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What the heart wants: adaptive significance of cordate leaf morphology in *Arnica* (Asteraceae)

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ABSTRACT.—Large, thin, horizontally oriented leaves under forest canopies select for an increasingly central petiole insertion point to minimize leaf construction costs for a given leaf area, driving the development of cordate leaf bases. However, whether leaf morphology limits leaf orientation and thus species distributions in shaded forest understories has been studied in few taxa. We studied how the leaf inclination of basal leaves of 2 congeners, heartleaf arnica (*Arnica cordifolia* Hook.), which possesses cordate leaf bases, and broadleaf arnica (*Arnica latifolia* Bong.), which does not, varied along a canopy cover gradient from subalpine forests to meadows in the Greater Yellowstone Ecosystem, Wyoming, United States. Though individuals of both species were found across understory light environments, individuals of heartleaf arnica were capable of reaching lower leaf inclinations than individuals of broadleaf arnica in the shadiest environments, consistent with biomechanical limitations to leaf inclination in leaves lacking cordate bases. Indeed, cordateness (the depth of leaf lobing) in heartleaf arnica increased with greater canopy cover, driving concomitant decreases in petiole-leaf angles. Further ecophysiological study of these and other congeners with conspicuously variable leaf morphology may prove particularly insightful into the adaptive significance of both individual and suites of plant traits.

RESUMEN.—Las hojas grandes, delgadas y con orientación horizontal debajo del dosel arbóreo seleccionan un punto de inserción del pecíolo cada vez más central para minimizar el costo de producción de las hojas de un área foliar determinada, impulsando el desarrollo de bases foliares cordiformes. Sin embargo, se ha estudiado en pocos taxones si la morfología de las hojas limita su orientación y, por lo tanto, la distribución de especies en sotobosque de bosques sombreados. Estudiamos cómo la inclinación de las hojas basales de dos congéneres: el árnica de hoja de corazón (*Arnica cordifolia* Hook.), que posee bases foliares cordiformes, y el árnica de hoja ancha (*Arnica latifolia* Bong.), que no las tiene, varió a lo largo de un gradiente de cobertura de dosel desde bosques subalpinos hasta praderas en el ecosistema del Gran Yellowstone, Wyoming, EE. UU. Si bien se encontraron ejemplares de ambas especies en ambientes luminosos del sotobosque, los ejemplares de árnica de hoja de corazón alcanzaron inclinaciones foliares más bajas que los ejemplares de árnica de hoja ancha en los ambientes más sombreados, lo que es consistente con las limitaciones biomecánicas de la inclinación de las hojas en aquellas que carecen de bases cordiformes. De hecho, la cordatez (la profundidad de los lóbulos de las hojas) en el árnica de hoja de corazón aumentó con una mayor cobertura del dosel, lo que provocó disminuciones simultaneas en los ángulos del pecíolo y la hoja. El estudio ecofisiológico adicional de estos y otros congéneres con morfología foliar notoriamente variable podría revelar la importancia adaptativa de los rasgos individuales y conjuntos de rasgos de plantas.

Leaves, the primary organ for carbon gain in plants, exhibit considerable morphological, physiological, and chemical variation across taxa. Leaf traits vary along environmental gradients and covary with each other, indicating both adaptive significance of and trade-offs among traits (Westoby et al. 2002, Diaz et al. 2016, Wang et al. 2022). Among the best examples of this are the worldwide leaf economics spectrum (Reich et al. 1997, Wright et al. 2004) and "fast" versus "slow" plant traits (Reich 2014), wherein individuals possess a certain suite of traits supporting either rapid resource acquisition or extended resource conservation. However, the fitness advantages of any individual trait are context dependent, with natural selection favoring traits that maximize plant growth rates and reproduction in certain environmental conditions. Plants must then allocate limited resources (i.e., carbon, water, and nutrients) to maximize continued resource acquisition, leading to trade-offs in the construction of different plant tissues (Bloom et al. 1985, Enquist and Niklas 2002).

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Fig. 1. Example leaves from each study species highlighting differences in leaf morphology, namely the cordate leaf base in heartleaf arnica (*Arnica cordifolia* Hook., left), which is absent in broadleaf arnica (*Arnica latifolia* Bong., right).

