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Plastid DNA inheritance and plastome-genome incompatibility in interspecific hybrids of *Zantedeschia* (Araceae)

Abstract Plastid DNA (ptDNA) probes were used in RFLP analysis to determine ptDNA inheritance in interspecific hybrids in *Zantedeschia*. Biparental and maternal ptDNA inheritance was found in albino hybrids between the evergreen species *Z. aethiopica* and several winter-dormant species. From two albino hybrids, different types of ptDNA were detected in shoots derived from different parts of an embryo. This result indicates that plastids were sorted out during embryo development. Only maternal ptDNA was detected in the hybrids of *Z. aethiopica* × *Z. odorata* (a summer-dormant species) but paternal, biparental, and maternal ptDNA were found in the hybrids of the reciprocal cross, *Z. odorata* × *Z. aethiopica*. By correlating these ptDNA inheritance patterns with the leaf colour (albino, pale-green, and green) of the hybrids, it is suggested that the *Z. odorata* plastome is incompatible with the *Z. aethiopica* genome. The *Z. aethiopica* plastome is partially compatible with the *Z. odorata* genome but the development of *Z. aethiopica* plastids appears to be blocked by the presence of the *Z. odorata* plastids.

Key words RFLP · Hybrid variegation · Plastid DNA · Interspecific incompatibility · *Zantedeschia*

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Introduction

In angiosperms, the majority of species have a maternal ptDNA inheritance and a minority of species have a biparental ptDNA inheritance. The absence and presence of ptDNA in generative or sperm cells generally correlate with maternal and biparental ptDNA inheritance respectively (Corriveau and Coleman 1988). Based upon detection of ptDNA in generative or sperm cells, Corriveau and Coleman (1988) reported that 18% of 235 species studied were potentially capable of biparental ptDNA inheritance. Of 398 species, 27% had the potential for biparental ptDNA inheritance (Harris and Ingram 1991). Paternal ptDNA inheritance in angiosperms is a rare event and has only been demonstrated in intraspecific hybrids of *Medicago sativa* (Schumann and Hancock 1989; Masoud et al. 1990) and in interspecific hybrids between *Daucus muricatus* and *D. carota* spp. *sativus* (Boblenz et al. 1990). In contrast to the angiosperms, the majority of gymnosperms have paternal ptDNA inheritance, e.g., the genera *Pinus* (Wagner et al. 1989), *Larix* (Szmidt et al. 1987), *Pseudotsuga* (Neale et al. 1986) and *Picea* (Stine and Keathley 1990).

Plastid-DNA inheritance is usually determined by using a parent with a plastome-encoded chlorophyll deficiency in reciprocal crosses. Biparental ptDNA inheritance is detected when green and white sectored leaves appear in the progeny. By this method, biparental ptDNA inheritance was noted in several genera, including *Pelargonium* (Tilney-Bassett 1973; Tilney-Bassett and Almouslem 1989), *Medicago* (Smith et al. 1986; Smith 1989a) and *Oenothera* (Kirk and Tilney-Bassett 1978; Chiu et al. 1988). RFLP (restriction fragment length polymorphism) analysis, using cloned ptDNA as a probe, has recently been used to examine ptDNA inheritance in a number of studies (Neale et al. 1986; Szmidt et al. 1987; Schumann and Hancock 1989; Wagner et al. 1989; Masoud et al. 1990; Stine and Keathley 1990). The parental origin of ptDNA can be determined unequivocally using this method.

