A physiological approach to the ecology and evolution of flowers

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Abstract

For most angiosperms, flowers are critical to reproduction because they increase rates of outcrossing. Flowers are highly variable in numerous traits, including size, shape, and color. Most of this variation is thought to have arisen due to selection by pollinators. Yet, non-pollinator selection is increasingly being recognized as contributing to floral trait evolution. One such non-pollinator agent of selection that often opposes pollinator selection includes the physiological and resource costs of producing and maintaining flowers. Yet, our understanding of the physiological function of flowers remains limited. Here I argue for a comparative, physiological framework for studying flowers and highlight recent work elucidating some of the basic physiological structure-function relationships of flowers and apply an energy balance model to show how two pollination traits (flower size and flower color) can interact with physiological traits. This modeling shows that (1) physiologically meaningful estimates of flower size can be easily gleaned from available floras, (2) the range of flower size most common in the California flora is the range in which complex, non-linear dynamics in flower energy balance occur, and (3) that intraspecific variation in flower color can, by these conservative estimates, cause large (up to 8°C) changes in flower temperature. The strong interaction between pollination traits (flower size and color) and physiological traits (surface conductance to water vapor) suggests that a more unified framework for understanding the evolution of floral form and function would include physiological traits that represent the costs of flower production and maintenance.

Introduction

It is commonly assumed that an organism's phenotype is the result of adaptation. Selection, it is thought, hones the various traits of an organism to best maximize fitness in the ecological context in which the organism thrives. The fundamental challenge facing an organism is, therefore, one of allocation: how to allocate its limited resources in order to maximize survival and reproduction. But simply observing the diversity of plant life makes obvious the fact that there is no single solution to this problem. Allocation even to reproductive structures–whose function is most immediately tied to fitness–can vary, in terms of biomass, from 1-60% among plant species (Bazzaz et al. 1987). One way to reconcile the presumption of maximizing fitness with the obvious diversity of phenotypes has been with optimality models (e.g. Parkhurst and Loucks 1972; Givnish and Vermeij 1976; Ashman and Schoen 1994). These models define cost and benefit functions, which, when solved under varying conditions, yield a variety of optimal solutions. In evolutionary models, the number of equally fit solutions increases and the maximum fitness of any one of them decreases as the number of constraints or selective agents increases (Niklas 1994). Put simply, phenotypic diversity increases as organisms must perform more tasks.

Defining the costs of plant structures for optimality models is inherently a question of physiology–what are the costs of producing and maintaining the structure? The most common currency of cost is carbon, which is a basic component of plant structures and is necessary for respiration. For photosynthetic structures, such as leaves, water is also considered a cost because the diffusion of CO_2 from the atmosphere into the leaf requires that water be evaporated. As a result, optimal leaf size and shape can be predicted for different environmental conditions based on the carbon and water costs of construction and maintenance, the carbon benefits of photosynthesis, and the various environmental factors (light, temperature, humidity) that influence the biochemical pathways inside leaves (Parkhurst and Loucks 1972; Givnish and Vermeij 1976). Thus, the factors that generate phenotypic diversity are those that influence the cost and benefit functions, which are typically in terms of carbon and water.

For flowers, however, benefit functions are defined by ovule fertilization and pollen dissemination (e.g. Ashman and Schoen 1994). Since the recognition and articulation of the role of flowers in plant reproduction over two centuries ago (Sprengel 1793; Sprengel 1996; Vogel 1996), there has, rightfully, been a strong emphasis on characterizing the diversity of floral form and the adaptive value of various floral traits. These studies have elaborated the numerous floral traits that can be involved in pollinator interactions (Kevan and Baker 1983; Fenster et al. 2004), have detailed how different floral morphological traits are associated with different pollinators (e.g. Whittall and Hodges 2007), and have shown how certain combinations of floral characters are likely more advantageous than others (Stebbins 1951a; O'Meara et al. 2016). Yet, the costs of flowers–the resources associated with their production and maintenace (Reekie and Bazzaz 1987a; Reekie and Bazzaz 1987b)–have received notably less attention (Gleason 2018), despite their key role in determining fundamental traits, such as longevity (Ashman and Schoen 1994) and despite the tradeoff between resource investments in reproduction and leaf function (i.e. gas exchange and growth; Bazzaz et al. 1987; Reekie and Bazzaz 1987c; Galen et al. 1999). Furthermore, the maintenance costs of flowers–e.g. rates of respiration–can better predict future reproductive effort than their static production costs (Ashman 1994). Thus, characterizing the adaptive accuracy of flowers for their pollination function may ignore important physiological factors that may also exert substantial influence over floral form and evolution.

Although pollinators are still considered the primary drivers of floral traits (Fenster et al. 2004), over the last few decades the role of resource availability have been increasingly acknowledged as important factors shaping floral traits (Sapir 2017; Sapir and Ghara 2017). Because non-pollinator agents of selection often oppose pollinator selection, there is often a tradeoff between these competing agents (Galen 1999; Strauss and Whittall 2006). Despite the importance of these non-pollinator agents of selection, little effort has been made to fully characterize the physiological costs of flowers and the evolution of traits underlying these costs. While studies focused on one or a few species help to elucidate physiological mechanisms (e.g. Galen et al. 1999; Chapotin et al. 2003; Roddy and Dawson 2012; Teixido and Valladares 2014a; Teixido and Valladares 2015; Roddy et al. 2018), a

comparative, macroevolutionary framework is critical to understanding the long-term, net impacts of variation in floral physiological traits on evolutionary dynamics and to distinguishing the developmentally possible from the selectively advantageous. Furthermore, the climate is changing faster than even the most aggressive models have predicted (Raupach et al. 2007), driving major shifts in phenology (Fitter and Fitter 2002; Parmesan and Yohe 2003) and plant investment in reproduction (Wright and Calderon 2006). These phenological shifts have physiological underpinnings and implications. Understanding the physiology of flowers is, therefore, critical to understanding the causes and consequences of shifting flowering time on plant function and evolution.

