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# Geographical variation in predictive seedling emergence in a perennial desert grass

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## Summary

**1** Mechanisms that link germination and emergence to environmental cues associated with seedling success (predictive germination) would be expected to evolve when seedlings have a greater mortality risk than seeds, but may be less important in perennial plants than in annual plants.

**2** We investigated variation in predictive seedling emergence among divergent populations of a short-lived perennial desert grass, *Digitaria californica*, from sites that differed in climatic and edaphic factors. This species is native to environments in which the amount and duration of adequate soil moisture may control germination and seedling establishment success.

**3** We utilized a special irrigation system that permits application of a range of amounts of water within a single experiment in a glasshouse. Emergence data were subjected to probit and survival analyses to describe differences among the populations in response to applied water.

**4** Significant variation in predictive emergence was shown to exist among populations of *D. californica* when measured as amount of water required for 50% emergence following 3 days of water application, or as time required to achieve this level of emergence. Both climatic and soil characteristics were important with populations that originated from sites with less summer precipitation, and soils with higher water-holding capacity tended to have lower water requirements for emergence.

**5** The report demonstrates the existence of subtle variation in predictive emergence among populations of a perennial grass representing a relatively narrow range of ecological amplitude. It also establishes the usefulness of line-source irrigation and probit analysis procedures in studying seedling emergence behaviour.

*Keywords:* germination, line-source irrigation, probit analysis, survival analysis

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## Introduction

Several of the germination strategies that have evolved allow plants to persist in highly variable environments. Predictive germination, defined as germination that is directly sensitive to environmental factors associated with conditions favourable for immediate seedling growth, may, in some species, increase the probability of successful seedling estab-

lishment and reduce that of seed and seedling mortality (Cohen 1966; Beatley 1974; Venable & Lawlor 1980; Freas & Kemp 1983; Philippi & Seger 1989). Given the highly variable nature of precipitation in arid environments (Noy-Meir 1973), amount and temporal distribution of available soil moisture are primary environmental variables upon which predictive germination behaviour is likely to be based (Evans & Young 1987; Gutterman 1993; Roundy *et al.* 1997). Controls of germination in plants native to desert environments have been investigated intensively for annual species, both theoretically (Cohen 1966; Venable & Lawlor 1980; Venable 1989; Philippi 1993) and empirically (Freas & Kemp 1983;

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Elberse & Breman 1990; McGee & Marshall 1993; Gutterman & Nevo 1994; Pake & Venable 1996). Most of this research has considered the significance of seed dormancy within and between years, while less attention has been paid to the evolution of direct sensitivity to environmental cues (Venable & Lawlor 1980), specifically the existence of minimum amounts of soil moisture needed to trigger germination. Theoretical treatments suggest that perenniality is associated with reduced selective pressure on germination traits (Venable & Brown 1988; Rees 1994) and this may explain why little data are available on predictive germination in long-lived plants.

For plants native to arid environments, analyses of variation in germination and seedling growth in response to variable soil moisture have tended to focus on interspecific comparisons (Watt 1982; Frasier *et al.* 1985, 1987). However, many of the confounding effects of variable life-history traits that may exist among species are eliminated when examining intraspecific variation in plant performance and available soil moisture, and such approaches are therefore likely to yield a clearer understanding of germination behaviour and its ecological significance (Venable 1984; Meyer & Monsen 1991; Evans & Cabin 1995; Meyer *et al.* 1995).

Sophisticated theoretical analyses of the evolutionary significance of variation in germination behaviour are now common (Rees 1994; Venable 1997). However, methods used in validation experiments are often primitive, overly artificial, or lacking sufficient control. In arid environments, where response to variation in soil moisture is critical, an alternative approach may involve the use of sophisticated environmental simulation equipment, such as line-source irrigation systems. These produce a consistent gradient of water application away from a sprinkler nozzle and have been used to evaluate the response of seedlings to variable amounts of soil moisture (Johnson *et al.* 1982). This technology might also be an efficient method of assessing germination and emergence behaviour over a range of soil moisture conditions. When coupled with probit and survival analysis procedures (Scott *et al.* 1984), it may be possible to use this experimental approach to describe subtle differences in predictive germination response to moisture that might not otherwise be discernible.

