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ORIGINAL PAPER

Inheritance of organelle DNA markers in a pea cross associated with nuclear-cytoplasmic incompatibility

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Abstract An unusual biparental mode of plastid inheritance was found in pea, in a cross associated with nuclear-cytoplasmic incompatibility manifested as deficiency of chlorophyll pigmentation. Plastid DNA marker *trnK* and mitochondrial DNA marker *cox1* were analyzed in F1 progeny that received cytoplasm from an accession of a wild subspecies *Pisum sativum* ssp. *elatius*. Plants with sectors of green tissue on leaves and seed cotyledons with green patches on an otherwise chlorotic background were found to carry paternally inherited plastid DNA, suggesting that photosynthetic function was affected by nuclear-cytoplasmic conflict and required proliferation of paternally inherited plastids for normal performance. The paternally inherited plastid DNA marker was also observed in the roots. The presence of the paternal marker in cotyledons, roots and leaves was independent of each other. Inheritance of the mitochondrial DNA marker *cox1* appeared to be of the maternal type.

Introduction

In the process of sexual hybridisation of plants, an organism is formed that combines nuclear-encoded genetic characteristics of both parents. At the same time, chloroplasts and mitochondria are usually inherited from only one parent (Birky 2001) and in this respect do not comprise any novelty. The role of cytoplasmic inheritance is commonly underestimated in part due to limited variability of organellar genomes (Wolfe et al. 1987), in part because mitochondrial and plastid genomes retain only restricted set of genes pertinent to the processes that take place in those organelles (Race et al. 1999). In some genetic context, the importance of the organellar gene contents becomes evident. A well-known example of a genetic conflict associated with certain nuclear-cytoplasm combinations is cytoplasmic male sterility (CMS), which usually results from chimaeric mitochondrial open reading frames (Schnable and Wise 1998), but also may be mediated by chloroplasts (van der Hulst et al. 2004; Ruiz and Daniell 2005). Such conflicts can be overcome through the activity of certain nuclear genes (Hanson and Bentolila 2004). Among grasses, genetically determined nuclear-cytoplasmic incompatibility can determine whether or not interspecific and intergeneric crosses are successful (Anderson and Maan 1995; Tsunewaki et al. 1996). This consideration is especially important in plant breeding. For instance, in cereals, alloplasmic lines were constructed combining the same nuclear genome with different cytoplasmic genomes originating from a related plant species. Comparisons of a number of quantitative traits in the set of barley alloplasmic lines (Goloenko et al. 2002), in different combinations of nuclear and cytoplasmic genomes of *Triticum* and *Aegilops* (Tsunewaki et al. 2002), maize and teosinte (Allen 2005) showed that various productivity traits were significantly affected by certain nuclei-cytoplasm combinations. Thus, even in case when interaction of nuclear and cytoplasmic genomes does not cause large disturbances such as incompatibility in crosses,

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cytoplasmic genetic factors appear to have a large contribution to the phenotypic characters, although it remains obscure what type of organelles are responsible for the effects observed and what is the nature of interaction.

Earlier we described a case of nuclear-cytoplasmic incompatibility in the crosses of a pea line belonging to a wild subspecies *Pisum sativum* ssp. *elatius* (Bogdanova and Berdnikov 2001) and showed that this genetic conflict could be compensated for via proliferation of chloroplasts inherited from the paternal plant (Bogdanova and Kosterin 2006). This situation closely resembles that occurring in interspecific crosses of *Oenothera* where visible signs of nuclear-cytoplasmic conflict were correlated with the share of paternally inherited chloroplasts (Chiu and Sears 1993). The major difference between the two is that in *Oenothera*, the plastids normally are inherited biparentally while in *Pisum*, plastid inheritance is normally maternal. A similar way to restore fertility and vigor was observed in a series of backcrosses in barley–wheat hybrids that employed an unusual paternally oriented shift in the composition of mitochondrial and chloroplast DNA markers (Aksyonova et al. 2005). Unusual biparental inheritance of mitochondria was also observed in wheat–rye hybrids (Siniavskaia et al. 2004).

