. Heritability of Yield

The inheritance of yield in cucumber has been measured using a number of different methods, crosses, and populations. Narrow-sense heritability was reported to be 0.02–0.88, depending on the trait and method of measurement (Table 8.6). However, yield is most efficiently measured as fruit number at green stage (the normal harvest stage for edible fruits, e.g., 10% oversized fruits), as recommended above in sections II, III, and IV for intermediate-stage trials. For that type of trial, heritability is 0.07–0.25 (depending on population and environment

Table 8.6. Heritability (h^2) for Yield in Cucumber.

Reference population[a]	Test unit[b]	Yield measurement[c]	Fruit harvest stage[d]	h^2	Reference
Mon. Pickle	FS	Weight	Green	0.02	Smith et al. 1978
Mon. Pickle	FS	Number	Green	0.17	Smith et al. 1978
Mon. Pickle	FS	Value	Green	0.19	Smith et al. 1978
Gy14 × LJ 90430	P-O	Number	Mature	0.88	Horton et al. 1980
6 gyn. pickles	F_2	No./stem	Green	0.32	El-Shawaf & Baker 1981b
6 gyn. pickles	F_1	No./lateral	Green	0.17	El-Shawaf & Baker 1981b
6 gyn. pickles	FS	Weight	Green	0.00	El-Shawaf & Baker 1981b
20 gyn. hybrids	F_1	Number	Green	0.56	El-Shawaf & Baker 1981c
20 gyn. hybrids	F_1	Weight	Green	0.48	El-Shawaf & Baker 1981c
W1540 × W1925	BC2S2	Weight/fruit	Mature	0.63	Owens et al. 1985a
W1540 × W1928	BC2S2	Weight/fruit	Mature	0.58	Owens et al. 1985a
NCES1	HS	Number	Green	0.07	Strefeler & Wehner 1986
NCES1	FS	Number	Green	0.16	Strefeler & Wehner 1986
NCMBS	HS	Number	Green	0.19	Strefeler & Wehner 1986
NCMBS	FS	Number	Green	0.07	Strefeler & Wehner 1986
NCWBS	HS	Number	Green	0.25	Strefeler & Wehner 1986
NCWBS	FS	Number	Green	0.11	Strefeler & Wehner 1986

[a] Populations are: 6 gyn. pickles=F_1 hybrids from all possible crosses of 6 gynoecious inbreds; 20 gyn. pickles=F_1 hybrids from 4 gynoecious inbreds × 5 hermaphroditic inbreds; Mon. pickle=population developed from monoecious inbreds; NCES1=North Carolina Elite Slicer 1 population; NCMBS=North Carolina Medium Base Slicer; NCWBS=North Carolina Wide Base Slicer.

[b] Test units are half-sib (HS), full-sib (FS), parent-offspring (P-O), or inbred-backcross (BC_2S_2) families.

[c] Yield measurement is total fruit weight or number per plot or per plant, except weight per fruit as listed.

[d] Harvest stage is once-over at the edible green stage or at the mature seed stage.

tested) for half-sib or full-sib family means.

Heritability estimates generally apply only to the populations, environments, and cycles from which the estimates were obtained. However, they have been found to be good predictors of gain over many cycles of selection if the population is kept large enough to prevent inbreeding

(Moll and Stuber 1974). Useful guidelines for population size were provided by Baker and Curnow (1969), who suggested that 16 to 64 plants (or families) be selected for intercrossing each cycle. In my recurrent selection program, we generally test 400 families and intercross the best 20 each cycle (Fig. 8.1).

El Shawaf and Baker (1981b) estimated heritability at 0.00–0.56 using crosses among selected inbred lines and testing in a single environment. The study provided useful information, but violated the assumptions used in the measurement of heritability, which include having a random-mated reference population in linkage equilibrium. In addition, estimates are biased upward when measured in only one environment since genotype-environment interactions cannot be separated from genotype effects in such cases. As expected, some of their estimates were on the high side. It is interesting to note that they report a higher heritability for fruit number than for weight as found by others. Also, main-stem fruit number was more heritable than lateral-branch fruit number.

Heritability estimates for different populations under various environmental conditions were similar in two studies (Smith et al. 1978; Strefeler and Wehner 1986). Heritability estimates were higher for diverse populations developed by crossing hundreds of lines (0.11–0.25) than for uniform populations developed by crossing several elite lines (0.07–0.19). Heritabilities in that range are considered low, but progress should be possible using recurrent selection. On the other hand, low heritabilities indicate that it would not be efficient to select for yield among single plants in the early generations of a breeding program.

