CUCUMBER

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1. INTRODUCTION

Cucumber (*Cucumis sativus* var. *sativus* L.) is a member of the economically important family Cucurbitaceae which includes squash (*Cucurbita* ssp.), watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai], and melon (*Cucumis melo* L.). After tomato (*Solanum lycopersicum L*) and watermelon, cucumber and melon are cultivated more broadly than any other vegetable species (http://faostat.fao.org; Pitrat et al., 1999) where 2,427,436 hectares were harvested in 2004 producing 40,860,985 Mg under field and greenhouse culture. Production of cucumber is the second largest of all cucurbits (23.2 million tons), where China (553 Mg), Iran (30 Mg), Turkey (38 Mg) and the United States (23 Mg) represented 66 % of the world production in 2003.

The Curcurbitaceae consists of two subfamilies, Zanonioideae and the Cucurbitoideae (Jeffrey, 1980; Kirkbride 1993) (Figure 1). The Cucurbitoideae houses eight tribes, one of which (Melothrieae) includes the genus *Cucumis*, where the basic chromosome number is 2n = 2x = 24 (Dane and Tsuchiya 1976). *Cucumis* is partitioned into two subgenera designated as *Cucumis* (2n = 2x = 14 and 24) and *Melo* (2n = 2x = 24) that contain five cross-sterile species groups (Jeffrey 1980). The subgenus *Cucumis* comprises three or four Sino-Himalayan species, including *C. sativus* (2n = 2x = 14) and *C. hystrix* Chakr. (2n = 2x = 24). *C. sativus* houses several botanical varieties including var. *sativus*, the cultivated cucumber (hereafter referred to as *C. s.* var. *sativus*), and the wild, free-living var. *hardwickii* (R.) Alef. (hereafter referred to as *C. s.* var. *hardwickii*) (Kirkbride 1993).

Wild African *Cucumis* species (mostly 2n = 2x = 24) are cross incompatible with cucumber and melon, which are themselves cross-incompatible (Kroon et al., 1979). Likewise, the wild, free-living *C. hystrix* is only sparingly fertile with cucumber (Chen et al., 1995; 1997a&b). This species is found only in the Yunnan Province of Southern China, and has unique genetic attributes that make its taxonomic determination complex.

2. ORIGIN AND DOMESTICATION

The biosystematics and phylogeny of *Cucumis* species based on morphology, crossability, and protein analysis (Deakin et al., 1971; Staub et al., 1987&1992a; Perl-Treves and Galun, 1985) has led to an understanding of species relationships that have been largely confirmed by nuclear DNA analysis (Jobst et al., 1998; Zhuang et al., 2004). Most recently, Garcia-Mas et al. (2004) defined phylogenetic relationships among *Cucumis* species using ribosomal internal transcribed spacer sequences and microsatellite markers. Although their data did not agree with some of the previously described genetic relationships obtained using isozyme and restriction fragment markers

(Staub et al., 1992; Perl-Treves et al., 1985; Jobst et al., 1998), their description of a clear separation between *C. sativus* and the rest of the *Cucumis* species supported the earlier studies.

The center of origin for *Cucumis* species is likely Africa for the wild species. However, initial sites of domestication for melon and cucumber are probably the Middle East and Southern Asia, respectively, where genes from exotic sources have contributed extensively to plant improvement (Dane et al., 1980; McCreight et al., 1993; Staub et al., 1999). Cucumber (*C. s.* var. *sativus*) may have originated in Africa (Tapley et al., 1937), China, India, or in the Near East (Vavilov, 1926&1951; Harlan, 1975; De Candolle as cited by Hedrick, 1919), with domestication occurring later throughout Europe. It was domesticated about 3,000 years ago, and is indigenous to India (primary center of diversity; Jeffrey, 1980; De Candolle as cited by Hedrick, 1919; Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997). Cucumber was brought to Greece and Italy by the Romans (2nd century BC; Mesopotamia), and it appeared in France in the 9th century, in England in the 14th century, and in North America by the mid-16th century. The Spanish brought cucumber to Haiti in 1494, and cucumber was reported in Montreal, Canada (by Cartier), in Florida, U.S. (by Desoto), and in Virginia, U.S. (by Amidas and Barlow) in 1535, 1539, and 1584, respectively (Whitaker and Davis, 1962; Robinson and Decker-Walters, 1997). Cucumber's dissemination westward from India is indicated by the profusion of ancient names that describe it. The English word "cucumber" comes from the Latin name *Cucumis*. Likewise, the Bohemian *agyrka*, German *gurke*, Greek *Aggouria*, and European *gherkin* trace back to an ancient Aryan word.

C. s. var. *hardwickii* is a wild relative of *C. s.* var. *sativus* that grows in the foothills of the Himalayan mountains and is used by native peoples of Northern India as a laxative (Deakin et al., 1971). This botanical variety is sympatric and cross-compatible with *C. s.* var. *sativus* and possesses a multiple fruiting and branching habit that is not common in cucumber (Horst and Lower, 1978). *C. s.* var. *hardwickii*, therefore, represents the extreme in variation in *C. sativus* germplasm (Dijkhuizen et al., 1996), and, thus, has potential for increasing genetic diversity in commercial cucumber (Staub et al., 1992b).

The genetic variation in *C. s.* var. *sativus* accessions from India and China (the secondary center of diversity for cucumber) has been assessed by protein and DNA marker analyses (Staub et al., 1997&1999; Horejsi and Staub, 1999). Data indicate that variation exists among accessions from different Indian states, the differences between Indian and Chinese accessions are distinct, and that Indian and Chinese accessions themselves are distinctly different from other *C. s.* var. *sativus* genotypes throughout the world. Genetic differences exist among cultivars grown in the same growing region [e.g., Shanghai and the Hunan region (Southern China) and Jiang Su, and Anhui (Northern China)]. These facts suggest that cultivar differences among Indian and Chinese cultivars can exist over a relatively limited geographical range.

It is has been hypothesized that the genetic variation present in cucumber germplasm in Southern China is endemic to that region and/or has been augmented by the infrequent immigration of germplasm from Northern India via ancient Himalayan trade routes (Staub et al., 1997&1999). This germplasm has subsequently been isolated by surrounding mountain ranges (i.e., Himalayas) and the region's political and social structure. In contrast, the genetic diversity of Northern Chinese cucumber germplasm is thought to be a direct beneficiary of the "Silk Road", where germplasm (genetic variation) has been continually introduced from India via Eastern Europe.

Two contrasting hypotheses regarding the origin of *C. s.* var. *sativus* and *C. melo* have been proffered; fragmentation of seven haploid chromosomes to form 12 (Bhaduri and Bose, 1947) and fusion of 12 haploid chromosomes to form seven (Trivedi and Roy, 1970). These species have been under reproductive and evolutionary isolation for a considerable amount of time (Garcia-Mas et al., 2004; Chung et al., 2006). The phylogenetic relationship between *C. hystrix* (H) and *C. s.* var. *sativus* (S) is not substantially different since fertile amphidiploids have been synthesized

between *C. hystix* and *C. s*. var. *sativus* to create a synthetic species called *C. hystivus* (Chen et al., 1997a&b; Chen and Kirkbride, 2000; Chung et al., 2006). Furthermore, the development of the fully fertile *C. hystivus* (2n = 4x =38; HHSS; Chen and Kirkbride, 2000), partially fertile allotriploids (2n = 3x = 26; HSS), fertile diploids (2n = 2x = 14; SS), and partially fertile monosomics (2n = 15; SS + 1H) from *C. hystivus* and *C. s*. var. *sativus* matings indicates that chromosome reduction can occur through inbreeding and selection for chromosome number in this genus (Chen et al., 2004a&b). These facts, together with variation observed in the chloroplast genome among a broad array of *Cucumis* species, lend support to the hypothesis that *C. hystrix* is a progenitor species of *C. sativus*, or that they at least share a common ancestral lineage (Chung et al., 2006).

3. MARKET CLASSES OR CULTIVAR GROUPS

There are two basic cucumber types; those eaten fresh (i.e., fresh or slicing market types; Wehner and Horton, 1986) and those consumed as a processed product (processing or pickling types; Staub and Bacher, 1997). The major fruit types are the American processing and fresh market types, the Dutch gherkin and greenhouse types, the German Schalgurken type, the Mideast Beit Alpha type, and the Oriental trellis (burpless) type.

Fresh market types are field or greenhouse grown, and are usually between 15 (i.e., U.S. and Mediterranean) to 40 (i.e., European) cm in length. Less common fresh market types include Sfran (compact fruit types marketed in the Persian Gulf), and "lemon" cucumber (shape similar to a lemon with pale, greenish-yellow skin; hermaphroditic). Processing types differ depending on cultural preferences (e.g., U.S. vs. Europe).

Europe

European market types include glasshouse cucumbers, Mediterranean or "Mini" types for glasshouse or poly-tunnel production, and processing cucumbers (i.e., gherkins). Mini cucumbers have 14-17 cm long fruit. All of those types are primarily marketed for commercial production in Europe, North America, Greece, Spain, and Turkey.

European glasshouse types (32 to 40 cm long) are gynoecious, parthenocarpic (seedless), resistant to diseases such as powdery mildew (*Sphaerotheca fuliginea* (Schl. ex Fr.) Poll.), and cucumber mosaic virus (CMV), and will produce fruit under controlled climate conditions where commercial production is an exacting and costly enterprise. Most of the commercial cultivars are of Dutch origin. Disease resistance, high yield, and ability to grow at low temperatures are common breeding objectives. Some representative cultivars in Europe as well as in the U.S. and Canada include 'Jessica', 'Optima', 'Flamingo', 'Toska 70', 'Averyl', 'Niagara', 'Ladner', 'Sandra', 'Camaro', 'Dominica', 'Bella', 'Activa', and 'Sinaloa'. Some typical, disease resistant, gynoecious, mini cultivars are 'Jawell', 'Manar', 'Alamir', and 'Melita'.

United States

The first cultivars used in the U.S. were brought from Europe (ca. 1700s), and included 'Early Short Prickley', 'Long Green Turkey', 'Smyrna', 'Roman', and 'White Spined' (Tapley et al., 1937). Additional cultivars sold in the U.S. were 'China Long' in 1862 and 'Chicago Pickling' in 1888 (Whitaker and Davis, 1962). Beginning in 1880, there was interest in cultivar development by and for American growers.

In the first few decades of the 1900's new cultivars were developed with improved fruit shape and color (Anonymous, 1954-1958, 1960-1964; Barnes, 1969-1971; Minges, 1965-1968, Lower, 1973&1975). 'Model', introduced in 1946 with good fruit shape and adaptation to the southern production regions of the U.S., is a good example of that era. Then, beginning in 1937, emphasis was placed on disease resistance with the introduction of 'Shamrock', a cultivar resistant to CMV. After the introduction of cultivars with scab (causal agent: *Cladosporium cucumerinum* Ellis & Arthur) and downy mildew [causal agent: *Pseudoperonospora cubensis* (Berk. & Curt) Rostow] resistance, germplasm was developed with resistance to several diseases. In 1955, resistance to scab and CMV were combined to produce the line Wis. SMR 12. Resistance to additional diseases was identified, and eventually combined to produce 'Sumter' (field resistances to seven diseases) and the gynoecious line Wis. 2757, with resistance to nine diseases [scab, CMV, bacterial wilt (causal agent: *Erwinia tracheiphila* {(E. F. Smith) Holland}, angular leaf spot (causal agent: *Pseudomonas lachrymans* {(E. F. Smith and Bryan) Carsner}, anthracnose (causal agent: *Colletotrichum lagenarium* {(Ross.) Ellis & Halst}, downy mildew, powdery mildew (causal agent: *Sphaerotheca fuliginea* {(Schl. ex Fr.) Poll.}, target leaf spot (causal agent: *Corynespora cassiicola* {(Berk. & Curt) Wei}, and Fusarium wilt (causal agent: *Fusarium oxysporum* {(Schlecht.) Snyd. & Hans f. sp. *cucumerinum* Owen}] (Table 1). Diseases where resistance needs to be incorporated into new cultivars include Rhizoctonia fruit rot [causal agent: *Rhizoctonia solani* Kuhn; telemorph *Thanatephorus cucumeris* {(A. B. Frank) Donk}], gummy stem blight [causal agent: *Didymelia bryoniae* (Auersw.) Rehm], watermelon mosaic virus (WMV) race 1, and zucchini yellow mosaic virus (ZYMV).

Relatively slow progress was made in the improvement of other traits such as sex expression and plant habit. 'Midget' was a dwarf-determinate cultivar introduced in 1940 (Table 1). The dwarf character was not used extensively, however, until later with the introduction of 'Castlepik', which was a semi-dwarf cultivar with determinate flowering habit. Monoecious hybrids were introduced in 1945, but seed was too expensive to permit wide commercial use. Development of gynoecious sex expression by Peterson and Anhder (1960) permitted hybrids to be produced economically. 'Spartan Dawn', developed from the gynoecious inbred 713-5, was the first (1962) gynoecious hybrid released for industry use. This initial release was followed by the continued development of public gynoecious inbred lines between 1960-2004 (e.g., the Gy series, Gy-2, -3, -7, -8, and -14). Recent breeding efforts (1970-2000) have focused on improved fruit quality, yield, earliness, and adaptation to a broad array of U.S. production environments. Yield in once-over harvest systems may be improved by the introduction of dwarf plant types. However, research with the compact mutant (*cp*; Kaufman and Lower, 1976) for high-density cultivation, or multi-branching types such as littleleaf (Goode et al., 1980) that possesses simultaneous fruiting has not resulted in successful culitvars.

