



Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Plastid capture and resultant fitness costs of hybridization in the *Hirta* clade of southern African *Oxalis*

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ARTICLE INFO

Article history:

Received 1 March 2017

Received in revised form 26 May 2017

Accepted 22 June 2017

Available online xxxx

Edited by AJ Potts

Keywords:

Plastid capture

Fitness

Hirta clade

Hybridization

Plastid inheritance

Oxalis

Cytonuclear discordance

Self-compatibility

ABSTRACT

Ancient hybridization leading to plastid capture is a likely cause of cytonuclear discordance, although discordance may also be attributed to other mechanisms. Cytonuclear discordance is ubiquitous in a clade of southern African *Oxalis* known as the *Hirta* clade, despite a notable lack of documented field hybrids for this genus. The aims of this study were to determine whether hybridization is possible between different *Hirta* clade species, what the fitness effects on seed set of possible hybridizations are, and to determine the mode of inheritance of plastid DNA in *Oxalis*. We tested these aims using manual interspecific and conspecific crosses, as well as self-pollination control crosses of species within this clade, conducted in a research collection context. Roughly 10% of interspecific crosses produced seed, most of which were confirmed as unambiguous hybrid plants using DNA sequencing of the Internal Transcribed Spacer (ITS). Low levels of self-compatibility were recorded in several species, while one accession showing very high levels of self-compatibility (accession MO1218). Interspecific crosses produced significantly less seed per capsule compared to conspecific crosses with respective parents, suggesting decreased fitness in the establishment of the F1 hybrids. Selfing seed set was significantly lower than interspecific and conspecific seed set upon removal of MO1218. Using plastid fragment length polymorphisms, *Oxalis* was found to have predominantly or exclusively maternally inherited plastid DNA. This study establishes the viability of the earliest stages of plastid capture in *Oxalis*, and provides context relevant to the lack of documented field hybrids in the southern African members of this genus. Future studies should focus on F1 survival and fertility and the maternal fitness effects of subsequent backcrosses to the maternal parent, as well as on hybridization rates under field conditions, to assess whether hybridization occurs at rates sufficient to affect *Oxalis* evolution in southern Africa.

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1. Introduction

Plastid capture is the process by which plastid DNA from one species is transferred to the F1 generation of an interspecific hybrid (Tsitrone et al., 2003), followed by fixation of the introgressive plastid, through repeated backcrossing with the paternal parent, often with no or very little evidence of nuclear introgression (Okuyama et al., 2005). Consequently, hybridization must occur before plastid capture through introgression can take place, and hybridization potential between prospective parent species should thus be studied when looking at plastid capture (Rieseberg and Wendel, 1993). Plastid capture has been suggested to be a major contributor to phylogenetic incongruence between nuclear and plastid sequences (cytonuclear discordance) (Oberlander et al., 2011; Okuyama et al., 2005; Soltis and Kuzoff,

1995; Tsitrone et al., 2003; Xu et al., 2012). Although cytonuclear discordance is often taken as evidence of plastid introgression, detecting this pattern can be complicated by varying amounts of nuclear introgression from the maternal parent in commonly used phylogenetic loci such as ITS (Okuyama et al., 2005). Additionally, ancestral polymorphisms that are randomly sorted (incomplete lineage sorting/ILS) (Joly et al., 2009; Maddison and Knowles, 2006; Pelsner et al., 2010) and sampling errors (Huson and Bryant, 2006) involving paralogs and pseudogenes (Álvarez and Wendel, 2003; Koonin, 2005) can also give rise to cytonuclear discordance. ILS arises when lineage sorting has not been completed across multiple species divergences, especially in rapidly radiating groups and where population sizes are large (Maddison, 1997). Paralogs and pseudogenes are formed by local gene or whole genome duplications and can generally only be detected through well-sampled phylogenetic analysis (Álvarez and Wendel, 2003; Koonin, 2005).

