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RESOURCE ALLOCATION TO INFLORESCENCE COMPONENTS IS HIGHLY INTEGRATED DESPITE DIFFERENCES BETWEEN ALLOCATION CURRENCIES AND SITES

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Premise of research. Sex allocation theory considers that, given limited resources, a trade-off must exist between allocations to competing functions, such as accessory and primary sexual organs, or between allocations to primary male and female sexual organs. However, phenotypic and genotypic correlations between floral components have often been found to be positive. A view of resource allocation from a phenotypic-integration perspective could shed light on these apparently paradoxical results. Resource allocation, and not only floral metric traits, can also be significantly integrated because of genetic or developmental constraints or functional contribution to offspring production. We describe the allocation of resources to inflorescence components and assess for the first time whether resources can also be phenotypically integrated in *Tussilago farfara* L. (Asteraceae), a species with inflorescences functioning as pollination units.

Methodology. We studied the absolute and proportional allocation of resources to inflorescence components in terms of dry mass, N, and P as well as their nutrient concentration. We applied indices of phenotypic integration, previously limited to metric traits, to resource allocation at the inflorescence level.

Pivotal results. Irrespective of currency and site differences, (1) scapes were always the inflorescence components receiving the highest allocation, whereas rays received the lowest allocation; and (2) allocation to inflorescence components was phenotypically integrated, ranging from 2.80% to 58.44% of the maximum possible integration.

Conclusions. Integration in terms of resources was similar to or higher than that reported for floral metric traits in other species. The phenotypic integration of resources might result from the fact that most inflorescence components of *T. farfara* may contribute significantly to different functions, such as support, pollen donation, and seed production. The generality of the integration of resources allocated to sexual reproductive components awaits future studies but might help in understanding the usual lack of negative correlations between floral components expected to be linked by trade-offs.

Keywords: Asteraceae, capitulum, phenotypic integration, trade-off, *Tussilago farfara*, sex allocation.

Introduction

Allocation of resources to different floral organs has concerned plant ecologists for a long time, from a sex allocation perspective (Charlesworth and Charlesworth 1981; Lloyd 1984; Charnov and Bull 1986; Sakai 1993, 2000). Sex allocation theory assumes that cosexual plants should allocate resources to floral organs in a way that maximizes individual fitness. Traditionally, a distinction between primary (ovules and stamens) and accessory (sepals, petals, and peduncle) sexual organs has been made (Lloyd 1984, 1987). Sex allocation theory has considered that, given a limited amount of resources, a trade-off must exist between allocations to accessory (e.g., attractive) and primary sexual organs (Charlesworth and Charlesworth 1987), as well as between those to primary male and female sexual organs (Charlesworth and Charlesworth 1981). However, phenotypic (Campbell 1997; Parra-Tabla and Bullock 2000) and genotypic (Ashman 2003; Ashman and Majetic 2006) correlations between allocations to floral organs have often been found to be positive. To further complicate this matter, resource allocation can be estimated using different currencies, such as energy (Bradbury and Hofstra 1976), dry mass, or nutrients (Bazzaz et al. 2000). Although some currencies provide concordant estimates of allocation (Hickman and Pitelka 1975; Méndez and Karlsson 2007), different currencies frequently yield different allocation patterns (Lovett Doust and Harper 1980; Ashman and Baker 1992; Méndez and Traveset 2003).

Inflorescences, and not only flowers, can also be studied from a resource allocation perspective (Méndez 2001; Harder et al. 2004). Inflorescences are not merely an aggregation of flowers. First, inflorescences involve an allocation of resources to accessory support structures, which adds complexity to sex allocation theory predictions (Lloyd 1984, 1987). Second,

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from a functional perspective, inflorescence traits, such as number of flowers, size, and sexual segregation, deeply influence mating performance and therefore are subject to natural and sexual selection (Thomson 1988; Ohara and Higashi 1994; Torices and Méndez 2011). The assessment of resource allocation patterns to the different inflorescence components offers the possibility of understanding the selective pressures on inflorescence traits, particularly when they are functionally integrated and act as pollination units (Méndez 2001). Unfortunately, allocation of resources to different inflorescence components remains understudied (Lovett Doust and Harper 1980; Lovett Doust and Cavers 1982; Méndez 2001).

In both flowers and inflorescences, which consist of a diverse array of structures, resource allocation patterns are unavoidably multivariate and should be described using a covariance matrix. Such matrices are not intuitively interpreted. We suggest that tools from quantitative genetics and from floral biology can be fruitfully utilized in interpreting these complex covariance matrices of resource allocation. First, Flury methods (Arnold and Phillips 1999; Phillips and Arnold 1999) can be utilized to compare the congruence of allocation patterns across sites, genotypes, or currencies. Second, phenotypic-integration measures allow the summarizing of multivariate allocation patterns into a single number expressing how tight the resource allocation is. Phenotypic integration is commonly defined as the phenotypic-correlation structure of multiple characters (Berg 1960; Murren 2002). Therefore, from a methodological perspective, the use of floral-integration tools also offers a convenient, synthetic way to analyze allocation patterns. Until now, the interest in floral integration has focused on metric traits (Pérez-Barrales et al. 2007; Bissell and Diggle 2010). Flowers (or inflorescences) are complex structures consisting of different organs that jointly work for the same aim: offspring production. Application of this framework to resource allocation patterns within flowers or inflorescences seems sensible because they could also be positively correlated and significantly integrated.

