

## TESTING LIFE HISTORY CORRELATES OF INVASIVENESS USING CONGENERIC PLANT SPECIES

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**Abstract.** We used three congeneric annual thistles, which vary in their ability to invade California (USA) annual grasslands, to test whether invasiveness is related to differences in life history traits. We hypothesized that populations of these summer-flowering *Centaurea* species must pass through a demographic gauntlet of survival and reproduction in order to persist and that the most invasive species (*C. solstitialis*) might possess unique life history characteristics. Using the idea of a demographic gauntlet as a conceptual framework, we compared each congener in terms of (1) seed germination and seedling establishment, (2) survival of rosettes subjected to competition from annual grasses, (3) subsequent growth and flowering in adult plants, and (4) variation in breeding system. Grazing and soil disturbance is thought to affect *Centaurea* establishment, growth, and reproduction, so we also explored differences among congeners in their response to clipping and to different sizes of soil disturbance.

We found minimal differences among congeners in either seed germination responses or seedling establishment and survival. In contrast, differential growth responses of congeners to different sizes of canopy gaps led to large differences in adult size and fecundity. Canopy-gap size and clipping affected the fecundity of each species, but the most invasive species (*C. solstitialis*) was unique in its strong positive response to combinations of clipping and canopy gaps. In addition, the phenology of *C. solstitialis* allows this species to extend its growing season into the summer—a time when competition from winter annual vegetation for soil water is minimal. Surprisingly, *C. solstitialis* was highly self-incompatible while the less invasive species were highly self-compatible. Our results suggest that the invasiveness of *C. solstitialis* arises, in part, from its combined ability to persist in competition with annual grasses and its plastic growth and reproductive responses to open, disturbed habitat patches.

**Key words:** annual grassland, California, USA; *Centaurea melitensis*; *Centaurea solstitialis*; *Centaurea sulphurea*; congeneric species; invisibility *cf.* life-history correlates; invasive species; invasiveness, predicting; Mediterranean-type climate; plant community; plant traits.

### INTRODUCTION

Predicting which exotic plant species will become invasive has proved to be very difficult. Techniques such as multivariate analyses of species characteristics, climate-matching models, and greenhouse experiments have been of limited value for establishing general patterns of invasiveness (Williamson 1996). Manipulative field experiments with congeners that differ in invasiveness have been suggested as an approach with great promise (Mack 1996), however only two studies have been attempted (Thébaud et al. 1996, Lambrinos 2002).

Perhaps one reason for the limited success in predicting invasiveness is that predictions often do not specify an environmental context and, as a result, important ecological characteristics of invaded communities are not considered. A particularly well researched community is California's Central Valley grassland,

which has been extensively altered by a series of plant invasions (Biswell 1956). Eurasian annual grasses now constitute ~90% of the biomass of this community and dominance by these annual grasses has been complete for almost 130 yr (Heady 1988).

Within the last 50 yr, a new invasion of summer-flowering exotic species has further altered the vegetation of California's grasslands (Burcham 1981). Three of these species are Eurasian annuals in the star-thistle section of the genus *Centaurea* in the Asteraceae family. The species are closely related, yet vary greatly in invasiveness as defined as their rate of spread after naturalization (Richardson et al. 2000). The most invasive of the three congeners, *Centaurea solstitialis* L., currently occupies  $\sim 9.6 \times 10^6$  ha of California (Pitcairn et al. 1998, DiTomaso and Gerlach 2000b). The other species, *C. melitensis* L. and *C. sulphurea* Willd., are present in annual grasslands but their abundances and distributions are strikingly different from those of *C. solstitialis*. Although *C. melitensis* is widely distributed in California, it is an infrequent species in

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annual grasslands and forms dense populations only on disturbed or xeric sites (DiTomaso and Gerlach 2000a). *C. sulphurea* is an extremely localized species that has persisted as three small populations since 1923 (Barbe 1989).

Because these closely related congeners exhibit such strong differences in their capacity to invade annual grasslands, we used them to test whether invasiveness is related to differences in life history traits. We hypothesized that during initial colonization, populations of these species must pass through a demographic gauntlet of establishment, survival and reproduction in order to persist and expand at a site. In particular we hypothesized that the most invasive species (*C. solstitialis*) might possess unique life history characteristics. Using this idea of a demographic gauntlet as a conceptual framework, we conducted a series of field and laboratory experiments designed to compare each congener at each life history stage within the gauntlet. Specifically, we compared congeners in terms of (1) seed germination and seedling establishment, (2) survival of rosettes subjected to competition from annual grasses, (3) subsequent growth and flowering in adult plants, and (4) variation in breeding system.

As noted earlier, an understanding of the role of life history variation in the invasion process should consider the potential interactive effects of environmental variation; for invasion dynamics the disturbance regime at a site can be an environmental parameter of particular importance. Disturbance regimes influence recruitment for many invasive species in California's grasslands (Hobbs and Mooney 1995, Kotanen 1997a, b). Generally, disturbances in this community are thought to enhance invasion and occur as various sizes of soil disturbances caused by burrowing animals (typically ground squirrels and gophers) or as openings in the grass canopy caused by cattle grazing. We explored how each *Centaurea* species responded to differences in the size of soil disturbances by planting each species into variably sized canopy gaps within a mixture of annual grass species. Cattle grazing effects were explored through clipping treatments. By combining congeneric life history comparisons with experimental manipulations of canopy removal by soil disturbance and clipping, we hoped to gain a more comprehensive understanding of how invasiveness is determined by the interplay of life history variation and disturbance regime.

## METHODS AND MATERIALS

### Study site

The study site was located within an old field on the campus of the University of California, Davis (38°33' N, 121°48' W), Yolo County, California, USA. The vegetation has been an annual grassland community for at least 15 yr and is dominated by Eurasian annual grasses (*Avena fatua* L., *Bromus diandrus* Roth, *B. hor-*

*deaceus* L., and *Hordeum murinum* L.) and *Centaurea solstitialis*. Other species present are Eurasian annual *Trifolium* and *Erodium* species. The soil at the study site is a Reiff loam soil series that is a coarse-loamy, mixed, nonacid, thermic Mollic Xerofluvent (Huntington et al. 1981). The climate at the site is typically Mediterranean with hot, dry summers and cool, wet winters (Major 1988). Average annual rainfall over the last 36 yr is 491 mm and most precipitation (>90%) occurs between 1 October and 31 May. Seasonal total rainfall during the year of the experiment was greater than average (749 mm).

