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## PLASTICITY OF CHASMOGAMOUS AND CLEISTOGAMOUS REPRODUCTIVE ALLOCATION IN GRASSES

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### ABSTRACT

Cleistogamy is more common in grasses than in any other angiosperm family. Both self-fertilized cleistogamous (CL) spikelets and open-pollinated chasmogamous (CH) spikelets are typically produced. Relative allocation to CL and CH varies among species and populations, and is influenced by ontogeny and environment. The balance between reproductive modes can be expressed as a CH/CL ratio. This ratio is very plastic and stressful conditions can result in values  $<1.0$ . In *Amphicarpum purshii*, an annual with subterranean CL spikelets, CH/CL declined as density increased because CH decreased more than CL as size was reduced by intraspecific competition. In the shade-tolerant annual *Microstegium vimineum*, CH/CL was lowest in large greenhouse-grown plants in an unlimited, sunny environment, but was highest in small plants from a shady forest interior; tiller vegetative mass often showed a negative allometric relation to CH and CL allocation. In the perennial *Dichanthelium clandestinum*, CH and CL allocation varied among populations, but there was no consistent effect of light on CH/CL. The phenology of reproduction strongly affects CH/CL. In *Danthonia spicata*, CH/CL was high early in the season as CH flowering commenced, but dropped quickly as axillary CL spikelets matured; *A. purshii* showed the opposite pattern because CL reproduction occurred first. The assumption that cleistogamy simply provides reproductive assurance should be reevaluated in light of new information on phenology and allometry. Changes in the balance between CH and CL caused by environmental factors may be indirect effects of size. Evolutionary models that do not explore the plasticity and allometry of CH and CL reproduction may not be useful in predicting the myriad patterns in nature.

Key words: allometry, chasmogamy, cleistogamy, grasses, phenotypic plasticity, Poaceae, reproductive allocation.

### INTRODUCTION

Cleistogamy (CL) is the production of flowers that do not open and undergo self-fertilization “in the bud” (Lord 1981). Most species that have CL flowers can and do continue to make open, potentially cross-pollinated chasmogamous (CH) flowers. Because an individual usually can make both floral forms and they may be present at the same time, CL species are often considered to have a mixed breeding system or “multiple strategy” (Lloyd 1984; Schoen 1984; Redbo-Torstensson and Berg 1995; Masuda et al. 2001). Due to the structural and developmental differences typically found between CH and CL flowers (and sometimes, between the resulting fruits and seeds), CL species are also considered to show reproductive dimorphism (Lord 1981; Clay 1983a; Schoen and Lloyd 1984; Cheplick 1994; Plitmann 1995).

In Poaceae, CL is more common than in any other angiosperm family and has been reported in over 320 species (Campbell et al. 1983). Cleistogamy may be due to spikelets that do not open because of modified floral parts, precocious maturation while retained within enclosing leaf sheaths, or lodicule failure (Campbell 1982; Heslop-Harrison and Heslop-Harrison 1996). For example, Campbell (1982) described how, in some species of *Andropogon* L., spikelets within the raceme sheath can go through anthesis and self-fertilize before the inflorescence fully emerges from the enclosing sheath. Without detailed observation, the above types

of CL may be difficult to detect in the field and have probably led to underestimates of the extent of self-fertilization in grasses. Other types of CL are more readily observed by casual inspection. “Sheath fertilization” involves the retention of spikelets on non-emergent, axillary inflorescences enclosed within leaf sheaths and is the most common type of CL in grasses (Campbell et al. 1983). Depending on the species, axillary spikelets may be found all along the stem axis or be mostly concentrated at the basal nodes (Dyksterhuis 1945; Dobrenz and Beetle 1966; Cheplick and Clay 1989; Cheplick 1996). In a few grasses, CL spikelets and caryopses (seeds) mature at the ends of specialized culms beneath the soil surface (Campbell et al. 1983; Cheplick 1994).

The relative extent of CL can vary greatly both between and within phylogenetically related species (Campbell 1982). Perhaps the best example is Clay’s (1983a) detailed comparison of multiple populations of four species of *Danthonia* DC. Percent CL was defined as the number of CL spikelets divided by the number of CH + CL spikelets. Hence, % CL shows the fraction of the total flowers that were CL at the time the population was sampled. For five populations of *D. sericea* Nutt., mean % CL ( $\pm$  SE) was only  $2.7 \pm 0.3\%$ , while for two populations of *D. compressa* Austin % CL was  $50.2 \pm 1.0\%$ . Populations were most variable for *D. spicata* (L.) P. Beauv., ranging from 5 to 43% CL ( $x \pm$  SE =  $24.5 \pm 0.4\%$ ). Because higher % CL in *D.*

*spicata* was associated with disturbed and mown habitats; Clay (1983a) suggested grazing pressure might generally favor increased levels of CL in grasses, a view shared by others (Dyksterhuis 1945; Campbell et al. 1983).

Other research has indicated that the extent of CL in grasses can vary among seed-derived sibships (Clay 1982; Cheplick and Quinn 1988) and among clonal replicates in perennials (Cheplick 1995). In *Amphicarpum purshii* Kunth, an annual, the ratio of seeds from CH spikelets to those from CL spikelets had a significant narrow-sense heritability of 0.56 (Cheplick and Quinn 1988). For the perennial *Danthonia spicata*, Clay (1982) reported broad-sense heritabilities of 0.53 and 0.72 in the field and greenhouse, respectively, for the proportion of CL spikelets produced per tiller. Although simple recessive inheritance of CL (one to three genes) has been reported in some grain crops (Merwine et al. 1981; Chhabra and Sethi 1991; Kurauchi et al. 1993; Ueno and Itoh 1997), like most life-history traits in wild species, CL is likely to be under quantitative genetic control (Mazer and LeBuhn 1999). Given the primacy of genetic variation to the microevolution of populations, it is surprising that so little effort has gone into documenting quantitative genetic variation in the extent of CL vs. CH in different species.