4. GENETIC RESOURCES

The primary, secondary, and tertiary gene pools of *Cucumis* have been defined by Bates et al. (1995), den Nijs and Custers (1990), and Raamsdonk et al. (1989). Although the primary gene *Cucumis* pool includes *C. s.* var. *sativus* and var. *hardwickii*, recent crossing and molecular analyses indicate that *C. hystrix* should perhaps be included in this gene pool (Chen and Kirkbride, 2000; Chen et al., 2004a). Wide hybridization in the *C. sativus* gene pool continues to be utilized for increasing the genetic diversity in cucumber (Nikolova et al., 2002). The secondary gene pool, however, includes wild African *Cucumis* species of varying ploidy levels, which are cross-incompatible with *C. sativus* (den Nijs and Custers, 1990).

The most recent compendium of cucurbit germplasm provides documentation of 68 world collections (Bettencourt and Konopka, 1990). It describes holdings in national genebanks, cites important breeding collections, and provides general information about these holdings, including their maintenance, availability, and evaluation. In Europe, the International Plant Genetic Resources Institute (IPGRI) coordinates institutional germplasm holdings. In the U.S., plant germplasm is maintained and evaluated by the U.S. National Plant Germplasm System (NPGS). The regional plant introduction (PI) station of NPGS at Ames, Iowa houses about 1,350 *C. sativus* accessions of worldwide origin. Molecular evaluation of this collection indicates that PI accessions are genetically diverse, not in Hardy-Weinberg equilibrium, and that they differ markedly from commercial germplasm in genetic structure (Meglic et al., 1996; Staub and Ivandic, 2000; Staub et al., 2002a). However, many of these accessions are as homozygous and homogeneous as elite inbred lines.

Plant introductions (i.e., PIs) have contributed significantly to cucumber improvement, and have been detailed by Tatlioglu (1993). Additional germplasm that has supplied traits for cucumber improvement include PI 183056 (India; large root size), PI 183967 (synom. LJ 90430; India; multiple lateral branching, sequential fruiting, nematode resistance), PI 197087 (India; downy mildew resistance), 200815 (Myanmar; powdery mildew and gummy stem blight resistance), PI 200818 (Myanmar; bacterial wilt resistance), PI 209065 (U.S.; high yield), PI 212233 (Japan; powdery mildew resistance), PI 220860 (South Korea; gynoecy), and PIs 418962, 419008, 419009, and 419135 from China [multiple disease resistances (Peterson et al., 1986a&b; Staub et al., 2002a)]. Other important germplasm used in cucumber improvement include 'Riesenschaal' (Germany), 'Zeppelin' (Germany), 'Chinese Long' (Japan), 'Tokyo Long Green' (Japan) 'Spotvrije' (The Netherlands), and ILG 58049 (The Netherlands; Peterson et al.,1986a&b).

5. CURRENT GOALS OF BREEDING

Cucumber improvement is a complex process involving the refinement of populations derived from intercrossing elite and/or exotic (unadapted) germplasm, the extraction of inbred lines from such populations, and the identification of commercially acceptable F_1 hybrids. Early genetic enhancement of cucumber (1850-1980) focused mainly on the incorporation of disease resistance and changes in plant architecture (e.g., sex expression, growth habit) that were augmented by improved cultural practices (Galun, 1961; McCollum, 1934; Sitterly, 1972; Peterson, 1975; de Ponti, 1975; George, 1970; Kubicki, 1980). General reviews of cucumber breeding (Lower and Edwards, 1986; Tatlioglu, 1993), and an examination of processing cucumber production (Staub and Bacher, 1997) have provided for rather complete treatments of cucumber improvement and culture. Therefore, the genetics and breeding information presented herein seeks to add to this early knowledge base, with an emphasis on new and emerging technologies as they relate to standard, commonly practiced breeding methods. Focus is placed on processing cucumber breeding since its breeding is relatively complex and the application of emerging technologies is well documented.

Yield and quality are a major focus of cucumber improvement and consist of many extensively reviewed, interrelated traits that are often the focus of the cucumber breeder (Lower and Edwards, 1986; Tatlioglu, 1993). These quantitatively and qualitatively inherited traits range from disease resistance to plant and fruit architecture and habit. Because of their diverse genetic nature, importance to plant improvement, and application in marker-assisted selection (MAS), the physiological interrelationships and genetics of a number of these traits are discussed below.

Yield

Yield has been a focus of cucumber breeders for over 50 years (Lower and Edwards, 1986; Wehner, 1989; Wehner et al., 1989). During the middle part of the 20th century, yield of U.S. processing cucumber maintained a steady increase from 4,685 kg/ha in 1949 to 11,455 kg/ha in 1979, an average annual increase of 226 kg/ha (Lower and Edwards, 1986). Similarly, yield trials of five popular gynoecious processing cultivars from the Southeastern United States released between 1969 and 1987 revealed an average annual yield increase of 400 kg/ha (Wehner, 1989). By 1980, the average yield of US processing cucumbers was 12,550 kg/ha, triple that of 4,076 kg/ha in 1920 (USDA, 1940, 1981). Most of the increase in yield during this period can be attributed to improved cultural practices and breeding for disease resistance (Lower and Edwards, 1986; Wehner 1989; Wehner et al., 1989). The introduction of the gynoecious flowering habit increased early yield, but did not affect total yield as measured over multiple harvests (Wehner et al., 1989).

As improved cucumber yield became increasingly important, it became the focus of many studies beginning in the late 1970's. Research conducted on many aspects of yield including breeding methodologies (e.g., selection methods and selection criteria), optimizing yield trials (e.g., methods to measure yield and optimal plot size), and the genetics of yield (e.g., heritability and genotype by environment interactions) from the late 1970's to the late 1980's are reviewed by Wehner (1989). Studies indicate that improvement by direct selection for yield is difficult. Yield is quantitatively inherited, has a low heritability [i.e., narrow-sense heritability (h^2) of 0.07 to 0.25], and is influenced mainly by genotype and environment, and to a lesser degree by genotype × environment interactions. Thus, selection for yield during population development should occur in intermediate stages of a recurrent selection scheme on a plot basis rather than on individual plants. Yield may effectively be evaluated in small (one row, single replication and harvest), multi-location (two to three) trials over seasons or years. The optimal time to harvest in trials depends upon a harvest index that is based on the number and weight of oversized fruit in check (control) plots.

Measurement of cucumber yield is often difficult because the fruits are harvested before they reach physiological maturity (yield measurement is reviewed by Wehner 1989). Cucumber growers usually measure yield by volume or weight per unit area, but the volume and weight of immature fruit can change rapidly from day to day, thus yield is dependent on the time of harvest. Converting yield to market value of processing cucumbers is further complicated because harvested fruit are graded by diameter where the smallest fruits have the greatest value, while oversized fruit have little or no commercial value. Although several methods for measuring yield (i.e., volume, mass, number, or dollar value) have been investigated, the most efficient measurement of yield in research studies is the total (marketable and oversize) number of fruits per plant, since it has a higher heritability, is more stable over time, and is easier to measure than other yield measurements. Furthermore, fruit number is highly correlated (genetic correlation = 0.87) with fruit weight (Wehner 1989).

Ironically, the increase in research on yield did not produce an increase in yield of U.S. processing cucumber, which has reached a plateau since the early 1980's (Shetty and Wehner, 2002; Fazio et al., 2003a; USDA, 2004). Mixed results have been obtained when selecting directly for yield, which may partially be explained by low heritability and environmental influence, combined with the difficulty in measuring yield (Wehner, 1989). The most effective approach to breeding for yield may be selecting for other traits correlated with yield that have a higher heritability (Wehner, 1989; Cramer and Wehner, 1998a&b; Cramer and Wehner, 2000a). Such traits correlated with yield are commonly referred to as yield components, and include number of harvests per plant, stem length, number of branches per plant, number of flowering nodes per

branch, time to anthesis, percentage of pistillate flowers, and percentage of fruit set (Cramer and Wehner 1998a; Cramer and Wehner, 2000a). These traits can be manipulated to create various genotypes that possess an array of architectural habits. Recent studies suggest that MAS may be used to augment phenotypic selection for yield components (Fazio et al., 2003b; Fan et al., 2006).

Yield Components

Correlations among traits are important when manipulating plant architecture for yield improvement, since source/sink relationships provide practical constraints on fruit development. Correlations between yield component traits as well as with yield have been investigated in a variety of cucumber germplasm including slicing populations (Cramer and Wehner, 1998a&b), processing populations (Serquen et al., 1997a; Cramer and Wehner, 1998b; Cramer and Wehner, 2000a; Fazio, 2001), hybrids (Cramer and Wehner 1999a), and germplasm derived from *C. s.* var. *hardwickii* (Fredrick and Staub 1989). Correlative effects, a plant's reproductive biology (e.g., days to anthesis and sex expression), and gene action must be considered during breeding. Thus, studied attention to yield components has included the evaluation of the U.S. cucumber germplasm collection and elite lines for their combining ability for yield to create high-yielding wide- and narrow-based populations with acceptable fruit quality (Shetty and Wehner, 2002; Walters and Wehner, 1994; Wehner, 1997; Wehner, 1998; Wehner et al., 2000a&b).

Sex Expression

The type (e.g., gynoecious or monoecious) and intensity of sex expression is important to commercial cucumber production since differences in sex type and flowering can affect harvest date and relative yield. Genes that are hormonally controlled and influenced by growing environment affect both the type and intensity of sex expression (Lower and Edwards 1986; Tatlioglu 1993; Staub and Bacher, 1997).

Genetics of Sex Expression. Cucumber sex phenotypes are mainly monoecious (staminate and pistillate flowers) or gynoecious (pistillate flowers only), but androecious (staminate flowers only), hermaphroditic (perfect flowers), andromonoecious (staminate and perfect flowers), and trimonoecious (staminate, perfect, and pistillate flowers) types also exist. Plants possessing pistillate and perfect flowers have also been observed and used in hybrid production (El-Shawaf and Baker, 1981a). These sex types are determined by three major loci (*F*, *M*, and *A*; Shifriss, 1961; Galun, 1961 and Kubicki, 1969). The *F* locus influences the degree of femaleness (*FF>Ff>ff*), while the *M* locus determines whether flowers are unisexual (*M_*) or bisexual (*mm*). The *A* locus conditions increased male tendency if a plant is homozygous recessive *aa* and *ff*. Interactions between these loci yield the basic sex types found in cucumber.

While this three-gene model describes the basic regulation of sex types, a plant's phenotype is also influenced by modifying genes and environmental factors (Serquen et al., 1997a&b). The existence of sex modifying genes is supported by the observation that inbred gynoecious plants differ in their level of gynoecy and their capacity to confer femaleness in F_1 hybrids (Kubicki, 1969, Zhang et al., 1992). Monoecious plants also vary quantitatively in sex expression, ranging from predominately staminate to predominately pistillate. In fact, there are at least five genes that modify the expression of gynoecy in cucumber (Serquen et al., 1997b; Fazio et al., 2003a). Thus, hybrids between monoecious and gynoecious lines can show considerable variation in the frequency of female flowers depending upon the level of gynoecy in the parents (the *F* locus and the constitution of alleles at sex modifying loci). This variation in the level of gynoecy in

gynoecious × gynoecious and gynoecious × monoecious hybrids remains a potential deficiency in many commercial cultivars.

Hormonal Factors Controlling Sex Expression. Genetic control and environmental variation of sex expression is mediated through changes in plant hormonal levels. Current theory holds that sex expression in cucumber is regulated by a balance between ethylene, auxins, absissic acid (ABA) and gibberellins (GA; Roy and Saran, 1990; Galun, 1959). While ethylene is considered the primary hormone affecting femaleness (Byers et al., 1972), gibberellins regulate male sex expression (Atsmon et al., 1968; Rudich et al., 1972a&b). Ethylene mediates primordial changes to determine gynoecy where the enzyme ACC (1-aminocyclopropane-1-carboxylic acid) synthase plays a critical regulatory role. Trebitsh et al. (1997) isolated and mapped a partial sequence of the gene *CsACS1*, which co-segregates with *F* in cucumber. Another ACC synthase (*CSACS2*) gene was described by Kamachi et al. (1997; 2000), and subsequently the gene for femaleness (dominant *F* allele) in cucumber was characterized and isolated (Mibus and Tatlioglu, 2004). Sequencing of gene regions and assessment of their function will likely further elucidate the genetics of flower development including sex formation (Przybecki et al., 2004; Yamasaki et al., 2003).