Light often limits productivity in forest understories, which may favor plant traits that maximize light capture (Chazdon 1986, Givnish 1987, Pearcy et al. 1987, Givnish 1988). Leaf morphology and inclination both vary with light environment. In shade, horizontally oriented, thinner leaves maximize light interception and minimize internal light competition, whereas vertically oriented, thicker leaves in sun maintain lower leaf temperatures and reduce photoinhibition (Givnish 1987, 1988, Björkman and Demmig-Adams 1995, Niinemets 1998, Leach and Givnish 1999, Valladares et al. 2002, Niinemets 2010). Horizontal leaf inclination in shade further selects for a centrally located petiole insertion point to reduce petiole and vein construction costs for a given leaf area (Givnish 1986), driving the evolution of increasingly cordate and eventually peltate leaf morphology. Cordate leaf bases are common in tropical forest lianas (Givnish and Vermeij 1976) and temperate forest vines (Goodwillie et al. 2004) and violets (*Viola* spp.; Givnish 1986, 1987), with peltate leaves present in >350 herbaceous species across 25 orders (Wunnenberg et al. 2021). While individuals may vary their inclination with changes in the light environment, leaf morphology is often phylogenetically conserved (Wyatt and Antonovics 1981, Givnish 1987, Jones et al. 2008, Nicotra et al. 2011), with cordate leaf bases having evolved in some taxa but not congeners (e.g., Givnish 1986, 1987). However, intraspecific (and intraindividual) variation in leaf morphology driven by variability in resource availability (e.g., light; Talbert and Holch 1957, Vogel 1968, Terashima et al. 2001) has been well documented. Despite its apparent importance for light interception, photosynthesis, and thus whole plant carbon gain, tests of the adaptive significance of cordate leaf morphology have been limited to few taxa.

Here, we investigated the potential adaptive significance of cordate leaf morphology in 2 closely related understory herbaceous plant species, heartleaf arnica (*Arnica cordifolia* Hook.) and broadleaf arnica (*Arnica latifolia* Bong.). As their names imply, the basal leaves of heartleaf arnica possess a cordate leaf base, while those of broadleaf arnica do not (Fig. 1). Leaf temperature and water dynamics as they vary with sun and shade have previously been explored in these congeners (Young and Smith 1979), but missing from that analysis was any consideration of variable leaf morphology. The ranges of these species overlap across much of the North American Rocky Mountains, and individuals co-occur locally in lower-montane to subalpine forests and meadows (Wolf and Denford 1984a). This presents a unique opportunity to assess potential limitations of leaf inclination and thus local distribution among congeners driven by leaf morphology. We hypothesized that, owing

TABLE 1. Average (±SE) petiole-leaf angle of and canopy cover experienced by individuals of heartleaf arnica ($n = 25$) and broadleaf arnica ($n = 21$) across subalpine forests and meadows of the Greater Yellowstone Ecosystem, Wyoming, United States.

	Heartleaf arnica	Broadleaf arnica	df	*t*	*P*
Petiole-leaf angle (°)	146.7 ± 0.9	150.8 ± 0.9	44	−0.76	0.45
Canopy cover (%)	41.7 ± 1.1	35.4 ± 1.1	44	0.51	0.61

to cordate leaf bases, individuals of heartleaf arnica would be able to reach more horizontal leaf inclinations and thus persist in shadier environments than individuals of broadleaf arnica do. In contrast, we hypothesized that individuals of broadleaf arnica would be biomechanically limited and unable to reach a horizontal leaf inclination. Finally, among individuals of heartleaf arnica, we hypothesized that cordateness (the depth of leaf lobing) would increase with increasing canopy cover, which would in turn allow for reduced leaf inclinations with increasingly cordate leaves.

To test these hypotheses, we opportunistically sampled individuals of heartleaf and broadleaf arnica in subalpine forests and meadows across the Greater Yellowstone Ecosystem, Wyoming, United States, in July and August 2022. Percent canopy cover above each individual was estimated using a densiometer placed at the level of the leaf surface. To quantify leaf inclination, we photographed individuals from the side (heartleaf, $n = 25$; broadleaf, $n = 21$), ensuring that the angle between the petiole and leaf planes (hereafter petiole-leaf angle) was clearly visible. If the petiole and leaf planes were perfectly perpendicular and the leaf horizontal, the petiole-leaf angle was 90°. As the 2 planes became parallel and leaf inclination became increasingly vertical, the petiole-leaf angle approached 180°. To quantify cordateness, we photographed the surface of basal leaves of heartleaf arnica ($n = 22$). Cordateness was defined as the ratio of total leaf length to midvein length, with cordateness increasing as the petiole insertion point became more centrally located and the proportion of leaf length behind the petiole (i.e., opposite the midvein) increased. Image analysis was done in ImageJ.