### Theory

Theoretical considerations of the evolution of CL have involved comparative cost-benefit analyses of CH vs. CL flower production (Schoen and Lloyd 1984) or variation in the relative fertility of the two floral types (Redbo-Torstensson and Berg 1995; Masuda et al. 2001). Because the paternal costs of producing prodigious amounts of pollen in outcrossed spikelets may be high in grasses (e.g., Schoen 1984), maternal reallocation of conserved resources to CL spikelets could enhance plant fitness by increasing the number or size of maturing seeds (Schoen and Lloyd 1984; Lloyd 1987). Indeed, seeds of CL spikelets are heavier than those of CH spikelets in a number of grass species (Campbell et al. 1983; Schoen 1984; Cheplick 1994). Assuming no inbreeding depression, this can translate into more successful establishment of seedlings that germinate from the seeds of CL spikelets (Cheplick and Quinn 1983; Clay 1983b; Schoen 1984).

The production of CL flowers might compensate for the loss in fruit set due to the unsuccessful fertilization of many CH flowers, providing "reproductive assurance" (Redbo-Torstensson and Berg 1995; Culley 2002). Where environments fluctuate between conditions that are favorable and unfavorable for each reproductive mode, CL may be envisaged as a "bet-hedging strategy" (e.g., Berg and Redbo-Torstensson 1998). The relative balance between CH and CL should depend on the ability of a plant to assess and respond to environmental variation (Schoen and Lloyd 1984). In the model presented by Masuda et al. (2001), seasonal variation in the fertility of CH flowers was used to explain why some species switch between reproductive modes during the course of the growing season.

There is no question that the relative production of CH and CL flowers, fruits, and seeds is markedly plastic in most facultatively CL plants (e.g., Schemske 1978), including

grasses (Clay 1982, 1983a; Bell and Quinn 1987; Cheplick 1995). Environmental factors known to affect the extent of CL in grasses include light, soil nutrition and moisture, and competition and herbivory. Because CL flowers are energy efficient for a plant to produce and provide reproductive assurance (Schemske 1978; Schoen 1984; Schoen and Lloyd 1984), it has long been noted that whenever environmental conditions are stressful there tends to be greater reproduction by CL compared to CH (Dyksterhuis 1945; Wilken 1982; Campbell et al. 1983). Hence, the ratio of CH to CL is expected to decline with increasing environmental stress. It is also recognized that both CH and CL depend on ontogeny, varying with plant size and phenological stages in ways that may be predictable for some species (Clay 1982; Jasieniuk and Lechowicz 1987; Cheplick and Clay 1989; Cheplick 1994; Diaz and Macnair 1998). As will be explored later in this paper, the challenge for the future generation of models of the evolution of mixed CH/CL breeding systems will be to account for the marked plasticity of the two reproductive modes in relation to environmental factors. In addition, they will need to explore the relations of plant size and phenological stage to observed changes in the extent of CL shown during plant development.

### Objectives

Given the predictions made by theoretical models for the evolution of CH/CL and the complexities inherent in trying to understand life-history traits that vary greatly with environmental conditions, one objective of this paper will be to summarize information on the relative allocation to CH and CL in a variety of grasses exposed to variable environments. The balance between reproductive modes will be expressed as a CH/CL ratio. Because many of the changes in this balance that are mediated by environmental factors may be the indirect effect of plant size, a second objective will be to present allometric relationships of CH and CL to vegetative mass for several grass species for which data are available. A final objective is to describe how temporal changes in CH/CL are related to the phenology of the two reproductive modes.

## MATERIALS AND METHODS

### Data Sources

Information on CH and CL allocation expressed as a proportion of plant (or tiller) dry mass in relation to environmental factors was obtained from published sources. Ratios of CH/CL were calculated from allocation or dry mass data. Allometric relationships between CH or CL allocation and vegetative mass were characterized by regression analysis and results are depicted in conventional  $\log_{10}$ - $\log_{10}$  plots (Niklas 1994). Vegetative mass is the sum of root and shoot mass.

The following environmental factors and grasses were examined: density for *Amphicarpum purshii* (Cheplick 1982; Cheplick and Quinn 1983), soil nutrients for *A. purshii* (Cheplick 1989), and *Triplasis purpurea* (Walter) Chapm. (Cheplick 1996), light and soil moisture for six *Dichanthelium clandestinum* (L.) Gould populations (Bell and Quinn 1987), and light for *Microstegium vimineum* (Trin.) A. Camus (Che-

plink unpubl. data; see below). In addition, phenological data on CH and CL allocation were used to depict temporal changes in CH/CL across a single growing season in *Amphibromus scabrivalvis* (Trin.) Swallen (Cheplick and Clay 1989), *Amphicarpum purshii* (Cheplick 1982), and *Danthonia spicata* (Cheplick and Clay 1989).

**Data for *Microstegium vimineum*.**—Japanese stiltgrass is an Asian species that has become very invasive in the eastern USA (Hunt and Zaremba 1992; Gibson et al. 2002). Although it is a summer annual C<sub>4</sub> grass, it is shade tolerant (Horton and Neufeld 1998) and tends to grow in mesic deciduous forests where it can form a dense, lawn-like monoculture underneath the canopy. In temperate regions, it recruits from seed in early spring and produces culms that can branch and root from the lowermost nodes. Terminal racemes that bear CH spikelets emerge in late summer. The spikelets undergo anthesis and mature seed in early autumn. In addition, CL spikelets form on sheath-enclosed axillary racemes beginning at the uppermost nodes in late summer. Mature seeds from CH and CL spikelets are present simultaneously on individual plants in early autumn.

