

## VARIATION IN SUMMER DORMANCY IN THE LILIOID GEOPHYTE *BURCHARDIA UMBELLATA* (COLCHICACEAE)<sup>1</sup>

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Plant dormancy is a form of phenotypic plasticity that minimizes exposure to seasonally stressful conditions. We examined variation in summer dormancy in two highland and two lowland populations of the lilioid geophyte *Burchardia umbellata* to test the prediction that facultative dormancy is advantageous in habitats with variable summer conditions. Consistent with this prediction fewer highland plants than lowland plants became dormant under wet common garden conditions. Also, significant among-family variance occurred within highland but not lowland populations, indicating genetic differences among and within populations. Most lowland plants became dormant when exposed to wet or dry conditions (~92%), indicating that dormancy was primarily obligate. In contrast, dormancy in highland plants increased from 44% under wet conditions to 93% under dry conditions, indicating that dormancy of some highland plants was facultative and induced by drought. Survival, growth, and flowering were reduced in lowland populations, and in dormant vs. nondormant highland plants, indicating costs of dormancy that could negate the advantages of dormancy under variable summer conditions. Summers in lowland populations are predictably hot and dry, favoring a phenotype that responds invariably to environmental cues that are correlated to future dry conditions. In highland populations, variable summer conditions probably maintain polymorphism in dormancy.

**Key words:** *Burchardia umbellata*; Colchicaceae; environmental cues; geophyte; habitat-specific selection; phenotypic plasticity; plant dormancy; threshold trait.

Phenotypic plasticity is the ability of an individual plant to alter its phenotype in response to changes in environmental conditions and is widely regarded as a mechanism to cope with heterogeneous environments (Bradshaw, 1965; Schlichting, 1986; Sultan, 1987). Plasticity can be selectively advantageous in habitats that encounter predictable environmental change (Levins, 1968; Lloyd, 1984; Lively, 1986; Schlichting, 1986; Bradshaw and Hardwick, 1989). Under such conditions, individuals use environmental cues to predict future conditions allowing them to make functionally appropriate adjustments to their phenotype. However, where environmental cues are unreliable or there are costs associated with producing a plastic phenotype, specialists with a fixed phenotype can have a selective advantage (Bradshaw, 1965; Levins, 1968; Lloyd, 1984; Bradshaw and Hardwick, 1989). Intraspecific variation in phenotypic plasticity can be pronounced and such variation is often interpreted as being the result of habitat-specific selection (Cook and Johnson, 1968; Schlichting and Levin, 1990; Sultan and Bazzaz, 1993; Linhart and Grant, 1996; Weinig, 2000).

Long-lived plants occurring in seasonal environments must adapt to the conditions posed by both favorable and unfavorable seasons. Plant dormancy minimizes exposure to seasonally stressful periods and is a form of stress evasion since dormant plants do not grow or reproduce (Hoffman and Parsons, 1993). Dormancy is a manifestation of plasticity via developmental conversion involving a threshold response to environmental change that produces discrete variation with two

phenotypic classes (Smith-Gill, 1983; Via et al., 1995; Schlichting and Pigliucci, 1998). Threshold traits often have a large additive genetic component, with strong environmental induction (Roff, 1996, 1997). For example, environmental cues such as photoperiod and temperature can induce dormancy in anticipation of the onset of freezing conditions in winter deciduous plants and of drought in summer deciduous plants (Bradshaw, 1965; Bradshaw and Hardwick, 1989; Schlichting and Pigliucci, 1998).

The life cycle of most geophytes includes a dormant period during which time the above ground parts of the plant die back in response to seasonally stressful conditions (Raunkiaer, 1934; Dafni, Cohen, and Noy-Meir, 1981). Regrowth occurs by means of the perennating bud that is borne on an underground storage organ such as a tuber or a corm. The storage organ conserves nutrients between seasons and allows rapid growth of leaves under favorable conditions. In southern Australia, geophytes are common on nutrient-poor soils and become dormant in response to the hot, dry summers. The benefit of summer dormancy is escape from drought stress and the consequent negative effects on plant survival, growth, and reproduction (Pate and Dixon, 1982). However, there may be costs for plants that are obligately summer dormant if plants fail to emerge from dormancy or miss opportunities for growth and reproduction if conditions are uncharacteristically favorable. Such costs are likely to be most severe in habitats where summer conditions are unpredictable and in this situation we predict that facultative dormancy should be selectively favored. Facultative dormancy occurs when plants exhibit plasticity in dormancy, depending on environmental conditions. Conversely, in habitats where summers are predictably hot and dry we expect obligate dormancy to be advantageous.

Here we test these predictions by investigating summer dormancy in two lowland and two highland populations in the geophyte *Burchardia umbellata* (Colchicaceae). We first monitored dormancy under moist common garden conditions to

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TABLE 1. Locations and altitude for the four study populations of *Burchardia umbellata*; lowland: Mont Park (MP) and Boomers Reserve (BR); highland: Mt Samaria (MS) and Tom Groggin (TG). Long-term average climatic data were available only for MP and MS. Data for BR and TG would have been similar to MP and MS, respectively.