### Study species

The three *Centaurea* species germinate in the fall and grow vegetatively as rosettes until they bolt in late spring and produce stiff, upright, multiple-branched, photosynthetic flowering stems. Individual flowers are grouped into heads that are produced for three to four weeks in *C. melitensis* and *C. sulphurea* and up to five months in *C. solstitialis*. The mixed mating system of *C. melitensis* is complex with cleistogamous heads produced early in the season, chasmogamous heads produced during peak bloom, and cleistogamous heads produced after peak bloom (Porrás and Álvarez 1999, Porrás and Muñoz 2000). *C. solstitialis* has been shown to be largely self-incompatible with some variability in compatibility between and within populations (Maddox et al. 1996, Sun and Ritland 1998). The breeding system of *C. sulphurea* was undocumented prior to this study. All three species produce seeds that bear a small plume or pappus to aid dispersal by adhesion (Roché and Thill 2001) although about 20% of the seed produced by each *C. solstitialis* head does not possess a pappus.

### Experimental design overview

A series of field experiments described below were used to examine differences among congeners at various life history stages. The canopy-gap field experiment examined how seedling establishment, plant vegetative growth, and flower production by the congeners responded to variation in microsite quality as affected by different levels of disturbance (i.e., different canopy-gap sizes). A smaller field experiment compared the effect of simulated grazing (i.e., clipping) on growth and reproduction among the congeners. Because the primary measure of reproductive output in both the canopy-gap and clipping experiments was flower-head production and not seed production, we conducted an additional pollination study that provided conversions from flower-head production to seed number and examined breeding-system variation among the three species. Finally, because germination characteristics can be important determinants of establishment success, we conducted a separate, comprehensive germination experiment under more-controlled conditions (e.g., germination in soil containers) to examine in de-

tail the differences among the thistle congeners in this critical life history stage.

#### *Canopy-gap field experiment*

**Experiment design and establishment.**—Seed of each *Centaurea* species was collected during the summer of 1997 from natural populations nearest to the study site. Mature heads were harvested from ~100 widely dispersed plants in each population, placed in paper bags, and stored in an unheated shed under ambient temperature conditions. Each seed was tested individually to determine if it contained an embryo by dropping it from a height of ~10 cm onto a metal pan. Dissection of a subsample of seeds confirmed that filled seeds bounced higher and made a distinctive sound when they struck the pan.

During September 1997, twenty-five 4 × 4 m blocks were established. All plant litter was mowed to a height of 5 cm and nine circular plots were arranged on a 3 × 3 grid within each block. The centers of the plots were 1 m apart and each plot consisted of an area 30 cm in diameter. All litter and seed were removed from each circular plot. A randomized complete block experimental design with treatments consisting of a factorial combination of the three *Centaurea* species and three gap treatments (no-gap, 10-cm gap, and 30-cm gap) was established in October 1997. In the no-gap treatment, an annual-grass planting mixture was spread uniformly across each circular plot. In the 10-cm gap treatment, the planting mixture was sown within a 32 cm diameter circle centered on the plot except that a 10 cm diameter circular area was left bare in the plot center. For the 30-cm gap treatment, the entire circular plot was left bare, and the planting mixture was sown in a 15 cm wide band immediately outside of each plot. The planting mixture consisted of 15 g of *Bromus hordeaceus* seed (the dominant annual grass at the site), a small amount of the larger seeds of three annual grass species (*H. murinum*, *B. diandrus*, and *A. fatua*), and 500 mL of annual grass litter. A constant planting-mixture density of ~25 000 germinable seeds/m<sup>2</sup> was obtained that is similar to moderate densities found in the field (Young et al. 1981).

From 7 through 9 November 1997, twenty-five seeds of one of the three *Centaurea* species were sown 1 cm apart in a 4 × 4 cm grid located in the center of each circular plot. To prevent loss of seed by birds, each seed was pressed into the soil until it was below the soil surface but not covered by soil. The *C. solstitialis* seed was a mixture of 5 no-pappus seeds and 20 pappus seeds to approximate the proportion of each type of seed produced by a head. Plots were weeded as necessary.

**Seedling establishment and early growth.**—During 9–11 February 1998 seedlings of *Centaurea* species in each plot were counted and harvested except for a single, randomly selected seedling. This remaining seedling was used to estimate subsequent growth and re-

production in the plot. At the time of harvest, the average height of the vegetation surrounding each *Centaurea* seedling was measured. Harvested seedlings were washed, separated into leaf and stem tissue, and their leaf areas were measured using a MK2 Delta T area meter (Decagon Devices, Pullman, Washington, USA). Leaf number was recorded and the distance from the top of the apical meristem to the stem base was measured. Harvested seedling material was oven dried at 50°C for 48 h and then weighed. In those samples where multiple seedlings were harvested from a single plot, one seedling was randomly chosen for statistical analysis.

**Rosette growth responses to varying light environments.**—During 14–16 April each *Centaurea* plant was measured to determine apical meristem height and height of the tallest leaf tip. Photosynthetically active radiation (PAR) levels were measured above the canopy, 5 cm above the soil surface, at the apical meristem, and at the level of the tallest leaf tip using an AccuPar Ceptometer (Decagon Devices). All measurements were made within 90 min of solar noon.

**Final plant size and reproductive output.**—*Centaurea* aboveground biomass was harvested from June to October as each plant senesced. After drying at 60°C for 72 h, the plant material was separated into stems and flower heads, weighed, and flower-head number per plant recorded. All seed was removed from the flower heads before weighing because significant amounts of seed had been shed prior to harvest.

**Data analysis.**—The initial overall design of the canopy-gap experiment was a randomized complete block design with 25 blocks and treatments consisting of a factorial combination of the three *Centaurea* species and three gap sizes (no gap, 10-cm gap, and 30-cm gap). Block number was reduced by 5 for analyses of final plant growth and reproduction because five blocks were clipped in April as part of a simulated grazing study (described below). All analyses were performed using the SAS System for Windows (SAS Institute 1999). Block was analyzed as a random factor and all response variables except number of leaves required log<sub>10</sub> transformation to stabilize treatment-group variances. Because of heterogeneous variances in the final harvest data, log-transformed values were analyzed using weighted ANOVA techniques (Yandell 1997). The weighting groups were determined using a combination of Levene's (1960) test and an inspection of the raw data; weights were calculated as  $w_i = \hat{\sigma}_i^{-2}$ . The error rate for treatment-group comparisons was controlled using Hochberg's (1988) step-up Bonferroni method.