Our primary objective in this research was to use a glasshouse line-source irrigation system to determine whether there is variation in germination and emergence behaviour among populations of *Digitaria californica* (Benth.) Chase., a perennial grass native to the Sonoran and Chihuahuan Deserts of North America and to similar environments in South America (Henrard 1950). Roundy & Biedenbender (1996) and Livingston (1992) showed that germination of *D. californica* is particularly

slow compared with other perennial grasses from these habitats, indicating that germination of this species may be especially sensitive to environmental cues. Caryopses were collected from 10 *D. californica* populations in Arizona, Texas and Mexico, and plants developing them in a common environment were used to produce equal-aged caryopses for use in this research. For each population we determined the amount of water required to produce emergence of 50% of the viable caryopses, and emergence speed, and then tested for relationships between these traits, caryopsis mass and climatic and edaphic factors at the site where the population was collected. A secondary objective of the research was to examine the practicality of using line-source irrigation technology and probit and life-table analyses to evaluate germination and seedling emergence behaviour under a range of water availability.

## Materials and methods

### EVALUATING SEEDLING EMERGENCE USING LINE-SOURCE IRRIGATION TECHNOLOGY

*Digitaria californica* (Arizona cottontop) is a perennial caespitose grass native to elevations between 300 and 1800 m a.s.l. in the Sonoran and Chihuahuan desert scrub and semi-desert grassland biotic communities of the south-western United States and north-western Mexico (Cable 1979; Brown 1994). This species is also native at somewhat higher elevations (1200–2800 m) in comparable biotic communities in Bolivia and Argentina (Henrard 1950). While mortality of *D. californica* plants has been shown to be high in the first year following emergence in Arizona (> 60%), about 20% of the plants that survive this period may live for more than 3 years and some may live more than 8 years (Canfield 1957). *Digitaria californica* appears to show most rapid germination at temperatures of about 23 °C, which occur during the summer months (when mean minimum temperature > 13 °C), and it does not require specific sequences of alternating temperatures for maximum germination. While germination may occur at lower temperatures, emergence and seedling survival is considered unlikely during winter and spring because seedling development proceeds slowly at temperatures characteristic of these seasons. As soil water is very rarely available for the long periods needed to support winter establishment (Roundy & Biedenbender 1996), plants that reach sexual maturity are likely to have originated only from caryopses that germinated in summer. (Caryopsis is used throughout to refer to the true caryopsis plus the villous glume and sterile lemma that represent the diaspore in this species.)

Soil for all emergence experiments was collected from a site at the Santa Rita Experimental Range (1155 m a.s.l.), 45 km south-east of Tucson, Arizona, USA, where *D. californica* is native. The soil, from the Combate-Diaspar Series (thermic Ustic Torrifuvent), was taken from the surface 5 cm. Soil that passed through a 2.5-mm screen was autoclaved and air dried before use.

Caryopses were obtained from *D. californica* populations from 10 locations representing a variety of habitats in the species range in North America (Table 1). A sample of these caryopses was sown in 1-litre pots containing the Combate-Diaspar soil in 1995. The resulting plants (20 per population) were grown with regular irrigation and fertilization in a glasshouse in Tucson, Arizona. Floral development suggests that *D. californica* is highly autogamous (S.E. Smith, unpublished data). Plants from each population were grown together but were isolated by at least 2 m from plants from any other population. Mature caryopses were harvested by hand from these plants in July–September 1996, and bulked for use in experiments. Caryopses of *D. cali-*

*formica* require a period of after ripening under temperature conditions that mimic those that occur in natural environments following dispersal in the autumn. Maximum germination percentage is observed following storage at 24–27°C for 10 weeks for caryopses harvested on 1 October (Gatica 1995). Caryopses were therefore stored under ambient conditions in paper envelopes in the glasshouse until January 1997, to facilitate after ripening. Continued storage at this temperature may result in loss of viability, but our experiments were conducted over two summers, and caryopses, once ripened, were therefore stored with desiccant at 4°C following after ripening until used. For emergence experiments, slightly tapered cylindrical plastic containers (20 × 4 cm, height × top diameter; Ray Leach Containers<sup>®</sup>, Stuewe and Sons Inc., Corvallis, OR) were first filled with 18 ml of pea gravel before 132 ml screened soil (water content < 0.05%) was added on top. Six caryopses were placed individually with the midline of the caryopsis 1–2 mm below the soil surface in each container, and an additional 9 ml of soil that passed through a 2.5-mm screen

**Table 1** Collection information for 10 accessions of Arizona cottontop used in studies of seedling emergence using a line-source irrigation system