Breeding For Improved Gynoecy. Associations between the number of female flowers per plant (sex expression) and fruit per plant (yield) have been identified in several studies. Selection for gynoecy has been successful in segregating progeny derived from European glasshouse by Chinese cultivar matings (Fang et al., 1995). In four U.S. slicing cucumber populations over several cycles of selection, Cramer and Wehner (1998a) found that the number of female flowers was positively correlated with yield in some population-season combinations. Highly significant, positive correlations (r) between percent pistillate nodes and yield were also identified in one of four pickling populations, with moderate, positive correlations in another (Cramer and Wehner, 2000b), suggesting sex expression has potential for increasing yield through indirect selection. In the other two populations, however, slight negative correlations between the two traits were identified. While Serquen et al. (1997b) found a slight negative phenotypic correlation ($r = –0.27$) between sex expression and the number of fruits per plant, Fazio (2001) found a positive correlation ($r = 0.24$) with the number of females nodes on lateral branches and total fruit per plant. Using similar germplasm, Fan et al. (2006) identified a positive correlation ($r = 0.40$) between gynoecy and fruit number. These data suggest that the association between yield and sex expression varies between populations and growing environments.

The most noticeable effect of sex expression on yield is not in total yield over multiple harvests, but on early yield. Gynoecious × gynoecious and gynoecious × monoecious hybrids produce significantly higher yields in the first harvest than monoecious × monoecious hybrids, but there is no significant difference among these hybrids for total yield over multiple harvests (Wehner and Miller, 1985). Because of their early, concentrated fruit set, gynoecious hybrids were instrumental in establishing a system for once-over mechanical harvesting of processing cucumber (Lower and Edwards 1986; Wehner 1989). Now almost all once-over mechanical harvest operations use exclusively gynoecious hybrids (Staub and Bacher, 1997).

Earliness

Earliness and stable gynoecious sex expression are important components of yield in processing cucumber, especially in once-over machine harvest operations. The introduction of early, gynoecious lines possessing a uniform, concentrated fruit set made once-over machine harvest systems economically practical (Lower and Edwards, 1986; Wehner, 1989). Earliness is

often measured as days to anthesis or days to first harvest. Days to anthesis was found to be negatively correlated ($r = –0.23$) with the number of fruit per plant (i.e., fewer days to anthesis correlates to more fruit per plant; Serquen et al., 1997b). Fazio (2001) found a comparable result in a similar population in 2000 ($r = –0.31$), but these two characteristics were not significantly correlated in 1999. Additionally, a significant, positive correlation ($r = 0.26$) was identified between days to first harvest and number of fruit per plant in 1999. Interestingly, days to first harvest and days to anthesis were not correlated.

Multiple Lateral Branching

Evidence from several studies indicates that selection for multiple lateral branching (MLB) types should increase cucumber yield (i.e., fruit per plant). Number of lateral branches was found to be positively correlated ($r = 0.58$ to 0.42) with the number of fruit per plant in a processing cucumber population in two locations over two years (Fazio, 2001). Likewise, significant, positive correlations between yield and MLB were also detected in several diverse populations (Fredrick and Staub, 1989; Cramer and Wehner, 1998a; Cramer and Wehner, 1999a; Cramer and Wehner, 2000a).

Path analysis was employed in eight processing and slicing cucumber populations to determine the magnitude of correlations of yield component traits with each other as well as with yield (Cramer and Wehner, 2000b). Of the yield components tested (branches per plant, nodes per branch, pistillate nodes, and fruit set), only branches per plant were consistently correlated ($r > 0.7$) with yield (i.e., over populations, cycles of selection, and environments). Furthermore, the correlation between MLB and yield increased (from $r = 0.67$ to 0.82) with continued selection for yield (i.e., from early to later cycles). From their analyses, Cramer and Wehner (2000b) suggested that efforts to improve yield in cucumber should focus on increasing MLB. Multiple lateral branching is, in fact, quantitatively inherited (at least four genes; Wehner et al., 1989; Serquen et al., 1997a; Fazio et al., 2003a) with mostly additive genetic variance and a narrow sense heritability (h^2) of 0.00 to 0.61 depending on the population exploited, making it a candidate for use in plant improvement.

Fruit Size

Processing cucumbers in the U.S. are graded based on their size, with the smaller fruit usually bringing a higher price (Lower and Edwards, 1986; Tatlioglu, 1993). Thus, fruit length:diameter (L:D) is considered a yield component, since it determines marketable yield. For example, U.S. processing cucumbers must have an L:D of 2.9 to 3.3 to be commercially acceptable (Staub and Bacher, 1997). Although important for marketable yield, L:D is generally associated with lower fruit number per plant ($r = –0.98$, Serquen et al., 1997a; $r = –0.27$ to $–0.36$, Fazio, 2001).

Parthenocarpy

Parthenocarpy (seedless fruit) is an economically important yield- and quality-related trait in cucumber. Parthenocarpy is regulated by endogenous plant growth regulators (e.g., diffusible auxin, IAA), and their balance is dramatically influenced by environment (Kim et al., 1994). Phenotypic selection has, however, resulted in the development of parthenocarpic hybrids (More and Budgujar, 2002) and genetic stocks (Sztangret et al., 2004).

It is clear that parthenocarpy is genetically controlled, but there is little agreement regarding the number and type of gene action involved. Hawthorn and Wellington (1930) and Meshcherov and Juldasheva (1974) suggested that parthenocarpy is recessive and controlled by a

single gene. Kvasnikov et al. (1970), however, proposed that many incompletely recessive genes control parthenocarpy. Pike and Peterson (1969) simultaneously proposed that a single dominate gene expressing incomplete dominance controls parthenocarpy in cucumber.

Results of de Ponti and Garretsen (1976) and El-Shawaf and Baker (1981a&b) indicate that parthenocarpy may be quantitatively inherited in this species. In fact, studies by Sun et al. (2006a&b) indicate that the genetics of parthenocarpy are complex. Generation means analyses in cross-progeny derived from elite processing cucumber lines indicated gene action generally could not be adequately explained by a simple additive-dominance model. Moreover, the analysis of F_3 families indicated that more than five genes control parthenocarpy, and that growing environment and epistatic interactions dramatically influence trait expression.

Fruit Quality

External quality

External fruit quality differs for various market types (Lower and Edwards, 1986). For European glasshouse types, uniform green fruit must be fine-spined and possess a relatively high L:D (> 4), while dark green Asian greenhouse types tend to bear comparatively more warts. In contrast, medium green processing cucumbers in the U.S. possess a shorter L:D, and are typically blocky in shape. Such differences necessitate distinct breeding objectives, even though many external fruit quality characteristics are simply inherited (1-3 genes; Pierce and Wehner, 1990).

Internal quality

The requirements for internal fruit quality differ dramatically between fresh market and processing types. For fresh market, breeding for traits such as keeping quality (e.g., no shrinkage) and internal taste (e.g., non-bitter) and color characteristics are important (Wehner, 1996). Processing practices must be considered when breeding for improved pickling fruit quality (e.g., fruit storage characteristics; Wehner et al., 2000b; Shetty and Wehner, 2002). The U.S. cucumber processing industry produces a wide variety of products using three main processing methods: brine (fermented), fresh-pack (pasteurized), and cold-pack (refrigerated; Lower and Edwards, 1986; Miller and Wehner, 1989; Staub and Bacher, 1997). Brining, in general, involves preserving harvested cucumbers in a high salt solution (5-16% sodium chloride), which is allowed to ferment for several weeks. Breeding requires close scrutiny and testing for traits related to postharvest mesocarp disorders (Serce and Staub, 1999) and processing quality (seed cavity disorders; Staub and Bacher, 1997). In processing cucumber, particular attention is paid to the evaluation of seed cavity size and maturation, and fruit anomalies such as placental hollow and carpel separation (Lower and Edwards, 1986). Even though genetics of these quantitatively traits are not well documented and trait expression is dramatically affected by environment, recurrent selection has successfully improved fruit quality in U.S. processing cucumber (Wehner et al., 1996).

Disease and Insect Resistance Traits

The genetic control for resistance to scab (*Ccu*), downy mildew (*dm*), bacterial wilt (*Bw*), angular leaf spot (*psl*), anthracnose (*Ar*, *cla*), target leaf spot (*Cca*), Corynespora leaf spot, and Fusarium (*Foc*) is conditioned by few genes (Robinson et al., 1976; Pierce and Wehner, 1990). Seedling cotyledon tests have been developed to screen for resistance to the pathogens of each of these diseases allowing for the release of a wide array of resistant cucumber market types (Lower

and Edwards, 1986). Seedling screening procedures are amendable to simple backcrossing and selfing strategies for line development.

In contrast, the genetics of resistance to viruses, such as CMV (*Cmv*), WMV (*Wmv*), Potyvirus, and ZYMV (*zymv*), or to powdery mildew (*pm-1*, *-2*, *-3*, *pm-h*), green mottle mosaic virus (GMMV), gummy stem blight, belly rot, cottony leak (causal agent: *Pythium* spp.), phytophthora rot (causal agent: *Phytophthora capsici* Leo.), and gray mold [causal agent: *Rhizopus stolonifer* (Ehrenb.: Fr) Vuill] is complex. Resistance to these diseases is quantitatively inherited and/or influenced dramatically by other pathogens (i.e., virus interactions) and by growing environment. Breeding for resistance to these diseases requires exacting test protocols and extensive replicated testing (field and greenhouse) in multiple environments employing artificial and/or natural inoculation (Wehner and Shetty, 2000; St. Amand and Wehner, 1995; Uchneat and Wehner, 1998; Zijlstra et al., 1995). Usually accessions are screened for resistance, populations are developed through recurrent selection procedures, and then lines are extracted by backcrossing with subsequent selfing (St. Amand and Wehner, 2001a&b; Wehner et al., 2004). Lines and hybrids are then rigorously tested to determine their suitability for release (Wehner et al, 1996).

There is little genetic resistance to insect pests in cucumber (Dhillon and Wehner, 1991; Walters et al., 1993). One notable exception is resistance to root-knot nematode [causal agent: *Meloidogyne javanica* (Treub) Chitwood] for which resistance was found in *C. s.* var. *hardwickii* (PI 183967; Walters et al., 1991). In this case, resistance was conditioned by a single recessive gene (*mj*). Introgression of this gene required the development of screening protocols (Walters et al., 1992) and rigorous greenhouse selection in replicated "split-pot" tests (i.e., evaluating resistance for different nematode species) with subsequent field evaluation (Walters et al., 1999). Introgression breeding resulted in the release of resistant populations (Walters et al., 1996) and lines (Walters et al., 1997) of major importance to Southern U.S. growing regions.

Stress Resistance

Abiotic stresses (e.g., temperature extremes, water deficiencies) often depress yield, increase plant susceptibility to disease, and reduce fruit quality (Staub, 1996; Staub and Wehner, 1996). There is stress tolerance variability in cucumber germplasm (Chung et al., 2003; Smeets and Wehner, 1997; Staub and Krasowska, 1990; Staub et al., 1991; Walters and Wehner, 1994), and breeding has allowed gain from selection to produce germplasm with improved tolerance for some stresses (Staub et al., 1988; Staub et al., 1991). However, the genetics of stress resistance is largely not understood, and is, in most cases, likely complex and substantially influenced by growing and/or postharvest storage environment. For instance, the phenotypic expression of "pillowy," a fruit disorder caused by water deficiency, is directly influenced by fruit calcium concentration and is affected by temperature and relative humidity (Thomas and Staub, 1992; Staub and Navazio, 1993). Although the intensity of pillowy can be mitigated by appropriate postharvest handling (Navazio and Staub, 1994), the effect is genotype dependent (Serce and Staub, 1999). Large environmental effects make breeding for improved stress resistance expensive and laborious.

6. BREEDING METHODS AND TECHNIQUES

Breeding objectives are determined by the requirements associated with cucumber market classes [e.g., U.S. processing (pickling), U.S. fresh market, European glasshouse, Mediterranean, Asian glasshouse]. Cucumber development for greenhouse and field growing environments involves specific cultural (e.g., chemically induced sex conversion) and market considerations

(e.g., fruit type) that have been critically reviewed elsewhere (Lower and Edwards, 1986; Tatlioglu, 1993; Staub and Bacher, 1997). Only in rare cases are traits not inherited as Mendelian factors (Chung et al., 2003; Havey, 1997). Breeding plans are driven by historically proven procedures and emerging technologies. Often, genotypes with unique plant architecture (e.g., determinate, multiple lateral branching types) must be evaluated to determine cultural conditions to optimize their performance prior to their release (Staub et al., 1992b; Schultheis et al., 1998).

Breeding Plan

Program objectives (i.e., market type) determine the choice of parental types (plant introductions, accessions, cultivars, and breeding lines) that are selected based on the traits they possess. Typically, breeding follows a series of steps that consist of population development and improvement, line extraction, and hybrid evaluation.

