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Morphological consequences of the trade-off between growth and reproduction in a columnar cactus (*Lophocereus schottii*)

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Abstract

Since cacti have very small surface/volume ratios, the amount of light they intercept is limited, and so is photosynthesis. However, many cacti shade themselves by means of dense hairy mats, called cephalia, which protect the floral buds. There is a trade-off between allocating a surface to photosynthesis or to the protection of reproductive structures. We found that proportion of the stem covered by cephalium affected fitness in the columnar cactus *Lophocereus schottii*. Too little cephalium holds few floral buds while too much reduces fecundity – probably through diminished photosynthesis – with an intermediate amount maximising reproduction. The optimal proportion of cephalium becomes smaller as the plant grows, probably because self-shading by new branches causes a further reduction in light interception. Smaller plants had significantly less cephalium than the optimal amount to maximise current reproduction. Since the largest individuals produced more reproductive structures, small cacti may find it more profitable to grow fast to achieve a large fecundity, than to assign resources to immediate reproduction via cephalium development.

Introduction

When compared to most plants, cacti stand out for their very low surface/volume ratio. This means that cacti have a small photosynthetic surface compared to the proportionally large respiratory demand of their water-storing parenchyma, and are therefore restricted by the amount of photosynthetically active radiation that is intercepted by the plant (Nobel 1988). Despite this, most cacti shade themselves by means of non-photosynthetic spines and hairs. Some species even produce cephalia, which are dense bristly, hairy, or woolly structures developed around the floral buds. In those species, flowering occurs almost invariably

within the hairy mass (Bravo-Hollis 1978). The cephalium may protect the reproductive parts from some potential causes of external damage such as herbivores, nectar-robbers, and radiation (Buxbaum 1961). In some cacti, a dense covering of spines and hairs has been shown to work as a sunshade capable of achieving a reduction of as much as 10°C on the plant surface. Despite these benefits, shading by spines may also have a negative impact on photosynthesis (Nobel 1983, 1988). Thus, the amount of cephalium cover is subject to a trade-off: While it protects the floral buds and may additionally help keep the stem cool, it also reduces the scarce and limiting photosynthetic surface (Zavala-Hurtado et al. 1998). As the

plant's overall fitness depends both on the rate of photosynthesis and on an adequate protection of the reproductive organs, it would be expected that the development of the cephalium, and the proportion of the stem that is covered by this structure, should reflect the trade-off between both conflicting functions.

Lophocereus schottii (Engelm.) Britton and Rose of the Sonoran Desert has a spiny pseudocephalium which may protect floral buds against high radiation and temperature while providing a safe site for the larvae and pupae of its pollinator, the seed-consuming moth *Upiga virescens* (Holland and Flemming 1999). In contrast with true cephalia, which are anatomically discontinuous with the lower stem, pseudocephalia are the upper part of single stems that become covered by a mat of hairs and spines, which may be lost as the plant grows. In *L. schottii*, however, stems get narrower once the cephalium is initiated and few spines are shed from the older part of the structure, so the pseudocephalium becomes larger as the stem grows. Once a branch apex initiates a cephalium, it does not turn back to producing green stems. These traits allow us to assess more easily the dynamics of cephalium development, making *L. schottii* an attractive species to study the way in which the plant manages its reproductive structures and their associated costs.

In this paper we explore the hypothesis that the production of cephalium affects the individual's reproductive output, and that there is an intermediate optimum amount of cephalium that maximises the production of reproductive structures.

Methods

We worked at *Llanos de Magdalena* in Baja California Sur, Mexico. These sandy flats are located at around 26° N, 112° W. The closest weather stations (located at 22 and 73 km from the study site) based on 40-year datasets report annual rainfall averages of 54.8 mm and 105.7 mm, although coastal fogs are frequent. Vegetation is a xeric scrub where a few species of columnar cacti are conspicuous elements.

