Evidence for Colinearity among Genetic Linkage Maps in Cucumber

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Abstract. Cucumber (*Cucumis sativus* L. var. *sativus*; 2n = 2x = 14), has a narrow genetic base (3% to 8% polymorphism). Nevertheless, several genetic maps exist for this species. It is important to know the degree of colinearity among these maps. Thus, the positions of random amplified polymorphic DNAs, sequenced characterized amplified regions, simple sequence repeat, restriction fragment length polymorphisms, and fluorescent amplified fragment length polymorphism markers were compared in four maps. A previously unreported map was constructed in a narrow cross (processing line 2A × Gy8; *C. s.* var. *sativus*; ≈7% polymorphism) and compared with the three published maps [two narrow-based (processing type; *C. s.* var. *sativus*; 8% to 12% polymorphism) and a broad-based (*C. s.* var. *sativus* × *C. s.* var. *hardwickii* (R.) Alef. ≈12%)]. Common makers were identified in seven linkage groups, providing evidence for microsynteny. These common markers were used as anchor markers for map position comparisons of yield component quantitative trait loci. The relative order of anchor markers in each of six linkage groups (linkage groups 1, 2, and 4–7) that had two or more anchor markers within each group was colinear, and instances of microsynteny were detected. Commonalities in the position of some yield component quantitative trait loci exist in linkage groups 1 and 4 of the maps examined, and the general synteny among these maps indicates that identification and mapping of additional anchor markers would lead to successful map merging to increase cucumber map saturation for use in cucumber breeding.

Genetic linkage mapping has historically been the basis for genomic investigation and the analysis of quantitative trait loci (QTL) (Doerge, 2002). The construction of a detailed linkage map is, in fact, the initial step for the use of genetic markers in marker-assisted selection (MAS) for crop improvement (Staub et al., 1996). In cucumber (*Cucumis sativus* var. *sativus* L.; 2n = 2x = 14; hereafter designated *C. s.* var. *sativus*; estimated genome length, 750–1000 cM), protein (isozyme) and morphological markers have been successfully used for mapping economically important traits (Knerr and Staub, 1992; Meglic and Staub, 1996). DNA marker-based cucumber linkage maps have also been constructed by Kennard et al. (1994), Serquen et al. (1997), and Park et al. (2000) to span 766 cM, 628 cM, and 816 cM, respectively. More recently, expanded

and integrated cucumber linkage maps [538.6 cM (narrow-based map) and 450.1 cM (broad-based map)] have been constructed using morphological traits, isozymes, and DNA markers (Bradeen et al., 2001).

Linkage maps have been used to define QTL–marker associations for yield and quality components in cucumber (Dijkhuizen and Staub, 2003; Fazio et al., 2003a; Kennard and Havey, 1995; Serquen et al., 1997). Such maps have been constructed using F_{2:3} progeny designs (Dijkhuizen and Staub, 2003; Serquen et al., 1997), and recombinant inbred lines (RIL) (Fazio et al., 2003a). Dominant [i.e., random amplified polymorphic DNAs (RAPD), sequenced characterized amplified regions (SCAR), and amplified fragment length polymorphism (AFLP)], as well as codominant [simple sequence repeat (SSR), single nucleotide polymorphism (SNP)] markers have been used extensively in these maps for the placement of yield component QTL and their successful introgression in elite germplasm using MAS (Fan et al., 2006; Fazio et al., 2003b).

Hybrid production in cucumber is typified by the ubiquitous use of closely related, elite lines (3%–8%) (Dijkhuizen et al., 1996). Diversity assessment has revealed unique accessions that define the extent of variation in cucumber, and these have been used in

genetic map construction (Horejsi and Staub, 1999). These accessions include H-19 (University of Arkansas, Fayetteville, Ark.) and Gy7 [University of Wisconsin (UW), Madison, Wisc.], and Gy14 (Clemson University, Clemson, S.C.) (Fazio et al., 2003a; Kennard et al., 1994; Serquen et al., 1997). The narrow genetic diversity in adapted lines has necessitated the strategic crossing of elite lines with exotic *C. s.* var. *sativus* (PI 482360; China) (Kennard et al., 1994) and *C. s.* var. *hardwickii* (R.) Alef. (PI 183967; India) (Dijkhuizen and Staub, 2003) germplasm to obtain enough variation for the construction of moderately saturated maps. Recently, the unique, elite processing cucumber lines 2A (UW) and Gy8 (UW) have also been identified as having potential for increasing parthenocarpic yield and fruit quality in cucumber (Sun et al., 2006a, b).

