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Floral scents of chafer-pollinated asclepiads and a potential hybrid

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Abstract

Floral scent is a key functional trait for pollinator attraction to flowers, but is poorly documented in many plant lineages and pollination systems. In South African grasslands, chafer beetles (Scarabaeidae: Cetoniinae), particularly *Atrichelaphinis tigrina*, *Cyrtothyrea marginalis* and *Leucoscelis* spp., are common floral visitors and specialized pollination by these beetles has recently been established in several asclepiad, orchid and protea species. Chafer beetles are known to be attracted by a variety of floral volatile compounds and scent has been suggested to be an important signal in these chafer-operated pollination systems. In this study, we used dynamic headspace extraction methods and coupled gas chromatography–mass spectrometry (GC–MS) to examine the chemical composition of the floral scents of seven putatively chafer-pollinated asclepiad species in the genera *Asclepias*, *Pachycarpus* and *Xysmalobium*. We identified 15–57 compounds in the scents of these species, of which seven were common to all species examined. The scent profiles of each species separate into discrete clusters in two dimensional space based on non-metric multidimensional scaling (NMDS), indicating clear distinctions between species and suggesting that plants may use different combinations of volatiles to attract beetles. Two plants suspected to be intergeneric hybrids were also examined. Data on pollination systems, morphology and scent chemistry are consistent with the hypothesis that these plants are hybrids between the chafer-pollinated species *Asclepias woodii* and *Pachycarpus concolor*. The results of this study are discussed in relation to the role of chafer beetles as generalist pollinators of specialized asclepiads.
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Keywords: Apocynaceae; Asclepiadoideae; Cantharophily; Floral volatiles; Introgression; Pollination guild

1. Introduction

Floral scent is increasingly being recognized as a functionally important trait in many plant–pollinator interactions, but remains poorly examined for many systems (Dudareva and Pichersky, 2006; Raguso, 2001). Recent studies in South African grasslands have revealed a guild of plants that are reliant on chafer beetles (Scarabaeidae: Cetoniinae), particularly *Atrichelaphinis tigrina* (Olivier, 1789), *Cyrtothyrea marginalis* (Swartz, 1817) and *Leucoscelis* spp. for pollination. These chafer beetles are ubiquitous and generalist floral visitors in South African grasslands (pers. obs.). Interestingly, while the beetles themselves are highly generalist, some of the plants they pollinate are highly specialized, in many cases being dependent almost entirely on just one beetle species for pollination. Chafer-pollinated species include asclepiads (Apocynaceae: Asclepiadoideae; Ollerton et al., 2003; Shuttleworth and Johnson, 2008, 2009a), orchids (Orchidaceae; Johnson et al., 2007; Peter and Johnson, 2009) and proteas (Proteaceae; Steenhuisen and Johnson, 2007).

Detailed studies of the mechanisms of chafer attraction by flowers have recently been conducted for proteas (Steenhuisen et al., 2008; Steenhuisen et al., 2010-in this issue) and have shown that floral scent is a key pollinator attractant. A role for scent in pollination of the chafer-pollinated orchid *S. microrrhynchum* was also suggested from antennal electrophysiological studies of *A. tigrina* (Johnson et al., 2007). Chafer-pollinated asclepiads are also often unusually fragrant in comparison to their congeners, further suggesting that volatiles may play an important role in the attraction of chafer beetles. The aims of this study were thus to examine the chemical composition of the floral scents of chafer-pollinated asclepiads and from the resultant patterns to evaluate the role of floral scent in the attraction of chafer beetles to asclepiad flowers.

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During the course of a previous study (Shuttleworth and Johnson, 2009a), we discovered two individuals of what appeared to be intergeneric hybrids between the two chafer-pollinated species *Asclepias woodii* and *Pachycarpus concolor*. These plants were growing at a site in Midmar Nature Reserve (Table 1) where both *A. woodii* and *P. concolor* co-occur and exhibited floral and vegetative traits intermediate between those of the suspected parent species (Fig. 1a,b,c). Hybridization is an important phenomenon which can result in novel traits being incorporated into parent species through backcrossing and introgression (Barton, 2001; Broyles, 2002; Lewontin and Birch, 1966; Rieseberg et al., 2003; Stebbins, 1959). Although hybridization in North American *Asclepias* species has frequently been examined (Kephart et al., 1988; Klips and Culley, 2004; Wyatt and Broyles, 1992; Wyatt and Hunt, 1991), it has seldom been reported in African asclepiads (but see Weale, 1873). We thus aimed to document these putative hybrids and examine the likelihood that they result from hybridization between *A. woodii* and *P. concolor* through comparison of pollination systems, morphologies and floral scent.