Lophocereus schottii has a polypodial growth, showing a cluster of branches that emerge at ground level from a common crown (Figure 1). We have observed in the field that shoots usually

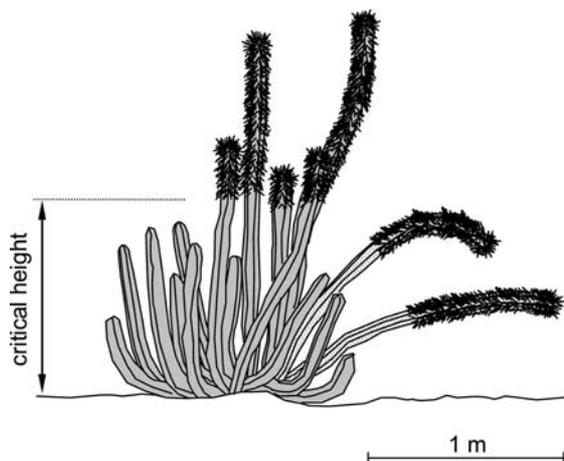


Figure 1. Branching pattern of *Lophocereus schottii* in Baja California. Note the uneven, markedly hierarchical distribution of branch lengths, and the initiation of cephalia above a critical height.

bend and die when they reach 2.5–4.0 m in height. In the study site, the development of the spiny mat that forms the cephalium begins when branches achieve a critical height of about 1 m. Cephalia are commonly distributed on a few elongated shoots, while smaller branches in the same individual are fully photosynthetic. Since the overall amount of cephalium-covered stems depends on the size of the plant, we tried to sample individuals across the whole size-range of the population. Since shoots are almost cylindrical, their length may be quite correlated with plant biomass. Thus, we calculated plant size as the sum of the individual lengths of the constituent stems, and used it as a factor in all analyses. For some of them we divided the individual plants into the following size categories: (I) 0–5 m total stem length ($n=157$), (II) 5–10 m ($n=88$), (III) 10–20 m ($n=52$), and (IV) more than 20 m ($n=20$). In total, we sampled 317 plants. We measured the total stem length, the length of every cephalium, and the number of flowers and fruits in each branch. Plant size was defined as the sum of the total lengths of the healthy branches; cephalium proportion (CP) was defined as the ratio of the sum of functional cephalium lengths to plant size. The number of fruits and fully-developed flowers was used as a measure of fitness. This instantaneous measure does not estimate the total reproductive effort of *L. schottii*, since it reproduces over a period of 5 months (Holland and Flemming 1999), but,

assuming that plants with different sizes or CP reproduce simultaneously, it gives us an unbiased estimate of the relative fitness of cacti differing in size and morphology. Measurements were conducted in late August, which is the end of the reproductive season, so most of the pollinated flowers may be recognisable in the field as mature or developing fruits.

Since analysing plant morphology in relation to size raises questions about the ontogenetic pattern of the individuals, we performed an allometric analysis. We performed a reduced major axis regression of total vegetative shoot length on total cephalium length using a log–log transformation. The slope, α_{RMA} , serves as a comparison of the growth rates of both kinds of stem.

All the cephalia in a plant seemed to begin at about the same height above ground. Since *L. schottii* drops a few cephalium spines as its reproductive branches grow, the lowest height of the cephalium on the stem is not necessarily a measure of the height at which it was first formed. As small cephalia (<50 cm) do not show evidence of having lost spines yet, their mean lower threshold was used to estimate in each plant the critical height at which cephalia are formed.

To assess the effect of cephalium proportion on reproduction, we regressed the number of flowers and fruits as dependent variables against size, CP, and the corresponding interactions. Quadratic terms were included to evaluate non-linear trends. Because the number of flowers and fruits is a discrete frequency count, we used Poisson regression (i.e., log-linear regression with continuous predictors and a χ^2 measure of fit; see Crawley 1993; Everitt 1994; and Krause and Molson 1997). When the residual errors in these models showed overdispersion (i.e., the variance of the residuals was significantly higher than that predicted by the Poisson distribution), the frequency data were rescaled to correct for biases in the statistical tests of hypotheses (Crawley 1993). In all cases, the analyses were made with the GLIM statistical package, release 4 (McCullagh and Nelder 1983; NAG 1986).