Four mapping populations have been used extensively for yield component analysis in cucumber (Dijkhuizen and Staub, 2003; Fazio et al., 2003a; Kennard et al., 1994; Serquen et al., 1997). Information from some of these and other maps (Horejsi et al., 2000) has been used to construct integrated broad- and narrow-based consensus maps (Bradeen et al., 2001). Given the paucity of polymorphism in elite cucumber germplasm, there is a need for comparative genomic analyses among existing maps and those developed from other potentially important elite parents (e.g., 2A × Gy8) (Sun et al., 2006a, b). Therefore, a map was constructed from a mating between the elite lines 2A and Gy8 for linkage grouping and marker order analysis, and for comparisons with maps reported by Fazio et al. (2003a; elite), Bradeen et al. (2001; elite and unadapted) and Dijkhuizen and Staub (2003; unadapted). These analyses provide for a preliminary comparative genomic analysis in cucumber as the initial step in map merging using elite mapping populations.

Materials and Methods

Germplasm and population development.

Two U.S. processing-type cucumber inbred lines originating from the UW-Madison Cucumber Breeding Program (UW-CBP) were used for map construction based on the economic importance of parthenocarp for open-field cucumber production (Sun et al., 2006b). The parthenocarpic line 2A is gynoeious (gy), normal leaf (L), and indeterminate (De), and has the ability to set multiple fruits without pollination under growing conditions typically found in North American climates. Likewise, the nonparthenocarpic U.S. processing-type inbred line Gy8 is stable gynoeious, normal leaf, and has an indeterminate plant habit, but does not produce or bears only few fruits without pollination. These lines are morphologically similar, except for their parthenocarpic character, and are genetically different from H-19 (processing type; monoecious, little leaf, indeterminate) and Gy7 (synom. G421; processing type; gynoeious, normal leaf, and determinate; UW-CBP, PI 482360 (long Chinese type;

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monoecious, normal leaf, and indeterminate) and PI 183967 (monoecious, little leaf, indeterminate, free-living plant of Indian origin that bears small, egg-shaped 3–5-cm-long fruit), which have been previously used as mapping parents.

The cost of constructing two coupling phase F_2 maps is half that of developing two backcross maps (Knapp et al., 1995), and thus an $F_{2:3}$ progeny design was implemented in this study for map construction using lines 2A and Gy-8. Hybrid seeds (F_1) derived from crossing 2A and Gy8 were produced in a greenhouse at Cartago, Costa Rica, during the spring of 1998. Subsequently, a single F_1 plant was used to produce F_2 progenies in a greenhouse at Madison, Wisc., during the fall of 1998. Meristem cuttings were taken from F_2 plants grown in a greenhouse at Arlington, Wisc., and in an open-field at Madison, Wisc., in the spring of 1999, and were then self-pollinated to produce 120 F_3 families.

DNA analysis. Young leaves from at least seven plants of each of 120 F_3 families were bulk sampled along with F_1 progeny and parental lines, and held for at least 12 h at -80°C before DNA extraction and analysis according to Fazio et al. (2003a). A set of 10-mer RAPD primers (A1-AZ20) was purchased from Operon Technologies (Alameda, Calif.), and the University of British Columbia (Vancouver, B.C., Canada; UBC200-UBC699). All polymerase chain reaction (PCR) solutions were purchased from Promega (Madison, Wisc.), and PCR and electrophoresis procedures were according to Horejsi et al. (1999). Only bright and consistent bands of 2.2 kb or less were scored for segregation analyses, where DNA fragment sizes were estimated by comparative analysis with *EcoRI* and *HindIII* digested lambda DNA band migrations. Each band was identified by the abbreviated company name, the name of RAPD primer, plus the fragment size of PCR product (e.g., OP-R13–580).

Seventy-seven SCAR markers previously developed from mapped RAPD markers (Horejsi et al., 1999) were examined for their potential utility in map construction. The electrophoresis procedure and banding nomenclature were the same as described for RAPD analysis.

A total of 224 previously described SSR markers [135 cucumber SSR markers plus 89 melon (*Cucumis melo* L.) SSR markers] were evaluated for their potential value in map construction (Danin-Poleg et al., 2000; Fazio et al., 2002). The protocol for SSR PCR master mix preparation was the same as for SCAR analysis, electrophoresis was according to Fazio et al. (2002), and gel images were processed as described for RAPD analysis.