#### *Clipping experiment*

On 18 April five pairs of blocks from the canopy-gap experiment were selected for a clipping experiment. The blocks were paired on the basis of similar floristic composition and canopy height. One block from each pair was randomly chosen to receive a clip-

ping treatment. All vegetation in a block, including the *Centaurea* target, was clipped to a height of 5 cm and removed. The number of heads produced by each *Centaurea* plant was counted after each plant senesced.

#### Pollination experiment

Unclipped plants with at least three simultaneously maturing heads were randomly selected from plots within the canopy-gap experiment to be used in a pollination study (11 plants each for *C. melitensis* and *C. sulphurea* and 22 plants for *C. solstitialis*). Three treatments (pollinators excluded, supplemental pollination from flowers on the same head, and open pollination) were randomly assigned to individual heads on each plant. Pollinator-exclusion bags were constructed from white nylon 1-mm mesh fastened over two heads on each plant approximately one week before the heads opened. The supplemental pollination treatment was accomplished by manually moving pollen from flowers actively extruding pollen to flowers with exposed stigmatic surfaces. Supplemental pollen was applied to each head between the hours of 1000 and 1200 daily for four days. The number of seeds produced by each head was determined after each plant was harvested.

*Data analysis for the clipping and pollination experiments.*—We intended to analyze the clipping experiment as a split-plot model but the presence of large heterogeneous variances and numerous zero responses severely violated ANOVA assumptions. Data gathered from the pollination experiment also contained many zero values. Following the advice of Mead (1988), we did not analyze these data with ANOVA but rather report the results for both experiments as the median response and range for each treatment combination.

#### Germination study

Seed was collected from a total of 15 populations in order to include population variation in germination responses. *C. melitensis* and *C. solstitialis* seeds were collected in northern (~38° N latitude) and southern (~33° N latitude) California. *C. melitensis* seeds were collected in southern California in coastal sage scrub located on a coastal bluff and at two inland sites. In northern California *C. melitensis* seeds were collected in oak woodlands near the coast and at two inland sites. *C. solstitialis* seeds were collected in southern California in an inland annual grassland community, an inland hay field, and a mountain meadow. In northern California *C. solstitialis* was collected in a coastal annual grassland, an inland annual grassland, and in a mixed-conifer woodland. Because of *C. sulphurea*'s very limited geographical distribution, seed could be collected only in northern California from three oak woodland sites.

Within each collection site, maternal plants were randomly selected. Mature heads just beginning to shed dried corollas were collected; heads from each maternal plant were bagged separately. Seed collections were

made between 28 May and 1 July for *C. melitensis*, between 16 June and 25 June for *C. sulphurea*, and between 27 July and 16 August for *C. solstitialis*. The seed was stored in an unheated shed under ambient temperature conditions. Rates of seed filling were determined using methods described in the canopy-gap study.

In October 1997 individual blocks of soil ~15 cm deep were excavated from the field study site and all plant litter was removed. Soil blocks were crushed and the soil was placed in germination blocks containing individual 2.4 cm diameter cells (Stuewe & Sons, Corvallis, Oregon, USA). On 23 November a single seed was sown in each cell from each of 50 maternal plants of the *C. melitensis* and *C. sulphurea* populations. From 50 maternal plants of each *C. solstitialis* population collected, pappus and no-pappus seed types were sown separately. Each seed was randomly assigned to a germination tube in a completely randomized experimental design. Pappus-bearing seeds were placed with their flat sides parallel to the soil surface (see Roché and Thill 2001). No-pappus seeds were placed with their flat sides parallel to the surface of the soil. The germination blocks were placed inside an open-sided rain shelter to expose seeds to naturally varying temperature and humidity regimes.

On 26 November the soil in each cell was watered until saturated; thereafter the cells were misted 3 times daily until the soil was saturated. Germination was noted when the tip of the radicle emerged from the seed coat. The weather from 26 November to 9 December was overcast and rainy with temperatures that ranged from a nighttime low of 2°C to daytime high of 18°C. On 9 December ungerminated seeds were treated with a 400-ppm solution of gibberellic acid and kept indoors near an east-facing window at temperatures that varied between 18° and 20°C, night and day, respectively. After 10 d no additional germination was observed and all seeds were dissected to determine viability. Any seed that did not contain a firm, white endosperm was nonviable and excluded from the analysis.

Germination data were analyzed as Kaplan-Meier survival curves and the log rank test was used to detect differences between survival curves when the predictors consist of two grouping variables or to test the hypothesis that all survival curves were the same for more than two predictor variables (Kleinbaum 1996). All analyses of germination data were performed using JMP for Macintosh (SAS Institute 1997).

## RESULTS

### Canopy-gap field study

*Seedling establishment and early growth.*—In the initial establishment phase there were no differences among species in the number of seedlings establishing in the no-gap treatment from 10 November to 31 December (MSE = 19.64; df: species = 2, block = 23,



TABLE 1. ANOVA *F* values of the effect *Centaurea* species identity, canopy-gap size, and their interactions on leaf area, number of leaves, total aboveground dry mass, apical bud height, and specific leaf area of *Centaurea* seedlings harvested in February.

Treatment	df	Leaf area	Number of leaves	Total aboveground dry mass	Apical bud height	Specific leaf area (SLA)
Species	2	65.91***	25.07***	70.30***	60.20***	19.41***
Gap	2	103.19***	107.56***	127.68***	11.01***	72.68***
Species × Gap	4	3.86**	2.93*	3.37*	3.60**	3.06*
Block	23	1.50	1.69*	1.78*	2.04**	2.80***
Error df		169	175	170	169	169
MSE		0.177	8.534	0.177	0.050	0.006

Note: Except for number of leaves, data were log-transformed before analysis.

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

error = 46;  $P = 0.26$ ) and the mean establishment percentage across species was 54%.

Species identity, gap size, and their interactions all significantly affected *Centaurea* seedling growth and morphology (Table 1, Fig. 1A–E). Although *Centaurea* seedling growth in all species increased with increasing canopy-gap size, the two-way interactions are important for comparing species responses and so our results are presented graphically as interaction profile plots (see Neter et al. 1996, Yandell 1997, Suding and Goldberg 2001). Species-specific growth and morphological responses show that *C. melitensis* seedlings consistently produced less leaf area and aboveground biomass than the other species across gap treatments (Fig. 1A and C). *C. melitensis* responded to the altered light environment in the no-gap and 10-cm gap treatments by increasing specific leaf area (SLA) (Fig. 1D) but did not significantly increase stem length (Fig. 1E).

