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The Role of Plastome-Genome Incompatibility and Biparental Plastid Inheritance in Interspecific Hybridization in the Genus *Zantedeschia* (Araceae)

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ABSTRACT

In most genera combinations of plastomes and genomes function to form normal plants, irrespective of the taxonomical distances between the plastidial genome and the nuclear genome. In some genera plastomes and genomes have co-evolved to such a degree that they can only function within specific combinations. Our aim was to determine plastid inheritance and plastome-genome incompatibility (PGI) among species of *Zantedeschia* from the section *Aestivae*. To this end, plastomes and genomes of five taxa (*Z. albomaculata* subsp. *albomaculata*, *Z. albomaculata* subsp. *macrocarpa*, *Z. elliotiana*, *Z. pentlandii* and *Z. rehmannii*) were combined by interspecific hybridisation. Plastomes were differentiated using plastome specific CAPS-markers. Degrees of plastome-genome incompatibility existed between the hybrid genomes of *Z. rehmannii* and *Z. albomaculata*, *Z. rehmannii* and *Z. elliotiana*, *Z. rehmannii* and *Z. pentlandii* and the plastomes of *Z. albomaculata*, *Z. elliotiana* and *Z. pentlandii*, respectively. The plastome of *Z. rehmannii* appeared compatible to all tested hybrid genomes in section *Aestivae*. It was only fully incompatible with the hybrid genome with *Z. aethiopica* (section *Zantedeschia*). The plastomes of *Z. albomaculata* and *Z. elliotiana* appeared compatible to the hybrid genome of *Z. albomaculata* and *Z. elliotiana*. Four plastomes were differentiated among the section *Aestivae*. Biparental plastid inheritance (3 to 90%) was observed among all crossing combinations, which produced more than 1600 interspecific offspring. Biparental inheritance of plastids thus appeared to be a general phenomenon among interspecific hybrids within the section *Aestivae*. A literature review shows that biparental plastid inheritance is not uncommon in interspecific hybrids. The genus *Zantedeschia* shows an unusual wide range of degrees of biparental plastid inheritance that is only recorded in genera that also show plastome-genome incompatibility.

Keywords: Aestivae, arum lily, calla lily, cpDNA, cytoplasmic, hybrid variegation

INTRODUCTION

As a member of the *Araceae* family, the genus *Zantedeschia* is endemic to southern Africa and consists of two sections (Letty 1973; Singh 1996). Cultivars have been bred for ornamental value of either the flowers or the entire plants mainly from *Z. rehmannii*, *Z. albomaculata*, *Z. elliotiana* and *Z. pentlandii*. Most cultivars are propagated vegetatively, although some are F_1 hybrid cultivars, thus propagated by seeds.

Zantedeschia spp. (**Fig. 1**) have a tuberous (section *Aestivae*) or rhizomatomous (section *Zantedeschia*) storage organ (Singh 1996), are frost tender and, except for *Z. aethiopica*, require a period of dormancy. *Z. aethiopica* is an evergreen, but will become dormant if its environment limits growth. Therefore, storage organs of all *Zantedeschia* spp. are lifted after onset of dormancy and are stored in a growth-limiting environment. The genus *Zantedeschia* con-

Fig. 1 *Zantedeschia* spp. used in this study. (**A**) *Z. aethiopica*; (**B**) *Z. rehmannii*; (**C**) *Z. albomaculata* subsp. *albomaculata*; (**D**) *Z. elliotiana*.

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sists of eight species in two sections. The section *Zantedeschia* consists of *Z. aethiopica* and *Z. odorata*, while the section *Aestivae* consists of *Z. albomaculata*, *Z. elliotiana*, *Z. jucunda*, *Z. pentlandii*, *Z. rehmannii* and *Z. valida* (Singh *et al.* 1996).

Infestations by viruses and bacteria hamper further horticultural development of *Zantedeschia*. In particular the bacterium that causes soft rot *Pectobacterium carotovorum* subsp. *carotovorum* (formerly *Erwinia carotovora* subsp. *carotovora*) can destroy entire harvests. Biological and chemical measures have been successfully applied in soft rot control, but only to a limited extent. Therefore, the most promising are cultivation measures, since some methods have success in decreasing disease incidences in *Zantedeschia* spp. These include mulching (Welsh and Clemens 1992; Wright *et al.* 2002), early cessation of irrigation (Wright *et al.* 2002), application of rockwool (Mori *et al.* 1999), course river sand (Welsh and Clemens 1992) or a combined application of peatmoss, vermiculite and perlite as growing media (Chen and Lin 2000), decreased nitrogen fertilisation (Van Leeuwen *et al.* 2001) and fertilisation by gypsum (Funnell and MacKay 1999). Unfortunately, none of these measures alone could fully control control soft rot (*P. carotovorum* subsp. *carotovorum*). Therefore, combining protective methods could result in better control of soft rot. The cultivation measures appear promising, since they are durable. Sensitivity to chemicals could be overcome by the pathogen, and use of chemicals is being restricted by international legislation. Biological control such as hot water treatment can become expensive due to its intensive energy use.