Population	Latitude (°S)	Longitude (°E)	Altitude (m asl <sup>a</sup> )	Annual rainfall (mm)	Summer temperatures		No. of days >35°C	No. of days <0°C
					Maximum (°C)	Minimum (°C)		
MP	37°72'	145°04'	90	715.7	25.6	13.1	9.8	4.7
BR	37°38'	145°12'	180					
MS	37°03'	146°05'	480	990.3	26.4	10.9	4.9	54.0
TG	36°33'	148°09'	600					

<sup>a</sup> asl: above sea level.

determine the extent of genetic variation among and within populations. Second, we assessed the costs and benefits of dormancy by examining summer survival, growth and flowering among populations and between dormant and nondormant phenotypes. Third, we grew plants under contrasting soil moisture regimes to determine the extent to which dormancy was obligate or facultative. Finally, we monitored plants in the field in order to assess the effect of natural environmental conditions on the occurrence of dormancy.

## MATERIALS AND METHODS

**Study species and site**—*Burchardia umbellata* is widely distributed in southern Australia and occurs on a variety of soil types in swamps, grassland, heathland, and woodland (MacFarland, 1987). Adult plants usually have several annual leaves, a corm, and several fleshy root tubers, which each last two or more years (Pate and Dixon, 1982). Plants emerge from summer dormancy after autumn or winter rains. Flowering occurs in spring (September–November) and plants produce a terminal umbel with 2–9 hermaphroditic flowers (Ramsey and Vaughton, 2000). Leaf senescence occurs after fruiting in late spring and early summer.

We studied two lowland and two highland populations of *B. umbellata* located in temperate eastern Victoria that were chosen for their differences in altitude, temperature, and rainfall (Table 1; lowland: Mont Park [MP] and Boomers Reserve [BR]; highland: Mt Samaria [MS] and Tom Groggin [TG]). The MP population was located in grassland while the other populations were located in woodland. The MP and MS populations were disturbed, while the BR and TG populations were relatively undisturbed. All populations contained >200 plants.

**Common garden experiment**—We assessed within- and among-population variation in summer dormancy under common garden conditions by growing progeny from each of seven open-pollinated maternal plants in each population. Seeds were collected from each population by harvesting ripe capsules from maternal plants after flowering in 1995. Sampled plants were at least 5 m apart and were from the middle of the populations. Seeds were surface-sterilized with 1.5% sodium hypochlorite and placed on moistened filter paper in plastic petri dishes in June 1996. Dishes were placed in a growth cabinet at 16°C : 8°C and a 12 h light : 12 h dark photoperiod. From each maternal family, 16 seedlings were transplanted into plastic pots (75 cm<sup>3</sup>) containing equal parts of sand and loam when they were ~3 wk old. Pots were placed in trays on a bench in an unheated shadehouse and kept moist. Temperatures inside the shadehouse resembled those occurring naturally in the MP and BR populations. Seedlings were fertilized with a half-strength solution of liquid fertilizer (Aquisol, Hortico Pty Ltd, Australia) every 3 mo and granules of controlled-release fertilizer containing trace elements (Osmocote Plus, Scotts-Sierra International, USA) were applied every 6 mo. Trays were moved every 4 wk to avoid position effects in the shadehouse.

Plants were examined every month for 24 mo, from September 1996 to

August 1998. Summer dormancy was assessed as the senescence of leaves. Dormant plants had no green leaves during at least one monthly census during summer; nondormant plants had at least one green leaf throughout summer. Surviving dormant plants produced new leaves during autumn; dead plants failed to emerge from dormancy. Survival was assessed as the number of plants that were alive in one year divided by the number alive in the previous year.

The effects of population and year (explanatory variables) on summer dormancy and survival (response variables) pooled over maternal families were assessed using maximum likelihood approaches. We used logit models and analyses of deviance, allowing for the binomial error structure of the binary response variables (“dormant”/“nondormant”; “dead”/“alive”), and carried out analyses using the logit link function. Deviance is a measure of discrepancy used to assess the goodness of fit of the model to the data. Analysis of deviance estimates the change in deviance caused by the inclusion of a given explanatory variable into the model. Deviances (*D*) approximate and are tested against the  $\chi^2$  distribution, allowing the significance of explanatory variables and their interactions to be examined (Collett, 1991).

Logit models do not allow estimation of genetic variance components, and we tested genetic differences in first-year dormancy and survival among maternal families in each population by one-way ANOVA. We used common garden conditions and open-pollinated progeny arrays, and significant differences among maternal families are related to broad-sense heritabilities and represent upper estimates of variation upon which selection can act (Falconer and Mackay, 1996; Roff, 1997). Plants within maternal families were classed as either dormant (0) or nondormant (1), and either dead (0) or alive (1). Such 0, 1 data violate the normality assumption of ANOVA. Normality is not required for estimating variance components, but is required for hypothesis testing (Service, 2000) and therefore we assessed statistical significance using sampled randomization tests. For each population, 1000 data sets were selected randomly with replacement from the original data to obtain distributions of *F* ratios, to which we compared the *F* ratios from the original one-way ANOVAs (Sokal and Rohlf, 1995; Roff, 1997).

