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Paternal inheritance of chloroplast DNA and maternal inheritance of mitochondrial DNA in the genus *Actinidia*

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Abstract PCR amplification of four chloroplast DNA (cpDNA) and two mitochondrial DNA (mtDNA) regions followed by restriction of the amplified products was used to identify restriction fragment length polymorphisms in 21 *Actinidia* taxa. Subsequently, the mode of organelle inheritance was investigated in both interspecific and intraspecific controlled crosses made between genotypes showing different cpDNA and/or mtDNA haplotypes. Fifty-six seedlings produced from three interspecific crosses, including in one case the pseudo reciprocal (different genotypes of the same species used as opposite parents), were checked for cpDNA inheritance, and 102 seedlings from the same interspecific crosses and 32 seedlings from two intraspecific crosses within the species *A. deliciosa* were checked for mtDNA inheritance. In all cases, cpDNA was inherited from the father and mtDNA was inherited from the mother. Maternal inheritance of mtDNA was expected, being the rule in plants, but *A. deliciosa* is the first genus in angiosperms for which a widespread and strictly paternal inheritance of cpDNA has been reported. Transmission of chloroplastic and mitochondrial genomes through opposite parents provides an exceptional opportunity for studying the paternal and maternal genetic lineages of species in the genus *Actinidia*.

Key words Kiwifruit · Chloroplast inheritance · Mitochondrial inheritance · mtDNA Intraspecific polymorphism · PCR-amplified RFLP

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Introduction

Cytoplasmic DNA which comprises the chloroplast and mitochondrial genomes, is an interesting subject of analysis for phylogenetic reconstruction at a variety of taxonomic levels and its study became widespread once the techniques of DNA analysis were generally available (Clegg and Zurawski 1992).

Extra-nuclear DNA has three main advantages for systematic studies: (1) it is inherited cytoplasmically and therefore apparently does not undergo recombination during sexual reproduction (Harris and Ingram 1991; Birky 1995); (2) in nearly all eukaryotes, it is usually inherited from only one parent (Birky 1995), (3) it shows little intraspecific variation (Crawford 1990) because the estimated rate of nucleotide substitutions is low, in chloroplasts being one-quarter to one-third and in mitochondria one-twelfth the rate in plant nuclear DNA (Palmer 1992).

In most angiosperms both plastids and mitochondria are maternally inherited (Corriveau and Coleman 1988). Molecular and cellular mechanisms exclude organelles during pollen development (reviewed in Hagemann 1992; Reboud and Zeyl 1994; Birky 1995), but most such controls are not stringent (Birky 1983) so that biparental inheritance of organelles has been reported, or at least postulated, in many different taxa (Kirk and Tilney-Bassett 1978; Sears 1980; Corriveau and Coleman 1988; Harris and Ingram 1991). The relaxed control of cytoplasmic DNA inheritance, which has been better documented for chloroplasts, results in the presence in the same progeny of individuals carrying chloroplast genes either exclusively from the mother or exclusively from the father, or else from both parents. The frequency of the three different kinds of offspring varies according to the species involved and often in different crosses of the same species (Schumann and Hancock 1989; Harris and Ingram 1991; Forsthoefel et al. 1992; Birky 1995).

Exclusively uniparental paternal inheritance of plastids is commonest in gymnosperms (reviewed in

Hipkins et al. 1994; Reboud and Zeyl 1994) and rare amongst angiosperms, having so far been reported only in *Actinidia* (Cipriani et al. 1995). Less information is available for mitochondria. Their inheritance is considered to be maternal in all plants with only a few reported cases of non-strict maternal inheritance (Reboud and Zeyl 1994). The sparsity of reports on mitochondrial inheritance is due mainly to the lack of suitable phenotypic and molecular markers (Reboud and Zeyl 1994) and the peculiar features of plant mtDNAs (Palmer 1992).