In the present work we analyze F1 pea plants resulting from crosses of the VIR320 line implicated in nuclear-cytoplasmic incompatibility to study the inheritance of plastid and mitochondrial DNA markers in different organs and show that paternally inherited plastids are found in non-photosynthetic organs as well as in photosynthetic and that their presence in cotyledons, roots and leaves is independent of each other. At the same time all F1 plants display only the mitochondrial DNA marker from the maternal parent.

Materials and methods

Plant material

Fifteen F1 hybrids were analyzed resulting from the cross of VIR320 line (*Pisum sativum* ssp. *elatius*) used as the maternal parent with the original line Sprint-1, four F1 plants from the reciprocal cross Sprint-1 × VIR320, and eight F1 seeds resulting from the cross VIR320 × WL1238. WL1238 (Weibullsholm, Landscrona, Sweden) is a tester line carrying the *i* gene that conditions green coloration of cotyledons. This marker is also present in VIR320. About 5 mg of flour was scratched from mature hybrid seeds with a scalpel and used for DNA extraction, while the remaining part of the seed was planted in a container filled with sand. Seven to 10 day-old seedlings were harvested, and DNA was extracted separately from the roots and aboveground parts.

Genomic DNA extraction

About 100 mg of leaf or root tissue was rubbed with a glass pestle through a stainless steel grid (1 × 1 mm) into a vessel containing 1.5 ml of 0.15 M NaCl. If cotyledon material was used, about 5 mg of seed flour was resuspended in 1.5 ml of 0.15 M NaCl. After centrifugation at 4,000 *g* the pellet was extracted with the buffer containing 100 mM Tris–HCl (pH 8.0), 100 mM NaCl, 5 mM EDTA, 0.5% SDS (w/v). Genomic DNA from the crude extract was purified with the aid of a DNA extraction kit (Medigen, Russia) according to manufacturer's recommendations.

PCR amplification and DNA sequencing

The intron of the *trnK* gene was used as a marker of chloroplast DNA. Primers used for amplication of the *trnK* intron were: 5′-ATGTCGTATCAACGGTGAA TTCTAA, matching the 5′-part of the intron (EMBL accession X03853), and 5′-GAGATCTAGATCGTT CTAAATATAC (Gen Bank accession AY386961), matching the 5′-part of the *matK* gene residing in the intron of the *trnK*. A PCR-product of about 650 bp was amplified from the genomic DNA of the VIR320 and Sprint-1 lines that was sequenced using BigDye Terminators version 3.0 at ABI PRISM equipment at the sequencing center ICG and IChBFM SD RAS. A 1,200 bp-fragment of the *cox1* gene was used as a mitochondrial DNA marker. This fragment was amplified using the primers 5′-TGGTAATTGGTCTGTTCCG ATTCT and 5′-CCACTGCTTGAAGTGATTGTTA CG, matching the nucleotide sequence of the EMBL X14409 accession. PCR-reactions were performed in a volume of 20 µl and contained 10–20 ng of genomic DNA, 0.5 µM of each primer, 200 µM of each dNTP, 1 unit of Taq polymerase (ICiG). The following conditions were applied: initial denaturation at 95°C 1 min, followed by 38 cycles including 59 s at 94°C, 59 s at 56°C, 60 s at 72°C.

Endonuclease digestion and DNA electrophoresis

PCR-products from the mitochondrial *cox*1 gene were digested with the *Psi*I endonuclease as follows: 5 µl of the PCR reaction were mixed with the buffer and 10 units of the restriction enzyme in the total volume of 12 µl and kept at 37°C for 2 h. The digestion products

were electrophoresed in 1.5% agarose gel in TAE buffer containing 0.5 μg ethidium bromide per millilitre. DNA bands were visualized in UV light. Five microlitres of PCR-reaction from the plastid *trnK* gene were digested with 10 units of the *Bsc*4I endonuclease in the presence of 100 μg/ml BSA in the total volume of 12 ml. Reactions were kept at 55°C for 2 h and then electrophoresed in 2% agarose gel.