Several breeding methods are usually employed in parallel to accomplish multiple objectives. That is, one program segment might use recurrent selection to develop a base population that possesses general adaptation, early yield, and appropriate fruit type. Pedigree selection might be used when crossing two parents to develop inbred lines with high, early yield borne on a unique plant habit (i.e., determinate) found in one parent, and high quality fruit (i.e., brine quality) along with other unique characteristics (i.e., high carotenes, disease resistance) that are typical of the other parent. A third program segment might use backcross breeding to make a disease resistant version of a parthenocarpic hybrid with top performance. Nevertheless, strategies that incorporate selection for disease resistance and improved yield require judicious implementation since selection for disease resistance can be negatively correlated with yield (Staub and Grumet, 1993). As molecular marker technologies become more efficient, effective, and affordable, they will be increasingly used to augment and enhance conventional phenotypic selection during population development and/or inbred line development.

Population Development

Recurrent Selection. Although cucumber is a cross-pollinated crop, population improvement methods that are popular in other cross-pollinated crops have not been frequently utilized. This is primarily due to the species' large plant size, and its low rate of natural outcrossing. In addition, the relatively few existing breeding programs (e.g., currently two public and four private breeders in the U.S.) often cannot bear the expense (i.e., additional years) of population development for quantitative traits during cultivar improvement.

The most effective method for the improvement of quantitative traits, such as yield in cucumber, may be recurrent selection. However, the initial populations must possess the necessary genetic diversity for selection (e.g., flesh color, fruit size, and disease resistance; Wehner and Cramer, 1996). Due to the inherent characteristics of cucumber (i.e., large plant size and five-month generation time), recurrent selection methods (i.e., mass, full- and half-sib) are inherently limited to a few generations (2-3) per year (Wehner, 1989).

Intercrossing two to four superior, unrelated hybrids can create elite populations. Wide-based populations are created by manual intercrossing 20 or more elite cultivars for two or more generations, and then using bees for intermating in an isolation block for two or more generations before applying mild selection pressure for important quantitative traits such as yield and internal fruit quality. Simple recurrent selection can be utilized for selection among single-plant hills for a set of highly heritable traits. In contrast, reciprocal recurrent selection permits

simultaneous improvement of two populations for traits with low heritability such as yield-associated combining ability (Cramer and Wehner, 1998a&c; Cramer and Wehner, 1999b). This is an expensive procedure, but produces two populations that are useful for male and female line development during elite hybrid construction.

Population development requires the identification of methods for yield testing that are efficient for large-scale yield trials (Wehner, 1989). Traditionally, recurrent selection procedures evaluate at least 200 individuals (or progenies of individuals) per population where 20 are intercrossed to create the next cycle of selection. Once a unique population is developed, the population can then be released and/or line extraction can proceed for hybrid evaluation and production (e.g., Wehner, 1998a&b).

Line extraction

Pedigree Breeding. Selection based on pedigree is the most common cucumber breeding method. To initiate pedigree breeding, two or more adapted parents are chosen which complement each other in their traits. For instance, where the objective is to produce new lines with high yield, early maturity, high fruit quality, and good disease resistance, one parent might be generally acceptable (yield, earliness, fruit quality) except for disease resistance and the other might be generally good (disease resistance, yield, earliness) except for fruit quality. Crossing the two parents results in a hybrid (F_1), which is then self- or sib-pollinated to produce a segregating (F_2) population, and subsequent selection for highly heritable traits produces the F_3 generation. If multiple progeny are tested from each selected F_2 plant (e.g., selection for anthracnose races 1 and 2), the best plants are typically chosen from each of the best F_3 families and are then used to produce the F_4 generation.

Beginning at the F_4 (or S_4) generation, selection emphasizes family-row performance for quantitative traits, and superior plants within family-rows are selected for the next generation. The F_6 (or S_6) are relatively uniform, and can then be handled as inbred lines. Selection typically involves the use of eight-plant plots for traits such as early flowering, number of pistillate flowers, and fruit number and quality. The number of plants or families selected typically in a cross might decrease from 54 F_2 plants to 36 F_3 families, 24 F_4 families, and then 18 F_5 lines during the selfing process.

Single-seed Descent. Single-seed-descent, a modification of pedigree breeding, is utilized to rapidly develop inbred lines by self-pollination in greenhouses and winter nurseries without selection until later generations (e.g., S_3 to S_6). This method can be employed to improve quantitative traits such as yield and earliness, rather than qualitative traits such as disease resistance. Selection for many qualitative traits (e.g., spine color) can be performed in early generations (e.g., F_2, F_3/ S_3) by eliminating plants or families with unsuitable trait values.

Backcross Breeding. Backcross (BC) breeding is used to transfer one qualitative (highly-heritable) trait [e.g., determinate character (*de*), downy mildew resistance, (*dm*), nematode resistance (*mj*)] into an otherwise superior inbred, which is referred to as the recurrent parent. Often, six generations of selection and backcrossing to the recurrent parent are required to recover the desired genotype (recurrent parent with the additional trait) and eliminate the undesirable traits inherited from the non-recurrent (donor) parent.

Two versions of the backcross method are utilized depending on whether the gene of interest is recessive or dominant. For the transfer of a trait controlled by a recessive gene, the recurrent parent is crossed with the donor parent, and the F_1 is backcrossed to the recurrent

parent. In one scheme, the F_1 is self-pollinated to produce the F_2, which segregates for the trait of interest. Individuals from the F_2 that possess the trait are backcrossed to the recurrent parent to produce the BC_1. The BC_1 generation is then self-pollinated to produce the BC_1S_1, which is evaluated for the trait. Individuals possessing the trait of interest are selected and backcrossed to the recurrent parent. This process is repeated until the BC_6 generation where the best individuals are self-pollinated and selected for the trait to produce the improved inbred.

For the transfer of a trait controlled by a dominant gene [e.g., anthracnose (*Ar*), bacterial wilt (*Bw*), or target leaf spot (*Cca*) resistance], the recurrent parent is crossed with the donor parent, and the F_1 is subsequently backcrossed to the recurrent parent. The BC_1 generation is then evaluated, and individuals possessing the trait are backcrossed to the recurrent parent. This process is repeated until the BC_6 generation where the best individuals are self-pollinated and selected for homozygous expression of the trait using progeny testing.

Hybrid Testing

Once developed, inbreds can be crossed in all possible combinations and evaluated to identify superior hybrid combinations. Hybrids are usually made as crosses between gynoecious and monoecious lines, or two monoecious inbred lines. In cases where many inbreds have been identified as potential parents, it may be necessary to limit the scope of the trialing [e.g., 20 inbreds could produce $(20 \times 19)/2 = 190$ different hybrids, without including reciprocal crosses]. Thus, hybrids for evaluation are usually made from pairs of inbreds having complementary traits. Consideration of potential combining ability is given when choosing lines for hybrid production.

Testing of experimental hybrids often progresses in stages, with fewer hybrids to test in later stages where more effort is spent on the evaluation of each hybrid. In the first trialing year, two replications are recommended in each of two locations. In the second year, the best hybrids should be evaluated under replication (2-4) in 8 to 12 diverse locations (i.e., grower fields, university experiment stations). In the third year, the hybrids are examined in grower trials (0.5-1.5 ha) in several production regions (~10-20). Information from the three years of trialing often leads to the release of the best one or two hybrids in the fourth year.

Even though publicly-released open-pollinated populations are often genetically broad-based and provide a source for further plant improvement, hybrids provide an avenue for proprietary protection of commercial inbred lines (Staub et al, 2005). Hybrid identification and production is, however, expensive, and thus cost/benefits are always critically assessed before initiating hybrid development.

Case Studies

Factors important to population improvement and inbred line extraction include the amount of genetic variation and gene action present, the heritability of the traits selected, and the degree of the linkage associations. These factors were considered in the development of populations and lines in the case studies given below. These studies highlight the use of the exotic *C. s.* var. *hardwickii* which possesses economically important genes not resident in *C. s.* var. *sativus*.

Architectural habit. WI 6383 is a gynoecious, multiple disease resistant, white spined cucumber population produced by intermating elite USDA *C. s.* var. *sativus* processing lines and *C. s.* var. *hardwickii* accessions (PI 183967 and PI 215589; Staub et al., 1992c). This population was released to provide breeders with a source from which they could extract multiple disease resistant lines with a multiple lateral branching and sequential fruiting habit. The development

of WI 6383 was supported by research on the inheritance of yield components in *C. s.* var. *sativus* × C. *s.* var. *hardwickii* derivatives (Kupper and Staub, 1988; Fredrick and Staub, 1989).

WI 6383 originated from a cross between four processing cucumber lines (WI 1606, WI 1589, WI 1983, and WI 1895) that also produced population WI 2843 (Peterson et al., 1985). These gynoecious, non-bitter lines are resistant to anthracnose, downy and powdery mildew, scab and Fusarium, and possess acceptable fruit quality. A selection from WI 2843 was crossed with the F_1 between PI 183967 and PI 215589 and subsequent pedigree selection produced disease resistant (via seedling screening tests), white spined, non-bitter, and gynoecious F_4 lines. About 100 F_4 plants were randomly mated to produce WI 6383, which is homogeneous for the traits selected. Seed of ~500 F_4 individuals were then subjected to three cycles (C) of recurrent, half-sib family selection for three-harvest yield. Self-pollination of selected C_3 plants led to F_7 families of which the highest yielding lines were designated WI 5098 and WI 5551. This population and attending lines are vigorous, indeterminate, produce between 4-6 primary lateral branches at the base (crown) of the plant (standard commercial types produce 1-3 primary lateral branches), and possess a sequential fruiting habit (no crown-set inhibition) not present in commercial cucumber.

Root-knot nematode resistance. Cultivars 'Lucia', 'Manteo', and 'Shelby' were developed with resistance to root-knot nematodes (*Meloidogyne* spp.; Walters and Wehner, 1997). Nematodes are important pests worldwide and cause about 11% crop loss annually in North Carolina (primary cucumber production state in U.S.). These elite lines possess resistance to *M. arenaria* races 1 and 2, *M. javanica*, and *M. hapla*. The development of these lines was supported by research that developed evaluation protocols (split-root technique; Walters et al., 1995) and identified the genetic control for resistance (Walters et al., 1993&1997).

'Lucia', 'Manteo', and 'Shelby' were developed from the NCH-1 population, which was created by intercrossing 12 cultivars, breeding lines, and plant introduction accessions with *C. s.* var. *hardwickii* PI 183967 (synom. LJ 90430). These F_1's were subjected to two cycles of bee-mediated intercrossing in open-field isolation. This resulted in a base population designated as NCH1 C_0 from which half-sib family recurrent selection (yield and fruit shape) was practiced to produce C_9. Random half-sib C_9 families were then self-pollinated and selected for nematode resistance using the split-root technique to produce indeterminate, monoecious S_7 lines from which 'Lucia', 'Manteo', and 'Shelby' were produced. Selection was initially applied for *M. javanica* (S_0-S_6), and then for *M. hapla* and races 1 and 2 of *M. arenaria* (S_6-S_7). In addition to nematode resistance, these three lines possess varying degrees of resistance to powdery mildew and anthracnose with acceptable fruit firmness, yield, and processing quality. The three cultivars differ mainly in their fruit L:D (i.e., short, medium-length or long).

7. SEED PRODUCTION

Hybrid seed production is facilitated in either greenhouse or field environments (open-field or cage isolation) by hand- or insect-pollination as reviewed by Lower and Edwards (1986). Typically, breeder's seed of inbred lines is increased to produce enough seed for foundation and production seed that is then used to produce hybrids.

Breeder's and foundation seed of inbred lines is usually produced by hand-pollination under greenhouse or cage isolation. Isolation blocks or screen cages are often employed for large seed increases (inbred and hybrid). Open-field isolation blocks are separated from other cucumber fields by at least 1.5 km. Where the number of wild bees is insufficient to ensure adequate pollination, beehives are introduced into the isolation block or cage.

In the case of hybrid seed production for large-scale commercial use, open-field increases employ the strategic placement of rows such that cross-pollination can occur between lines of opposite sex types. Typically, one or two male rows are alternated with four to five female rows from which hybrid seed is harvested.

Hybrids commonly result from gynoecious × gynoecious, gynoecious × monoecious, monoecious × monoecious, and gynoecious × hermaphrodite line matings. In the case of gynoecious × gynoecious hybrids, the sex expression of one line is chemically altered by ethylene inhibitors such as silver nitrate, silver-thiosulfate, or aminoethoxyvinylglycine (Beyer, 1976; Lower and Edwards, 1986). The seed of gynoecious lines is also produced using such compounds. Likewise, staminate flowering lines (e.g., monoecious, hermaphrodite, androecious) can be converted to pistillate flowering by application of ethylene releasing compounds such as alpha-naphthalene acetic acid and ethephon (2-chloroethylphosphonic acid; Byers et al., 1972). Chemicals are usually applied at least three times, beginning at the first true-leaf stage, and then once a week thereafter to induce sex conversion.