The kiwifruit (*Actinidia deliciosa*) is a recently domesticated species. The world industry is based on a single female genotype, the cultivar 'Hayward', but the genus contains more than 60 species and 100 taxa, almost all with edible fruit and characterised by great variability in agronomic and qualitative traits (Ferguson 1990). Such variability allows for the introgression of novel characters into kiwifruit. Many *Actinidia* species can be successfully crossed but for the better design of breeding programmes it is useful to know more about relationships between the species. Analysis of four cpDNA regions in *Actinidia* has already demonstrated that cytoplasmic DNA is a source of polymorphisms well suited to phylogenetic analysis (Cipriani and Morgante 1993; Cipriani 1994). Chloroplast inheritance has also been investigated and was found to be strictly paternal in four different interspecific crosses involving *A. arguta*, *A. chinensis*, *A. deliciosa* and *A. kolomikta* as parents (Cipriani et al. 1995).

We report here further evidence of paternal inheritance of chloroplast DNA in *Actinidia* and the first evidence of maternal inheritance of mitochondrial DNA in both interspecific and intraspecific crosses.

Materials and methods

PCR amplification of cpDNA and mtDNA regions, followed by the restriction of amplified products with different restriction enzymes, was used to identify restriction fragment length polymorphisms (RFLPs) in 21 *Actinidia* taxa and to determine the mode of organelle inheritance in interspecific and intraspecific crosses between genotypes showing different cpDNA and/or mtDNA haplotypes.

Plant material

Two to eight genotypes of each of the following taxa, *A. arguta* var. *arguta*, *A. arguta* var. *purpurea*, *A. arguta* var. *cordifolia*, *A. hypoleuca*, *A. rufa*, *A. melanandra*, *A. kolomikta*, *A. polygama*, *A. valvata*, *A. macrosperma*, *A. callosa* var. *henryi*, *A. chrysantha*, *A. indochinensis*, *A. hemsleyana*, *A. fulvicoma*, *A. latifolia*, *A. lanceolata*, *A. eriantha*, *A. chinensis* var. *chinensis*, *A. deliciosa* var. *deliciosa* and *A. deliciosa* var. *chlorocarpa*, were screened for polymorphisms at the cpDNA and mtDNA regions reported below.

Four interspecific crosses (*A. chinensis* × *A. eriantha* and its reciprocal *A. eriantha* × *A. chinensis*, *A. chrysantha* × *A. polygama*, and *A. chrysantha* × *A. valvata*), of the dozens attempted on the basis of the parent species having different cpDNA and mtDNA haplotypes, produced progeny which were analysed in this study. The ploidy levels of genotypes used as parents were checked by flow cytometry.

One male cultivar, 'Tomuri', of *A. deliciosa* var. *deliciosa* (hereinafter shortened to *A. deliciosa*) showed an insertion of approximately 30 base pairs at the mtDNA *nad*1 gene and was therefore used as male parent in two intraspecific crosses ('Allison' × 'Tomuri' and 'Hayward' × 'Tomuri') in order to confirm the mode of inheritance of mtDNA found in interspecific hybrids.

Seeds were collected from mature fruits of seed-plants, stored at 4°C for 2 months, kept at alternating temperatures for 2 weeks to overcome dormancy and then allowed to germinate in the greenhouse.

DNA extraction

Total DNA was extracted from approximately 0.3 g of young leaves with CTAB buffer, separated with chloroform/isoamylic alcohol, centrifuged at 6000 g for 20 min, precipitated in isopropanol and washed with ethanol according to the procedure described by Doyle and Doyle (1990).

PCR amplification and DNA restriction

Pairs of primers were synthesised (Operon Technologies, Calif.) for four cpDNA and two mtDNA regions. The cpDNA regions were selected in the rubisco large subunit gene (*rbcL*), the photosystem II D1 protein gene (*psbA*), and the spacers between *trnT* and 5′-*trnL* exon (*a-b*) and between *trnL*-3′ exon and *trnF* (*e-f*). The criteria adopted for selecting chloroplast sequences and the lengths of these sequences are described in Cipriani and Morgante (1993). The mtDNA regions were selected in the *nad*1 and *nad*4 genes, according to the data of Demesure et al. (1995). The primer pair sequences are reported in Table 1.

