Theor Appl Genet (1992) 84:280–285

THEORETICAL AND APPLIED GENETICS



# Chloroplast DNA inheritance in *Populus*

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Received November 9, 1991; Accepted November 15, 1991
Communicated by H.F. Linskens

**Summary.** The inheritance of chloroplast (cp) DNA was examined in $F_1$ hybrid progenies of two *Populus deltoides* intraspecific controlled crosses and three *P. deltoides* × *P. nigra* and two *P. deltoides* × *P. maximowiczii* interspecific controlled crosses by restriction fragment analysis. Southern blots of restriction digests of parental and progeny DNAs were hybridized to cloned cpDNA fragments of *Petunia hybrida*. Sixteen enzymes and five heterologous cpDNA probes were used to screen restriction fragment polymorphisms among the parents. The mode of cpDNA inheritance was demonstrated in progenies of *P. deltoides* × *P. nigra* crosses with 26 restriction fragment polymorphisms of cpDNA differentiating *P. deltoides* from *P. nigra*, as revealed by 12 enzyme-probe combinations, and in progenies of *P. deltoides* × *P. maximowiczii* crosses with 12 restriction fragment polymorphisms separating *P. deltoides* from *P. maximowiczii*, as revealed by 7 restriction enzyme-probe combinations. In all cases, $F_1$ offspring of *P. deltoides* × *P. nigra* and *P. deltoides* × *P. maximowiczii* crosses had cpDNA restriction fragments of only their maternal *P. deltoides* parent. The results clearly demonstrated uniparental-maternal inheritance of the chloroplast genome in interspecific hybrids of *P. deltoides* with *P. nigra* and *P. maximowiczii*. Intraspecific *P. deltoides* hybrids also had the same cpDNA restriction fragments as their maternal parent. Maternal inheritance of the chloroplast genome in *Populus* is in agreement with what has been observed for most other angiosperms.

**Key words:** *Populus* – Chloroplast DNA – Maternal plastid inheritance – Restriction fragment length polymorphism

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## Introduction

Chloroplast genomes of plants carry approximately 50 protein-coding genes which play major roles in photosynthesis and related biosyntheses and a complete set of rRNA and tRNA genes (Palmer 1985). Chloroplast genes are potentially useful for plant improvement. The chloroplasts of higher plants are targets for genetic engineering (Svab et al. 1990; Ye et al. 1990) and are the site of action of selective herbicides (Smith 1989). Also, chloroplast (cp) DNA restriction site variation is useful for constructing molecular phylogenies (Palmer 1987). Therefore, understanding the inheritance and structure of the cp genome is of fundamental biological importance, and there is an increasing interest in this direction.

Most angiosperm species typically display uniparental-maternal inheritance of plastids, with some species having regular or occasional biparental plastid inheritance (Tilney-Bassett 1978; Sears 1980; Whatley 1982; Smith 1989). Most studies on plastid inheritance have relied upon the use of plastid mutants in reciprocal crosses or ultrastructural analysis (Tilney-Bassett 1978; Sears 1980; Whatley 1982). Recently, restriction fragment length polymorphism (RFLP) analysis has provided precise molecular techniques to determine the mode of inheritance of organellar genomes. RFLP analysis of cpDNA has been employed to ascertain the mode of inheritance of the cp genome with a high degree of certainty in intra- and interspecific crosses of angiosperms (review in Smith 1989; Schumann and Hancock 1989; Polans et al. 1990; Soltis et al. 1990; Horlow et al. 1990) and gymnosperms (review in Strauss et al. 1989; Neale and Sederoff 1989; Neale et al. 1989; Stine and Keathley 1990). RFLP analysis has provided an increasing number of exceptions to generalizations about plastid inheritance in angiosperms (e.g. Medgyesy et al. 1986; Schmitz and Kowallik 1986; Horlow et al. 1990), and has revealed that the chloroplast genome typically is paternally inherited in gymnosperms (review in Strauss et al. 1989; Neale and Sederoff 1989; Neale et al. 1989; Stine and Keathley 1990). In addition, a rapid screening procedure involving DNA fluorochrome has been developed to detect potential biparental inheritance of plastid DNA, and results for 235 an-

giosperm species have been provided (Corriveau and Coleman 1988).