Hybridization and ILS can both produce well-supported, but incongruent phylogenies, making it difficult to decipher the true reason for incongruence (Joly et al., 2009; Pelsner et al., 2010; Yu et al., 2011).

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Determining whether hybridization or ILS is the reason for cytonuclear discordance can be done using coalescent-based approaches. If more than two unlinked genomic data sets are available, testing can take place to determine whether incongruence patterns are random or non-random, indicating ILS or hybridization, respectively (Buckley et al., 2006). A less direct, but less expensive option is to test whether viable hybrid offspring can be formed from the prospective parent species, using crossing experiments.

One of the assumptions underlying theoretical models of plastid capture is an increase in fitness of introgressed individuals, in most cases via plant female function due to cytoplasmic male sterility and re-assignment of resources to ovule and seed production (Tsitrone et al., 2003), although a blanket fitness advantage leading to a plastid selective sweep has also been suggested (Percy et al., 2014). However, for female fitness advantage to be expressed in subsequent generations, the potential negative effects of hybridization on the viability and fertility of the F1 generation must be overcome. One mechanism that contributes to the maintenance of hybrids is heterosis, also known as hybrid vigour, which has been extensively studied in crop plants due to its importance in the development of improved crops (Chen, 2010; Schnable and Springer, 2013). It has been suggested that earlier hybrid generations would be less fit than the original parent plants, but would see higher fitness in later generations, which can increase hybrid persistence (Rieseberg and Carney, 1998; Seehausen, 2004). Long-term persistence of hybrids in the environment is linked to whether hybrid lineages are fit enough to either outcompete parents or to colonize a different, often novel habitat (Rieseberg, 1997), meaning that parents and hybrid lineages rarely co-exist in sympatry. On the contrary, hybrid breakdown has been found in several instances, even in later generations, which could result in only short-term persistence of hybrids in the environment (Johansen-Morris and Latta, 2006). Hybrid fitness needs to be evaluated, as it is directly linked to the success and persistence of hybrids in both cultivation and nature, and it needs to be assessed on a per-species basis, as hybrid fitness appears to vary between different organisms (Johansen-Morris and Latta, 2006; Rieseberg, 1997; Rieseberg and Carney, 1998; Seehausen, 2004).

One major reason for cytonuclear discordance stems from the generally uniparental nature of inheritance of the plastome, which typically results in smaller effective population sizes and shorter times to coalescence (Charlesworth, 2009). Plastid inheritance in plants can be maternal, paternal or biparental, although studies on angiosperms have found mostly maternal plastid inheritance (Chen et al., 2002; Corriveau and Coleman, 1988; Möller et al., 2004; Sears, 1980; Zhang et al., 2003). Although for most unstudied angiosperms plastid inheritance is assumed to be maternal, such assumptions are often based on very small sample sizes in distantly related species and do not take conspecific variation in plastid inheritance into account (Harris and Ingram, 1991). In a study on the rare *Helianthus verticillatus* Small, 6 plants from a sample of 323 showed paternal plastid inheritance (Ellis et al., 2008). As a result, explicit testing of plastid inheritance processes is vital in unstudied/poorly studied groups (Ellis et al., 2008; Harris and Ingram, 1991).

Oxalis L. (Oxalidaceae) is a morphologically variable cosmopolitan genus consisting of more than 500 species found primarily in South America and southern Africa (Lourteig, 1994, 2000; Salter, 1944). At least 220 species are known from southern Africa, most of which are located in the Greater Cape Floristic Region (GCFR) (Dreyer and Makgagga, 2003; Manning and Goldblatt, 2012; Oberlander et al., 2011; Snijman, 2013). Southern African (SA) *Oxalis* form a clade derived from a South American lineage (Oberlander et al., 2011). Historically hybridization has seldom been invoked as an explanation for the massive morphological variation in this genus and there are no known SA *Oxalis* hybrids recorded in the field (Salter, 1944). Recent phylogenetic work (Oberlander et al., 2004, 2011; Schmickl et al., 2015) has retrieved a clade of species, informally called the *Hirta* clade (Oberlander et al., 2004, 2011; Schmickl et al., 2015), scattered across three of the sections/subsections proposed by Salter (1944). This clade shares a