Here I have three aims. First, I argue for a more comparative approach to studying floral physiology and show how existing data may be used to address basic but unanswered questions about floral ecology and evolution. Second, I summarize recent research elucidating the physiological traits of flowers, focusing primarily on hydraulic architecture, and layout a series of hypotheses about the evolution of hydraulic structure-function relationships in flowers. Finally, I apply an energy balance modeling approach to show how traits important to pollinator interactions can have physiological implications. My approach here is, by no means, comprehensive; rather, I aim to showcase how a biophysical perspective can elucidate new insight into floral form, function, and evolution.

Towards a comparative physiology of flowers

Since the pioneering studies of Kohlreuter and Sprengel (Sprengel 1793; Sprengel 1996; Vogel 1996), floral biology has been predominated by focused studies on single species or closely related taxa. Broad, macroevolutionary studies of floral trait evolution have focused on highly conserved and/or easily measurable traits (Stebbins 1951a; Sargent 2004; Reyes et al. 2016). The diversity and complexity of floral form, the difficulty of measuring structures as delicate and as ephemeral as flowers, and concerns over homology have all likely precluded efforts of broader, macroevolutionary studies of flowers. While intense, focused studies on single species and closely related taxa remain fundamentally important for experiments, these studies should be complemented by broader analyses of more species and traits.

However, the great diversity of flowers inevitably raises concerns in evolutionary studies about comparisons of non-homologous structures. These concerns about homology are inherently related to developmental homology. Our continued exploration of the genetic mechanisms underlying floral development in new, non-model lineages has required that the elegant ABC model of flower development be ever altered to accommodate the nuances from more lineages (Soltis et al. 2007; Specht and Bartlett 2009). That differentiated corollas have evolved multiples times among the angiosperms (Irish 2009) should not dissuade us from macroevolutionary studies, nor should concerns over homology severely limit what taxa we sample. Planar leaves likely evolved multiple times, but that has not precluded comparisons of traits among these independent origins of leaf form. The diversity of floral development and the numerous times certain floral traits have evolved should be heralded as hallmarks of convergent evolution: while flowers may not be *developmentally* homologous they are, in many ways, *functionally* homologous. That morphologically similar structures have repeatedly evolved could be taken as evidence of their importance but, even more assuredly, should be taken as evidence of the genetic and developmental lability that has allowed the repeated evolution of complex traits. Focusing on the physiological functions of structures can enable new avenues of research, much as it has done in other aspects of the plant sciences.

The field of plant functional biology has, over the last three decades, developed a set of standard protocols for measuring leaf traits–both anatomical and physiological–which has galvanized research on the variation in these traits and led to the development of a conceptual framework describing the evolution of suites of traits (Wright et al. 2004; Reich 2014). While this approach has extended to research on stems and roots (Chave et al. 2009; Roumet et al. 2016), flowers and fruits have remained notably absent from this framework. Ignoring concerns over homology, we should develop a more cohesive framework of what traits may be useful for determining the functional dimensions and tradeoff axes of flowers. From an ecophysiological perspective, traits related to the metabolic currencies–carbon, water, nutrients–are most interesting, as are traits that are directly related to pollination, such as flower size. One immediate source for data on many species are floras, which

commonly contain basic information about floral traits such as color and size. But can data from floras be reliably used to estimate flower size?

I tested the utility of flower size estimates available from floras by comparing measurements of the surface area of flowers to reports of flower size from the regional flora of California (Jepson eFlora, 2015). I measured the two-dimensional, projected surface area of floral perianths on fully expanded flowers of 43 species from 29 families growing at the University of California Botanical Garden. Flowering shoots were excised, the cut shoot surfaces immediately recut underwater, and the shoots transported back to the laboratory where flowers were dissected. The calyx and corolla structures were individually placed on a flatbed scanner, and their areas measured using ImageJ (Rueden et al. 2017), totaled per flower and averaged per species. This provided two potential estimates of flower size: one in which the corolla and calyx structures were summed and one in which only the corolla structures were included (for flowers lacking a differentiated perianth, such as monocots and magnoliids, I included all tepals). For these 43 species, I extracted estimates of flower size from the Jepson eFlora (2015), which were reported as either petal length or flower diameter and often included a minimum and maximum. Because measurements of flower size were in units of area (i.e. square centimeters), reports from the flora needed to be converted into similar units for comparison. I averaged the minimum and maximum measurements reported in the flora and made two assumptions to convert these estimates into units of area: (1) that flowers are circular, and (2) that the length of a petal was equivalent to the radius of this circle. These assumptions were probably safer for actinomorphic flowers than zygomorphic flowers. I used standard major axis regression (R package "smatr"; Warton et al. 2012) to compare the slopes and intercepts in the relationships between predicted and measured flower size. Flower size estimated from the flora was a strong predictor of actual flower size, for whole flowers ($R^2 = 0.63$, $P < 0.0001$; Figure 1a) and for corollas ($R^2 = 0.65$, $P < 0.0001$; Figure 1b). For neither relationship was the slope significantly different from unity ($P = 0.45$ and $P = 0.69$, respectively), suggesting that with a sufficient number of species, estimates of flower size from floras may be reliable estimates for physiologically meaningful measurements. This result enables mining published floras for data on flower size, a trait that is known to be

176 important to pollination but for which there has been no consistent method for
177 measurement.

