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Pollination ecology and hybridization between *Narcissus cavanillesii* A. Barra & G. Lopéz and *N. serotinus* L. in Portugal

Abstract

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Pollinator activity can have a major effect on the reproductive success of plant species, not only assuring their survival but also influencing gene flow and hybridization between species. *N. cavanillesii* is considered a threatened species in Portugal with only two reported populations, forming highly-fragmented, isolated patches. This autumnal flowering species develops small yellow flowers with a short perianth tube and an inconspicuous corona, allowing total exposure of the sexual structures. Although *N. cavanillesii* is self-compatible and self-pollinated, cross-pollination processes are favoured and necessary to promote higher fruit set (50%). *N. serotinus* is distributed along the Mediterranean coast and in Portugal is considered a common species. Its fragrant flowers are white and have a very short yellow corona and a long, narrow perianth tube that hides the sexual organs. Self-pollination processes are favoured, although this species can also set fruits by cross-pollination. Floral visitors are necessary to promote self-crossings. *N. serotinus* has an average fruit set of about 70%. In Portugal, these two species are sympatric and their flowering periods overlap. Artificial crossings revealed weak reproductive barriers that do not prevent interspecific crosses especially when *N. cavanillesii* is the receptor species. However, in natural conditions, hybridization events are reduced by the activity of different pollinators. *N. cavanillesii* flowers are mainly visited by the hymnoptera, *Halictus* sp., while *N. serotinus* is mostly visited by the coleoptera, *Meligethes* sp. Only the hymenoptera, *Megachile* sp. is common to both species, but less than 3% of the visits are shared between these two species. The present study shows that these two co-generic species, which are well-adapted to the same environment, have developed divergent reproductive strategies, minimizing pollinator competition and assuring survival outside the main Mediterranean flowering season.

Introduction

The genus *Narcissus* L. (*Amaryllidaceae*) is one of the most recognized insect-pollinated genera. It is geographically concentrated in the Mediterranean region, particularly in the Iberian Peninsula where it reaches its highest diversity (Barrett & al. 1996). Species taxonomy and circumscriptions vary widely and thus, there is little agreement on the number of species within the genus. Estimates range from 16-150 species (reviewed in Blanchard 1990), but most authors accept 35-70 species, divided between 2 subgenera and 10 sections

(Fernandes 1968; Barrett & al. 1996). A recent work using modern phylogenetic approaches has helped resolve systematic relationships in *Narcissus* (Graham & Barrett 2004).

Narcissus is one of the most important genus used in horticulture with more than 20000 registered names representing over a century of breeding efforts (Barrett & al. 1996). Yet, the floral biology and breeding systems of most *Narcissus* species are unknown. There is also little information concerning pollination ecology, although most species have showy flowers, some of which are highly scented (Dobson & al. 1997). Pollinators are mainly referred to as bees in *N. longispathus* (Herrera 1995), *N. triandus* and *N. pallidulus* (Barrett & al. 1997); hawkmoths in *N. assoanus* (Baker & al. 2000), *N. dubius* (Worley & al. 2000), *N. papyraceus* (Arroyo & al. 2002), *N. rupicola* (Pérez & al. 2003) and *N. tazetta* (Arroyo & Dafni 1995); and diurnal moths and pierid butterflies in *N. watieri* (Pérez & al. 2003). However, different populations of the same species can have different floral visitors, as in *N. tazetta* whose lowland marsh populations are mainly pollinated by a hawkmoth and whose hill populations are visited by a syrphid and some solitary bees (Arroyo & Dafni 1995).

Most species have white (e.g. *N. papyraceus*), pale yellow (e.g. *N. triandus*) or deep yellow flowers (e.g. *N. fernandesii*), except the deep green *N. viridiflorus*, which is thought to be pollinated by crepuscular moths (Vogel & Müller Doblies 1975). Most species flower in late winter or spring but five species flower in autumn: *N. broussonetti*, *N. cavanillesii*, *N. elegans*, *N. serotinus* and *N. viridiflorus*.