In this study, we investigate resource allocation to inflorescence components of the monoecious *Tussilago farfara* L. (Asteraceae), a species with inflorescences (heads) functioning as pollination units. Monoecious heads conveniently allow the unambiguous separation of male and female components in studies of resource allocation. Previous research on this species (Torices and Méndez 2011) showed (1) a positive influence of allocation to male flowers on female reproductive success and (2) different allometric patterns in sexual allocation across sites. Thus, we expect that (1) resource allocation to inflorescence components will be phenotypically integrated and (2) the extent of this integration will be different among populations, indicating a potential adaptive role of resource integration at inflorescence level. This suggests phenotypic integration of resource allocation to inflorescence components but also potential variation in the extent of integration among populations. We addressed the following specific questions: (1) What is the absolute and proportional allocation to each inflorescence component? (2) Is the allocation pattern similar independent of the allocation currency utilized? (3) Is resource allocation integrated at the inflorescence level? and (4) Does integration differ across sites or allocation currencies?

Material and Methods

Species and Study Sites

Tussilago farfara L. (Asteraceae) is a perennial rhizomatous herb that prefers clayey and loamy soils but is also frequent on stony soils. Each ramet bears a rosette of leaves and, in reproductive individuals, one to more than 10 inflorescences. Inflorescences are solitary rayed heads (capitula) on scapes with achlorophyllous scales. Heads produce two kinds of flowers: inner, tubular flowers that are functionally male and four or five rows of outer, female flowers, which have a narrow ray (Nordenstam 2007). The species is mainly visited by Hymenoptera (Wild et al. 2003).

Two populations on roadsides were sampled in northern Spain in 2004: Noreña (universal transverse Mercator coordinates: 30TTP71, 200 m asl) and Saús (30TTP80, 420 m asl). The substrate at Noreña had more gravel and a very low plant cover, with *Salix atrocinerea* and *Viburnum opulus* as dominant species. In Saús, the roadside had a closed canopy of *Acer pseudoplatanus* and an understory with 100% plant cover, dominated by grasses and two forbs: *Primula vulgaris* and *Helleborus viridis*. Floral visitors were scarce in both populations, and only a small bee was observed in our surveys of floral visitors.

Resource Allocation to Inflorescence Components

We studied the absolute and proportional allocation of dry mass, N, and P to, as well as the nutrient concentration of, each inflorescence component. At each site, from January 22 to March 7, 2004, we harvested one inflorescence (head and its scape) approaching anthesis per ramet from 40 different ramets. We sampled inflorescences at least 1.5 m apart to increase the probability of sampling different genets. At the lab, we separated each inflorescence into the following components: scape, receptacle, male flowers, and female flowers. In addition, 50 female flowers per inflorescence were dissected into the ray (attractive function) and the rest of the flower (reproductive function)—hereafter the ovary. All components were oven-dried at 60°C for 48 h and weighed to the nearest 0.1 mg. Total N and P were determined, after micro-Kjeldahl digestion, in a Skalar segmented-flow nutrient auto-analyzer (Skalar Analytics, Breda, Netherlands). We calculated three allocation measures per inflorescence component: (1) absolute allocation, the amount of resources (dry mass, N, or P) allocated to the inflorescence component; (2) proportional allocation, the amount of resources (dry mass, N, or P) allocated to the inflorescence component divided by the total amount of resources allocated to the whole inflorescence; and (3) nutrient concentration, the amount of nutrients (N and P) allocated to the inflorescence component per unit mass (measured in mmol/g).

To test for differences in dry-mass, N, and P allocation among inflorescence components (scape, receptacle, male flowers, ovaries, and rays) and among currencies (dry mass, N, and P), we used generalized estimating equations (GEEs) as implemented in the SAS procedure GENMOD (SAS, ver. 9.1). GEEs allow the exploration of differences in resource allocation among inflorescence components while accounting for the dependence among components coming from the same inflo-

rescence by means of a correlation matrix (Zuur et al. 2009). Furthermore, GEEs share the flexibility of other generalized linear methods, e.g., response variables with distributions other than normal and the incorporation of several predictors in the model (Quinn and Keough 2002). In our models, besides testing for differences in resource allocation to inflorescence structures, we introduced the site and the currency as predictor variables in the model.

Inflorescence components (scape, receptacle, male flowers, ovaries, and rays) were considered as measurements taken on the same inflorescence using the REPEATED statement, taking the inflorescence as the SUBJECT effect and selecting "exchangeable" as the covariance structure (Zuur et al. 2009). Two kinds of models were fitted. First, we jointly included all data from the three currencies to test the main effects of currency on resource allocation to each inflorescence component. In this model, the explanatory variables included were inflorescence component, site, currency, and the interactions site × inflorescence component and currency × inflorescence component. Second, for each currency we assessed the resource allocation to different inflorescence components at each site by building three different models, one per currency, since allocation was currency dependent (see "Results"). In these separate models, the explanatory variables included were inflorescence component, site, and their interaction. To account for the variation in resource acquisition between inflorescences, inflorescence size (measured as total biomass, total N content, or total P content) was added to all models as a covariate.

We assumed normal errors and identity link functions for the three response variables: absolute and proportional allocation and nutrient concentration. We used the TYPE 3 option of PROC GENMOD to analyze the main effects in all the GEEs. This analysis is similar to a type III sum of squares but is more appropriate for unbalanced designs. We studied specific differences between inflorescence components using the DIFF option in the LSMEANS statement of the GENMOD procedure.