Cumulative length of leaves was measured on three occasions in October 1996, October 1997, and August 1998, as an indicator of growth. The proportion of plants that flowered was recorded in 1997 and 1998. A repeated-measures ANOVA was used to examine the effects of year, population, and maternal families on length of leaves. Year and population were crossed, fixed factors, and maternal family was a random factor nested within populations. Each maternal family was considered as being measured repeatedly over years. Due to mortality, we used the mean leaf length for each maternal family ( $N = 3$ –16). Length of leaves was transformed using natural logarithms prior to analysis.

Most plants became summer dormant in the lowland populations. Therefore we examined the costs of dormancy in the highland MS and TG populations by comparing survival, flowering, and growth of dormant and nondormant plants. We examined the effects of population and dormancy (explanatory variables) on percentage survival pooled over years and percentage flowering in the third year (response variables) using logit models and analyses of deviance. For growth, we used cumulative length of leaves in 1998 and classified plants as nondormant in both summers, dormant in one summer, or dormant in both summers. Growth was compared using a partially hierarchical ANOVA, with population and dormancy as crossed, fixed factors, and maternal family as a random factor nested within populations.

**Effect of soil moisture**—We investigated the effect of soil moisture on dormancy by growing plants under wet and dry conditions. In July 1997, we germinated seeds from bulk collections from the four populations; seeds were collected from ~50 plants that flowered in the previous year. For each population, 4-wk-old seedlings ( $N = 90$ ) were planted into plastic pots (75 cm<sup>3</sup>) containing sand and loam. Pots were placed into a glasshouse, relocated weekly to avoid position effects and kept moist for 3 mo. Some seedlings died, and final sample sizes were 84 plants per population, all of which were vigorous when treatments were imposed.

At the beginning of summer (November), we randomly assigned pots from each population to either a wet or dry soil treatment. In the wet treatment,

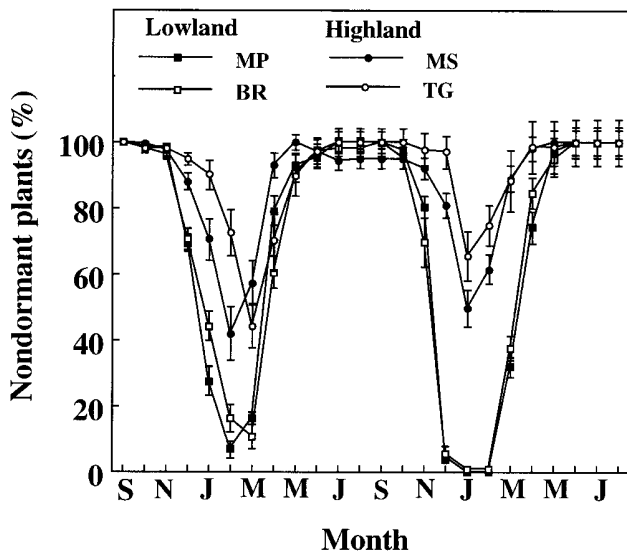


Fig. 1. Summer dormancy of plants from the lowland (Mont Park [MP], Boomers Reserve [BR]) and the highland (Mt Samaria [MS], Tom Groggin [TG]) populations in eastern Victoria, Australia, from September 1996 to August 1998 in a common garden is shown. Data are the mean ( $\pm 1$  SE) percentages of nondormant plants pooled over seven maternal families from each population at each monthly census. Initially, 16 seedlings from each maternal family were planted.

pots were watered every 3–5 d for the duration of the experiment. In the dry treatment, pots were watered every 9–15 d until autumn (mid-April) after which they were watered every 3–5 d until the end of the experiment (August). We simulated natural changes in soil moisture in the dry treatment by watering every 9 d at the beginning and end of summer, and every 15 d during midsummer. Daily minimum and maximum temperatures were 13.0°C and 28.6°C in summer and 8.3°C and 20.6°C in winter.

We monitored seedlings every 2 wk throughout the experiment and recorded summer dormancy and survival as described above. We assessed whether dormancy and survival (response variables) were dependent on watering treatment and population (explanatory variables) using logit models and analyses of deviance. We assessed plant mass at the completion of the experiment by harvesting, drying at 65°C, and weighing individual plants. For analysis, MP and BR plants were pooled because survival was low in the dry treatment. We examined the effects of watering treatment and population on plant size using two-way ANOVA with treatment and population as fixed factors. Plant mass was transformed using natural logarithms prior to analysis.

**Field studies**—We assessed whether there was variation in summer dormancy and winter growth in the field. We visited populations in December 1997 and March and September 1998 and examined previously marked adult plants. Dormant plants had yellow or brown leaves and nondormant plants had green leaves. During each visit at least 50 plants were examined, except for the TG population in September, when only 30 plants were located.