A large stand within a forest in Millstone Township, central New Jersey, USA, was selected for detailed study. Complete tillers with mature seeds were collected every 20 m along a transect through the shady forest understory on 5 Oct 2001 until seeds from 20 plants had been sampled. All seeds were stratified at 4°C for four months on moistened filter paper in petri dishes. Seedlings obtained from these seeds were used to establish a greenhouse population of *M. vimineum* on 3 May 2002. There were 120 plants, 6 per family. Details of this experiment are reported elsewhere (Cheplick 2005). For the present purpose, it should be recognized that these plants experienced a high-resource environment, growing in high light and supplied with mineral nutrients (fertilizer) on two occasions. As terminal racemes with seeds of CH spikelets matured (4 Sep–15 Oct 2002), a single, large senesced tiller was sampled. Tiller length, number of branches, and culm, leaf, terminal CH, and axillary CL seed dry mass (after two days at 60°C) were obtained. Data were collected for 20 randomly selected individuals (one per maternal family).

To compare the very large plants from the high-resource, greenhouse environment to plants in the more stressful natural environment, two tiller populations were sampled at the field site in autumn 2002, when tillers bore mature CH and axillary CL racemes. On 15 Oct, tillers were collected from the forest edge where plants experienced full sun (1100–1800  $\mu\text{mol}/\text{m}^2/\text{s}$ ) for at least 2–4 hr/day. On 24 Oct, 20 additional tillers were collected from within the shaded forest interior where light levels during the previous growing season (barring sunflecks) were only 5–30  $\mu\text{mol}/\text{m}^2/\text{s}$  for the entire day (Cheplick unpubl. data).

These tillers from the “edge” and “shaded” populations were dried for two days at 60°C and data were recorded as for the greenhouse population described above. It should be noted that the genetic background for all three experimental groups (greenhouse, edge, shaded) should be similar because all plants sampled had been part of the large original *M. vimineum* stand at the field site.

Table 1. Dry mass (mg) of vegetative (root + shoot) parts, and CL and CH spikelets and seeds of *Amphicarpum purshii* reared in a greenhouse at variable densities. Pots were 11.4 cm in diameter. Data adapted from Cheplick (1982). Values are  $x \pm \text{SE}$ ;  $N = 10$ . Coefficients of variation are in parentheses.

Density	Vegetative	CL	CH
Control (1/pot)	722.9 $\pm$ 61.4 (26.8)	92.2 $\pm$ 11.0 (37.8)	56.3 $\pm$ 4.8 (26.9)
Low (5/pot)	338.7 $\pm$ 20.5 (19.1)	44.0 $\pm$ 2.2 (15.5)	11.5 $\pm$ 1.3 (34.6)
Medium (15/pot)	216.5 $\pm$ 4.6 (6.7)	31.4 $\pm$ 1.4 (14.2)	2.4 $\pm$ 0.3 (43.4)
High (30/pot)	174.7 $\pm$ 8.4 (4.8)	27.1 $\pm$ 1.7 (19.3)	1.1 $\pm$ 0.2 (62.0)

## RESULTS

### Density

Plasticity of CH and CL allocation in relation to density was determined from an experiment with the amphicarpic annual *Amphicarpum purshii* (Cheplick and Quinn 1983), a species with subterranean CL spikelets and aerial, terminal CH spikelets (Cheplick 1994). In an intraspecific competition experiment, plants were reared in a greenhouse at four densities: 1, 5, 15, and 30 per 11.4 cm diameter pot. These will be referred to as control, low, medium, and high densities, respectively, and correspond to 98.0, 489.9, 1469.6, and 2939.2 plants/m<sup>2</sup>. These treatments nicely bracket the natural range in density from 152/m<sup>2</sup> to 2808/m<sup>2</sup> (calculated from data in Cheplick 1982). The experiment lasted three months and there were ten replications of each density (Cheplick and Quinn 1983). At harvest, despite a decrease in the dry mass of both CH and CL reproductive components with increasing density (Table 1), CL allocation was remarkably constant, varying only from 13 to 16% (Fig. 1). In contrast, CH allocation declined from 8% in the control to 0.6% at the highest density. Thus, CH/CL showed a precipitous decrease with increasing density (Fig. 2).

Because *A. purshii* size was also reduced significantly with density (Table 1; Cheplick and Quinn 1983), the allometry of CH/CL to vegetative dry mass (i.e., root + shoot mass) was determined across densities. The relationship of CH/CL to vegetative mass (VM) was best described by a polynomial regression (Fig. 3):  $\log(\text{CH}/\text{CL}) = -26.0 + 17.8 \log \text{VM} - 3.1 \log(\text{VM})^2$  ( $N = 30$ ,  $r^2 = 0.84$ ,  $P < 0.001$ ). In this species, CH/CL tends to increase up to a point, but then levels off to where the allocation to CH is about 60% that of allocation to CL in the largest plants (Fig. 3). It is also noteworthy that CH allocation was more variable than CL allocation at low, medium, and especially high density, as assessed by coefficients of variation (Table 1).

### Soil Fertility

Plasticity of the balance in CH and CL in relation to soil fertility was explored for *Triplaxis purpurea*, an annual with axillary CL. In this greenhouse study, plants were exposed to three treatments: low nutrients (water only), medium nutrients (1.5 g/liter 20-20-20 N-P-K fertilizer) and high nutrients (3 g/liter 20-20-20 N-P-K fertilizer). Details of the