Results

We have previously shown that in in crosses between the pea line VIR320 as the maternal parent and any of the vast majority of cultivated pea forms, there occurred a nuclear-cytoplasmic conflict resulting in almost sterile chlorotic plants with reduced leaflets and stipules (Fig. 1a) (Bogdanova and Berdnikov 2001). The roots of these plants are also underdeveloped with very short (1–4 mm) lateral outgrowths (Fig. 1a). In some cases the conflict is overcome so that sectors of various size of normal green tissue are formed, and occasionally almost the entire plant has a normal appearance (Fig. 1b, c).

Fig. 1 Phenotype of F1 plants from the cross VIR320 × WL1238. **a** Plant manifesting nuclear-cytoplasmic conflict. **b** Plant with partial recovery from the conflict. **c** Plant with almost complete recovery from the conflict

It was shown earlier that formation of green tissue was associated with the presence of paternally inherited chloroplasts, as judged from the presence of plastid DNA marker *rbcL*. The paternal leakage of chloroplast DNA occurred only in the crosses associated with nuclear-cytoplasmic conflict, in the reciprocal crosses plants were phenotypically normal and the paternal form of the *rbcL* in them was not registered (Bogdanova and Kosterin 2006).

To assess what organellar genomes are involved into the conflict we analyzed the inheritance of mitochondrial genome in the cross VIR320 × Sprint-1 associated with the nuclear-cytoplasmic incompatibility. As a marker of mitochondrial DNA, a fragment of the *cox*1 gene coding for cytochrome oxidase subunit I was used. A 1,200 bp PCR-product obtained from the lines VIR320 and Sprint-1 was further digested with a number of restriction endonucleases, and we found that the product amplified from DNA of the VIR320 line contained a recognition site for the *Psi*I endonuclease. Thus, after treatment of the PCR-products with *Psi*I, the maternal form of the *cox1* gene was digested into two fragments of 260 and 940 bp, while the paternal form remained undigested and had the size of 1,200 bp. We analyzed DNA extracted from cotyledons, roots and leaves of 15 F1 progenies of the cross VIR320 × Sprint-1 and leaves of four F1 progenies of the reciprocal cross (Fig. 2). Cleavage of PCR-products with *Psi*I was somewhat incomplete and a faint band can be seen in Fig. 2, lanes 1–10, corresponding to the intact form. Nevertheless, in all cases, digestion profile of the PCR-amplified *coxI* marker was indistinguishable from that of the maternal parent, indicating that the the nuclear-cytoplasmic conflict did not affect inheritance of mitochondria, at least as refers to the *cox*1 marker.

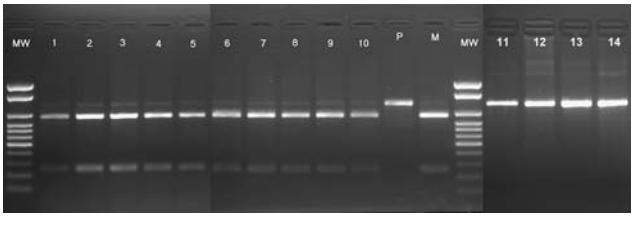

Fig. 2 Restriction fragments formed after *Psi*I digestion of the PCR-amplified *cox1* mitochondrial DNA marker. *Lanes 1–10* representative F1 plants from the cross VIR320 × Sprint-1. *Lanes 11–14* F1 plants from the reciprocal cross Sprint-1 × VIR 320. *P* Sprint-1, *M* VIR320, *MW* molecular weight marker 100–1,000 bp + 1.5 kb + 2 kb

Earlier we found that patches of green tissue on otherwise chlorotic leaves were associated with the presence of paternally inherited chloroplasts (Bogdanova and Kosterin 2006). We were further interested to analyze distribution of plastid DNA in non-photosynthetic tissues. We obtained nucleotide sequences of the 5′ part of the intron of the *trnK* gene (tRNA for lysine) from the VIR320 and Sprint-1 lines (submitted to EMBL database as AM295252 and AM294945). A nucleotide substitution G/A in the position 143 from the start of the upstream primer distinguished the maternal and paternal forms. We utilized this difference to identify the maternal or paternal origin of the *trnK* marker by means of the restriction endonuclease *Bsc*4I. The PCR product from VIR320 was digested into four fragments of 204, 194, 140, 109 bp, while that from the Sprint-1 produced three fragments of 249, 204, 194 bp that enabled us to register the presence of the paternally inherited plastid DNA marker.