Results

Lophocereus schottii begins cephalium production when it reaches an overall size of 170 ± 36 cm, and

has 3.1 ± 0.8 branches on average (all errors correspond to the 95% confidence interval). Critical height for cephalium initiation averages 93.2 cm, although it ranges from 77 cm in small plants to 114 cm in the largest ones. The differences in critical height between size groups were highly significant (Kruskal-Wallis $H = 27.95$, $p < 0.0001$).

The number of reproductive branches is always small, with over one third of the individuals having just one cephalium. As these cacti grow, they develop more cephalia (from a mean of 1.47 cephalia in size I plants to 7.28 in size IV plants, $\chi^2 = 97.02$, $p < 0.0001$). However, the ratio of reproductive to total branches consistently decreased with size (from 0.40 in size I plants to 0.26 in size IV plants; Spearman's $\rho = -0.18$, $p = 0.008$). That is, although large plants show more reproductive branches, these represent a smaller proportion of the cactus' stems. Nevertheless, the growth rate of cephalium is greater than that of photosynthetic stems, as shown by the allometric regression slope of 0.853 (95% C.I.: 0.758–0.947, Figure 2). As a result, CP increases with plant size.

Most (60.5%) of the branches are shorter than the minimum size required for cephalium initiation. The maximum frequency of stems occurs just below or at the plant's critical height (Figure 3), with 34.2% of the total stems having a size 0–30 cm smaller than their size-class critical heights. If we consider that branches may measure as much as 4 m, it becomes clear most of them are restricted within a quite narrow range of lengths.

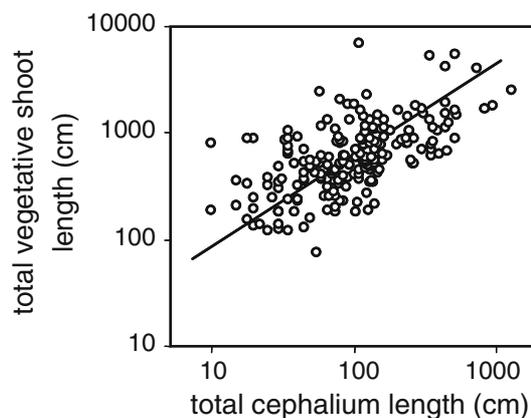


Figure 2. Allometric relationship between cephalium and photosynthetic stem length. The slope is significantly smaller than one (0.853 ± 0.095).

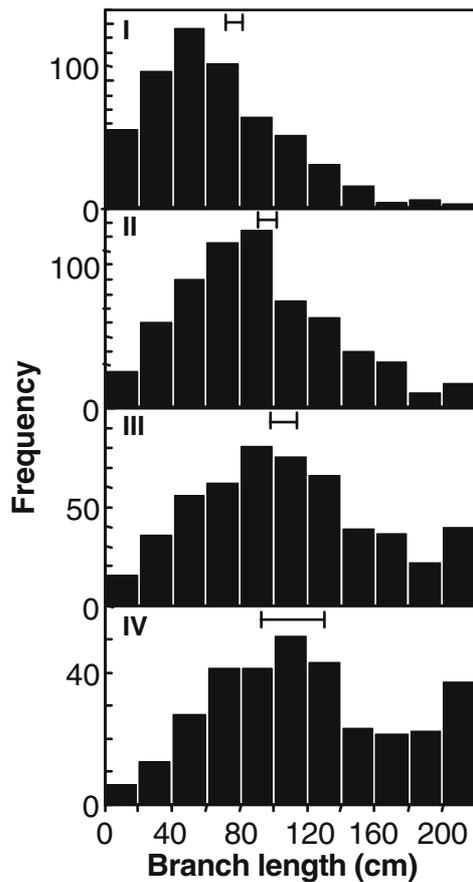


Figure 3. Frequency of branches with different lengths for the four plant size classes: (I) 0–500 cm total stem length ($n=157$), (II) 500–1000 cm ($n=88$), (III) 1000–2000 cm ($n=52$), and (IV) more than 2000 cm ($n=20$). The lines above the histogram correspond to the 95% confidence interval for the critical height needed for cephalium initiation. Note that for young plants the most frequent branch-length classes occur below the critical height.