Welch's 2-sample *t* tests were used to assess differences in the petiole-leaf angle and canopy cover between heartleaf and broadleaf arnica ($\alpha = 0.05$). Simple linear regression was then used to quantify the direction and strength of the effects of canopy cover on petiole-leaf angle for both species and on cordateness for heartleaf arnica, as well as the direction and strength of the influence of cordateness in heartleaf arnica on leaf inclination. Squared predictor terms were included when data appeared nonlinear and kept only if that term was significant ($\alpha = 0.05$) in the model. All statistical analyses and data visualization were conducted in R version 3.6.3 (R Core Team 2020) using the '*ggplot2*' (Wickham 2016), '*ggpubr*' (Kassambara 2020), '*tidyverse*' (Wickham et al. 2019), and '*stats*' packages (see Supplementary Materials 1, 2).

We found no difference between heartleaf and broadleaf arnica in mean petiole-leaf angle, nor differences in canopy cover between species (Table 1). However, our regression analyses revealed species-specific responses of petiole-leaf angle to canopy cover, with a negative linear relationship for heartleaf arnica ($R^2_{adj} = 0.68$, $F_{1,23} = 51.8$, $P < 0.001$) and a negative nonlinear relationship for broadleaf arnica ($R^2_{adj} = 0.60$, $F_{2,18} = 15.9$, $P < 0.001$), the latter of which reached a minimum petiole-leaf angle and then plateaued (Fig. 2). Cordateness in individuals of heartleaf arnica increased with canopy cover ($R^2_{adj} = 0.28$, $F_{1,20} = 9.357$, $P = 0.01$; Fig. 3), driving decreases in petiole-leaf angle with increasing cordateness ($R^2_{adj} = 0.24$, $F_{1,20} = 7.701$, $P = 0.01$; Fig. 4).

Cordate leaf bases in basal leaves of heartleaf arnica allowed individuals to possess lower leaf inclinations in shadier environments, as cordateness increased and petiole-leaf angle decreased with increasing canopy cover. Further, basal leaves of broadleaf arnica appeared incapable of lowering their leaf inclination beyond a certain point, likely owing to their lack of cordate leaf morphology. Lower leaf inclination in shaded environments should increase light interception and photosynthesis relative to more vertically oriented leaves in the same light environment. However, the lack of a cordate leaf base in basal leaves of broadleaf arnica did not exclude it from shaded environments, suggesting that other mechanisms may allow for coexistence of individuals across variable canopy cover. For example, individuals of broadleaf arnica in