Location (population name)	Accession information (year collected)*	Weather station†	Mean summer precipitation (mm) (number of months)‡	Soil water content (% of dry weight at matric potential of -1.5 MPa)§
Durango, MX	PI 216638 (1953)	Francisco I. Madero, Durango	377 (5)	–
Chihuahua, MX	PI 216622 (1953)	Chihuahua, Chihuahua	265 (5)	–
Douglas, AZ	PI 399305 (1973)	Douglas	244 (4)	4.0 d
Sierra Vista, AZ	PI 399300 (1972)	Y Lightning Ranch	232 (4)	4.4 d
Santa Rita Exp. Range, AZ	Exclosure 2B (1990)	Eriopoda Station	225 (4)	3.8 e
Van Horn, TX	PI 469253 (1958)	Van Horn	194 (5)	–
Robles Junction, AZ	Robles Junction (1990)	Anvil Ranch	180 (4)	3.0 f
Oracle Junction, AZ	PI 399302 (1972)	Willow Springs Ranch	151 (4)	5.9 c
San Simon, AZ	Highway 86, w. San Simon (1994)	Santa Rosa School	143 (3)	7.6 a
Bowie, AZ	PI 399304 (1972)	Bowie	140 (4)	6.4 b

\*Collection details for plant introductions (PIs) available from USDA-National Plant Germplasm System

< [http://www.ars-grin.gov/npgs/acc/acc\\_queries.html](http://www.ars-grin.gov/npgs/acc/acc_queries.html) >. Details for other accessions can be obtained from S.E. Smith.

†Unless otherwise noted, average long-term (> 22 years) precipitation from WorldClimate

< <http://www.worldclimate.com> >. Eriopoda Station data from records kept at SRER for the period 1943–93.

‡ = Total precipitation in months with mean minimum temperature > 13°C at the site of precipitation measurement, if available. If minimum temperature data were not available, data were used for the nearest station within the network available from the National Climate Data Center.

§Data available for Arizona accessions only. Means followed by different letters are not significantly different by sequential Mann–Whitney *U*-tests among adjacent means ( $P \leq 0.05$ ).

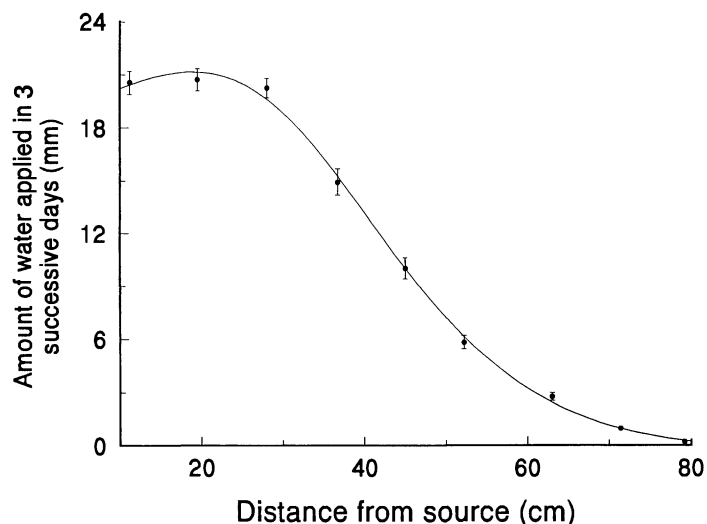
was then applied to cover them completely. Any excess soil was removed by running a straight edge over the top edge of each container.

A line-source irrigation system was built in an evaporatively cooled glasshouse in Tucson, Arizona, using the basic design outlined by Johnson *et al.* (1982), in which a single nozzle moves perpendicular to the irrigation gradient. (Details on design or operation of the irrigation system can be obtained from S. E. Smith.) The system was programmed to apply water between 02.00 and 03.00 h, when glasshouse fans were not running, at a rate at which there was no runoff from the exposed soil surface. Water application was measured by weighing soil-filled containers (without caryopses), placed at the same distance from the line source as those containing caryopses, each morning on each of 3 successive days. This weight was transformed to a depth (equivalent to total millimetres of precipitation over the 3 days) and all discussion refers to these values (Fig. 1).