Plant size was the factor that explained most (28.4% altogether with its quadratic term) of the variation in reproductive output, followed by CP (22.9% altogether with its quadratic term, Table 1). The coefficients of both size-squared and CP-squared were significant and negative in sign, indicating a non-linear, convex trend for both factors. Fecundity increases rapidly with size in the smaller plants, but tends to level-off in the larger categories. It also increases with increasing cephalium proportion, but it declines in plants with an unduly high proportion of stems covered by the reproductive spiny-mat (Figure 4). As the significant interaction between size and CP shows, larger

Table 1. Log-linear regression of plant size and cephalium proportion (CP) on reproduction.

Source	χ^2	DF	p	Deviance explained	Coefficient
Size	146.2	1	< 0.0001	17.24%	1.996×10^{-3}
CP	133.9	1	< 0.0001	15.79%	1.836×10^1
Size ²	94.6	1	< 0.0001	11.16%	-2.162×10^{-7}
CP ²	60.66	1	< 0.0001	7.15%	-2.999×10^1
Size \times CP	25.32	1	< 0.0001	2.99%	-2.166×10^{-3}

Non-significant terms were excluded from the model. Model was re-scaled to correct for overdispersion ($R^2=67.57$).

plants achieve maximum reproduction by having smaller proportions of cephalia.

It is noteworthy that in most cases the observed CP was lower than the theoretical value needed for

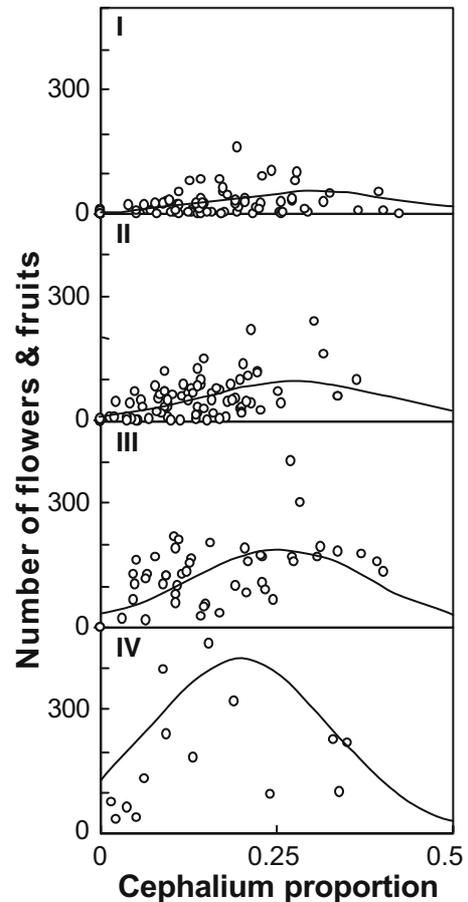


Figure 4. Estimated changes in fecundity (flowers plus fruits) related to the proportion of the plant's stem covered by cephalia for the four plant size classes. Each line corresponds to the behaviour predicted for plants having a size equal to the size-class midvalue by the multiple regression model.

maximum reproductive output, which was computed for each individual from the model generated through the log-linear regression. The divergence between the observed and the optimal CP was calculated for each individual. While proportion of cephalium in the smaller individuals is well below the value yielding a maximum reproductive output, this discrepancy becomes smaller for large cacti, turning non-significant for size IV plants (Table 2 and Figure 5).

Discussion

Our results show that reproductive output is related to plant size and cephalium proportion. As the cactus gets larger, it produces more flowers and fruits, which is a pattern found in most plants (Heywood 1986; Stearns 1992). Cephalium proportion behaved as we expected: having some is necessary for reproduction to take place, but having too much has a negative effect on the number of reproductive structures produced (Figure 4). This pattern supports our hypothesis that cephalium is a costly structure that entails a trade-off between photosynthesis and reproduction.