Despite the wealth of knowledge of the mode of cpDNA inheritance in angiosperms, no data are available on the mode of inheritance of the chloroplast genome in the Salicaceae, particularly in the genus *Populus* L. To our knowledge, there are no published data on cpDNA inheritance in any forest tree angiosperm. Poplars (*Populus*) are dioecious (with one exception), fast-growing, and economically important multipurpose trees that are suitable for a wide variety of products.

*Populus deltoides* Marsh. (Section *Aigeiros* Duby), *P. nigra* L. (Section *Aigeiros*), and *P. maximowiczii* Henry (Section *Tacamahaca* Spach.) are important both biologically and economically for the breeding of hybrid poplar varieties for intensive poplar culture programs (Dickmann and Stuart 1983). These poplar species are sexually compatible with each other (Zsuffa 1975), and many interspecific breeding programs concentrate on these species. The natural range of *P. deltoides* is in North America, that of *P. nigra* in Europe and western Asia, and that of *P. maximowiczii* in northeastern Asia.

The objective of the study reported here was to determine the mode of inheritance of cpDNA in $F_1$ hybrid progenies of *P. deltoides* controlled crosses with *P. deltoides*, *P. nigra*, and *P. maximowiczii* through restriction fragment analysis. Cloned cpDNA fragments from *Petunia hybrida* were used as heterologous probes for cpDNA of *Populus*. We present here data which demonstrate uniparental-maternal inheritance of cpDNA in $F_1$ interspecific hybrids of *P. deltoides* × *P. nigra*, and *P. deltoides* × *P. maximowiczii*.

## Materials and methods

### *Plant material and controlled crosses*

Parents and 10 $F_1$ progeny of each of three *Populus deltoides* × *P. nigra* (D17 × N166, D17 × N167, and D32 × N167) and two *P. deltoides* × *P. maximowiczii* (D17 × M10 and D17 × M11) interspecific controlled crosses and female parents and 10 $F_1$ progeny of each of two *P. deltoides* (D17 × D476 and D17 × D477) intraspecific controlled crosses were analyzed. The male parents of the *P. deltoides* intraspecific controlled crosses were not available for this study. The controlled crosses were made in 1983 (Rajora 1990), and the $F_1$ progeny were located in a field test in Ontario, Canada. The plant material of $F_1$ progeny for this study was collected from this test and that of the parents was collected from the arboreta of the Ontario Forestry Institute, Ontario Ministry of Natural Resources, Maple, Ontario. The sampled $F_1$ trees had been confirmed earlier by allozyme analysis to be hybrids of their respective parents of the controlled crosses (Rajora 1990).

Dormant shoot cuttings were collected from each of the six parent trees and 70 $F_1$ hybrid progeny of the seven controlled crosses in March 1989. The shoot cuttings were rooted in a greenhouse at the University of Alberta.

### *DNA isolation, restriction, electrophoresis, and Southern blotting*

Very young leaves from the rooted cuttings were used for DNA extraction. Total cellular DNA was isolated from 1.0 to 1.5 g leaf tissue (f.w.) from each individual by a modification of the CTAB DNA isolation methods of Murray and Thompson (1980) and Doyle and Doyle (1987). DNAs (approximately 5 µg) of individual plants were digested with 10–15 units of restriction enzymes *Ava*I, *Bam*HI, *Bcl*I, *Bgl*II, *Cla*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Kpn*I, *Pst*I, *Pvu*II, *Sac*I, *Sal*I, *Sma*I, *Xba*I, and *Xho*I for 4 to 5 h according to the manufacturer's recommendations (Boehringer Mannheim Canada).

The DNA restriction fragments and *Hin*dIII Phage λ DNA fragments as standard size markers were then separated on 20 × 20 cm 0.7% agarose gels by electrophoresis at 1.25 V/cm for about 18 h in TBE buffer (Maniatis et al. 1982). Gels were stained with ethidium bromide and photographed. The DNA fragments were then transferred to nylon membranes (Gene Screen Plus, DuPont Canada) using the alkaline transfer method of Chomezynski and Qasba (1984).