The protocol for fluorescent amplified fragment length polymorphism (fAFLP; i.e., restriction digestion of genomic DNA, ligation adapters, and preamplification and selective fAFLP reactions) analysis was according to radioactive AFLP methodologies described by Vos et al. (1995) and the fAFLP

technique of Berres (http://ravel.zoology.wisc.edu/sgaap/AFLP_html/fALP_introduction.htm).

Linkage analysis, segregation distortion tests, and map analysis. Linkage analyses were performed using MapMaker/EXP 3.0 (Lander et al., 1987) and JoinMap 3.0 (Van Ooijen and Voorrips, 2001). All fAFLP, RAPD, and SCAR band morphotypes were scored as 1 (present) or 0 (absent) for dominant marker analyses. Codominant SSR bands were scored as 0, 1, or 2 as representative of the homozygous parthenocarpic parent (2A), the homozygous nonparthenocarpic parent (Gy8), or the heterozygote respectively. Segregation ratio distortion tests were performed as standard tests of dominant and codominant marker ratios (3:1, 1:2:1).

The validity of coupling phase associations during F_2 mapping decreases as the recombination frequency increases (Mather, 1936), and therefore relatively stringent recombination frequency and logarithmic odds (LOD) thresholds were selected (Knapp et al., 1995). All heritable markers (designated as coupling plus repulsion phase) were initially used to construct linkage groups (LGs) using JoinMap 3.0 with LOD threshold values ranging between 3.0 and 4.0 (LOD grouping step, 0.5), with a maximum recombination fraction of 0.49. Recombination fraction frequencies were converted to Kosambi map functions (Kosambi, 1944) to allow for consideration of crossover interference among adjacent marker positions. Default values were then chosen for the remaining mapping parameters, and the marker order within each LG was calculated.

Assignment of marker to LGs using MapMaker used LOD and recombination frequency threshold values of 3.5 and 0.4 respectively. The best seed order was initially selected, and then the remaining markers from each LG were sequentially added to the seed order. During each iteration, a marker with the most likely unique position was placed, and then the map order was retested at a LOD of 2.0.

Coupling plus repulsion phase markers were divided into coupling phase with respect to female (2A designated as 2A coupling) and male parent (Gy8 designated as a Gy8 coupling), respectively. The “best-fit” map was created using an LOD of 3.0 and a recombination frequency of 0.37, and a LOD of 3.5 and a recombination frequency of 0.37 thresholds for 2A and Gy8 coupling phase data, respectively. Mapping then proceeded for both phases as described earlier for coupling plus repulsion phase linkage analyses. Map information from the coupling plus repulsion phase linkage analysis was used to assign LG designations in the 2A and Gy8 coupling phase maps.

To provide common anchor points between the 2A $\times$ Gy8 map and the Gy7 $\times$ H-19 map of Fazio et al. (2003a), an additional 37 fAFLP markers (Tables 1 and 2) were mapped (MapMaker and JoinMap) in each of these mapping populations, resulting in a “revised” LG order from that used in the map of Fazio et al. (2003a) (Fig. 1). These and other common markers inherent in all maps were

used for comparative analyses, and a graphic representation of the LGs was created using MapChart software for Windows (Voorrips, 2002). For continuity, the LG designations and nomenclature used herein were those of Fazio et al. (2003a).

Percentage of polymorphic markers in the 2A $\times$ Gy8 mapping population was compared with those mapping populations of Kennard et al. (1994), Serquen et al. (1997), and Fazio et al. (2003a). The 2A $\times$ Gy8, and the revised Fazio et al. (2003a) and Bradeen et al. (2001) linkage maps were then compared using common fAFLP, SSR, and RAPD and SCAR markers. The positions of common QTL as derived from at least two common markers were compared in the 2A $\times$ Gy8, Fazio et al. (2003a), and Dijkhuizen and Staub (2003) maps.

Results and Discussion

Broad- and narrow-based cucumber consensus maps have been created for appraisal of this species’ genome, and for assessment of their potential application to MAS (Bradeen et al., 2001). However, additional maps have been constructed for QTL analyses using elite mapping parents, and have been successfully used in MAS (Fazio et al., 2003b; Fan et al., 2006). Because comparative map analysis can provide information regarding their potential for map merging, the percentage of polymorphism, LGs, marker order, and relative differences among maps for marker types and associated QTL were evaluated.