Zantedeschia is commonly known as arum or calla lily and is an important flower crop in New Zealand. The genus *Zantedeschia* includes two sections: one containing an evergreen species, *Z. aethiopica*, and a second containing five winter-dormant species (Letty 1973). A summer-dormant species, *Z. odorata*, was recently described which falls between the previous two sections, having some characters from each group (Perry 1989). Our current breeding program involves interspecific hybridisation between the two sections. Embryo culture was used to rescue hybrids but all hybrids rescued to-date have been albino (Chi 1990; Yao 1992). Further hybridisation experiments have attempted to use *Z. odorata* as a bridge species and produced virescent, albino, and variegated (virescent/albino) hybrids (Yao 1992). Virescent plants are initially albino or pale-green but become greener as the plants mature. Hybrid chlorophyll deficiency has been observed in other genera and is believed to be caused by plastome-gemone incompatibility (Kirk and Tilney-Bassett 1978; Hagemann 1992). In order to classify plastome incompatibility in *Zantedeschia*, a study of ptDNA inheritance in these hybrids was performed.

Materials and methods

Plant material

The parents and hybrids used in this study are listed in Table 1. Codes have been assigned to each species (two letters) or cultivar (three letters). Albino hybrids between *Z. aethiopica* and winter-dormant species were rescued by embryo culture (Chi 1990; Yao, 1992). MS medium (Murashige and Skoog 1962) with 0.3–3.0 mg/l of benzylaminopurine was used to rescue embryos, and to multiply and maintain albino hybrids. From two of these embryos, no. 43 and no. 47 of CHR × CHI, multiple albino shoots were produced from both the embryo axis and the haustorial tip of cotyledon (Chi 1990). Hybrid embryos from *Z. aethiopica* × *Z. odorata* were germinated in

vitro and transferred into a greenhouse at 3 weeks after germination. Hybrids from *Z. odorata* × *Z. aethiopica* were grown from seed in a greeenhouse (Yao 1992). Seedlings were classified as albino, virescent, or variegated.

DNA clones

DNA of a 1.5-kb *EcoRI/XbaI* fragment of the 18s rDNA of apple (Simon and Weeden 1992) was used for hybrid confirmation. For determining ptDNA inheritance, six kiwifruit ptDNA clones, λKIWI4, λKIWI6, λKIWI15, λKIWI17, λKIWI19 and λKIWI24, were obtained from Dr. R. Gardner. These six clones comprise about 60% of the kiwifruit plastome (Crowhurst et al. 1990). Two other ptDNA clones, pZAC1 and pZAC2, were isolated from a library which was constructed using *Hind*III fragments of total-leaf DNA of CHI. The plastid origin of pZAC1 and pZAC2 was confirmed by hybridisation of kiwifruit ptDNA clones (Yao 1992).

Southern hybridisation

Total-leaf DNA of green and albino plants was isolated using the CTAB (cetyltrimethylammonium bromide) nucleic-acid-extraction procedures of Rogers and Bendich (1988). Rescued albino hybrids were cultured for more than 6 months and leaf tissue from more than 20 shoots were collected for DNA extraction. DNA was digested with *Hind*III or *Eco*RI according to the recommendations of the supplier. Digested plant DNA fragments, as well as DNA markers (1-kb DNA ladder or *Hind*III-digested lambda DNA from BRL), were separated on an 0.8% agarose gel. The resulting gel was Southern-blotted onto a nitrocellulose membrane (BAS85, Schleicher and Schuell) according to Maniatis et al. (1982). The hybridisation was carried out using an Enhanced Chemiluminescence (ECL) Gene Detection System (Amersham). Probe labelling, hybridisation (in the presence of 0.3 M NaCl), washing, and signal detection were carried out according to the manufacturer's instructions. DNA markers were also included in the probe mixture in order to reveal these markers on Southern blots.