In Portugal there are seventeen recognized *Narcissus* species occurring in diverse areas which range from open sites, Mediterranean scrub communities and low elevation marshes or river banks to rocky hillsides and high mountains. Only two flower in autumn: *N. cavanillesii* and *N. serotinus*. Information on the insect pollinators of these species is scarce (for *N. serotinus* see Pérez Chiscano 1985). The present study aims to clarify the relationship between these two species with regard to flower attraction, breeding system and pollinator behavior.

Species

Narcissus cavanillesii A. Barra & G. López is a small geophyte of 4-15 cm height with one or two leaves that are not present in flowering bulbs. It normally produces one single flower and the corolla comprises six bright yellow perianth segments. The flower does not present the typical morphology of a *Narcissus* species, which normally has a long floral tube and a highly exuberant corona. *N. cavanillesii* has a very short floral tube (less than 2 mm) and an inconspicuous corona which are normally very difficult to see. This may explain why this species has only recently been accepted within the genus *Narcissus*. This morphology allows an open corolla and total exposure of sexual organs. The fruit is a small ellipsoidal capsule that releases the seeds by three longitudinal splits, when the pericarp is dry.

The species is restricted to the SE Iberian Peninsula, Algeria and Morocco and is listed under Annexes II and IV of the Habitats Directive of the European Union (CEE 92/43). In Portugal there are only two known localities (Ajuda and Montes Juntos) both reported in the Alentejo region (Malato-Beliz 1977; Rosselló-Graell & al. 2003). This species is considered Critically Endangered in Portugal according to IUCN categories due to its low area of occupancy, population size and fragmentation (Rosselló-Graell & al. 2003a). The recent construction of the Alqueva dam has also affected these two populations (Rosselló-Graell & al. 2002).

Narcissus serotinus L. presents white solitary flowers (8-25 cm height) which are highly scented even at night. Like *N. cavanillesii*, leaves are not present in flowering individuals. Flowers are erect and comprise a long, narrow floral tube that hides the internal structures, a yellow corona under 2 mm and six perianth segments. Like its congener, it has an actinomorphic structure with six stamens, located in two whorls. The upper stamens are higher or at the same height as the style but rarely exceed the floral tube. The lower stamens are shorter than the style and the nectaries are located above them. Contrary to *N. cavanillesii*, the floral tube of *N. serotinus* hides the sexual structures.

N. serotinus is considered a widespread species throughout the Mediterranean basin, distributed from Portugal to Turkey. In Portugal, this species appears mainly in the Alentejo region and is not considered a threatened species, although the construction of the Alqueva dam has led to a population decrease of 20% in this area.

Data for the present study were collected from 2001-2003 in the Ajuda population where the two species co-exist. In the studied area, *N. serotinus* is more abundant than *N. cavanillesii* (60:20 reproductive individuals, respectively) but has a lower density since *N. cavanillesii* forms denser patches due to higher vegetative reproduction.

Flowering phenology

Both species presented a very short flowering period. In 2001 *N. cavanillesii* started to flower at the end of September reaching its peak from 8 to 12 October and ending on 25 October. Flowering had a mean duration of 32 days. Floral synchrony within species (Albert & al. 2001) had a very low value of about 38%. The reproductive individuals of *N. serotinus* appeared after the flowering peak of *N. cavanillesii*. They flowered for 16 days from 12 October to 1 November. As in *N. cavanillesii*, floral synchrony within species was very low at about 48%, limiting gene flow between plants. The flowering period of the two species overlapped during 15 days allowing gene flow between them.

Floral biology

Flowering span was similar for both species (5.1 *vs* 5.5 days in *N. cavanillesii* and *N. serotinus*, respectively). In *N. cavanillesii* flowers the stigma became receptive one day before pollen was available (protogynia), thereby favoring cross-pollination. In *N. serotinus*, pollen and stigma were functional at the same time facilitating self-pollination. These results are in concordance with the flower morphology of each species. However, contrary to what was expected, the P:O value was lower in *N. cavanillesii* than in *N. serotinus* (mean ± SE respectively 211.80 ± 46.80 *vs* 417.55 ± 115.62).