### *Probe preparation and hybridization*

Five *Petunia hybrida* cpDNA fragments cloned into plasmid pBR322 (Palmer et al. 1983) were used as hybridization probes for cpDNA fragments of *Populus*: P3, a 21-kb *Pst*I fragment from the large single-copy (LSC) region containing a part of the *rbcL* gene; P6, a 15.3-kb *Pst*I fragment from the LSC region; P8, a 9.2-kb *Pst*I fragment from the LSC region; P10, a 9.0-kb *Pst*I fragment from the LSC region containing a part of the *psbA* gene; and P12, a 7.6-kb *Pst*I fragment from the inverted repeat. Plasmid DNA containing *Petunia* cpDNA inserts was isolated by the alkaline-lysis method (Maniatis et al. 1982) and purified by ultracentrifugation in a cesium chloride gradient in the presence of ethidium bromide. The probes were prepared by radiolabelling the above *Petunia* cpDNA fragments with $dCT^{32}P$ by random priming following the specifications of the manufacturer (Boehringer Mannheim Canada). Unincorporated nucleotides were removed from the labelled recombinant probes using Elutip D Columns (Schleicher and Schuell, Keene, N.H.). Prehybridizations and hybridizations were conducted at 60 °C in 1 *M* NaCl, 50 m*M* TRIS-HCl pH 7.5, 1% SDS, and 10 mg denatured salmon/herring sperm DNA. The membranes were prehybridized for 8–20 h and then hybridized for 18–20 h. Hybridized blots were then washed for (1) 15 min at room temper-

**Table 1.** Enzyme-probe combinations and the number of interspecific restriction fragment polymorphisms[a] used to demonstrate the mode of inheritance of chloroplast DNA (cpDNA) in interspecific controlled crosses of *Populus*

| Enzyme | Probe | Number of restriction fragment polymorphisms of cpDNA | |
|---|---|---|---|
| | | *P. deltoides* × *P. nigra* | *P. deltoides* × *P. maximowiczii* |
| *Ava*I | P6 | 1 | 1 |
| *Bam*HI | P6 | 2 | 3 |
| *Bcl*I | P3 | 3 | – |
| *Bcl*I | P6 | 3 | 2 |
| *Bgl*II | P6 | 1 | – |
| *Bgl*II | P8 | 3 | 1 |
| *Bgl*II | P10 | 2 | – |
| *Cla*I | P6 | 2 | – |
| *Eco*RI | P3 | 2 | 2 |
| *Hin*dIII | P3 | 2 | – |
| *Hin*dIII | P6 | 1 | – |
| *Sma*I | P6 | – | 1 |
| *Xba*I | P6 | 4 | 2 |

[a] The details of these and other interspecific cpDNA restriction fragment polymorphisms among *P. deltoides*, *P. nigra*, and *P. maximowiczii* will be presented elsewhere

ature (RT) with 1 × washing solution (WS: 0.15 *M* NaCl, 10 m*M* sodium phosphate buffer pH 6.5, 1 m*M* EDTA, and 0.5% SDS), (2) twice for 30 min each at 65 °C with 1 × WS, and (3) twice for 15 min each at RT with 0.1 × WS. Hybridized membranes were exposed to X-ray films with and without intensifying screens for 3 h–48 h at −70 °C.

After screening cpDNA restriction fragment polymorphisms among the parents of the controlled crosses along with other individuals of *P. deltoides, P. nigra,* and *P. maximowiczii* with 16 restriction endonucleases and five *Petunia* cpDNA probes, we used the 13 most suitable enzyme-probe combinations (Table 1) to determine the mode of inheritance of cpDNA in progenies of interspecific controlled crosses of *Populus*. Most of the enzyme-probe combinations were used to examine cpDNA inheritance in intraspecific *P. deltoides* crosses.

The membranes were then stripped off the cpDNA probes according to the manufacturer's instructions and hybridized separately with each of the two maize mitochondrial (mt) DNA probes: CoxI, a 10-kb *Bam*HI fragment containing the cytochrome c oxidase subunit I (*coxI*) gene (Issac et al. 1985); and Atp6, a 2.7-kb *Hin*dIII fragment containing ATPase subunit 6 (*atp6*) gene (Dewey et al. 1985).