Differences in seedling growth between *C. sulphurea* and *C. solstitialis* were much more dependent on gap size. *C. sulphurea* seedlings produced greater leaf area and aboveground mass than *C. solstitialis* seedlings in the 10-cm gap treatment but both species were very similar in the no-gap and 30-cm gap treatments. *C. sulphurea* increased its SLA in response to altered light environments as gap size decreased and it also grew taller than the other species across gap size treatments. In terms of leaf production, seedlings of *C. solstitialis* responded in a more plastic fashion than the other two species by exhibiting a greater increase in leaf number in the 30-cm gap treatment. *C. solstitialis* seedlings responded to the altered light environment of the no-gap and 10-cm gap treatments by increasing SLA but, like *C. melitensis*, seedlings did not grow taller.

In sum, for all species there was an increase in growth and a decrease in SLA with increasing canopy-gap size. Although *C. melitensis* seedlings were consistently smaller than the other two species across gap treatments, differences between *C. sulphurea* and *C. solstitialis* were dependent on gap size. Compared to the other species, *C. sulphurea* tends to produce fewer but larger and thicker leaves. In contrast, *C. solstitialis*

tends to respond to canopy gaps by producing a larger number of small, thin leaves.

**Rosette growth responses to varying light environments.**—Photosynthetically active radiation (PAR) at 5 cm above the soil surface was only affected by gap size and not by species identity (Table 2, Fig. 2A–D). Additionally, canopies of the sown annual grasses had closed around the 10-cm gap treatments so that soil surface PAR values of the no-gap treatments and 10-cm gap treatments were approximately equal and ~15% of ambient PAR (1646  $\mu\text{mol}/\text{m}^2$ ). In the 30-cm gap treatment, soil surface PAR was higher at ~30% of ambient PAR. The amount of PAR reaching the uppermost plant surface (“apex PAR”) was significantly affected by the interaction of species identity and gap size. All three species received approximately equal amounts of apex PAR in the 30-cm gap treatment. Although *C. melitensis* and *C. solstitialis* received approximately equal amounts of apex PAR in the no-gap treatment and in the 10-cm gap treatment, because of greater stem height, *C. sulphurea* experienced significantly more apex PAR in these treatments because of greater stem height.

Each species responded to changes in its light environment in different ways (Fig. 2C and D). *C. sulphurea* grew as a less compact rosette than the other species in the no-gap and 10-cm gap treatments. *C. solstitialis* grew as a compact rosette regardless of gap size and it increased its access to PAR in the 10-cm gap treatment by elevating its leaf tips. *C. melitensis* grew as a less compact rosette than *C. solstitialis* in the 30-cm gap treatment, but in the no-gap and 10-cm gap treatments the bud heights of *C. melitensis* and *C. solstitialis* were not statistically different. Despite having a higher bud than *C. solstitialis* in the 10-cm gap treatment, *C. melitensis* was a shorter plant because of *C. solstitialis*’ ability to elevate its leaf tips.

**Adult plant size and reproductive output.**—Species identity, gap size, and their interactions all significantly affected *Centaurea* plant size and reproduction (Table 3, Fig. 3A–D). However, the most striking result is the