Breeding system

Both species produce fruits and seeds from self- and cross-pollinations indicating the absence of self-incompatibility systems (Tab. 1). Furthermore, preliminary observations did not find wind to be a pollinator vector, as none of the emasculated seeds set fruit when insect visitation was prevented.

In *N. cavanillesii*, plants covered to prevent insect visits produced capsules with fewer seeds compared to fruits produced by cross-pollination (U=1020, *P*<0.001 and U=1350, *P*<0.01 respectively for insect exclusion and xenogamy; Tab. 1). No significant differences were found between control and xenogamy treatments (U= 1560, *P*=0.142; Tab. 1).

In *N. serotinus*, only 25% of bagged, unmanipulated flowers produced fruit (Tab. 1). However, autogamy increased fruit set to 42% (Tab. 1), which is not significantly different from that of cross-pollinations (U=1500, P=0.067). Thus, although *N. serotinus* is self-compatible, insect activity is important to self-pollination processes. No significant differences were found between control and cross-pollinated plants (U= 1740, P=0.700). Although there is considerable variation in seed production, *N. serotinus* usually produced more seeds per plant than *N. cavanillesii* (16 *vs* 6 respectively).

Floral advertisement

To examine the role of ultraviolet patterns (UV) in flower advertisement, a total of 50 plants from each species were illuminated at night with a UV lamp (365 nm wavelength) and the resulting images were captured using a video camera with a 24-bit definition. The UV photographs show strong pigmentation in *N. serotinus* flowers with all flower segments reflecting UV radiation except in the corona and around the flower tube (Fig. 1). Another important stimulus that attracts insects from a long distance is flower scent (Dobson 1994). Neutral-red staining of flowers of both species showed the location of osmophors in the corona, as observed by Vogel (1962) for *N. jonquilla*. However, in *N. cavanillesii* these structures are not relevant since the corona is inconspicuous.

Table 1. Mean fruit set and standard deviations for flowers of *Narcissus cavanillesii* and *N. serotinus* after different pollination treatments (n=60).

Pollen transfer	*N. cavanillesii*	*N. serotinus*
Control	0.50 ± 0.50	0.68 ± 0.47
Insect exclusion	0.38 ± 0.49	0.25 ± 0.43
Autogamy	0.20 ± 0.40	0.48 ± 0.50
Xenogamy	0.63 ± 0.48	0.65 ± 0.48

Fig. 1. Flowers of *Narcissus cavanillesii* (left) and *N. serotinus* (right) under human visible radiation (above) and ultraviolet radiation, 365 nm (below).

Hybridization experiments

Interspecific pollination experiments conducted between *N. cavanillesii* and *N. serotinus* resulted in fruit set, suggesting a degree of genetic compatibility between these two species. In *N. serotinus* only 12% of the flowers developed fruit when they received pollen from *N. cavanillesii as* compared to 45% when they received their own pollen (U=1200, *P*<0.001). In contrast, almost 45% of *N. cavanillesii* flowers developed fruits, either from the pollen of their own species or from their congener (U=1685, *P*=0.519). Thus, the hybridization process seems to be asymmetric causing a greater impact on endangered *N. cavanillesii*.

Pollinator activity and behavior

N. cavanillesii and *N. serotinus* were visited by a small number of insects. In 2002, most of the visits in *N. cavanillesii* were performed by two Hymenoptera, *Halictus* sp. (83% of recorded pollination visits), followed by *Megachile sp* (10.6%). The remaining visits were performed by two species of Diptera (Syrphydae and Calliphoridae) and one Hymenoptera (Apidae) (Tab. 2). These results are similar to a preliminary list of insect visitors reported in 2000, although the frequency of visits was higher (Rosselló-Graell & al. 2003a). The disturbances in this region, namely the construction of the Alqueva dam and the subsequent work of machinery, may have influenced insect activities.