8. MOLECULAR MARKER-ASSISTED BREEDING

The application of genetic markers for MAS follows three major recurring cycles regardless of marker type (Figure 2). Markers are identified as potentially useful, and subsequently developed into efficient and effective genotyping systems. These markers are then placed on a genetic map and associated with QTL through progeny analysis for their subsequent use in MAS.

Development of Molecular Markers

Marker development in cucumber has occurred in several marker systems [isozymes, restriction fragment length polymorphisms (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLP), simple sequence repeats (SSR), and single nucleotide polymorphisms (SNP)], where changes between marker systems were driven by the steady progression of technological advances (Figure 3). In each case, the goal was the development of moderately saturated maps (i.e., ~150 to 200 markers to provide 90-95% coverage at 10-15 cM intervals).

During the period between 1984 and 1992, work in the U.S. progressed on the development of isozyme and RLFP markers leading to the construction of unsaturated maps (Knerr and Staub, 1992; Meglic and Staub, 1996; Kennard et al., 1994). The use of these codominant markers was assessed, and their development was terminated because of their utilization costs and the paucity of polymorphic markers when RAPD technologies were introduced (1992-2000; Figure 3). Although dominant in nature, RAPD and subsequent AFLP markers were attractive because of their comparatively low technological costs and methodological simplicity (RAPDs) and their potential to produce multiple, polymorphic markers from single assay (RAPDs and AFLPs). In the case of RAPD technology, putative polymorphism declaration (i.e., number of bands) was relatively high (10-15 bands per primer), but reproducibility and fit to 3:1 genetic ratios for many putative marker loci was also low (recovery rate = ~ 50 of 1,000 markers evaluated; Staub et al., 1996). This level of recovery is typical of many other marker systems in cucumber.

Dominant markers (RAPD and AFLP) were useful initially in the development of moderately saturated maps (Serquen et al., 1997b; Bradeen et al., 2001), but are not preferred in breeding programs. The mapped RAPD loci were, nevertheless, strategically important during early map construction (Serquen et al., 1997b; Figures 2&3), and were therefore subjected to conversion to

more preferable sequence amplified characterized region (SCAR) markers by silver staining-mediated sequencing (Horejsi et al., 1999). Although 62 (83%) of the 75 RAPDs were successfully cloned, only 48 (64%) RAPD markers were successfully converted to SCARs markers and 11 (15%) of these reproduced the polymorphism observed with the original RAPD marker. The emergence of automated sequencing technologies made possible the development of codominant SSR and SNP technologies (Fazio et al., 2002&2003a) and the reassessment of RAPD to SCAR as well as SCAR to SNP marker conversion (Robbins, 2006). Two sources of sequence data [SCAR marker fragments and BAC library (Nam et al., 2006) clones] were employed to convert RAPD to SCAR and SNP markers for increased efficiency (multiplexing) and effectiveness (stable and codominant markers; Figure 4). A total of 39 new markers (SCAR and SNP) have recently been developed, seven of which have proven effective when multiplexed in MAS. The multiplexing potential of the remaining markers and those recently created from EST libraries (unpublished) has yet to be determined

Development of Genetic Maps

The first genetic linkage maps in cucumber were reported almost 20 years ago and were based solely on phenotypic markers (Fanourakis and Simon, 1987; Vakalounakis, 1992; Pierce and Wehner, 1990). The first molecular markers mapped were isozymes (Knerr and Staub, 1992), which were subsequently combined with phenotypic markers (Meglic and Staub 1996). As DNA-based molecular markers were developed (RFLP and RAPD), they were combined with existing marker types in linkage maps (Kennard et al., 1994) (Figure 5). More recent maps possess an array of phenotypic and DNA-based markers (RAPD, RFLP, AFLP, SCAR, SSR, and SNP; Serquen et al., 1997a; Park et al., 2000; Fazio et al., 2003a). As genetic maps continued to be refined and molecular markers were included, the total map distance generally expanded to approach the estimated genome size (750 to 1000 cM; Staub and Meglic, 1993). The total genetic distances of these maps spanned 166 (Fanourakis and Simon, 1987), 95 (Vakalounakis, 1992), 168 (Knerr and Staub, 1992), 766 (narrow-based), 480 (wide-based; Kennard et al., 1994), 584 (Meglic and Staub, 1996), 600 (Serquen et al., 1997b), 816 (Park et al., 2000), and 706 cM (Fazio et al., 2003a). These maps show varying degrees of colinearity (Table 2).

The map constructed by Park et al. (2000) employed 347 RAPD, RFLP, AFLP, and loci conditioning virus resistances, which were placed on 12 linkage groups with a mean marker interval of 4.2 cM. A map constructed by Serquen et al. (1997a) defined nine linkage groups with an average distance between markers of 8.4 cM (RAPD only). Information from this map was recently merged with other maps (Fanourakis and Simon, 1987; Knerr and Staub, 1992; Kennard et al., 1994; Meglic and Staub, 1996; Horejsi et al., 2000) to synthesize a consensus map containing 255 markers, including morphological traits, disease resistance loci, isozymes, RFLPs, RAPDs, and AFLPs on 10 linkage groups (Bradeen et al., 2001). The mean marker interval in this consensus map was 2.1 cM spanning a total length of 538 cM. More recently, Fazio et al. (2003a) constructed a map containing 14 SSR, 24 SCAR, 27 AFLP, 62 RAPD, one SNP, and three morphological markers (131 total markers) spanning seven linkage groups (the theoretical number based on the haploid chromosome number) using recombinant inbred lines (RIL). This map spanned 706 cM with a mean marker interval of 5.6 cM.

QTL Mapping

The development of genetic linkage maps has provided tools for the molecular analysis of important characteristics in cucumber including fruit quality (Wenzel et al., 1995), disease

resistance, (Park et al., 2000), and yield components (Serquen et al., 1997b; Fazio et al., 2003a; Figure 5). The marker-QTL associations identified in these studies form the foundation for cucumber improvement through MAS.

Molecular mapping of economically important traits in cucumber has occurred using several inbred lines (Kennard et al., 1994; Horejsi et al., 2000; Park et al., 2000). These include lines GY-14, WI 1983, Zudm1, Straight-8, PI 183967 (*C. s*. var. *hardwickii*, India), and PI 432860 (China). These lines were chosen because of their disease resistance (e.g, downy mildew and virus resistance) or morphological (e.g., yield and quality) attributes. Although extensive virus resistance mapping is still occurring (M. J. Havey, USDA, ARS), these maps have not been used extensively for QTL mapping (Figure 5). One notable exception involves the use of two inbred processing lines, Gy-7 (synom. G421; R.L. Lower, University of Wisconsin, Madison, Wisc.) and H-19 (synom. AR 7975; Goode et al., 1980), which have been exploited extensively as parents to create F_3 families for use in genetic analysis (Serquen et al., 1997a) and QTL mapping (Serquen et al. 1997b) of several yield components (Table 3). The traits mapped included multiple lateral branching, gynoecious sex expression, L:D, and earliness, and were further characterized by QTL analysis using RIL derived from the same parental lines (Fazio et al., 2003a). Subsequently, derivatives of these and other lines were used successfully in introgression of yield components by backcrossing using MAS (Fazio et al., 2003b; Fan et al., 2006), and are, therefore, employed herein for demonstration of specific accomplishments (Figure 6).

Yield Components

Sex expression. Genetic analyses and QTL mapping studies have indicated that several loci are involved in sex expression. In a population fixed for the *M* and *A* genes (i.e., segregating only at the *F* locus), Serquen et al. (1997a) estimated five effective factors involved in gynoecious sex expression in each of two locations. Most of the gene action was attributed to dominance variance, with approximately a 1:3 ratio of additive to dominance variance. The narrow sense heritability (h^2) was estimated at 0.14 and 0.16 in two distinct environments, suggesting selection for sex expression would be difficult. In the same population, Serquen et al. (1997b) identified four QTL for sex expression common across two environments, plus a fifth QTL unique to one environment. These QTL accounted for over 85% of the observed variation in each environment with 67% and 74% of the variation attributed to a QTL near the *F* locus. In a QTL study of a RIL population derived from the same parents, three QTL were detected for the number of female nodes on the mainstem, accounting for 31% of the variation, 16% of which was attributed to a QTL at the *F* locus (Fazio et al., 2003a). Two of these QTL, including the one at the *F* locus, showed significant effects on the number female nodes on primary lateral branches. Although a large portion of the genetics of sex expression is controlled by the *F* locus, it is clear there are other regions of the genome involved in the expression of gynoecy.

Earliness. A QTL analysis for days to anthesis revealed a single QTL explaining 13% of the variation common in two environments, and a second QTL of smaller magnitude (R^2 = 8.1) in another environment (Serquen et al., 1997b). Fazio et al. (2003a) identified four QTL for days to anthesis, two of which were common in two environments tested. These two QTL accounted for 12% to 15% of the variation observed, with the environment specific QTL explaining an additional 4% and 15% of the variation. Fazio et al. (2003a) also identified four QTL in a single environment for days to first harvest. These QTL accounted for 21% of the variation observed, one of which mapped to the same genomic region as a QTL for days to anthesis common to two

environments. Although a few earliness QTL (1-2) were identified in these studies, others likely remain undetected.

Multiple lateral branching. Four QTL affecting MLB have been identified by F_3 family analysis that explained 48% to 66% of the observed variation depending upon environment (Serquen et al., 1997b). Although a total of 13 QTL for MLB were subsequently identified by Fazio et al. (2003a) using RIL derived from the same parents, only five were detected in at least two locations with a combined R^2 of 37% to 55% depending on location. In both QTL studies, one major QTL was detected that accounted for 32% (Fazio et al., 2003a) to 40% (Serquen et al., 1997b) of the variation, which mapped near the little leaf locus (*ll*).

The number of lateral branches can be relatively stable across growing environments (Georgia and Wisconsin; Serquen et al., 1997b) and planting dates (early and late; Fredrick and Staub 1989). For instance, four QTL were found to be stable in diverse U.S. growing environments (Wisconsin in 1999 and 2000 and Utah in 1999; Fazio et al., 2003a). However, Fazio et al. (2003a) identified a QTL specific to Wisconsin (LOD 2.7-3.0 in both years), and seven other QTL (LOD 2.8-6.1) unique to a single environment. This result, coupled with the trait's moderate heritability and additive gene action (Serquen et al., 1997a), indicates that some QTL are affected by the environment [i.e., seasons (López-Sesé and Staub, 2002) and plant density (Staub et al., 1992b)]. Indeed, MLB has varied in *C. s.* var. *hardwickii* derived genotypes across years in another study in Wisconsin (Fredrick and Staub, 1989).

Fruit size. As with earliness, QTL analysis for fruit L:D suggests a few stable QTL are involved with environmental factors playing a role in trait expression. In the QTL analysis of Serquen et al. (1997a), fruit length and fruit diameter were analyzed separately as well as L:D. One QTL was identified for fruit length in both environments tested (R^2 = 21% and 31%) and three QTL were identified for fruit diameter, one in both environments (R^2 = 15.7% and 9.6%) and one unique to each environment (R^2 = 21.9% and 9.6%). Two QTL were identified for L:D, but only in one environment (R^2 = 13.7% and 14.4%), both of which mapped to the same genomic regions as two QTL for fruit diameter, including the QTL identified in both environments. Although a total of 12 QTL for L:D were declared significant by Fazio et al. (2003b), only five were identified in both test locations with a combined R^2 of 31% and 30%. The total R^2 from all QTL was 36% and 57% in the two test environments. As with MLB number, L:D is effected by growing location (Serquen et al. 1997a&b; Fazio et al., 2003a&b) and plant density (Dijkhuizen and Staub, 2003). Efforts to isolate the specific genes regulating fruit growth in cucumber that have resulted in the cloning of cDNAs for preferentially expressed genes (Suyama et al., 1999).

Disease Resistance

Horesji et al. (2000) identified RAPD markers linked to the downy mildew resistance gene (*dm*). Two F_3 family populations (WI 1983G × Straight 8 population and Zudm1 × Straight 8 population) were evaluated over five locations in North America and Europe to identify RAPD markers linked to *dm*. Five markers were identified 15 to 33 cM away from *dm*, which was subsequently mapped (0.1 and 1.9 cM away) and cosegrated with ten other markers (Bradeen et al., 2001). A scab resistance gene (*Ccu*) was also mapped by Bradeen et al. (2001). Park et al. (2000) found that resistances to papaya ringspot virus (PRV) and ZYMV were closely linked to each other (2.2 cM), and were also tightly linked (~5.2 cM) to three AFLP markers. Given their relatively closely linkage associations with resistance genes, markers from these studies are likely exploitable in MAS.

Fruit Quality

Wenzel et al. (1995) used a wide cross [GY-14 (U.S. elite processing) × PI 432860 (China)] to identify QTL associated with fruit quality. The two-year, single-location study identified five, three, three, and two QTL for fruit length, diameter, seed-cavity size, and color, respectively.

The fruits of parthenocarpic genotypes are typically of higher quality than their seeded counterparts. There have been 10 QTL detected for parthenocarpy in a narrow cross (2A × Gy8; Sun et al., 2006c), three of which map to the same genomic regions as QTL detected for fruit yield at first-harvest by Fazio et al. (2003a). Four of 10 QTL reside on Linkage Groups (LG) 1 and 4.