The irrigation regime selected was based largely on the research of Frasier *et al.* (1985, 1987), Roundy & Biedenbender (1996), Roundy *et al.* (1997) and a pilot study conducted in 1996 (S.E. Smith & D.M. Fendenheim, unpublished data). While many factors are involved in determining whether seedlings will emerge and establish in arid environments (Guterman 1993), existing data indicate that precipitation (water application) on at least 3 consecutive days is needed for seedling establishment of warm-season perennial grasses such as *D. californica* in south-eastern Arizona. Experiments were begun only when mean relative humidity exceeded approximately 60% and when these condi-

tions were forecast to persist for at least 3 consecutive days. Glasshouse cooling was adjusted to mimic outside temperatures as much as possible (Table 2). Water was applied using the line-source system for 3 consecutive days (days 1–3) during each of seven 25-day experiments that were initiated and completed between 16 August and 13 September 1997 (three experiments) and 25 July and 16 September 1998 (four experiments). No water was applied on days 4–11, the post-irrigation drought period, and it was during this period that initial emergence was recorded. Water was then applied liberally on days 12–24 to saturate the soil thoroughly and uniformly and permit emergence from any remaining viable caryopses. Under these conditions maximum seedling emergence was observed at the highest levels of water application, and levels of emerged seedling mortality were low at all moisture levels throughout the post-irrigation drought period.

Each experiment contained the 10 populations arranged in a randomized complete block design with three replications. Within each replicate of each population, nine containers were placed parallel to the irrigation gradient (perpendicular to the route of travel of the sprinkler nozzle). These were located between 11.2 and 79.2 cm from a line directly below the nozzle. This group of nine containers is referred to as a 'plot.' The nine containers represented nine water application levels, with the containers closest to the nozzle receiving in excess of 20 mm of water during the 3-day irrigation period, while those furthest from the nozzle received < 1 mm during the same period (Fig. 1). Maximum soil water content (weight of water/weight of dry soil) in the container at the 11.2 cm position aver-



**Fig. 1** Mean ( $\pm$  SE) amount (depth) of water applied by a line-source irrigation system from 11.2 to 79.2 cm from a line directly below the water source. Means are totals for 3 days of water application for three replicate experiments in 1997. Function:  $r^2 = 0.982$ .

**Table 2** Mean ( $\pm$  SE) temperature and relative humidity within the glasshouse on days with and without water application or precipitation for the first 8 days of each of the three experiments in 1997, and of the four experiments in 1998 and for all 8-day periods in July and August 1987–98 at an outdoor weather station in Tucson, Arizona, that began with 3 consecutive days with precipitation ( $n = 8$ )

Days with water application/precipitation	Temperature ( $^{\circ}$ C)		Relative humidity (%)	
	Means during experiments	1987–98 means*	Means during experiments	1987–98 means
Yes	26.9 $\pm$ 0.1	26.9 $\pm$ 0.6	71.4 $\pm$ 0.3	70.8 $\pm$ 3.2
No	27.2 $\pm$ 0.1	29.3 $\pm$ 0.3	66.7 $\pm$ 0.2†	54.2 $\pm$ 1.8

\*Data from the Arizona Meteorological Network, Tucson station (AZMET 1998).

†Significant differences were observed between experimental values and means from the Arizona Meteorological Network only for relative humidity without water application/precipitation ( $P \leq 0.05$ ) based on Mann–Whitney  $U$ -test.

aged  $8.10 \pm 0.26\%$  after 3 days with irrigation and  $3.40 \pm 0.65\%$  at the end of the post-irrigation drought. At the 79.2 cm position, maximum and minimum soil moisture averaged  $0.08 \pm 0.01\%$  and  $0.06 \pm 0.01\%$  at these times, respectively.

Variation in the depth of summer precipitation among sites where *D. californica* is native may be due to variation in the total number of precipitation events, the mean depth of precipitation per event, or both. Existing meteorological data suggest a positive correlation between these factors in the region where this species occurs (Smith & Schreiber 1974; Hanson *et al.* 1994), indicating that sites with lower summer rainfall have both fewer precipitation events and less precipitation per event. Water application within the line-source gradient represents a range of precipitation depths that would be expected during 3 consecutive days with precipitation. The dryer portion of the gradient would therefore tend to mimic average conditions at sites with lower summer precipitation, while the wetter portion of the gradient would correspond to sites with higher summer precipitation.

Seedlings were considered emerged when any portion of the coleoptile could be observed. Counts of the number of emerged seedlings in each container were conducted on days 4–8 and on day 25. Caryopsis mortality was represented by the percentage of caryopses sown within a container that had not emerged by the end of the experiment.