Larger plants have higher reproductive output when they have proportionally less cephalium (Figure 4). The reason for this may be the self-shading produced by the numerous branches in large individuals (Geller and Nobel 1986). As is the case with spines and hairs, shading by branches also reduces PAR interception. In order to keep the same balance between shaded (both by cephalium and by other stems) and unshaded photosynthetic surfaces, a large *L. schottii* should reduce its cephalium proportion.

The field data show that smaller plants are, on average, below the cephalium proportion that

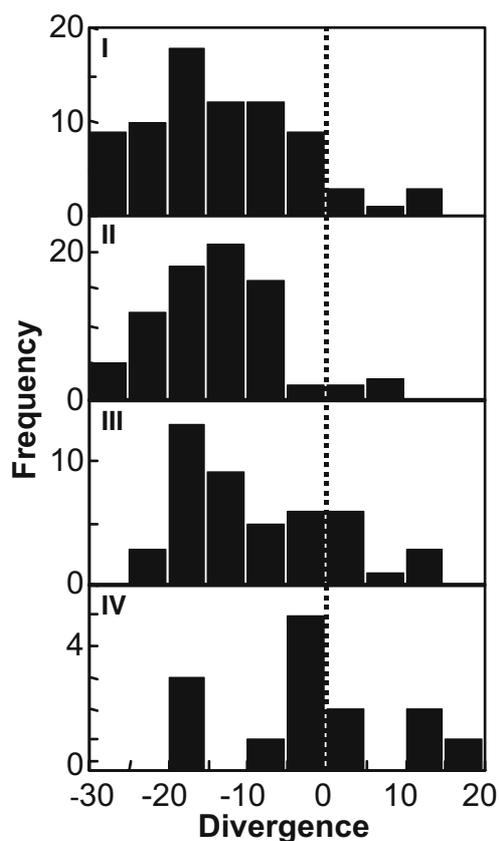


Figure 5. Distribution of the divergence between the observed and the optimal cephalium proportion for the individual plants in the four plant size classes. The dotted line shows zero divergence. Note that while most of the younger plants (I–II) lie markedly below optimal cephalium proportion, the older plants (IV) cluster around zero divergence and do not differ from the predicted optimum (see also Table 2).

yields maximum fecundity (Figure 5). This pattern may be related to the trade-off between present versus future reproduction. When size has a large impact upon reproduction, as it happens in *L. schottii* (Table 1), some organisms defer breeding, allocating their resources to growth

Table 2. Observed and optimal cephalium proportion.

Size class	Optimal cephalium proportion	Observed mean cephalium proportion	<i>t</i>	<i>p</i>
(I) 0–500 cm	0.30	0.167 (±0.010)	13.09	<i>p</i> < 0.0001
(II) 500–1000 cm	0.28	0.141 (±0.008)	17.61	<i>p</i> < 0.0001
(III) 1000–2000 cm	0.25	0.172 (±0.013)	6.00	<i>p</i> < 0.0001
(IV) over 2000 cm	0.20	0.151 (±0.029)	1.70	0.1050

Optimal cephalium proportion was estimated from log-linear regression model as the point at which the number of flowers and fruits was maximum, when size is equal to size class midpoint. The values in parentheses correspond to one standard error.

(Stearns 1992). The main cost of reproducing later, i.e., the risk of dying before procreating, seems quite reduced in juvenile columnar cacti (Pierson and Turner 1998; Godínez-Álvarez et al. 1999; Esparza-Olguín et al. 2002). A young *L. schottii* may find it more profitable to grow fast than to have an instantaneously optimal cephalium proportion for its size. By having smaller cephalia, it does not only increase its photosynthetic surface, but has no choice other than directing the resultant photosynthates to functions different from reproduction, such as growth. The production of cephalium seems to have been regulated by natural selection not so much as to maximise short-term fecundity but to maximise the plant's overall reproductive value.