## RESULTS

**Common garden experiment**—Dormant plants were observed in December in all populations and as the summer progressed the proportion of dormant plants increased (Fig. 1). In both years, lowland MP and BR populations had a greater proportion of dormant plants in December than highland MS and TG populations, and this trend was evident throughout the summer. Plants emerging from dormancy were first observed in February and March. The proportion of nondormant plants increased in populations until May (Fig. 1).

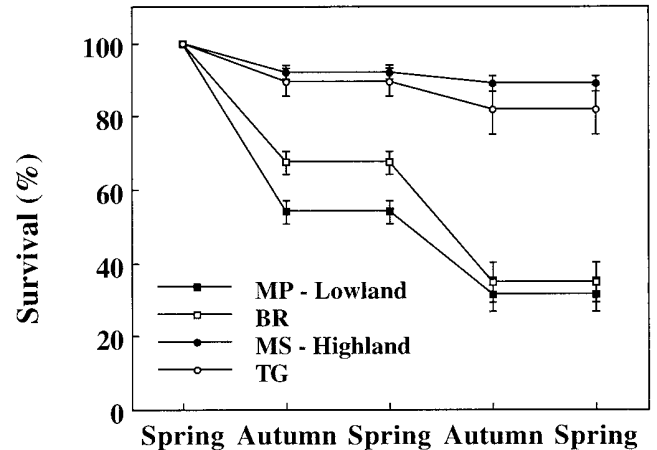


Fig. 2. Survival of plants from the lowland (MP, BR) and the highland (MS, TG) populations in spring (September) and autumn (May) from 1996 to 1998 in a common garden is shown. Data are the mean ( $\pm 1$  SE) percentages of surviving plants pooled over seven maternal families from each population.

The proportion of plants that became summer dormant depended on population and year (population: deviance,  $D = 208.3$ ,  $df = 3$ ,  $P = 0.000$ ; year:  $D = 18.79$ ,  $df = 1$ ,  $P = 0.000$ ). Dormancy was greater for lowland plants (years 1 and 2; MP: 96 and 100%; BR: 92 and 100%) than for highland plants (years 1 and 2; MS: 66 and 43%; TG: 59 and 37%). The population  $\times$  year interaction was significant ( $D = 13.61$ ,  $df = 3$ ,  $P < 0.004$ ); in the second year dormancy increased in lowland MP and BR populations but decreased in highland MS and TG populations.

Significant among-family variance for first year dormancy, indicating genetic variation, was observed in the highland MS and TG populations but not the lowland MP and BR populations. Among-family variance components as percentages were: MS, 44.7% (randomization test for one-way ANOVA,  $P = 0.000$ ); TG, 8.3% ( $P = 0.029$ ); MP, 0.0% ( $P = 0.667$ ); and BR, 0.5% ( $P = 0.322$ ). The ranges in the percentage of dormant plants among families were: MS, 42–100%; TG, 31–80%; MP, 93–100%; and BR, 87–100%.

Mortality occurred during the summer and was due to plants failing to emerge from dormancy (Fig. 2). No mortality occurred during winter when plants were actively growing. Cumulative survival was  $>80\%$  for highland plants and  $\sim 34\%$  for lowland plants after 24 mo in the common garden (Fig. 2).

The proportion of plants that survived the summer depended on population but not year (population:  $D = 129.8$ ,  $df = 3$ ,  $P = 0.000$ ; year:  $D = 0.09$ ,  $df = 1$ ,  $P = 0.769$ ). Fewer lowland MP and BR plants survived than highland MS and TG plants (percentage survival of living plants for years pooled: MP, 56%; BR, 60%; MS, 95%; TG, 91%). The population  $\times$  year interaction was not significant ( $D = 6.46$ ,  $df = 3$ ,  $P = 0.092$ ).

Significant among-family variance for first year survival was observed in the highland TG population (8.3%,  $P = 0.033$ ). Among-family variances for the other populations were not significant (MS, 0.0%,  $P = 0.956$ ; MP, 0.0%,  $P = 0.912$ ; BR, 1.5%,  $P = 0.256$ ). The ranges in the percentage of surviving plants among families were: TG, 69–100%; MS, 87–100%; MP, 50–69%; and BR, 56–87%. Survival was neg-