Mapping using 2A and Gy8

Percentage of polymorphism. Of the 1077 RAPD markers examined, 77 (7.1%) were polymorphic between the mapping parents (2A and Gy8; Table 3). Thus, the polymorphism level in this mapping population was less than that reported in narrow crosses by Kennard et al. (1994) (Gy14 $\times$ PI 432860; $\approx 9\%$), Serquen et al. (1997) (Gy7 $\times$ H-19; $\approx 11\%$), and Fazio et al. (2003a) (Gy7 $\times$ H-19, $\approx 12\%$). Moreover, upon segregation analysis, 1.6% (17 of 1077) of the RAPD markers examined yielded chi-square P values larger than 0.01 when compared with the 5.1%, 4.8%, and 3.7% reported by Kennard et al. (1994), Serquen et al. (1997), and Fazio et al. (2003a), respectively. The comparatively low polymorphism level reported herein is the result of the genetic similarities between the parental lines used, which typifies the close genetic relationships among U.S. processing cucumber germplasm (Staub et al., 2005).

Identification of mappable markers. Initially, 1378 markers (RAPD, SCAR, and SSR) were evaluated for map construction using 2A $\times$ Gy8 $F_{2:3}$ progeny segregations based on their successful application in previous studies (Fazio et al., 2002; Horejsi and Staub, 1999; Serquen et al., 1997) (Table 1). In contrast to Fazio et al. (2003a) (Gy7 $\times$ H-19), where 10.4% of the available cucumber SSR markers were useful for mapping,

Table 1. Identity, polymorphism level, and selected *EcoRI* (E) and *MseI* (M) primers used for fluorescent amplified fragment length polymorphisms analysis in cucumber (*Cucumis sativus* L.).

<i>MseI</i> primer	<i>EcoRI</i> primer ^a											
	E11-AA	E12-AC	E13-AG	E14-AT	E15-CA	E16-CC	E18-CT	E19-GA	E23-TA	E24-TC	E25-TG	E26-TT
M17-CG	4	6	2	4	4	1	4	1	2	3	4	5
M47-CAA	4	4	1	4	2	2	1	2	4	1	4	1
M48-CAC	1	6	4	2	2	3	5	0	2	1	3	0
M49-CAG	3	1	1	3	3	2	3	4	3	2	1	2
M50-CAT	2	2	1	0	4	2	2	3	4	5	3	4
M51-CCA	0	2	6	4	8	5	1	1	8	4	4	0
M52-CCC	2	5	0	2	4	0	0	1	2	0	0	8
M54-CCT	5	0	3	3	2	0	0	4	3	1	3	3
M58-CGT	4	3	0	2	1	0	6	0	3	0	2	5
M59-CTA	1	2	1	4	3	1	2	2	11	0	6	5
M60-CTC	5	3	1	4	0	5	5	0	3	1	3	4
M61-CTG	2	1	2	2	0	3	5	7	5	2	0	1
M62-CTT	3	3	4	9	2	4	4	9	7	0	3	4

^aSequences of the E and M adaptors and primers according to Vos et al. (1995).

only 2.2% of those identified herein could be exploited for the linkage analysis (no melon and four cucumber). Likewise, of the 77 cucumber SCAR makers available (Horejsi et al., 1999), only K7-SCAR-560 (1.3%) was used in mapping. The fact that sparingly few potential polymorphisms could be used in map construction typifies results obtained in other such efforts using isozyme (Knerr and Staub, 1992; Meglic and Staub, 1996), restriction fragment length polymorphism (RFLP) (Kennard et al., 1994), RAPD (Serquen et al., 1997), and SSR (Fazio et al., 2003a) markers in cucumber.