In *N. serotinus* seven different insect species were attracted to their flowers. The main visitor was the Coleoptera, *Meligethes* sp. (52%), followed by the Syrphidae, *Eristalis pratorum* (21.95%) and the Hymenoptera, *Megachile* sp. (13.75%). The remaining species were mainly butterflies that can be regarded as sporadic pollinators (Table 2). However, in other nearby populations (Badajoz), butterflies like *Macroglossum stellatarum* were once recorded as the main visitors of this plant (Pérez Chiscano 1985).

Floral visitor activity started at 10 a.m., reached a peak between 12 a.m. and 2 p.m., and ended at 4-5 p.m. Visitors were normally only observed on sunny days with weak winds., No nocturnal insect activity was observed in either species. The three flower structures that could attract and be touched by pollinators were the nectaries, the anthers and the stigma.

Table 2. Pollinators observed in *Narcissus cavanillesii* and *N. serotinus*: values in bold the visitor common to both species.

Insects	*N. cavanillesii*		*N. serotinus*	
	% total visits	Time/flower	% total visits	Time/flower
Hymenoptera				
Halictus sp.(Halictidae)	83.3	1-3s	-	-
Lassioglossum sp.(Halictidae)	-	-	7.6	1-8s
Anthopora sp.(Anthophoridae)	-	-	4.8	3-4s
Mechachile sp.(Megachilidae)	**10.6**	**3-4s**	**13.7**	**2-4s**
Ceratina cucurbina (Apidae)	2.0	1-3s		
Diptera				
Episyrphus balteatus (Syrphidae)	2.1	2-4s	-	-
Stomorhina lunata (Caliphoridae)	2.0	2-4s	-	-
Eristalis pratorum (Caliphoridae)	-	-	20.8	1-4s
Coleoptera				
Meligethes sp. (Nitidulidae)	-	-	48.8	52-124s
Lepidoptera				
Pieris rapae (Pieridae)	-	-	2.2	1-3s
Aricia cramera (Lycaenidae)	-	-	2.1	1-4s

The majority of the reported insects sucked the nectar, and the main visitors can be considered effective pollinators. However, the main pollinator in each species seems to follow a different strategy. In *N. cavanillesii*, *Halictus* sp. usually landed on the flower and started to search for nectar. As the nectaries are located at the bottom, it was forced to crawl towards the flower base, rubbing itself around the stigma and the stamens. In this way, the pollen grains adhered to the insect´s head and the dorsal side of its thorax. When it landed on the next flower, the pollen grains were deposited on the stigma..This behaviour favours cross-pollination processes. In contrast, in *N. serotinus* the main visitor is a Coleoptera species, *Meligethes* sp., which behaves as a pollen thief. When gathering pollen, the insect moved between the upper and lower stamens several times. The pollen grains adhered to the thorax and were deposited on the stigma of the same plant by the upward-downward movements of the insect. However, not all the pollen was deposited and thus, when the insect visited another plant, the pollen on its body was placed on the stigma. Cross-pollinations and mainly self-pollinations are favoured by this behaviour. The activity of this pollen thief enables *N. serotinus* to rely on more “specific” and efficient pollination that may contribute to the high fruit development seen in natural conditions.

This study not only detected different insect visitors but also showed different pollination strategies for these two species. However, one insect was common for both species: *Megachile* sp. (Tab. 2). Only 2.49% of the visits were shared between the two *Narcissus* species. The remaining visits were usually constant to one of the two species, limiting natural hybridization processes between them. In fact, the few hybrid individuals in natural conditions are usually found in small clustered, isolated groups. Other nearby geophytes such as *Leucojum autumnale* or *Scilla autumnalis* also seemed to compete for these pollinators but to a lesser degree.

Discussion and Conclusions

Ecological and evolutionary implications

Geophytes are said to have an ecological advantage. The presence of a storage organ allows them to have distinct phases of growth and reproduction (Dafni & al. 1981; Burtt 1970) as well as the possibility of flowering outside the growth season (Shmida & Dafni 1989). Autumnal flowering is a peculiar feature since the autumnal and winter pollination market is scarce and also because these are harsh seasons from an environmental point of view. However, flowering outside the main season (spring) can be an advantage due to lower pollinator competition and improper pollen flow (Shmida & Dafni 1989). Can two sympatric species share this reduced market and still maintain their genetic integrity? The two species studied here occur together in the same region and in similar habitats, their flowering periods overlap and we have direct evidence that artificial cross-pollination between the two species produces viable seeds. The most effective mechanism to maintain their genetic integrity appears to be the activity of different pollinators.