Phenotypic Integration of the Allocation to Inflorescence Components

We studied the phenotypic integration of the allocation to each inflorescence component by means of three approaches: (1) the index of phenotypic integration proposed by Wagner (1984); (2) a hierarchical comparison of phenotypic variance-covariance matrices, using the Flury hierarchy (Arnold and Phillips 1999; Phillips and Arnold 1999); and (3) a correlation analysis. First, we studied the magnitude and statistical significance of inflorescence integration, using the eigenvalue variance of its correlation matrix (i.e., integration index, hereafter INT; Wagner 1984; Cheverud et al. 1989). Character correlation matrices for different sites and currencies were based on different numbers of plants, causing the expected eigenvalue variance on the hypothesis of random covariation among characters to vary among data sets (Wagner 1984; Cheverud et al. 1989). Thus, empirical values of INT were corrected by subtracting the site- and currency-specific expected value, which is determined by the number of characters and individuals measured (INTexp = (no. of characters − 1)/no. of plants; Cheverud et al. 1989; Pavlicev et al. 2009). The unbiased INT for each site and currency was considered to reflect significant inflorescence integration if its 95% confidence interval did not include 0. Confidence intervals and standard errors were obtained by bootstrapping (n = 10,000 permutations per test), with functions written by R. Torices for R (available upon request). The maximal eigenvalue variance is determined by the number of measured traits minus 1 (Pavlicev et al. 2009). Thus, the magnitude of the phenotypic integration was also expressed as a percentage of the maximum possible value (hereafter Rel INT), by scaling INT values on the number of measured traits minus one (Pavlicev et al. 2009). Furthermore, we propose a modification of INT (hereafter size-controlled INT) in which the eigenvalue variance is calculated from a partial-correlation matrix instead of the correlation matrix. We used the partial-correlation matrix between the inflorescence components and the inflorescence size (see below for further details about partial correlations). In this way, we could assess the magnitude of phenotypic integration after controlling by differences in organ size.

Second, we tested whether the structure of phenotypic covariation between the absolute allocations to different inflorescence components was maintained among the three currencies and between the two sites. For that purpose, we tested for differences in the overall structure of the covariance matrix of resource allocation between currencies for each population and between populations for each currency, using Flury's hierarchical common principal components (CPC) analysis (Arnold and Phillips 1999; Phillips and Arnold 1999). This approach can reveal shared similarities across covariance matrices that go beyond the simple question of matrix equality (Phillips and Arnold 1999). Phenotypic-covariation matrices can share complex relationships, such as the orientation of particular principal components (Phillips and Arnold 1999). We used the CPC "jump-up" approach of Phillips and Arnold (1999). The model assuming that the matrices are unrelated (i.e., complete heterogeneity among covariance matrices) was sequentially compared, using log-likelihood ratio tests, with models that specify different relationships among the currencies or population covariance matrices. Thus, the procedure started by testing the hypothesis of shared partial CPCs between matrices against unrelated structure and followed with more inclusive hierarchical models of relationships between matrices, such as CPCs, proportionality, and equality, until a statistically significant deviation was found. This analysis was carried out in the CPC program written by P. Phillips (available at http://pages.uoregon.edu/pphil/programs/cpc/cpc.htm).

Third, we utilized Pearson correlation to determine whether the absolute allocation to each inflorescence component was correlated at both studied sites and for the three currencies. Correlation between components can result from large differences in resource acquisition between individuals. To assess whether the correlation structure was maintained beyond the variation in resource acquisition, we estimated pairwise partial correlations (Magwene 2001) between inflorescence components, after controlling by inflorescence size, utilized as a proxy of resource acquisition.

Results

Allocation to Inflorescence Components

Absolute and proportional allocation to different inflorescence components. Absolute reproductive allocation differed significantly among inflorescence components and marginally among currencies and sites (table 1). Inflorescence size also significantly influenced absolute allocation to inflorescence components (table 1). The description of allocation patterns was complicated by the significant interaction between inflorescence component and both site and currency (table 1). Scapes were always the inflorescence component receiving the highest allocation for all currencies at both sites, whereas rays received the lowest allocation (table 2). The relative importance of the other inflorescence components was dependent on site and currency (table 2). Ovaries were the component receiving the second-highest allocation for all currencies and sites, except for dry mass and P at Noreña. Patterns of proportional allocation basically repeated those found for absolute allocation and are not detailed in this article (table 1; fig. 1).

Regarding primary sexual components, allocation to ovaries was significantly higher than that to male flowers for all currencies at both sites, except for N allocation at Noreña, where there was not a significant difference between the two components (table 2). Regarding support and attractive components, allocation decreased in the order scape > receptacle > rays, except for P at Saús, where receptacle and rays had similar allocation (table 2).

Nutrient concentrations. Nutrient concentration differed significantly among inflorescence components and currencies but not between sites (table 1). Inflorescence size also influenced nutrient concentration of different inflorescence components (table 1). For N, concentration decreased from primary sexual structures through rays to receptacle and scape (table 3). For P, ovaries had the highest concentration, followed by rays; the remaining components had different [P], depending on the site (table 3).

Currency Differences in the Allocation Pattern

Absolute and proportional allocations to inflorescence components were affected by the currency (table 1). Proportional allocation patterns of P were significantly different from resource allocation in terms of dry mass and N (LSMEANS difference tests: $\chi^2 = 0.22$, $P = 0.637$ for dry-mass vs. N allocation; $\chi^2 = 8.63$, $P = 0.003$ for dry-mass vs. P allocation; $\chi^2 = 8.97$, $P = 0.003$, for N vs. P allocation).

Phenotypic Integration of the Allocation to Inflorescence Components

Integration indices. We detected integration of allocation components in the inflorescence in *Tussilago farfara*. Resources allocated to each inflorescence component were significantly integrated at both sites irrespective of the currency used (table 4). Nevertheless, the magnitude of the integration differed widely among sites and currencies, ranging from 2.80% to 58.44% of the maximum possible integration. Integration was commonly higher at Saús (table 4). Within sites, integration decreased in the order dry mass > P > N (table 4). However, these differences in integration among currencies were not significant (table 4).