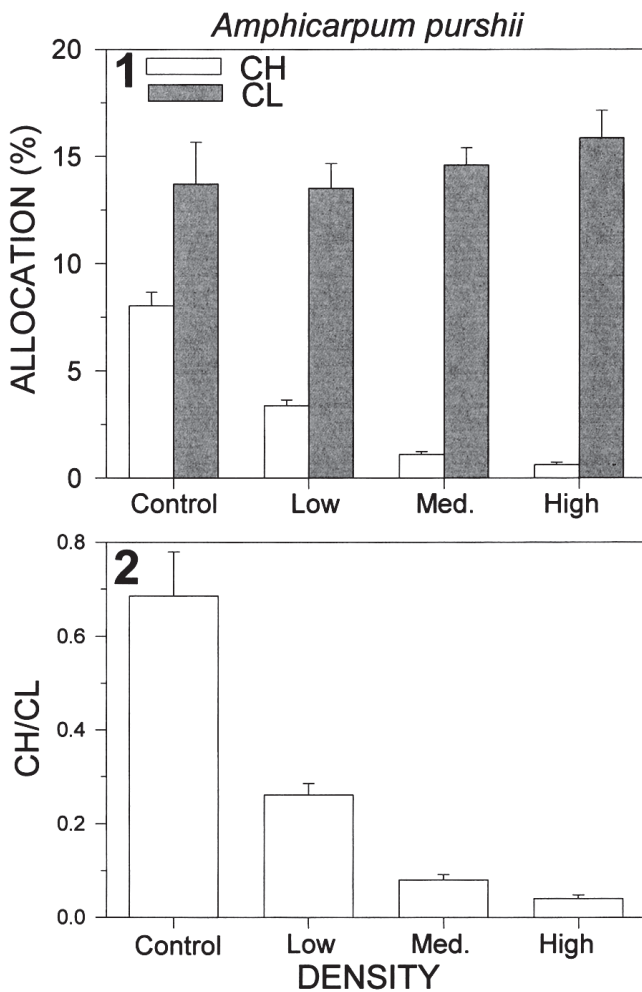


Fig. 1, 2.—Relation of CH and CL allocation, and CH/CL, to intraspecific density in *Amphicarpum purshii*. All bars are  $\bar{x} \pm SE$ ;  $N = 10$ .—1. Percent allocation of vegetative mass to CH and CL.—2. Ratio of CH to CL.

growing conditions are available in Cheplick (1996). Although plant size data were not recorded, the number of seeds matured in CH and CL spikelets and their dry masses were determined. The mean total number of seeds/tiller, % CL seeds/tiller, and CH/CL mass ratio are shown in Table 2. Not surprisingly, higher nutrient levels enhanced seed output (for  $\log_{10}$  transformed no. seeds,  $F = 8.49$ ,  $P < 0.001$ ); however, the percent of seeds matured in CL spikelets was high (75–81%) regardless of nutrient conditions (for arcsine, square-root transformed proportion of CL seeds,  $F = 1.34$ ,  $P > 0.2$ ; Table 2). With medium or high levels of nutrients, CH/CL showed no significant increase relative to low nutrients (for arcsine, square-root transformed CH/CL,  $F = 0.53$ ,  $P > 0.5$ ).

In a study of the effects of nutrient availability in *Amphicarpum purshii*, plants were subjected to high (3 g/liter 20-20-20 N-P-K fertilizer) or low (water only) nutrients and harvested when senesced (Cheplick 1989). Although high nutrients resulted in significantly greater vegetative mass ( $\bar{x} \pm SE$ : 384.1  $\pm$  9.7 mg in high vs. 287.3  $\pm$  15.6 mg in low nutrients), the dry mass of CL and CH seeds was not correlated with vegetative mass (Cheplick 1989). From these

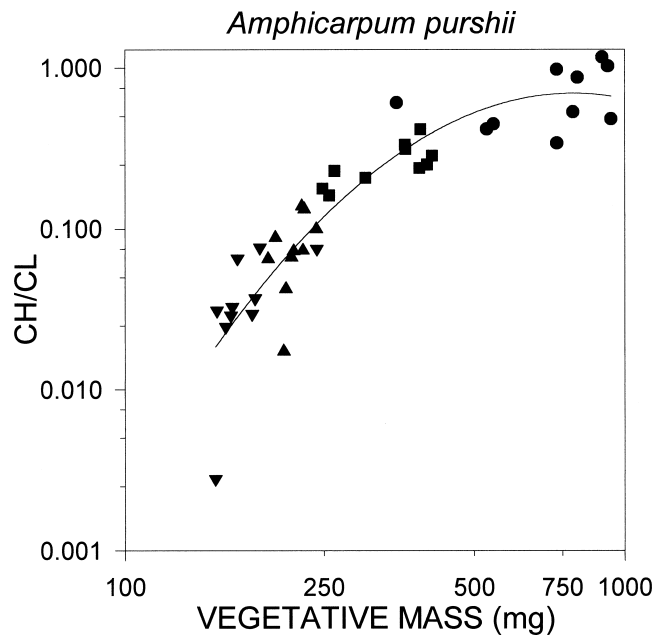


Fig. 3.—Allometry of CH/CL ( $\log_{10}$ - $\log_{10}$  plot) in the intraspecific competition experiment with *Amphicarpum purshii*. Symbols show plants from control (●), low (■), medium (▲), and high (▼) density treatments (see Cheplick and Quinn 1983).

data, CH/CL ratios were calculated. There was no significant difference in CH/CL in high nutrients (0.2468  $\pm$  0.0207) vs. low nutrients (0.2289  $\pm$  0.0106) ( $t = 0.76$ ,  $P > 0.5$ ).

*Light and Soil Moisture*

In a detailed study of the effects of soil moisture and light intensity on the plasticity of CH and CL allocation patterns, Bell and Quinn (1987) investigated six populations of the caespitose perennial *Dichanthelium clandestinum*. Seeds were collected from six sites in central New Jersey that differed in soil moisture and light levels. Some plants were reared in a greenhouse along a soil moisture gradient, while others were subjected to one of three light treatments: high (68–86% full sun), medium (31–40% full sun), or low (11–14% full sun). Allocation to CL was always much greater than allocation to CH in all treatments. Across the soil moisture gradient, allocation to CH remained relatively constant, but was <1% in all populations. However, the proportion of the reproductive allocation comprising CL flowers increased as soil moisture decreased, in accordance with the expectation of greater CL under stressful conditions. Nevertheless, it may be suspected that the changes in CH/CL across the moisture gradient were simply indirect effects of plant size

Table 2. Mean ( $\pm$  SE) number of seeds per tiller, percent of seeds from CL spikelets, and CH/CL mass ratio for *Triplasis purpurea* reared in a greenhouse at three levels of soil nutrients ( $N = 13$  per nutrient level). See Cheplick 1996.