To identify additional usable markers, 156 *EcoRI* and *MseI* primer combinations were used for fAFLP examination of the mapping parents (Table 1). This survey allowed for the identification of 433 polymorphic fAFLP fragments providing, on average, 2.8 polymorphic fragments per primer combination. Ninety-four (60.2%) of these primer combinations amplified more than two polymorphic fragments that discriminated between the parental lines. These putative marker loci were then subjected to chi-square ratio distortion tests (Table 2). Of the 374 fAFLP fragments examined, 270 (72.2%) fit the expected ratio (3:1) at *P* values larger than 0.01. These markers (on average, 2.9 polymorphic fAFLP fragments per primer combination) were used to ana-

lyze 2A × Gy8-derived F₃ families in linkage analysis. This was dramatically less than the average of 7.8 AFLP fragments (163 AFLP fragments derived from 21 primer combinations) available to Bradeen et al. (2001) in the development of a narrow-based consensus map using data from the Gy7 × H-19 F₂ (Serquen et al., 1997), WI 1983 × Straight 8 F₂ (Horejsi et al., 2000), and ZUDM × Straight 8 F₂ (Horejsi et al., 2000) mapping populations. This disparity in marker identification and utilization parallels that found when using the RAPD, SCAR, and SSR markers described earlier, and is likely the result, once again, of the close genetic relationship between the parental lines used herein.

Linkage group analysis

Markers with chi-square *P* values greater than 0.01 (Krutovskii et al., 1998; Marques et al., 1998) and 0.05 (Vuylsteke et al., 1999) have been used in map construction. In this study, putative markers with chi-square *P* values less than 0.01 were excluded from linkage analysis to minimize false-positive marker placement. This constraint resulted in the deployment of 187 molecular markers (17 RAPD, three SSR, one SCAR, and 166 fAFLP markers) for LG assignment using 2A × Gy8-derived F₃ families.

JoinMap and MapMaker provided only slightly different results in linkage grouping analysis when coupling plus repulsion phase markers (168) were used in initial map construction [JoinMap (11 LGs) vs. MapMaker (10 LGs)]. Two LGs assigned by JoinMap were combined by MapMaker into one single group. The sparingly few differences in the results obtained using these algorithms may be the result of the inability of MapMaker to assess segregation distortion correctly, which in turn leads to the spurious assignment of markers into LGs (Vuylsteke et al., 1999). Identical results were obtained when Gy8 coupling phase markers were used in JoinMap and MapMaker analyses (106 markers, nine LGs). In contrast, JoinMap and MapMaker initially assigned 89 markers during 2A coupling phase analysis to eight LGs.

Marker order analysis

Differences in marker order were evident in LGs created by JoinMap and MapMaker. These differences were, however, minor (i.e., couplet marker order differences) and infrequent, and are likely the result of the unique program-based decision criteria used for adding markers to a map. Given the similarity among the maps created by the software used and the simplicity of its use, MapMaker was employed for the presentation of marker

Table 2. Identity of *EcoRI* (E) and *MseI* (M) primers used for fluorescent amplified fragment length polymorphisms that fitted a 3:1 segregation ratio test using a 2A × Gy8-derived bulked F_{2:3} cucumber (*Cucumis sativus* L.) progeny.

<i>MseI</i> primer	<i>EcoRI</i> primer ^a											
	E11-AA	E12-AC	E13-AG	E14-AT	E15-CA	E16-CC	E18-CT	E19-GA	E23-TA	E24-TC	E25-TG	E26-TT
M17-CG	0	4	nd	3	2	nd	1	nd	nd	3	0	5
M47-CAA	4	2	1	3	nd	nd	nd	2	4	nd	4	nd
M48-CAC	nd	3	2	2	nd	5	5	nd	nd	1	1	nd
M49-CAG	3	nd	nd	3	3	nd	2	0	3	0	nd	nd
M50-CAT	nd	2	1	nd	4	nd	nd	2	4	3	2	4
M51-CCA	nd	2	4	4	8	3	0	nd	0	4	3	nd
M52-CCC	2	1	nd	2	4	nd	nd	nd	nd	nd	nd	8
M54-CCT	5	nd	1	1	nd	nd	nd	2	2	nd	3	3
M58-CGT	4	2	nd	nd	nd	nd	4	nd	3	nd	2	2
M59-CTA	nd	nd	0	3	3	nd	nd	2	11	nd	4	5
M60-CTC	1	2	nd	4	nd	2	3	nd	3	nd	2	4
M61-CTG	nd	nd	1	nd	nd	2	5	4	5	nd	nd	nd
M62-CTT	3	3	3	4	nd	3	4	7	4	nd	0	3

^aSequences of the E and M adaptors and primers were published by Vos et al. (1995). nd, no data.