Further evidence of low heritability is provided by uniformity trials for yield (fruit number per plot) in North Carolina using 'Calypso' gynoecious hybrid pickling cucumber (Wehner 1984b). The field was typical of those available to researchers in North Carolina, and was given fertilizer and irrigation according to recommended cultural practices. Yield (fruits per 1.5 × 1.5 m plot in a once-over harvest) varied from 9 to 35, with a mean of 25 and a standard deviation of 4, among the 150 plots harvested. The variation was due entirely to environment, and depended on which row and tier the plot was in. Studies such as this one point out the usefulness of check plots as covariates, as well as incomplete-block designs for control of variability within replications.

Additional study is needed to determine the underlying cause of variability for yield. A number of factors undoubtedly contribute, including nonuniform emergence, root establishment, vine growth, sex expression, and pollination. Sex expression is an important contributor to yield variability, with number of pistillate flowers per plant decreasing with increased environmental stress. For example, sex expression of gynoecious hybrids was affected by plant density, where plants had fewer pistillate nodes as density increased from 84,000 to 256,000 plants/ha (Lower et al. 1983). Also, plants become less gynoecious if they are spaced unevenly within rows (Nienhuis et al. 1984). The percentage of gynoecious plants of Gy 14-2 dropped from 97 to 88 when hills were planted with 2 instead of 1 plant, even though the average density was the same in both cases (84,000 plants/ha). Thus, some variability in yield can be controlled by using improved planters that drop exactly 1 seed at each location in the row.

High heritabilities have been reported for crosses using adapted × unadapted germplasm (such as LJ 90430) and measuring yield as number of mature fruits per plant at wide spacing (Horton et al. 1980). Unfortunately, LJ 90430 has very small fruits and there is a negative correlation between fruit number and weight per fruit in progenies of crosses involving LJ 90430 (Fredrick 1986). Therefore, as selection proceeds for larger fruit size (required for marketability), number of fruits per plant will likely decline.

Weight per fruit is highly heritable (Owens et al. 1985a), indicating that selection for this yield component would provide rapid progress. However, weight per fruit is not a trait that can be changed much in the pursuit of yield, but is more useful for those who are trying to produce lines having fruits of a particular size to suit their markets.

VI. SELECTION METHODS

A procedure for planting, pollinating, and seed harvesting of cucumbers in the field for a breeding program was described by Barnes (1947), and is used currently with a few modifications by many programs. Similar methods are used for growing plants in the greenhouse. Greenhouses provide additional generations per year in the temperate climates, thus speeding the advance of generations in a breeding program. Goulden (1939) originated the idea of using growth chambers in the early stages of a breeding program to speed generation time by crowding plants together in small containers. Grafius (1965) was the first to apply that method to breeding using oats (*Avena sativa* L.) and barley (*Hordeum vulgare* L.) grown in flats of sand to keep the plants small and cause them to produce seeds faster. In cucumbers, small plants are produced by planting in small (102-mm diameter) pots, but the plants do not go to seed any faster than large plants grown in large (203-mm diameter) pots (Wehner and Horton 1986a). We use 152-mm diameter pots in the greenhouse to keep the plants small enough to handle easily, and to get one fruit containing approximately 100 seeds per plant. Larger pots (203-mm diameter or more) should be used if two fruits per plant, or more seeds per pollination are desired.

Seeds can be harvested from the fruits 3–7 weeks after pollination. We usually harvest at 6 weeks, but it is possible to speed generation time by harvesting earlier. Edwards et al. (1986) reported that germination of two normal cucumber populations was 10% when fruits were harvested at 3 weeks and seeds allowed to ferment in the juice in closed containers for 1 day before washing and drying. Germination was 85, 95, and 100% at 4, 5, and 6 weeks, respectively. A third population studied was of the compact plant type (discussed in more detail in section VIII), and had 10–55% lower germination percentage at all harvest times. Other factors affect seed harvest time. Seeds will mature more rapidly in pollinated fruits if the plants are grown in greenhouses with high temperature (e.g., 32°C).

Quantitative traits having low heritability are best improved using recurrent selection in a population, since that method permits the plant breeder to accumulate even small gains obtained from each cycle of selection to make significant long-term improvements. Recurrent selection has been applied to yield improvement in cucumber over the last few years with mixed results. Nienhuis (1982) evaluated recurrent selection for yield improvement in cucumber using S_1 line selection and reciprocal full-sib selection. S_1 line selection provided the most gain, and a similar study was continued by Lertrat and Lower (1983, 1984) who used recurrent selection for specific combining ability in two pickling cucumber populations. They used the gynoecious inbred, Gy 14, as the tester to select for improved yield. The procedure was described later in more detail by Lower and Edwards (1986). Families (S_1 lines, full-sib families, or testcross progenies) were produced in the off-season, and tested in the summer using two or more planting dates with 2–4 replications each in 1 year at one location. Plots consisted of 30 plants, of which the middle 25 were harvested. In midsummer, a final planting was made to intercross the best families. Families that perform poorly in the test block were removed from the intercross block before pollination.