Use of resistant cultivars would conceivably decrease the risk of infestation by soft rot and would ease cultivation of *Zantedeschia* spp. considerably. Combined use of resistant cultivars and protective cultivation measures could help in controlling soft rot even more. Indeed, genetic variation exists among *Zantedeschia*, from highly susceptible (*Z. pentlandii* and some accessions of *Z. albomaculata* subsp. *albomaculata*), to partially resistant (*Z. rehmannii* and other accession of *Z. albomaculata* subsp. *albomaculata*) and almost completely resistant (some accessions of *Z. aethiopica*) (Snijder *et al.* 2004).

Breeding for partial resistance among section *Aestivae* is possible, but laborious. The partial resistance of *Z. rehmannii* and *Z. albomaculata* is controlled by multiple genes (Snijder *et al.* 2004) and a strong environmental effect exists for the phenotypical expression of resistance. Thus, multiple repetitions are needed in resistance testing (Snijder and Van Tuyl 2002).

Besides being resistant to soft rot, *Z. aethiopica* harbours other highly desired characteristics as well, such as a strong vigour and a short generation time from seed to flower of only 9-11 months. Unfortunately interspecific hybrids of *Z. aethiopica* and species of section *Aestivae* are not viable due to their inability of producing green plants. The plastomes and genomes of *Z. aethiopica* and cultivars of the section *Aestivae* were demonstrated to be incompatible to such a high degree that hybrids were chlorophyll deficient (albino) and could only survive heterotrophically (Yao *et al.* 1995).

Interspecific hybrids among thesection *Aestivae* show degrees of chlorophyll deficiency as well. Chlorophyll deficient plants were more susceptible than healthy green plants of the same family (Snijder *et al.* 2004). Therefore, insight in the directions of plastome-genome incompatibility and plastid inheritance are essential for efficient design of a breeding programme of *Zantedeschia*.

For a more elaborate understanding of the role of plastome-genome incompatibility and biparental plastid inheritance in the genus *Zantedeschia* and particularly in the section *Aestivae*, 1600 reciprocal interspecific hybrids were developed from five taxa of the section *Aestivae*. Plastome-specific CAPS markers were used to verify plastome-genome incompatibility and plastid inheritance. A literature review on plastid inheritance in interspecific hybrids among flowering plants demonstrates that biparental plastid inheritance is not uncommon but *Zantedeschia* demonstrates an unusually wide range.

PLANT MATERIAL AND CULTIVATION

Accessions of *Aestivae* species were obtained from nurseries and a botanical garden (**Table 1**).

All plants were raised in poor soil in a greenhouse with temperatures ranging from 20-30ºC during the day and 15-18ºC during the night. Seedlings were raised in standard potting soil in the first growing season and in poor soil in the second growing season. Tubers were lifted after leaves had withered completely and the tubers were surface-dried in a ventilated climate room (18ºC, 30% relative humidity (RH)) before storage (9ºC, 70% RH). Tubers were pre-treated at 18ºC for four weeks, before planting. Parental plants were promoted to flower by incubating tubers 10 min in 100 ppm GA_3 (Berelex, Bayer) just before planting.

INTERSPECIFIC HYBRIDISATION

Flowers were pollinated at opening of the spathe after emasculation. Hybridisations were carried out in the greenhouse (with day temperatures ranging from 20-30ºC and night temperatures from 15-18ºC) with fresh pollen using a 70%-ethanol sterilised brush. Fruits were harvested after the plants had wilted, seeds were collected from ripe fruits and directly sown in standard potting soil. The hybrid character was judged from plant morphology and the origin of the plastomes was verified using plastome specific CAPS markers. Hybrids of *Z. rehmannii* and *Z. aethiopica* were retrieved as described by Yao *et al.* (1995).

Table 1 Plant material used for producing interspecific hybrids.

PRInr	Code	Genotype	Source[1]
99008	AT	*Z. aethiopica* 'Crowborough'	N, The Netherlands
00060	Aa1	*Z. albomaculata* subsp. *albomaculata*	N, The Netherlands
00061	Aa2	*Z. albomaculata* subsp. *albomaculata*	N, The Netherlands
00031	Aa3	*Z. albomaculata* subsp. *albomaculata*	G, South Africa
00056	Aa4	*Z. albomaculata* subsp. *albomaculata*	N, South Africa
018002	Am1	*Z. albomaculata* subsp. *macrocarpa*	N, South Africa
018006	Am2	*Z. albomaculata* subsp. *macrocarpa*	N, South Africa
00062-1	E1	*Z. elliotiana*	N, The Netherlands
99004	E2	*Z. elliotiana*	N, The Netherlands
00073	E3	*Z. elliotiana*	N, South Africa
00069-2	P	*Z. pentlandii*	N, The Netherlands
00063	R1	*Z. rehmannii*	N, The Netherlands
00078	R2	*Z. rehmannii*	N, The Netherlands
99022	R3	*Z. rehmannii*	N, New Zealand
00057	R4	*Z. rehmannii*	N, South Africa
00074	R5	*Z. rehmannii*	N, South Africa

[1] N=nursery, G=botanical garden.