The observed pattern of integration was maintained when INT was calculated using the partial-correlation matrix, in which inflorescence size was included as the third control variable (size-controlled INT), instead of the correlation matrix (table 4). However, two main differences should be highlighted (table 4): (1) at Noreña, the size-controlled INT was always higher than INT, independent of the currency, but differences were not statistically significant; (2) at Saús, the two indices were very similar, except for dry-mass allocation, in which the size-controlled INT showed a significantly lower integration than INT.

Differences in integration across sites and currencies. No common pattern in the covariance matrices of allocation to inflorescence components was found between different currencies within each site, as indicated by the Flury hierarchy analysis. The unrelated model (complete heterogeneity among covariance matrices) could not be rejected against the next model in the Flury hierarchy (Noreña: $\chi^2_8 = 26.3$, $P = 0.0009$; Saús: $\chi^2_8 = 23.4$, $P = 0.0029$).

There was significant heterogeneity among sites for dry-mass and N phenotypic-covariance matrices (dry mass: $\chi^2_4 = 23.4$, $P = 0.0001$; N: $\chi^2_4 = 20.4$, $P = 0.0004$). However, the covariance matrices for P allocation to inflorescence components of both sites shared the same CPCs, since this model did not show a statistically significant deviation from complete heterogeneity among sites ($\chi^2_{10} = 10.4$, $P = 0.409$), whereas a

Table 1

Results of Generalized Estimated Equation Models Testing Whether Allocation Was Affected by the Inflorescence Component, Site, Currency, and Inflorescence Size (Total Biomass, Total N Content, or Total P Content)

	Absolute allocation			Proportional allocation			Nutrient concentration		
Effect	χ_2	df	P	χ_2	df	P	χ_2	df	P
Component	56.67	4	<.0001	56.58	4	<.0001	40.46	4	<.0001
Site	2. 84	1	.092	7.24	1	.007	2.17	1	.140
Currency	5.86	2	.054	14.75	2	.012	25.76	1	<.0001
Site × component	38.87	4	<.0001	31.75	4	<.0001	23.57	4	<.0001
Currency × component	64.18	8	<.0001	42.30	8	<.0001	34.75	4	<.0001
Inflorescence size	13.37	1	.0003	5.34	1	.021	11.99	1	.0005

Note. Inflorescence components are scape, receptacle, male flowers, ovaries, and rays. The model for nutrient concentration included only two levels for currency: N and P. Significant P values are underlined.

Table 2

Dry Mass, N, and P Allocation to Different Inflorescence Components of *Tussilago farfara* at Two Sites (Noreña and Saús)

	Dry mass (mg)			N (μg)			P (μg)		
Inflorescence component	Noreña	Saús	*P*	Noreña	Saús	*P*	Noreña	Saús	*P*
Scape	111.9 ± 65.5 (40)^{A}	89.2 ± 32.3 (40)^{A}	.036	1065 ± 666 (39)^{A}	2949 ±1382 (27)^{A}	<.0001	190 ± 112 (39)^{A}	332 ± 160 (29)^{A}	<.0001
Receptacle	15.6 ± 4.7 (40)^{B}	12.4 ± 3.6 (40)^{B}	.218	272 ± 111 (39)^{B}	344 ± 120 (29)^{C}	<.0001	52 ± 18 (39)^{B}	45 ± 21 (29)^{C}	<.0001
Male flowers	8.7 ± 3.6 (40)^{D}	9.5 ± 2.9 (40)^{C}	.035	258 ± 113 (38)^{B}	320 ± 129 (25)^{C}	<.0001	37 ± 14 (38)^{C}	35 ± 15 (25)^{C}	<.0001
Ovaries	10.2 ± 3.5 (29)^{C}	13.9 ± 4.9 (39)^{B}	.001	288 ± 89 (24)^{B}	545 ± 175 (29)^{B}	.0004	141 ± 79 (24)^{A}	178 ± 122 (28)^{B}	.949
Rays	6.7 ± 2.6 (29)^{D}	7.6 ± 3.5 (39)^{D}	.059	130 ± 52 (26)^{C}	225 ± 104 (26)^{D}	<.0001	33 ± 34 (21)^{C}	73 ± 82 (25)^{C}	.843

Note. Data are presented as mean ± SD (*n*). Significant effects for site on each inflorescence structure are presented. Within columns, means of dry mass, N, or P that do not share the same letter were significantly different at the $P < 0.001$ level, as determined by LSMEANS differences. Female flowers were included in the model as ovaries and rays. Significant *P* values are underlined.