Polymerase chain reactions of cpDNA regions were carried out in a 50-µl vol containing 200 ng of genomic DNA, 0.2 µM of each primer, 200 µM of each dNTP, 50 mM of KCl, 10 mM of Tris-HCl pH 9.0, 2.5 mM of $MgCl_2$ and 1 unit of *Taq* polymerase (Pharmacia Biotech) with the following thermal-cycle profile: 95°C for 5 min for one cycle; 80°C for 3 min for one cycle; 94°C for 1 min, 50°C for 1 min, 72°C for 1 min 30 s for 26 cycles; 72°C for 7 min for one cycle.

The PCR mixture for mtDNA regions was slightly modified, using 40 ng of genomic DNA and 2.0 mM of $MgCl_2$. The thermal-cycle profile was as follows: 94°C for 4 min for one cycle; 80°C for 3 min for one cycle; 93°C for 1 min, 58°C for 1 min, 72°C for 2 min for 33 cycles; 72°C for 7 min for one cycle.

The *Taq* polymerase was added during the 3 min at 80°C cycle (hot start).

The amplification products for all taxa screened were digested with different restriction enzymes (data not reported). Those adopted for the determination of organelle inheritance are reported in Tables 2 and 3.

The digests were electrophoresed in 3% agarose gel (Metaphor, FMC Bioproducts) containing ethidium bromide.

Results

The crosses studied gave large numbers of highly viable seed except for the cross *A. chrysantha* × *A. polygama* in which each fruit set contained a small number of seed, of which only a very few (14%) germinated. This was due to the unbalanced ploidy of the parents: flow cytometry showed that the *A. chrysantha* genotype used was tetraploid and the *A. polygama* diploid (data

Table 1 List of the cpDNA and mtDNA regions adopted in this study and the primer-pair forward/reverse sequences designed for the PCR amplification

DNA regions[a]	Primer-pair sequence	Reference
Chloroplast DNA		
rbcL	for. 5′-TTGGCAGCATTCCGAGTAA rev. 5′-TGTCCTAAAGTTCCTCCAC	Cipriani et al. (1993)
psbA	for. 5′-CCATGACTGCAATTTTAGAG rev. 5′-ACTTCCATACCAAGGTTAGC	Cipriani et al. (1993)
a-b spacer	for. 5′-CATTACAAATGCGATGCTCT rev. 5′-TCTACCGATTTCGCCATATC	Taberlet et al. (1991)
e-f spacer	for. 5′-GGTTCAAGTCCCTCTATCCC rev. 5′-ATTTGAACTGGTGACACGAG	Taberlet et al. (1991)
Mitochondrial DNA		
*nad*1	for. 5′-GCATTACGATCTGCAGCTCA rev. 5′-GCAGCTCGATTAGTTTCTGC	Demesure et al. (1995)
*nad*4	for. 5′-CAGTGGGTTGGTCTGGTATG rev. 5′-TCATATGGGCTACTGAGGAG	Demesure et al. (1995)