Intercrossing the best families in isolation can be done by hand, but limited project resources can be conserved by using natural outcrossing by bees, and can be effective if done properly. In one experiment, monoecious cucumbers had 50% self- and sib-pollination when planted in plots in an isolation block (Wehner and Jenkins 1985). To avoid such inbreeding in maize (*Zea mays* L.), Lonnquist (1964) used a mixture of all the families being tested (called composite pollen rows) planted in alternating rows with the families being tested. The composite pollinator gives each family in the adjacent rows a good chance of being outcrossed with plants that belong to other families. We use composite pollen rows sprayed with silver nitrate, an ethylene inhibitor that induces the formation of staminate flowers, to provide pollen in our intercross blocks. We spray the families in the plot rows with ethephon, an ethylene releaser that induces the formation of pistillate flowers, to make them gynoecious (Tolla and Peterson 1979). Fruits harvested from the plot rows will be outcrosses with the composite pollen rows, each constituting a half-sib family. An example of the North Carolina State University breeding program involving testing and intercrossing of S_1 lines is shown in Fig. 8.1.

Recurrent selection involves early testing, since families are evaluated in each selection cycle before much, if any, inbreeding has been done. In the North Carolina Medium Base Pickle population, early (e.g., S_1 line) testing of yield (fruit number per plot) for combining ability was generally more efficient than late (e.g., S_8 line) testing, especially using an inbred line as a tester (Rubino and Wehner 1986a). Early testing was not efficient for testing inbred yield *per se*, and was not always more efficient than late testing for general combining ability (using the original population as the tester).

In 2- and 3-way crosses with 13 inbred lines of pickling cucumbers, general combining ability was relatively more important than specific combining ability for fruit number per plot in once-over harvest (Tasdighi and Baker 1981). Therefore, the average performance of finished inbreds can be used as a good predictor of their yield in hybrid combination. However, it is advisable to use combining ability as the measure of yield in the early stages of inbred development (Rubino and Wehner 1986a).

It may be possible to use recurrent selection to improve yield over a wide range of testing locations. However, genotype-environment interaction may prevent gains from being made. Wide-area improvement using convergent-divergent selection (Lonnquist et al. 1979) was evaluated using a pickling cucumber population tested in Wisconsin, Ohio and North Carolina. No gain for yield was made after four cycles of selection (Wehner et al. 1986, 1988). Lack of progress was partially due to selection methods, since yield was measured as mature fruit number per plant in the first two cycles, and a low selection intensity using half-sib families was used in the last two cycles. Such a convergent-divergent program may be more successful using efficient testing methods, and a set of similar testing environments (e.g., locations within the southeast U.S.). Consequently, research is needed to identify regions that have similar conditions for genotype performance.

The inbred-backcross method was proposed for improvement of quantitative traits in cucumber using adapted × unadapted lines (Owens et al. 1985b). That method may be useful for yield improvement, while maintaining a useful level of expression of the numerous other traits required in current cultivars.

VII. YIELD PHYSIOLOGY

Carbohydrate produced in source (leaf) tissue is translocated to sink (growing fruits, apical meristems) tissue. Fruits compete with other tissues, especially other fruits, for carbohydrates. A single-growing cucumber fruit, either pollinated (McCollum 1934) or parthenocarpic (Ells 1983), will suppress the growth of subsequent fruits. If the fruit is removed during harvest, or reaches seed maturity, the next oldest fruit will begin to grow within a few days. Those developing fruits and seeds impose a strong demand on the plant, which is associated with accelerated leaf carbon exchange rate (Barrett and Amling 1978). Fruits growing on cucumber plants in the greenhouse were highly competitive with vegetative parts, such as leaves and stems for carbohydrates (Pharr et al. 1984). When compared to fruitless controls, plants that were supporting a growing fruit had reduced vegetative growth.