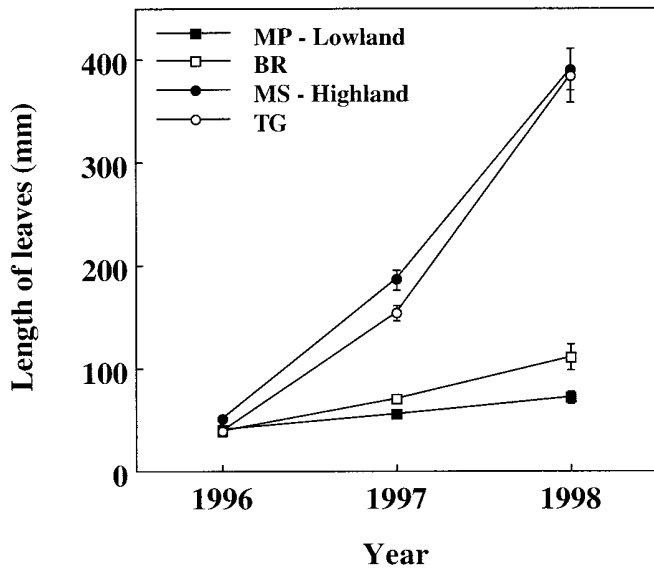


Fig. 3. Mean ( $\pm 1$  SE) cumulative length of leaves (mm) over 3 yr for plants from lowland (MP, BR) and highland (MS, TG) populations in a common garden are shown.

atively correlated with summer dormancy. Pooled over populations, the proportion of plants that survived the summer decreased with an increasing proportion of first year dormant plants in each maternal family (Pearson correlation,  $r = -0.72$ ,  $P = 0.000$ ,  $n = 28$  maternal families).

Population, maternal families within populations, and year significantly affected plant growth (Fig. 3, Table 2). The increase in length of leaves over the three years was greater for highland TG and MS plants than for lowland MP and BR plants, as indicated by the significant year  $\times$  population interaction.

No plants flowered in the lowland populations. In the highland MS and TG populations, 2.0 and 1.0% of plants flowered in their second year and 43 and 50% of plants in their third year, respectively. There was a mean of  $7.1 \pm 1.6$  flowers per umbel ( $N = 39$ ) in the MS population and  $8.9 \pm 1.9$  ( $N = 44$ ) in the TG population.

Costs were associated with dormancy in the highland populations as indicated by differences in survival, flowering, and growth of dormant and nondormant plants. Survival was similar in both populations ( $D = 1.19$ ,  $df = 1$ ,  $P = 0.275$ ), but was greater for nondormant than dormant plants (100 vs. 87%;  $D = 30.58$ ,  $df = 1$ ,  $P = 0.000$ ). The dormancy  $\times$  population interaction was not significant ( $D = 0.00$ ,  $df = 1$ ,  $P = 1.00$ ). Flowering was independent of population ( $D = 0.06$ ,  $df = 1$ ,

TABLE 2. Results of a repeated-measures ANOVA showing the effects of population, maternal family nested within population, and year on plant growth. Values for maternal families were the mean of 3–16 seedlings each measured on three occasions over 24 mo.

Source of variation	df	MS	F	P
Population	3	6.41	34.90	0.000
Family (Population)	24	0.18	1.86	0.033
Year	2	12.46	126.42	0.000
Year $\times$ Population	6	1.40	14.25	0.000
Error	48	0.10		

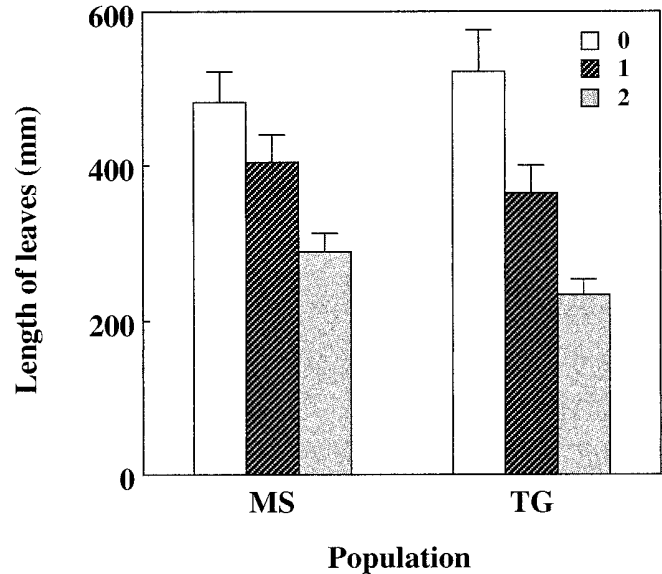


Fig. 4. Mean ( $\pm 1$  SE) cumulative lengths of leaves (mm) for highland MS and TG plants that were nondormant in both summers (0), dormant in one summer (1), and dormant in both summers (2) in a common garden are shown.

$P = 0.800$ ), but was more likely if plants were nondormant in the previous summer than if they were dormant (66 vs. 17%;  $D = 43.43$ ,  $df = 1$ ,  $P = 0.000$ ). The dormancy  $\times$  population interaction was significant ( $D = 4.87$ ,  $df = 1$ ,  $P = 0.027$ ); more nondormant TG than MS plants flowered (70 vs. 62%), but fewer dormant TG than MS plants flowered (8 vs. 27%). Plant growth was significantly affected by dormancy (Fig. 4, Table 3). Growth of plants that were nondormant in one summer or both summers increased by 46 and 91%, respectively, compared to plants that were dormant in both summers. Plant growth did not differ between populations. Variation among maternal plants was weakly significant. The dormancy  $\times$  population and the dormancy  $\times$  plant interactions were not significant.