[a] See text for more details about the DNA regions

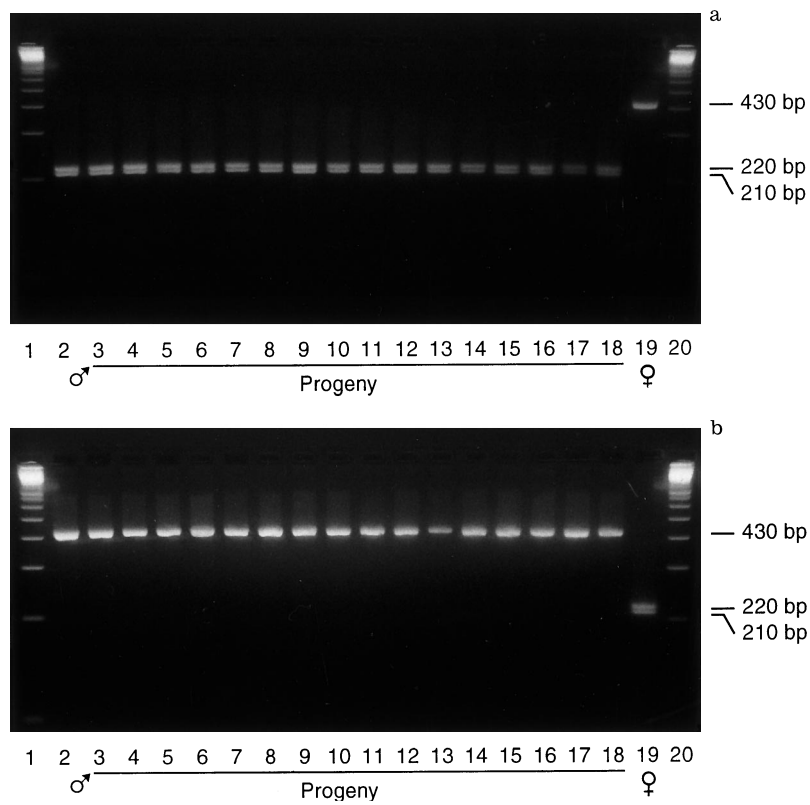

Fig. 1 Analysis of inheritance of the cpDNA *e-f* spacer restricted with *Taq*I in the interspecific crosses (**a**) *A. chinensis* #54.16 (female parent) × *A. eriantha* #105.5 (male parent) and (**b**) *A. eriantha* #105.4 (female parent) × *A. chinensis* #54.19 (male parent). In both figures from left: *lane 1* = 100-bp ladder; *lane 2* = male parent, *lanes 3–18* = progeny; *lane 19* = female parent; *lane 20* = 100-bp ladder

not reported). Of the other genotypes used as parents, *A. chinensis* and *A. eriantha* were diploid, *A. valvata* was tetraploid, and *A. deliciosa* was hexaploid.

In studies of chloroplast DNA inheritance, the parents of *A. chinensis* and *A. eriantha* were differentiated at the cpDNA *e-f* spacer by a restriction site recognised by *Taq*I in *A. eriantha* but not in either of the *A. chinensis* genotypes (Fig. 1, Table 2). *A. chrysantha* was distinguished from both *A. polygama* and *A. valvata* by a more complex fragment pattern generated by *Hin*fI (Table 2).

Strictly paternal inheritance of cpDNA was observed in all four interspecific crosses, with a total of 56 seedlings being examined. This result confirms a previous study in which 63 seedlings were analysed from different interspecific crosses involving the species, *A. arguta*, *A. deliciosa*, *A. chinensis* and *A. kolomikta* (Cipriani et al. 1995).

Table 2 Inheritance of cpDNA in *Actinidia* interspecific hybrids

Cross, parents[a]	cpDNA region	Restriction enzyme	Maternal fragment pattern (bp)	Paternal fragment pattern (bp)	No. of offsprings with fragment pattern[b]		
					M	P	Bip
C80 *A. chinensis* #54.16 × *A. eriantha* #105.5	*e-f* spacer	*Taq*I	430	210/220	0	16	0
C95 *A. eriantha* #105.4 × *A. chinensis* #54.19	*e-f* spacer	*Taq*I	210/220	430	0	16	0
C88 *A. chrysantha* #104.6 × *A. polygama* #70	*a-b* spacer	*Hin*fI	390/120/100[c]	350/140/120[c]	0	8	0
C89 *A. chrysantha* #104.6 × *A. valvata* #123.1	*a-b* spacer	*Hin*fI	390/120/100[c]	350/140/120[c]	0	16	0

[a] For each cross, the female parent is written first. The symbol # precedes the accession/genotype code
[b] M maternal, P paternal, Bip biparental
[c] Fragments shorter than 100 bp were disregarded

