Cytoplasmic effects on plant performance and fertility are well documented (Kihira, 1982). An example of a useful organellar trait is cytoplasmic male sterility, which is widely used to produce hybrid seed of many crops (Havey, 2004). There are numerous examples of deleterious traits associated with cytoplasms, such as the reduced vigor of maize (Zea mays) inbreds possessing the teosinte cytoplasm (Allen, 2005; Edwards et al., 1996) and low-temperature chlorotic phenotypes associated with the ogura cytoplasm of the brassicas [Brassica sp. (Bannerot et al., 1977)]. Mitochondrion-associated phenotypes include the chloroplast mutator of Arabidopsis thaliana (Abdelnoor et al., 2003; Martinez-Zapater et al., 1992), non-chromosome stripe of maize (Newton and Coe, 1986), and mosaic (MSC) mutants of cucumber (Lilly et al., 2001; Malepszy et al., 1996), all of which show chlorotic sectors on leaves, reduced vigor, and relatively poor fertility. These mutants are often due to deletions or rearrangements in the mitochondrial DNA that negatively affect gene expression and mitochondrial function (Gu et al., 1993; Hartmann et al., 1994; Hunt and Newton, 1991; Janska et al., 1998; Lauer et al., 1990; Lilly et al., 2001; Marienfeld and Newton, 1994; Newton et al., 1990; Sakamoto et al., 1996).

Whereas the chloroplast DNAs of most plants are similar in size and structure (Raubeson et al., 2007), the mitochondrial DNAs vary greatly in size from about 219 kbp (Palmer and Horben, 1987) to well over 11 Mbp (Sloan et al., 2012). The larger sizes of plant mitochondrial DNAs are due in part to the accumulation of repetitive motifs (Andre et al., 1992) and DNA transfers from the chloroplast (Cummings et al., 2003). Recombination among repetitive motifs can give rise to structurally rearranged mitochondrial DNAs, which can exist as relatively low-copy subgenomic molecules (sublimons) (Abdelnoor et al., 2003, 2006; Bartoszewski et al., 2004b; Fauron et al., 1995). These sublimons can shift in relative abundance, a process referred to as substoichiometric shifting (Janska et al., 1998; Shedge et al., 2007), to produce mitochondrially associated phenotypes (Abdelnoor et al., 2003; Janska et al., 1998; Kanazawa et al., 1994). The predominance of a specific mitochondrial DNA can be under nuclear control (Abdelnoor et al., 2003; Shedge et al., 2007) to presumably maintain beneficial interactions between the mitochondrial and nuclear genomes.
Cucumber possesses several characteristics useful for organellar genetics, including differential transmission of the organellar DNAs; a large mitochondrial DNA with repetitive sequences that undergo recombination to produce structurally rearranged molecules; and the existence of the mitochondrially associated, MSC phenotypes. Whereas most plants show maternal transmission of both the chloroplast and mitochondrial DNAs (Birky, 1995; Reboud and Zeyl, 1994), cucumber chloroplasts are maternally and mitochondria paternally transmitted (Havey, 1997; Havey et al., 1998). This unique mode of transmission allows for the separation of chloroplast and mitochondrial effects by reciprocal crossing. The cucumber chloroplast DNA is similar to most plants in size and structure (Kim et al., 2006); however, its mitochondrial DNA is one of the largest among all eukaryotes at 1685 kbp (Alverson et al., 2011; Ward et al., 1981). The mitochondrial DNA of cucumber possesses clusters of repetitive DNAs (Alverson et al., 2011; Bartoszewski et al., 2004a; Lilly and Havey, 2001) that recombine to produce structurally polymorphic molecules among elite cucumber populations (Havey et al., 1998) and are associated with the MSC phenotypes (Bartoszewski et al., 2004b; Lilly et al., 2001). Because of maternal transmission of the organelles in the vast majority of plants, it is difficult to unequivocally separate chloroplast or mitochondrial effects on phenotypes. Cucumber provides a unique system to identify and characterize chloroplast and mitochondrial effects on plant growth and development by exploiting differential transmission of these organelles. In this study, we produced doubled haploids from divergent cucumber populations and crossed among them to generate a complete diallel mating design. The diallel is a useful tool to estimate the combining abilities of inbreds and heterosis (Griffing, 1956). The general combining ability (GCA) of an inbred is a measure of the average performance of hybrids from crosses with other inbreds. Specific combining ability (SCA) measures the performance of specific hybrid combinations relative to the average performance expected from the inbred parents. Here we report significant differences for plant growth between reciprocal hybrids possessing identical nuclear genotypes, revealing the potential of beneficial organellar effects on plant performance.

Materials and Methods

Doubled haploid plants were produced by culturing immature female flowers (Dirks, 1988) from each of five cucumber populations (GY14, MM76, ST8, TMG1, and 9930). Because these plants are derived from the female gametophyte, they must possess mitochondrial DNA from the plant producing the female flower. Each putative DH was self-pollinated to produce a DH line, and one DH line from each of the five populations was randomly chosen for genotyping and crossing. MSC3 is a highly inbred mitochondrial mutant of cucumber (Bartoszewski et al., 2004b). We detected no heterozygosity in the five DH lines and MSC3 were grown in the greenhouse and crossed with each other both as the male and female to produce a complete diallel of 30 hybrids. Three plants of each hybrid and parental line (108 plants total) were grown in each of three greenhouses (blocks). The experiment was repeated three times. Growth conditions were optimal for cucumber (16-h days at 28 °C with light intensity of 270 μmol·s⁻¹·m⁻² at the level of the greenhouse bench; nights at 24 °C). Plants were destructively harvested at 30 d (Expt. 1) and 22 d (Expts. 2 and 3) after planting by cutting stems at the cotyledons, and fresh and dry weights of each plant were measured. The mean weights of the three plants in each block were calculated for hybrids and parents. GCA, SCA, and reciprocal-cross effects were calculated using a SAS (version 9.3; SAS Institute, Cary NC) program based on Griffing′s (1956) method 1; fixed effects model 1. Average heterosis was estimated using the program of Burow and Coors (1994).