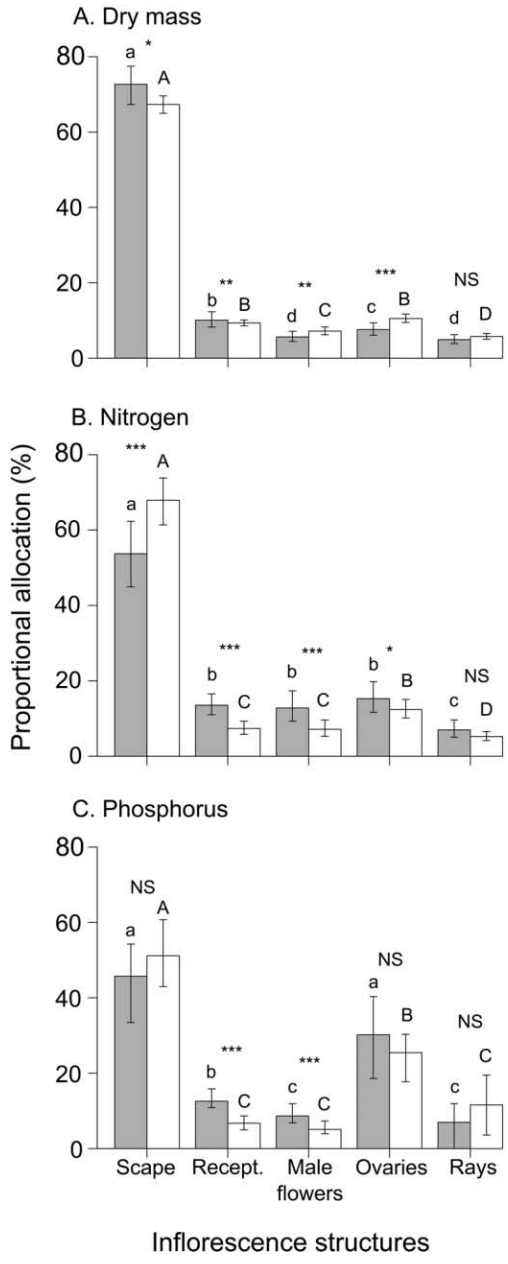

Fig. 1 Percentage of dry mass (*A*), nitrogen (*B*), and phosphorus (*C*) allocated to inflorescence component in *Tussilago farfara*. Gray bars: Noreña; white bars: Saús. Segments show confidence intervals at 0.001. Significance of differences between sites for each inflorescence component is as follows: NS indicates $P > 0.05$, a single asterisk $P < 0.05$, two asterisks $P < 0.01$, and three asterisks $P < 0.001$. Means of dry-mass, N, or P proportional allocation that do not share the same letter within sites (lowercase for Noreña, uppercase for Saús) are significantly different at the $P < 0.001$ level, as determined by LSMEANS differences. Recept. = receptacle.

statistically significant deviation was found in the test against the next hierarchical model, proportionality among matrices ($\chi^2_{14} = 30.0$, $P = 0.008$).

Correlation analysis. In terms of dry mass, almost all inflorescence components were positively correlated at both sites (table 5). The only exception was that the dry mass of ovaries and rays at Noreña was not correlated with the dry mass of scapes and male flowers (table 5). Correlations in terms of N qualitatively agreed with those in terms of dry mass, although some correlations lost significance, namely, those between scape and male flowers at both sites and those between receptacle and ovaries and rays at Noreña (table 5). In terms of P, most correlations between inflorescence components were not significant (table 5). Only three significant and positive correlations were found at Saús: between scape and receptacle, between scape and ovaries, and between receptacle and male flowers (table 5). The correlation between male and female (ovaries plus rays) flowers was significant and positive in terms of dry mass and N for both sites (results not shown). In terms of P, this correlation was not significant for Saús ($r = 0.078$, $n = 22$, $P = 0.729$), whereas it was significantly negative for Noreña ($r = -0.407$, $n = 28$, $P = 0.032$).

Many positive correlations disappeared when correlations between components were estimated as partial correlations controlled by inflorescence size (table 6). In all currencies, scapes were in general negatively correlated with all the other components in both sites (table 6). However, some significantly positive correlations between inflorescence components remained in the partial-correlation analyses: at Noreña, positive partial correlations were found only in terms of dry mass, between receptacles and male flowers and between ovaries and rays (table 6). At Saús, we found positive partial correlations between receptacles and rays in terms of dry mass and N and between rays and ovaries and male flowers and between ovaries and receptacles in terms of N (table 6). Regarding primary sexual components, we found a positive partial correlation between male flowers and ovaries in terms of N for Saús. In terms of P, partial correlation between male flowers and ovaries was significantly negative for both sites (table 6).

Discussion

Resource Allocation to Inflorescence Components

Functional evolution of inflorescences has been approached from different perspectives in evolutionary ecology (Wyatt 1982; Thomson 1989; Harder et al. 2000, 2004; Diggle 2003). Important insights into this question can result from the study of resource allocation to support, attraction, and primary sexual components in inflorescences, a natural, yet largely unexplored, prolongation of similar studies on single flowers. We illustrate the potential of this approach by highlighting three aspects of our results with *Tussilago farfara*.

Patterns of allocation to primary sexual versus accessory structures in inflorescences are almost completely unknown. In single flowers, dry-mass allocation is often biased toward petals (Lovett Doust and Cavers 1982; Campbell 1997; Parra-Tabla and Bullock 2000), particularly in exogamous plants (Cruden and Lyon 1985). Independent of mating system, accessory structures usually account for 60%–70% of dry-mass allocation (Cruden and Lyon 1985). Within primary sexual structures, dry-mass allocation is biased toward male organs in exogamous species, while the opposite occurs in selfing species (Cruden and Lyon 1985). For inflorescences, the limited evidence available indicates that the bias toward accessory

Table 3

Concentrations (mmol/g) of N and P in Inflorescence Structures of *Tussilago farfara* at Two Sites (Noreña and Saús)

Inflorescence component	[N] (mmol/g)			[P] (mmol/g)		
	Noreña	Saús	*P*	Noreña	Saús	*P*
Scape	.571 ± .233 (39)^{C}	1.832 ± .563 (27)^{AB}	<.0001	.058 ± .026 (39)^{D}	.120 ± .046 (29)^{B}	.199
Receptacle	1.078 ± .448 (39)^{B}	1.645 ± .445 (29)^{B}	.232	.112 ± .033 (39)^{C}	.115 ± .042 (29)^{B}	.015
Male flowers	1.799 ± .611 (38)^{A}	2.041 ± .575 (25)^{A}	.837	.137 ± .036 (38)^{B}	.119 ± .030 (25)^{B}	<.0001
Ovaries	1.728 ± .343 (24)^{A}	2.282 ± .457 (30)^{A}	.237	.483 ± .282 (24)^{A}	.400 ± .245 (29)^{A}	.109
Rays	1.152 ± .235 (26)^{B}	1.703 ± .569 (27)^{B}	.142	.147 ± .135 (21)^{BCD}	.288 ± .258 (26)^{AB}	.164