SPECIES-SPECIFIC PLASTID CAPS MARKERS

DNA extraction

Total DNA was extracted from ca. 0.3 g lyophilised young leaf material that was ground using the RETCH method (Qiagen). DNA was extracted from each sample by thoroughly mixing with 400 µl extraction mix (0.13 M Tris. HCl, 0.02 M EDTA, 0.9 M NaCl, 0.9% CTAB, 0.15 M sorbitol, 5% $Na_2S_2O_5$, and 0.6% sarkosyl) and incubating for one hour at 65ºC. After applying one volume chloroform/isoamylalcohol (24:1 v/v), the resulting suspension was centrifuged for 20 min at 5500 × *g*. DNA was precipitated from the supernatant by one volume ice-cold (-20ºC) isopropanol and collected by centrifuging for five min at $21 \times 10^3 \times g$. After discarding the supernatant, the DNA was washed in 70% ethanol and suspended in TE (1 M Tris, 0.1 M EDTA).

Primers

The intergenic region of *trn*D and *trn*C (about 3.1 kb, further called DC) was amplified by PCR using primer pair DC_{ron} ($DC_{ron\text{-}F}$: 5′-AGAGCACCGCCCTGTCAAG-3′ and $DC_{ron\text{-}R}$: 5′-GCATGGCCRAGYGGTAAGG-3′). DC_{ron} was designed after alignment of flowering plant sequences of *trn*C and *trn*D using Primerselect (DNASTAR). The sequences were obtained from GenBank (NCBI).

PCR amplification

The polymerase chain reaction was carried out in 25 µl volume (10 mM Tris-HCl, pH 9.0, 50 mM KCl, 3.5 mM $MgCl_2$, 0.1% Triton X-100, 1 mM dNTP (Invitrogen), 5 pM DC_F for DC, 10 pM DC_R for DC, 0.5 U SuperTaq (HT Biotechnology), 0.05 U *Pfu* polymerase (Promega) and 100-500 ng template DNA). *Pfu* polymerase was added to improve the amplification of products up to 35 kb (Barnes 1994). The MJ Research PTC-200 thermal cycler was programmed to carry out a temperature profile of 3 min at 94ºC, 40 cycles of one min 94ºC, 1 min at 64.5ºC and 3.5 min and with a final 15 min at 72ºC.

Restriction digestion of PCR products

The intergenic regions were assessed for restriction site polymorphisms by digesting 10 µl PCR product overnight by 10U of the restriction enzyme. DC was digested by *Alu*I and *Hae*III. Digested PCR products were separated on agarose gels (Invitrogen, Ultra Pure, electrophoresis grade).

DETERMINATION OF THE PLASTOME OF INTERSPECIFIC F_1 HYBRIDS

The plastome types of interspecific F_1 hybrids were determined using plastome-specific CAPS-markers and by judging from the leaf morphology. The plastome types in a part of each progeny of all hybrid combinations were verified by CAPS markers and associated with leaf morphology and chlorophyll content. Leaf morphology and chlorophyll content appeared to be distinctive for the plastome in all hybrid combinations, so the plastome types of individual interspecific hybrids were determined by judging from the leaf morphology and chlorophyll content as listed in **Table 2**.

Reciprocal interspecific F_1 hybrids of four species were generated to determine plastid inheritance and directions of plastome-genome incompatibility within the section *Aestivae*. Progeny originating from self-pollinations did not segregate for leaf colour, indicating that plastome-genome interactions within taxa were compatible. All interspecific progenies, however, segregated in three classes of leaf colour: green, variegated, and virescent or pale green. Virescence occurs when a leaf is initially pale or yellow, but turns green while ageing and can result from incompatible plastome-genome combinations (Kirk and Tilney-Bassett 1978).

Table 2 Association between plastome-genome combination as determined by CAPS-markers and leaf morphology in interspecific hybrids of *Z. aethiopica* (AT), *Zantedeschia rehmannii* (R1), *Z. albomaculata* subsp. *albomaculata* (Aa1, Aa2), *Z. albomaculata* subsp. *macrocarpa* (Am1, Am 2), *Z. elliotiana* (E) and *Z. pentlandii* (P).