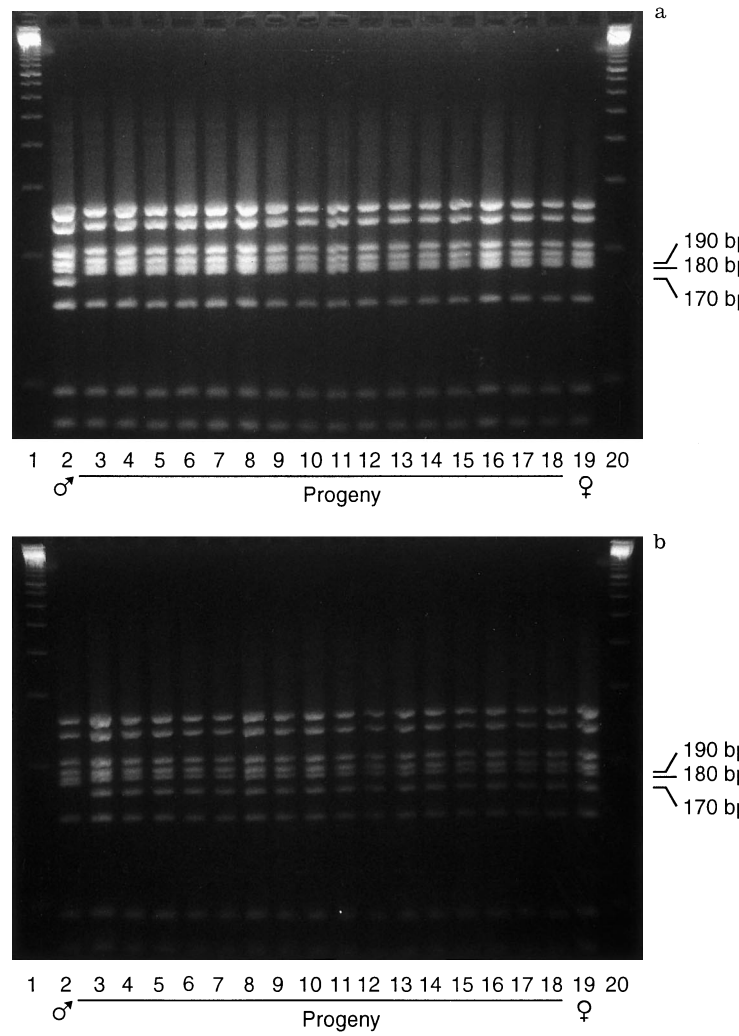

Fig. 2 Analysis of inheritance of the mtDNA *nad*1 gene restricted with *Hae*III in the interspecific crosses (**a**) *A. chinensis* #54.16 (female parent) × *A. eriantha* #105.5 (male parent) and (**b**) *A. eriantha* #105.4 (female parent) × *A. chinensis* #54.19 (male parent). In both figures from left: *lane 1* = 100-bp ladder; *lane 2* = male parent, *lanes 3–18* = progeny; *lane 19* = female parent; *lane 20* = 100-bp ladder

In studies of mtDNA inheritance, differentiation of *A. chinensis* from *A. eriantha* was probably due to an insertion/deletion polymorphism in the mtDNA *nad*1 gene, since restriction patterns produced by different enzyme systems gave only a 10-bp difference in the length of a single fragment, the remainder being the same (Fig. 2, Table 3). *A. chrysantha* was different from both *A. polygama* and *A. valvata* in one of the six fragments generated by *Hae*III (Table 3).

Strictly maternal inheritance of mtDNA was observed in all interspecific crosses examined (Table 3).