Note. Data are presented as mean ± SD (*n*). Significant effects for site on each inflorescence structure are presented. Within columns, mean [N] and [P] that do not share the same letter were significantly different at the $P < 0.001$ level, as determined by LSMEANS differences. Significant *P* values are underlined.

structures is even larger: from 76%–83% (this study) to more than 90% (Méndez 2001). In *T. farfara*, scape height can be important to raise flowers above the surrounding herbs and enhance pollinator attraction (Wild et al. 2003). This is consistent with a previous study, where we found that female reproductive success increased with increasing scape height (Torices and Méndez 2011).

In sex allocation theory, cosexuality has been hypothesized to be stabilized by preferential allocation to shared structures that contribute to both genders (Charlesworth and Charlesworth 1987). For inflorescences acting as pollination units, this prediction seems to hold in a limited test within Araceae (Méndez 2001). Scapes are considered to be unilateral (male) fixed costs, and high allocation to this component in the monoecious *T. farfara* thus contradicts theoretical predictions. Nevertheless, to what extent the scape can be considered to be a male fixed cost is debatable in *T. farfara* (Torices and Méndez 2011). A more comprehensive test would be obtained by comparing this and other monoecious Asteraceae with the allocations in hermaphroditic species, monoecious species with separate male and female heads (e.g., *Ambrosia*), and dioecious species (e.g., *Antennaria*, *Petasites*).

The analysis of resource allocation in inflorescences acting as pollination units can shed light on the evolution of the widespread presence of rayed heads, i.e., heads with peripheral zygomorphic corollas (rays), in the sunflower family (Burtt 1977; Funk et al. 2009). Rays enhance attractiveness to pollinators (Lack 1982; Marshall and Abbott 1984; Stuessy et al. 1986; Celedón-Neghme et al. 2007; Andersson 2008) and are usually associated to female unisexual flowers (Mani and Saravanan 1999; Torices and Anderberg 2009). Thus, Bawa and Beach (1981) proposed that selection for attractive petaloid ray flowers might have led to the sterilization of stamens to pay for the cost of ray production. According to this hypothesis, ray production should presumably be at least as costly as male components. Our results lend partial support to that prediction. Within female flowers, resources allocated to larger rays were not detracted from allocation to sexual organs, since ovaries and rays were positively correlated in terms of dry mass and N (table 5). Nevertheless, although rays were generally cheaper than male flowers, ray cost might be enough to limit nutrient allocation to primary sexual functions, as indicated by their negative partial correlation in terms of P (table 6). Further studies are needed to ascertain whether the reallocation hypothesis is applicable to rays in this family.

Currency Differences in the Allocation Pattern

The adequate currency in studies of reproductive allocation has been debated for decades (Thompson and Stewart 1981; Karlsson and Méndez 2005). In sexual allocation, the few studies available show that absolute resource allocation to floral organs in terms of nutrients yields patterns qualitatively similar to those in terms of dry-mass allocation (Ashman and Baker 1992; Méndez and Traveset 2003). The main difference with respect to dry-mass allocation is that primary sexual organs are enriched in nutrients compared to accessory organs, par-

Table 4

Degree of Phenotypic Integration among Absolute Allocation of Resources to Inflorescence Components for Three Currencies (Dry Mass, N, and P) and Two Sites (Noreña and Saús), as Measured with the Phenotypic Integration Index (INT) or Its Size-Controlled Version

Site, currency, size-controlled	INT	Standard error	95% CI	Rel INT (%)
Noreña:				
Dry mass:				
No	.921	.061	.512–1.783	23.04
Yes	1.504	.074	.797–2.367	37.61
N:				
No	.112	.047	.010–.788	2.80
Yes	.623	.054	.417–1.317	15.57
P:				
No	.366	.040	.273–.964	9.14
Yes	.839	.077	.331–1.686	20.96
Saús:				
Dry mass:				
No	2.338	.062	1.590–3.086	58.44
Yes	.728	.032	.462–1.238	18.20
N:				
No	.512	.049	.342–1.222	12.80
Yes	.593	.055	.354–1.351	14.84
P:				
No	1.768	.105	.965–2.783	44.19
Yes	1.647	.084	.963–2.436	41.18

Note. Standard errors and 95% confidence intervals (CI) were obtained by bootstrapping. INT for each site and currency was considered to reflect significant inflorescence integration if its 95% CI did not include 0. Rel INT indicates the relative eigenvalue variance, in which the observed eigenvalue variance was rated by the maximum variance expected, given the measured traits, and is expressed as a percentage.