Crossing directions	Cross	Leaf morphology	Plastome	# plants
rehmannii × *albo*. subsp. *albo*	R1 × Aa1	Green	R1	20
	Aa1 × R1	Virescent	Aa1	9
		Variegated (green and virescent sectors)	R1 (green sector) + Aa1 (virescent sector)[1]	2
	R1 × Aa2	Green	R1	4
rehmannii × *albo.* subsp. *macro*	R5 × Am1	Green	R5	1
	R5 × Am1	Variegated (green and virescent sectors)	R5 (green sector) + Am1 (virescent sector)[1]	7
	R3 × Am2	Green	R3	1
	R3 × Am2	Variegated (green and virescent sectors)	R3 (green sector) + Am1 (virescent sector)[1]	5
rehmannii × *elliotiana*	R1 × E1	Green	R1	2
		Variegated (green and virescent sectors)	R1 (green sector) + E1 (virescent sector)[1]	4
rehmannii × *pentlandii*	R1 × P	Green	R1	10
		Variegated (green and virescent sectors)	R1 (green sector) + P (virescent sector)[1]	2
elliotiana × *albo*. subsp. *albo*	Aa1×E1	Green	Aa1	13
		Variegated (green + pale green sectors)	Aa1 (green) + E1 (pale green)[2]	5
	Aa2 × E1	Green	Aa2	1
	E1 × Aa2	Green	Aa2	1
		Variegated (green + pale green sectors)	Aa2 (green) + E1 (pale green)[2]	13
albo.subsp.*albo* × *pentlandii*	Aa1 × P	Green	Aa1	11
		Virescent	P	3
elliotiana × *albo*. subsp. *macro*	E3 × Am2	Green	E3	6
	E3 × Am2	Green	E3+Am2	6
	E3 × Am2	Green	Am2	2
	E3 × Am2	Variegated (fine mosaic)	E3+Am2	3
	E3 × Am2	Variegated (fine mosaic and pale green sector)	E3+Am2 (mosaic) + E3 (pale green)	1
rehmannii × *aethiopica*	R3 × AT	Albino	R3	8
		Albino	AT+R3	9
		Albino	AT	1

[1] Green sectors contained plastids of *Z. rehmannii*, virescent sectors contained plastids of the other parent (**Fig. 2**).

[2] Green sectors contained plastids of *Z. albomaculata* subsp. *albomaculata*, pale green sectors contained plastids of *Z. elliotiana*.

PLASTOME-GENOME INCOMPATIBILITY BETWEEN AESTIVAE SPECIES

To determine the plastome composition of hybrid plant tissue, species-specific CAPS markers were developed from the plastidial intergenic region of *trn*D and *trn*C (DC). Sequence variations between the species were demonstrated on the intergenic region by polymorphic restriction patterns of *Alu*I and *Hae*III (**Table 3**).

Z. rehmannii and *Z. albomaculata* subsp. *albomaculata* demonstrated similar DC-*Hae*III restriction patterns and could be differentiated by the *Alu*I polymorphism of the largest and smallest fragment (**Table 3; Fig. 2**). *Z. albomaculata* subsp. *macrocarpa*, *Z. elliotiana* and *Z. pentlandii* demonstrated similar DC-*Hae*III patterns, but the DC-*Alu*I pattern of *Z. albomaculata* subsp. *macrocarpa* was different from *Z. elliotiana* and *Z. pentlandii*. *Z. elliotiana* and *Z. pentlandii* demonstrated similar restriction patterns and could therefore not be differentiated, but they showed a DC-*Alu*I and a DC-*Hae*III restriction pattern that was different from *Z. rehmannii* and *Z. albomaculata* subsp. *albomaculata* (**Table 3**).

Green tissue of progeny of *Z. rehmannii* (R1, R3, R5) and *Z. albomaculata* (Aa1, Aa2, Am1, Am2) contained the plastome of *Z. rehmannii*. Virescent tissue contained the plastome of *Z. albomaculata* (**Table 2**). The plastome of *Z. rehmannii* appears compatible to the hybrid genome with both subspecies of *Z. albomaculata*, resulting in normal green tissue. The plastomes of both subspecies of *Z. albomaculata* are correspondingly partially incompatible to their hybrid genomes with *Z. rehmannii*, resulting in virescent tissue.

Green tissue of progeny of *Z. rehmannii* (R1, R2) and *Z. elliotiana* (E1) or *Z. pentlandii* (P) contained the plastome of *Z. rehmannii*. Virescent tissue contained the plastome of *Z. elliotiana* (E1) or *Z. pentlandii* (P) (**Table 2**). The plastome of *Z. rehmannii* is apparently compatible to the hybrid genomes with *Z. elliotiana* or *Z. pentlandii*, resulting in green tissue. The plastomes of *Z. elliotiana* and *Z. pentlandii* are correspondingly partially incompatible to their hybrid genomes with *Z. rehmannii*, resulting in virescent tissue.

Tissue of progeny of *Z. elliotiana* (E1) and *Z. albomaculata* subsp. *albomaculata* (Aa1, Aa2) demonstrated two leaf types: green and pale green. Green tissue contained the plastome of *Z. albomaculata* subsp. *albomaculata*, pale green tissue contained the plastome of *Z. elliotiana*. The plastome of *Z. elliotiana* thus appeared partially compatible to its hybrid genome with *Z. albomaculata* subsp. *albomaculata*, resulting in normal growing green tissue. The plastome of *Z. elliotiana* correspondingly appeared partially compatible to its hybrid genome with *Z. albomaculata* subsp. *albomaculata*, resulting in pale green, somewhat slower growing tissue.

Green tissue of progeny of *Z. elliotiana* (E3) and *Z. albomaculata* subsp. *macrocarpa* (Am2) could contain the plastome of both parents. Pale green or mosaic light-green tissue could also contain the plastome of either parent. One pale green section, though, was found to only contain the plastome of *Z. elliotiana*. Either the plastomes of both species are equally compatible to the hybrid background, or the plastomes do not sort out as clearly as in the other interspecific hybrid combinations.