Use of Molecular Markers in Breeding

The pyramiding of simply inherited genes (e.g., disease resistance) during germplasm enhancement is common, and has proven useful in the improvement of many crop species. In cucumber, the pyramiding of disease resistance genes resulted in important inbred lines and populations [e.g, In the U.S. WI 2757 (Peterson et al., 1982), WI 1983 (Peterson et al., 1986a), WI 5207 (Peterson et al., 1986b), M-17 (Wehner et al., 1996), 'Lucia', 'Manteo', and 'Shelby' (Walters and Wehner, 1997), NCWBP, NCMBP, and NCEP1 (Wehner and Shetty, 1997), NCWBS, NCMBS, and NCES1 (Wehner, 1998a)]. Less well reported and understood are genetic approaches for the incorporation of quantitatively inherited traits. Molecular markers provide a tool for the dissection of quantitative variation, and thus are potentially important to cucumber improvement (Figure 6).

Cucumber possesses several characteristics that are favorable to MAS including a small genome size (~880 Mega base pairs; Staub and Meglic, 1993), low chromosome number, and rapid life cycle (three cycles per year). In addition, fairly saturated genetic linkage maps have been developed, and QTL analyses have identified several genomic locations involved with important traits (Serquen et al., 1997b; Fazio et al., 2003a; Table 3). Based on these associations, three experiments have been conducted to provide evidence for the potential benefits of MAS during population development and inbred line extraction in cucumber (Fazio et al., 2003b; Fan et al., 2006; Robbins, 2006).

Population Development

To evaluate the effectiveness of MAS, four genetically diverse processing cucumber inbred lines were intermated then bulked maternally to create four base populations (C_0; Robbins, 2006). Each of these populations underwent phenotypic selection (PHE), MAS (using marker-QTL associations identified by Fazio et al., 2003a; Table 3), and random mating without selection (RAN) for three cycles. The four traits under selection were MLB, gynoecy (GYN), earliness (EAR), and L:D (Table 3). Using the same C_0 populations and selection scheme allowed a direct comparison of the effectiveness of MAS and PHE. Since each C_0 population varied for any given trait, the response to MAS and PHE was not the same for each population. In general, C_0 populations that were inferior for a trait either responded favorably to selection or remained constant while those with superior trait values either did not change or decreased. Both MAS and PHE provided improvements in all traits under selection in at least one population with the exception of MAS for EAR. MAS and PHE were equally effective at improving MLB and L:D, but PHE was generally more effective than MAS for GYN and EAR. When considering all traits, responses to PHE were superior in three of the four populations. However, the population for which MAS was superior

showed the only increase in yield (fruit/plant), which was not under direct selection. Thus, both MAS and PHE can be useful for multi-trait population improvement, but their effectiveness depends upon the traits and populations under selection.

Inbred Line Extraction

Fazio et al. (2003b) compared the response of MLB to PHE under open-field conditions, RAN, and MAS employing five markers (two SSRs, two RAPDs and one SNP) in two backcross generations (Table 3). No significant differences were detected in either backcross generation between the mean values of MLB from PHE and MAS, which were both significantly higher than the RAN control. Since two cycles of MAS required one year compared to three for PHE, MAS increased overall breeding efficiency.

The effect of MAS for four yield components (MLB, GYN, fruit L:D, and EAR) was evaluated in two backcross processing cucumber populations (line extraction) after two cycles of phenotypic recurrent selection (population improvement) for the same traits (Fan et al., 2006) (Table 3). Even after PHE provided gains in MLB and L:D, MAS continued to improve both these traits in one backcross population and L:D in the other. MAS also provided an increase in gynoecy (GYN) in both populations. Thus, MAS operated to fix favorable alleles that were not exploited by phenotypic selection.

The use of MAS requires the construction of robust markers (preferably codominant), the identification of marker-trait associations, and the development of strategies for their effective deployment in plant improvement programs (Figure 2). Although initial marker development efforts were largely ineffective, sequencing technologies and the availability of cucumber BAC libraries and expressed sequence tags (ESTs) will allow for the development of codominant SSR and SNP-based markers that will be extremely useful in MAS. RIL populations are now available which facilitate the identification of marker-trait associations. Phenotyping of individuals remains time consuming, but genotyping has been made more efficient through marker multiplexing during PCR (Staub et al., 2002b; Robbins, 2006). Recent MAS studies focusing on quantitatively inherited yield component traits are indicative of its potential for cucumber improvement as a tool to enhance selection efficiency. MAS will be most effective when it is used in conjunction with phenotypic selection, especially for quantitatively inherited traits where important genotype × environment interactions are known to exist.

9. MAJOR BREEDING ACHIEVEMENTS

The early cucumber breeding achievements reviewed by Lower and Edwards (1986) include the: 1) development and use of disease screening technologies to develop resistant cultivars; 2) identification of biochemical pathways which regulate sex expression; 3) development and implementation of controlled pollination procedures, and; 4) characterization of genetics which stabilize gynoecious sex expression. Early selection for disease resistance was primarily performed in the open-field under conditions where the presence of economically important pathogens was unpredictable. In the 1970-1980's scientific collaborations between Drs. C. E. Peterson (cucumber breeder) and P. W. Williams (pathologist) at the University of Wisconsin resulted in the development of seedling screening methodologies that allowed for the highly controlled, high-throughput assessment of pathogen resistance in segregating progeny. This led to the development of germplasm (i.e., lines, hybrids, and populations) with resistance to several important diseases, and the eventual transfer of this technology to the private sector by the late 1980's. Biochemical and comparative analyses of sex morphotypes in early 1960's led

to the discovery of pathways that regulate sex expression in cucumber. This allowed for a better understanding of the biochemistry and physiology underlying sex expression that led to the ability to convert sex types for genetic manipulation. Chemical sex conversion allowed for more rapid cultivar improvement since plant types could be more predictably recovered from selection using more sophisticated selection techniques (e.g., reciprocal recurrent selection, tandem selection). The combination of the ability to manipulate sex expression, methodologies for accurate prediction of disease resistance, and sophisticated selection techniques allowed for the development of sex stable gynoecious lines that could be crossed to produce hybrids with distinctly improved attributes. Among those that provided such improvements were Drs. C. Barnes (Clemson University), B. Kubicki (Warsaw Agricultural University), H. Munger (Cornell University), C. E. Peterson (Michigan State University then USDA, ARS at the University of Wisconsin) and R. L. Lower (North Carolina State University and then the University of Wisconsin). Beginning in the early 1980s improved techniques for germplasm evaluation (e.g., improved field plot techniques) were documented and instituted for the systematic application of complex breeding systems resulting in improved germplasm (e.g., incorporation of exotic genes). These techniques and publicly released germplasm (gynoecy, disease resistance) have been used widely by the seed industry. It is likely that genes for parthenocarpy will be increasingly used to increase yield and fruit quality in the next decade.

More recently, the creation of sophisticated computer algorithms and the development of molecular marker technologies has allowed for an in-depth quantification of some economically important metric traits, the development of unique genetic stocks, and an improved understanding the cucumber genome (Figure 2). Much of the U.S. research on molecular marker development, map construction, and QTL analysis between 1980 and 2000 was partially funded by the seed industry. The use of new technologies (e.g., molecular markers) and genetic stocks [e.g., RIL and nearly-isogenic lines (NIL)] will likely increase in the future as they augment conventional breeding. Their wide-scale use will result from the availability of precise phenotypic data (i.e., cost and time), the development of a highly saturated map with attending marker-QTL associations (i.e., the identification of trait-linked SNP markers), and the ability to detect and characterize epistatic interactions (i.e., development of NIL and the availability of more sophisticated computer algorithms).

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Table 1. Important steps in the genetic improvement of cucumber in the U.S.

Cultivar or line	Developer or seed source	Year introduced	Noteworthy trait(s)[1]
Improvement of disease resistance			
Shamrock	Iowa State Col., Ames	1937	CMV
Maine No. 2	Maine Agr. Exp. Sta.	1939	Scab
P.R. 39	Puerto Rico Agr. Exp. Sta.	1944	DM
Wis. SMR 12	Univ. of Wis., Madison	1955	Scab CMV
Ashe	N. C. Agr. Exp. Sta.	1959	Scab DM
Tablegreen	Cornell Univ., Ithaca	1960	CMV PM
Polaris	S. C. Agr. Exp. Sta.	1961	DM PM Anth
Poinsett	S. C. Agr. Exp. Sta.	1966	DM PM Anth ALS
Chipper	S. C. Agr. Exp. Sta.	1968	DM PM Anth ALS CMV
Sumter	S. C. Agr. Exp. 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. Exp. Sta.	1940	Dwarf-determinate habit
Burpee Hybrid	W. Atlee Burpee Co.	1945	Mon-Hyb CMV DM
Model	Associated Seed Growers	1946	Fruit shape
MSU 713-5	Mich. Agr. Exp. Sta.	1960	Gyn
Spartan Dawn	Mich. Agr. Exp. Sta.	1962	Gyn-Hyb CMV Scab
Castlepik	A. L. Castle & Co.	unknown	Dwarf-determinate, Gyn-Hyb
Littleleaf	Univ. Arkansas	1980	Multibranched habit

[1] CMV = cucumber mosaic virus resistance, DM = downy mildew resistance, Scab = scab resistance, PM = powdery 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.

Table 2. Common genetic markers across four linkage maps in cucumber [*Cucumis sativus* var. *sativus* and *C. sativus* var. *hardwickii* (R.) Alef.]

Sun, 2004 (2A x Gy8) F2 var. *sativus* x var. *sativus*	Revised Fazio et al. 2003 (Gy7 x H19) RIL var. *sativus* x var. *sativus*	Bradeen et al. 2001 Narrow-based Consensus F2/BC var. *sativus* x var. *sativus*	Bradeen et al. 2001 Broad-based Consensus F2/BC var. *sativus* x var. *hardwickii*
Linkage Group 1			
	F (LG1,0.0)		F (LGA,30.0)
CSWCT25-350 (LG1,6.5)*	CSWCT25-350 (LG1,9.4)		
	J5-SCAR (LG1,11.2)	**J5_1 (LGA,5.6)**	
	de (LG1,28.8)	de (LGA,15.6)	
	E14M62-214 (LG1,37.2)	*E14/M62-F-214--P2 (LGA,52.2)*	*E14/M62-F-214-P2 (LGA,77.9)*
	E14M62-112 (LG1,43.0)	*E14/M62-F-112-P1 (LGA,41.2)*	
E12M62-230 (LG1,56.2)	*E12M62-230 (LG1,49.0)*		
E18M48-188 (LG1-2A,64.6)	*E18M48-188 (LG1,54.7)*		
	I1B-SCAR (LG1,57.5)	**I1_1 (LGA,54.4)**	
	OP-AJ6 (LG1,59.5)	**AJ6 (LGA,52.2)**	
	E12M48-107 (LG1,62.2)	*E12/M48-F-107-P2 (LGA,53.0)*	
	BC523-SCAR (LG1,64.1)	**BC523 (LGA,52.2)**	
	OP-AD12-1 (LG1,68.4)	**AD12 (LGA,49.2)**	
	OP-W7-2 (LG1,76.2)	**W7_2 (LGA,71.8)**	
	E14M62-224 (LG1,76.9)	*E14/M62-F-224-P2 (LGA,48.2)*	
	ll (LG1,82.0)	ll (LGA,68.5)	
E18M48-303 (LG1-2A,68.5)	*E18M48-303 (LG1,84.0)*		
		BC551 (LGA,69.1)	**BC551 (LGA,92.1)**
	BC592-SCAR (LG1,100.1)	**BC592 (LGA,81.8)**	
	OP-AH14 (LG1,112.7)	**AH14 (LGA,96.2)**	
Linkage Group 2			
E18M58-101 (LG2-Gy8,0.0)	*E18M58-101 (LG2,8.9)*		
	OP-F4 (LG2,20.8)	**F4 (LGB,9.8)**	
	E11M60-114 (LG2,31.9)	*E11/M60-F-114-P1 (LGB,11.1)*	
	E11M60-125 (LG2,44.4)	*E11/M60-F-125-P1 (LGB,22.4)*	
	OP-AO7 (LG2,47.1)	**A07_1 (LGB,30.8)**	
E23M59-228 (LG2-Gy8,9.6)	*E23M59-228 (LG2,48.1)*		
	AW14-SCAR (LG3,0.9)	**AW14_1 (LGC,0.0)**	
	X15-SCAR (LG3,2.4)	**X15 (LGC,40.2)**	
	G14-SCAR (LG3,6.7)	**G14 (LGC,38.3)**	

