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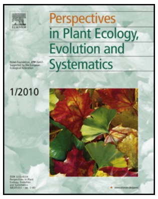

Research article

Disproportionate carbon and water maintenance costs of large corollas in hot Mediterranean ecosystems

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ABSTRACT

Larger corollas increase the reproductive success of entomophilous plants, but are also associated with increased carbon and water costs, especially under hot and dry conditions. Minimizing floral carbon and water loss by reducing corolla size should be potentially advantageous for plants living in these environments. We quantify maintenance costs of corollas (water and carbon) in large-flowered rockroses (*Cistus* spp.) in a Mediterranean ecosystem. We performed field studies of two coflowering sympatric *Cistus* of contrasting corolla size to analyze water costs. Additionally, we used the larger-flowered species (*C. ladanifer*) to analyze the effects of intraspecific variation in corolla size on floral net carbon exchange and transpiration rates. We also assessed the mean daily percentage of plant water and carbon consumed by corollas by comparing with that of leaves at the time of flowering in *C. ladanifer*. Temperature and corolla area increased water maintenance costs, following an allometric relationship where transpiration rate per unit of area increased with corolla area. Larger flowers tended to heat less under strong irradiance than smaller ones in both species, especially in *C. ladanifer*, demonstrating a stronger transpirational cooling effect on larger flowers. In terms of carbon, temperature significantly affected net carbon exchange rates, which were not affected by corolla size. Daily water and carbon expenses of corolla were ca. 50% of those of leaves on an organ surface area basis. Our results suggest that water and carbon maintenance costs of large flowers in the Mediterranean impose significant constraints to corolla size, ecophysiologically favoring smaller-flowered individuals in these ecosystems.

Introduction

Flower size is closely related to pollinator attraction and thus this trait plays a decisive role in the reproductive ecology of entomophilous plants. Larger corollas increase pollen deposition and removal and, as a result, increase both female and male fitness (Stanton et al., 1986; Young and Stanton, 1990; Kudoh and Wigham, 1998; Arista and Ortiz, 2007; Nattero et al., 2010). Accordingly, many studies have documented pollinator-mediated phenotypic selection toward larger corollas (e.g. Galen, 1989; Campbell et al., 1991; Conner and Rush, 1997; Totland, 2001; Nattero et al., 2010). However, since yet small-flowered plants persist in populations, Galen (1999) pointed out that a unilateral view of the evolution of flower size from a pollinator perspective was probably oversimplistic. Advantages associated with pollinator attraction can be offset by increased resource costs. For example, larger corollas are associated with greater requirements of biomass and water for floral development (Galen, 1999; Carroll et al., 2001; Elle and Hare, 2002), as well as with larger demographic costs due to water use under dry conditions (Galen, 2000).

Carbon use during flowering plays a key role in floral attraction and respiratory demands of corollas may consequently be high and even exceed the daily production of photosynthates at the whole plant (Galen et al., 1993; Vemmos and Goldwin, 1994; Lambers et al., 2008). Likewise, water is a limiting essential resource that is needed for the maintenance of corolla turgor and temperature (Galen, 2005). Temperature regulation is especially important in flowers, as thermal optima for processes contributing to sexual reproduction are narrower than optima for growth functions (Lacey, 1996; Erickson and Markhart, 2002; Young et al., 2004). Work on floral temperature has usually focused on thermogenic flowers (reviewed by Seymour, 2010) and flowers in alpine

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and subarctic climates where an increase of floral temperature has a positive effect on the development (Kevan, 1975; Stanton and Galen, 1989; Kudo, 1995; Tsukaya et al., 2002; Galen, 2006). However, floral overheating in hot climates can be damaging so transpirational cooling becomes crucial to minimize it (Patiño and Grace, 2002; Galen, 2005), whereas water shortage in dry environments can lead to an inefficient transpirational cooling. Heat and drought, acting together, can disrupt the normal performance of flowers, affecting both fruit and seed production (Konsens et al., 1991; Galen, 2000; Erickson and Markhart, 2002; Fang et al., 2010).

Mediterranean climates involve high temperatures and water and carbon shortages, imposing constraints in plant reproduction by speeding up development, shortening flowering duration (Larcher, 2000; Thompson, 2005; Aragón et al., 2008) and, occasionally, delaying the initiation of flowering until the rainy season to maximize water use efficiency (Blionis et al., 2001; Verdú et al., 2002). Minimizing floral water loss by reducing corolla size should be potentially advantageous for plants living in these environments (Galen, 2000, 2005; Elle and Hare, 2002; Herrera, 2005). However, many common Mediterranean plants such as rockroses (*Cistus* spp.) do exhibit large corollas. Large flowers in these hot and dry environments may suffer increased respiration and excessive evaporative demand. While there can be stomata on corollas, evidence suggests that there are too few to regulate the corolla temperature by thermoregulation (Galen et al., 1993; Patiño and Grace, 2002; Nobel, 2009). Some large-flowered plants in these and other hot and dry ecosystems show adaptations to prevent overheating and excessive water loss. Nocturnal flowering and pollination are features of several caperbushes (*Capparis* sp.) of semi-arid areas (Rhizopoulou et al., 2006), and most desert large-flowered cacti (Valiente-Banuet et al., 1997; Fleming et al., 2001). Floral cooling mechanisms appeared to be critical for the reproductive success of large convolvulaceous flowers in hot tropical environments (Patiño and Grace, 2002).