178 Centering metabolism in macroevolutionary studies of flowers

179 The origin and early diversification of the flowering plants may not have presaged the
180 grandeur of their future. The first angiosperms were most likely ruderal and adapted to
181 living under the dominant ferns and gymnosperms (Stebbins 1951b; Feild et al. 2004). The
182 many unique traits that have come to characterize the angiosperms either predated the
183 crown group angiosperms or were not all present in their origin (Doyle and Donoghue
184 1986; Sanderson and Donoghue 1994; Crane et al. 1995). Yet the angiosperms rapidly
185 diversified, accumulating novel traits–new reproductive structures, new anatomical
186 features that facilitated higher rates of metabolism–that enabled them to dominate
187 ecosystems globally and further promoted their diversity and dominance (Bond 1989;
188 Crepet and Niklas 2009; Brodribb and Feild 2010; Boer et al. 2012; Simonin and Roddy
189 2018). Traditionally, innovations in floral reproductive traits were thought to have been
190 the primary drivers of angiosperm diversity (Sanderson and Donoghue 1994; Crepet and
191 Niklas 2009), but more recent work has suggested that their ecological dominance–and
192 also possibly their diversity–may be due to factors linked to metabolism (Brodribb and
193 Feild 2010; Boer et al. 2012; Simonin and Roddy 2018). While the earliest angiosperms
194 were likely drought-intolerant with low physiological rates (Feild and Arens 2007; T. S.
195 Feild, D. S. Chatelet, et al. 2009), subsequent lineages rapidly developed smaller, more
196 densely packed cells that allowed unprecedented rates of primary metabolism and
197 expanded their metabolic scope (Simonin and Roddy 2018).

198 Central to this emerging perspective about early angiosperm evolution and subsequent
199 dominance is that the need to supply resources for primary metabolism (photosynthesis) is
200 a main selective agent driving innovation throughout the bauplan. Because the diffusion of
201 CO_2 into the leaf mesophyll requires that stomata on the leaf surface open, the wet internal
202 surfaces of the leaf are exposed to a desiccating atmosphere. In this way CO_2 uptake is
203 mechanistically coupled to the transport of water throughout the leaf such that traits
204 associated with water supply and loss are coordinated (Sack et al. 2003; Brodribb et al.

205 2005; Brodribb et al. 2007; Scoffoni et al. 2016). Given that most flowers assimilate little
206 carbon and need not transport large fluxes of water, does this water balance framework
207 apply to flowers? Early evidence suggests that it does: vein and stomatal densities exhibit
208 similar interspecific correlations among flowers as they do among leaves (Roddy et al.
209 2016; Zhang et al. 2018), and flowers obey the same scaling relationships between
210 hydraulic traits as leaves (Roddy et al. In revision). However, a few key differences exist
211 between leaves and flowers. While ANA grade and magnoliid leaves have lower vein and
212 stomatal densities than most eudicots, ANA grade and magnoliid flowers have higher vein
213 and stomatal densities than monocot and eudicot flowers (Figure 2). The higher rates of
214 metabolism that smaller, more densely packed cells enable (Simonin and Roddy 2018) are
215 likely unneccessary in flowers; flowers have lower vein and stomatal densities and larger
216 cells than their conspecific leaves (Lipayeva 1989; T. S. Feild, David S. Chatelet, et al. 2009;
217 Roddy et al. 2013; Roddy et al. 2016; Zhang et al. 2018), further suggesting that selection
218 on metabolism affects anatomical traits in heterotrophic as well as autotrophic organs. This
219 pattern also suggests that developmental modularity has enabled flower and leaf hydraulic
220 traits to diverge (Berg 1960; Roddy et al. 2013). Whether high vein and stomatal densities
221 in flowers are plesiomorphic, however, remains unclear without estimates of these traits
222 from ancestral lineages.

223 Reducing the abundance of stomata may have been a key physiological innovation with
224 cascading consequences on other floral traits. Relaxed from the need to supply high rates of
225 water to support photosynthesis, flowers could have reduced water loss through their
226 stomata, which would have allowed the densities of veins to be reduced. This transition
227 would have reduced both water and carbon costs of flowers and possibly would have
228 allowed alternative modes of hydration. While *Illicium* (Schisandraceae) and magnoliid
229 flowers are hydrated by the xylem (T. S. Feild, D. S. Chatelet, et al. 2009; T. S. Feild, David S.
230 Chatelet, et al. 2009; Roddy et al. 2018), some have argued based on water potential
231 gradients that eudicot flowers are hydrated by the phloem (Trolinder et al. 1993; Chapotin
232 et al. 2003). Such a transition in the basic plumbing of a flower would have been a critical
233 event in floral evolution, but unequivocal evidence for this pattern remains lacking.

Further, other physiological properties, such as high hydraulic capacitance could generate similar patterns as those considered indicative of phloem-hydration (Roddy et al. 2018).

On an area basis, these transitions in both water and carbon costs seem to have occurred in the common ancestor of monocots and eudicots, although better sampling of these divergences is strongly needed (Figure 2). While reducing stomatal densities would have curtailed maximum transpiration rate, stomata play a critical role in dynamically regulating water loss in leaves and flowers (Roddy et al. 2018). Without stomata, water loss from flowers may be entirely unregulated and controlled by epidermal and cuticular traits. The non-stomatal epidermal conductance of leaves is increasingly being considered an important trait that may influence drought tolerance (Duursma et al. 2019), and some evidence suggests it is linked to flower water balance, as well, because it correlates with vein density and whole-flower hydraulic conductance (K_{flower}; Roddy et al. 2016). If selection has driven reduced water loss from flowers, then the loss of stomata would have drastically reduced maximum transpiration rates and any further selection on reduced water loss may have revealed epidermal and cuticular traits to selection on water balance.

The macroevolutionary patterns in floral hydraulic traits suggest that innovations in floral water balance may have been a key dimension of floral evolution among early angiosperms, but do these dynamics play out over contemporary timescales? Correlations between traits and climate are often taken as strong evidence of natural selection, and within species larger flowers and floral displays occur in wetter habitats (Lambrecht 2013). Because larger flowers can more readily heat up (see discussion below), the disproportionate maintenance costs of large flowers leads them to have shorter longevities (Teixido and Valladares 2014a; Teixido and Valladares 2015), suggesting that physiological traits related to water balance interact with other traits linked to pollination success (Teixido and Valladares 2013; Teixido and Valladares 2014b). Because insect pollinators frequently prefer warmer flowers (Kevan 1975; Dyer et al. 2006), there is likely a tradeoff between the need to prevent overheating and the benefit of being warmer to attract pollinators (Patiño and Grace 2002; Patiño et al. 2002). These early results suggest that the need to maintain water balance may influence key pollination traits and affect floral form and function over both contemporary and historical timescales.