While younger plants seem to refrain from maximising reproductive output in favour of vegetative growth, the larger, older plants show cephalium proportions not differing significantly from the optimal value. These plants have little to gain in terms of fitness by delaying their reproductive effort. Parker's (1988, p. 340) growth equation for *L. schottii* shows that juvenile individuals grow faster. Cephalium-less plants with a size of 100 cm have a relative growth rate of $0.181 \text{ cm cm}^{-1} \text{ yr}^{-1}$, while the more cephalium-covered plants with a size of 3000 cm achieve only $0.132 \text{ cm cm}^{-1} \text{ yr}^{-1}$. This result is in strong agreement with our hypothesis that having a smaller than optimal CP releases resources that may then be assigned to growth.

Small *L. schottii* do not reproduce until a certain size (both in number of branches and in overall length) is reached. Afterwards, the cacti maintain a large number of stems just below the critical height at which cephalia are initiated (Figure 3). The branches can be conceived as members of a population, which is the plant, and as such they have a size structure. Population models tell us that branch frequency should show a monotonically decreasing trend as size increases, unless the population growth rate is negative, a large recruitment pulse occurred in the past, or growth rate of individuals in the population is faster when they are small. The latter process is the one that most frequently is found to occur (Martínez-Ramos and Álvarez-Buylla 1995; Condit et al. 1998). Parker (1988), working in Arizona, detected that growth rate of the branches of *L. schottii* actually diminishes as they approach the size class where

cephalium initiation occurs. As a result, the branch-size structures found in Parker's study closely resemble those of Baja California, with large numbers of branches in the class just below cephalium initiation height. This means that *L. schottii* manages to keep a large bank of stunted, slow-growing, photosynthetic branches for each reproductive cephalium. As a result, the overall growth rate of photosynthetic shoots is smaller than that of cephalia, as it was evinced by the allometric analysis. Besides guaranteeing that enough photosynthesis takes place in non-reproductive branches to support the development and maintenance of photosynthetically-costly cephalia, this strategy may be the cause for the small proportion of branches that actually develop a cephalium.

There is evidence of water movement among branches, and some inconclusive data that suggest sugar translocation in other cacti (Nobel and Pimienta-Barrios 1995; Nerd and Neumann 2004). This suggests that physiological integration may occur in *L. schottii*, and that small, vegetative stems may actually subsidise cephalia located in other branches. However, if translocation is lacking in this cactus, the pattern we have observed should be explained by other factors such as storage. Data are required to solve definitively this point.

In other species of cacti the stem under the cephalium is completely devoid of chlorophyll, but *Lophocereus* does have photosynthetic pigments in that area. This opens the question of whether the cephalium promotes rather than reduces photosynthesis by means of decreasing stem temperature. However, this seems unlikely since then all of the plant should be heavily covered by spines in order to increase its photosynthetic activity. This would occur especially in small branches, which are closer to the ground and therefore exposed to the highest temperatures (Nobel et al. 1986). This pattern has been observed in some *Opuntia* which have their lower cladodes covered by a spiny mat (Bravo-Hollis 1978). Besides, Parker's (1988) and our own results show that plants heavily covered by cephalium experience reduced reproduction and growth, a fact that does not agree with a hypothesis of increased photosynthetic activity under the cephalium. On the contrary, it shows the high energetic cost of this spiny structure.

Lophocereus schottii may increase its photosynthetic area by producing new juvenile branches

below the critical height. It can also increase its reproductive surfaces by selectively lengthening some shoots, or can reduce those surfaces by detaching some of the larger reproductive stems. Thus, the arrangement and size structure of the cephalia within the individual plant may be an important variable influencing the capability of the cactus to regulate reproduction.

Our results show that cephalium is a costly structure that is involved in both the trade-offs between growth and reproduction, and between present versus future reproduction. Although there is an optimal proportion of cephalium for each age class that maximises short-term reproductive output, young plants defer reproduction by developing cephalia significantly below this threshold, and allocating resources to increased growth.

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