Delaying the set of fruits on plants to "build a bigger factory" will not necessarily result in increased yield. Plants that were forced to remain vegetative longer than normal in the greenhouse had higher dry-matter accumulation in vegetative parts than the control plants, even when given time to develop fruits afterwards (Ramirez and Wehner 1984b; Ramirez et al. 1989a). Control plants that were allowed to begin fruiting when they were ready produced the greatest fruit weight per plant. In plants with delayed fruiting, the total plant weight was the same as the controls, but more photosynthate was diverted away from fruits to leaves and stems. Partitioning of dry matter for 'Calypso', LJ 90430, and M 21 plants after 88 days in the greenhouse was mostly to the fruits, with 'Calypso' having the greatest fruit weight per plant, and M 21 the least (Ramirez and Wehner 1984a; Ramirez et al. 1987a). LJ 90430 had the greatest dry weight in stems and leaves per plant, and had the greatest fruit number, but did not have the greatest fruit weight per plant. Similar results were obtained by Schuman et al. (1985), who reported that LJ 90430 had 8–30% less plant dry weight, and 61–64% less leaf area than 'Calypso' in two field tests in Wisconsin.

Delayed fruiting does not offer much promise for increased yield. However, plants that are allowed to grow large due to low planting density do produce higher yield per plant. For example, plants harvested once-over at the green stage had 3.4, 3.2, 2.2, and 1.7 fruits per plant when grown at 10300, 20580, 61750, and 123500 plants/ha, respectively (Wehner 1986b). There were 3.6, 3.6, 2.1, and 1.9 fruits/plant when the same treatments were harvested once-over at the mature seed stage.

Fruit yield is limited by plant efficiency and size because every leaf on the cucumber plant is involved with fruit growth. Defoliation (25–75%) of 'Calypso' plants grown in the greenhouse caused a decrease in the fruit weight per plant (Ramirez et al. 1987b). Removal of 25% of the leaves reduced fruit weight by 21%. Also, removal of lateral or apical buds caused a decrease in fruit weight per plant (Ramirez et al. 1989b). The earlier the apical bud was removed, the lower the fruit weight at harvest. Early bud removal also reduced the leaf area significantly compared to the control, which may have been partially responsible for reduced fruit weight.

When plants of 'Marketmore 76' were defoliated 25, 50, 75, and 100% at anthesis, then fruit weight was reduced by 23, 34, 44, and 76%, respectively (Roberts and Gorski 1985). Plants were grown in Ohio on raised beds covered with black plastic mulch and harvested 8 times. Removal of the shoot tips of the main stem and lateral branches at anthesis did not affect yield. Defoliation treatments had less effect when performed at first- or third-harvest stage than at anthesis. Thus, increased yield will be produced only if the plant is redesigned to produce a heavier fruit load, either with more leaves or more efficient leaves.

Cucumber is one of the few plant species known to translocate stachyose rather than sucrose in its phloem (Weidner 1964). Stachyose is a raffinose-saccharide that consists of galactose molecules attached to sucrose. If it were possible to change the translocation sugar from stachyose to sucrose, that might result in a saving of energy for the plant. It might be speculated that the unused energy could be directed to increased fruit production per plant (D. M. Pharr, personal communication).

VIII. YIELD IDEOTYPE

A. Plant Type

A number of potentially useful cucumber plant types exist which could increase yield per unit area. Those include dwarf, multibranched, little leaf, and determinate. Dwarf types can be produced using compact (*cp*) (Kauffman and Lower 1976) or dwarf (*dw*) genes and might be used to increase fruit yield by increasing plants per unit area while keeping fruit weight per plant constant. Compact is very different from the normal (tall) plant type of cucumber (Fig. 8.2).

No reports of planting density for optimum yield are available for dwarf plants (*dwdw*), but compact plants (*cpcp*) were reported to have an optimum density far above the normal planting rate (Edwards and Lower 1982a). Compact plants had more fruits per unit area than normal plants at densities above 40,000 plants/ha under both once-over and multiple-harvest systems in Wisconsin. It was not possible to determine the optimum density since yield increased linearly up to the maximum den-