Results and Discussion

Putative DH plants were produced by culturing immature female flowers (Dirks, 1988) from each of five cucumber populations (GY14, MM76, ST8, TMG1, and 9930). Because these plants are derived from the female gametophyte, they must possess mitochondrial DNA from the plant producing the female flower. Each putative DH was self-pollinated to produce a DH line, and one DH line from each of the five populations was randomly chosen for genotyping and crossing. MSC3 is a highly inbred mitochondrial mutant of cucumber (Bartoszewski et al., 2004b). We detected no heterozygosity in the five DH lines and MSC3 were grown in the greenhouse and crossed with each other both as the male and female to produce a complete diallel of 30 hybrids. Three plants of each hybrid and parental line (108 plants total) were grown in each of three greenhouses (blocks). The experiment was repeated three times. Growth conditions were optimal for cucumber (16-h days at 28 °C with light intensity of 270 μmol·s⁻¹·m⁻² at the level of the greenhouse bench; nights at 24 °C). Plants were destructively harvested at 30 d (Expt. 1) and 22 d (Expts. 2 and 3) after planting by cutting stems at the cotyledons, and fresh and dry weights of each plant were measured. The mean weights of the three plants in each block were calculated for hybrids and parents. GCA, SCA, and reciprocal-cross effects were calculated using a SAS (version 9.3; SAS Institute, Cary NC) program based on Griffing′s (1956) method 1; fixed effects model 1. Average heterosis was estimated using the program of Burow and Coors (1994).

Results and Discussion

Putative DH plants were produced by culturing immature female flowers (Dirks, 1988) from each of five cucumber populations (GY14, MM76, ST8, TMG1, and 9930). Because these plants are derived from the female gametophyte, they must possess mitochondrial DNA from the plant producing the female flower. Each putative DH was self-pollinated to produce a DH line, and one DH line from each of the five populations was randomly chosen for genotyping and crossing. MSC3 is a highly inbred mitochondrial mutant of cucumber (Bartoszewski et al., 2004b). We detected no heterozygosity in the five DH lines and MSC3 were grown in the greenhouse and crossed with each other both as the male and female to produce a complete diallel of 30 hybrids. Three plants of each hybrid and parental line (108 plants total) were grown in each of three greenhouses (blocks). The experiment was repeated three times. Growth conditions were optimal for cucumber (16-h days at 28 °C with light intensity of 270 μmol·s⁻¹·m⁻² at the level of the greenhouse bench; nights at 24 °C). Plants were destructively harvested at 30 d (Expt. 1) and 22 d (Expts. 2 and 3) after planting by cutting stems at the cotyledons, and fresh and dry weights of each plant were measured. The mean weights of the three plants in each block were calculated for hybrids and parents. GCA, SCA, and reciprocal-cross effects were calculated using a SAS (version 9.3; SAS Institute, Cary NC) program based on Griffing′s (1956) method 1; fixed effects model 1. Average heterosis was estimated using the program of Burow and Coors (1994).

Table 1. General combining abilities expressed as deviations from overall mean of zero for fresh and dry weights of progenies from diallel crossing among parental inbred (MSC3) and doubled haploids selected from populations TMG1, ‘Marketmore 76’ (MM76), 9930, ‘Straight 8’ (ST8), and Gy14 of cucumber.

| Parent     | Fresh wt | Dry wt |
|------------|----------|-------|
| TMG1       | 1.52     | 0.51  |
| MM76       | 1.81     | 0.19  |
| 9930       | 1.48     | 0.39  |
| ST8        | -0.72    | -0.08 |
| Gy14       | -1.88    | -0.27 |
| MSC3       | -5.90    | -0.74 |
lines and MSC3 for 190 SSRs (Yang et al., 2012), confirming their highly inbred status. A dendrogram based on 25 SSRs commonly polymorphic among the lines (Supplemental Table 2) revealed two main groups relative to Csh (Fig. 1). The North American cucumbers clustered together (GY14, MM76, and ST8), as did the Asian types (TMG1 and 9930). The mitochondrial mutant MSC3 was placed with the Asian germplasms (Fig. 1). These results are consistent with previous research demonstrating significant genetic divergence between Asian and North American cucumbers (Lv et al., 2012; Staub et al., 1999). Growth of young plants was measured 22–30 d after planting in greenhouses. Across experiments, overall average fresh and dry weights were 30.4 and 3.0 g, respectively. Fresh and dry weights were significantly correlated at 0.70; coefficients of variation were 15.2% and 19.7%, respectively, and this level of variation may have contributed to the lower correlation between fresh and dry weights. For both traits, genotypes (parents and hybrids), experiments, genotype-by-experiment interactions, and blocks within experiments [block(experiment)] were highly significant ($P < 0.001$). The significance of experiments may have resulted from the weather conditions outside of the greenhouses; cloudy days were typical during Expts. 1 and 2, while clear sunny weather predominated during Expt. 3. Also during Expt. 2, one greenhouse (block) was cooler by an average of 5 °C than the other two greenhouses, which may have contributed to the significant block (experiment) effect.

Across experiments, GCA, SCA, and reciprocal effects, as well as their interactions with experiments, were all highly significant ($P < 0.001$). The DH lines from TMG1, MM76, and 9930 showed positive GCA effects for both fresh and dry weights; while ST8, GY14, and MSC3 had negative GCA effects for both traits (Table 1). The parental DHs and MSC3 showed negative SCA effects for both fresh and dry weights (Table 2), indicating that hybrids consistently out-performed parental lines. Across experiments, average heterosis over the midparent value was between 14% and 30% (Table 3). Although the DH from TMG1 showed the highest GCA effects (Table 1), it performed significantly better as a female than male (Table 4). The opposite was true for ST8, which performed better as a male (due to paternal transmission of mutant mitochondria), but not when used as the female parent (mitochondria transmitted from the wild-type male parent). As a male, MSC3 decreased fresh and dry weights of progenies by 21% and 27% (respectively) relative to experiment-wide means. We detected significant differences between reciprocal hybrids from crosses among wild-type DH lines (Tables 4 and 5). Although the DH from TMG1 showed the highest GCA effects (Table 1), it performed significantly better as a female than male (Table 4). The opposite was true for ST8, which performed better as a male than female (Table 4). As a result, reciprocal hybrids between ST8 and TMG1 were significantly ($P < 0.001$) different for dry and fresh weights across experiments (Table 5), differing by ≈30% of the overall experimental means for both traits. Other reciprocal hybrids showing significantly different fresh and dry weights were from crosses of TMG1 by Gy14 or 9930, as well as Gy14 and MM76 for dry weights (Table 5). Therefore, cucumber inbreds showing good GCA and/or SCA should be crossed in both directions to determine if a hybrid produced in one direction outperforms the reciprocal cross (Table 4).

Possible explanations for the significant reciprocal-cross differences include nuclear-cytoplasmic interactions or parent-of-origin effects. The differential transmission of the cucumber organelles (Hayve, 1997) allows for the production of reciprocal hybrids with contrasting chloroplast and mitochondrial combinations and identical nuclear genotypes. The significantly better performance of a DH as the male parent could be due to superior mitochondria and/or beneficial mitochondrial interactions with the nucleus. Conversely, better performance as the female parent could indicate better performing or interacting chloroplasts. Well defined heterotic groups exist in maize, and better performing hybrids are produced by crossing inbreds from distinct groups (Hallauer et al., 1988). Our results indicate that different organellar types may exist in cucumber.