Results

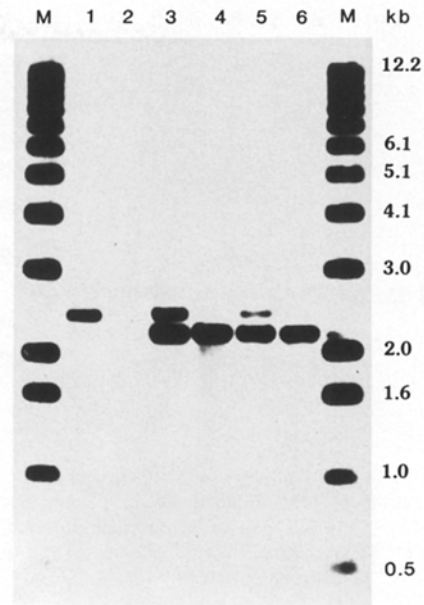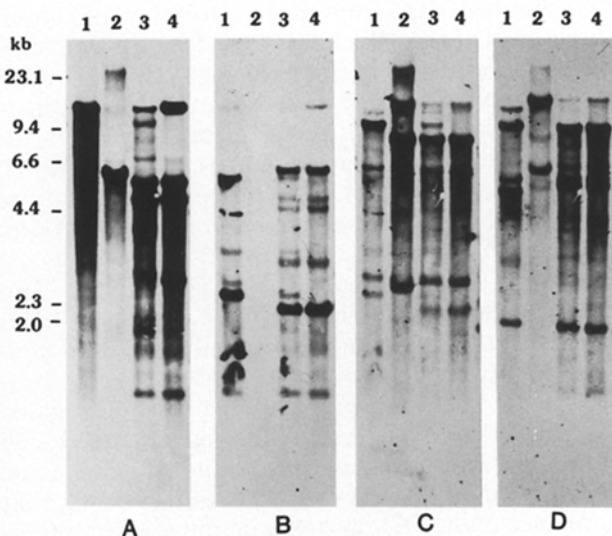The ptDNA inheritance pattern of two albino hybrids, no. 43 and no. 47, of CHR × CHI was investigated. A

Table 1 Parents and hybrids used in this study

Parents	Code	Description
Z. aethiopica (L.) Spreng	AE	Evergreen, a commen form of the species grown in New Zealand
Z. aethiopica (spotted leaf)	AES	Evergreen, a spotted-leaf form of the species
Z. aethiopica 'Childsiana'	CHI	Evergreen, dwarf form (Bailey and Bailey 1976)
Z. odorata Perry	OD	Summer dormant (Perry 1989)
Z. elliottiana (Watson) Engl.	EL	Winter dormant (Letty 1973)
Z. 'Chromatella'	CHR	Winter dormant, a cultivar closely related to *Z. albomaculata* (Hook.) Baill
Z. 'Galaxy'	GAL	Winter dormant, a hybrid of unknown parentage

Hybrids	Description
CHR × CHI	Multiple albino shoots derived from embryo axis and haustorium (Chi 1990)
GAL × AES	Multiple albino shoots derived from embryo axis (Yao 1992)
AE × EL	Multiple albino shoots derived from embryo axis (Yao 1992)
CHI × EL	Multiple albino shoots derived from embryo axis (Yao 1992)
CHI × OD	Virescent plants produced by embryo germination in vitro (Yao 1992)
AE × OD	Virescent plants produced by embryo germination in vitro (Yao 1992)
AES × OD	Virescent plants produced by embryo germination in vitro (Yao 1992)
OD × AE	Virescent plants produced by seed germination (Yao 1992)
OD × CHI	Virescent, albino, and chimeric plants produced by seed germination (Yao 1992)

Southern blot of HindIII-digested DNA of the two parents and their hybrids was probed sequentially using pZAC2 and three kiwifruit ptDNA probes: λKIWI6 + λKIWI15, λKIWI17 + λKIWI19, λKIWI4 + λKIWI24. The two kiwifruit ptDNA clones pooled in each proble partially overlap each other. Biparental ptDNA inheritance was demonstrated in no. 47 (Fig. 1). A deletion of ptDNA corresponding to λKIWI6 + λKIWI15 (Fig. 1B) was detected in no. 43. For probes pZAC2, λKIWI17 + λKIWI19 and λKIWI4 + λKIWI24, some bands of hybrid no. 43 matched maternal bands but none matched paternal bands (Fig. 1A, C, D). It would appear that a major structural rearrangement had occurred. λKIWI6 and λKIWI15 are in the inverted repeat region and part of the small single-copy region of the plastome (Crowhurst et al. 1990). Deletion of DNA corresponding to these clones indicated that the small single-copy region and the two inverted repeats were deleted in the plastome of hybrid no. 43.

