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 14. The geological durations of species in our analysis, from the base of the stage of first appearance to the top of the stage of last appearance, vary from 2.0 to 32 My, with a median [± 1 SE (SOM)] of 8.7 ± 0.4 My (27). Median durations are 9.3 ± 0.4 My for the shaded species in Fig. 1, and 8.3 ± 0.4 for the remaining species. The median time taken to attain peak occupancy, measured from the base of the stage of first appearance to the midpoint of the peak stage, is 4.0 ± 0.5 My for all species, 3.9 ± 0.5 My for the shaded species in Fig. 1, and 4.6 ± 0.6 My for the remaining species. The median time between the midpoint of the peak stage and the top of the stage of last appearance is 4.5 ± 0.3 My for all species, 4.6 ± 0.4 My for the shaded species in Fig. 1, and 4.5 ± 0.6 My for the remaining species. The subsets of species are statistically indistinguishable from each other in median duration, time from first appearance to peak occupancy, and time from peak occupancy to last appearance (SOM). Nor are there any significant differences between the median time from first appearance to peak and the median time from peak to last appearance (SOM).
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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S20

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References

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Transgenerational Plasticity Is Adaptive in the Wild

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Plants exhibit adaptive responses to light, but it is not known whether parental plants transmit environmental cues that elicit adaptive responses in offspring. We show that offspring life history (annual versus biennial) is influenced by the maternal light environment (understory versus light gap). This transgenerational plasticity is adaptive when offspring are grown in their maternal light environment, where seeds typically disperse. Projections of population growth show that plants that are appropriately cued for their light environment through maternal effects have 3.4 times greater fitness than otherwise. Transgenerational plasticity has evolved in response to natural variation in light and provides a flexible mechanism by which sedentary organisms cope with heterogeneous environments.

All organisms experience environmental heterogeneity. Some move to cope with variable environments, but those that cannot move require other mechanisms to ensure success. Plants have little choice in their growth environment, and seed dispersal is often limited, with most seeds falling relatively close to the maternal plant (1, 2). Thus, a seedling's growth environment may frequently be similar to its mother's, especially where habitat patches are constant between generations and larger than the scale of seed dispersal. Under these conditions, adaptive maternal cues elicited by the local habitat may evolve if they increase offspring fitness (3). In a heterogeneous environment, flexible maternal effects will confer a greater fitness advantage than fixed genetic specialization to local habitats (4, 5), because gene movement between habitats through pollen may result in sampling different environments between generations.

Plants respond to heterogeneity in their immediate environment through plasticity. This plasticity may be adaptive, enhancing individual performance (6), or simply a passive consequence of resource limitation (7, 8). Plasticity may also occur between generations if the parental environment influences the expression of offspring

traits. Transgenerational plasticity in response to maternal environments is common in plants (9–12), and maternal effects may increase maternal fitness (10). There is little evidence that transgenerational plasticity enhances offspring fitness in plants, although conditions, such as sedentary growth form, spatially patchy habitats, and limited seed dispersal, favor its evolution (10, 13). The demonstration of adaptive maternal effects requires that (i) the maternal environment influences offspring trait expression, (ii) these maternal influences are genetically based, and (iii) maternal effects enhance offspring fitness.

Campanulastrum americanum is a monocarpic herb whose populations span distinct light environments and include annual and biennial life histories. Seeds that germinate in the fall are annuals, whereas those germinating in the spring are biennials and flower during their second summer. Annual and biennial plants co-occur, and an individual's seeds may germinate in either or both seasons. We hypothesized that adaptive maternal effects may influence the life-history schedule, because germination time de-

Table 1. Analysis with generalized linear models of the influence of offspring life history and of maternal and offspring light environment on fitness components in *C. americanum*. For seedling yield, life history indicates the probability of germination and early survival as annuals and biennials. Dashes indicate factors not included in the model. *, $P < 0.10$; †, $P < 0.05$; ‡, $P < 0.01$; §, $P < 0.001$.