## Results and discussion

### *CpDNA inheritance in intraspecific P. deltoides controlled crosses*

All 20 $F_1$ offspring of the two intraspecific *P. deltoides* crosses (D17 × D476, D17 × D477) had the same cpDNA fragments as their maternal parent D17. Due to unavailability of the *P. deltoides* male parents D476 and D477 for this study, we could not ascertian whether the cpDNA restriction fragments of these trees were the same as or different from those of the female D17. However, based on our observations of no cpDNA restriction fragment polymorphisms among 10 individuals of *P. deltoides* var *'deltoides'* from diverse sources, we presume that the female (D17) and male parents (D476, D477) had the same cpDNA restriction fragments. These trees belonged to the same variety *'deltoides'*, and originated from the same population. Therefore, it was not possible to clearly demonstrate maternal inheritance of cpDNA in intraspecific *P. deltoides* controlled crosses.

### *CpDNA inheritance in interspecific controlled crosses*

*P. deltoides* × *P. nigra*. The *P. deltoides* females differed from the *P. nigra* males by 36 species-specific restriction fragment polymorphisms revealed by 19 restriction enzyme-probe combinations. The details of these interspecific cpDNA restriction fragment polymorphisms will be presented elsewhere. Twenty-six of these restriction fragment polymorphisms, revealed by 12 enzyme-probe combinations (Table 1), were found to be the most useful in differentiating *P. deltoides* from *P. nigra* and, therefore, were used to examine the mode of cpDNA inheritance in progenies of *P. deltoides* × *P. nigra* crosses. These 12 enzyme-probe combinations differentiated *P. deltoides* females from the *P. nigra* males by 18 species-specific restriction fragment length polymorphisms (RFLP) (inferred to be 13 deletions of 110 base pairs (bp) to 9.1 kb and 5 insertions of 100 bp to 2.5 kb in *P. nigra* relative to *P. deltoides*) and 8 restriction site (presence or absence) differences (10 polymorphisms shown in Fig. 1). In all cases, all of the 30 $F_1$ hybrid progenies of the three *P. deltoides* × *P. nigra* crosses had cpDNA restriction fragments that only their maternal parents D17 and D32 had (Fig. 1), suggesting the uniparental-maternal inheritance of cpDNA in these interspecific *Populus* hybrids. Figure 1 shows the selected autoradiographs of the cpDNA restriction fragments of the parents and progeny of *P. deltoides* × *P. nigra* crosses revealed by 4 enzyme-probe combinations (*Ava*I-P6, *Bcl*I-P6, *Bgl*II-P10, and *Xba*I-P6), demonstrating maternal cpDNA inheritance.

*P. deltoides* × *P. maximowiczii*. CpDNA of *P. deltoides* female D17 was distinct from that of *P. maximowiczii* males M10 and M11 by 16 species-specific restriction fragment polymorphisms revealed by 11 enzyme-probe combinations (data not shown). Twelve of these restriction fragment polymorphisms, identified by 7 restriction enzyme-probe combinations, (Table 1) were found to be the most discriminating between *P. deltoides* and *P. maximowiczii* and, therefore, were employed to examine cpDNA inheritance in progenies of *P. deltoides* × *P. maximowiczii* crosses. Eight of these polymorphisms were identified as RFLPs (5 inferred to be deletions of 70–200 bp, and 3 inferred to be insertions of 300–500 bp in *P. maximowiczii* relative to *P. deltoides*) and 4 as restriction site (presence or absence) mutations (7 polymorphisms are shown in Fig. 2). In all instances, as was observed for progenies of *P. deltoides* × *P. nigra* controlled crosses, all 20 $F_1$ hybrid offspring of the two *P. deltoides* × *P. maximowiczii* crosses inherited the cpDNA restriction fragments of only their maternal parent D17 (Fig. 2), suggesting uniparental-maternal cpDNA inheritance. Autoradiographs of the cpDNA restriction fragments of the parents and $F_1$ progeny of the *P. deltoides* × *P. maximowiczii* crosses, as revealed by 3 enzyme-probe combinations (*Bam*HI-P6, *Xba*I-P6, *Eco*RI-P3), demonstrate the maternal inheritance of cpDNA (Fig. 2).