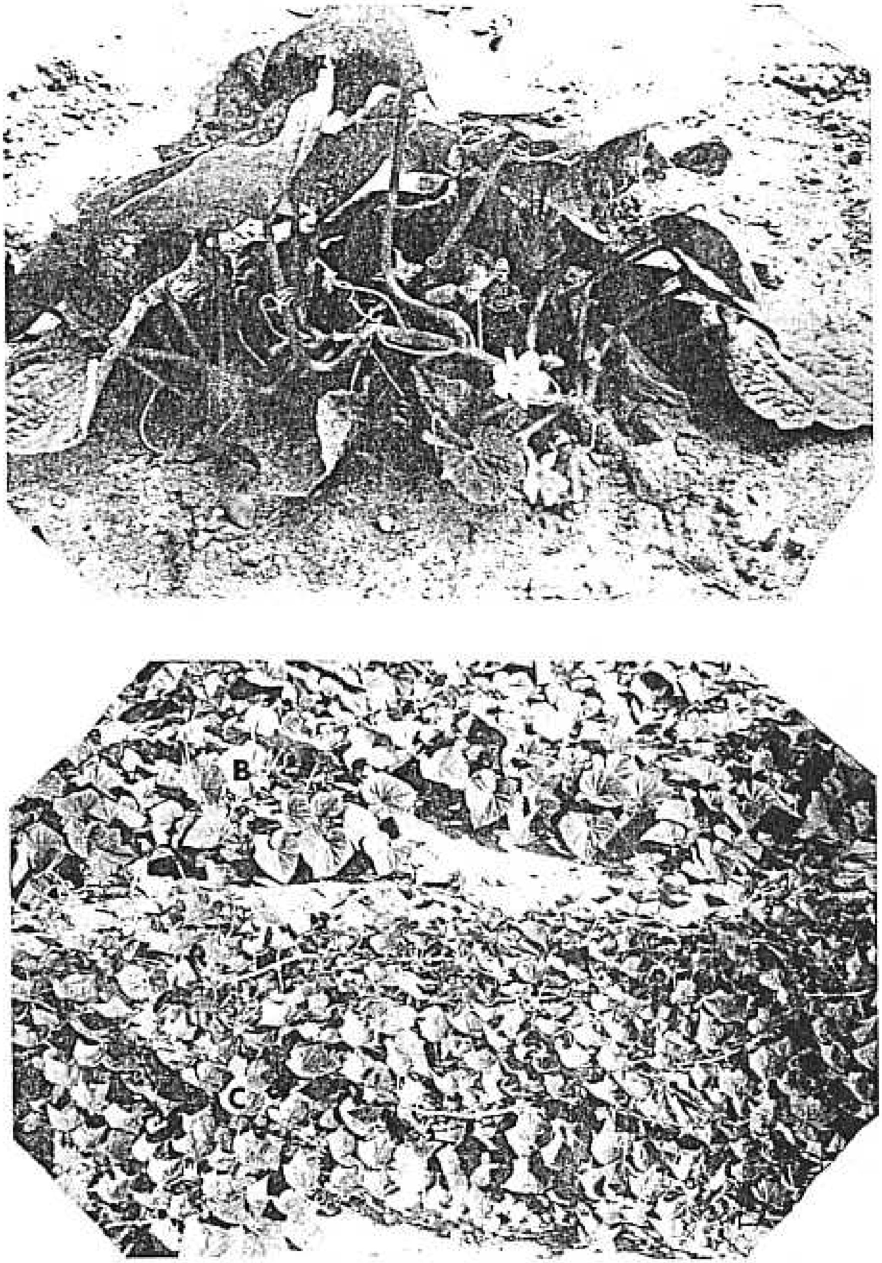

Fig. 8.2. Compact (A), normal (B) and little-leaf (C) plant types growing in the field in North Carolina.

sity tested of 296,000 plants/ha. However, the optimum density for yield (weight and value/ha) from once-over harvest of normal (tall, indeterminate) pickling cucumbers was as high as 850,000 plants/ha in Canada (Cantliffe and Phatak 1975b). Plants were grown in equidistant spacing from 460 × 460 mm (50,000) to 100 × 100 mm (850,000 plants/ha), with yield/ha increasing as plant density increased. Generally, however, it is recommended that normal plant types be grown at densities of 50,000 plants/ha for multiple harvest (Hughes et al. 1983; Morrison and Ries 1968) to 300,000 plants/ha for once-over harvest (O'Sullivan 1976).

The major problem with the use of the compact plant type is the high incidence of seed abnormalities such as cylindrical (instead of the typical flat) seed shape, and low (approximately 40%) percentage germination associated with the trait (Edwards and Lower 1981). The abnormalities were influenced mainly by maternal effects in the general sense, which could include cytoplasmic or maternal environment effects (Edwards and Lower 1982b). The observed inbreeding depression was partially responsible for smaller seed sizes in compact plants, but not for their lower percentage of emergence (Edwards and Lower 1983). If the seed problems cannot be solved by breeding, commercially acceptable stands of compact types could be attained by increasing the planting rate. Alternatively, two or more seeds could be pelleted using an artificial seed coating to make the small seeds easier to handle in planting equipment. However, the costs involved in seed coating may preclude its use in cucumber.

The determinate plant habit is controlled by the *de* gene (George 1970a, 1970b), and has been associated with higher yield and shorter vines (Denna 1971; Prend and John 1976). However, many gene loci are involved in modifying vine length, and it is possible to develop short-or long-vined lines that are determinate (Miller and George 1979). Unfortunately, determinate types do not tolerate high-density plantings any better than indeterminates. The optimum density for production was found to be the same as for the normal plant type in fresh-market (Munger et al. 1982) and pickling (Wehner and Miller 1987) cucumbers. Higher yield of the determinate type is due to concentrated fruit set with a greater fruit weight per plant at each harvest.

