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PHENOTYPIC PLASTICITY MAY FACILITATE INVASION BY *AEGILOPS TRIUNCIALIS*

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ABSTRACT

One great obstacle to understanding the invasion of nonnative species into native ecosystems is the lack of information on the population biology of the invading species. In particular, morphological and physiological adaptations and potential for phenotypic plasticity will strongly influence a species' ability to persist and spread in newly invaded ecosystems. Phenotypic plasticity can buffer populations from selection thereby allowing them to survive the establishment phase of the invasion. The annual grass *Aegilops triuncialis* (Poaceae, Triticeae) has become highly invasive in California (USA) and provides an opportunity to investigate the importance of phenotypic plasticity to persistence and spread in new habitats. This species produces dispersal units containing dimorphic caryopses ("seeds") with different degrees of dormancy. Germination of the smaller seeds is suppressed by maternal tissues and by the larger sibling, but how this induced dormancy varies across populations is unknown. I used 12 populations from northern California to compare size relationships between seeds and to investigate variation in the strength of the maternal and sibling effects on germination. The larger seeds were never dormant while induced dormancy of the smaller seeds varied across populations and years. Thus, the factors governing induced dormancy were not genetically fixed, but appeared to be environmentally influenced. For *A. triuncialis*, reproductive strategies, such as seed-size dimorphism, may facilitate initial invasions into new environments, but variation in the strength of controls over germination may be important for facilitating post-invasion persistence and spread.

Key words: *Aegilops triuncialis*, competition, dimorphism, dormancy, invasion, phenotypic plasticity.

INTRODUCTION

A wide range of morphological traits have been identified as being directly or indirectly beneficial for invasive plant species success, including high dispersal ability, rapid germination and growth, rapid maturation, high allocation to reproduction, and high reproductive output (Baker 1965; Lodge 1993; Sakai et al. 2001). Phenotypic plasticity is also included as an important trait, but its contribution to invasibility has rarely been quantified in a meaningful way (e.g., Rice and Mack 1991; Sexton et al. 2002). One reason researchers give more attention to adaptive morphology is the notion that form follows function and that fixed traits must result in a quantifiable tradeoff between survival and fitness. If true, such a tradeoff implies that narrowly adapted or specialized organisms may show reduced trait plasticity (Marshall et al. 1986; Sultan 1995). Therefore, in highly successful invasive species, if there are identifiable suites of physical traits that confer a selective advantage, then trait plasticity is predicted to be a less important component of that success. In contrast, however, if invasive species are generalist species, then plasticity itself may be a critical component of the suite of traits characterizing invasive species (Baker 1965; Sakai et al. 2001). To create a predictive framework for invasive species ecology, it will be important to investigate more fully the relationship between plasticity and invasiveness.

The potential role of plasticity in invasion must be viewed over the time required for establishment and spread. During the so-called "lag phase" (Mack 1985) typical of most invaders prior to aggressive spread, the invader is faced with

novel environmental conditions influencing growth, resource availability, and competition with locally adapted native species. Over this period, selection pressure to adapt to local conditions must be unusually high and trait plasticity probably contributes to the year-to-year success of the introduced species. Whether a new species is adapted to competition for light in highly productive conditions or to rapid colonization after repeated disturbance, plastic responses to growing conditions must play an important role in short-term success. Two very important traits that are likely to contribute to establishment and which show high variability in annual plants are the speed of germination and the rate of stem elongation because both contribute to more rapid growth and resource acquisition (Harper 1977).

One habitat type where the importance of plasticity should be easily observed is in grasslands typical of Mediterranean climatic zones. In these environments, invasion by annual grasses, in particular, has occurred repeatedly and patterns of above- and below-ground resource partitioning are not particularly complex. In California, USA, invasion by annual Eurasian plants has been massive and has occurred in a very short span of time (Burcham 1957; Mack 1986). Mack (1986) called it one of the most complete and rapid habitat conversions in recorded history. The totality of the conversion to dominance by nonnative species suggests that invasions in the future could be less common or will involve species with unusual suites of traits. As new invasions occur, these grasslands can provide opportunities for observing the process of invasion, the morphological traits that contribute to success, and the subsequent effects on the community (Montalvo et al. 1997).