Panel a

Panel b

Fig. 1. Comparison of cucumber (*Cucumis sativus* L.) linkage groups constructed from morphological (F = gynocious, ll = little leaf, de = determinate), RAPD (OP, BC), SSR (CSW), SCAR, SNP, faFLP (E), and AFLP markers segregating in bulked $F_{2,3}$ progeny derived from a $2A \times Gy8$ *C. sativus* var. *sativus* mating (coupling and coupling plus repulsion phases), G421 $\times$ H-19 *C. sativus* var. *sativus*-derived RIL (revised from Fazio et al., 2003a), Gy14 $\times$ PI 432860-derived $F_{2,3}$ (narrow-based consensus map), and Gy14 $\times$ *C. s. var. hardwickii* (R.) Alef. PI 183967 (broad-based consensus map) (Bradeen et al., 2001) populations. Bold letters indicate common markers on linkage groups 1 (panel a), 2 (panel b), 3 (panel c), 4 (panel c), 5 (panel c), 6 (panel d), and 7 (panel e).

order analysis of 2A coupling, Gy8 coupling, and coupling plus repulsion phase maps.

After the assessment of LG analyses, 78, 97, and 168 markers from 2A coupling,

Gy8 coupling, and coupling plus repulsion phase respectively were selected for initial marker ordering analyses. These markers spanned seven LGs with at least three

markers per LG (Fig. 1; unlinked markers not shown).

Of the 168 markers used in marker order analyses, 48, 47, and 54 markers were mapped

Fig. 1. (Continued)

in 2A coupling, Gy8 coupling, and coupling plus repulsion phase using the F_3 family data respectively (Fig. 1). In total, 100 markers (53.5%) were mapped to a unique position in the coupling and coupling plus repulsion phase maps at a LOD of more than 2.0. The total marker coverage in the 2A coupling, Gy8 coupling, and coupling plus repulsion phase map was 388.6 cM, 412.2 cM, and 496.6 cM, respectively. These maps have a mean marker interval of 8.1 cM (2A coupling), 8.8 cM (Gy8 coupling), and 9.2 cM (coupling plus repulsion). Given that the genome length of cucumber is between 750 to 1000 cM (Staub and Meglic, 1993), these maps must be considered relatively unsaturated. The precision and confidence placed on best marker order determinations increases as the LOD threshold used in marker ordering, and the size of the population used is increased (Liu, 1998). Thus, high marker order precision and the development of a high-density linkage map in cucumber using elite inbred lines would require a large population size using an $F_{2:3}$ mating design, perhaps 250 individuals analyzed using a LOD of 3.0 for marker ordering.

The use of dominant markers for map construction is problematic because they provide less genotypic information than codominant markers when F_2 progeny are used,

which in turn increases biases during linkage estimation (Knapp et al., 1995). Dominant markers have, however, proved to be valuable for map construction in elite cucumber germplasm in this and other studies (Fazio et al., 2003a; Park et al., 2000). Thus, the use of a more efficient mating design (e.g., RIL and backcross) of considerable population size (200–300 individuals) may be prescriptive for increasing the precision of marker order and the development of highly saturated linkage maps in elite cucumber populations, especially when a high proportion of the markers used are dominant. The allocation of resources for the construction of such maps, however, requires a critical analysis of return on investment (i.e., potential for direct market benefit) and considerations for their use in other research (e.g., colinearity for map merging). In the case of cucumber, access to codominant markers and appropriate, genetically diverse high-value immortalized populations (i.e., RIL segregating for many horticultural important traits) in elite germplasm may limit the broad implementation of marker-based selection in cucumber breeding programs.

Comparative genome analysis

Markers were dispersed in seven LGs, where 19, 43, 18, and three markers were

found to be common between the 2A $\times$ Gy8 map and that of Fazio et al. (2003a) (comparison 1), Fazio et al. (2003a) and Bradeen et al. (2001) (narrow-based; comparison 2), Bradeen et al. (2001) narrow- and broad-based (comparison 3), and Bradeen et al. (2001) (broad-based) and Fazio et al. (2003a) (comparison 4) respectively (Fig. 1). Marker types in comparisons 1 [fAFLP (17), SSR (1), and RAPD (1)], 2 [fAFLP (11), SCAR (13), RAPD (17), little leaf (*ll*) and determinate (*de*)], 3 [fAFLP (2), RFLP (9), RAPD (6), and downy mildew (*dm*)], and 4 [fAFLP (1), RAPD (2), and gynoecious (*F*)] differed markedly.