	Seedling yield (χ^2)	Rosette survival (χ^2)	Adult survival (χ^2)	Fruit number (F)	Seeds per fruit (F)
Life history (LH)	13.14§	-	9.54‡	41.13§	14.55§
Offspring light (OL)	10.40‡	0.00	0.58	39.09§	16.89§
Maternal light (ML)	2.86 [†]	0.00	0.07	0.41	0.31
OL × ML	8.86‡	1.98	0.00	0.23	0.06
OL × LH	947.80§	-	15.43§	0.16	0.78
ML × LH	7.61‡	-	0.29	0.63	0.40
OL × ML × LH	0.02	-	0.11	0.15	0.00
Block	845.26§	19.69	167.08§	2.50‡	1.70†
Herbivory	-	-	-	9.02§	0.80

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termines life history and maternal effects are usually strongest in seeds (9, 10). To evaluate possible adaptive maternal effects, we asked (i) whether maternal light environment influences offspring life history, (ii) if there is genetic variation for maternal light effects, and (iii) whether these maternal effects increase offspring fitness.

Our central hypothesis was that offspring fitness would be enhanced when plants were grown in the same light environment as that of the maternal plant. *C. americanum* individuals either grow in the forest understory, which receives no direct sunlight, or in tree-fall light gaps and are in full sunlight for part of each day. On average, light gaps receive 10 times the irradiance as understory habitats (14) (fig. S1). Plasticity to light is relatively well understood at the phenotypic and molecular level (15), and plastic shade-avoidance responses are often adaptive (16, 17). Light gaps are large relative to the scale of *C. americanum*'s seed dispersal (13), therefore off-

spring typically grow in the same light environment as that of their mother. It is less likely that offspring share their father's light environment, because *C. americanum* outcrosses (18) and is pollinated by bumblebees (19) that forage over areas encompassing both understory and light-gap habitats.

We pollinated full-sib mothers in the two environments with the same sire to create genetically similar offspring that differed in their maternal light environment. We planted seeds in light-gap and understory areas of the population with a partial reciprocal transplant experimental design (14). Both maternal and offspring light environments influenced the number of annuals and biennials that germinated and survived as seedlings (seedling yield). Most seeds in light gaps germinated in the fall as annuals, and most seeds in the understory germinated in the spring as biennials (offspring light; Table 1 and Fig. 1). Seedling yield was also determined by the maternal light environment (offspring light × maternal light; Table 1). Seeds in light gaps had greater germination rates and early survival if their mother was from a light gap for both annuals (offspring light × maternal light; $F = 7.14$, $P < 0.008$) and biennials (maternal light; $F = 4.42$, $P < 0.04$; Fig. 1). Seeds in the understory had greater germination and survival if their

mother was from the understory, but this was true only for annuals (Fig. 1). Maternal effects influenced offspring life-history schedule and enhanced offspring germination and survival when seeds were grown in the same light environment as that of their mother for three of the four combinations.

We evaluated the performance of annuals (fall germinating) and biennials (spring germinating) in understory and light-gap habitats by manipulating life history such that annuals and biennials bloomed in the same year (14). Seeds were obtained from maternal plants that were reared in understory and light-gap environments. These seeds were germinated under controlled conditions in the spring so that they expressed a biennial life history. Seeds germinating in the fall were used as annuals. Biennial and annual seedlings were transplanted in subsequent years into light-gap and understory areas of the natural population. Maternal light environment did not directly influence adult fitness traits (Tables 1 and 2). In contrast, offspring growth environment affected almost all fitness components. Adult survival was greater for annuals in light gaps and for biennials in the understory (offspring light × life history; Tables 1 and 2), mirroring seedling yield. Plants in light-gap habitats had at least 5.5 times greater fruit production and 1.5 times as many seeds per fruit as understory plants (Tables 1 and 2).