	BC450-2 (LG3,7.8)	**BC450 (LGC,4.7)**	
	E11M60-342 (LG3,9.1)	*E11/M60-F-342-P2 (LGC,5.6)*	
		E14/M49-F-105-P1 (LGC,27.9)	*E14/M49-F-105-P2 (LGH,16.6)*
	AA9B-SCAR (LG4,18.1)	**AA9 (LGC,33.7)**	**OP_AA9 (LGH,14.7)**
	OP-H13 (LG4,24.5)	**H13 (LGC,38.3)**	
	OP-C1 (LG4,34.4)	**C1 (LGC,47.2)**	
	AJ18-SCAR (LG4,41.2)	**AJ18 (LGC,55.1)**	
		E14/M51-F-344-P1 (LGC,55.1)	*E14/M51-F-344-P2 (LGH,19.2)*
	OP-Y5 (LG4,44.5)	**Y5 (LGC,55.1)**	
	Y3-SCAR (LG4,48.2)	**Y3 (LGC,55.1)**	
	BC526-SCAR (LG4,48.8)		**BC_526 (LGH,15.8)**
	OP-L18-1 (LG4,52.9)	**L18_1 (LGC,46.5)**	
Linkage Group 4			
E14M52-85 (LG4-2A,13.8)	*E14M52-85 (LG4,74.0)*		
	OP-K7 (LG4,113.4)		**OP_K7-3 (LGH,14.7)**
		dm (LGC,55.1)	dm (LGH,27.7)
E23M50-210 (LG4,0.0)	*E23M50-210 (LG4,140.6)*		
E23M50-184 (LG4-2A,95.7)	*E23M50-184 (LG4,146.1)*		
OP-R13-580 (LG4-2A,86.7)	**OP-R13-580 (LG4,154.3)**		
E18M48-226 (LG4,12.9)	*E18M48-226 (LG4,193.7)*		
	E12M48-119 (LG5,6.0)	*E12M48-119 (LGE,15.8)*	
	BC503 (LG5,11.0)	**BC503 (LGE,7.2)**	
Linkage Group 5			
E23M50-181 (LG5-2A,0.0)	*E23M50-181 (LG5,14.5)*		
		CsC558/H3 (LGF,0.0)	**CsC558/H3 (LGE,3.9)**
		CsC137/H3 (LGF,2.4)	**CsC137/H3 (LGE,5.6)**
Linkage Group 6			
E26M54-345 (LG6,7.1)	*E26M54-345 (LG6,17.6)*		
	N6-A-SCAR (LG6,26.3)	**N6_2 (LGF,4.4)**	
	E11M60-332 (LG6,29.3)	*E11/M60-F-332-P2 (LGF,8.4)*	
	AK5-SCAR (LG6,33.5)	**AK5 (LGF,9.3)**	**OP_AK5-1 (LGE,13.0)**
E18M58-227 (LG6-Gy8,7.1)	*E18M58-227 (LG6,57.5)*		
		CsC362/E1 (LGF,19.2)	**CsC362/E1 (LGE,23.0)**
		CsP441/E1 (LGF,20.5)	**CsP441/E1 (LGE,23.8)**
		CsP280/H3 (LGF,22.1)	**CsP280/H3 (LGE,25.4)**
		BC_523 (LGF,28.1)	**BC_523 (LGE,30.6)**

		AP13 (LGF,32.4)	**AP13 (LGE,36.6)**
	BC605 (LG6,74.8)	**BC605 (LGG,0.0)**	
E18M17-227 (LG6-Gy8,11.1)	*E18M17-227 (LG6,85.1)*		
	E11M50-558 (LG6,91.7)	*E11M50-558 (LGG,15.7)*	
Linkage Group 7			
E13M50-277 (LG7,20.0)	*E13M50-277 (LG7,7.8)*		
	BC515 (LG7,15.8)	**BC515 (LGH,0.0)**	
		CsP308/E1 (LGH,4.1)	**CsP308/E1 (LGI,5.1)**
E25M60-545 (LG7-2A,7.5)	*E25M60-545 (LG7,21.7)*		
	L19-1-SCAR (LG7,27.0)	**L19_1 (LGH,11.9)**	
	OP-AT15-3 (LG7,28.2)	**AT15 (LGH,9.9)**	
	BC388-SCAR (LG7,28.4)	**BC388 (LGH,11.3)**	**BC388 (LGI,13.8)**
	BC231 (LG7,29.2)	**BC231 (LGH,11.9)**	
E23M49-237 (LG7,34.3)	*E23M49-237 (LG7,37.0)*		
E18M58-394 (LG7,68.4)	*E18M58-394 (LG7,56.3)*		
		CsP105/E1 (LGH,13.8)	**CsP105/E1 (LGI,16.4)**
		H5_4 (LGH,13.8)	**H5_4 (LGI,11.4)**
		CsC166/E1 (LGH,23.2)	**CSC166/E1 (LGI,25.0)**

* Underline = single sequence repeat, italic = amplified fragment length polymorphism, bold = random amplified polymorphic DNA or sequence characterized region, and bold & underline = restriction fragment length polymorphism. Parenthesis indicates linkage group and position.

Table 3. Characteristics of molecular markers defined in a genetic map of cucumber constructed by Fazio et al. (2003b) and used in marker-assisted selection for population improvement.

Marker	Type[a]	Linkage group	Map position (cM)	Parent[b]	Multiplex group[c]	Ideotype	QTL (mapping parent and LOD score) and *gene* associations [d]
CSWCT28	SSR	1	5.0	G&H		G&H	EAR(G, 7.1), MLB(H, 10.4), GYN(G, 13.0), L:D(H, 5.7), *F*
L18-SNP-H19	SNP	1	7.4	H	1	H	EAR(G, 7.1), MLB(H, 10.4), GYN(G, 13.0), L:D(H, 5.7)
OP-AG1-1	RAPD	1	31.8	G		H	EAR(G, 6.4), MLB(H, 11.6), GYN(G, 7.3), *de*
AJ6SCAR	SCAR	1	61.4	G	3	H	MLB(H, 3.3)
BC523SCAR	SCAR	1	66.5	G	2	H	MLB(H, 3.3)
OP-AD12-1	RAPD	1	70.2	H		G	EAR(G, 4.1), MLB(H, 32.9), GYN(G, 3.7), L:D(G, 8.6), *ll*
AW14SCAR	SCAR	3	3.9	G&H	1	G	GYN(G, 5.1)
CSWTAAA01	SSR	4	34.1	G&H	2	H	MLB(H, 4.6)
OP-AI4	RAPD	5	101.0	G		G	GYN(G, 3.0)
OP-AO12	RAPD	5	117.3	G		G	GYN(G, 3.0)
OP-AI10	RAPD	6	22.5	H		G	L:D(G, 7.3)
AK5SCAR	SCAR	6	33.0	G	2	H	MLB(H, 3.0)
M8SCAR	SCAR	6	39.1	H		H	MLB(H, 3.0)
OP-W7-1	RAPD	6	83.4	H		G	GYN(G, 4.1)
L19-2-SCAR	SCAR	6	115.0	H	1	G	MLB(G, 4.2), GYN(G, 4.1)
NR60	SSR	6	137.4	G&H		G	MLB(G, 4.2)
BC515	RAPD	7	0.0	H		H	L:D(H, 4.2)
L19-1-SCAR	SCAR	7	9.9	H	3	H	L:D(H, 4.2)

[a] SSR = simple sequence repeat, SNP = single nucleotide polymorphism, RAPD = random amplified polymorphic DNA, and SCAR = sequence characterized amplified region

[b] Allelic constitution based on mapping parents H-19 and Gy-7 (synom. G421) (Fazio et al. 2003b), where G = present in Gy-7, H = present in H-19, G&H = present in Gy-7 and H-19 (codominant marker)

[c] Markers used in multiplex were placed in multiplexing groups (1, 2, or 3)

[d] Markers associated with QTL for DTF = earliness, MLB = multiple lateral branching, GYN = gynoecious, and L:D = length to diameter ratio. The parentheses contain the parent contributing the QTL (G = Gy-7, H = H-19) followed by the highest LOD score for each QTL obtained from multiple field trials (Serquen et al. 1997a; Fazio et al. 2003b). Genes are *F* = femaleness, *de* = determinate, and *ll* = little leaf

Cucurbitaceae (Family)
- Zanonioideae (Subfamily)
- Cucurbitoideae (Subfamily)
  - Melothrieae (Tribe)
    - *Cucumis* (Genus)
      - *Cucumis* (Subgenus)
        - *C. sativus* L. (Species)
          - var. *sativus*
          - var. *hardwickii*
        - *C. hystrix* Chakr. (Species)
      - *Melo* (Subgenus)
        - *C. melo* L. (Species)
          - subsp. *agrestis*
          - subsp. *melo*

Figure 1. Taxonomic classification of cucumber (*C. sativus* L.) and melon (*C. melo*) L. in the family Cucurbitaceae according to Chung et al. (2006).

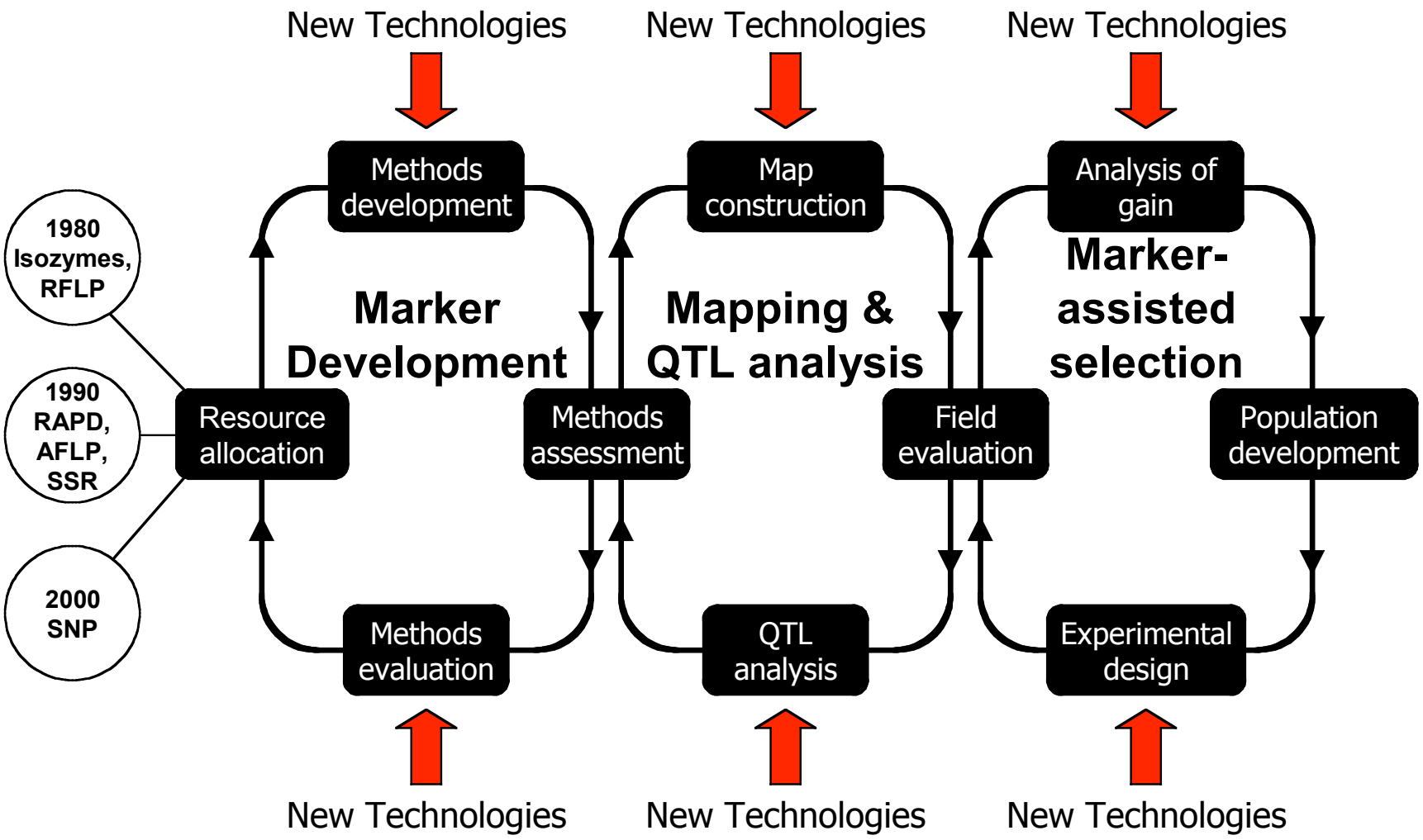

Figure 2. Schematic of marker development and application in cucumber breeding.