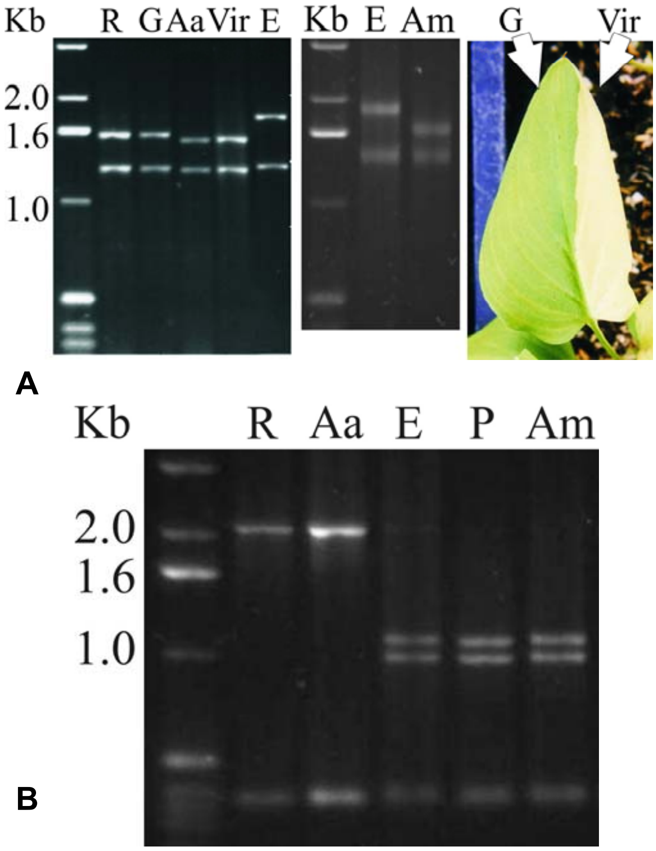

Fig. 2 Caps markers retrieved after PCR-amplification of the plastidial intergenic spacer of trnD and trnC and digestion by *Alu*I and *Hae*III. (A) *Z. rehmannii* (R), *Z. Albomaculata* subsp. *Albomaculata* (Aa) and their chimerical hybrid (virescent sector (VIR) - green sector (G)), *Z. elliotiana* (E) and *Z. albomaculata* subsp. *macrocarpa* (AM), digested by *Alu*I. (**B**) *Z. rehmannii* (R), *Z. albomaculata* subsp. *albomaculata* (AA), *Z. albomaculata* subsp. *macrocarpa* (AM), *Z. elliotiana* (E), and *Z. pentlandii* (P), digested by *Hae*III.

Albino tissue of progeny *Z. rehmannii* and *Z. aethiopica* contained the plastome of either parent or both. Both the plastome of *Z. rehmannii* and the plastome of *Z. aethiopica* appear incompatible to the hybrid genome, resulting in albino tissue.

PLASTID INHERITANCE IN AESTIVAE SPECIES

The variegation that was demonstrated in some progeny (**Fig. 2; Table 2**), originated from sorting out of plastomes, where differentially coloured leaf tissue contained different parental plastomes. Apparently, biparental plastid inheritance took place in all of these cases. To determine modes of plastid inheritance more precisely, hybrids from many crosses were assessed for leaf morphology. Considering the directions of plastome-genome incompatibility it is possible to use leaf colour as an indicator for the plastome type, given a known hybrid background (**Table 2**). More hybrids were developed and modes of plastid inheritance in these crosses were deduced and listed in **Table 4**.

Table 3 CAPS: *Alu*I- and *Hae*III-restriction patterns of the plastid *trn*D-*trn*C intergenic region from *Zantedeschia albomaculata*, *Z. elliotiana*, *Z. rehmannii* and *Z. pentlandii*.

Species	**Accessions**	**Size (kb)**	**Restriction pattern (in kb)**	
			***Alu*I**	***Hae*III**
Z. rehmannii	R1-R5	3.2	1.6, 1.25, 0.21	2.1, 0.37, 0.37
Z. albomaculata subsp. *albomaculata*	Aa1-4	3.2	1.55, 1.25, 0.21, 0.05	2.1, 0.37, 0.37
Z. albomaculata subsp. *macrocarpa*	Am1-2	3.2	1.65, 1.35, 0.2	1.1, 0.97, 0.41, 0.36
Z. elliotiana and *Z. pentlandii*	E1-3, P	3.2	1.7, 1.35	1.1, 0.97, 0.41, 0.36
Z. aethiopica	AT	~2.4		

Z. rehmannii and *Z. albomaculata* subsp. *albomaculata* demonstrated similar DC-*Hae*III.

Table 4 Percentage of hybrids demonstrating maternal, biparental and paternal plastid inheritance as judged from leaf colour in interspecific hybrids of *Z. rehmannii* (R), *Z. albomaculata* subsp. *albomaculata* (Aa), *Z. albomaculata* subsp. *macrocarpa*, *Z. elliotiana* (E) and *Z. pentlandii* (P).