Table 5

Pearson Correlation Coefficients between Dry Mass, N, or P (Measured in mg) of Different Inflorescence Components in *Tussilago farfara* at Two Sites

	Scape	Receptacle	Male flowers	Ovaries	Rays
Dry mass:					
Scape		.468 (.002, 40)	.381 (.015, 40)	.261 (.172, 29)	.222 (.247, 29)
Receptacle	.802 (.000, 40)		.503 (.001, 40)	.622 (.000, 29)	.592 (.001, 29)
Male flowers	.516 (.001, 40)	.548 (.000, 40)		.233 (.224, 29)	.334 (.077, 29)
Ovaries	.758 (.000, 39)	.772 (.000, 39)	.502 (.001, 39)		.751 (.000, 29)
Rays	.773 (.000, 39)	.825 (.000, 39)	.591 (.000, 39)	.758 (.000, 39)	
Nitrogen:					
Scape		.595 (.000, 39)	.045 (.789, 38)	.138 (.521, 24)	.087 (.672, 26)
Receptacle	.475 (.012, 27)		.321 (.049, 38)	.251 (.237, 24)	.230 (.259, 26)
Male flowers	.337 (.125, 22)	.550 (.005, 24)		.336 (.117, 23)	.235 (.258, 25)
Ovaries	.579 (.002, 26)	.597 (.001, 28)	.644 (.001, 24)		.456 (.033, 22)
Rays	.570 (.004, 24)	.619 (.001, 25)	.626 (.002, 22)	.759 (.000, 26)	
Phosphorus:					
Scape		.306 (.058, 39)	.107 (.522, 38)	−.065 (.763, 24)	−.073 (.752, 21)
Receptacle	.529 (.003, 29)		.225 (.175, 38)	−.071 (.740, 24)	−.143 (.537, 21)
Male flowers	.288 (.172, 24)	.520 (.009, 24)		−.231 (.288, 23)	−.017 (.944, 20)
Ovaries	.515 (.006, 27)	.255 (.199, 27)	.077 (.728, 23)		−.018 (.939, 20)
Rays	−.118 (.576, 25)	.191 (.361, 25)	.068 (.757, 23)	.267 (.207, 24)	

Note. Data in parentheses are significance (*P*) and sample size. Above diagonal: Noreña; below diagonal: Saús. Significant coefficients are underlined.

ticularly petals (Ashman and Baker 1992; Carroll and Delph 1996; Méndez and Traveset 2003). Our results indicate that these patterns were also valid for the inflorescences of *T. farfara* (see, however, Lovett Doust and Harper 1980).

The currency problem becomes bigger when the correlation structure of allocation to different floral organs is analyzed. In *Paeonia cambessedesii*, the correlation structures of dry-mass and P allocation were more similar to each other than to that of N allocation (Méndez and Traveset 2003). In *T. farfara*, dry mass and N showed similar correlation structures, whereas that for P was markedly different. Similarity of allocation or correlation structures across currencies can be dependent, among other factors, on what the limiting nutrient is, a matter that warrants further study. According to the view of plants as balanced systems in terms of resource acquisition and use (Bloom et al. 1985), correlation structures across nutrients should be strong, indicating that all nutrients are similarly limiting. On the other hand, female reproductive organs usually are particularly enriched in N, while male reproductive organs are particularly enriched in P (Ashman and Baker 1992;

Table 6

Partial Correlation Coefficients between Dry Mass, N, or P of Different Inflorescence Components While Controlling by Inflorescence Size (Total Mass, N, or P) in *Tussilago farfara* at Two Sites

	Scape	Receptacle	Male flowers	Ovaries	Rays
Dry mass:					
Scape		−.418 (.005, 40)	−.375 (.014, 40)	−.862 (.000, 29)	−.855 (.000, 29)
Receptacle	−.591 (.000, 40)		.337 (.029, 40)	.469 (.007, 29)	.448 (.011, 29)
Male flowers	−.542 (.000, 40)	.078 (.635, 40)		.067 (.731, 29)	.203 (.290, 29)
Ovaries	−.657 (.000, 40)	.168 (.306, 39)	−.001 (.997, 39)		.680 (.000, 29)
Rays	−.661 (.000, 39)	.334 (.034, 39)	.188 (.250, 39)	.204 (.211, 39)	
Nitrogen:					
Scape		−.201 (.294, 27)	−.597 (.000, 27)	−.807 (.000, 21)	−.627 (.001, 21)
Receptacle	−.692 (.000, 20)		−.100 (.624, 27)	−.383 (.078, 21)	−.268 (.238, 21)
Male flowers	−.833 (.000, 20)	.347 (.127, 20)		.321 (.150, 21)	.136 (.560, 21)
Ovaries	−.834 (.000, 20)	.435 (.047, 20)	.600 (.002, 20)		.317 (.156, 21)
Rays	−.713 (.000, 20)	.412 (.063, 20)	.550 (.007, 20)	.421 (.055, 20)	
Phosphorus:					
Scape		.252 (.185, 29)	.255 (.187, 28)	−.664 (.000, 20)	−.168 (.481, 20)
Receptacle	.086 (.708, 22)		.058 (.772, 28)	−.345 (.123, 20)	−.137 (.567, 20)
Male flowers	.092 (.687, 22)	.410 (.050, 22)		−.472 (.032, 19)	.044 (.860, 19)
Ovaries	−.420 (.044, 22)	−.479 (.017, 22)	−.466 (.022, 22)		−.604 (.002, 20)
Rays	−.858 (.000, 22)	−.050 (.826, 22)	−.046 (.842, 22)	−.037 (.872, 22)	

Note. Data in parentheses are significance (*P*) and sample size. Above diagonal: Noreña; below diagonal: Saús. Significant coefficients are underlined.