Table 3 Inheritance of mtDNA in *Actinidia* interspecific and intraspecific hybrids

Cross, parents[a]	mtDNA region	Restriction enzyme	Maternal fragment pattern (bp)	Paternal fragment pattern (bp)	No. of offsprings with fragment pattern[b]		
					M	P	Bip
Interspecific hybrids							
C80 *A. chinensis* #54.16 × *A. eriantha* #105.5	*nad*1	*Hae*III	180[c]	170[c]	32	0	0
		*Msp*I	350[d]	340[d]	32	0	0
C95 *A. eriantha* #105.4 × *A. chinensis* #54.19	*nad*1	*Hae*III	170[c]	180[c]	30	0	0
		*Msp*I	340[d]	350[d]	30	0	0
C88 *A. chrysantha* #104.6 × *A. polygama* #70	*nad*4	*Hae*III	120[e]	130[e]	8	0	0
C89 *A. chrysantha* #104.6 × *A. valvata* #123.1	*nad*4	*Hae*III	120[e]	130[e]	32	0	0
A. deliciosa intraspecific hybrids	*nad*1	*Hae*III	170[f]	200[f]	16	0	0
'Allison' #4 × 'Tomuri' #3		*Mnl*I	220[g]	240[g]	16	0	0
		*Msp*I	340[h]	360[h]	16	0	0
'Hayward' #6 × 'Tomuri' #3	*nad*1	*Mnl*I	220[g]	240[g]	16	0	0
		*Msp*I	340[h]	360[h]	16	0	0

[a] For each cross, the female parent is written first. The symbol # precedes the accession/genotype code
[b] M maternal, P paternal, Bip biparental
[c] Other restriction fragments common to both parents (bp): 150/190/200/210/240/260. Fragments shorter than 100 bp were disregarded. Total fragment length approximaely 1.6 kb
[d] Other restriction fragments common to both parents (bp): 220/250/270. Fragments shorter than 100 bp were disregarded. Total fragment length approximately 1.6 kb
[e] Other restriction fragments common to both parents (bp): 100/150/200/250/490/600. Fragments shorter than 100 bp were disregarded. Total fragment length approximately 2.0 kb
[f] Other restriction fragments common to both parents (bp): 150/190/200/210/240/260. Fragments shorter than 100 bp were disregarded. Total fragment length approximately 1.6 kb
[g] Other restriction fragments common to both parents (bp): 130/140/150/190/220/230. Fragments shorter than 100 bp were disregarded. Total fragment length approximately 1.6 kb
[h] Other restriction fragments common to both parents (bp): 110/130/220/240/250. Fragments shorter than 100 bp were disregarded. Total fragment length approximately 1.6 kb

Maternal inheritance of mtDNA was likewise demonstrated by studying the progeny of two intraspecific crosses within *A. deliciosa* (Table 3), by exploiting an insertion of approximately 30 bp that differentiated the male cultivar 'Tomuri' from any of the other genotypes assayed in that species (data not reported), including the two female genotypes used as parents (Fig. 3).

Discussion

The data presented in this paper and those reported in Cipriani et al. (1995) demonstrate strictly paternal inheritance of chloroplasts in *Actinidia* amongst 119 seedlings from eight different interspecific crosses involving eight taxa, but strictly maternal inheritance of mitochondria in 134 seedlings involving both interspecific and intraspecific crosses and six different taxa.

Strictly paternal inheritance of chloroplasts is uncommon in angiosperms (Reboud and Zeyl 1994). Chloroplasts are usually inherited from the mother, although relaxed control of organelle transmission to the zygote could account for the low incidence of biparental inheritance observed in many species (Kirk and Tilney-Bassett 1978; Sears 1980; Harris and Ingram 1991; Reboud and Zeyl 1994). There are also reports of uniparental inheritance from the mother or from the father depending on the particular genotypes involved (reviewed in Cipriani et al. 1995). Initial studies (Boblenz et al. 1990) indicated that in *Daucus*, chloroplasts were always inherited from the father but subsequent work has shown instead that they are strictly maternally inherited (Steinborn et al. 1995). *Actinidia* therefore remains the only angiosperm genus consistently showing inheritance of chloroplasts from the father alone. Maternal inheritance of mitochondria was expected, being the rule in all plants so far studied.