Table 2. Specific combining abilities expressed as deviations from overall mean of zero for fresh and dry weights of progenies from diallel crossing among inbred (MSC3) and doubled haploids selected from populations TMG1, ‘Marketmore 76’ (MM76), 9930, ‘Straight 8’ (ST8), and Gy14 of cucumber.

|     | Fresh wt |       |       |       |       |       |       |
|-----|----------|-------|-------|-------|-------|-------|-------|
|     | TMG1 | Gy14 | ST8 | MM76 | 9930 | MSC3 |
|     | 3.44 | 0.09 | 1.36 | 1.59 | 0.72 |       |
|     | 0.39 | 0.61 | 0.61 | 0.61 | 0.61 |       |

Table 3. Heterosis observed for fresh and dry weights of progenies across three experiments from diallel crossing among parental doubled-haploid and inbred lines of cucumber.

| Expt. no. | Wt | Parents | Hybrids | Overall | Heterosis (%) |
|-----------|----|---------|---------|---------|---------------|
|           |    |         |         |         |               |
| 1         | Dry | 2.7     | 3.8     | 3.7     | 29.7          |
| 2         | Dry | 20.1    | 26.7    | 25.8    | 25.6          |
| 3         | Dry | 1.7     | 2.1     | 2.1     | 19.0          |
|           | Fresh | 21.0    | 24.5    | 24.0    | 14.6          |
|           | Fresh | 2.5     | 3.5     | 3.4     | 29.4          |
|           | Fresh | 35.5    | 45.7    | 44.4    | 23.0          |

*Heterosis reported as percentage of overall mean fresh or dry weight.
and inbreds possessing specific organelles may perform better as the male or female to produce more vigorous hybrids.

In animals, different phenotypes may occur depending on whether an allele is inherited from the mother or father, and these parent-of-origin effects are often due to imprinting in which an allele from one parent is epigenetically modified (Mott et al., 2014). In plants, most parent-of-origin differences are restricted to the endosperm and show maternal expression (reviewed by Köhler et al., 2012). There is an example of parent-of-origin expression in the embryo, the *maternally expressed in embryo 1* gene of maize (Jahnke and Scholten, 1995); however there is no evidence for significant effects on subsequent growth and development of the plant. Nevertheless, the significant reciprocal-cross differences reported in this study could be affected by parent-of-origin effects acting independently of or interacting with the organelles.

The significantly different performances of reciprocal hybrids from DH parents offer a unique opportunity to study biological differences associated with organelar and/or parent-of-origin effects. Transcriptome analyses should reveal important nuclear gene-expression differences associated with contrasting organelar combinations in identical nuclear genotypes. Epigenetic modification of alleles associated with parent-of-origin effects can be determined using tools such as methylation-sensitive enzymes or bisulfite sequencing (Lauria et al., 2014). These studies should provide insights about specific nuclear genes or pathways that interact with the organelles to enhance expression. Expression levels of these genes or pathways could then be assessed as targets for selection in plants showing strict maternal transmission of the organelles, toward the development of superior-performing hybrids.

**Literature Cited**

Abdelnoor, R.V., A.C. Christensen, S. Mohammed, B. Munoz-Castillo, H. Moriyama, and S.A. Mackenzie. 2006. Mitochondrial genome dynamics in plants and animals: Convergent gene fusions of a MutS homologue. J. Mol. Evol. 63:165–173.

Abdelnoor, R.V., R. Yule, A. Elo, A.C. Christensen, G. Meyer-Gauen, and S.A. Mackenzie. 2003. Substoichiometric shifting in the plant mitochondrial genome is influenced by a gene homologous to MutS. Proc. Natl. Acad. Sci. USA 100:5968–5973.

Allen, J.O. 2005. Effect of teosinte cytoplasmic genomes on maize phenotypes. Genetics 169:863–880.

Alverson, A.J., D.W. Rice, S. Dickinson, K. Barry, and J.D. Palmer. 2011. Origins and recombination of the bacterial-sized multichromosomal mitochondrial genome of cucumber. Plant Cell 23:2499–2513.

Andre, C., A. Levy, and V. Walbot. 1992. Small repeated sequences and the structure of plant mitochondrial genomes. Trends Genet. 8:128–131.

Bannerot, H., L. Boulidard, and Y. Chupeau. 1977. Unexpected difficulties met with radish cytoplasm in *Brassica oleracea*. EUCARPIA Cruciferae Nwsl. 2:16.

Bartoszewski, G., N. Katzir, and M.J. Havey. 2004a. Organization of repetitive DNAs and the genomic regions carrying ribosomal RNA, cob, and atp9 genes in the cucumber mitochondrial genomes. Theor. Appl. Genet. 108:982–992.

Bartoszewski, G., S. Malepszy, and M.J. Havey. 2004b. Mosaic (MSC) cucumbers regenerated from independent cell cultures possess different mitochondrial rearrangements. Curr. Genet. 45:45–53.

Birky, C.W. 1995. Uniparental inheritance of mitochondrial and chloroplast genes: Mechanisms and evolution. Proc. Natl. Acad. Sci. USA 92:11331–11338.

Burow, M.D. and J.G. Coors. 1994. Diallel: A microcomputer program for the simulation and analysis of diallel crosses. Agron. J. 86:154–158.

Cramer, C.S. and T.C. Wehner. 1999. Little heterosis for yield and yield components in hybrids of six cucumber inbreds. Euphytica 110:99–108.

Cummings, M.P., J.M. Nugent, R.G. Olmstead, and J.D. Palmer. 2003. Phylogenetic analysis reveals five independent transfers of the chloroplast gene rbcL to the mitochondrial genome in angiosperms. Curr. Genet. 43:131–138.

Dirks, R. 1988. Method for the production of double-haploid cucumbers. Patent US5492827 A. U.S. Patent Trademark Office, Washington, DC.

Edwards, J.W., J.O. Allen, and J.G. Coors. 1996. Teosinte cytoplasmic genomes. I. Performance of maize inbreds with teosinte cytoplasts. Crop Sci. 36:1088–1091.

Fauron, C., M. Casper, Y. Gao, and B. Moore. 1995. The maize mitochondrial genome: Dynamic, yet functional. Trends Genet. 11:169–173.

Ghaderi, A. and R.L. Lower. 1978. Heterosis and phenotypic stability of F1 hybrids in cucumber under controlled environment. J. Amer. Soc. Hortic. Sci. 103:275–278.

Ghaderi, A. and R.L. Lower. 1979. Heterosis and inbreeding depression for yield in populations derived from six crosses of cucumber. J. Amer. Soc. Hortic. Sci. 104:564–567.