In this study we quantify maintenance costs of corollas in terms of water and carbon in large-flowered rockroses (*Cistus* spp.) in a Mediterranean ecosystem. We consider the metabolism of stored photosynthates to support petal respiration to be the main carbon costs of flowers (i.e., a negative net carbon exchange, as in Galen et al., 1993), while in other studies carbon costs of corollas were indirect costs taken as decreased photosynthetic rates of leaves at the whole plant associated to large corollas (Galen et al., 1999; Lambrecht and Dawson, 2007). A direct measurement of carbon maintenance costs of corollas gives us a precise assessment of floral maintenance costs in terms of carbon loss and allows us to compare them and evaluate them in the context of the plant. We expect that in dry Mediterranean ecosystems large corolla size coupled with a high ambient temperature involve significant costs in terms of carbon and water supplies. We hypothesize that large and numerous flowers are highly costly, not only regarding water use, but also, since corollas barely contribute to photosynthesis (Galen et al., 1993; Vemmos and Goldwin, 1994), regarding carbon for the maintenance of respiring tissues.

We performed field studies of two *Cistus* species (Cistaceae) to test our hypotheses. Species of *Cistus* are iteroparous evergreen shrubs and their disc-shaped five-petaled flowers are hermaphrodite and depend on multiple insect pollinators to set fruits (Bosch, 1992; Herrera, 1992; Talavera et al., 1993, 2001). Corolla size is positively related to intraspecific variation in pollinator visit rates, but this is not translated into a differential female fitness in the study species (Talavera et al., 2001; Arista and Ortiz, 2007). Specifically, we chose two coflowering sympatric species of contrasting corolla size, *C. albidus* (smaller) and *C. ladanifer* (larger), as a reference system to analyze water costs. *C. ladanifer*'s flowers are one of the largest in the Mediterranean (Arrington and Kubitzki, 2003), reaching up to approx. 11 cm in diameter (Teixido et al., 2011). Additionally, we used *C. ladanifer* to analyze the effects of intraspecific variation in corolla size on floral transpiration and net carbon exchange rates. High within-individual variation in corolla size in this species (48%: A.L. Teixido, personal observations) creates an opportunity to test whether the physiological costs of large flowers vary not only among species but also among individual flowers within a population and even within an individual plant.

Materials and methods

Study system

C. albidus L. and *C. ladanifer* L. (Cistaceae) are related species with contrasting flower size (mean diameter ± SD: 5.30 ± 0.49 vs 9.19 ± 0.77 cm, respectively, $n = 42$). *C. albidus* is a shrub 40–100 cm tall that inhabits calcareous and dry soils. Flowering phenology spans from February to June and each plant produces purplish-pink flowers in terminal heads pollinated by beetles and bees (Bosch, 1992; Muñoz-Garmendía and Navarro, 1993). *C. ladanifer* is a shrub 100–250 cm tall that inhabits acidic and dry soils. Flowering phenology spans from March to June and each plant produces solitary white flowers often exhibiting dark colored spots at their bases (Muñoz-Garmendía and Navarro, 1993). Flowers are mainly pollinated by bees, beetles and flies (Talavera et al., 1993). Both *C. albidus* and *C. ladanifer* are self-incompatible, but self-pollinated flowers of the former species can set some seeds (Bosch, 1992; Herrera, 1992). Flowers open synchronously each morning within populations and lose their petals in the afternoon.

The study was conducted between April and May of 2011 in the Madrid province, central Spain (39°53′–41°09′ N, 3°03′–4°34′ W). Two different sites were utilized to study floral maintenance costs in terms of water and carbon. Due to volume of work, we could not carry out both measurements at the same site. However, our objective and subsequent results were not affected by this matter since we aimed to evaluate the effects of corolla size and air temperature on floral maintenance costs so we have worked on the very same area and study system (i.e., large flowers under stressful conditions), ensuring that plants and environmental conditions during flowering peak were almost identical. Both differences in floral transpiration rates between coflowering sympatric species and between sunny and cloudy days in *C. ladanifer* were monitored in San Agustín de Guadalix (740 m a.s.l.; 40°41′ N 3°36′ W; hereafter Pop1-transpiration) between April and May. The area is on a limestone and gypsum soil with granitic outcrops and is covered by an open scrubland vegetation on a south facing hilly slope. Climate is dry, with an annual mean precipitation of 567 mm and an annual mean temperature of 13 °C (Ninyerola et al., 2005). Floral net carbon exchange rates in *C. ladanifer* were monitored in Becerril de la Sierra (1120 m a.s.l.; 40°44′ N 3°57′ W; hereafter Pop2-net carbon exchange) in May. This area is on a granite soil covered by sparse trees on a south facing slope. Climate is subhumid, with an annual mean precipitation of 820 mm and an annual mean temperature of 11 °C (Ninyerola et al., 2005). We are aware that conditions at both sites clearly differed but we focused on the main objective of the study: quantifying maintenance costs of corollas in terms of water and carbon in large-flowered species in a Mediterranean environment, independent from the population context.

Microclimate was recorded during the study period at each population to relate it to floral maintenance costs. Microclimatic variables measured were air temperature (°C), air relative humidity (%), soil moisture (%) and solar irradiance (μmol PAR m^{-2} s^{-1}). We also calculated VPD from air temperature and relative humidity. Sensors were used for air temperature and relative humidity