Nutrients	No. seeds	% CL	CH/CL
Low	44.75 $\pm$ 4.67	80.95 $\pm$ 2.98	0.2678 $\pm$ 0.0631
Medium	80.92 $\pm$ 6.43	74.59 $\pm$ 3.01	0.3439 $\pm$ 0.0591
High	78.00 $\pm$ 9.12	77.64 $\pm$ 2.69	0.3012 $\pm$ 0.0422

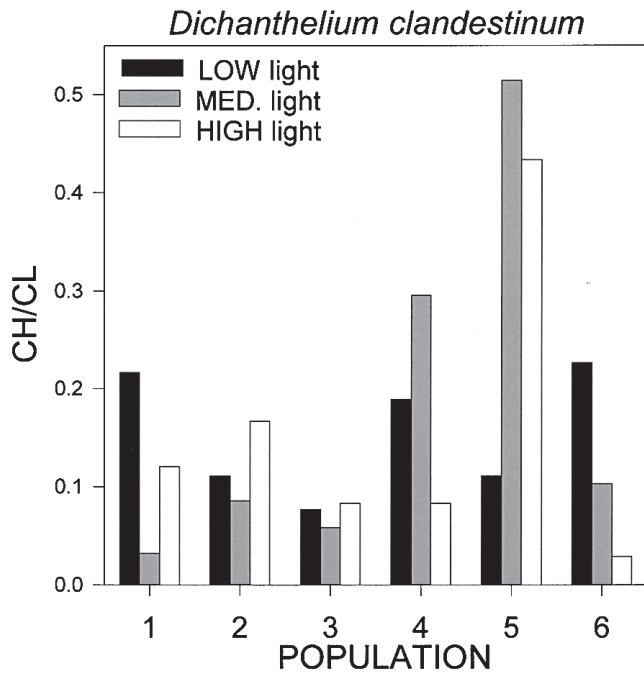


Fig. 4.—Relation of CH/CL to light intensity for six populations of *Dichanthelium clandestinum* in New Jersey, USA. Data were calculated from mean values for % CH and % CL reported in Bell and Quinn (1987).

because biomass was significantly lower whenever soil moisture was limited (Bell and Quinn 1987).

Populations showed variable patterns of plasticity in CL allocation along the moisture gradient. The two populations that showed a relatively high allocation to CL at low soil moisture were from sites where soil moisture was typically low, suggesting increased CL as a possible adaptation to dry conditions.

In the light intensity experiment, populations of *D. clandestinum* differed significantly in allocation to CH and CL within and across all light treatments (Bell and Quinn 1987). Hence, there were genetically based differences in population allocation patterns to CH and CL. Ratios of CH/CL were calculated from the allocation data (Fig. 4) in Bell and Quinn (1987). Populations varied from no effect of light on CH/CL (population 3 in Fig. 4), a decrease in CH/CL with increasing light (population 6), and an increase in CH/CL with increasing light (population 5). Population 5 was the only example of the predicted increase in CH under high resource conditions (Fig. 4).

For the three populations of the invasive annual *Microstegium vimineum*, mean ( $\pm$  SE) vegetative mass for the greenhouse-, edge-, and shade-reared tillers was  $796.2 \pm 56.3$  mg,  $281.2 \pm 25.8$  mg, and  $140.1 \pm 17.8$  mg, respectively. The greenhouse tillers had the lowest allocation to both CH ( $2.1 \pm 0.1\%$ ) and CL ( $5.1 \pm 0.4\%$ ) (Fig. 5). Tillers from the sunny edge habitat had the highest allocation to CH ( $7.7 \pm 0.9\%$ ) and CL ( $15.1 \pm 1.3\%$ ). Tillers from the shaded forest interior allocated a similar amount of biomass to CH ( $6.0 \pm 0.6\%$ ) and CL ( $6.9 \pm 0.7\%$ ). Interestingly, CH/CL was lowest in the resource-rich greenhouse and did not differ from that of field tillers from the edge habitat (Fig. 6). However, tillers from the shaded habitat had the highest CH/CL

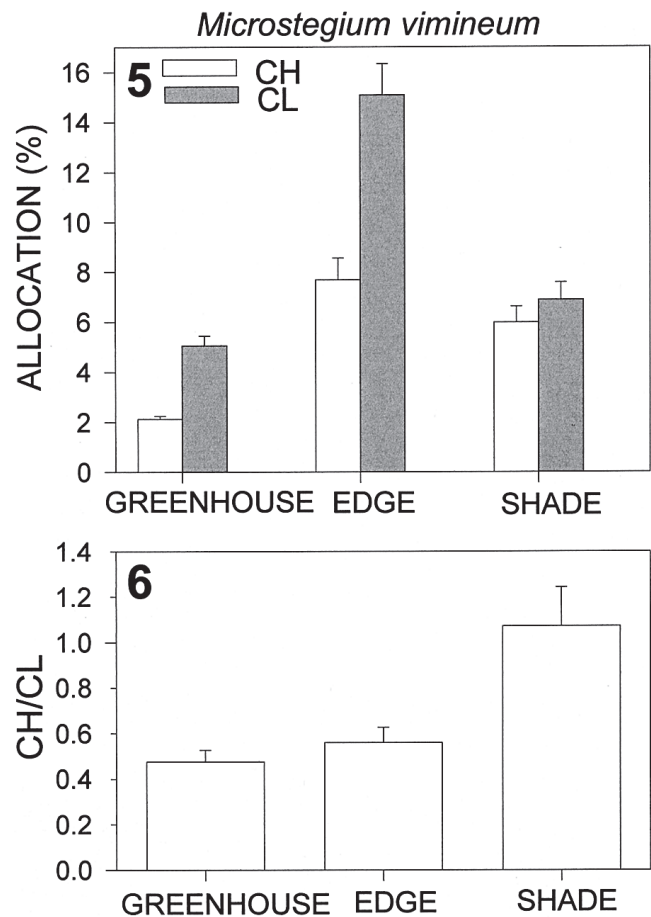


Fig. 5, 6.—Relation of CH and CL allocation, and CH/CL, to population source in *Microstegium vimineum*. Bars are  $x \pm$  SE;  $N = 20$  (except for edge where  $N = 15$ ).—5. Percent allocation of tiller vegetative mass to CH and CL.—6. Ratio of CH to CL.

ratio, despite being collected from a population with a very high intraspecific density (Cheplick 2005).