	Mother	**Father**	**M**[1]	**B**	**P**	**n**
Z. rehmannii × *Z. albomaculata*	R3	Aa3	83	17		332
	Aa3	R3	89	11		37
	R3	Aa4	73	27		157
	R4	Aa4	58	42		83
	Aa4	R4	69	26	6	35
	R4	Aa3	77	23		13
	R1	Aa1	98		2	41
	Aa1	R1	87	11	2	45
	R1	A2	95	5		57
	Aa2	R2	89	11		57
	R3	Am1	56	44		90
	R5	Am2	59	41		58
Z. rehmannii × *Z. elliotiana*	R1	E1	90	10		58
	E1	R1	87	11	2	129
	E2	R3	79	21		197
	R1	P	89	9	2	66
Z. elliotiana × *Z. albomaculata*	Aa1	E1	96[2]	3[3]	1[4]	149
	E1	Aa2	10[4]	90[3]		42

[1] M=maternal, B=biparental, P=paternal plastid inheritance.

[2] Plants were green and presumably contained the plastome of *Z. albomaculata* (**Table 3**).

[3] Plants were variegated green and pale green and presumably contained both plastomes.

[4] Plants were pale-green and presumably contained the plastome of *Z. elliotiana* (**Table 3**).

Table 5 Directions of plastome-genome incompatibility in the genus *Zantedeschia* as deduced from the present study (**Table 3**) and earlier studies (Yao *et al*. 1994; Yao and Cohen 2000).

Genome[1]	**Plastome**[1]					
	Zantedeschia		***Aestivae***			
	aethiopica	***odorata***	***rehmannii***	***albo*. subsp. *albo***	***albo*. subsp. *macro***	***elliotiana / pentlandii***
aethiopica × *odorata*	++	-				
aethiopica × *rehmannii*	-		-			
odorata × *Aestivae*		-	-[2]			
rehmannii × *albo*. subsp. *albo*			++	±		
rehmannii × *albo*. subsp. *macro*			++		±	
rehmanni × *elliotiana/pentlandii*			++			±
albo. subsp. *albo* × *elliotiana*				++		+
albo. subsp. *macro* × *elliotiana*					++?	+/±?[3]

1 '++' = compatible, green leaf tissue; '+'= compatible, pale green leaf tissue; '±' = partially compatible, virescent leaf tissue; '-'= incompatible, albino leaf tissue.

[2] For cultivars of section Aestivae, the plastome of *Z. rehmannii* was marked, since the plastome of *Z. rehmannii* appeared compatible to all of the assessed genomic backgrounds (**Table 3**) and is most representative for the Aestivae genomes concerning compatibility.

[3] A pale-green sector of a variegated plant contained the plastome of E.

All families showed some degree of biparental plastid inheritance (**Table 4**). Considerable differences existed between families within similar species crossings, however. While R1 × Aa1 had a strong maternal bias (98%), only 58% of the offspring of R4 × Aa4 showed maternal plastid inheritance (**Table 4**). A high percentage (90%) of the offspring of E1 × Aa2 showed biparental plastid inheritance. The pseudo-reciprocal (Aa1 × E1) showed a maternal dominance in plastid inheritance (96%).

DISCUSSION

In the present analysis, we have demonstrated that biparental inheritance of plastids and plastome-genome incompatibility are prevalent among interspecific hybrids of the section *Aestivae*. Biparental inheritance of plastids and plastome-genome incompatibility were described in interspecific hybrids of *Z. aethiopica* and *Z. odorata* (Yao and Cohen 2000) as well as in interspecific hybrid *Aestivae*-cultivars and *Z. aethiopica* (Yao *et al*. 1994). In the present study, we presented more extended data on five taxa belonging to section *Aestivae*. It can thus be concluded that biparental plastid inheritance and plastome-genome incompatibility is prevalent in the entire genus *Zantedeschia*.

Based on the present study and the previously mentioned studies of Yao *et al*. (1994) and Yao and Cohen (2000), an overview of all directions of plastome-genome compatibility in the genus *Zantedeschia* can be constructed (**Table 5**). Yao *et al.* (1994) assessed hybrids of *Aestivae*-cultivars and *Z. aethiopica* and *Z. odorata*.

Based on the directions of plastome-genome incompatibility and restriction site polymorphisms, at least four plastomes were differentiated within section *Aestivae*. The plastome of *Z. rehmannii* appeared compatible to all of the tested hybrid backgrounds within section *Aestivae*. The plastome of *Z. albomaculata* subsp. *albomaculata* appeared compatible to its hybrid background with *Z. elliotiana*, but partially incompatible to its hybrid background with *Z. rehmannii*. The plastome of *Z. albomaculata* subsp. *macrocarpa* appeared equally compatible to its hybrid background with *Z. rehmannii*, but possibly not as compatible to its background with *Z. elliotiana*. The restriction pattern of *Z. albomaculata* subsp. *macrocarpa* appeared intermediate between *Z. albomaculata* subsp. *albomaculata* and *Z. elliotiana* and *Z. pentlandii*. Plastomes of *Z. elliotiana* and *Z. pentlandii* showed similar directions of plastome-genome incompatibility and restriction patterns, also with other tested restriction enzymes (*Hinf*I, *Mse*I, *Dpn*II). These two latter plastomes were only fully compatible to their associating genome and most likely similar.