**Effect of soil moisture**—In all populations, more plants became dormant under dry conditions than wet conditions (Fig. 5a;  $D = 53.22$ ,  $df = 1$ ,  $P = 0.000$ ). Under dry conditions, dormancy was similar in all populations. Under wet conditions, more lowland plants became dormant than highland MS and TG plants, and more MS plants became dormant than TG plants ( $D = 34.57$ ,  $df = 3$ ,  $P = 0.000$ ). The population  $\times$

TABLE 3. Results of a partially hierarchical ANOVA showing the effects of dormancy, population, and maternal family nested within population on plant growth. Only the highland MS and TG plants were analyzed because most plants from the lowland populations became dormant. Plants were either nondormant in both summers, dormant in one summer or dormant in both summers.

Source of variation	df	MS	F	P
Dormancy	2	3.798	17.52	0.000
Population	1	0.934	2.08	0.175
Family (Population)	12	0.449	1.79	0.057
Dormancy $\times$ Population	2	0.036	0.17	0.845
Dormancy $\times$ Family (Population)	24	0.217	0.86	0.652
Error	127	0.252		

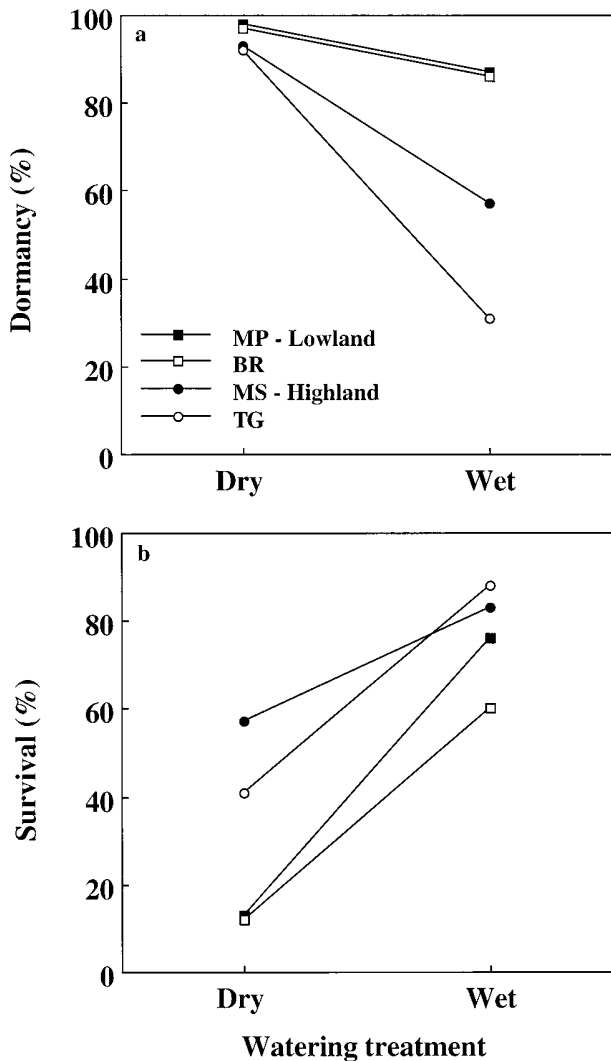


Fig. 5. Percentages of lowland (MP, BR) and highland (MS, TG) plants that were (a) summer dormant and that (b) survived the summer under wet and dry conditions are shown.

treatment interaction was not significant, indicating that the overall effect of watering on dormancy was similar in all populations ( $D = 4.00$ ,  $df = 3$ ,  $P = 0.262$ ).

Plant survival was greater under wet conditions than dry conditions in all populations (Fig. 5b;  $D = 84.25$ ,  $df = 1$ ,  $P = 0.000$ ). Overall, more highland MS and TG plants survived than lowland MP and BR plants ( $D = 27.55$ ,  $df = 3$ ,  $P = 0.000$ ). The population  $\times$  treatment interaction was not significant, indicating that watering affected survival similarly in all populations ( $D = 5.60$ ,  $df = 3$ ,  $P = 0.133$ ).

Plant mass was significantly affected by watering conditions and population (Fig. 6; treatment:  $F_{1,168} = 11.60$ ,  $P = 0.001$ ; population:  $F_{2,168} = 47.98$ ,  $P = 0.000$ ). Under both wet and dry conditions, mass of the highland MS and TG plants was greater than the mass of the pooled lowland plants. There was a weak population  $\times$  treatment interaction; mass of MS and TG plants was less under dry than wet conditions, but mass was similar under both conditions for the pooled lowland plants ( $F_{2,168} = 2.79$ ,  $P = 0.064$ ).