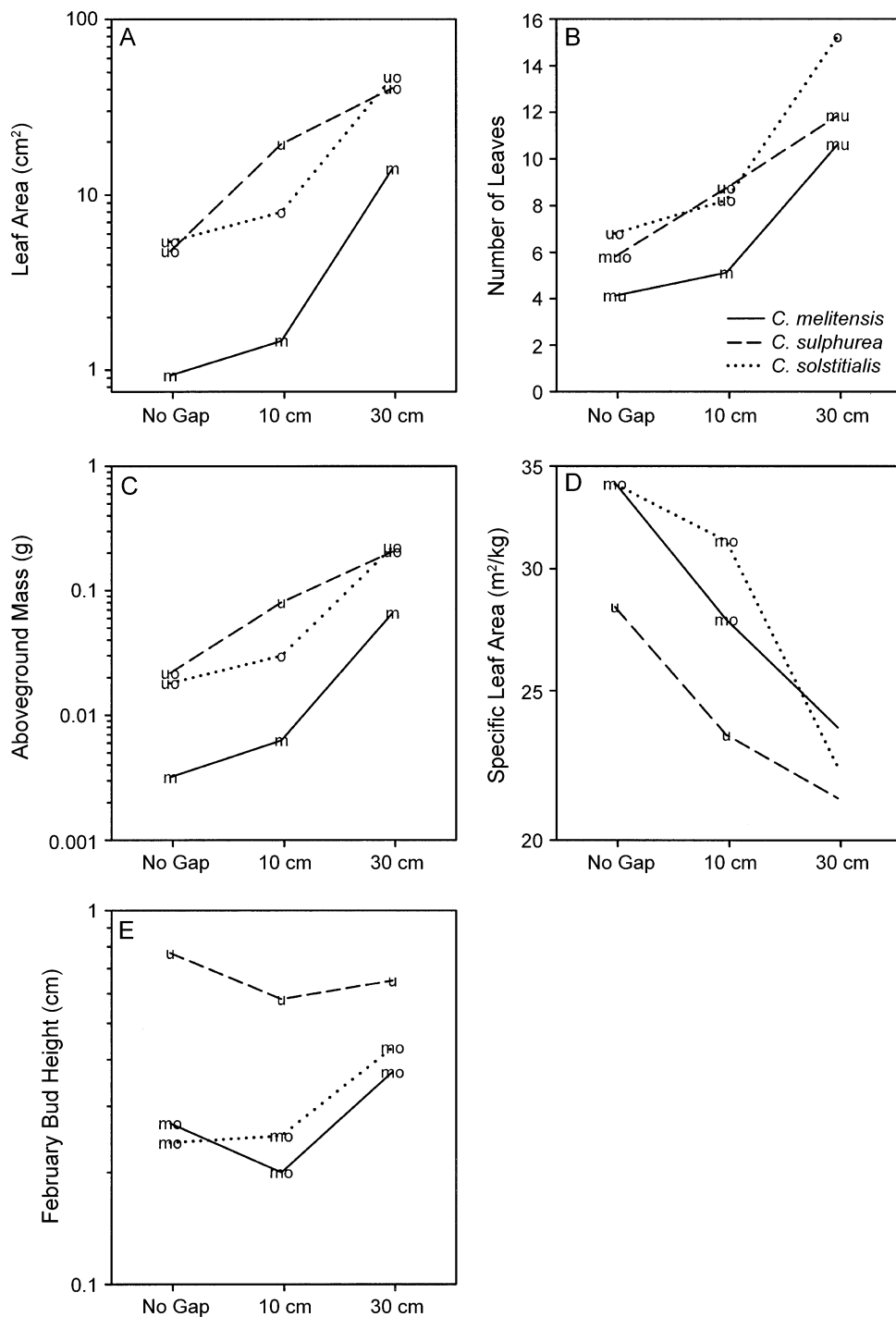


FIG. 1. Per-plant responses of *Centaurea melitensis*, *C. sulphurea*, and *C. solstitialis* to gap size (note log scales in panels (A), (C), (D), and (E): (A) leaf area; (B) number of leaves; (C) aboveground biomass; (D) specific leaf area; and (E) bud or apical meristem height. The significance of species comparisons within each level of gap size is indicated by the presence of m (*C. melitensis*), u (*C. sulphurea*), or o (*C. solstitialis*) in any combination. Species responses that share the same letter are not significantly different, and the absence of all letters within a gap size indicates that none of the species were significantly different (at  $P < 0.05$ ).

TABLE 2. ANOVA  $F$  values of the effect of *Centaurea* species identity, canopy-gap size, and their interactions on photosynthetically active radiation (PAR) at the soil surface and the plant apex, apical bud height, and leaf height of rosettes measured in April.

Treatment	df	PAR at soil surface	PAR at plant apex	Apical bud height	Leaf height
Species	2	0.11	15.70***	54.79***	18.95***
Gap	2	31.72***	32.78***	4.03*	16.27***
Species $\times$ Gap	4	1.05	2.04	3.96**	2.41†
Block	24	9.12***	3.02***	2.27**	1.97*
Error df		192	176	176	176
MSE		0.094	0.049	0.091	0.065

Note: Data were log-transformed before analysis.

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ ; †  $P = 0.051$ .

capacity of *C. solstitialis* to respond very strongly to canopy gaps. For example, flower-head production for *C. solstitialis* in the 30-cm gap treatment averaged 100.4 heads while *C. melitensis* and *C. sulphurea* produced only 4.8 and 10.5 heads, respectively (Fig. 3A). Without canopy-gap disturbance, differences in head production by *C. sulphurea* and *C. solstitialis* in the

no-gap treatment were not statistically different. Although not always statistically significant, the general patterns of flower-head dry mass, stem dry mass, and total dry mass were similar across the gap treatments with *C. solstitialis* > *C. sulphurea* > *C. melitensis* (Table 3, Fig. 3). The much longer growing and flowering season observed for *C. solstitialis* probably con-

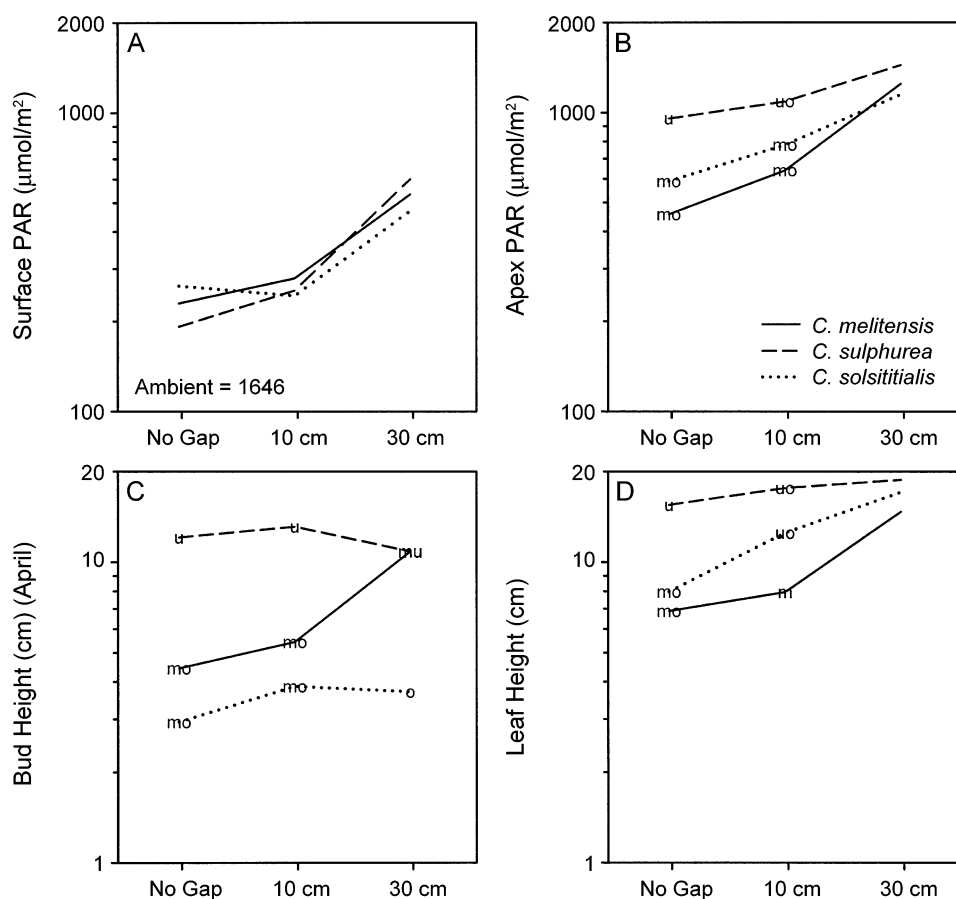


FIG. 2. Per-plant responses of *Centaurea melitensis*, *C. sulphurea*, and *C. solstitialis* to changes to gap size (note log scales): (A) surface PAR; (B) apex PAR; (C) bud or apical meristem height; and (D) leaf height. The significance of species comparisons within each level of gap size is indicated by the presence of m (*C. melitensis*), u (*C. sulphurea*), or o (*C. solstitialis*) in any combination. Species responses that share the same letter are not significantly different, and the absence of all letters within a gap size indicates that none of the species were significantly different (at  $P < 0.05$ ).

TABLE 3. Weighted ANOVA  $F$  values of the effect of species identity, canopy-gap size, and their interactions on flower-head number, flower-head dry mass, stem dry mass, and final aboveground dry mass of *Centaurea* plants harvested after senescence.

Treatment	df	Head number	Head dry mass	Stem dry mass	Final aboveground dry mass
Species	2	22.59***	24.05***	33.78***	28.36***
Gap	2	42.50***	31.52***	36.48**	34.08***
Species $\times$ Gap	4	4.12**	4.45**	4.26**	2.81*
Block	18	1.40	1.17	1.17	1.32
Error df	140	140	140	140	140
MSE		0.682	0.842	0.887	0.760

Note: Data were log-transformed before analysis.