Figure 3 shows the digestion profiles of PCR products amplified from DNA samples extracted from cotyledons (Fig. 3a), leaves (Fig. 3b) and roots (Fig. 3c) of

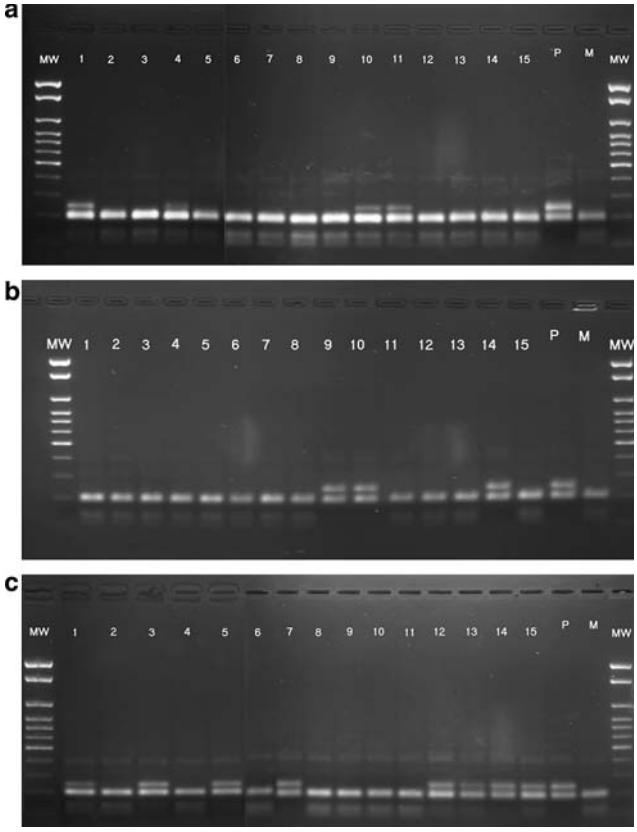

Fig. 3 Restriction fragments formed after *Bsc*4I digestion of PCR-amplified *trnK* plastid DNA marker in F1 progeny of the cross VIR320 × Sprint-1. DNA was extracted from: **a** cotyledons, **b**. leaves, **c**. roots. *Lanes1–15* individual plants, *P* paternal form (Sprint-1), *M* maternal form (VIR320), *MW* molecular weight marker 100–1,000 bp + 1.5 kb + 2 kb

Fig. 4 F1 seed resulting from the cross VIR320 × WL1238. Green sectors are seen on a *yellowish background*

the F1 hybrids from the cross VIR320 × Sprint1. The paternally inherited *trnK* marker was observed in all tissues studied, photosynthetic or not. It was present in four samples of cotyledons (Fig. 3a, lanes 1, 4, 10, 11), 8 samples of roots (Fig. 3c, lanes 1, 3, 5, 7, 12, 13, 14, 15). Three samples of leaves carried the paternal *trnK* marker (Fig. 3b, lanes, 9, 10, 14) and these were three plants that acquired patches of green tissue on their leaves. Notably, the presence of the paternally inherited *trnK* marker in one organ of an F1 plant is not correlated with its presence in other organs of the same plant (the same lane numbers in Fig. 3).

To further analyze the relation between photosynthetic function and paternal inheritance of plastids as a way to overcome nuclear-cytoplasmic conflict we studied the presence of the paternal *trnK* marker in eight F1 seeds resulting from the cross VIR320 × WL1238. Both parental lines carry the *i* gene that determines green color of the cotyledons (Blixt 1972), the progeny is homozygous for *i* and should have green cotyledons. However, anomalies in chlorophyll pigmentation observed in the seedlings can also be seen as a pale yellowish coloration in the cotyledons sections. Among 8 seeds studied, two had green sectors on a yellowish background (Fig. 4); the PCR/endonuclease analysis showed that these two seeds were heteroplasmic in respect of the paternal *trnK* marker while the remaining six seeds lacking green patches in the cotyledons lacked it (not shown). This result further supports the conclusion that normal photosynthetic function in the hybrid seeds requires the presence of paternal plastids.