Physiological implications of pollination traits

In cold habitats, flower shape and orientation are under selection to increase the temperature of the flower microenvironment in order to attract pollinators (Kevan 1975; Stanton and Galen 1989; Atamian et al. 2016). In many cases, then, elevated flower temperatures are beneficial, as they also can be involved in the release and dissemination of floral volatiles (Jakobsen and Olsen 1994; Sagae et al. 2008; Schiestl 2015), a component of pollination interactions that likely predates the angiosperms (Terry et al. 2007; Penalver et al. 2012). But flower temperatures cannot exceed critical temperatures that might hinder pollination and seed development, and so there is a tradeoff between elevating temperatures to attract and reward pollinators and maintaining temperatures cool enough to prevent overheating.

For an individual plant, flowers are almost always positioned at the top of the canopy, where air temperature is warmest and humidity lowest. This placement can have important implications on the energy and water balance of flowers because of high solar radiation and exposure to high windspeeds. For example, in seasonally dry tropical forests, most species flower in the dry season, when rainfall and atmospheric humidity are low and air temperature and solar radiation high, creating conditions of high evaporative demand (Wright and Van Schaik 1994; Wright and Calderon 1995; Wright and Calderon 2006). In the understory, conditions are generally thought to be more stable, but even understory flowers can still overheat to temperatures that induce mortality in carpels and pollen (Patiño and Grace 2002).

One way to regulate temperature is through latent heat loss due to the evaporation of water. Leaves transpire substantial amounts of water through their stomata, but the relatively low abundance of stomata on flower petals (Lipayeva 1989; Roddy et al. 2016; Zhang et al. 2018) suggests their ability to regulate water loss and temperature is limited. Yet, stomatal densities and, thus, maximum transpiration rates, have been measured on relatively few species. Furthermore, many traits that influence energy balance (e.g. color, shape) are more variable in flowers than in leaves, suggesting that the dynamics of floral temperature may be more complicated, particularly because of the multiple selective

293 pressures acting on flowers. One first step in understanding these dynamics would be to
294 determine the sensitivity of flower energy balance to variation in traits linked to pollinator
295 preference. The lower vein and stomatal densities of flowers suggest that they have lower
296 rates of transpiration, which would hinder their ability to dissipate energy through latent
297 heat loss. Using energy balance as a framework, I focus here on two flower traits important
298 to pollinator interactions: flower color and flower size.

299 To test the sensitivity of flower energy balance to variation in flower size and flower color, I
300 modeled energy balance using the R package 'tealeaves' (Muir 2019), which enables
301 manipulation of physiological and environmental parameters. Because these models are
302 generally applied only to leaves, there is an implicit assumption that the structure being
303 modeled is planar, and so the temperature modeled is most applicable to a flat petal. In
304 reality, more complex, three-dimensional shapes would cause deviation from the modeled
305 temperatures, most likely by reducing transpiration such that the assumption of a flat petal
306 used in the present analyses would produce lower flower temperatures (T_{flower}) than those
307 measured under natural conditions. In all model runs, I kept constant solar radiation (1000
308 W m^{-2}), air temperature (T_{air}, 25°C), relative humidity (50%), and windspeed (2 m s^{-1}). To
309 examine how flower size and color may interact with water balance to influence T_{flower}, I
310 varied the total surface conductance to water vapor responsible (g_t) for transpiration and
311 latent heat loss by using five values for g_t (5, 10, 25, 50, 100 μmol m^{-2} s^{-1} Pa^{-1}) that span the
312 range of values measured from a phylogenetically diverse set of species (Roddy et al. 2016;
313 Roddy et al. 2018). For flowers lacking stomata, the epidermal conductance is the primary
314 contributor to g_t. Further details about the energy balance calculations (e.g. characteristic
315 dimension, absorptance) are discussed in the relevant sections below. It should be noted
316 that the environmental parameters I held constant in all models (solar radiation, air
317 temperature, relative humidity, and windspeed) all influence the calculated flower
318 temperature (T_{flower}). The modeled T_{flower} results, therefore, reflect the relative effects of the
319 varied parameters (color, size, g_t) and not the absolute temperatures the flowers may
320 experience.

Flower color

In order to be seen and visited by a pollinator, a flower must stand out against the green backdrop of leaves and be distinct from other flowers in the community or from closely related species (Spaethe et al. 2001; Peter and Johnson 2008; Hopkins and Rausher 2012; Muchhala et al. 2014). Differences between pollinators in their ability to see colors can help to drive diversity in flower color, often in association with other morphological traits (Whittall and Hodges 2007), but pollinators are not the only selective agent on flower color. Flower color can also change in response to environmental stress, such as temperature, drought, or ultraviolet light, because plant pigments such as anthocyanins are commonly upregulated in response to stress, and they can be expressed in flowers as well as in leaves (Wettberg et al. 2010). Flower color polymorphisms are often linked to environmental gradients (Dick et al. 2011; Arista et al. 2013; Koski and Ashman 2015), further contributing to the high lability of flower color (Rausher 2008; Smith and Goldberg 2015).

The optical properties of flowers are influenced by a variety of factors, including surface texture (e.g. cell shape and cuticle structure; Whitney et al. 2009), internal structure of the mesophyll (Kooi et al. 2016), which can scatter absorbed light, and the type and distribution of pigments throughout the petal (Kay et al. 1981). These factors that influence floral color profiles can also influence flower energy balance and water relations. The surface texture of petals can have a significant impact on the amount of light–and, by extension, energy–that is reflected or absorbed (Gorton and Vogelmann 1996; Kooi et al. 2015; Vignolini et al. 2015). Epidermal cell structure and cuticle properties directly influence wettability (Taneda et al. 2015), which determines whether water droplets roll off the petal or can be absorbed. Absorption of water through the epidermal surface can be a critical source of water for leaves (Berry et al. 2018), mitigating water potential declines that develop throughout the course of the day by harvesting small amounts of intercepted precipitation that might not otherwise penetrate the soil surface be accessible by the roots. Furthermore, how pigments are distributed in the different tissues would influence light penetration through the petal (Kooi et al. 2016) and where energy is absorbed and

dissipated through evaporation. Darker pigmentation leads to higher absorptance, elevating flower temperature, but latent heat lost to transpiration prevents overheating of the floral microenvironment (Patiño and Grace 2002). Yet, the effects of flower color on energy balance have not been fully explored.