We compared the fitness of annual and biennial plants in each light environment using a population projection approach. In most monocarpic plants, fitness is measured as fecundity, with individuals that do not survive to reproduce scored as zero. However, in *C. americanum*, population growth rate (λ), estimated by projection matrix analysis, is a more appropriate measure than fecundity because of the differences in life span between annuals and biennials. The contribution of annual and biennial life histories to population growth was determined with demographic loop analysis (14, 20), where the loop elasticity indicates the proportion of population growth contributed by each life history. 93.5% of the projected population growth in light gaps is due to annuals (Fig. 2A), despite the greater fruit and seed production of biennials (Tables 1 and 2). In contrast, annuals growing in the forest understory contribute only 0.3% to population growth. Overall, projected population growth is larger in light gaps than in the understory (Fig. 2A). Greater frequency and fitness of biennials in light-limited regions of the population, and annuals in light gaps where resources are more abundant, support predictions of life-history theory (21, 22) and suggest that seasonal germination plasticity, in response to the ambient light environment, enhances fitness. Furthermore, the differential performance of annuals and biennials between light habitats indicates that environmental heterogeneity helps maintain the polymorphic life history in this species.

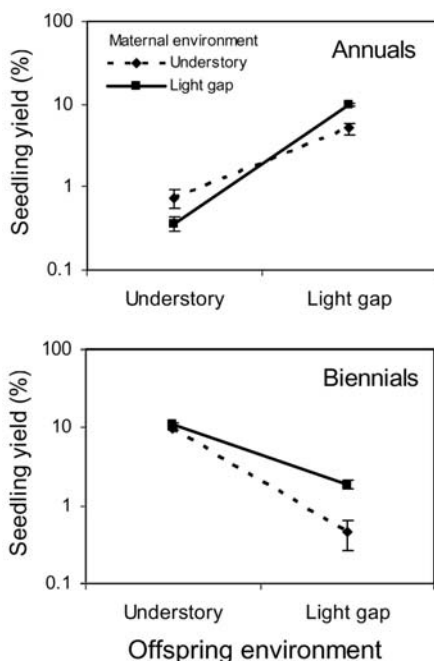


Fig. 1. The influence of maternal and offspring light on the number of annual (fall-germinating) and biennial (spring-germinating) *C. americanum* seedlings. Maternal and offspring plants were grown in forest understory or light-gap habitats. Seedling yield (\pm SEM) is the percentage of seeds that germinated and survived through the seedling stage of the life cycle.

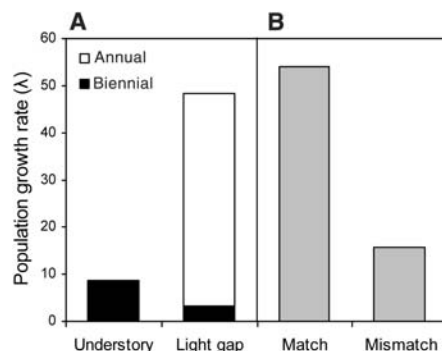


Fig. 2. (A) The contribution of annual and biennial life histories to projected population growth in *C. americanum* in forest understory and light-gap habitats. (B) Projected population growth when offspring are grown in their maternal light environment (match) or when the light environment is switched between generations (mismatch). [Natural populations are expected to have growth rates (λ) of near unity; larger growth rates are a product of experimental conditions favoring germination and survival.]

Table 2. Mean (SEM) rosette survival, adult survival, fruit number, and number of seeds per fruit for *C. americanum* growing in light-gap and understory habitats. N.A., not applicable.

	Annual		Biennial	
	Light gap	Understory	Light gap	Understory
Rosette survival (%)	N.A.	N.A.	96.9	97.4
Adult survival (%)	69.8	50.0	63.0	83.3
Fruit number	38.1 (2.5)	3.1 (0.3)	192.9 (9.6)	35.0 (1.0)
Seeds per fruit	25.5 (1.1)	8.1 (1.4)	38.1 (1.0)	25.4 (0.6)

To determine the adaptive value of maternal light effects, we analyzed λ in plants with both matching and mismatched maternal and offspring light environments. Frequency and fitness were greater for annuals in light gaps and biennials in the understory. The projection matrix mimicked these conditions with data for annuals from seeds of sunlight-grown mothers planted in light gaps and for biennials from seeds of shade-grown mothers planted in the understory (14). The conditions of a second projection matrix were the same as those of the first, except that offspring were not grown in their mother's environment. A demographic loop analysis was conducted on each matrix. λ for mismatched maternal and offspring environments was less than a third of that when they matched (Fig. 2B), indicating that maternal environmental effects enhance offspring fitness.