Sequences highly homologous to cpDNA have been reported to be present in the mitochondrial genome (Stern and Palmer 1984; Sederoff 1987). The concern that some of the restriction fragment polymorphisms observed among *P. deltoides, P. nigra,* and *P. maximowiczii* that were used for demonstrating the mode of cpDNA inheritance in *P. deltoides* × *P. nigra* and *P. deltoides* × *P. maximowiczii* hybrids may be of mitochondrial origin was addressed by using a highly conserved mtDNA probe, CoxI, containing the *cox*I gene, as well as another

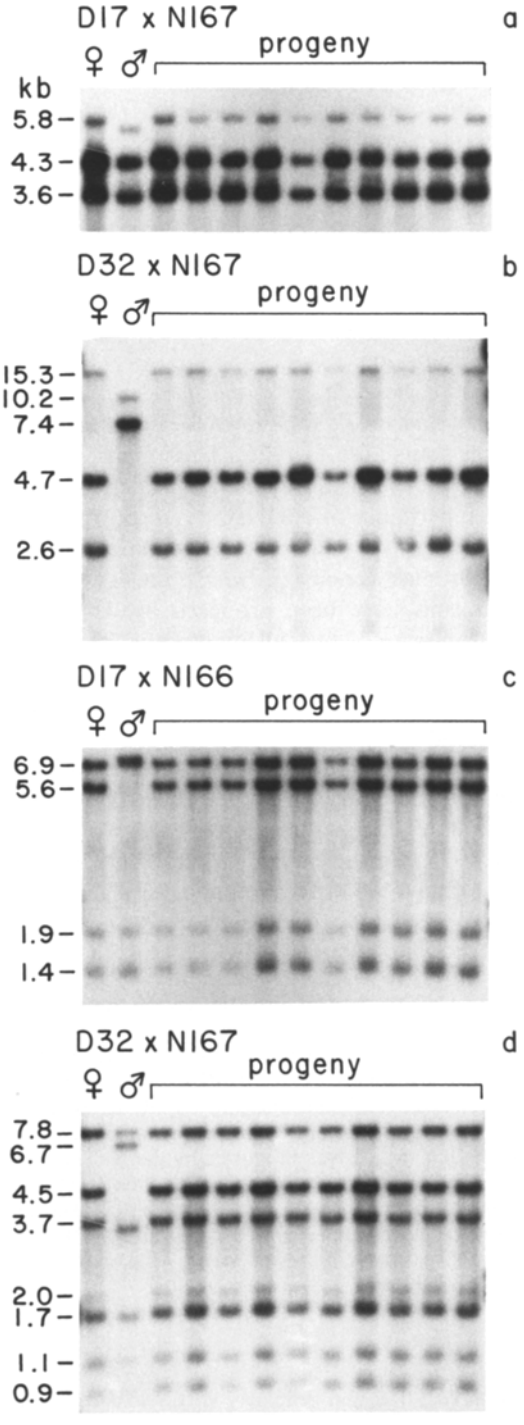


**Fig. 1 a–d.** Autoradiograms demonstrating uniparental-maternal inheritance of cpDNA in *P. deltoides* × *P. nigra* controlled crosses. **a** Parents and offspring DNAs restricted with *Ava*I and hybridized with *Petunia* 15.3-kb cpDNA fragment P6. The *P. deltoides* female parent differs from the *P. nigra* male parent for one *Ava*I-P6 fragment. The female parent D17 and all its progeny have a 5.8-kb fragment, whereas the male parent N167 has a 5.3-kb fragment. **b** Parents and offspring DNAs restricted with *Bcl*I and hybridized with *Petunia* 15.3-kb cpDNA fragment P6. The *P. deltoides* female parent differs from the *P. nigra* male parent for four *Bcl*I-P6 fragments. The female parent D32 and all its progeny have 15.3-kb, 4.7-kb, 2.6-kb, and 1.4-kb fragments, whereas the male parent N167 has 10.2-kb, 7.4-kb, and 1.3-kb fragments. The 1.4-kb and 1.3-kb fragments are not shown in the picture. **c** Parents and offspring DNAs restricted with *Bgl*II and hybridized with *Petunia* 9.0-kb cpDNA fragment P10. The *P. deltoides* female parent differs from the *P. nigra* male parent for two *Bgl*II-P10 fragments. The female parent D17 and all its progeny have 6.9-kb and 5.6-kb fragments, whereas the male parent N166 has a 7.1-kb fragment. **d** Parents and progeny DNAs restricted with *Xba*I and hybridized with *Petunia* 15.3-kb cpDNA fragment P6. The *P. deltoides* female parent differs from the *P. nigra* male parent for four *Xba*I-P6 fragments. The female parent D32 and all its progeny have 4.5-kb, 3.7-kb, 2.0-kb, and 0.7-kb fragments, whereas the male parent N167 has 6.7-kb, and 3.5-kb fragments. The 0.7-kb fragment is not shown in the picture