To test for the effects of flower color on energy balance, I measured incoming solar irradiance on a representative sunny day and reflectance and transmittance profiles of white, pink, and red flowers of *Dodecatheon* sp. (Primulaceae) using an Ocean Optics S2000 spectrometer (Ocean Optics, Largo, Florida, USA) with sensitivity between 400 and 900 nm. Absorptance profiles were calculated as the difference between unity and the sum of the reflectance and transmittance profiles. While the white flower had near uniform reflectance and absorptance across the visible waveband, the red and pink flowers had higher absorptance below 650 nm (Figure 3a,b). The red flower had near complete absorptance in the 400-600 nm band. These differences in absorptance were expected to drive differences in temperature. Using a representative spectrum for incoming solar radiation, I calculated a weighted average absorptance as:

$$\overline{A} = \frac{\sum(A \cdot \%E_e)}{\sum(\%E_e)}$$

where A is the absorptance at each wavelength and $\%E_e$ is the intensity of that wavelength scaled to the maximum intensity of the incoming solar radiation. The weighted average absorptances for the white, pink, and red flowers were 0.29%, 26.8%, and 64.2%, respectively. I tested how these differences in absorptance may interact with the total conductance to water vapor by calculating leaf temperature at all combinations of these traits, using the conditions listed above.

Both flower color (absorptance) and g_t had strong effects on T_{flower}. Darker flowers were hotter, but these elevated temperatures were offset by higher g_t (Figure 3c). Varying g_t twenty-fold caused T_{flower} to change about 3.5°C for white flowers, about 5.5°C for pink flowers, and almost 8°C for red flowers. Meanwhile, at a g_t of 100 μmol m^{-2} s^{-1} Pa^{-1}, red flowers were more than 3°C warmer than white flowers, but at a g_t of 5 μmol m^{-2} s^{-1} Pa^{-1}, red flowers were about 7°C warmer than white flowers. The effects of flower color were

most pronounced at low g_t values, in the range of values for many monocots and eudicots (Roddy et al. 2016), suggesting that small changes in stomatal abundance and epidermal conductance can have large impacts on energy balance. It is important to note that these energy balance simulations were run with a windspeed of 2 m s^{-1}, and windspeeds lower than this would lead to higher T_{flower}.

Flower size

Two of the most well studied morphological characteristics of flowers are their size and shape. Flower size can vary at all taxonomic scales, including within individual plants. Flower size is thought to be under strong pollinator selection, particularly for pollinators that use visual cues, with larger flowers attracting more pollinators. But flowers are not universally large, and the complexity of their shape has hindered progress toward understanding the evolution of flower size. Furthermore, flower size can evolve extremely rapidly (Davis et al. 2007). Yet, despite its importance to plant-pollinator interactions, flower size has been absent from macroevolutionary studies of floral traits (Sauquet et al. 2017).

Beyond the structural costs of building a large flower, are there physiological costs and tradeoffs associated with the maintenance of flowers that are driven by variation in flower size? To examine how variation in flower size interacts with g_t to influence T_{flower}, I used the estimates of flower size from the California flora described above to parameterize the range in flower size used in the energy balance model. Most species in the dataset had relatively small flowers, below 20 cm^2 (Figure 4a). To test for the effects of flower size on energy balance, I set absorptance to 0.268, which is equivalent to the pink flower modeled above, and varied flower size in the energy balance model by assuming that the characteristic dimension that represents size in energy balance models was equivalent to flower diameter. I varied this characteristic dimension from 0.5 cm to 12 cm, which represents variation in corolla surface area from approximately 0.2 cm^2 to 113 cm^2, the range observed among the California flora (Figure 4a).

Variation in flower temperature depended primarily on g_t and, secondarily, on flower size for a given flower color (Figure 4b). The effects of a proportional change in g_t were much

larger at lower values of g_t. For example, reducing g_t from 25 to 5 μmol m^{-2} s^{-1} Pa^{-1}, within the range of epidermal conductances reported for monocots and eudicots caused an approximtely 2.5°C increase in T_{flower}. Thus, reducing g_t by reducing stomata can have large and significant impacts, and the proportional reduction of g_t by eliminating a single stoma are even greater among small-flowered species. Above a surface area of approximately 15 cm^2, flower temperature increased for all values of g_t, although the effects were relatively small (less than 0.5°C). However, below approximately 15 cm^2, flower size impacts on T_{flower} were more variable. For very small flowers, increasing flower size decreased T_{flower}, but this effect quickly dissipated such that increasing corolla area up to approximately 15 cm^2 drove increases in T_{flower} by almost 0.5°C. Coincidentally, these large effects of small changes in flower size on T_{flower} occurred in the range of flower sizes that are most common among the species sampled (Figure 2a).

The morphological complexity of flowers complicates more accurate modeling of flower energy balance. For these simulations, I assumed flowers were planar, but many flowers are curved or tubular, both of which would reduce latent heat loss by increasing boundary layer resistance causing an incrase in T_{flower}. Nonetheless, this sensitivity analysis shows that nonlinear dynamics in the energy balance model may be particularly important for small-flowered species, which predominate the Mediterranean-type climate of California.

Conclusions

Despite their ephemerality, flowers are a critical component of the plant life cycle, and their physiology is intimately tied to their performance. While pollinators are likely the primary selective agents acting on flowers, the physiological costs of flower production and maintenance often oppose pollinator selection and, therefore, can directly impact their form and function. Centering metabolism in our study of flowers has begun to yield new insights into the function of flowers. I have shown here that physiological traits and pollination traits can interact in complex ways. These results highlight the need to more fully characterize the diverse tradeoffs between pollination traits and physiological traits and how the interactions between these types of traits influence floral trait disparity and diversity. Furthermore, more rigorous quantification of the physiological costs of flowers

will help to address fundamental questions in floral evolution. Early evidence from macroevolutionary patterns of floral physiological traits suggests that reducing the costs of flowers would have relaxed the strength of non-pollinator selection and allowed floral traits to more rapidly and more closely track pollinator preference. Only by more fully understanding the physiological traits of flowers will we be able to more completely understand the many dimensions of their past and future evolution in response to a changing climate.