The DNA of no. 43 used in the above experiment was extracted from haustorial shoots whilst the DNA of no. 47 was extracted from embryo-axis shoots. We considered that ptDNA in haustorial shoots may have been different to that in embryo-axis shoots from the same embryo. Therefore, a Southern blot was prepared using four HindIII-digested DNA samples of haustorial shoots and embryo-axis shoots of no. 43 and no. 47. When the Southern blot was probed with pZAC1, the embryo-axis shoots of both hybrids showed biparental ptDNA (Fig. 2). However, only maternal ptDNA was found in haustorial shoots of no. 47. Haustorial shoots
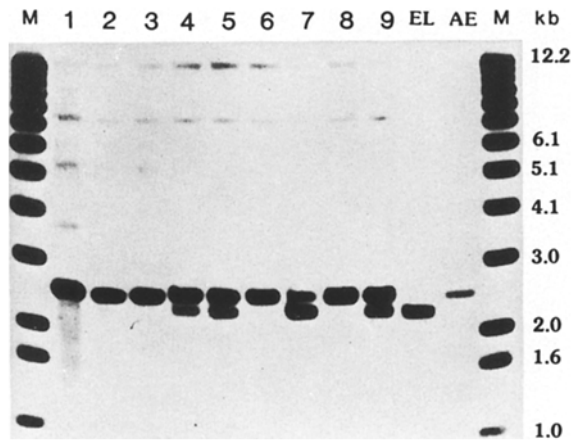

Fig. 2 Differences in ptDNA between embryo-axis shoots and haustorial shoots of 'Chromatella' (CHR) × 'Childsiana' (CHI) hybrids. HindIII-digested DNA was separated on an 0.8% agarose gel and transferred to a nitrocellulose membrane. The membrane was probed with pZAC1. 1, CHI; 2, haustorial shoots of hybrid no. 43; 3, embryo-axis shoots of hybrid no. 43; 4, haustorial shoots of hybrid no. 47; 5, embryo-axis shoots of hybrid no. 47; 6, CHR

of no. 43 gave no signal with the pZAC1 probe indicating that a deletion had occurred in this region. pZAC1 was located within the inverted repeated region (Yao 1992). Therefore, this result supports that obtained in the first experiment and further indicates a difference in ptDNA between shoots derived from different parts of the same embryo.

Nine albino hybrids of AE × EL, derived from embryo axes, were tested with pZAC1, pZAC2, λKIWI17 + λKIWI19 and λKIWI4 + λKIWI24 in Southern hybridisations. These four probes gave the same results for ptDNA inheritance of all nine albino plants. Four plants (nos. 4, 5, 7, 9) showed biparental ptDNA bands, but the remaining five plants showed only the maternal bands (Fig. 3). For plant no. 7 the paternal bands were stronger than the maternal bands, whereas in plants nos. 4, 5 and 9, the maternal bands were stronger than the paternal bands. None of these probes detected any deletion in the nine albino hybrids. Four albino hybrids of CHI × EL were also checked with pZAC1. They all showed maternal ptDNA inheritance. One of the two albino hybrids of GAL × AES showed biparental ptDNA inheritance (Table 2).