Temperature and relative humidity were measured every 12 min throughout each experiment using Hobo<sup>®</sup>-XT and -RH data loggers (Intermountain Environmental Inc., Logan, UT). Daily means for these variables were compared with daily means observed during the 8-day periods in July and August 1987–98 in Tucson that began with 3 consecutive days with precipitation (AZMET 1998) (Table 2).

#### SOIL COLLECTION AND ANALYSIS

Original caryopses collections were made between 1953 and 1994 (Table 1) by six different collectors.

For Arizona collections made by persons other than authors of this paper, exact locations of each population were determined using information provided by US Department of Agriculture (USDA)-Natural Resources Conservation Service personnel from original unpublished notes, or from the Plant Inventory (USDA 1954, 1975, 1982). Soil was sampled from the surface 5 cm directly under at least five *D. californica* plants at each of these sites in August 1997 ( $> 1$  kg total). Dried soil that passed through a 2-mm mesh screen was evaluated for the relationship between matric potential and soil moisture content at a matric potential of  $-1.5$  MPa using a pressure plate apparatus (Klute 1986).

#### STATISTICAL ANALYSES

Maximum percentage emergence within each container was determined over days and water levels for each plot. Plots that did not have at least five containers with 100% emergence ( $n = 3$  over both years) were excluded from all analyses. Reduced emergence in these plots was most probably due to caryopsis placement at sowing, and would be expected throughout the plot. Caryopsis mortality, temperature, relative humidity and soil water content were evaluated using Kruskal–Wallis  $k$ -sample or Mann–Whitney  $U$ -tests (Sokal & Rohlf 1981). Functions describing relationships between water application and distance from the water source (Fig. 1) and emergence and water application (Fig. 2) were generated using TableCurve 2D (SPSS Inc., Chicago, IL).

Probit analysis can be applied to seedling emergence (germination) experiments to estimate the amount of an environmental factor required for some level of response (Scott *et al.* 1984; Still & Bradford 1998). In these experiments, the amount of water required for 50% emergence by day 8 was estimated using probit procedures assuming the normal distribution for the probit model in SAS (SAS Institute 1989). Individual estimates were made for each population and experiment after pooling data

from the three replications in that experiment. These 70 estimates (seven experiments  $\times$  10 populations) were then subjected to mixed model ANOVA (experiments = random effect) using PROC GLM (SAS Institute 1989) to determine significant differences among populations. Comparison of performance between years was made by calculating rank correlation coefficients for the amounts of water required for 50% emergence for populations in each year. Life-table analysis was used to evaluate the time required to achieve 50% emergence of viable carypopses in each population (Scott *et al.* 1984). This was done for two levels of water application where emergence of at least 50% was possible for all populations (level 2, *c.* 20.6 mm, and level 5, *c.* 14.0 mm water applied during the initial 3-day irrigation period, with the latter level representing water application considered 'moderate'). Non-parametric multiple comparison of emergence times among populations based on Wilcoxon rank scores and using a Bonferroni adjustment was done using a SAS program developed by Fox (1993). Spearman's rank correlation coefficients were calculated for pairs of primary emergence variables. Statistical significance was assigned at  $P \leq 0.05$  in all cases.

## Results

### EXPERIMENTAL CONDITIONS

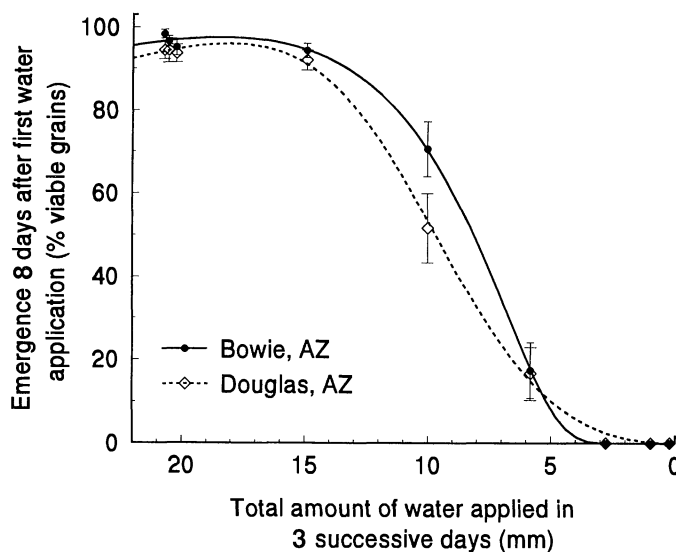
Mean temperatures on days with and without water application during the first 8 days of the experiments were not significantly different from the long-term average (1987–98) for 8-day periods in July and

August that began with 3 consecutive days with precipitation (Table 2). Mean relative humidity also did not differ on days with water application and precipitation, although mean relative humidity during periods without water application was significantly greater during experiments than during comparable periods at the outdoor weather station.

