Biochemical Systematics and Ecology 66 (2016) 33–36

Contents lists available at ScienceDirect

Biochemical Systematics and Ecology

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

Chemical evidence for hybridity in *Drosera* (Droseraceae)

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ARTICLE INFO

Article history:
Received 15 December 2015
Received in revised form 20 January 2016
Accepted 5 March 2016
Available online 17 March 2016

Keywords:
Chemotaxonomy
Drosera
Hybrids
Naphthoquinones

ABSTRACT

Naphthoquinone patterns found in *Drosera* hybrids between quinone-heterogenous parent species are reported here for the first time. Quinone patterns are constant in and characteristic for all taxa investigated. Each investigated parent species contains only one quinone isomer (either plumbagin or 7-methyljuglone), whereas all investigated hybrids between quinone-heterogenous parent species contain both isomers at almost equal concentrations, which indicates co-dominant heredity resulting from expression of both parental loci affecting regioselectivity in the biosynthesis of these acetogenic metabolites. This allows predictions on hybridity (and possibly on parentage) in some taxa of the genus.

1. Introduction

It has long been known that the genus *Drosera*, together with the family (*Droseraceae*) and the order containing it, *Nepenthales* (= "non-core *Caryophyllales*" *sensu* APG III, 2009), are characterized by the frequent presence of acetogenic naphthoquinones (Hegnauer, 1969, 1990; Schlauer, 1997). This is in contrast to *Caryophyllales* ("core *Caryophyllales*"), in which *Nepenthales* are frequently included (APG III, 2009; Chase and Reveal, 2009), but that are devoid of these metabolites and that frequently contain betalains instead. *Drosera* is one of the few genera from which both regioisomers plumbagin (5-hydroxy-2-methyl-1,4-naphthoquinone, 2-methyljuglone, **1**, CAS No. 481-42-5) and 7-methyljuglone (5-hydroxy-7-methyl-1,4-naphthoquinone, ramentaceone, **2**, CAS No. 14787-38-3) are known Fig. 1.

Both have also been reported from the genus *Nepenthes* of *Nepenthaceae* (Schlauer et al., 2005), which are consecutive sister to *Droseraceae* (Meimberg et al., 2000) and from the more distantly related family *Ebenaceae* of the asterid order *Ericales* (Hegnauer, 1989). While in the latter cases both isomers are frequently found in the same plant, their distribution in *Drosera* is more strictly limited to certain species, and for most species only one (main) quinone is characteristic (Culham and Gornall, 1994): Sometimes the quinone pattern reflects phylogenetic relationship, as *e.g.* in the almost exclusively Australian *Drosera* subgenus *Ergaleium*, that is composed of sections (*e.g.* the "tuberous sundews" and *Drosera binata*) typically containing **1** (and not **2**) and of sections devoid of any of the two isomers (*e.g.* the "pygmy sundews"). In *Drosera* subgenus *Drosera*, that accounts for most of the species occurring outside Australia (and for only very few in Australia), mutual exclusivity of the two quinone isomers has been found in the vast majority of species. Natural hybrids are known between some quinone-heterogenous species, and this is the first report on their chemical constituents.

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http://dx.doi.org/10.1016/j.bse.2016.03.005
0305-1978/

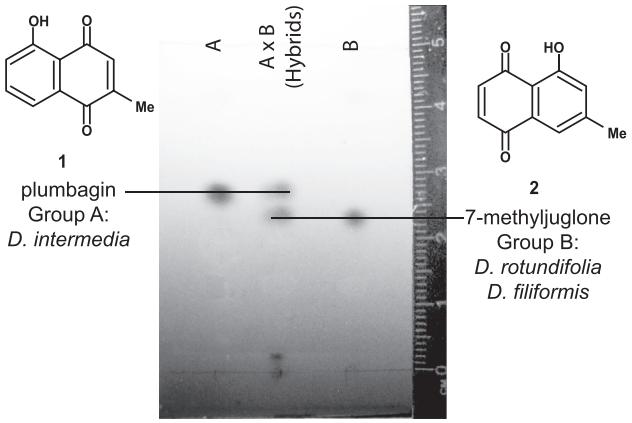

Fig. 1. Chemical structures of plumbagin (**1**) and 7-methyljuglone (**2**) and representative TLC of extracts from quinone-heterogenous *Drosera* species and their respective hybrids.