Acknowledgments

T.A. Kursar gave me an incredible opportunity and taught me most of the ecophysiological methods I use. I thank N.M. Holbrook for the initial suggestion to work on flowers. T.E. Dawson, D.D. Ackerly, D.D. Baldocchi, P.V.A. Fine, K.A. Simonin, C.R. Brodersen, and S. Mambelli have provided valuable feedback and insight in thinking about plant form, function, and evolution. C.M. Guilliams, T. Lilittham, J. Farmer, V. Wormser, and T. Pham helped with data collection of flower size. J.H. Matthes helped with measurements of floral spectral. K.P. Tu has guided me in thinking about energy balance considerations, among other topics. I thank the organizers of the symposium from which this special issue developed. K. Prats provided valuable feedback on an earlier draft.

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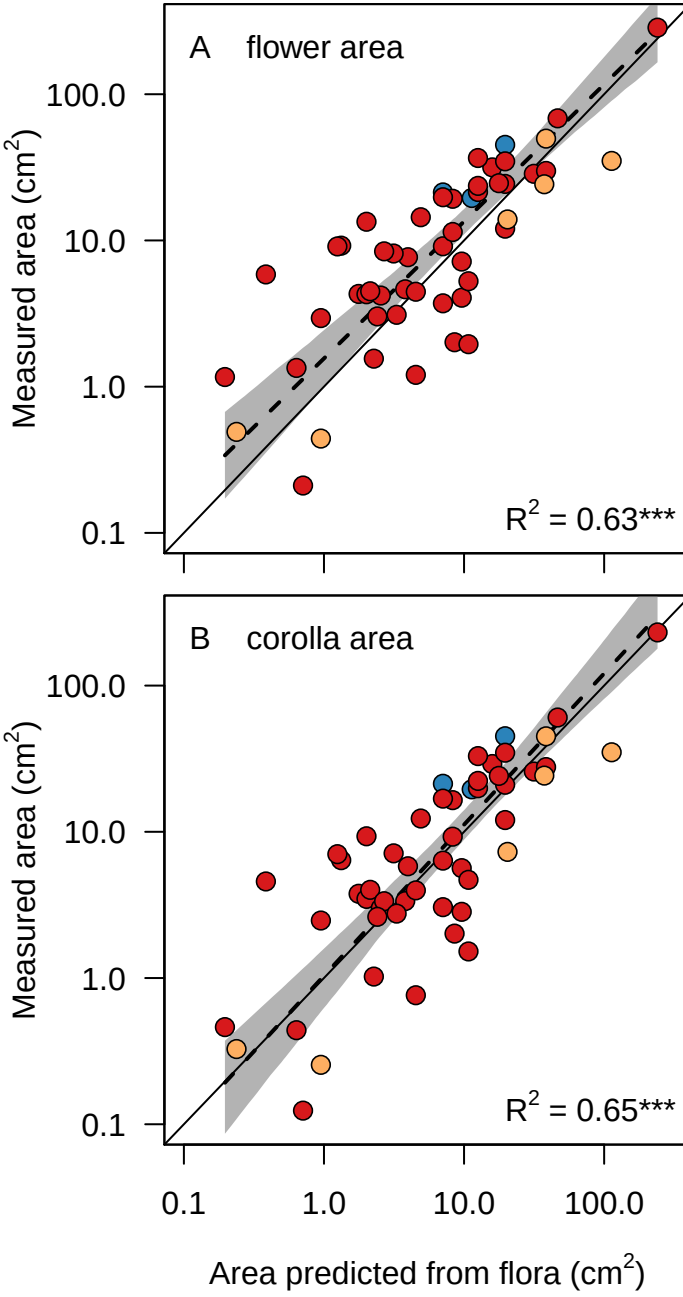
Figure legends