Because the three tiller groups differed greatly in size, allometric relationships of CH and CL allocation to vegetative mass (VM) were plotted (Fig. 7, 8). For shaded tillers there was a significant decrease in % CH with increasing VM ( $\log[\% \text{ CH}] = 1.64 - 0.44 \log \text{ VM}$ ;  $r^2 = 0.28$ ,  $P < 0.05$ ), but this relationship was insignificant for edge ( $r^2 = 0.13$ ,  $P > 0.05$ ) and greenhouse ( $r^2 = 0.03$ ,  $P > 0.05$ ) tillers. In contrast, there was a highly significant decrease in % CL with increasing VM for greenhouse tillers ( $\log[\% \text{ CL}] = 3.33 - 0.92 \log \text{ VM}$ ;  $r^2 = 0.50$ ,  $P < 0.01$ ). Percent CL and VM were not correlated in edge ( $r^2 = 0.11$ ,  $P > 0.05$ ) or shaded ( $r^2 = 0.14$ ,  $P > 0.05$ ) tillers. Due to these allometric patterns, CH/CL was positively related to VM in the greenhouse tillers ( $\log[\text{CH/CL}] = -2.59 + 0.77 \log \text{ VM}$ ;  $r^2 = 0.29$ ,  $P < 0.01$ ). Thus, the largest plants in the most resource-rich environment preferentially allocated more to CH relative to CL, in agreement with the idea of CH as an opportunistic mode of reproduction.

#### Phenology

In the previous studies of CH and CL allocation patterns, data were collected at a single point in time, typically when

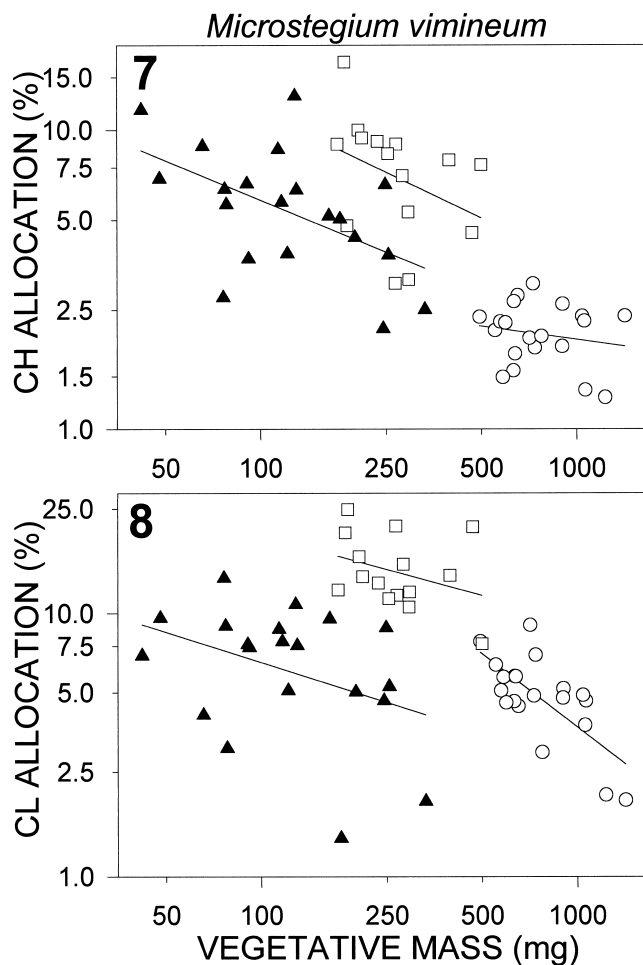


Fig. 7, 8.—Allometry of percent CH and CL allocation ( $\log_{10}$ – $\log_{10}$  plots) for three population sources in *Microstegium vimineum* from central New Jersey, USA. Tillers were from the shaded woods ( $\blacktriangle$ ), sunny edge habitat ( $\square$ ), or greenhouse ( $\circ$ ).—7. Percent allocation of tiller vegetative mass to CH.—8. Percent allocation of tiller vegetative mass to CL.

plants were mature and had produced seeds in both CH and CL spikelets. However, the phenology of CH and CL flowering can vary greatly between species, further complicating research into the evolution of mixed breeding systems. As an example, contrasting temporal patterns of CH and CL reproduction are presented for three cleistogamous grasses.

In the caespitose perennial *Danthonia spicata*, apical CH flowering precedes CL flowering and axillary CL seeds continue to mature at the upper nodes as plants age (Cheplick and Clay 1989). In a population originally collected from Durham, North Carolina, USA, but maintained in a garden plot in Bloomington, Indiana, USA, CH/CL dropped from 2.8 to 1.1 over a three-week period (Fig. 9). For another population collected from the field in Monroe County, Indiana, USA, CH/CL was 7.9 in mid-Jun, but declined to 3.3 by Jul (Fig. 10). This drop in CH/CL is predominantly due to an increase in CL allocation over time; CH allocation only varied between 9.3 and 11.0% in the garden population and decreased from 15.1 to 13.3% in the field population over five weeks. At the same time, CL allocation increased from

3.3 to 9.1% in the garden and from 1.9 to 3.3% in the field (Cheplick and Clay 1989).