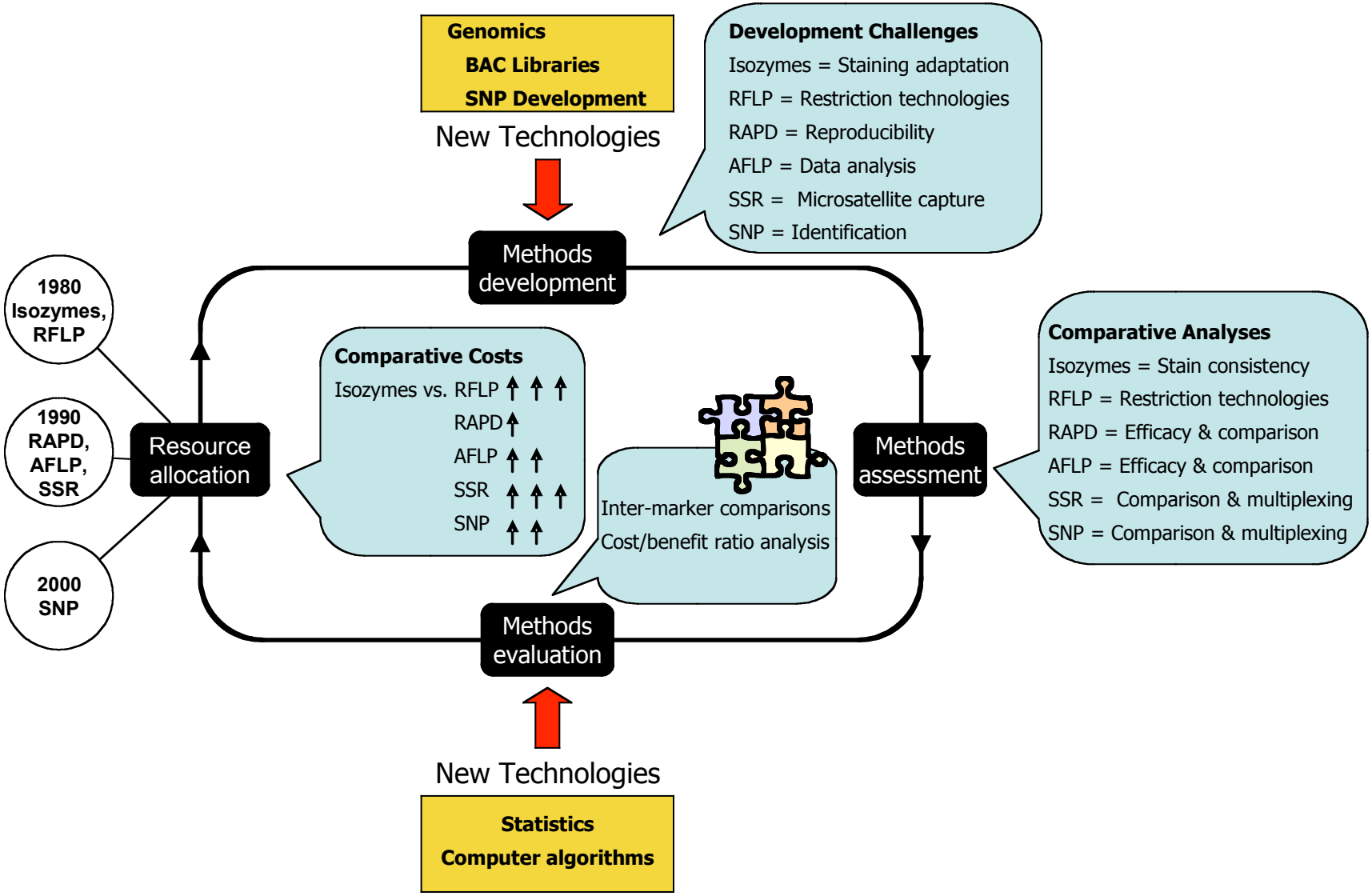

Figure 3. Events surrounding marker development in cucumber where the puzzle icon indicates the critical element.

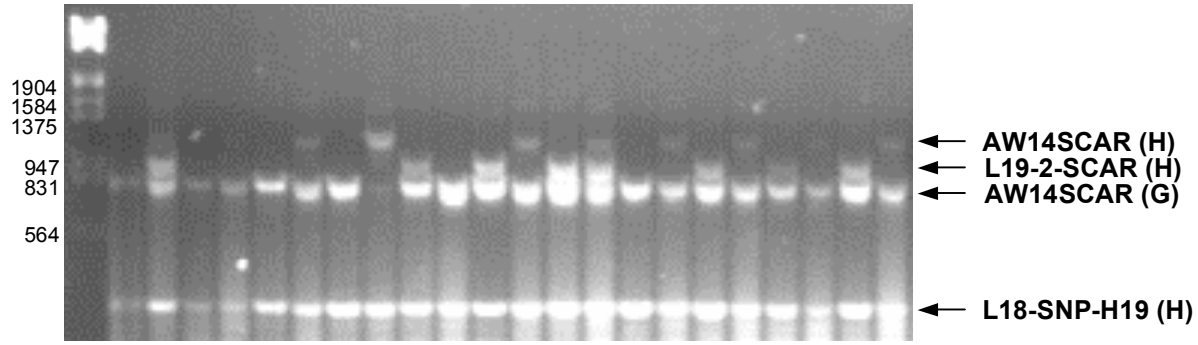

Figure 4. Example of a multiplexing reaction in a cucumber population. The far left lane is a molecular weight marker (lambda DNA digested with *Eco*RI and *Hin*dIII) with the molecular weight of each band in base pairs. The four bands are (top to bottom) the H-19 (H) allele of AW14SCAR (a codominant marker), L19-2-SCAR (dominant H-19 marker), the Gy-7 (G) allele of AW14SCAR, and L18-SNP-H-19 (dominant H-19 marker).

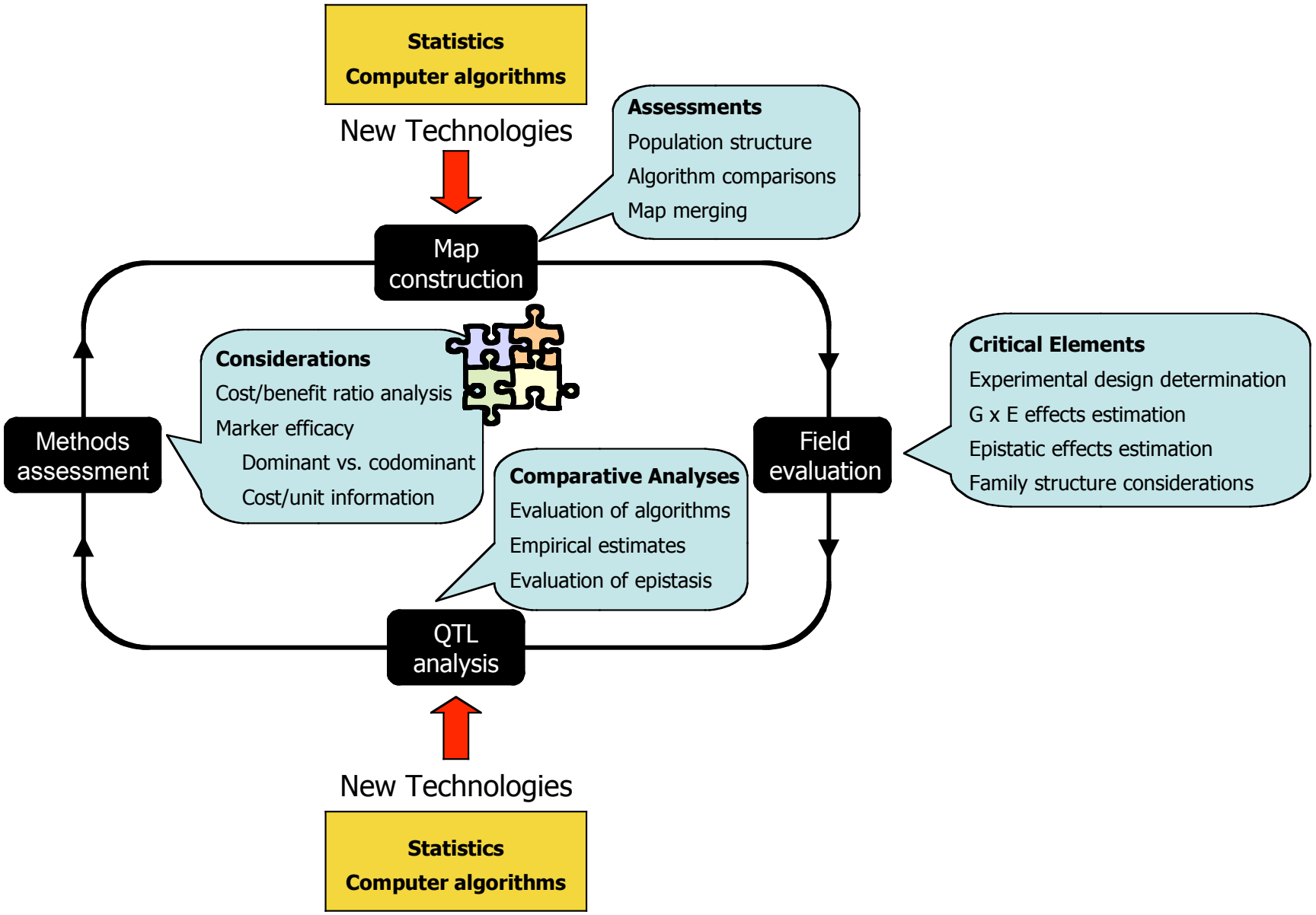

Figure 5. Assessments during mapping and QTL analysis in cucumber where the puzzle icon indicates the critical element.

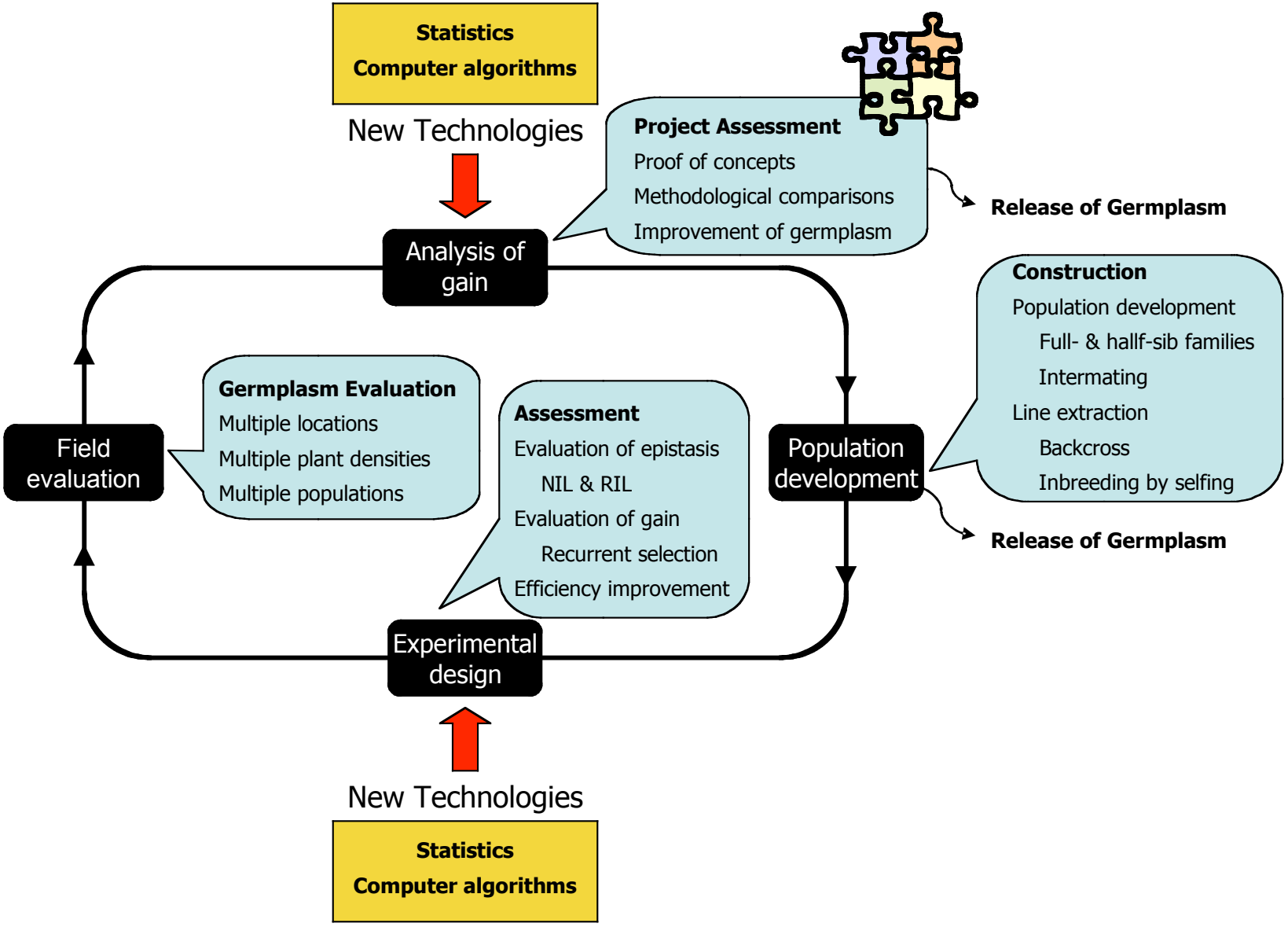

Figure 6. The evaluation of marker-assisted selection in cucumber where the puzzle icon indicates the critical element.