The specific aims of this study were thus (1) to determine the chemical composition of the floral scents of the five known chafer-pollinated asclepiads and an additional two species suspected to be chafer-pollinated, (2) to identify compounds in the floral scents of the seven species that may be attractive to chafer beetles and, (3) to compare floral and vegetative morphologies, and scent of the putative hybrids to those of the parent species.

2. Methods

2.1. Study species and their pollination systems

This study involved seven grassland asclepiads (Apocynaceae subfamily Asclepiadoideae *sensu* Endress and Bruyns, 2000) in the genera *Asclepias*, *Pachycarpus* and *Xysmalobium* (Fig. 1; Table 1). One of these species, *A. woodii*, is endemic to the KwaZulu-Natal midlands and is listed as vulnerable in the Red list for South African plants (Nicholas et al., 2009). *Pachycarpus* sp. nov. is a recently discovered species still in the process of formal description (M. Glenn, J. Lamb, A. Nicholas and A. Shuttleworth, unpubl. data), but is currently known from only a single locality and must also be considered threatened.

The pollination systems of five of these plant species have been examined in previous studies and shown to be operated primarily by the chafers *A. tigrina*, *C. marginalis* and *Leucoscelis* spp. (Scarabaeidae: Cetoniinae; Ollerton et al., 2003; Shuttleworth and Johnson, 2009a). The pollination system of *Asclepias albens* has not been examined in detail, but *A. tigrina* beetles have frequently been observed visiting these flowers and we have collected individuals of this beetle species carrying considerable numbers of *A. albens* pollinaria (unpubl. data). The pollination system of *Pachycarpus plicatus* is also unverified, but morphological similarities between this species and the beetle-pollinated *P. concolor* (such as a bowl shaped corolla and flattened gynostegial column with widely spaced anther wings) suggest that it is also adapted for pollination by chafer beetles. Voucher specimens of the study species are deposited in the Bews Herbarium (University of KwaZulu-Natal, Pietermaritzburg).

2.2. Floral scent collection, GC–MS analysis and comparison of fragrance data between species

Scent samples were collected between October and December 2007 at six sites in KwaZulu-Natal, South Africa (Table 1). Floral scent was collected using dynamic headspace sorption methods by enclosing individual inflorescences in polyacetate bags (Kalle, Germany) and pumping air from the bags through

Table 1
Pollinators and sampling details of floral scent collection for the study species.

Species	Pollinators		Scent sampling and plant localities					
	Principal pollinator	Source[a]	*n*	Sample duration min[b]	Sample date[b]	Locality[c]	Co-ordinates	Altitude (m.a.s.l.)
Asclepias albens (E.Mey.) Schltr.	*Atrichelaphinis tigrina* suspected	3	6	20	24 Oct 2007	VCNR	30°16′06.5″S; 30°37′14.5″E.	447
A. woodii (Schltr.) Schltr.	*Atrichelaphinis tigrina, Cyrtothyrea marginalis*	1	6	25 (1–3), 80 (4–5)	13 Nov 2007 (1–3), 26 Nov 2007 (4–5)	MNR	29°32′15.8″S; 30°10′13.1″E.	1088
Pachycarpus concolor E.Mey.	*Atrichelaphinis tigrina*	2	7	25 (1–3), 60 (4–6), 80 (7)	13 Nov 2007 (1–3), 23 Nov 2007 (4–6), 26 Nov 2007 (7)	MNR	29°32′15.8″S; 30°10′13.1″E.	1088
P. plicatus N.E.Br.	Unknown	–	5	60	1 Dec 2007	MCNR	30°29′58.2″S; 29°25′12.3″E.	1455
P. scaber (Harv.) N.E.Br.	*Cyrtothyrea marginalis, Leucoscelis* spp.	2	5	20	1 Nov 2007	B	29°45′13.3″S; 30°21′29.9″E.	810
Pachycarpus sp. nov.	*Atrichelaphinis tigrina*	2	5	30	3 Dec 2007	H	30°16′10.3″S; 30°12′09.3″E.	976
Xysmalobium involucratum (E.Mey.) Decne.	*Atrichelaphinis tigrina, C. marginalis*	1	5	20	29 Oct 2007	WF	29°36′35.9″S; 30°07′59.4″E.	1350
A. woodii X *P. concolor* hybrid	–	–	1	25	13 Nov 2007	MNR	29°32′15.8″S; 30°10′13.1″E.	1088

[a] 1 = Ollerton et al. (2003); 2 = Shuttleworth and Johnson (2009a); 3 = Pers. obs.
[b] Numbers in parentheses refer to the sample number.
[c] B = Baynesfield; H = Highflats; MCNR = Mount Currie Nature Reserve, Kokstad; MNR = Midmar Nature Reserve, Howick; VCNR = Vernon Crookes Nature Reserve, Umzinto; WF = Wahroonga Farm.

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