A major limitation to mechanization of the pickling cucumber harvest has been the lower yield associated with machines that do once-over harvest. Yield of marketable fruits from 'Earlipik' pickling cucumber under irrigated conditions in Ontario, Canada, was 39.7 vs. 23.2 Mg/ha for multiple-harvest vs. once-over, respectively (Tan et al. 1983). The gynoecious, determinate plant type may offer a solution to the lower yield of once-over machine harvest systems by producing a concentrated set of fruits.

Multibranched types produce more fruits per plant than normal types, but may require a lower planting density for optimum yield. Sources of multibranched plant habit include the little leaf mutant, 'Little John' (Goode et al. 1980), and the *Cucumis sativus* L. var. *hardwickii* line, LJ 90430. Inheritance of multibranched habit in 'Little John' was quantitative and ranged from 0.00–0.61 in several crosses evaluated for narrow-sense heritability (Wehner et al. 1987). Little leaf has not been evaluated as thoroughly in field trials as determinate and compact types, but it has a distinct appearance compared with the normal leaf (Fig. 8.2). 'Little John', having many small leaves, has been reported to be drought tolerant (Goode et al. 1980), and deserves additional research.

LJ 90430 had 11 laterals/plant compared with 2 for the monoecious inbred 'PG' (Horst and Lower 1978). LJ 90430 has been tested at densities of 4,000–86,000 plants/ha, and the optimum for fruit yield (number/ha) at mature seed stage was approximately 55,000 plants/ha (Delaney et al. 1983).

In addition to multibranched habit, LJ 90430 has the ability to set many fruits per plant, with an average of 80 fruits per plant at the mature seed stage in North Carolina trials (Horst and Lower 1978). It has been suggested that LJ 90430 and other lines of *Cucumis sativus* L. var. *hardwickii* be used in crosses to improve yield (weight per unit area) of cucumber by increasing the number of fruits per plant (Staub and Kupper 1985). Increase in fruit number would be fairly easy, given a narrow-sense heritability of 0.88 for fruit number from a newly formed population of Gy 14 × LJ 90430 (Horton et al. 1980). However, increased fruit number is only one component of yield per hectare, and the fruit weight per plant of LJ 90430 at mature seed stage and wide plant spacing was estimated to be the same as for Gy 14 (Nienhuis et al. 1980). Further, Gy 14 would probably have had a higher yield under conditions more favorable to its plant habit (denser plant spacing and harvest at immature fruit stage). In greenhouse studies of fruit growth, elite cultivars such as Calypso had greater fruit weight per plant than LJ 90430, even though they had fewer fruits per plant (Ramirez et al. 1987a).

Other multiple-fruiting lines of *Cucumis sativus* L. var. *hardwickii* are available to the cucumber breeder. When three of those lines (LJ 91176, PI 183967, and PI 215589) were used in backcrosses to three *C. s.* var. *sativus* recurrent parents, the BC_1 progeny had 32–65% more fruits per plant than the recurrent parent (Staub and Kupper 1985). A major problem was that the diameter and length of the fruits of the BC_1 progeny were smaller than those of the recurrent parent. Using number of fruits per plant × fruit volume (calculated from the diameter and length measurements) as an estimate of fruit yield, yield of the BC_1 progeny ranged from 12% less to 39% more than the *C. s.* var. *sativus* recurrent parent. The 39% increase was from the *C. s.* var. *hardwickii* line PI 215589, the line from which LJ 90430 was selected.

Greatest number of mature fruits per hectare on multibranched families derived from LJ 90430 were produced with a density of approximately 55,000 plants/ha, involving a spacing of 0.15 × 1.5 m per plant (Delaney et al. 1983). Yield of Gy 14 was still increasing as density was increased to 86,000 plants/ha, so it was not clear what the optimum density was for fruit number at the mature seed stage. LJ 90430 derivatives produced around 750,000 fruits/ha vs. 250,000 fruits/ha for Gy 14. In a study comparing 4 lines derived from 2 cycles of recurrent selection of a *Cucumis sativus* var. *hardwickii* × *C. s.* var. *sativus* population, the lines equaled or exceeded the yield of 'Calypso' in a multiple-harvest trial with 0.23 × 1.5 m plant spacing (Staub 1985). Fruit quality and length:diameter ratio were unacceptable for industry use, however. Overall, it appears that yield of commercially useable fruits has been improved by using LJ 90430 in breeding programs.