Progeny from the crosses AES × OD, AE × OD and CHI × OD were virescent. These progenies showed rDNA bands from both parents when an 18s rDNA probe was used in RFLP analysis (data not shown), confirming the hybrid nature of these plants. The Southern blot used for the confirmation of hybrid nature was reprobed using pZAC1. Thirty hybrids from these three

Fig. 1 Biparental ptDNA inheritance and ptDNA deletion in albino hybrids of 'Chromatella' (CHR) × 'Childsiana' (CHI). HindIII-digested DNA was separated on an 0.8% agarose gel and transferred to a nitrocellulose membrane. The membrane was probed with pZAC2 (A) and reprobed sequentially with λKIWI6 + λKIWI15 (B), λKIWI17 + λKIWI19 (C) and λKIWI4 + λKIWI24 (D). 1, CHI; 2, hybrid no. 43 (haustorial shoots); 3, hybrid no. 47 (embryo-axis shoots); 4, CHR

Fig. 3 Biparental ptDNA inheritance in albino hybrids of Z. *aethiopica* (AE) × Z. *elliottiana* (EL). *Hind*III-digested DNA was separated on an 0.8% agarose gel and transferred to a nitrocellulose membrane. The membrane was probed with pZAC1. (1–9): nine albino hybrids

Table 2 Plastome-genome incompatibility and ptDNA inheritance in *Zantedeschia* hybrids

Cross	Leaf colour	No. of hybrids tested	ptDNA inheritance[a]		
			M	B	P
CHR × CHI	Albino	2	0	2	0
GAL × AES	Albino	2	1	1	0
AE × EL	Albino	9	5	4	0
CHI × EL	Albino	4	4	0	0
CHI × OD	Virescent	7	7	0	0
AE × OD	Virescent	18	18	0	0
AES × OD	Virescent	5	5	0	0
OD × CHI	Virescent	7	0	0	7
	Albino	1	1	0	0
	Variegated	3	0	3[b]	3[b]
OD × AE	Virescent	4	0	0	4

[a] M, maternal ptDNA inheritance; B, Biparental ptDNA inheritance; P, Paternal ptDNA inheritance
[b] Virescent leaf segments had paternal ptDNA inheritance; albino leaf segments had biparental ptDNA inheritance

crosses showed only maternal ptDNA inheritance (Table 2).

Progeny from OD × AE were virescent and progeny from OD × CHI were either virescent, albino, or variegated (virescent/albino). The hybrid nature of these plants was confirmed by Southern hybridisation using the rDNA probe (Fig. 4 A). When the Southern blot was reprobed using pZAC1, four OD × AE hybrids and seven virescent hybrids of OD × CHI showed paternal ptDNA bands only. DNA samples were prepared from both virescent and albino leaf segments of three variegated hybrids of OD × CHI. Virescent leaf segments contained paternal ptDNA but the albino leaf segments contained biparental ptDNA. DNA from one albino

hybrid showed only maternal ptDNA bands (Fig. 4 B, Table 2).

Discussion

This study demonstrated maternal, biparental, and paternal ptDNA inheritance in interspecific hybrids of *Zantedeschia* (Table 2). Bipaternal ptDNA inheritance has been detected in a number of angiosperm genera (Corriveau and Coleman 1988; Smith 1989 b; Harris and Ingram 1991). The percentage of progeny containing biparental ptDNA varies from species to species. If more than 5% of progeny contain biparental ptDNA, this is defined as regular biparental ptDNA inheritance, whereas less than 5% of progeny with biparental ptDNA is defined as occasional biparental ptDNA inheritance (Smith 1989 b). In the crosses CHR × CH1, GAL × AES and AE × EL biparental ptDNA inheritance appeared to be regular. Based on four hybrid plants, CHI × EL had only maternal ptDNA inheritance. The possibility of biparental ptDNA inheritance in this cross cannot be excluded until a larger number of hybrid plants are tested. In previous studies, predominantly paternal ptDNA inheritance has been demonstrated only in *Medicago* (Schumann and Hancock 1989; Masoud et al. 1990) and *Daucus* (Boblenz et al. 1990) among angiosperms. In the present study, only paternal ptDNA was detected in virescent hybrids of OD × CHI and OD × AE (11 plants tested).