modified, highly specialized, supra-areolate pollen type unique within the angiosperms (Dreyer, 1996). Also, bootstrap support values (BS), from a wide diversity of markers, always exceeded 96% for this clade (Oberlander et al., 2004, 2011; Schmickl et al., 2015). Taken together, this highly derived pollen type and DNA sequence data strongly support the *Hirta* clade as a natural entity.

There is some evidence that hybridization/plastid capture is possible in the *Hirta* clade. Salter (1944) anecdotally found hybridization to take place in cultivation between two morphologically distinct and allopatrically distributed *Hirta* clade members. ITS and plastid DNA-derived phylogenetic trees showed strong incongruence within the *Hirta* clade (Fig. 1) and it has been suggested that this could be due to hybridization and subsequent plastid capture (Oberlander et al., 2011). Preliminary work by Schmickl et al. (2015) has shown multiple, successive instances of within-species cytonuclear discordance, implying strongly, but indirectly, that plastid capture has occurred in the *Hirta* clade. To our knowledge no work has directly tested to what extent SA *Oxalis* species are capable of hybridization. Also, to our knowledge, no previous study has systematically assessed the mode of plastid inheritance in SA *Oxalis*. Corriveau and Coleman (1988) determined *Oxalis europaea* Jordan, which displayed maternal plastid inheritance, but it is unclear whether these results, from a single, distantly-related species and a small sample size, can be generalized to the mode of plastid inheritance of SA *Oxalis*.

This study had three primary aims that are all linked to plastid capture. The first was to determine, as a first step towards plastid capture, whether viable F1 hybrids can be formed between different species in the *Hirta* clade. The second was to determine what the fitness consequences of hybridization are on seed set, at least with regard to the maternal parent. The third aim was to determine the mode of plastid inheritance in members of the *Hirta* clade. If the substantial incongruence between plastid and ITS data in this clade is the result of plastid capture, we hypothesize that hybridization is possible between some species in the *Hirta* clade. We also hypothesize that if interspecific crosses are successful, a decrease in female parent fitness will be observed in terms of significantly lower number of seeds produced compared to conspecific crosses. Finally, we hypothesize that plastid DNA is maternally inherited in *Oxalis*.

2. Materials and methods

2.1. Species selection

Species selected for this study (Table 1) were based on the phylogenetic study of Oberlander et al. (2011). The *Hirta* clade was chosen due to known incongruence between plastid and ITS sequence data as well as between hundreds of low-copy nuclear genes and plastomes, respectively (Oberlander et al., 2004; Schmickl et al., 2015), and in addition due to at least some evidence for successful hybridization between different *Hirta* clade species in cultivation (Salter, 1944). *Hirta* clade members produce recalcitrant (exendospermous) seeds that germinate within 24–48 h of release from the seed capsules (Salter, 1944), making quantification of seedling germination and tissue sampling for PCR feasible within a few weeks after seed set. Although distribution data for SA *Oxalis* are generally poorly known, *Hirta* clade sister species pairs exhibit a range of distribution patterns, from complete allopatry to substantial sympatry.

2.2. Crossing and cultivation

Manual pollination was conducted during the peak flowering period (April–June 2016) using accessions of multiple *Hirta* clade species maintained in the open-air *Oxalis* research collection in the Stellenbosch University (SU) Botanical Gardens. Fine, alcohol-sterilized forceps were used to harvest and transfer pollen-laden anthers to virgin stigmas for the chosen crosses. To avoid potential complications resulting from tristylly (Barrett, 1993), all interspecific and conspecific crosses were

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