In the rhizomatous perennial *Amphibromus scabrivalvis*, a population collected from Louisiana, USA, was reared outdoors in Bloomington, Indiana, USA. Reproductive tillers were sampled at three stages (Cheplick and Clay 1989): early (before terminal CH panicles had emerged), mid (at the time of terminal panicle maturation), and late (one month later). Percent allocation to CL increased from 7.0 to 14.3% while CH allocation increased from 0 to 20.6%. Hence, CH/CL showed a pronounced increase between early and late developmental stages (Fig. 11).

Data on CH and CL allocation over time were also extracted for the annual amphicarpic grass *Amphicarpum purshii* from Appendix A in Cheplick (1982). Fifteen plants were harvested from a field population 2 km south of Lakehurst in the Pinelands of New Jersey, USA, once every two weeks throughout the summer growing season. In this species, CL spikelets and seeds are matured on subterranean culms throughout the summer, while aerial spikelets and seeds on open panicles are produced only in late summer or early autumn. Between 16 and 30 Jul, CL allocation increased from 12.1 to 29.1%, but CH/CL was zero because CH panicles were not yet present (Fig. 12). Between 13 Aug and 10 Sep, CH allocation increased from 1.3 to 6.8%. Therefore, CH/CL increased substantially from 0.03 to 0.16 during this period (Fig. 12).

#### DISCUSSION

Chasmogamous and cleistogamous reproductive allocation in grasses with mixed breeding systems varies greatly among species and populations within species. Variation among populations is not surprising given the plasticity of CH and CL in relation to environmental factors such as light, soil moisture and fertility, and competitive stress. Within natural populations, underlying all of the environmental influences on CH/CL is variation in the plasticity of genotypic responses. Genetically based differences in the phenotypic plasticity of CH and CL across populations can be detected by common garden experiments (Fig. 4; Bell and Quinn 1987). Variation in CL among seed-derived sibships (Clay 1982; Cheplick and Quinn 1988) or cloned genotypes (Cheplick 1995) reveal that the raw material for population microevolution exists in the few CL grasses examined to date.

In addition to environmental and genetic considerations, temporal changes during development (ontogeny) and the life cycle (phenology) can contribute to observed variation in the balance of CH and CL, as depicted by the CH/CL ratio. The mass of vegetative parts such as leaves, stems, and roots increases during the development of both annual and perennial grasses as tillers increase in size and number. Given an allometric relationship between vegetative mass and % CH or % CL, any environmental factor that slows (or speeds) development and changes plant size can indirectly alter the CH/CL ratio (Fig. 3). The drastic reduction in size associated with increasing intraspecific competition in *Amphicarpum purshii* (Table 1) and the relative decrease in % CH (but not % CL) explains the decrease in CH/CL as density increases (Fig. 2).