### EMERGENCE AND HABITAT CHARACTERISTICS

Seedling emergence exhibited a distinctly sigmoidal response to decreasing water application in all populations (two populations are shown in Fig. 2). Differences in emergence among populations along the moisture gradient were suggested by visual comparison of responses either over all levels of water application or at individual levels. Probit analysis permitted definitive comparisons of the populations' responses to the entire range of water application levels. The amount of water required for 50% emergence can be regarded as a measure of the minimum amount of moisture required for significant emergence to occur. Moreover, as emergence could be recognized as soon as the coleoptiles appeared and the coleorhiza emerges between 2 and 6 h before the coleoptile in *D. californica* (S.E. Smith, unpublished data), it is assumed that variation in this variable among populations could be attributed primarily to variation in germination and that seedling emergence represents a reasonable proxy for germination.

Considerable variation was observed among the populations in the water requirement for 50% emer-



**Fig. 2** Mean ( $\pm$  SE) percentage emergence 8 days after the first water application over the range of amounts (depths) of water applied for two populations of *D. californica*. These two populations represent the extremes in mean emergence at levels of water application below 10 mm that were observed among the 10 populations studied. Functions:  $r^2 > 0.98$ .

**Table 3** Amount of water required for and median time to achieve emergence of 50% of caryopses and caryopsis mortality in 10 populations of *D. californica* evaluated using a line-source irrigation system in seven experiments in 1997 and 1998

Population	Mean total water required in days 1–3 for 50% emergence by day 8 (mm)*	Median number of days following the first water application to achieve 50% emergences		Mean caryopsis mass $\pm$ SE (mg 100 caryopsis <sup>-1</sup> ) $\dagger$
		14.0 mm water applied in days 1–3	20.6 mm water applied in days 1–3	
Chihuahua	11.90 a	4.78 ab	4.72 a	70.1 $\pm$ 0.5
Durango	11.82 a	4.71 abcd	4.55 abc	85.8 $\pm$ 0.4
Robles Junction	11.43 ab	4.77 ab	4.57 abc	80.3 $\pm$ 0.2
Van Horn	11.35 ab	4.52 d	4.55 abc	83.6 $\pm$ 0.3
Douglas	10.89 ab	4.77 ab	4.53 bc	71.5 $\pm$ 0.1
Sierra Vista	10.10 bc	4.52 d	4.44 c	78.7 $\pm$ 0.1
Santa Rita Exp. Range	10.07 bc	4.73 abc	4.55 bc	82.8 $\pm$ 0.1
San Simon	10.06 bc	4.66 bcd	4.60 abc	82.3 $\pm$ 0.1
Oracle Junction	10.03 bc	4.72 abcd	4.71 ab	82.7 $\pm$ 0.2
Bowie	8.89 c	4.55 cd	4.45 c	85.0 $\pm$ 0.2
(Mean)	10.10	4.70	4.57	80.3

\*Means of estimates from five experiments assuming the normal distribution for the probit model. Means followed by different letters are significantly different ( $P \leq 0.05$ ) based on Duncan's multiple range test.

$\dagger$ Estimated using life-table analysis. Medians followed by different letters are significantly different ( $P \leq 0.05$ ) based on non-parametric multiple comparison using Wilcoxon rank scores and a Bonferroni adjustment (Fox 1993).

gence within 8 days (CV = 19.2%). This was reflected in several significant differences in mean water requirement among populations based on a Duncan's multiple range test (Table 3). Relative performance of populations between years was highly consistent for this variable ( $r_s = 0.98$ ,  $P \leq 0.05$ ). There was much less variability and fewer statistically significant differences among populations when emergence was measured by the median time required to achieve 50% emergence under either a relatively wet (c. 20.6 mm, CV = 2.0%) and a somewhat lower ('moderate') level of water application (c. 14.0 mm, CV = 2.5%) (Table 3). Substantial variability and several significant differences also existed among populations for soil water content (CV = 30.1%; Table 1) and caryopsis mass (CV = 6.7%; Table 3). Mean caryopsis mortality ranged from 4.6% to 37.6% over the nine levels of water application, and was most variable at low levels of water application. However, no significant differences were observed in this variable among populations for which mean mortality exceeded 6% (data not shown).