\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

tributed substantially to this species' greater reproductive output. Plant size and reproduction responses of *C. melitensis* were always less than the other species but the statistical significance of the differences varied across the response variables.

#### Effects of simulated grazing (clipping) on adult plant size and reproduction

There were striking differences in the species' responses to clipping treatments (Table 4). In the no-gap

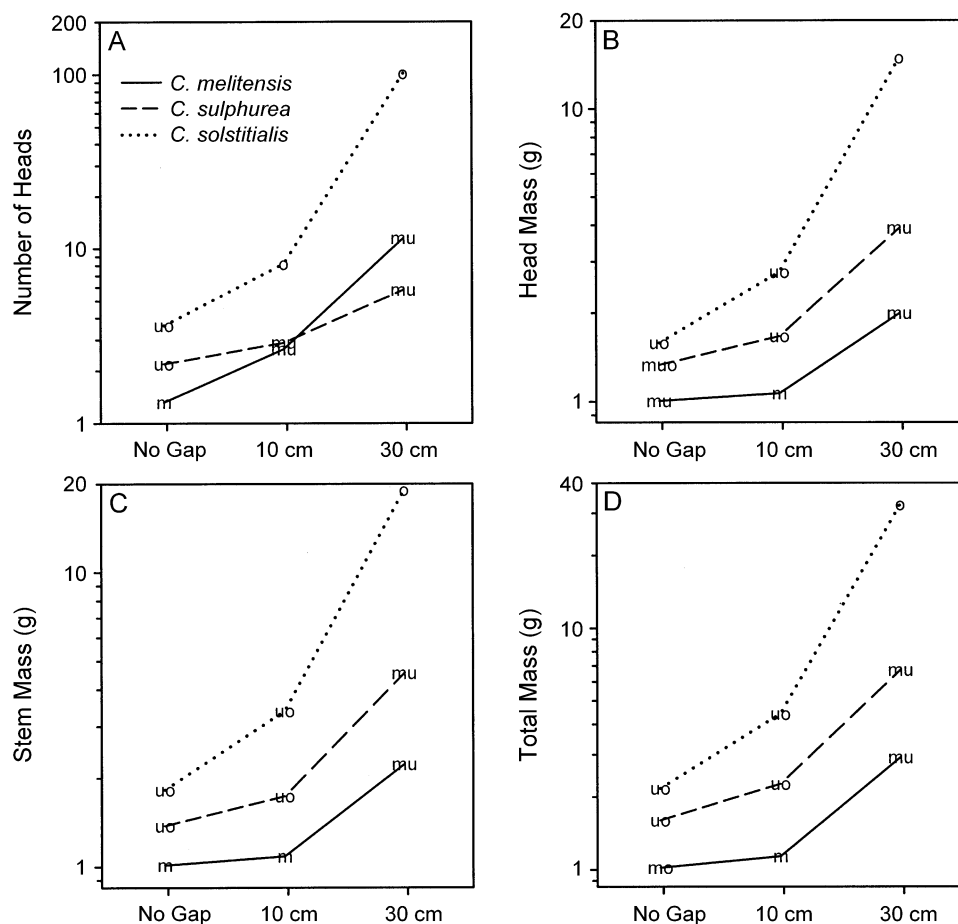


FIG. 3. Per-plant responses of *Centaurea melitensis*, *C. sulphurea*, and *C. solstitialis* to changes to gap size (note log scales): (A) number of heads; (B) head biomass; (C) stem biomass; and (D) total aboveground biomass. The significance of species comparisons within each level of gap size is indicated by the presence of m (*C. melitensis*), u (*C. sulphurea*), or o (*C. solstitialis*) in any combination. Species responses that share the same letter are not significantly different, and the absence of all letters within a gap size indicates that none of the species were significantly different (at  $P < 0.05$ ).



TABLE 4. *Centaurea* flower-head production in response to the interactive effects of species identify, gap size, and the April clipping treatment.

Treatment groups	Clip	No clip
No gap		
<i>C. melitensis</i>	0 (0–3)	1 (0–3)
<i>C. sulphurea</i>	0 (0–0)	1 (1–2)
<i>C. solstitialis</i>	20 (0–52)	4 (0–6)
10-cm gap		
<i>C. melitensis</i>	2 (0–15)	3 (1–8)
<i>C. sulphurea</i>	1 (0–3)	2 (1–3)
<i>C. solstitialis</i>	24 (0–141)	5 (0–621)
30-cm gap		
<i>C. melitensis</i>	0 (0–57)	11 (0–91)
<i>C. sulphurea</i>	8 (0–16)	3 (1–43)
<i>C. solstitialis</i>	103 (51–346)	161 (35–259)

Note: The results are presented as medians (followed by the range, in parentheses; i.e., smallest response–largest response).

and 10-cm gap treatments *C. solstitialis* increased its head production four- to fivefold when the plots were clipped to 5 cm. In contrast, under the same gap treatments, clipping reduced flower-head production of both *C. melitensis* and *C. sulphurea*. In the 30-cm gap treatment, flower-head production in *C. solstitialis* dropped from 161 to 103 heads per plant when clipped. *C. melitensis* head production also dropped from 11 heads to 0 heads in the 30-cm clipped treatment; in contrast, *C. sulphurea* flower-head production increased from 3 heads to 8 heads in the clipped treatment. The 5 cm high clipping treatment was above *C. solstitialis*' mean apical meristem (bud height), below *C. sulphurea*'s mean apical meristem, and at or just above *C. melitensis*' mean apical meristem height (Fig. 2C).

### Pollination responses and breeding systems

The first-blooming *C. solstitialis* heads at the study site produced no seed in open-pollination treatment while first-blooming *C. melitensis* and *C. sulphurea* heads produced a median of 25 and 26 seeds, respectively (Table 5). When open pollinated at peak bloom, *C. solstitialis* produced a median of 42 seeds per head, *C. sulphurea* produced 36 seeds per head, and *C. melitensis* produced 24 seeds per head. During peak bloom, *C. solstitialis* produced a median of 2% of its maximum open-pollinated seed production when bagged and 0 seeds per head when self-pollinated with pollen from other flowers in the same head. Median seed production in *C. sulphurea* relative to the open-pollination maximum was 68%, 64%, and 68% for bagged, selfed, and open-pollinated heads, respectively. Median seed production in *C. melitensis* was 29%, 61%, and 29% for bagged, selfed, and open-pollinated heads, respectively.