Recently, the determinate habit has been combined with multibranched habit from LJ 90430 to produce determinate plants with many lateral branches (Delaney and Lower 1984). There may be problems incorporating the traits into new lines, however. In crosses involving LJ 90430 and determinate inbred lines, the F_2 failed to fit a 3:1 ratio for determinate plant habit. The missing plants were those with determinate habit and multiple branches (Delaney and Lower 1985).

B. Sex Expression

Gynoecious sex expression was first reported by Peterson (1960) and developed into the inbred line MSU 713-5. That inbred provided a method for hybrids to be produced without hand pollination. In addition to making hybrid production economical, gynoecious sex expression provided a more concentrated fruit set and earlier maturity than the normal, monoecious type. Wehner and Miller (1985) reported that gynoecious × gynoecious and gynoecious × monoecious hybrids had significantly higher yield in the first harvest of a multiple-harvest trial than monoecious × monoecious hybrids, and remained higher in subsequent harvests. However, the differences observed in the later harvests were not significant.

Pollen must be available in fields of gynoecious cultivars in order for fruits to be set unless a parthenocarpic cropping system is being used. Adequate amounts of pollen are assured by mixing a monoecious and a gynoecious line to form a cultivar blend. Multiple-harvest yield of mixtures of monoecious pollinators with gynoecious hybrids was highest at 12.5%, and lowest at 100% pollinator (Miller 1976). Currently, blends of

12–15% pollinator are used in gynoecious hybrids in the U.S.

Aside from early maturity, gynoecious sex expression is also useful for providing the concentrated fruit set needed for once-over harvest systems. The main hindrance for the implementation of once-over mechanical harvesting systems has been the lack of economically acceptable yields when compared to those obtained by multiple hand harvest. Chemicals such as chlorflurenol have been used to induce simultaneous fruiting to increase yield for once-over harvest (Cantliffe and Phatak 1975a; Ells 1983). Such chemically controlled systems are not reliable due to the lack of stable gynoecious sex expression in cultivars tested, unfavorable environment × chemical interactions, and nonuniform stands.

Gynoecious inbreds are homozygous for the dominant genes *F* and *M*, or the recessive gene *gy* (Kubicki 1974; Robinson et al. 1976; Wehner et al. 1985). Plants are predominantly (not completely) gynoecious if they are heterozygous at the *F* locus (Kubicki 1969; Scott and Baker 1975). Commercial hybrids are usually produced by crossing gynoecious and monoecious inbreds in isolation, so the resulting hybrid is predominantly gynoecious. Completely gynoecious hybrids are considered desirable for once-over harvest. That can be accomplished by substituting gynoecious, androecious, andromonoecious or hermaphroditic inbreds for the monoecious parent in crosses with gynoecious inbreds (Pike and Mulkey 1971; Scott and Baker 1976; Staub et al. 1986; Tasdighi and Baker 1981). If a gynoecious × gynoecious hybrid is being produced, pollen can be obtained from the gynoecious paternal parent by spraying those plants several times with silver nitrate, silver thiosulfate, aminoethoxyvinylglycine, or other ethylene-inhibiting compounds, starting at the cotyledon stage (Kubicki 1965; Owens et al. 1980).

The *gy* gene has not been used commercially in the United States, but offers the possibility of economical production of monoecious hybrids by crossing a gynoecious inbred with a monoecious one. Monoecious hybrids may be useful as a component in a blend with a gynoecious hybrid to provide pollen for fruit production. Monoecious hybrids might also be useful for long-season fruit production with less chance of missing the optimum harvest stage due to weather and labor scheduling problems as happens with gynoecious hybrids.

The emphasis on gynoecious hybrids has hidden partly the fact that monoecious lines do well in multiple-harvest yield trials, especially for fresh-market cucumbers. For example, some of the higher-yielding lines in the 1983 through 1986 southern U.S. cooperative trials (29 environments) included 'Poinsett 76' (a monoecious inbred) and 'Dasher II' (a gynoecious hybrid), with average yields of 21.0 and 26.2 T/ha, respectively. The average yield of 'Dasher II' (released in 1982) was 25% higher than 'Poinsett 76' (an isoline of the cultivar released in 1966). Some of the yield difference is no doubt due to the fact that 'Dasher II' had 16 more years of breeding work behind it, which probably included selection for improved yield. A second point to consider is that predominantly gynoecious hybrids do as well as completely gynoecious hybrids in multiple-harvest trials, with little or no correlation ($r = 0.04$ spring, 0.36 summer) between yield and number of male nodes in a test of 56 gynoecious hybrids (data from 1983 North Carolina pickling cucumber trials).