Although generally accepted that flowering plants mainly receive plastids uniparentally, a review shows that biparental plastid inheritance in interspecific hybrids is not uncommon at all (**Table 6**). Of the 40 different genera listed

Table 6 Plastid inheritance among flowering plants; percentage of plants showing maternal (M) and biparental (B) or paternal inheritance (P) and size of assessed populations (n), determined with genetic evidence.

Mother	Father	M	B	P	n	Plastome-genome incompatibility	Reference
Acacia 2 spp.	*A.* 2 spp.		>5			+	Smith 1988 (in Kirk 1967)
Actinidia 4 spp.	*A.* 5 spp.			100%	114		Cipriani *et al.* 1995; Testolin and Cipriani 1997
Allium fistulosum	*A. cepa*	100%			?[1]		Yamashita *et al.* 1998
Iris fulva	*I. hexagona*	97%	2%	1%	100		Cruzan *et al.* 1993; Guillon and Raquin 2000
Brassica 4 spp.	*B.* 4 spp.	100%			300		Song *et al.* 1993; Oszminkowski and Jourdan 1994; Scott and Wilkinson 1999; Johannessen *et al.* 2005
Brassica rapa (=*campestris*)	*B. oleracea*	90	10		10		Song *et al.* 1993
Carica papaya	*Vasconcellea* 4 spp.	100%			23		Wills *et al.* 2005
Chamelaucium uncinatum	*C. megalopetalum*	100%			33		CPIN 142
Cicer arietinum	*C. reticulatum*		+		?		Kazan 1994
Epilobium 5 spp.	*E.* 5 spp.	100			>2000	+	Schmitz and Kowallik 1986
Epilobium hirsutum		99.93		0.07	1451	+	Schmitz and Kowallik 1986
Epilobium hirsutum		99.77	0.23		1774	+	Michaelis 1954
Epilobium hirsutum		100			301	+	Michaelis 1958
Epilobium parviflorum		100			295	+	Michaelis 1954
Epilobium watsonii	*E. montanum*	Frequent	Rare		2000	+	Schmitz and Kowallik 1986
Eucalyptus globules	*E. nitens*	100%			231		McKinnon *et al.* 2001
Fraxinus excelsior	*F. angustifolia*	100%			17		Morand-Prieur *et al.* 2002
Geranium bohemicum	*G. lanuginosum*		+		?[1]	+	Dahlgren 1923, 1925
Glycine max	*G. soja*	100%			?		Hatfield *et al.* 1985
Glycine tabacina	*G. canescens*	100%			?		Harris and Ingram 1991
Gossypium 4 sp.	*G.* 4 sp.	100%			?		Wendel 1988; Galau and Wilkins 1989
Helianthus annuus	*H.* 2 sp.	100%			108		Rieseberg *et al.* 1994
Hypericum perforatum		18.6	81.4?[3]		447	+	Correns 1937; Kirk and Tilney-Bassett 1978
Hypericum tetrapterum		59.8	39.9	0.3	1568	+	Noack 1932
Hypericum tetrapterum		3.6	93.9	2.7	590	+	Noack 1932
Liriodendron tulipifera	*L. chinense*	97.1%		2.9%	34		Sewell *et al.* 1993
Larrea 2 spp.	*L.* 2 sp.			100%	20		Yang *et al.* 2000
Lens lamottei	*L. nigricans*	50%	25%	25%	8		Van Oss *et al.* 1997
Leucadendron sp.	*L.* sp.	100%			100		Pharmawati *et al.* 1997
Lilium 2 spp.	*L.* 2 spp.	100%			? + 5		Haruki *et al.* 1998; Liu *et al.* 1998
Lotus cornicatus	*L. alpinus*	100%			~200		Gauthier *et al.* 1997
Magnolia tripetala	*M. fraseri*	99%		11%	9		Sewell *et al.* 1993
Magnolia 2 spp.	*M.* 3 spp.	100%			?		Tobe *et al.* 1993
Nicotiana plumbaginifolia (with cytoplasm from *N. gossei*)	*N. tabacum*	99.93	0.07%		1500		Medgyesy *et al.* 1986
Oenothera spp.		97-14	3-86		5827	+	Chiu and Sears 1993
Pelargonium zonale	*P. inquinans*	82	7	11	28	+	Pohlheim 1986
Pelargonium inquinans	*P. zonale*	23	35	15	13	+	Pohlheim 1986
Pelargonium cultivars	*Pelargonium* cultivars	Variable	Variable		~4000	+	Kirk and Tilney-Bassett 1978; Tilney-Bassett 1994; Dumolin Lapegue *et al.* 1997
Passiflora edulis	*P.* sp.	+	+			+	Do *et al.* 1992
Passiflora coccinea	*P. edulis*			+		+	Do *et al.* 1992
Passiflora menispermifolia	*Passiflora oerstedii*		+		?	+	Mrácek 2005
Phalaenopsis 2 spp.	*Phalaenopsis* 2 spp.	100			20		Chang *et al.* 2000
Phalaenopsis equestris	*Doritis pulcherrima*	100			10		Chang *et al.* 2000
Phlox drummondii	*P. cuspidata*	100%			62		Ferguson *et al.* 1999
Poncirus trifoliata	*Citrus reticulata* × *C. paradise*	100%			26		Moreira *et al.* 2002
Populus 1 sp.	*P.* 2 spp.	100%			50		Rajora and Dancik 1992
Populus trichocarpa	*P. max.* × *P. trich.*	100%			?		Mejnartowicz 1991
Populus max. × *P. berolinensis*	*P. trichocarpa*	100%			?		Mejnartowicz 1991
Rhododendron japonicum	*R.* 11 spp.	>95	<5		?	+	Smith 1988
Rhododendron kiusianum	*R. japonicum f. flavum*	73		27	45	+	Ureshino and Miyajima 2002
Rhododendron serpyllifolium	*R.* sp.	79	5	16	1991	+	Ureshino and Miyajima 2002
Stellaria porsildii	*S. longifolia*	66.7	16.6	16.6%	12		Chong *et al.* 1994
Stellaria longifolia	*S. porsildii*	100%			24		Chong *et al.* 1994
Streptocarpus sp.	*S.* sp.	100%			?		Moeller *et al.* 2003
Triticum 3 spp.	*Secale cereale*	100%			?		Harris and Ingram 1991
Z. odorata	*Z. aethiopica*	8	23	69	26	+	Yao *et al.* 1994; Yao and Cohen 2000
Zantedeschia aethiopica	*Z. odorata*	100			60	+	Yao *et al.* 1994; Yao and Cohen 2000
Zantedeschia aethiopica	Cultivars (section *Aestivae*)	59	41		171	+	Yao *et al.* 1994
Zantedeschia 3 spp.	*Z.* 5 spp.	10-98	3-90	1-6	1307	+	This study