Table 4. Reciprocal effects expressed as deviations from overall mean of zero in grams for fresh and dry weights of progenies from diallel crossing among doubled haploids selected from populations TMG1, ‘Marketmore 76’ (MM76), 9930, ‘Straight 8’ (ST8), and Gy14 of cucumber.

|                | Male | Female | Dry wt |
|----------------|------|--------|--------|
|                | TMG1 | Gy14   | ST8    | MM76 | 9930 | MSC3 | TMG1 | Gy14 | ST8 | MM76 | 9930 | MSC3 |
| Fresh wt       |      |        |        |      |      |      |      |      |      |      |      |      |
| TMG1           | —    | −2.37  | −4.42  | −1.36 | −1.93 | 4.63 | —    | −0.36 | −0.49 | −0.21 | −0.44 | 0.60 |
| Gy14           | 2.37 | —      | −0.84  | 1.50  | 0.79  | 3.44 | 0.36 | —     | −0.06 | 0.26  | 0.18  | 0.40 |
| ST8            | 4.42 | 0.84   | —      | 0.01  | −0.04 | 4.66 | 0.49 | 0.06  | —     | 0.00  | 0.10  | 0.49 |
| MM76           | 1.36 | −1.50  | −0.01  | —     | 1.31  | 1.62 | 0.21 | −0.26 | 0.00  | —     | 0.33  | 0.16 |
| 9930           | 1.93 | −0.79  | 0.04   | −1.31 | —     | −0.14 | 0.44 | −0.18 | −0.10 | −0.33 | —     | −0.06 |
| MSC3           | −4.63| −3.44  | −4.66  | −1.62 | 0.14  | —    | −0.60| −0.40 | −0.49 | −0.16 | 0.06  | —    |

Table 5. Significance of reciprocal-cross differences for fresh (above diagonal) and dry (below diagonal) weights of progenies from diallel crossing among doubled haploids selected from populations TMG1, ‘Marketmore 76’ (MM76), 9930, ‘Straight 8’ (ST8), and Gy14 of cucumber.

|                | Male | Female | Dry wt |
|----------------|------|--------|--------|
|                | TMG1 | Gy14   | ST8    | MM76 | 9930 | MSC3 | TMG1 | Gy14 | ST8 | MM76 | 9930 | MSC3 |
|                |      |        |        |      |      |      |      |      |      |      |      |      |
| TMG1           | —    | 0.032  | 0.001  | ns*   | 0.021 |
| Gy14           | 0.007| —      | ns     | ns    | ns    |
| ST8            | 0.005| ns     | —      | ns    | ns    |
| MM76           | ns*  | 0.003  | ns     | —     | ns    |
| 9930           | 0.002| ns     | ns     | ns    | —     |

ns* = nonsignificant at P < 0.05.
Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing schemes. Austral. J. Biol. Sci. 9:463–493.

Gu, J., D. Miles, and K.J. Newton. 1993. Analysis of leaf sectors in the Cucumis sativus mitochondrial mutant of maize. Plant Cell 5:963–971.

Hartmann, C., H. Recipon, M.F. Jubier, C. Valon, E. Delcher-Besin, Y. Henry, J. De Buyser, B. Lejeune, and A. Rode. 1994. Mitochondrial DNA variability detected in single wheat regenerant involves a rare recombination event across a short repeat. Curr. Genet. 25:456–464.

Hallauer, A.R., W.A. Russel, and K.R. Lamkey. 1988. Corn breeding, p. 463–564. In: G.F. Sprague and J.W. Dudley (eds.). Corn and corn improvement. Amer. Soc. Agron., Madison, WI.

Havey, M.J. 1997. Predominant paternal transmission of the mitochondrial genome cucumber. J. Hered. 88:232–235.

Havey, M.J. 2004. The use of cytoplasmic male sterility for hybrid seed production, p. 623–634. In: H. Daniel and C. Chase (eds.). Molecular biology and biotechnology of plant organelles. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Havey, M.J., J.D. McCreight, B. Rhodes, and G. Taurick. 1998. Differential transmission of the Cucumisorgenanome genomes. Theor. Appl. Genet. 97:122–128.

Hormuzdi, S.G. and T.A. More. 1989. Heterosis studies in cucumber (Cucumis sativus L.). Proc. Amer. Soc. Hort. Sci. 36:660–664.

Hunt, M.D. and K.J. Newton. 1991. The NCS3 mutation: Genetic evidence for the expression of ribosomal protein genes in Zea mays mitochondria. EMBO J. 10:1045–1052.

Hutchins, A.E. 1938. Some examples of heterosis in the cucumber (Cucumis sativus L.). Indian J. Hort. 4:73–79.

Jahnke, S. and S. Scholten. 2009. Epigenetic resetting of a gene imprinted in plant embryos. Curr. Biol. 19:1677–1681.

Janska, H., R. Sarria, M. Wolsoszynka, M. Arrieta-Montiel, and S.A. Mackenzie. 1998. Stoichiometric shifts in the common bean mitochondrial genome leading to male sterility and spontaneous reversion to fertility. Plant Cell 10:1163–1180.

Kanazawa, A., N. Tsutsumi, and A. Hirai. 1994. Reversible changes in the composition of the population of mtDNAs during dedifferentiation and regeneration in tobacco. Genetics 138:865–870.

Kihira, H. 1982. Importance of cytoplasm in plant genetics. Cytologia (Tokyo) 47:435–450.

Kim, J.S., J. Jung, J.A. Lee, H.W. Park, K.H. Oh, W.J. Jeong, D.W. Choi, J. Liu, and K. Cho. 2006. Complete sequence and organization of the cucumber (Cucumis sativus L. cv. Baekmibaekdadagi) chloroplast genome. Plant Cell Rpt. 25:334–340.

Köhler, C., P. Wolff, and C. Spillane. 2012. Epigenetic mechanisms underlying genomic imprinting in plants. Annu. Rev. Plant Biol. 63:331–352.

Lauer, M., C. Knudson, K.J. Newton, S. Gabay-Laughnan, and J.R. Laughnan. 1990. An abnormal growth mutant in maize has a defective mitochondrial cytochrome oxidase gene. Plant Cell 2:107–113.

Palmer, J.D. and L.A. Herbon. 1987. Uncircular structure of the Brassica hirta mitochondrial genome. Curr. Genet. 11:565–570.

Raubeson, L.A., R. Peery, T.W. Chunley, C. Dziubek, H.M. Forcade, J.L. Boore, and R.K. Jansen. 2007. Comparative chloroplast genomics: Analyses including new sequences from the angiosperms Nuphar advena and Ranunculus macranthus. BMC Genomics 8:174.

Reboud, X. and C. Zeyl. 1994. Organelle inheritance in plants. Heredity 72:132–140.

Rubino, D.B. and T.C. Wehner. 1986. Effect of inbreeding on horticultural performance of lines developed from an open-pollinated pickling cucumber population. Euphytica 35:459–464.