We tested whether maternal light effects were genetically variable, focusing on germination of light-gap annuals and understory biennials from families with all combinations of maternal and offspring environments. The effect of the maternal light environment on the proportion of fall-germinating seeds in light gaps and spring-germinating seeds in the understory varied among families (life history \times family \times maternal light; $\chi^2 = 37.20$, $df = 1$, $P < 0.011$; table S1), indicating genetic variation for maternal environment effects on seedling traits that influence fitness.

We demonstrated that offspring have greater rates of germination and early life survival when planted into their maternal environment and that

these early life effects influence fitness as measured by λ . Because seed dispersal is limited, most *C. americanum* individuals will experience their maternal light environment. Maternal effects that enhance performance in this environment represent transgenerational adaptive plasticity and allow for phenotypic adaptation to local environmental conditions. In plants, which lack the ability to escape their environment, maternal effects may serve as a form of environmental cuing between generations that enhance offspring performance. Maternal environmental effects should be favored over fixed specialization when genes move between environments via pollen and occasionally via seed. Seeds that disperse outside the maternal environment will suffer reduced fitness for a generation, but recovery is expected in locally produced offspring. As such, maternal effects represent a flexible evolutionary mechanism for sedentary organisms to cope with heterogeneous environments.

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Materials and Methods

Fig. S1

Table S1

References

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Widespread Monoallelic Expression on Human Autosomes

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Monoallelic expression with random choice between the maternal and paternal alleles defines an unusual class of genes comprising X-inactivated genes and a few autosomal gene families. Using a genome-wide approach, we assessed allele-specific transcription of about 4000 human genes in clonal cell lines and found that more than 300 were subject to random monoallelic expression. For a majority of monoallelic genes, we also observed some clonal lines displaying biallelic expression. Clonal cell lines reflect an independent choice to express the maternal, the paternal, or both alleles for each of these genes. This can lead to differences in expressed protein sequence and to differences in levels of gene expression. Unexpectedly widespread monoallelic expression suggests a mechanism that generates diversity in individual cells and their clonal descendants.

In diploid eukaryotic organisms, it is generally assumed that the maternally and paternally derived copies of each gene are simultaneously expressed at comparable levels. However, there are exceptions where only one of the alleles is

expressed. Monoallelically expressed genes fall into three distinct classes. One class is the autosomal imprinted genes (such as *IGF2* and *H19*) whose monoallelic expression is regulated in a parent-of-origin-specific manner (1). A second class is X-inactivated genes regulated by a random process: Early in development, around the time of implantation, half of the cells inactivate the maternal X chromosome and half inactivate the paternal X chromosome (2). A third class is autosomal genes subject to random

monoallelic expression (3–9), including the odorant receptor genes, as well as genes encoding the immunoglobulins, T cell receptors, interleukins, and natural killer cell receptors. For genes in this class, some cells express the maternal allele and other cells express the paternal allele. For some genes, cells expressing both alleles are also present [e.g., members of the interleukin gene family (5, 6)]. This third class was considered to comprise isolated examples of genes involved in the immune or nervous systems. Here, we present the development of a method for genome-wide identification of such genes, which revealed that more than 5% of assessed genes were subject to random monoallelic expression.

To carry out a genome-wide search for genes subject to random monoallelic expression, we used the Affymetrix Human Mapping 500 K array set, modifying the protocol to allow examination of RNA rather than DNA (10) (fig. S1). The locations of single-nucleotide polymorphisms (SNPs) on the Affymetrix 500 K SNP array are arbitrary with respect to locations within genes, with ~1% falling within exonic sequence and ~36% within intronic sequence. To allow the use of intronic SNPs, we purified nuclei so as to enrich intronic RNA. This RNA was then converted into double-stranded cDNA and used

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