The theoretical expectation that the relative proportion of

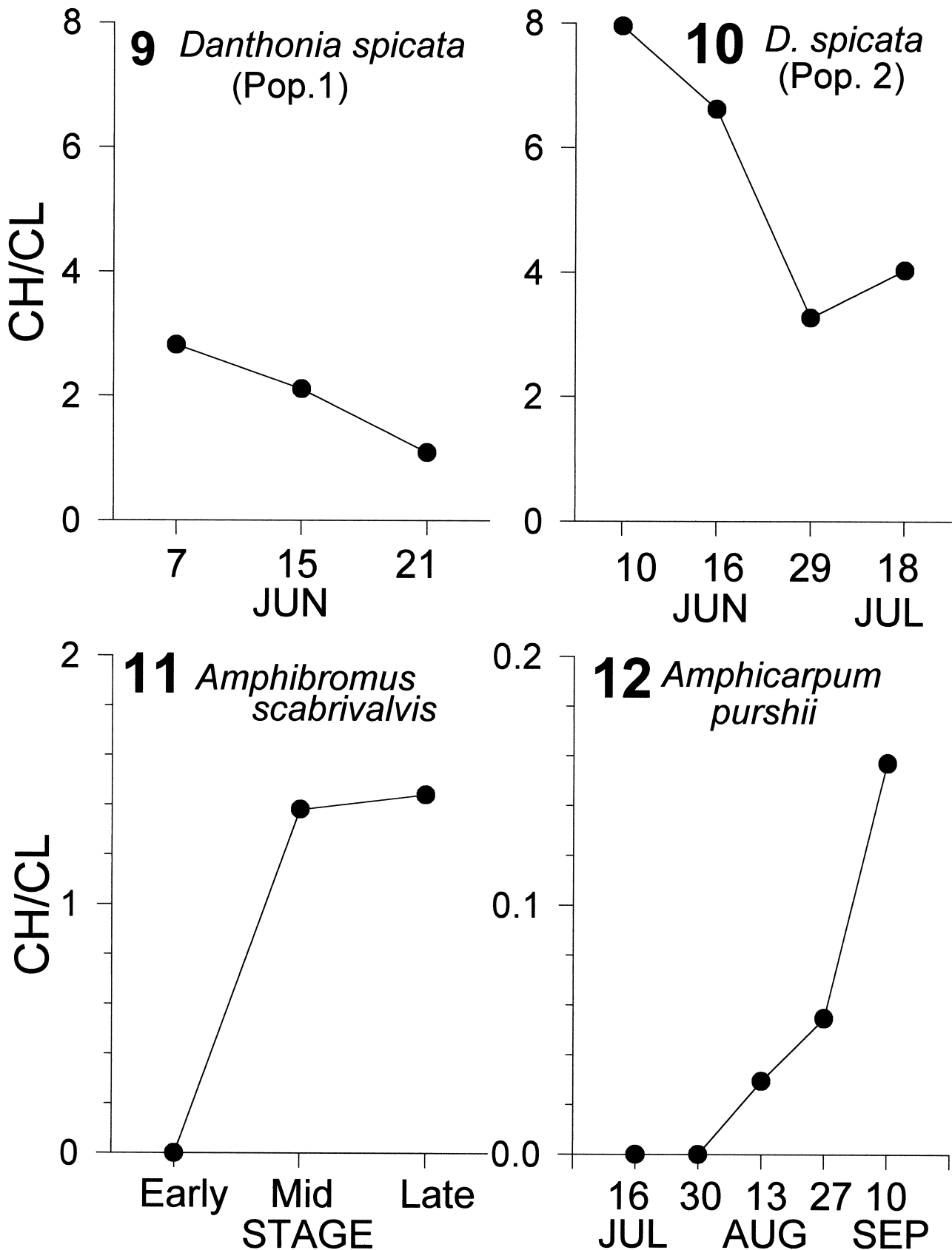


Fig. 9–12.—Contrasting patterns in the phenology of CH and CL in three grasses over a single growing season.—9. *Danthonia spicata* in a garden plot in Bloomington, Indiana, USA ( $N = 15, 14,$  and  $13$  for 7 Jun, 15 Jun, and 21 Jun, respectively).—10. *Danthonia spicata* from a field site in Monroe County, Indiana ( $N = 30$  per date).—11. *Amphibromus scabrivalvis* from Louisiana, USA, but reared outdoors in Bloomington, Indiana. “Early” is before terminal CH panicle emergence ( $N = 10$ ), “mid” is at the time CH panicles were mature ( $N = 16$ ), and “late” is one month later ( $N = 10$ ).—12. *Amphicarpum purshii* from a field site in the Pinelands of New Jersey, USA ( $N = 15$  per date).



the reproductive allocation devoted to CL would be greatest under environmentally stressful conditions is restricted to certain grasses exposed to specific conditions. This expectation is certainly not universal and cannot be unequivocally applied to all CL grasses studied to date. In *A. purshii*, most reproductive allocation was to CL at high density (Fig. 2). However, low soil nutrient availability did not significantly change the CH/CL ratio in this species, despite the smaller size of plants relative to those in higher nutrient conditions (Cheplick 1989). Likewise, in *Triplasis purpurea*, CH/CL was not significantly changed by decreasing soil fertility (Table 2). In *Dichanthelium clandestinum*, the proportion of the reproductive allocation composed of CL spikelets increased with soil moisture stress, in agreement with theoretical expectations; however, there was no consistent effect of light on CH/CL and the ratio was *greatest* under low light conditions for some populations (Fig. 4; Bell and Quinn 1987). Finally, data for *Microstegium vimineum* revealed that the lowest CH/CL ratios were obtained for the largest plants in the most resource-rich environment (Fig. 7, 8)!

In short, the proximate reason for plasticity in the CH/CL balance across variable environments can be exposed when the allometry of reproductive allocation is explored. Size dependence of both CH and CL has been recognized in other herbaceous plants with mixed breeding systems (Wilken 1982; Jasieniuk and Lechowicz 1987; Cheplick 1994; Berg and Redbo-Torstensson 1998; Diaz and Macnair 1998). Clearly, future studies of putative adaptive responses of CH and CL to environmental conditions should not ignore the role of size in mediating resource partitioning to both reproductive modes.

The patterns detected in the reproductive allocation to CH and CL for a particular species will also be closely linked to flowering phenology, which may be relatively fixed and not necessarily related to size. When CH precedes CL, a seasonal decline in CH/CL is expected (Fig. 9, 10), while the reverse is expected when CH follows CL (Fig. 11, 12). The phenological timing may be especially important in annual herbs of disturbed environments where the risks of early mortality can be high (Bazzaz 1996). For example, because *Amphicarpum purshii* allocates resources to CL much earlier in the growing season than it does to CH (Fig. 12), early death might mean that an individual has reproduced, but only via seeds matured in CL spikelets. The consistency in CH/CL phenology of species such as *A. purshii* provides a solid argument for an evolutionarily fixed strategy of reproduction. To date, it is not known to what extent mortality risks have contributed to the evolution of this particular phenological pattern in *A. purshii*, or any other annual CL species. For perennials in which seed recruitment is comparatively rare, early production of seeds by CL to provide reproductive assurance may not be a tenable evolutionary hypothesis (e.g., Berg and Redbo-Torstensson 1998).

Clearly, when trying to compare species or different experimental treatments within a species, investigators must be careful to only compare data recorded at equivalent phenological stages. Researchers should also be well aware of the relative timing of CH and CL reproduction for the species under study and how phenology might impact experimental results.

## Conclusions

Identifying the selective forces responsible for the evolution of mixed breeding systems in the grasses has been confounded by the tremendous phenotypic plasticity found among genotypes, populations, and species. It is clear that environmental factors, both abiotic and biotic, can alter the balance between CH and CL and that some proportion of the phenotypic changes in reproductive allocation can be attributed to changes in plant size. However, the ecological and evolutionary consequences of plasticity in CH and CL allocation have not been thoroughly characterized.

Population genetic structure is strongly affected by the highly inbred nature of CL breeding systems (Sun 1999; Green et al. 2001; Lu 2002). Although within-population molecular genetic diversity may be low, high levels of genetic differentiation can occur between populations (Godt and Hamrick 1998; Sun 1999). It is likely that such species exist as genetically different inbred lines that occasionally outcross (Green et al. 2001; Lu 2002). Significant quantitative genetic variation in life-history traits occurs among sibships in highly inbred species (Clay 1982; Cheplick and Quinn 1988; Charlesworth and Charlesworth 1995). Hence, the evolutionary potential of CL grasses may be considerable.

Further research is needed to test the models for the evolution and maintenance of CL, as noted over 20 years ago in the review by Campbell et al. (1983). The assumption that CL mostly provides reproductive assurance should be re-evaluated in light of information on allometric relationships and phenological patterns. Characterization of the molecular and quantitative genetic variation within and among populations, and the plasticity of life-history traits, will be necessary to further refine evolutionary models and understand the ecological success of species with mixed breeding systems.

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