In a number of studies, ptDNA in green plants has been found to be highly conserved in the course of tissue culture (Rode et al. 1985; Kemble et al. 1988; Harada et al. 1991). However, large-scale ptDNA deletions have been observed in albino plants regenerated from anther cultures of wheat and barley (Day and Ellis 1984, 1985), in rice (Harada et al. 1991) and in albino plants derived from scutellar calli of *Hordeum marinum* (Shimron-Abarbanell and Breiman 1991). The haustorial tip of the cotyledon in *Zantedeschia* is homologous to the scutellum in cereals. A deletion of ptDNA was detected in albino shoots derived from the haustorial tip of hybrid-embryo no. 43 of CHR × CHI. This deletion should be noted even though its mechanism is not clear.

Albino leaves of hybrids indicate an inhibition of chloroplast development, and virescent leaves indicate an inhibition or a partial inhibition of chloroplast development at seedling stages. This inhibition is considered to be caused by plastome-genome incompatibility (Kirk and Tilney-Bassett 1978; Hagemann 1992). Virescent hybrids of CHI × OD contained CHI ptDNA. This result indicate that the CHI plastome is partially compatible with the OD genome. One albino hybrid contained OD ptDNA, indicating that the OD plastome is incompatible with CHI genome. From the variegated hybrids of OD × CHI, virescent leaf segments contained the CHI plastome but albino leaf segments contained both CHI and OD plastomes. This result indicates that the presence of the OD plastome inhibited the develop-

Fig. 4 Plastid DNA inheritance in hybrids of crosses *Z. odorata* (*OD*) × 'Childsiana' (*CHI*) and *Z. odorata* × *Z. aethiopica* (*AE*). *Eco*RI-digested DNA was separated on an 0.8% gel and transferred to a nitrocellulose membrane. **A** the membrane was probed with 18*s* rDNA to confirm the hybrids. **B** the membrane was reprobed with pZAC1 to determine ptDNA inheritance. *1*, an albino hybrid; *2, 4, 6*, virescent leaf segments of three variegated hybrids; *3, 5, 7*, albino leaf segments of three hybrids corresponding to *2, 4, 6*; *8–14*, seven virescent hybrids of OD × CHI. *15–18*, four virescent hybrids of OD × AE
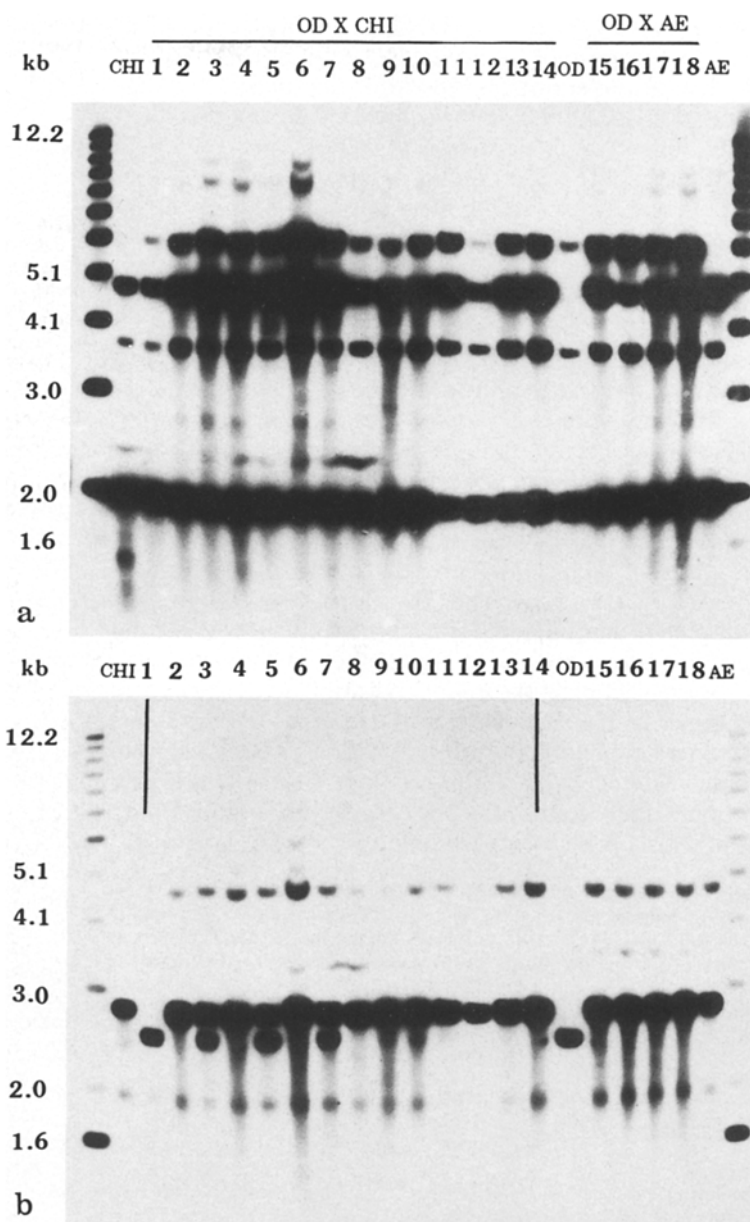
ment of CHI plastids. The mechanism of this inhibition is not clear.