Other traits, such as multipistillate flowering (due to the recessive *mp* gene), have been studied for possible use in increasing yield of cucumber for once-over harvest (Nandgaonkar and Baker 1981; Uzcategui and Baker 1979). It appears that the primary limitation in gynoecious plants for producing additional fruits during development is their inability to supply additional photosynthates. This problem also exists in lines with indeterminant plant habit (Ramirez et al. 1987a; Pharr et al. 1984). As a result, excess pistillate flowers simply abort. If the source (e.g., active leaves) is the limiting factor, simultaneous fruit set could be obtained by making the plant more efficient photosynthetically, or by slow but consistent fruit development (T. C. Wehner and D. M. Pharr, unpublished data).

C. Parthenocarpy

Parthenocarpy, ovary development without fertilization, provides cucumber growers with the ability to produce seedless fruits. Parthenocarpy is controlled by a single dominant major gene (*Pc*), as well as a number of minor modifying genes (Pike and Peterson 1969; Ponti et al. 1975). Theoretically, in parthenocarpic lines a larger proportion of photosynthates could be diverted to fruit tissue instead of producing seeds. Unfortunately, side-by-side comparisons of parthenocarpic lines with normal ones have been difficult to run because either bees must be kept out of test areas, or pollen must be excluded using completely gynoecious, sex-stable lines. On the other hand, pollen and bees are needed for the normal plants if they are to produce fruits. Tests run using nylon mesh cages to isolate the parthenocarpic lines showed a higher yield on the normal lines (G. E. Tolla, personal communication).

Parthenocarpy is useful in locations where bee activity is reduced (often due to cool, wet weather). For that reason, it is commonly used in northern Europe, where field production of that type is common. In Michigan, high yields (fruit weight and number per plant) of parthenocarpic fruits were obtained from 20 gynoecious × hermaphroditic F_1 hybrids tested in one environment (El-Shawaf and Baker 1981b). MSU

581H and MSU 662H had the highest general combining ability for yield of 17 hermaphroditic inbreds tested (El-Shawaf and Baker 1981a). MSU 364G and MSU 402G had the highest general combining ability for yield of 6 gynoecious inbreds tested (El-Shawaf and Baker 1981c).

Parthenocarpic habit has become indispensable to greenhouse cucumber production because it alleviates the need for bees. Individual plants in the greenhouse produce many fruits simultaneously, with yields of 5.5–23.7 kg/m^2 in experimental plots (see for example Peet and Willits 1987), compared with 1.2–7.0 kg/m^2 for slicer types or 3.8–5.1 kg/m^2 for pickling types in experimental field plots (Wehner 1985, unpublished trial results). The comparison is complicated by the fact that more intensive care is given greenhouse plants, and they are grown vertically on a trellis, which increases the leaf area/m^2 of soil surface. In small-plot experiments, fresh-market cucumbers grown vertically on a trellis yield 8–9 kg/m^2 compared with 4–6 kg/m^2 (depending on environment) when grown on the ground (Konsler and Strider 1973). Similar results were obtained by Hanna et al. (1987), who observed that 3.9–6.1 kg/m^2 marketable yield was produced on a trellis vs. 1.6–3.7 kg/m^2 when plants rest on the soil surface. Trellised plants had 29% more area per leaf, and 18–51% more plant weight than plants allowed to grow along the ground. Experiments with trellised cucumbers indicate that plant breeders might increase yield by developing cultivars with upright plant habit, a trait not known to exist in the species but perhaps obtainable from squash (*Cucurbita* spp.) through the use of genetic engineering techniques.

IX. SUMMARY

There are many approaches that should result in improved yield of cucumbers for fresh-market and processing uses. Ultimately, all approaches require a better understanding of the physiological limitations of cucumber plants, and how carbohydrates are manufactured by leaves, translocated through the phloem, and used by enlarging fruits.

Cucumber breeders interested in the development of high-yielding cultivars should make use of efficient trialing methods so they can maximize their gain. The breeder should resist the temptation to select for many traits in order to maximize gain on essential traits. It may be most efficient to develop cultivars for particular regions, both to restrict the number of breeding objectives, and to minimize the effects of genotype-environment interaction.

Plant architecture affects yield as well as suitability for particular types of production systems. Those who would like to maximize yield for once-over harvest systems might want to make use of slow fruit growth;

gynoecious sex expression; parthenocarpy; and determinate, dwarf, or multibranched plant habit. For multiple harvest, the objectives might be the same as for once-over harvest. However, traits like rapid fruit growth, indeterminate habit, little leaves, multiple branching, and long vines also should be considered.

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