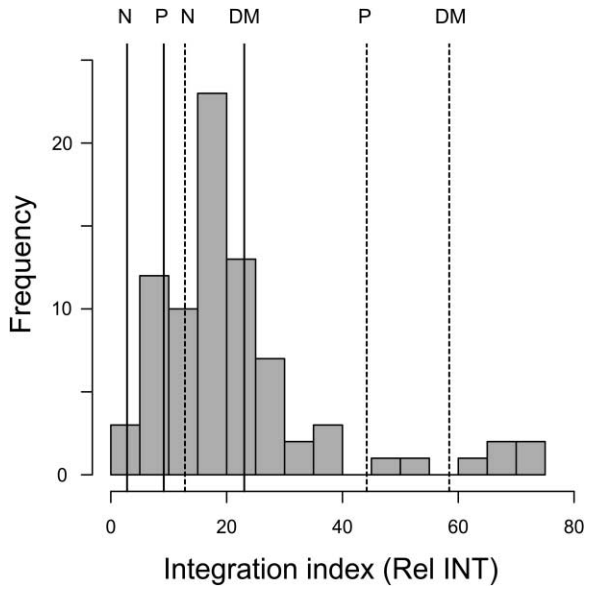

Fig. 2 Phenotypic integration for metric- and resource-based traits, measured as percentage of maximum integration possible (Rel INT). Observed integration levels for floral metric traits in 55 studies (bars; reviewed by Ordano et al. 2008) and observed integration for resources allocated to *Tussilago farfara* inflorescence components (vertical lines: solid lines for Noreña and dashed lines for Saús). DM = dry mass; N = nitrogen; P = phosphorus.

see, however, Méndez and Traveset 2003). These different requirements for specific nutrients could limit the degree of phenotypic correlation across currencies and lead to the presence of modularity (sensu Berg 1960) in the correlation matrix. In any case, discrepancies among currencies in correlation structure are relevant to any assessment of phenotypic integration, as we address in the next section.

Phenotypic Integration of the Allocation to Inflorescence Components

Despite the differences between currencies and sites, resources allocated to inflorescence components in *T. farfara* were phenotypically integrated. Our results indicate that integration in terms of resources can be similar to or higher than that found in a recent review for floral metric traits (fig. 2; Ordano et al. 2008). The generality of this pattern must await future comparative studies, including the analysis of integration in floral metric traits in *T. farfara*. Another question that should be addressed is whether dry mass or some nutrient might be usually more integrated. In this study, dry mass showed, in general, higher integration than nutrients, particularly N. Experimental manipulation of nutrient availability and genotypes could allow the factors that underlie the differential integration of nutrients and dry mass to be disentangled.

Floral organs or inflorescence components may be integrated because they work together toward the common goal of achieving successful reproduction (Murren 2002; Pigluicci 2003). Integration is easily understood for accessory components supporting both gender functions. Furthermore, it could also be present in components expected to be linked by trade-offs according to sex allocation theory. The reason is that, although unequivocal functions are commonly assigned to inflorescence components, those components may, in fact, have several functions. For instance, the function of male flowers is usually considered to be pollen donation. Nevertheless, in *T. farfara* male flowers may have an important role in pollinator attraction (Wild et al. 2003) and may eventually increase female reproductive success (Torices and Méndez 2011).

Adaptive resource integration might be the consequence of resource allocation to maximize both male and female reproductive success, given a limited amount of resources, whereas the adaptive integration of metric floral traits has been mainly attributed to an accurate placement of pollen deposition on pollinator bodies. Thus, an adaptive pattern of resource integration should be expected when the resources allocated to different components will enhance equally both primary sexual functions, i.e., pollen donation and seed production. Under this scenario, there might be no reason to expect a negative correlation between floral components, since there is no trade-off.

Negative correlations between floral organs have, nevertheless, been found (Parra-Tabla and Bullock 2000). A promising venue for studies of floral or inflorescence integration is to ascertain to what extent modularity (Berg 1960) can be present in flowers (Bissell and Diggle 2010) or more sophisticated structures such as inflorescences, in particular those acting as pollination units. Those studies should take advantage of advances in assessment of male reproductive success to test the hypothesis that higher integration should be expected in organs or components contributing significantly to mating success through both male and female sex functions.

Positive phenotypic correlations among competing structures or functions might also result from large differences in resource acquisition between the sampled individuals. This effect was present in our study, because partial-correlation analysis revealed negative correlations among inflorescence components, particularly in terms of P allocation. We found mainly changes from positive Pearson correlations to negative partial correlations in those correlations that involved scapes (tables 5, 6). Scapes generally contribute more than any other component to the total inflorescence size (fig. 1), and larger inflorescences might disproportionally allocate resources to scapes in comparison with other components, leading to a negative correlation between scapes and the other components when inflorescence size was taken into account in partial-correlation analysis. To overcome the obstacle of variation in resource availability, the use of common-garden designs in which resource acquisition and genotypes can be controlled has been suggested (Ashman et al. 2001). However, this approach does not allow exploration of phenotypic patterns in natural populations. Méndez (2001) suggested that looking at the slopes of the increases in allocation to competing structures when overall resource allocation increases can give a hint as to which structures are prioritized and get a disproportionate share of the extra resources. Here, we used a new integration index, in which size is taken into account via the partial correlations between traits and the size of the organ to estimate the variance of the eigenvalues. This approach may be useful for analyses of resource integration from field data but will require future scrutiny of its particularities in com-

parison with those of other integration indices based on the variance of eigenvalues (Haber 2011).

In conclusion, although resource allocation to *T. farfara* inflorescences was influenced by the currency used and the study site, as well as by differences in resource acquisition, we found that allocation to inflorescence components was phenotypically integrated. The examination of both resource- and metric-based measures of phenotypic integration among floral traits might provide new insights about the functional and genetic relationships between different phenotypic modules. We might expect a concordance of patterns a priori, since resource allocation underlies phenotypic metric traits. Nevertheless, those situations where resource- and metric-based traits would produce different correlation outcomes could be of particular interest. Therefore, understanding floral diversity and how the selection of floral phenotypes is produced could be improved by the "integration" of the two approaches.

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