2. Material and methods

2.1. Hybrids between Drosera species producing different naphthoquinone isomers

2.1.1. Drosera intermedia × rotundifolia

Drosera intermedia Hayne and *Drosera rotundifolia* L. are two of the globally most widespread species in the genus, and both are distributed through eastern North America and Europe, *D. intermedia* crossing the Caribbean and reaching eastern South America, while the range of *D. rotundifolia* is almost circumboreal with a few additional stations in tropical East Asia. Despite this wide distribution, early comparative investigations of quinones in both species were flawed by considerable confusion. A report of **1** from *D. intermedia* (Zenk et al., 1969) was attributed to the ambiguous name *Drosera longifolia* L. (that is more commonly synonymized with *Drosera anglica* Huds., a different species which does not contain **1**, but **2**). Even more surprisingly, *D. rotundifolia* was reported (Durand and Zenk, 1974) to contain **1**, while all later investigations of material from America, Europe and Asia yielded predominantly or exclusively **2**. The hybrid between *D. intermedia* and *D. rotundifolia*, *D.* × *belezeana* E.G.Camus, was reported from Britain (Pearman and Rumsey, 2004), Germany (Marabini, 2014) and the eastern United States (Kaelin, 2014). Whether the hybrid also occurs in Canada (USDA, 2015) or not could not be established with certainty yet. Anyway, all available evidence indicates the hybrid is very rare compared to the global range of overlap of both parent species. In all instances the hybrid shows clear indications of reduced fertility, and no offspring from seed is known in naturally occurring populations.

Morphological characteristics used for identification (Pearman and Rumsey, 2004): Leaf shape is most like that of *D. rotundifolia* but with a more cuneate base, more abruptly contracted to the petiole than in either *D. intermedia*, or *D. anglica* (a frequently co-occurring species). The hybrid has inherited the laterally produced peduncle from its *D. intermedia* parent. The abortive seeds of *D. intermedia* × *rotundifolia* have a faintly tuberculate surface reflecting the papillose surface of its *D. intermedia* parent as opposed to the reticulate surface of *D. anglica* (and *D. rotundifolia*).

2.1.2. Drosera intermedia × filiformis

Drosera filiformis Raf. is an eastern North American species, and throughout its range it frequently co-occurs with *D. intermedia*. *D. filiformis* contains **2** (Zenk et al., 1969; Culham and Gornall, 1994). The hybrid between *D. filiformis* and *D. intermedia*, *D.* × *hybrida* Macfarl. was hitherto discovered at only few localities, all in disturbed habitats of the Pine Barrens of southern New Jersey, USA (Brittnacher, 2011). No generative reproduction has been observed in these populations, either.

Morphological characteristics used for identification (Macfarlane, 1899): The summer leaves of *D. intermedia* × *filiformis* are on the average 90 mm (27 mm in *D. filiformis*, 40 mm in *D. intermedia*) long, of which 25 mm (13 mm in *D. filiformis*, 35 mm in *D. intermedia*) may be petiole. Numerous multicellular, branched hairs occur at the leaf base, but they are considerably shorter and less branched than in *D. filiformis* and more numerous and longer than in *D. intermedia*, where they are unbranched or only very slightly branched. The peduncles are produced laterally as in *D. intermedia*. The ovules and seeds of both parents mature well, those of the hybrid remain small and in most instances develop as empty or nearly empty shells.

2.2. Material investigated

Voucher specimens of all investigated hybrids were deposited at the Herbarium of the Botanische Staatssammlung (M), Munich, Germany. Plants of *D. intermedia* × *rotundifolia* vegetatively derived from naturally occurring populations in Germany (Schlauer *3349*), Britain (Schlauer *3350*) and the United States (Schlauer *3351*) and of *D. intermedia* × *filiformis*