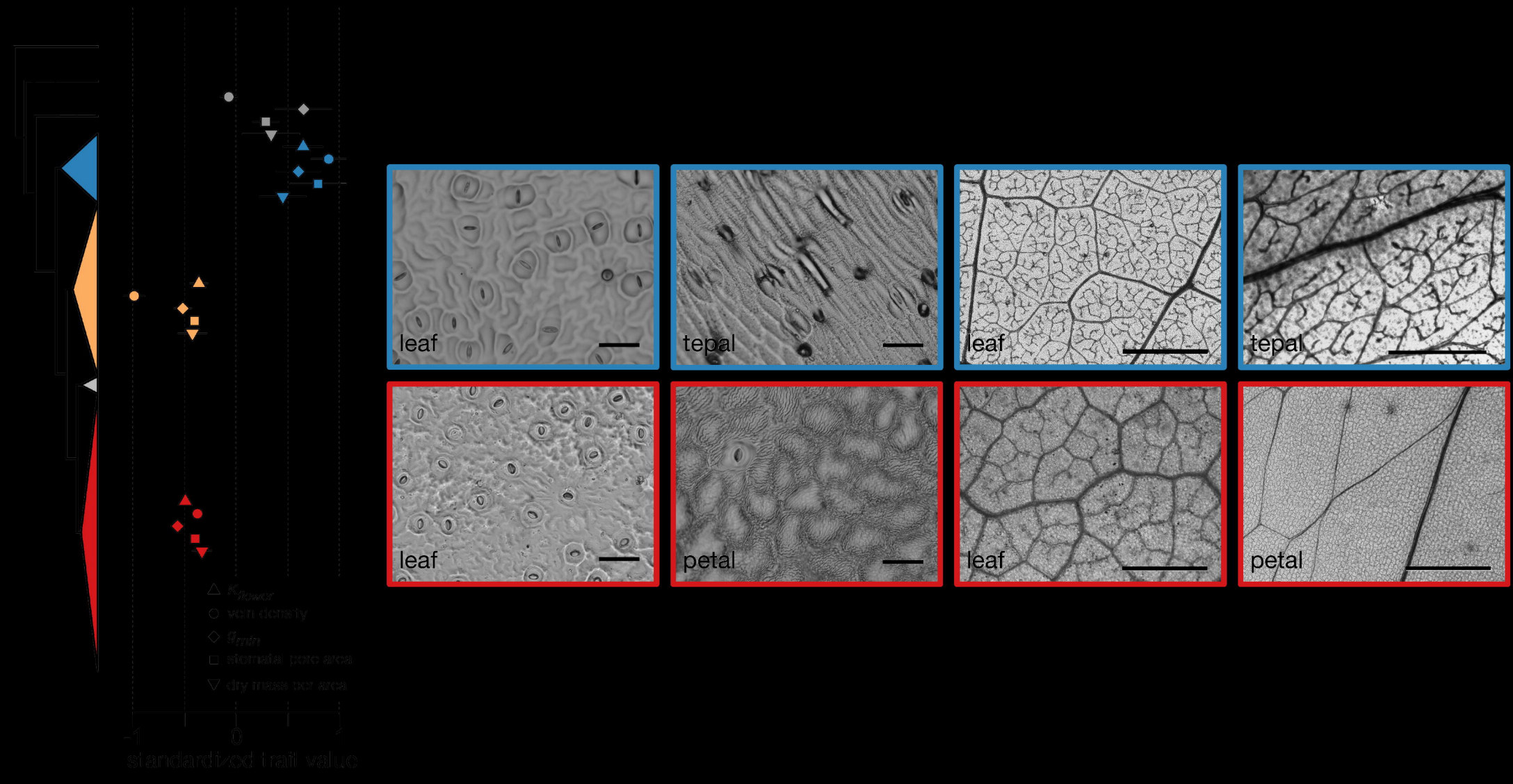
Figure 1. The scaling of measured flower surface area and the surface area predicted from descriptions for 43 species in the California flora. (A) The measured surface area is the total surface area of the calyx and corolla structures. (B) The measured surface area of only the corolla structures. In both figures, point colors correspond to clade membership (blue = magnoliids, orange = monocots, red = eudicots), the solid line is the 1:1 relationship, the dashed line and the grey shading represent the estimated standard major axis regression and its 95% confidence intervals.

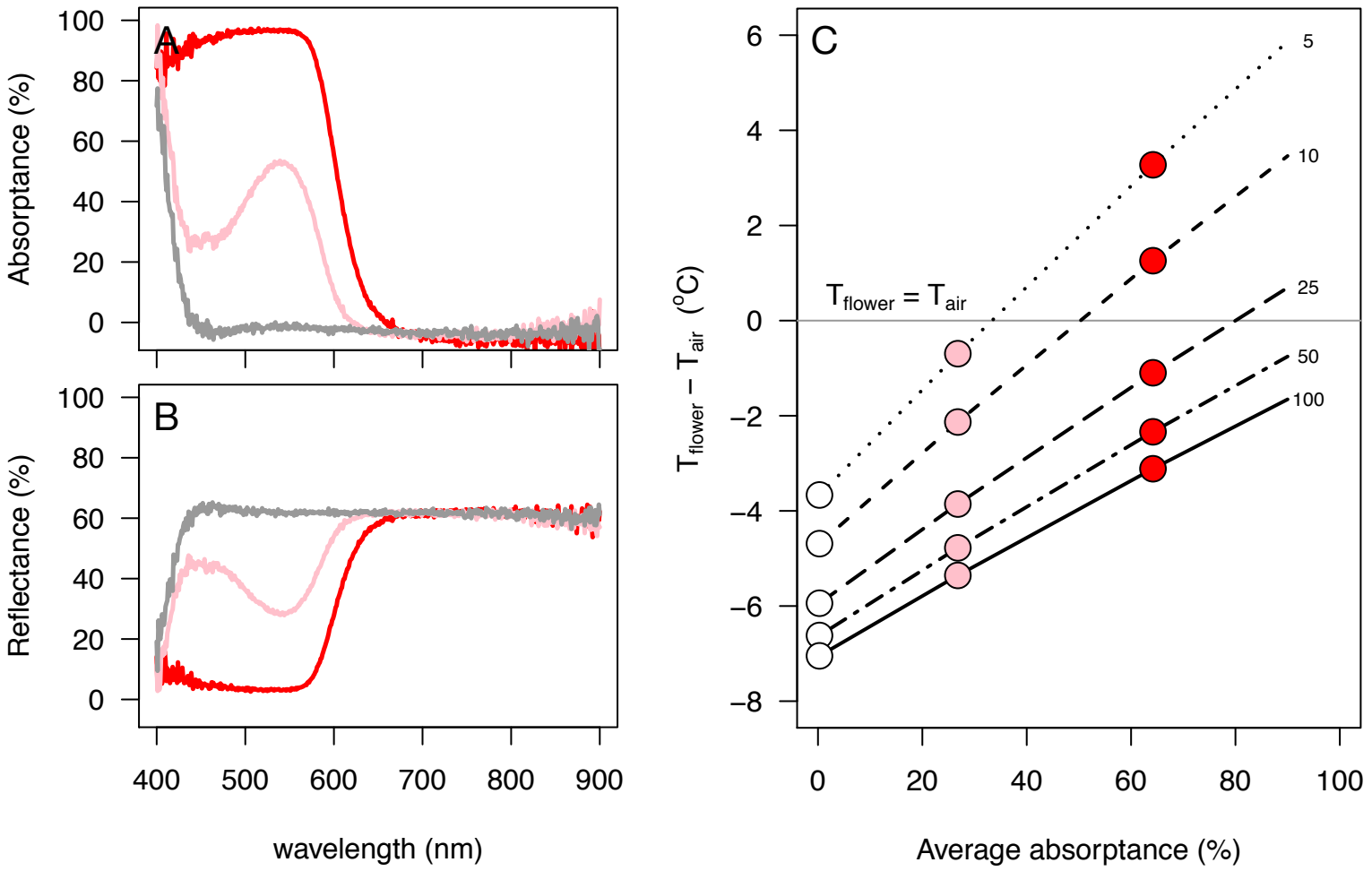
Figure 2. Variation in floral physiological and structural traits among extant angiosperm clades (modified from Roddy et al. (2016) with permission from the publisher). Traits are standardized and include whole-flower hydraulic conductance (K_{flower}), vein density, minimum epidermal conductance to water vapor (g_{min}), stomatal pore area index (a function of stomatal density and stomatal size), and corolla dry mass per projected surface area. Images show stomata (left) and veins (right) for leaves and flowers of two species, (top) *Calycanthus occidentalis* (Calycanthaceae) and (bottom) *Rhododendron davidsonianum* (Ericaceae). Outlines and colors indicate clade affinity (grey = ANA grade, blue = magnoliids, orange = monocots, red = eudicots). Scale bars for images of stomata are 100 μm and for images of veins are 1 mm.