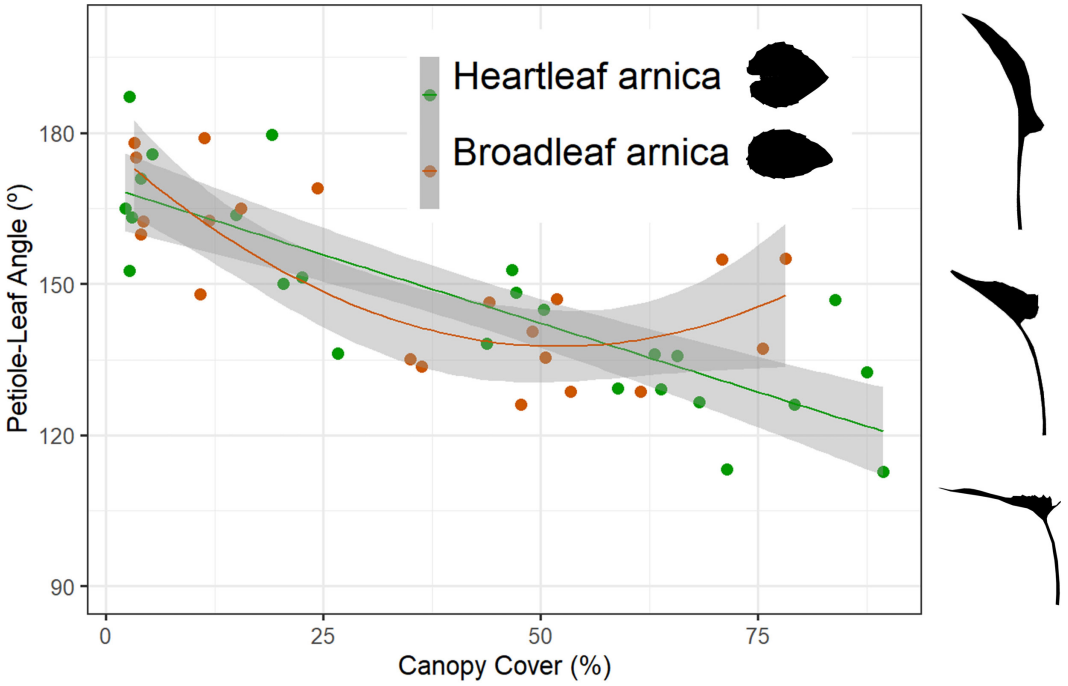

Fig. 2. Petiole-leaf angle across variable canopy cover for basal leaves of heartleaf arnica ($R^2_{adj} = 0.68$, $F_{1,23} = 51.8$, $P < 0.001$) and broadleaf arnica ($R^2_{adj} = 0.60$, $F_{2,18} = 15.9$, $P < 0.001$) from individuals distributed across the Greater Yellowstone Ecosystem, Wyoming, USA.

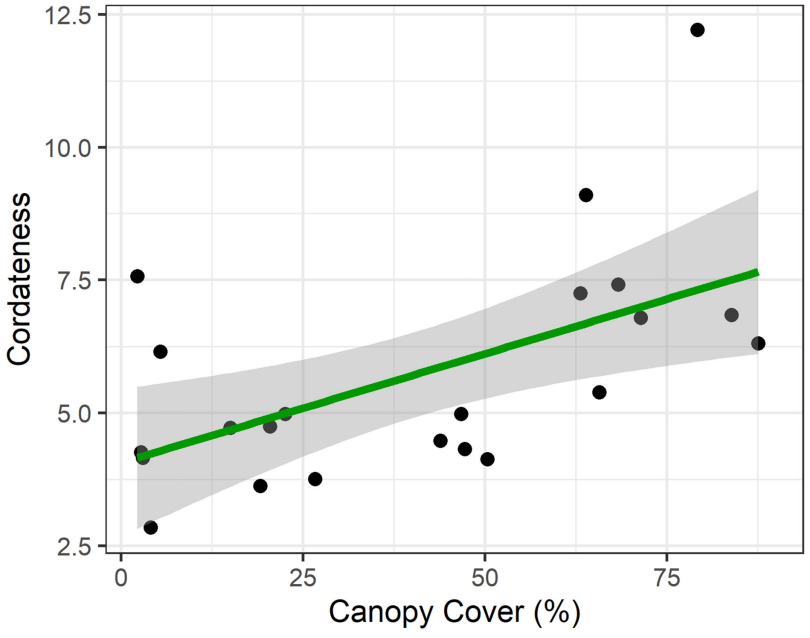

Fig. 3. Cordateness across variable canopy cover ($R^2_{adj} = 0.28$, $F_{1,20} = 9.357$, $P = 0.01$) for basal leaves of heartleaf arnica from individuals distributed across the Greater Yellowstone Ecosystem, Wyoming, USA.