In hybrids containing biparental plastids, the two types of plastids usually segregate, with different tissues containing a single plastid type. This is known as plastid 'sorting-out' (Kirk and Tilney-Bassett 1978). If only one parental plastome is incompatible with the hybrid genome (unidirectional incompatibility) the hybrid will be variegated with green and white sectors. This type of variegation has been observed in *Pelargonium* (Metzlaff et al. 1982) and in the hybrids of OD × CHI in the present study. Hybrids from CHI × CHR, AE × EL and GAL × AES were completely albino. No green sectors were observed on any of the 20–100 multiple shoots arising from single embryos in vitro (Chi 1990; Yao 1992) even though they contained biparental ptDNA

(Table 2). This result indicated that plastomes of both parents were incompatible with the hybrid genome in these crosses, i.e., bidirectional plastome-genome incompatibility.

Sorting out of plastids is usually apparent by the plant having green and white sectors in leaves (Kirk and Tilney-Bassett 1978). Further evidence for this comes from RFLP analysis using DNA from different shoots of one *Medicago* plant (Schumann and Hancock 1989). Plastid sorting-out in hybrids of OD × CHI was documented in this study at both phenotypic and DNA levels. Paternal ptDNA was detected in embryo-axis shoots but not in haustorial shoots of the hybrid embryos no. 43 and no. 47 of CHR × CHI (Figs. 1 and 2). As DNA samples were prepared from leaf tissue pooled from more than 20 shoots with the same origin, the

elimination of paternal ptDNA probably occurred in the haustorial tip of the cotyledon before the formation of adventitious shoots. It is possible that plastid sorting-out took place during embryo development and resulted in the difference in plastid composition between different regions of the embryo.

Different factors are significant in controlling ptDNA inheritance in different angiosperm species, e.g., the paternal genome in *Petunia hybrida* (Cornu and Dulieu 1988) and *Pelargonium* species (Tilney-Bassett and Almouslem 1989; Tilney-Bassett et al. 1992), the maternal genome (Masoud et al. 1990) or paternal genome (Smith 1989a) in *Medicago* species, and the plastome in *Oenothera* speices (Chiu et al. 1988). The number of maternal plastids exceeds paternal plastids by a ratio of 54:1 after fertilization in *Plumbago zeylanica* (Russell 1987). We assumed that the zygotes of OD × CHI would contain many more OD plastids than CHI plastids. Nevertheless, only CHI ptDNA was detected in the virescent hybrids of OD × CHI. The OD plastids were apparently completely eliminated. This result indicates a strong selective advantage for CHI plastids in these hybrids, since the OD plastids are incompatible with the hybrid genome. In the reciprocal cross, CHI × OD, all plants were virescent and only contained CHI plastids. Thus in these *Zantedeschia* interspecific hybrids, plastome-genome incompatibility appears to be significant in controlling ptDNA inheritance.

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