Comparisons among narrow-based maps. The orientation of linkage maps and the relative order of common markers between the 2A $\times$ Gy8 and Gy7 $\times$ H-19 mapping populations were compared (Fig. 1). Because of the limited number of common markers among these linkage maps, map-merging experiments were not possible. Instead, comparisons of putative homologous map regions were made via side-by-side visual inspections of LGs to allow for a preliminary assessment of map colinearity. The 14 common markers used were distributed among six LGs (LG1, 2, 4, 5, 6, and 7; Fig. 1). LG1, 2, 4, 6, and 7 each had at least two common markers, and LG5 had one such

Panel d

Panel e

Fig. 1. (Continued)

marker. Common markers were not detected in LG3. The order of anchor markers was colinear between the 2A x Gy8 population and the Gy7 x H-19 population in LG1, 6, and 7. Although five common markers mapped to LG4 in each population, the marker order was inverted between OP-R13-580 and E23M50-184, suggesting the occur-

rence of a genomic rearrangement in that region.

Comparisons between narrow- and broad-based maps. Although colinear marker orders were detected between the Gy7 x H-19 and Gy14 x PI 432860 maps, the limited common markers between 2A x Gy8 and Gy14 x PI 432860 did not allow for broad-

based comparative analyses (Fig. 1). Many common markers were identified between the narrow- and broad-based maps of Bradeen et al. (2001). Moreover, comparative analysis indicates that LG 1, 2, 3, 6, and 7 of the narrow-based map of Fazio et al. (2003a) are the same as those defined in the broad-based map of Bradeen et al. (2001). Such

comparison analyses provide evidence for colinearity and varying degrees microsynteny between these maps.

Comparisons of relative QTL position. The QTL positions associated with parthenocarp in cucumber are located on LG1 and 4 as defined by 2A × Gy8 progeny segregations (Sun et al., 2006c). Comparisons of QTL positions for parthenocarp and first-harvest

yield of seeded fruit (Fazio et al., 2003a) indicate that these and another yield-related QTL (i.e., days to anthesis, and fruit size and number) are positioned on LG1 (Fig. 2). Moreover, the genomic position of the *F* locus is in the same region as QTL for parthenocarp, which is consistent with the results of de Ponti and Garretsen (1976). The associated position of these loci, as well as

earliness and fruit number and length QTL located on LG1 and 4 in narrow- and broad-based maps, suggest that these QTL–marker associations will be important in plant improvement. This is especially true for programs interested in developing early, high-yielding, gynoecious germplasm for once-over machine harvest operations.

The syntenic nature of cucumber LGs among available genetic maps in general indicates that, although expensive and laborious, merging of existing maps would likely lead to a valuable narrow-based saturated consensus map in this species. This will, however, require the identification and characterization of additional anchor codominant markers (SSRs and/or SNPs, perhaps 50–70) in this genetically narrow species. Such an integrated, narrow-based map would find utility in MAS introgression of yield components (Fan et al., 2006) and quality traits (Sun et al., 2006c) that are conditioned by relatively few genes.

Table 3. Type and number of DNA markers evaluated for use in map construction using 2A × Gy8-derived cucumber (*Cucumis sativus* L.) progeny.

Marker type	Total marker examined	No. of polymorphisms ^z	No. of markers mapped ^y
RAPD	1077	77	17
SCAR ^x	77	2	1
Melon SSR ^w	89	1	0
Cucumber SSR ^v	135	4	3

^zAt least one major band polymorphism between parents.

^yFitted to either 1:2:1 (codominant marker) or 3:1 (dominant marker) ratio at $\alpha = 0.01$.

^xSequenced characterized amplified regions according to Horejsi et al. (1999).

^wMelon SSR sequences according to Danin–Poleg et al. (2000).

^vCucumber SSR sequences according to Fazio et al. (2002).

Fig. 2. Comparison map position of yield component QTL in cucumber (*Cucumis sativus* L.) in linkage groups 1 and 6 of maps from 2A × Gy8 *C. sativus* var. *sativus* mating (coupling and coupling plus repulsion phases), G421 × H-19 *C. sativus* var. *sativus*-derived RIL (revised from Fazio et al., 2003a), and Gy14 × *C. s. var. hardwickii* (R.) Alef. PI 183967 (Bradeen et al., 2001) progeny analyses. Bold letters indicate common markers.

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