Overall, the data suggest that *C. solstitialis* is a highly self-incompatible species while *C. melitensis* and *C. sulphurea* are highly self-compatible. Additionally, the increased seed production of *C. melitensis* when self-pollinated and its lower levels of seed production and occasional failure to produce seed when bagged or open pollinated suggests that it may be pollen limited.

### Germination experiment

The Kaplan-Meier survival curves of the pappus-bearing seed of the three species were significantly different ( $P < 0.05$ ; Fig. 4A). Because the log rank test emphasizes failures (germinations) in the tails of the survival curves (Kleinbaum 1996), most of the significance is probably due to *C. melitensis*' slower ger-

TABLE 5. Seed production per head for bagged *Centaurea* flower heads, selfed heads that were hand pollinated with pollen from other flowers in the same head, and open-pollinated heads; the data are expressed as medians followed by the range (in parentheses; smallest response–largest response).

Bloom time and species	Seed production per head (%)†			Open (no. seeds)‡	n§
	Bagged	Selfed	Open		
Peak bloom					
<i>C. melitensis</i>	29 (0–79)	61 (16–93)	29 (0–10)	24 (0–56)	11
<i>C. sulphurea</i>	68 (57–89)	64 (45–93)	68 (59–100)	36 (31–53)	11
<i>C. solstitialis</i>	2 (0–18)	0 (0–29)	58 (0–100)	42 (0–72)	22
First-heads bloom¶					
<i>C. melitensis</i>	...	...	54 (13–100)	25 (6–46)	11
<i>C. sulphurea</i>	...	...	54 (42–100)	26 (20–48)	7
<i>C. solstitialis</i>	...	...	0 (0–0)	0 (0–0)	8

† Percentages relative to the maximum number of seed produced by a single head in the open-pollination treatment.

‡ Number of seeds produced per head in the open-pollination treatment.

§ The number of plants of the species measured.

|| Peak bloom = the time when all other plants of the same species were activity producing heads.

¶ First-head bloom was determined by the first few heads produced at the site by individual plants of the same species. Only the first head produced by an individual plant was used for the first-heads bloom treatment.

mination rates after day 4. Overall, however, final germination percentages were very similar and at day 13 were 99%, 96%, and 98% for *C. melitensis*, *C. sulphurea*, and *C. solstitialis*, respectively. For *C. solstitialis* seed there were significant differences between the pappus and no-pappus seed with final germination percentages of 98% and 85%, respectively.

#### DISCUSSION

We used the idea of a demographic gauntlet to develop a conceptual framework for our study on life history correlates of invasiveness in three closely related *Centaurea* congeners. We anticipated that certain life history stages would be more important than others in determining a species' invasiveness. Habitat quality was manipulated in both the canopy-gap and the clipping experiments in order to understand if life history differences among the congeners might be accentuated under varying levels of disturbance. Results discussed below suggest that, especially with some sort of disturbance, certain traits are indeed more likely candidates than others in causing differences in invasiveness.

##### *Germination and seedling establishment*

Although we initially expected that variation in germination patterns among congeners might be an important correlate of invasiveness, the germination responses of the pappus seed of the three species were very similar. *C. solstitialis* seed began to germinate a day earlier than the other species but none of the pappus-bearing seed of the species evidenced seed dormancy under the conditions of our experiment. The general pattern in California appears to be that most of the seed produced by these *Centaurea* species germinates with the dominant annual grasses soon after the first significant rains in the fall (see Young et al. 1981).

For *C. solstitialis*, the germination response of the no-pappus seed was significantly different from the pappus seed and 15% of the no-pappus seed did not germinate during the November experiment. Because these seeds contained filled embryos, this ungerminated seed is probably viable but dormant. Seed dormancy is often thought to be a trait contributing to invasiveness and *C. solstitialis* does possess a seed bank (Sheley et al. 1999). The higher dormancy in the no-pappus seed might contribute in a modest way to invasiveness in *C. solstitialis*. In our experiment, we simulated the germination conditions experienced by most *Centaurea* seeds on the soil surface. However, it is also likely that some seed will be buried by the burrowing activities of gophers and ground squirrels and that some *C. solstitialis* no-pappus seed will be retained in the heads (Roché and Thill 2001). These factors have been shown to create complex germination responses in *C. solstitialis* seed (Joley et al. 1997).

We found no differences in seedling survivorship among the three species in the no-gap treatment. Our

result of 54% establishment in the no-gap treatment is similar to the 44% establishment recorded by Pitcairn et al. (1999) in a nearby natural *C. solstitialis* population during the same time period.

##### *Rosette growth responses to annual-grass competition*

Rosettes of each *Centaurea* species responded differently to the light environments created by our gap treatments. By February, young rosettes of *C. sulphurea* responded to smaller gap sizes primarily by growing less robust and taller stems than *C. solstitialis* whereas *C. melitensis* stems were similar in height to *C. solstitialis* but were much less robust. All three species increased their specific leaf area (SLA) in response to reductions in gap size but *C. sulphurea*'s increase was much less than the other species. Responses measured in February occurred while the annual grasses were very short (7 cm) and the target *Centaurea* plants in the 10-cm gap treatments were not shaded. Different responses among species in the 10-cm gap treatment suggest the ability of each species to anticipate future competition through detection of changes in the spectrum of light reflected from the annual grasses (Ballaré et al. 1987, Aphalo and Ballaré 1995, Ballaré 1999).

Our light measurements in the no-gap and 10-cm gap treatments during April show that the exotic annual grasses reduced photosynthetically active radiation (PAR) at 5 cm above the soil surface to ~15% of ambient levels. This reduction in irradiance would also be accompanied by a change in the quality of light reaching the soil surface through selective absorption by the grass canopy. Rosette plants with leaves growing close to the soil surface in dense shade suffer reductions in growth and fecundity.