mtDNA probe, Atp6, from maize. These mtDNA probes were hybridized to the restricted DNA fragments of *Populus* parents and progeny on the same membranes that were used for examining cpDNA inheritance. In no case did the mtDNA probes hybridize to the same fragments and show the same or similar polymorphisms as did *Petunia* cpDNA probes P3, P6, P8, and P10. Homologies to cpDNA in the nuclear DNA of some plant species have also been observed (e.g., Timmis and Scott 1983). However, uniparental-maternal transmission of RFLP markers as observed in our study would not be expected for nuclear DNA. Moreover, most of the restriction enzymes used were methylation sensitive that cut nuclear DNA infrequently. These observations suggest that probes P3, P6, P8, and P10 hybridized with the cpDNA of the *Populus* species and their $F_1$ hybrids and that the observed restriction fragment polymorphisms were of cpDNA origin.

The results of this study clearly demonstrate that cpDNA is transmitted uniparentally in $F_1$ interspecific hybrids of *P. deltoides* × *P. nigra* and *P. deltoides* × *P. maximowiczii* controlled crosses only through their maternal *P. deltoides* parents. Although it was not possible to clearly establish the mode of cpDNA inheritance in *P. deltoides* intraspecific crosses, the maternal inheritance of cpDNA in *P. deltoides* as well as in *P. nigra* and *P. maximowiczii* may be inferred from the results of the interspecific crosses. Additional work is needed to demonstrate the mode of cpDNA inheritance in intraspecific crosses of these species. This is the first demonstration of the mode of inheritance of the cpDNA/cp genome in the Salicaceae and, to our best knowledge, in any forest tree angiosperm. The results are in agreement with similar observations of maternal inheritance of plastids/cpDNA in most angiosperms studied (Tilney-Bassett 1978; Conde et al. 1979; Sears 1980; Whatley 1982; Soliman et al. 1987; Corriveau and Coleman 1988; Smith 1989; Polans et al. 1990; Soltis et al. 1990). Occasional low frequency transmission of paternal cpDNA has been