Discussion

A nuclear-cytoplasmic conflict that occurs in some crosses of remotely related plants may be resolved by paternal transmission of organellar genomes (Chiu and Sears 1993; Aksyonova et al. 2005; Bogdanova and Kosterin 2006). Proliferation of a certain type of organelle can indicate which of the cytoplasmic genomes is involved in the conflict. In *Oenothera*, the transmission efficiency of each plastome correlated strongly with its compatibility with the nuclear genome of the progeny (Chiu and Sears 1993). For barley–wheat hybrids, both mitochondria and chloroplasts of the paternal origin

were associated with fertility restoration of the hybrids (Aksyonova et al. 2005). In *Pisum*, a paternal leakage of chloroplast DNA appears to be the mechanism that compensates for a nuclear-cytoplasmic conflict (Bogdanova and Kosterin 2006).

Paternal plastid DNA that is inherited by the hybrid progeny can be further transmitted to the following generation. A preliminary analysis of five F2 progenies resulting from self-pollination of an almost entirely green F1 plant (like that in Fig. 1c) showed that three of the F2 carried chloroplast DNA marker predominantly of the paternal type and were phenotypically normal, while two plants had predominantly the maternal type. Of these two plants, one had variegated phenotype with chlorophyll deficiency and the other had normal green coloration but was completely sterile, implying that segregation of nuclear genes is also involved in the nuclear-cytoplasmic conflict.

To distinguish between the maternal and paternal forms of mitochondrial DNA we used a polymorphic *Psi*I recognition site. As seen in the Fig. 2, some portion of the PCR-product amplified with the *cox*1-specific primers in the VIR320 line remains undigested so that the corresponding band has the same size as in the Sprint-1 line. This result could point to the presence of so-called promiscous DNA in the nucleus (e.g. Ayliffe et al. 1998). To exclude the nuclear origin of the major polymorphic band employed in the analysis we checked the pattern of *Psi*I digestion of the *cox*I marker in F1 plants resulting from a reciprocal cross Sprint-1 × VIR320 (Fig. 2, lanes 11–14). In these plants, the *cox*I marker was indistinguishable from the Sprint-1 (maternal) form, indicating that the polymorphic band was of cytoplasmic rather than nuclear origin, in which case digestion patterns of F1 plants from reciprocal crosses would be identical. Although the exact origin of the minor undigested band is unclear and it could proceed from the paternal leakage of mitochondrial DNA, maternal inheritance of existing polymorphism (Laser et al. 1997) or promiscous nuclear DNA, this band hardly has any relation to the nuclear-cytoplasmic conflict, since it is uniform in all the F1 and indistinguishable from the maternal parent. It seems to us most probable that the restriction endonuclease fails to digest completely the DNA template, the situation described in (Storm et al. 1998; Fojtova et al. 2001), and that the *coxI* marker is inherited strictly maternally in the cross studied. Although it could not have been predicted a priori, this result is not surprising because mitochondria are inherited independently from plastids (Nagata et al. 1999). We conclude that mitochondrial genome was not involved into the genomic conflict, at least as refers to the *cox*1 marker. However, this does not exclude the possibility that other mitochondrial genes could be affected, because different mitochondrial genes were observed to be involved to different extent in fertility restoration in barley–wheat hybrids (Aksyonova et al. 2005).

To assess the relationship of photosynthetic function to the development of the observed nuclear-cytoplasmic conflict we tested the presence of paternally inherited plastids in non-photosynthetic tissues. Among 15 F1 progenies tested, 4 plants (corresponding to lanes 5, 7, 10, 14 in Fig. 3c) had the root system that appeared to be normally developed with long branched lateral roots. The paternal *trnK* plastid DNA marker was found in the roots of 8 plants and the presence of paternally inherited plastids was not correlated with the root phenotype. Thus, it appears that underdevelopment of the root system in F1 progeny of the cross VIR320 × Sprint-1 is due some other cytoplasmic factor involved into the nuclear-cytoplasmic conflict. This might be a plastid gene located far from *trnK* in the plastid genome or a mitochondrial gene remote from *coxI*. Mitochondrial genomes are often represented by subgenomic molecules of variable size (Backert et al. 1997) that makes it possible for different genes to be independently inherited. Such a kind of recombination was observed in a series of backcrosses in barley-wheat hybrids (Aksyonova et al. 2005). Plastid DNA can also display a considerable structural plasticity (Bendich 2004), so, the restoration of root phenotype might be due, for example, to some plastid gene involved into performance of root-specific plastid functions, among which are biosynthesis of starch, fatty acids and the synthesis of amino acids from inorganic nitrogen (Neuhaus and Emes 2000).