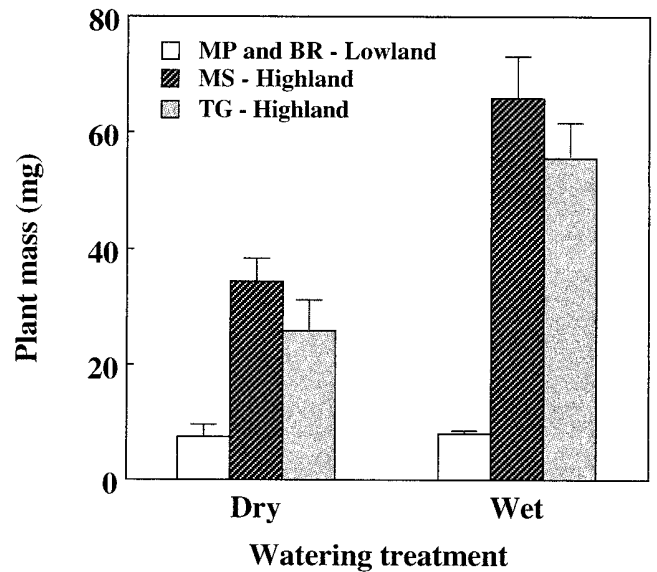


Fig. 6. Mean (+1 SE) masses (mg) of plants from the highland (MS, TG) and pooled lowland (MP, BR) populations under wet and dry conditions are shown.

**Field studies**—In the field, plants became dormant earlier in the lowland MP and BR populations than in the highland MS and TG populations. In December, dormancy was 100, 73, 18, and 0% in the MP, BR, MS, and TG populations, respectively. In March, all plants in all populations were dormant, and in September all plants were nondormant.

DISCUSSION

We found genetic variation in summer dormancy, a threshold trait, within and among populations of the lilioid geophyte *Burchardia umbellata*. In lowland MP and BR populations most plants were obligately dormant, whereas highland MS and TG populations contained both obligately dormant and facultatively dormant genotypes. The latter genotypes enter dormancy in response to drought conditions, but remain nondormant during conditions conducive for growth. Facultative dormancy allowed plants to avoid drought stress, while at the same time avoiding the costs of dormancy if conditions remained moist. Our results are consistent with predictions that obligate dormancy is selectively disadvantageous when environmental cues are unreliable and there are costs associated with becoming seasonally dormant. In this situation, selection should favor facultative dormancy probably via selection on an individual's sensitivity to the quality of its immediate environment. Although intraspecific variation in plant dormancy has been reported in other geophytes, little information exists on the extent to which differences are genetically or environmentally determined (Parsons, 2000). In other plant life forms, variation in plant dormancy within and among populations has been reported to have a genetic basis and has been interpreted as an adaptive response to habitat-specific selection (e.g., Clausen, Keck, and Hiesey, 1948; Clausen and Hiesey, 1958).

We found pronounced differences among populations in dormancy under moist conditions in a common garden with a greater proportion of dormant lowland MP and BR plants (92–100%) than highland MS and TG plants (37–66%). Differences of a similar magnitude occurred between lowland and

highland populations under moist conditions in the wet-dry experiment. Variation in a common garden such as reported here is usually taken as evidence for genetic differentiation. However, the design of our study does not exclude the possibility of maternal effects that can influence seed mass and seedling growth characters (Roach and Wulff, 1987; Donohue and Schmitt, 1998). In our study, *B. umbellata* plants took 3 yr to flower and it was not possible to monitor a second generation, which would have been necessary to discount maternal effects (Roff, 1997).

We also found significant differences among families for summer dormancy in the MS and TG populations (percentage among-family variance 44.7 and 8.3%, respectively), whereas differences in lowland populations were not significant (both ~0%). Variation occurring among families within populations is related to broad-sense heritability, which includes nonadditive and additive genetic variance, the latter upon which selection can act (Falconer and Mackay, 1996). The lack of genetic variation for dormancy within lowland populations may reflect past selection for obligate dormancy or genetic drift. Also, a larger sample than the seven maternal plants per population that we used may have detected variation within the lowland populations. Nevertheless, dormancy in the common garden and the wet/dry experiments were similar, indicating that most plants in lowland populations become dormant and that little variation probably exists for this trait. Conversely, among-year variation in summer conditions may maintain genetic variation for dormancy within highland populations.

In the lowland populations, the lack of differences in dormancy between the wet and dry conditions indicates that plants become dormant before they encounter drought stress and that dormancy is obligate. The benefit of obligate dormancy is increased survival resulting from escape from seasonally stressful conditions (Hoffman and Parsons, 1993). Obligate dormancy in *B. umbellata* is probably induced by an environmental cue(s) such as increasing photoperiod or temperature, both of which are correlated to future soil moisture conditions during the summer in lowland populations. Such environmental cues are used by winter deciduous trees and reliably predict the onset of freezing conditions (Bradshaw, 1965; Bradshaw and Hardwick, 1989; Schlichting and Pigliucci, 1998). Alternatively, dormancy may be endogenous and occur spontaneously without an environmental stimulus, as might result from strong directional selection for an environmentally induced threshold trait (Falconer and Mackay, 1996).