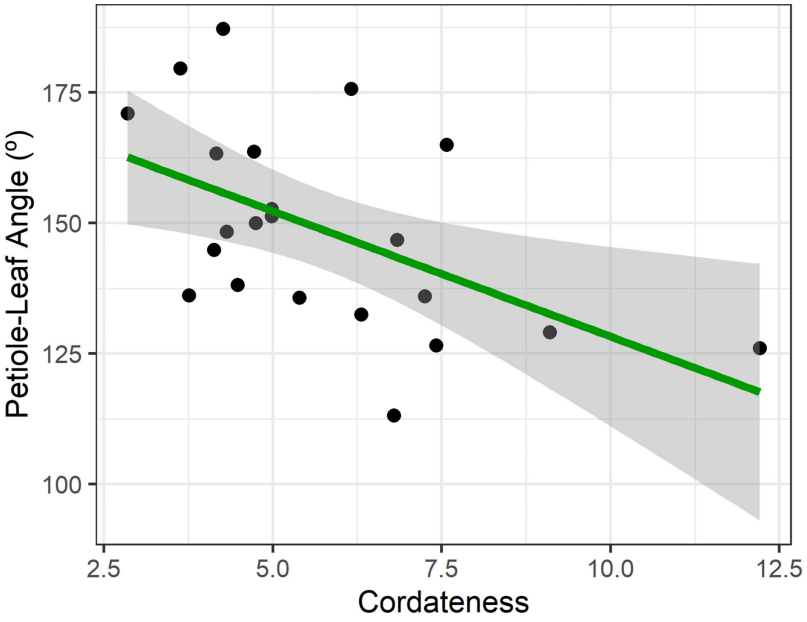

Fig. 4. Petiole-leaf angles across variable cordateness ($R^2_{adj} = 0.24$, $F_{1,20} = 7.701$, $P = 0.01$) for basal leaves of heartleaf arnica from individuals distributed across the Greater Yellowstone Ecosystem, Wyoming, USA.

shade were noticeably tilted at the base (N. Kiel personal observations), potentially compensating for their inability to lessen the petiole-leaf angle and allowing for leaf horizontality comparable to that of individuals of heartleaf arnica.

Our case study informs potential future research directions on these and other closely related species with different leaf morphologies. For example, population sizes for each species across light environments would better capture competitive ability than simple presence or absence. Indeed, heartleaf arnica is very common in subalpine forests but found occasionally in subalpine meadows, whereas broadleaf arnica is common in montane forests but more commonly found in subalpine meadows (Wolf and Denford 1984a), distributions which follow our findings here. However, others have found heartleaf arnica to be more abundant in relatively sunnier, drier understory environments than broadleaf arnica (Young and Smith 1979, Knapp et al. 1989), with individuals of heartleaf arnica in open environments growing nearly 25% larger and producing twice the number of seeds as those from shaded environments (Young 1983). Whether plant mass and seed production in sun compared with shade differ among individuals of broadleaf arnica or among individuals of heartleaf arnica has not been investigated, but such information is necessary to elucidate the relative fitness of each species across light environments.

The presence or absence of a cordate leaf base is but one example of the adaptive significance of variable leaf morphology across environmental gradients. For example, leaf margin, another conspicuous leaf trait, varies latitudinally, with entire, evergreen leaves in trees of the tropics transitioning to toothed or lobed deciduous leaves in temperate forest trees (Bailey and Sinnott 1916). The potential ecological and phylogenetic mechanisms underpinning this trend have been thoroughly explored (e.g., Givnish 1979, Royer and Wilf 2006, Schmerler et al. 2012, Edwards et al. 2016, 2017, Givnish and Kriebel 2017, Zohner et al. 2019), suggesting considerable interest in and value of such comparative studies of leaf morphology. Given their close phylogenetic relationship (Wolf and Denford 1984a, 1984b), unique leaf morphologies (this study, Wolf and Denford 1984a), differences in fine-scale spatial distributions (Young and Smith 1979, Wolf and Denford 1984a, Knapp et al. 1989), and varied physiological responses to sun versus shade (Young and Smith 1980, 1982, 1983, Young 1983), heartleaf

and broadleaf arnica may be an exceptional study system for understanding the evolutionary history and adaptive significance of plant leaf traits.

Supplementary Material

Two online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol84/iss2/9).

Supplementary Material 1. We assessed whether assumptions of selected statistical analyses were met. Each response variable used in Welch's *t* tests and regression modeling were normally distributed (Figs. S1, S2, S3, S4, S5), as were model residuals of each regression model (Figs. S6, S7). Finally, model diagnostics for each regression model revealed no violation of other assumptions (Figs. S8, S9, S10, S11).

Supplementary Material 2. Data on the petiole-leaf angle and cordateness of individuals of *Arnica cordifolia* and *Arnica latifolia* measured across a gradient of canopy cover in subalpine forests of the northern Rocky Mountains, USA.

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