Among all populations, precipitation during the summer at the site of collection was positively and significantly correlated with the water requirement for 50% emergence (Table 4 and Fig. 3). For the populations from Arizona, the water required for 50% emergence was also negatively correlated with the soil water-holding capacity (soil water content) at the site where plants were collected (Table 4 and Fig. 3). Emergence speed and caryopsis mass (Table 4) and mortality were not significantly corre-

lated with any of the emergence-related or environmental variables measured.

## Discussion

Our experiments demonstrate that significant variation exists in predictive emergence among populations of *D. californica*. This was manifested mainly in differences in the amounts of water required to achieve 50% emergence, but there was also a non-significant trend in the time needed to attain this with moderate water application. Variation in water requirement was associated with both average summer precipitation (for all populations) and soil characteristics at the site of origin (for the populations where this relationship could be assessed, i.e. the seven from Arizona). With a positive correlation between average summer precipitation and the depth of precipitation per rainfall event (Smith & Schreiber 1974; Hanson *et al.* 1994), our data suggest that the evolution of predictive emergence is linked to the average precipitation per day in 3 consecutive days with precipitation. Conclusions regarding responses to other precipitation regimes are not possible. Among the Arizona populations, there was also a negative, but non-significant, trend that suggests a positive association between soil water-holding capacity and summer precipitation, but it was not possible definitively to separate any independent effects of each of these factors on emergence behaviour.

One mechanism by which predictive emergence may be achieved in *D. californica* is by altering the



**Table 4** Spearman's rank correlation coefficients (probability of statistical significance) among measurements of emergence behaviour, environmental variables and caryopsis mass in 10 populations of *D. californica* evaluated using a line-source irrigation system

	Days to 50% emergence 14.0 mm of water ( <i>n</i> = 10)	Days to 50% emergence 20.6 mm of water ( <i>n</i> = 10)	Summer precipitation ( <i>n</i> = 10)†	Soil water content ( <i>n</i> = 7)‡	Caryopsis mass ( <i>n</i> = 10)
Amount of water for 50% emergence§	0.49 (0.15)	0.28 (0.43)	0.78* (0.01)	-0.80* (0.03)	-0.28 (0.42)
Days to 50% emergence 14.0 mm of water ( <i>n</i> = 10)		0.58 (0.08)	0.30 (0.40)	-0.71 (0.07)	-0.45 (0.19)
Days to 50% emergence 20.6 mm of water ( <i>n</i> = 10)			0.01 (0.99)	0.12 (0.79)	-0.21 (0.56)
Summer precipitation ( <i>n</i> = 10)				-0.62 (0.14)	-0.26 (0.47)
Soil water content ( <i>n</i> = 7)					0.35 (0.44)

\*Significant at  $P \leq 0.05$ .

†Mean precipitation in months with a mean minimum temperature  $> 13^\circ\text{C}$ .

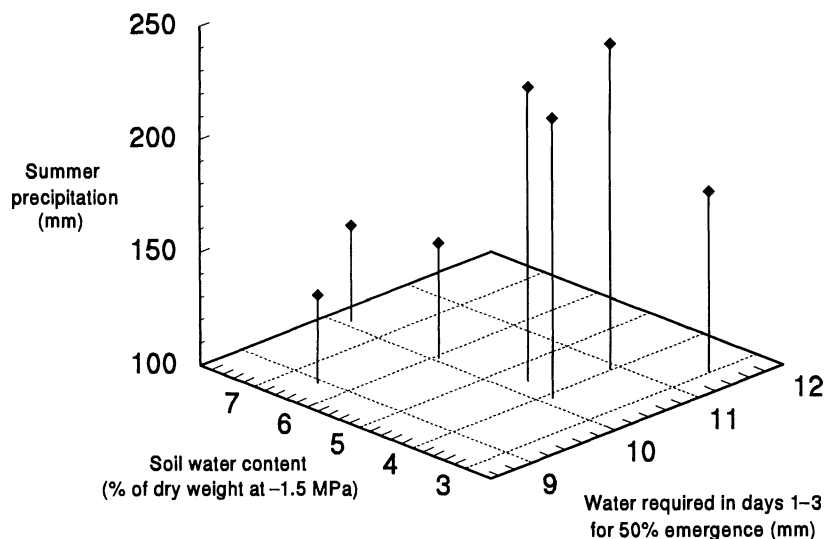
‡Expressed as percentage of dry weight of soil at a matric potential of  $-1.5\text{ MPa}$ ; populations from Arizona only.