[1] including reciprocals

in **Table 6**, there were reports in as much as 16 genera about some level of biparental plastid inheritance.

Few genera have been described where biparental inheritance of plastids is as prevalent as in the genus *Zantedeschia* (**Table 6**). Mainly genera in which plastome-genome incompatibility has been reported as well, show as wide a range of biparental and paternal plastid transmission patterns: *Pelargonium* (Pohlheim 1986), *Oenothera* (Chiu and Sears 1993), *Rhododendron* (Michishita *et al*. 2002; Ureshino and Miyajima 2002) and possibly *Acacia* (Smith 1988), *Hypericum* (Noack 1934), *Passiflora* (Mrácek 2005), and *Geranium* (Dahlgren 1923, 1925).

An interspecific hybrid might have a higher chance of receiving the compatible plastome type when the plastome is inherited biparentally as compared to uniparentally. In these genera the formation of interspecific hybrids may be promoted by permitting plastids to be inherited biparentally and hereby enabling selection of the most compatible plastome type.

It appears that the level of plastome-genome incompatibility between species of the same section is lower than the level of plastome-genome incompatibility between species of different sections. Plastomes and genomes of species within the section *Aestivae* are incompatible only to some degree, because all plants survived autotrophically. The plastome of *Z. aethiopica* and the hybrid genome of *Z. aethiopica* and *Z. odorata* (section *Zantedeschia*) were also only partially incompatible, because plants survived autotrophically. Intersectional hybrids were incompatible to a high degree, resulting in albino plants that can only survive heterotrophically (Yao *et al.* 1994). The level of plastome-genome incompatibility in interspecific hybrids appears correlated to the relatedness of the parental species in *Zantedeschia* spp.

It is becoming evident that genes have migrated from the plastid to the nucleus during evolution of plants (Martin *et al*. 2002; Huang *et al*. 2003). These translocations could result in plastomes containing genes that in other species are restricted to the nucleus. Plastomes and genomes that both do not contain the genes involved, would hence have become incompatible, where the level of incompatibility would depend on the function of the genes involved. The further that species have diverged, the greater the possibility that a translocation has taken place and plastomes and genomes have become incompatible.

CONCLUSION

In conclusion, all interspecific hybrid families of the genus *Zantedeschia* that were assessed showed a biparental mode of plastid inheritance with a maternal bias and levels of plastome-genome incompatibility. Based on the level of plastome-genome incompatibility, restriction site polymorphisms and directions of compatibility, four plastome types were differentiated among the section *Aestivae* and two were differentiated in section *Zantedeschia*. The *Aestivae* species hybridise readily and hybrids are fertile enabling genetic studies. Therefore, we propose the genus *Zantedeschia* and especially the section *Aestivae* as an object for further study of the phenomena of plastome-genome incompatibility and plastid inheritance.

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