Sakamoto, W., H. Kondo, M. Murata, and F. Motoyoshi. 1996. Altered mitochondrial gene expression in a maternal distorted leaf mutant of Arabidopsis induced by chloroplast mutator. Plant Cell 8:1377–1390.

van Dooijeweert, Z. Zhang, and S. Huang. 2012. Genetic diversity and population structure of cucumber (Cucumis sativus L.). PLoS ONE 7:e49199.

Malepszy, S., W. Burza, and M. Śmiech. 1996. Characterization of a cucumber (Cucumis sativus L.) somaclonal variant with paternal inheritance. J. Appl. Genet. 37:65–78.

Marienfeld, J.R. and K.J. Newton. 1994. The maize NCS2 abnormal growth mutant has a chimeric nad4-nad7 mitochondrial gene and is associated with reduced complex 1 function. Genetics 138:855–863.

Martinez-Zapater, J.M., P. Gil, J. Capel, and C.R. Somerville. 1992. Mutations at the Arabidopsis CHM locus promote rearrangements of the mitochondrial genome. Plant Cell 4:889–899.

Mott, R., W. Yuan, P. Kaisaki, X. Gan, J. Cleak, A. Edwards, A. Baud, and J. Flint. 2014. The architecture of parent-of-origin effects in mice. Cell 156:332–342.

Newton, K.J. and E.H. Coe, Jr. 1986. Mitochondrial DNA changes in abnormal growth (nonchromosomal stripe) mutants of maize. Proc. Natl. Acad. Sci. USA 83:7363–7366.

Newton, K.J., C. Knudson, S. Gabay-Laughnan, and J.R. Laughnan. 1990. An abnormal growth mutant in maize has a defective mitochondrial cytochrome oxidase gene. Plant Cell 2:107–113.

Palmer, J.D. and L.A. Herbon. 1987. Uncircular structure of the Brassica hirta mitochondrial genome. Curr. Genet. 11:565–570.

Raubeson, L.A., R. Peery, T.W. Chunley, C. Dziubek, H.M. Forcade, J.L. Boore, and R.K. Jansen. 2007. Comparative chloroplast genomics: Analyses including new sequences from the angiosperms Nuphar advena and Ranunculus macranthus. BMC Genomics 8:174.

Reboud, X. and C. Zeyl. 1994. Organelle inheritance in plants. Heredity 72:132–140.

Rubino, D.B. and T.C. Wehner. 1986. Effect of inbreeding on horticultural performance of lines developed from an open-pollinated pickling cucumber population. Euphytica 35:459–464.

Sakamoto, W., H. Kondo, M. Murata, and F. Motoyoshi. 1996. Altered mitochondrial gene expression in a maternal distorted leaf mutant of Arabidopsis induced by chloroplast mutator. Plant Cell 8:1377–1390.

Shedge, V., M. Arrieta-Montiel, A.C. Christensen, and S.A. Mackenzie. 2007. Plant mitochondrial recombination surveillance requires unusual 

RecA and MatS homologs. Plant Cell 19:1251–1264.

Singh, J.P., H.S. Gill, and K.S. Ahluwalia. 1970. Studies in hybrid vigour in cucumbers (Cucumis sativus L.). Indian J. Hort. 27:36–38.

Sloan, D.B., A.J. Alverson, J.P. Chuckalovcak, M. Wu, D.E. McCauley, J.D. Palmer, and D.R. Taylor. 2012. Rapid evolution of enormous, multichromosomal genomes in flowering plant mitochondria with exceptionally high mutation rates. PLoS Biol. 10:e1001241.

Staub, J.E., F.C. Serquen, T. Horejsi, and J.F. Chen. 1999. Genetic diversity in cucumber (Cucumis sativus L.). IV. An evaluation of Chinese germplasm. Genet. Resources Crop Evol. 46:297–310.

Ward, B., R. Anderson, and A. Bendich. 1981. The mitochondrial genome is large and variable in a family of plants (Cucurbitaceae). Cell 25:793–803.

Wehner, T.C. 1989. Breeding for improved yield in cucumber. Plant Breed. Rev. 6:323–359.

Yang, L., D.H. Koo, Y. Li, X. Zhang, F. Luan, M.J. Havey, J. Jiang, and Y. Weng. 2012. Chromosome rearrangements during domestication of cucumber as revealed by high-density genetic mapping and draft genome assembly. Plant J. 71:895–906.
### Supplemental Table 1. Primer sequences and chromosome locations of simple sequence repeats (SSR) used to establish homozygosity of doubled haploid and inbred lines of cucumber. Primers and locations were previously reported by Yang et al. (2012) and are included here for convenience only.