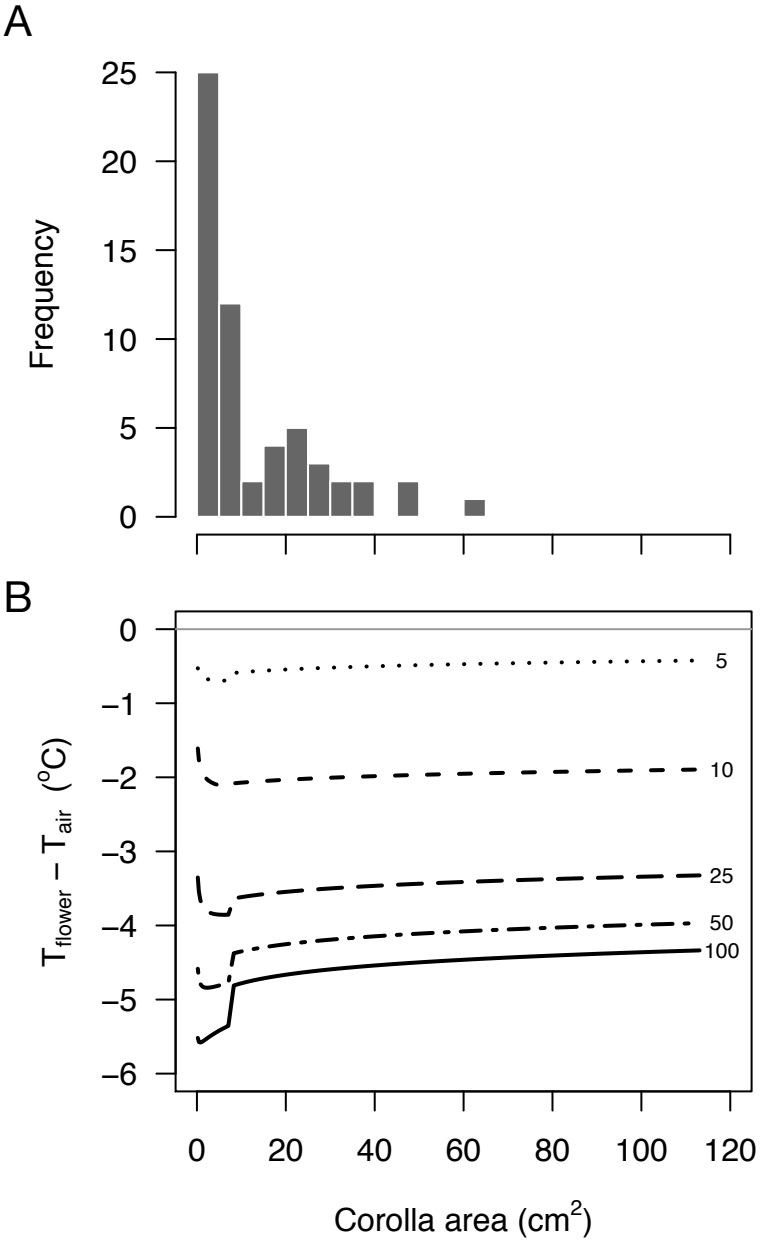
Figure 3. (A) Absorptance and (B) reflectance spectra for three *Dodecatheon* sp. flowers that differ in flower color (grey lines = white flower, pink lines = pink flower, red lines = red flower). (C) The modeled differences between between flower temperature (T_{flower}) and air temperature (T_{air}) as a function of absorptance and the total surface conductance to water vapor (g_t). Numbers indicate the value of the g_t isoclines (5, 10, 25, 50, 100 μmol m^{-2} s^{-1} Pa^{-1}), and colored points represent the values for the three measured flowers.

Figure 4. (A) Histogram of the two-dimensional projected surface area of flowers from the California flora (n = 43 species). (B) The modeled differences between flower temperature (T_{flower}) and air temperature (T_{air}) as a function of flower size and the total surface conductance to water vapor (g_t). Numbers indicate the value of the g_t isoclines (5, 10, 25, 50, 100 μmol m^{-2} s^{-1} Pa^{-1}).


A flower area
B corolla area
Measured area (cm2)
Area predicted from flora (cm2)
0.1
1.0
10.0
100.0
R2 = 0.63***
R2 = 0.65***


κ_{flower}
vein density
g_{min}
stomatal pore area
dry mass per area
-1
0
1
standardized trait value
leaf
tepal
leaf
tepal
leaf
petal
leaf
petal


A
B
C
Absorptance (%)
Reflectance (%)
wavelength (nm)
$T_{flower} - T_{air}$ (°C)
Average absorptance (%)
$T_{flower} = T_{air}$
5
10
25
50
100


A
Frequency
25
20
15
10
5
0
B
$T_{flower} - T_{air}$ (°C)
0
−1
−2
−3
−4
−5
−6
5
10
25
50
100
0
20
40
60
80
100
120
Corolla area (cm^2)