§Based on probit analysis of emergence after 8 days, with irrigation on days 1–3.

amount of time required to germinate. The apparent positive trend between time and amount of water required to achieve 50% emergence with moderate water application (*c.* 14.0 mm in 3 successive days) suggests that this may occur. Previous research (Gatica 1995) has shown that the glume and lemma surrounding the caryopsis of *D. californica* slows imbibition of the diaspore compared with that of naked caryopses. Collectively, these data indicate that caryopsis appendages may be very important in expression of predictive emergence in this species.

At the most arid extremes of the distribution of *D. californica* (summer precipitation  $< c.$  150 mm),

germination behaviour recorded here may indicate that this species can persist only on soils with relatively high water-holding capacities. This may even override the fact that at dry sites the efficiency of water utilization by established plants would be expected to be higher on sandier soils because of decreased runoff and evaporation (Noy-Meir 1973). Our data suggest that at least part of the reason for this is that there is unlikely to be sufficient precipitation to provide enough soil moisture to support germination and seedling emergence of *D. californica*, except on soils with relatively high water-holding capacities. As average summer precipitation



**Fig. 3** Means for summer precipitation, soil water content and total water required in 3 consecutive days for 50% emergence of *D. californica* populations from Arizona when evaluated using a line-source irrigation system.

increases above about 150 mm, the soils that support *D. californica* populations have lower water-holding capacities (Fig. 3), and mature plants may be able to utilize more effectively the increased water infiltration associated with these soils (Noy-Meir 1973). This could explain the observation that *D. californica* may become a much more dominant component of the vegetation at these sites (Cable 1979).

The caryopses used in these experiments were produced under the same environmental conditions, and our data therefore indicate that the differences among populations in predictive emergence in response to water are genetically based and thus the products of selection. This strongly suggests that precise predictive germination may have evolved in perennial grasses, although theoretical analyses of factors controlling germination do not lead to this expectation (Venable & Brown 1988; Rees 1994). However, *D. californica* is a short-lived perennial with high seedling mortality (Canfield 1957) and might therefore be expected to show behaviour more characteristic of an annual. The possibility exists that an interaction between the genotypes of each population and the artificial environment used for caryopsis production or evaluation of emergence may have been responsible for the emergence behaviour observed (Quinn & Colosi 1977). Nevertheless, given the close positive correlation between the water required for 50% emergence and precipitation and edaphic characteristics at the site of origin (Table 3), this seems unlikely.

Caryopses used in this experiment represent a bulk sample from up to 20 genotypes for each population, and therefore it is not possible to determine whether genetic variation in any of the traits measured exists within populations. Estimates of population performance presented here represent approximations of the average behaviour of the entire population. As each plot contained at least two containers with 100% emergence, it can be assumed that essentially all caryopses used in these experiments were viable and non-dormant. However, using these methods it is not possible to determine whether individual caryopses that do not emerge given the amount of water necessary for 50% emergence do so because of genetic differences in response to moisture or to experimental or sampling error. Nevertheless, the use of probit analysis made it possible to describe differences in population performance that would not have been possible using more traditional analysis approaches (Watt 1982; McGee & Marshall 1993; Emmerich & Hardegree 1996).

The amount of water available in the top 1–3 cm of soil, which ultimately drives germination and seedling emergence in *D. californica*, is determined by a complex interaction of meteorological, soil, physical and biological processes. Emergence under

the moisture regimes utilized in this experiment probably involved a set of biophysical events that mimicked those in natural seed beds in arid environments (Roundy *et al.* 1997). A series of hydration and dehydration events in the caryopsis may be needed to trigger germination and emergence. At levels of soil moisture below that where 50% emergence results, desiccation-associated mortality of physiologically active but ungerminated caryopses would be expected to increase (Allen *et al.* 1993). Evolution of the ability to detect and germinate in response to the appropriate amount of soil moisture is one component of an effective predictive germination strategy. The ability to reduce the probability of caryopsis mortality when insufficient water is available to trigger germination may also be evolutionarily important. However, our experiments were unable to demonstrate significant differences in survival at levels of water application that did not result in significant emergence following the initial 3-day irrigation.

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