| No. | SSR   | Forward     | Reverse       | Chromosome |
|-----|-------|-------------|---------------|------------|
| 1   | 9A10  | GACTAATGGCTCAGCTGTCAGG | CGACAGGAAATCATCTAGCA | 1          |
| 2   | 9C01  | GTGCCTCAGTCGATGGGGTGGT | GGGAAGGGAAGATGATCAATA | 1          |
| 3   | 25C04 | TGAATTTCTTTTGTGTGAATTTCA | ACCTCCCAAGGTCAACTGCA | 2          |
| 4   | 9B07  | CAAAATTTGGAGACTAAAAATGGT | TGGTTGTAGTCACTTTGCGCCA | 2          |
| 5   | 9E09  | AGCATGATGAGGATCCCTTG | CCGAATCTGCAACAAAGTATGG | 2          |
| 6   | 9G03  | GCTAAGTTTTGAGACTCTTCTT | CCAAAATGCAAGGAAAATCTGAGA | 3          |
| 7   | 25B09 | GTCTACTGGTCAGCCTTCTTAC | CCAAAATGCAAGGAAAATCTGAGA | 3          |
| 8   | 25D02 | GGGTAAAGGTTGTTTTGTTG | CAAACAGCCGTTCCTTGTTAAGA | 3          |
| 9   | 25G07 | CAAATGGGCTTTCTACTTCTT | GGGTGATGTCACAAAAAAGGAA | 3          |
| 10  | 9A03  | AGAAGAAGACCCCAAGAC | AGGCAATGCAAGGAAAATCTGAGA | 3          |
| 11  | 9B03  | ACAGATTGATTATTTTAAAAATCTT | CGGTTGAGACAAAGGAAAATCTGAGA | 3          |
| 12  | 25B11 | CATGTGAGGATGATGCCACAGT | CCAAAATGCAAGGAAAATCTGAGA | 4          |
| 13  | 25G06 | TTTTGGAATCAACATTTTTT | GCAAAATGCAAGGAAAATCTGAGA | 4          |
| 14  | 21A09 | GCAAGAAGAAATGACTCCTC | GTGACAAATTTTCTTCCTTCAA | 4          |
| 15  | 25C01 | CTGCCTGAGATGATCCAGGAA | GACAAATGCAAGGAAAATCTGAGA | 5          |
| 16  | 25F06 | GTTGTGAATTGTTGATGATT | GTGACAAATTTTCTTCCTTCAA | 5          |
| 17  | 9C04  | TCAGGATTGAAATGAAACCA | ATGACGCTGTCACAAAAAAGGAA | 5          |
| 18  | 9F01  | GCAGATGCAATTTTTCTGCTT | GCTGTCACAAAAAAGGAA | 5          |
| 19  | 25B12 | ATACATGCGACTGAGCTT | TCACAGGGTTGGTGAGGAC | 6          |
| 20  | 9A02  | GCAACTGAGAAGGATGTTG | GCTGTCACAAAAAAGGAA | 6          |
| 21  | 25B06 | ACCTGCTATGACAGATCGG | GCTGTCACAAAAAAGGAA | 7          |
| 22  | 25C11 | ATGAGGGAAGACCTTGGGTT | TTTCGTGAAGAAGGAAAATCTGAGA | 7          |
| 23  | 25G09 | TTTTGAAATCTTTTACATTG | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 24  | 25A10 | CAGCTCTGACAGATTCCGAG | GACAAATGCAAGGAAAATCTGAGA | 7          |
| 25  | 25C03 | TTCTGATGAGGGTTGAGTTG | CTGTCGACAAAAAAGGAA | 7          |
| 26  | 25C05 | TTCTGCTGAGCTTTTCTGTGG | CCATGTCATGTCACAAAAAAGGAA | 7          |
| 27  | 25C10 | GCTGATGACAGATTCCGAG | GACAAATGCAAGGAAAATCTGAGA | 7          |
| 28  | 25C07 | CACGCAGGATGATCAGTCCAG | GACAAATGCAAGGAAAATCTGAGA | 7          |
| 29  | 25C08 | TTTTGCAATCAACATTTCATTT | GACAAATGCAAGGAAAATCTGAGA | 7          |
| 30  | 25C09 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 31  | 25C10 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 32  | 25C11 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 33  | 25C12 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 34  | 25C13 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 35  | 25C14 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 36  | 25C15 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 37  | 25C16 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 38  | 25C17 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 39  | 25C18 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 40  | 25C19 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 41  | 25C20 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 42  | 25C21 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 43  | 25C22 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 44  | 25C23 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 45  | 25C24 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 46  | 25C25 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 47  | 25C26 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 48  | 25C27 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 49  | 25C28 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 50  | 25C29 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 51  | 25C30 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 52  | 25C31 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 53  | 25C32 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 54  | 25C33 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 55  | 25C34 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |
| 56  | 25C35 | ATGACGCTGTCACAAAAAAGGAA | ATGACGCTGTCACAAAAAAGGAA | 7          |

*Continued next page*
## Supplemental Table 1. Continued.

| No. | SSR      | Forward | Reverse | Chromosome |
|-----|----------|---------|---------|------------|
| 57  | 25B05    | TTATGCAACATTGGAGAACG | TGTATTTGTCGTCGCAACA | 2 |
| 58  | 25B10    | ACGTGAGAACACCCCTTCC | CTGGCAGGATGATTGATGGA | 2 |
| 59  | 25E02    | GAAAGGATGGTAGATGAAAGGG | CTTCTCCCCTCTCTGGCTT | 2 |
| 60  | 25G01    | TGAACAACTCACCTACCTCA | AAAGTGGAACCTTGGAGG | 2 |
| 61  | 25G08    | GCCTTTTCCTCTAATCTTATCC | TGAAGAAAAGGACAAAGAAAGAA | 2 |
| 62  | 25G11    | ACTATTGAGCATACGATTGGTTT | TGAATGACGAGATAAAGGAGTG | 2 |
| 63  | 25H03    | AATTCTCTCAGATTTTGGCA | GGTTTGGTAAGCAGCGAAA | 2 |
| 64  | 9A11     | TGCCAGCAAGAAGTTCACAC | CGCATGCTATGAGGACTCAA | 2 |
| 65  | 9B04     | GGAGAAATTTGATGGTGTAGCC | TGTGGAGGATGATGGTGTG | 2 |
| 66  | 9B06     | TCAACCTTCTAATTTGCAACCC | GTCTTCAAGCAGCACCACAAATGG | 2 |
| 67  | 9C12     | AAGGAAACAAGACCACTTAAACAAAAA | GGGTTCTAGAACAGGAGACA | 2 |
| 68  | 9D04     | TTTAATTTCCAAGGAAACG | TGAAGGAGAAGAGTTAAACAAGA | 2 |
| 69  | 9E02     | TGAACCTTCCCCACCTTAAACC | TGAATTTTGAGGAAACCTTC | 2 |
| 70  | 9F06     | TGCCCTTTACACTCAATAGTG | CAGGATCAACCTTCAATGGG | 2 |
| 71  | 9G01     | GCCAAAAATCCGAGAACGAGA | TCTCCAGGATTTTGGCTT | 2 |
| 72  | 25A02    | TACACAGAGGAGGGGTGTCC | TGTGTTGGATCCATTTCCTG | 3 |
| 73  | 25A05    | TGAGTTGATGAGTTGAGTTG | ATAAACCCCTTTTTCCCTT | 3 |
| 74  | 25B03    | GCTGCTTGATCCGGTTCTGT | GAGGAGGTAAATCATGCTCCA | 3 |
| 75  | 25B04    | GTCTATTCTCCCTGCTT | TGAAGGGAGAAACGACTTC | 3 |
| 76  | 25B07    | AAGGAAACAACCACTTACGCT | TGAAGGAGAAGAGTTAAACAAGA | 3 |
| 77  | 25C02    | TGAATGAGGGATGAGATGAA | TCTTTGCTTTGAGTATTTG | 3 |
| 78  | 25C08    | CAAACCCCAATCTGGTAA | ATTTGGAGATGTACTTGGG | 3 |
| 79  | 25C12    | CTTGGGATTCTTTGACCT | CGTTGAGAAATGTCTAAATGG | 3 |
| 80  | 25D01    | CCAAAATTTTAGGATCTCATGGG | AACCAATAATGCTTCTTCA | 3 |
| 81  | 25D04    | TACAGCCTCAAGATGAAACAGA | GGAAGAGGATGTTGGTGA | 3 |
| 82  | 25D07    | AATGGTGTGAGTTGAGTTG | AGGCCATCTTCTCCCTTCA | 3 |
| 83  | 25D10    | TCACCCTTCTTCATTTCTT | GAGATGAGTTGAGGAGTTT | 3 |
| 84  | 25E03    | TGAATCTCCTACTTCTCCT | CATGAAGGAGAAACGACTTC | 3 |
| 85  | 25E05    | CAGGAGGGATTGAGTTGAGG | GGGTTGGGAAAGACGTCTTG | 3 |
| 86  | 25E07    | CAGTTGAGAGGAGGATGTTT | CCGAGCTCAAACCACTTATC | 3 |
| 87  | 25E08    | GGCGTGGATCTTTGACCT | GACCCTTATACGCTGTTTAA | 3 |
| 88  | 25E07    | CAGTTGAGAGGAGGATGTTT | CCGAGCTCAAACCACTTATC | 3 |
| 89  | 25E09    | GGCGTGGATCTTTGACCT | GACCCTTATACGCTGTTTAA | 3 |
| 90  | 25E11    | GCACGCTCAAGATGAAACAGA | GCAACGTTGACTACAAT | 3 |
| 91  | 25E04    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 92  | 25E05    | AAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 93  | 25E07    | TTTGCAGAGGGCAAAGAAAG | TTTTGGTCTTCTCTCGACG | 3 |
| 94  | 25E06    | CTCCGGATCTCTACCAAATG | TCAGAGCAAAATCGTCTC | 3 |
| 95  | 25E08    | TGCTTCACAGAGATTGCGAC | CACCCTTCTCTCTCTCT | 3 |
| 96  | 25E09    | TGCTTCACAGAGATTGCGAC | CACCCTTCTCTCTCTCT | 3 |
| 97  | 25E10    | GTTGATGTAATTTGAGGAGT | TCAAGTCTCTGTTTGGAAAC | 3 |
| 98  | 25E11    | GTTGATGTAATTTGAGGAGT | TCAAGTCTCTGTTTGGAAAC | 3 |
| 99  | 25E12    | GTTGATGTAATTTGAGGAGT | TCAAGTCTCTGTTTGGAAAC | 3 |
| 100 | 25E04    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 101 | 25E05    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 102 | 25E06    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 103 | 25E07    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 104 | 25E08    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 105 | 25E09    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 106 | 25E10    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 107 | 25E11    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 108 | 25E04    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 109 | 25E05    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 110 | 25E06    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 111 | 25E07    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 112 | 25E08    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |
| 113 | 25E09    | GAAAGGATGCTGATTGACAGC | TTTTGGTCTTCTCTCGACG | 3 |