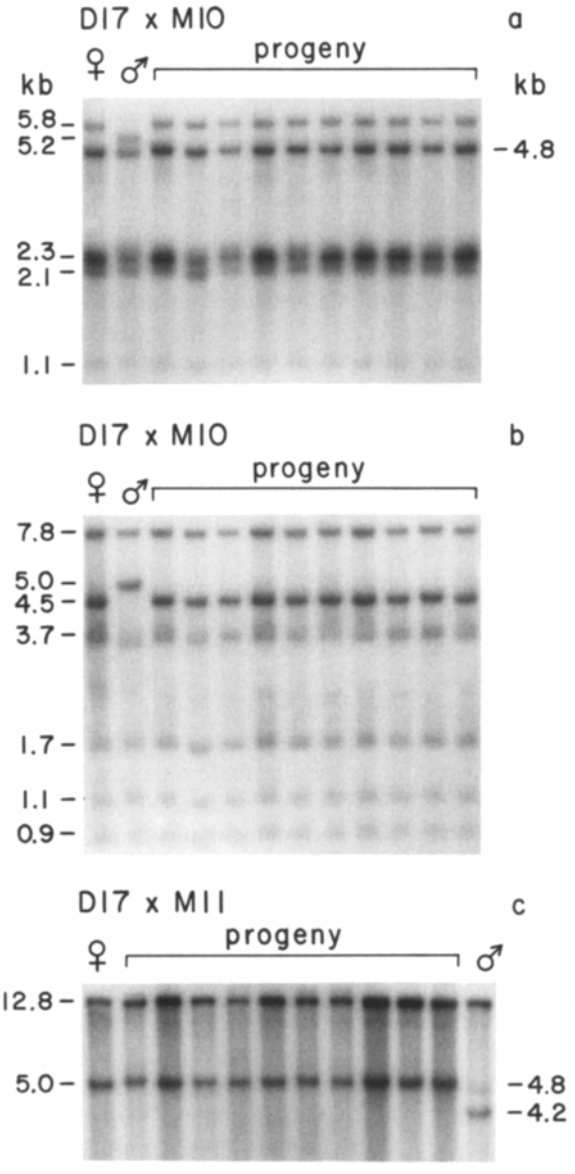


**Fig. 2a–c.** Autoradiograms demonstrating uniparental-maternal inheritance of cpDNA in *P. deltoides* × *P. maximowiczii* controlled crosses. **a** Parents and offspring DNAs restricted with *Bam*HI and hybridized with *Petunia* 15.3.0-kb cpDNA fragment P6. The *P. deltoides* female parent differs from the *P. maximowiczii* male parent for three *Bam*HI-P6 fragments. The female parent D17 and all its progeny have 5.8-kb and 4.8-kb fragments, whereas the male parent M10 has 6.1-kb, 5.2-kb, and 4.7-kb fragments. The 6.1-kb fragment is not clearly visible in the picture. **b** Parents and progeny DNAs restricted with *Xba*I and hybridized with *Petunia* 15.3-kb cpDNA fragment P6. The *P. deltoides* female parent differs from the *P. maximowiczii* male parent for two *Xba*I-P6 fragments. The female parent D17 and all its progeny have 4.5-kb and 3.7-kb fragments, whereas the male parent M10 has 5.0-kb and 3.6-kb fragments. **c** Parents and progeny DNAs restricted with *Eco*RI and hybridized with *Petunia* 21.0-kb cpDNA fragment P3. The *P. deltoides* female parent differs from the *P. maximowiczii* male parent for two *Eco*RI-P3 fragments. The female parent D17 and all its progeny have a 5.0-kb fragment, whereas the male parent M11 has 4.8-kb and 4.2-kb fragments

reported for interspecific hybrids of *Nicotiana* and *Epibolium* species when large number of $F_1$ progenies were screened (Medgyesy et al. 1986; Schmitz and Kowallik 1986). Also, four out of seven intergeneric *Hordeum* × *Secale* $F_1$ hybrids showed biparental cpDNA inheritance (Soliman et al. 1987). Our results are based on 50 $F_1$ offspring of five interspecific controlled crosses and 20 $F_1$ progeny of two intraspecific crosses of *Populus*. To absolutely ensure that occasional paternal transmission of cpDNA does not occur in *Populus*, large numbers of $F_1$ hybrids would have to be examined, and there may be limitations in doing so.

Interspecific *P. deltoides* × *P. nigra* and *P. deltoides* × *P. maximowiczii* hybrids are known for their vigor and other desirable traits (Zsuffa 1975). These hybrids have chloroplast genes of only *P. deltoides*, as evidenced from the maternal inheritance of cpDNA.

The mechanisms of uniparental-maternal transmission of the chloroplast genome in *Populus* are not known. Many mechanisms have been proposed by which the maternal transmission of plastids may occur. These are the exclusion of plastids from the male gamete during microsporogenesis, the loss of plastids from the male gamete, the exclusion of plastids during fertilization, the debilitation/destruction/inactivation of plastids/cpDNA during development, syngamy or zygote formation, intracellular random drift, and selective silencing (Sears 1980; Birky 1983; Connett 1987). Further research is needed to determine the exact mechanisms of maternal transmission of plastids in *Populus*.

*Acknowledgements.* The authors wish to thank Dr. G. P. Buchert and the staff of the Ontario Ministry of Natural Resources, Maple, Ontario for their assistance in procuring plant material, Dr. F. C. Yeh for discussions and interest, Karin Thirwell for technical assistance, Dr. J. D. Palmer for providing *Petunia* chloroplast DNA fragments, and Dr. R. R. Sederoff and Dr. C. S. Levings III for providing maize mitochondrial DNA fragments. This study was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) through an operating grant (A0342) to B. P. Dancik, and an NSERC Postdoctoral Research Fellowship (Grant 30793) to O. P. Rajora.

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**Note added in proof**

After this paper was accepted for publication, an article reporting maternal inheritance of cpDNA in other *Populus* hybrids, *P. trichocarpa* × (*P. maximowiczii* × *P. trichocarpa*) and (*P. maximowiczii* × *P. berolinensis*) × *P. trichocarpa*, appeared (Mejnartowicz M (1991) Theor Appl Genet 82:477–480).