Flower development, morphology and the exposure of rewards (pollen and nectar) all indicate that *N. cavanillesii* is a facultative cross-pollinated species. This is in agreement with our bagging experiment that showed partial dependence on insect pollination for fruit set. *N. cavanillesii* is mainly cross-pollinated by a hymenoptera attracted by the nectar in the bottom of the flower. In *N. serotinus*, a long and narrow tube hides the rewards. This indicates more specific flower visitors like butterflies with long proboscis or small beetles as recorded. On the other hand, more diverse insect species visited *N. serotinus* flowers possibly due to their higher advertisement capability. The flower arrangement in a symmetric, erect pattern provides a large platform where insects can land and a contrasting corona assists in locating the sexual organs. These advertisements are also supported by the presence of pigmentation patterns detected under UV filters in *N. serotinus*.

In any event, the ability to produce fruits and seeds by autonomous self-pollination may reduce the dependence of *Narcissus* on insect pollen vectors. Selfing presumably evolved because of the advantages of reproductive assurance but they are counteracted by the risk of inbreeding depression (Charlesworth & al. 1990; Lloyd 1992). Because autonomous self-pollination is facultative, the option of outcrossing, which improves seed "quality" is still preserved in both species. However, the lower fruit production in *N. cavanillesii* by spontaneous self-pollination means that protogynous mechanisms are partially effective in preventing fertilization. The role of pollinators seems particularly important for the subsistence of this species.

How is species integrity maintained?

The artificial cross-pollination experiment showed that hybridization could occur and negatively affect *N. cavanillesii*. As there are no strong geographic, ecological or compatibility barriers between the two species, the most effective mechanism for limiting pollen flow between *N. cavanillesii* and *N. serotinus* is the pollinator market and pollinator behaviour. The overlapping of their flowering periods also influences interspecific pollen competition. It is important for *N. cavanillesii* to flower earlier than *N. serotinus*, otherwise improper pollen transfer would be more prejudicial for the rare species (Murali & Sumukar 1994). In this 3-year study, the flowering periods of these two species overlapped during approximately 15 days, which seemed to limit (in addition to pollinator activity) important hybridization events. What would happen if environmental conditions changed allowing a total flowering overlap? One possibility is that interspecific gene flow would be quantitatively less efficient than within species gene flow, thus limiting the formation of hybrids. This could allow large populations of the two species to remain distinct even if they came into contact and hybridized. However, if one species is much more abundant than the other, the scarce species may be genetically displaced and absorbed (Rieseberg 1997).

Conservation needs: pollination facilitation or threat to endangered N. cavanillesii?

Several studies provide evidence of positive interactions between plants usually involving physical or resource profits from one species to the other (e.g., Bertness & Callaway 1994; Callaway & al. 2002). Most recently, the influence of shared pollinators has been suggested as an important force in community structure (reviewed in Palmer & al. 2003). Moreover, some authors have sustained the possibility of positive interactions but evidence is still limited to studies where plants with no rewards benefit from the closest rewarding species (Laverty 1992; Johnson & al. 2003). If small populations of *N. cavanillesii* have low reproductive success and coexisting *N. serotinus* facilitates reproduction, then sharing pollinators can be advantageous for these populations. However, absolute reproductive barriers between *N. cavanillesii* and *N. serotinus* do not exist and our results revealed that hybridization patterns could have a negative impact on *N. cavanillesii*. Thus, pollinators seem to play an important role in the reproductive success of *N. cavanillesii* and in preventing widespread hybridization. Furthermore, reduced pollination visits in small populations of *N. cavanillesii* where *N. serotinus* is not present (unpublished data) constitutes a warning of possible declines in pollinator services. These results indicate the importance of pollination ecology studies especially if we want to conserve and restore endangered species or communities.

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