Continued next page
| No. | SSR | Forward | Reverse | Chromosome |
|-----|-----|---------|---------|------------|
| 114 | 25F09 | ACATCGATCATCAAGCCACA | GGCATTTTGTGAACCTTGT | 4 |
| 115 | 25G10 | GGATTGGGAAAAGGGATGTT | GGGAAGGTTGAAGGAAAAGC | 4 |
| 116 | 9B10 | TTGAAGAAACCAAAGCCACC | CAAGCGAGTCACTCTTCTGA | 4 |
| 117 | 9C05 | GATGTCCACCACCAAGAGTAGA | CCAAGAAGCAGGTTTGAAGGT | 4 |
| 118 | 9D06 | TAGGCCAGTTGTTGCTAGT | GCTGCAATTGGAATCTTGT | 4 |
| 119 | 9D12 | CCTCAAGACTCCATCTCTC | AGGTTTCAAGTGTGACCC | 4 |
| 120 | 9E08 | GATGAAGAACGTTGGCGTTT | TCCCCTCAACATCATCTCA | 4 |
| 121 | 9E10 | GATGTCACCGAACCAAGTGA | CCCACAAAGAGGTTTCAAGA | 4 |
| 122 | 9F09 | TTGAAGAAACCAAAGCCACC | CAAGCGAGCTCATCTTCTGA | 4 |
| 123 | 9G04 | TTGAAGAAACCAAAGCCACC | CAAGCGAGCTCATCTTCTGA | 4 |
| 124 | 9G11 | GGGCCGATTGGGACTCTTACA | CTAACGAGAGACCAACATTG | 4 |
| 125 | 9G12 | GGGCCGATTGGGACTCTTACA | CTAACGAGAGACCAACATTG | 4 |
| 126 | 9H01 | GATGTCACCGAACCAAGTGA | CCCACAAAGAGGTTTCAAGA | 4 |
| 127 | 19E08 | GATGTCACCGAACCAAGTGA | CCCACAAAGAGGTTTCAAGA | 4 |
| 128 | 25A03 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 129 | 25A11 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 130 | 25A12 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 131 | 25B01 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 132 | 25B02 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 133 | 25B03 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 134 | 25B04 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 135 | 25B05 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 136 | 25B06 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 137 | 25B07 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 138 | 25B08 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 139 | 25B09 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 140 | 25B10 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 141 | 25B11 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 142 | 25B12 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 143 | 25C01 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 144 | 25C02 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 145 | 25C03 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 146 | 25C04 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 147 | 25C05 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 148 | 25C06 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 149 | 25C07 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 150 | 25C08 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 151 | 25C09 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 152 | 25C10 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 153 | 25C11 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 154 | 25C12 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 155 | 25D01 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 156 | 25D02 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 157 | 25D03 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 158 | 25D04 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 159 | 25D05 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 160 | 25D06 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 161 | 25D07 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 162 | 25D08 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 163 | 25D09 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 164 | 25D10 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 165 | 25D11 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 166 | 25D12 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 167 | 25E01 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 168 | 25E02 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 169 | 25E03 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |
| 170 | 25E04 | TCCTCAGGCTTGTTGCTAGA | ACCTCAAAAGATGCTCAGC | 5 |

Continued next page
### Supplemental Table 1. Continued.