In the highland populations, the increase in dormant plants under dry compared with wet conditions (93% vs. 44%) indicates that these populations contain two phenotypes: those that are similar to lowland plants and that become dormant regardless of soil moisture (i.e., obligate dormancy) and those in which dormancy does not occur until soil moisture levels decrease (i.e., facultative dormancy). Both obligate and facultative dormancy are probably under polygenic control, involving regulatory genes or allelic sensitivity (Via et al., 1995; Roff, 1996, 1997; Schlichting and Pigliucci, 1998). It is unclear if different cues induce dormancy or if different environmental thresholds apply for obligately and facultatively dormant individuals. Nevertheless, facultatively dormant individuals appear to be more sensitive to the quality of their immediate environment, which in turn allows these plants to remain nondormant while conditions are suitable for growth. To more fully examine the control of this variation in dormancy, a split-family design in which related progeny are

grown under different soil moisture conditions would be informative (e.g., Sultan and Bazzaz, 1993).

The evolution of facultative dormancy in *B. umbellata* populations depends on the costs of dormancy, and the reliability of environmental cues predicting future conditions. Our results indicated that there were costs associated with obligate dormancy, including reduced survival, growth and reproduction. Summer survival, growth, and flowering were all less in the lowland populations where most plants were obligately dormant compared to highland populations that contained both obligately and facultatively dormant individuals. Similarly within the highland populations, obligately dormant individuals had lower survival, were smaller, and were less likely to flower than facultatively dormant individuals. This lower survival of dormant individuals could account for the slight decline in dormancy in the highland populations in the second year of the common garden experiment. Dormant individuals may have acquired fewer reserves in their underground storage organs because their growing season was shorter than nondormant individuals. In geophytes, underground storage organs must reach a critical size during the growing season to ensure survival in a dormant state through the summer to the next growing season. The size of storage reserves is also important in determining flowering and seed set (Dafni, Cohen, and Noy-Meir, 1981; Pate and Dixon, 1982; Boeken, 1990). Factors that affect seedling growth and storage reserves such as maternal effects and/or genetic differences among maternal families may interact with dormancy to influence the likelihood of plant survival over the summer. Plants that have small storage reserves at the beginning of summer may be less able to survive dormancy than plants with larger reserves. The high levels of mortality that we observed in dormant plants particularly in the lowland populations concur with other studies of *B. umbellata* (Pate and Dixon, 1982; Hitchmough, Berkeley, and Cross, 1989).

The expected cost of facultative dormancy is death if the onset of adverse environmental conditions occurs rapidly and plants are unable to enter dormancy quickly enough to evade the resulting stress (Bradshaw and Hardwick, 1989; Schlichting and Pigliucci, 1998). A lesser cost is increased metabolic expenditure associated with a nonlethal decline in conditions (Sachs and Ho, 1986; Lindquist and Craig, 1988). We found no evidence of costs associated with facultative dormancy under dry conditions. Indeed, we found that survival and plant size were greater in the highland populations under both wet and dry conditions, consistent with genetic differences that were not associated with dormancy. In our experimental manipulation, we gradually dried out the soil over the summer, which may have allowed plants to acclimate to the drought conditions. Consequently, it is possible that we did not stress the facultatively dormant plants sufficiently to incur costs that may occur only if the onset of drought is sudden and prolonged.

We found that all plants became summer dormant under natural conditions in the field. For the highland populations this suggests that dry conditions during the summer were sufficient to induce dormancy in plants that were facultatively dormant. The extent to which our results are representative of other years is not known. However, we infer from our experimental results that some highland plants would remain nondormant in years with particularly wet summers. The onset of dormancy in the field was delayed in highland plants compared with lowland plants as indicated by a lower proportion

of dormant plants in December. In the common garden, highland plants entered dormancy later and emerged from dormancy earlier, indicating genetic differences for the duration of summer dormancy.

Genetic differences for summer dormancy among populations of *B. umbellata* are likely to be related to habitat-specific selection pressures. Conditions for plant growth are more suitable during the summer in the highland populations than in the lowland populations. Rainfall is 30% higher in the highland populations, and summer conditions are more unpredictable because of the occurrence of storms than in the lowland populations, which are predictably hot and dry. In addition, in the highland populations the colder winter conditions are less favorable for plant growth, and the ability to exploit growth opportunities during the summer is likely to be more important than in the lowland populations. Further, these habitat-specific differences in climate between lowland and highland populations were probably accentuated during periods of Pleistocene aridity (Chappell, 1991). Under these conditions, selection in lowland populations has favored phenotypes that respond invariably to environmental cues that are highly correlated to future conditions not conducive for growth or survival. In contrast, the occurrence of obligate and facultative dormancy within highland populations is probably a consequence of temporal heterogeneity. No single phenotype is the most fit on all occasions as suggested by theoretical models examining polymorphism (Levins, 1968; Lloyd, 1984). In highland populations, dry years should favor obligate dormancy and wet years should favor facultative dormancy.

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