Faced with a deteriorating light environment, *Centaurea* plants in our canopy-gap experiment responded in a variety of ways that included growing taller primary stems to escape shading (Ballaré et al. 1991, Aphalo and Ballaré 1995, Ballaré 1999), elevating their leaf tips (Ballaré et al. 1991), or increasing their SLA (Sims et al. 1998). *C. solstitialis* increased its height in the 10-cm gap treatment by elevating its leaf tips. *C. sulphurea* acclimated to low light levels primarily by growing taller primary stems while *C. melitensis* and *C. solstitialis* acclimated by greatly increasing their SLA. By February, both *C. sulphurea* and *C. solstitialis* produced significantly more aboveground biomass than *C. melitensis* through the use of their different acclimation strategies. Also, *C. sulphurea*'s much larger seed mass may have provisioned its seedlings with additional resources that enabled them to acclimate to low light environments without ceasing growth. However, the difference in biomass between *C. melitensis* and *C. solstitialis* is likely due to *C. solstitialis*' greater growth rate because initial seed masses were very similar. Growth-rate differences may be due to either greater metabolic efficiencies or, perhaps, to different tol-

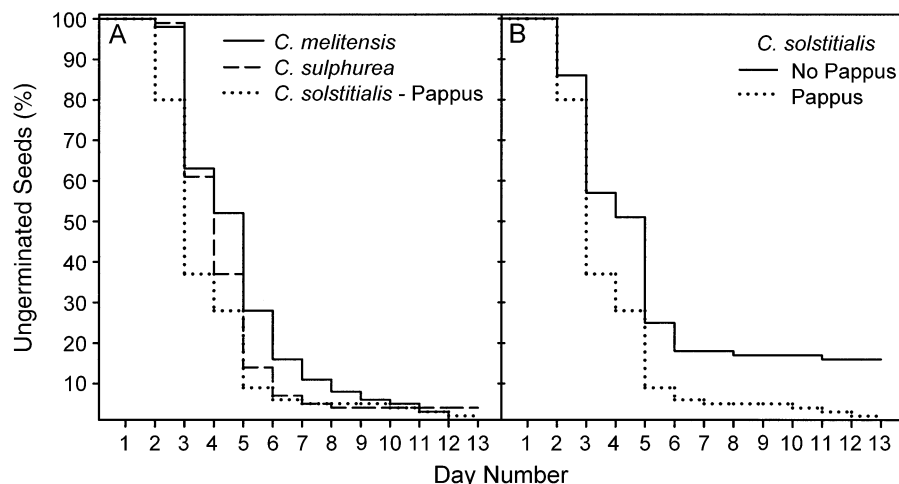


FIG. 4. Germination responses of *Centaurea melitensis*, *C. sulphurea*, and *C. solstitialis*: (A) pappus seed for all three species; (B) *C. solstitialis* pappus seed vs. no-pappus seed.

erances to cold temperatures. *C. melitensis*' home range is restricted to north Africa, Spain, and the warmer coastal areas of the central Mediterranean while the home range of *C. solstitialis* extends much further northward and eastward (de Bolòs and Vigo 1995).

#### Adult growth and fecundity

The shorter stems produced by *C. solstitialis* in all gap treatments allowed its apical meristems to avoid damage when the vegetation was clipped to simulate grazing. Clipping also apparently reduced the competitive effects of annual grasses and allowed *C. solstitialis* to greatly increase its fecundity in the clipped, no-gap, and 10-cm gap treatments.

*C. solstitialis* produced many more heads than *C. melitensis* in all of the gap treatments. It also produced many more heads than *C. sulphurea* except in the no-gap treatment. In the canopy-gap and clipping experiments, *C. solstitialis* exhibited a stronger plastic response in growth and reproduction to disturbance than did its congeners. The greater capacity of *C. solstitialis* to respond reproductively to disturbance is due, in part, to its long and indeterminate life span (Roché et al. 1997) that allows it to continue growing through the dry season using residual soil water not used by the annual grasses (Gerlach 2000). The other *Centaurea* species are also capable of using the residual soil water, but their shorter and more determinate life spans may limit their maximum reproductive capacity (Gerlach 2000).

#### Breeding systems and invasiveness

It is rather surprising that the most invasive species, *C. solstitialis*, is highly self-incompatible while the less invasive species are self-compatible. The self-incompatibility mechanism in *C. solstitialis* has not been studied but, because it is a member of the Asteraceae family, it likely possesses a homomorphic sporophytic system

controlled by S-alleles with a multi-locus hierarchical dominance structure (Richards 1997, de Nettancourt 2001). A simulation study predicted that small populations (<50 individuals) with this type of breeding system are unable to maintain a high diversity of S-alleles and therefore there should be a decrease in the frequency of available mates with time (Byers and Meagher 1992). Byers and Meagher (1992) concluded that very small populations of self-incompatible species are not stable and are likely to become extinct due to increased variance and limited availability of mates.

*C. solstitialis* populations that contain individuals that are partially self-compatible were identified in our study and in other studies (Harrod and Taylor 1995, Maddox et al. 1996, Sun and Ritland 1998). Recent findings indicate that small levels of self-compatibility in predominantly self-incompatible species may be increased by environmental stress and inbreeding (Levin 1995, Hiscock 2000). Strong selection for self-compatibility in *C. solstitialis* may result in satellite populations sustained by higher rates of self-compatibility than exist in larger core populations.

#### CONCLUSIONS

We found that the three *Centaurea* species differed in their responses to our hypothetical demographic gauntlet and that differences in invasiveness were determined by a subset of potential life history correlates. Greater invasiveness by *C. solstitialis* in the annual grassland community appears to be related to the combination of persistent fecundity in less favorable habitat and maximum fecundity in favorable habitat patches created by disturbance. *C. solstitialis* produced many more heads than the other species in the 10-cm gap and 30-cm gap treatments and as many or more heads as *C. sulphurea* in the no-gap treatment. In general, these manipulations indicated that the invasive nature of *C. solstitialis* was dependent on this species' plastic

capacity to respond readily to any disturbance that opens up the canopy and reduces competition from annual grasses. Because of its extended growing and flowering season, *C. solstitialis* is also able to persist within relatively closed grassland vegetation and take advantage of residual soil moisture resources not used by annual grass species (Gerlach 2000).

The rate of spread of an invader has been shown to be sensitive to the size and distribution of disturbance patches in a heterogeneous environment due to how the patches are sampled by the seed dispersal shadow of individual plants (Bergelson et al. 1993). California's annual grassland community is renowned for its spatial and temporal heterogeneity across many scales (Bartolome 1989, Huenneke 1989). Every year there is a complete turnover of individuals and large shifts in species composition. Ground squirrels, gophers, and voles create patches of bare ground that vary greatly in size (Lidicker 1989, Hobbs and Mooney 1995) while disease and herbivory create patchy distributions of potential competitors. Because of their highly plastic growth and indeterminate phenology, individual *C. solstitialis* plants growing in favorable patches are able to grow larger and produce many more heads than the other *Centaurea* species. These initial colonists create broad, dense seed shadows that thoroughly sample the distribution of potentially favorable patches and facilitate the spread of this highly invasive species (see Willson and Traveset 2000).

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