| No. | SSR | Forward | Reverse | Chromosome |
|-----|-----|---------|---------|------------|
| 171 | 9A09 | TCAGACGGGGTTGATTTTC | ACCAGCACAAGGAAAACCTG | 6 |
| 172 | 9B09 | GAGTTTCAACAAATGTTGCTCTT | CTTTTGCTTTGTGGACCAT | 6 |
| 173 | 9D02 | ACACCATTTTTTCATCGAGATT | GGGATGAGGAGCAAATGGTA | 6 |
| 174 | 9D10 | CCCACAATTTTAAATGACTCCAA | AATTACCAATCCACGCCATTC | 6 |
| 175 | 9E01 | AAAACCTTAAGCTCAAACATTGAA | TGTTGCTGTTATCTTTTCTTGC | 6 |
| 176 | 9E05 | TATGCCATCAAAACGACACC | GTAGAGATGGGTGCGAAGC | 6 |
| 177 | 9E12 | TTCTTCTCCATAATTTAAGTCCAA | CAAAATAAAAAAACGCAAAAA | 6 |
| 178 | 9F07 | TATTTCTCATCGGAAAGAACGCC | TTTGCCCTACTACCCCTCTT | 6 |
| 179 | 9F12 | AGAAATGGGGATTGAATATTATATTAAC | CACCAAGCTACATATTTCAGCA | 6 |
| 180 | 9G09 | GGTGTTGATAACCTCAAATAGAGAATG | GGCGAAAGGAGTTATACCA | 6 |
| 181 | 9H08 | CACCTCAAACGCACTCCATC | TGGCTGTTATGAGACTTGC | 6 |
| 182 | 25C07 | CTTCTCTCGGCCAGTGAC | TTAATGTCACACTGGCA | 7 |
| 183 | 25D11 | CCCACATGCAAACCTCTTT | GTCCCTCCGCACCTTACCT | 7 |
| 184 | 25E08 | CTTCTCTCCGAGCTCCTTCC | GGCAGAAAGGAGTTATACCA | 7 |
| 185 | 25F10 | ATTGGATTTTAGCGCGCTT | AACAATGAGGAAAGGTGCC | 7 |
| 186 | 25H07 | TTTTTGGAATATACGGCGCT | TCCAAAGATTTCCATTGCT | 7 |
| 187 | 9B12 | TCATCTAAATATAAAGTTGAATGGTTG | CTCCTCACACACTTGC | 7 |
| 188 | 9D11 | CCGGTAGGTTGGTCTTGAATG | TTGGAAAGGAAATGGAAA | 7 |
| 189 | 9G10 | AGCTAGCCACATATTAGGACAGT | CACTCTCAAATTTAGGCACACA | 7 |
| 190 | 9H06 | TTTTGGTAGAATCAAAGAACG | GGGAAATCACAATTCATG | 7 |

### Supplemental Table 2. Presence (1) versus absence (0) of polymorphic simple sequence repeats (SSR) used for genetic-distance estimates.

| SSR | Fragment | Csh | ST8 | MM76 | Gy14 | 9930 | TMG | MSC3 |
|-----|----------|-----|-----|------|------|------|-----|------|
| 9G03 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9G03 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| 9G03 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 9F01 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9F01 | 5 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| 9F01 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 9C04 | 7 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9C04 | 8 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| 9C04 | 9 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 9C04 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 9C01 | 11 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 9C01 | 12 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 9C01 | 13 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9C01 | 14 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 9B07 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9B07 | 16 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| 9B07 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 9B07 | 18 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 9B03 | 19 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9B03 | 20 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 9B03 | 21 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 9B03 | 22 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 9A10 | 23 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| 9A10 | 24 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 9A10 | 25 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9A10 | 26 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 9A03 | 27 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| 9A03 | 28 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 9A03 | 29 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 9A02 | 30 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 9A02 | 31 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
Supplemental Table 2. Continued.

| SSR    | Fragment | Csh | ST8 | MM76 | Gy14 | TMG | MSC3 |
|--------|----------|-----|-----|------|------|-----|------|
| 9A02   | 32       | 0   | 1   | 0    | 0    | 0   | 0    |
| 9A02   | 33       | 0   | 0   | 0    | 0    | 0   | 0    |
| 9A02   | 34       | 0   | 0   | 1    | 0    | 0   | 0    |
| 25G09  | 35       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25G09  | 36       | 0   | 0   | 0    | 1    | 1   | 1    |
| 25G09  | 37       | 0   | 1   | 1    | 0    | 0   | 0    |
| 25G09  | 38       | 0   | 0   | 0    | 0    | 0   | 0    |
| 25G07  | 39       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25G07  | 40       | 0   | 1   | 0    | 1    | 0   | 1    |
| 25G07  | 41       | 0   | 0   | 1    | 0    | 1   | 0    |
| 25G06  | 42       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25G06  | 43       | 0   | 1   | 0    | 1    | 0   | 0    |
| 25G06  | 44       | 0   | 0   | 1    | 0    | 1   | 0    |
| 25G06  | 45       | 0   | 0   | 0    | 0    | 1   | 1    |
| 25G02  | 46       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25G02  | 47       | 0   | 1   | 0    | 0    | 0   | 0    |
| 25G02  | 48       | 0   | 0   | 1    | 0    | 1   | 1    |
| 25G02  | 49       | 0   | 0   | 0    | 1    | 0   | 0    |
| 25F06  | 50       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25F06  | 51       | 0   | 1   | 1    | 1    | 1   | 1    |
| 25F09  | 52       | 1   | 0   | 1    | 0    | 0   | 0    |
| 25F09  | 53       | 0   | 1   | 1    | 0    | 1   | 1    |
| 25D05  | 54       | 0   | 1   | 0    | 0    | 1   | 0    |
| 25D05  | 55       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25D05  | 56       | 0   | 0   | 1    | 0    | 1   | 1    |
| 25C11  | 57       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25C11  | 58       | 0   | 0   | 1    | 1    | 1   | 0    |
| 25C11  | 59       | 0   | 1   | 0    | 0    | 1   | 1    |
| 25C04  | 60       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25C04  | 61       | 0   | 1   | 1    | 0    | 1   | 0    |
| 25C04  | 62       | 0   | 0   | 0    | 1    | 0    | 1    |
| 25C01  | 63       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25C01  | 64       | 0   | 0   | 1    | 0    | 1   | 0    |
| 25C01  | 65       | 0   | 1   | 0    | 1    | 0   | 0    |
| 25C01  | 66       | 0   | 0   | 0    | 0    | 1   | 0    |
| 25B12  | 67       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25B12  | 68       | 0   | 1   | 1    | 1    | 0   | 0    |
| 25B12  | 69       | 0   | 0   | 0    | 0    | 1   | 1    |
| 25B12  | 70       | 0   | 0   | 0    | 0    | 0   | 1    |
| 25B11  | 71       | 1   | 0   | 0    | 0    | 1   | 1    |
| 25B11  | 72       | 0   | 1   | 1    | 1    | 0   | 0    |
| 25B09  | 73       | 1   | 0   | 0    | 0    | 0   | 1    |
| 25B09  | 74       | 0   | 0   | 1    | 0    | 0   | 0    |
| 25B09  | 75       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25B09  | 76       | 0   | 1   | 0    | 1    | 0   | 0    |
| 25B06  | 77       | 1   | 0   | 0    | 0    | 0   | 0    |
| 25B06  | 78       | 0   | 1   | 1    | 1    | 0   | 0    |
| 25B06  | 79       | 0   | 0   | 0    | 0    | 1   | 0    |
| 25B06  | 80       | 0   | 0   | 0    | 0    | 0   | 1    |
| 25B06  | 81       | 1   | 0   | 0    | 0    | 0   | 0    |
| 21A09  | 82       | 0   | 1   | 1    | 1    | 1   | 1    |
| 9E09   | 83       | 1   | 0   | 0    | 0    | 0   | 1    |
| 9E09   | 84       | 0   | 1   | 1    | 0    | 1   | 0    |
| 9E09   | 85       | 0   | 0   | 0    | 1    | 0   | 0    |