In *Pisum*, cytological studies revealed the presence of cytoplasmic DNA in pollen tubes suggesting potential possibility of biparental inheritance of organelles (Corriveau and Coleman 1988). In some pea cultivars the number of organellar nucleoids per pollen tube can attain 7 (Corriveau et al. 1989), but even in this case chloroplasts are still maternally inherited (Polans et al. 1990), indicating that normally a mechanism exists that discards paternal plastids during later pollen tube growth, during or after fertilization. Such mechanisms include loss of cytoplasmic organelles from the generative or sperm cells, degradation of organelle DNA within generative and/or sperm cells, and exclusion of male cytoplasm at gametic fusion (summarized in Mogensen 1996). In intergeneric hybrids of plant species characterized by uniparental maternal organelle inheritance, there may occur a paternal leakage of organelle DNA (Soliman et al. 1987; Moreira et al. 2002; Siniavskaia et al. 2004; Aksyonova et al. 2005). In mice, paternal

leakage of mitochondrial DNA was described in an interspecific cross (Gyllensten et al. 1991), and a hypothesis had been put forward that a genetically determined system of recognition of sperm mitochondria was inefficient in the interspecific hybrids (Kaneda et al. 1995). It seems probable that in the situation of the conflict between nuclear and plastid genomes in pea, a mechanism providing exclusively maternal inheritance of plastids fails to operate and a zygote is formed containing plastids from both parents. Further, random or stochastic processes can fix organelles of one or the other parent in a fraction of cells in the developing embryo (Birky 1995). Thus we can expect that different parts of the plant would be more or less enriched in the paternal plastid DNA depending on the plastid segregation in the embryo that may be associated with spatial distribution of the plastids. For example, in alfalfa, plastids localized in the apical part of the zygote are preferentially trasmitted to the embryo, while the basal part of the zygote contributes to the suspensor, which eventually degenerates (Zhu et al. 1993). In addition, intracellular selection in favour of paternal plastids that, in contrast to the maternal ones, are capable of photosynthesis might take place, such as in case of antibiotic-resistant mitochondria in yeast (Birky 1973) or systematic increase in frequency of certain mtDNA genotypes in some tissues in mice (Jenuth et al. 1997).

The nature of nuclear-cytoplasmic conflict described here remains obscure. It is possible that in the VIR320 line, as a carrier of genetically determined ability to cause nuclear-cytoplasmic incompatibility in the crosses, some gene(s) is mutated responsible for signal transduction from nucleus to plastids, metabolite transport or structural features of the plastid membranes. In somatic cell hybrids combining nuclear genome of *Atropa belladonna* and cytoplasmic genomes of tobacco, there developed chlorophyll deficiency conditioned by the inability of the nightshade nuclear genome to support effective editing of the tobacco *atpA* (ATP synthase CF1 alpha chain) transcript in plastids (Schmitz-Linneweber et al. 2005). The number of genes responsible for incompatibility of the cellular genomes appears to be rather small. In *Triticum*, it was shown that a system of two nuclear genes, *scs* and *Vi* is involved into maintenance of nuclear-cytoplasm compatibility (Simons et al. 2003; Gehlhar et al. 2005), but the molecular function of these genes remains unknown.

The case of nuclear-cytoplasmic incompatibility found in the garden pea appears to be a useful model that allows observation of interactions between cellular genomes in different compartments that are normally masked by low variability of organellar genomes. This model has an advantage over traditionally used interspecies hybrids of cereals, which have decreased fertility, and allows genetic analysis at the intraspecies level.

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