Organelle inheritance is a complex phenomenon (Tilney-Bassett 1978; Sears 1980; Birky 1995), and two limits to experimental approaches should be stressed: the sensitivity of analytical procedures and the number of progeny assayed (Milligan 1992).

The technique adopted in the present work, of comparing RFLPs of PCR-amplified DNA regions, seems less prone to the fault, attributed to the Southern-blotting technique, of failing to detect DNA templates present at low-copy numbers in the presence of vast excesses of the templates supplied by the competing parent (Milligan 1992; Birky 1995). On the other hand, both molecular approaches are considered to be more reliable than cytological analyses. For instance, the

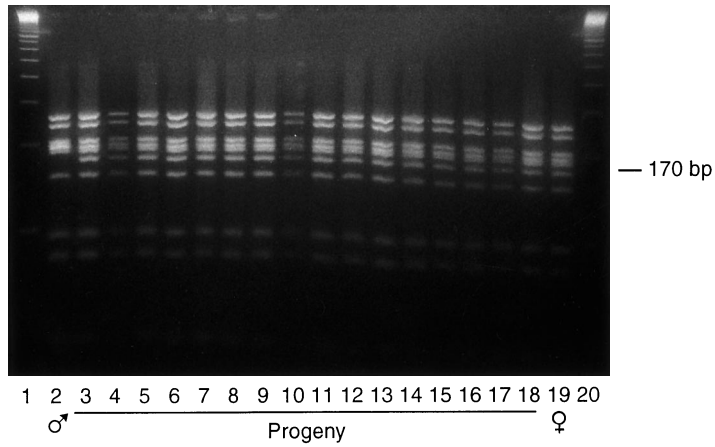

Fig. 3 Analysis of inheritance of the mtDNA *nad*1 gene restricted with *Hae*III in the intraspecific cross *A. deliciosa* 'Allison' #4 × 'Tomuri' #3. From left: *lane 1* = 100-bp ladder; *lane 2* = 'Tomuri' #3 (male parent), *lanes 3–18* = progeny; *lane 19* = 'Allison' #4 (female parent); *lane 20* = 100-bp ladder. The 170 bp-long fragment is lacking in the male parent. The presence of two fragments 200 bp-long, which overlap, is postulated in the male parent according to the full length of the unrestricted PCR amplification product (data not shown) and the intensity of the band at 200-bp in 'Tomuri #3'

presence of fluorochrome-dye-stained bodies in pollen does not necessarily indicate that paternal plastids are transferred into the embryo, since there are at least four mechanisms which should exclude paternal plastids during fertilisation (Sears 1980; Harris and Ingram 1991). As to the number of progeny tested, if the complexity of organelle transmission mechanisms is ignored and the phenomenon is regarded simply as a binomial sampling process, examination of a few dozen offspring should be sufficient to identify any prevailing uniparental inheritance of organelles, whereas the detection of rare deviations from strictly uniparental inheritance would require the analysis of very large numbers – many hundreds or even thousands – of offspring (Milligan 1992). As organelle inheritance must be seen as a continuum rather than an 'all-or-nothing' process (Harris and Ingram 1991), the occasional occurrence of biparental inheritance can be expected for many, if not all, species (Milligan 1992) and the aim of studies such as the present one is instead to determine the usual mode of organelle inheritance in particular taxa. Reports of strictly uniparental inheritance based on progeny sizes of between 7 and 100 [see Milligan (1992) for the statistical meaning of these values] can be accepted as demonstrating that the transmission pattern observed experimentally is indeed the most common pathway for the taxon being studied.

Because of the large numbers of progeny and interspecific cross combinations examined, the technical approaches adopted, and the results for mtDNA being the same in both interspecific and intraspecific crosses, we are confident that paternal inheritance of plastids and maternal inheritance of mitochondria could be the general rule in the genus *Actinidia*.

The transmission of chloroplast and mitochondrial genomes through different parents provides an exceptional opportunity for studying paternal and maternal genetic lineages of species within *Actinidia*.

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