Table 1. Seed collection sites of *Aegilops triuncialis* in northern California, USA. Eleven populations were sampled, with one (Bear Valley) sampled in two years. Population numbers correspond with the regressions in Fig. 1.

Population	°N latitude	°W longitude
Sacramento Valley		
1. Jepson Prairie	38.29	121.82
2. Mather Field	38.55	121.28
Northern Sierra Nevada Foothills		
3. Bear Creek	38.88	120.13
4. Sierra AD	39.23	121.28
5. Sierra Shubert	39.25	121.28
Northern Coast Range		
6. Hopland-Foster	39.03	123.10
7. Hopland-BA	39.02	123.09
8. Hopland-WSII	39.02	123.08
Central Coast Range (inland)		
9–10. Bear Valley	39.12	122.44
11. McLaughlin	38.86	122.41
12. Snell Valley	28.70	122.41

Grasslands in Mediterranean climates are characterized by high seasonal competition intensity and by a high proportion of annual species showing seed dormancy. However, seasonal variation in the timing and distribution of precipitation, and subsequent productivity, can be very unpredictable (George et al. 1989). Thus, seeds must be able to respond quickly when conditions are appropriate because early germination and establishment has been correlated with survival later in the season (e.g., Ross and Harper 1972; Kadmon 1993). However, some fraction of the species seed bank often remains dormant even under optimal conditions as a bet-hedging strategy against catastrophic loss of early cohorts (Cohen 1967). In addition, the very high variation in inputs to the soil seed bank of annuals, and subsequent seedling densities, suggest that seeds should exhibit some sensitivity to the potential competitive environment represented by the neighborhood seed bank (Dyer et al. 2000; Turkington et al. 2005).

Dyer (2004) found that the aggressively spreading, non-native, annual grass *Aegilops triuncialis* L. (barbed goat-grass; Poaceae, Triticeae) is unusual among nonnative annual grasses in California because spikelets contain dimorphic caryopses ("seeds") that remain together after dispersal. These traits lead to the expectation of both maternally influenced (Westoby 1981) and sibling-influenced (Cheplick 1992) germination of subordinate seeds. This species showed both influences (Dyer 2004) and was subsequently used in this study to investigate plasticity of seed dormancy and the strength of maternal and sibling influences across 12 populations in four regions of its California distribution.

MATERIALS AND METHODS

Dry inflorescences of *Aegilops triuncialis* were collected from 12 populations in four regions of northern California in 2000 and 2001 (Table 1). Inflorescences usually contained

four to six spikelets with the lower two often containing a pair of dimorphic seeds. The large seed was never dormant (Dyer 2004) and the small seed showed complete germination only after removal from the spikelet. In the spikelet, dormancy of the small seed was likely induced by chemicals on the surrounding tissues (i.e., a maternal effect, Lavie et al. 1974) and by the presence of the large seed (i.e., a sibling effect, Dyer 2004).

Two treatments were applied to 200 spikelets from each population. To eliminate the effect of the sibling seed, the large seed was manually removed from 100 spikelets. To reduce the strength of the maternal effect, 50 intact spikelets and 50 with the large seed removed were soaked in deionized water for 18 hr; the process was repeated three times. This process resulted in four treatment combinations: intact/unwashed, intact/washed, seed removed/unwashed, and seed removed/washed. The four treatment groups of 50 spikelets from each population were sown individually to the depth of the spikelet (ca. 1 cm) in seedling tubes (Stuewe and Sons, Corvallis, Oregon, USA) filled with commercial potting soil. Each group of 50 seedling tubes was arranged on racks as five groups of 10 spikelets per treatment. Racks were placed in a Conviron environment chamber (Controlled Environments Inc, Pembina, North Dakota, USA) set at 20°C day (12 hr) and 10°C night (12 hr) temperatures. Seedling tubes were watered daily and emergence was monitored over a 14-day period. After fully drying the soil, seeds, and seedlings, emergence of the remaining seeds was monitored over a second watering period of 14 days.

Fifty pairs of seeds from each population were weighed to estimate the slope and variation of the relationship between large and small seeds. The relative strength of the dormancy-inducing factors within each population was analyzed with a two-way ANOVA (JMP vers. 3.02, SAS Institute Inc., Cary, North Carolina, USA) using emergence (arcsine transformation of percent values) of small seeds after the first and second wet periods. No statistical comparisons among populations were made.

RESULTS

Mean seed mass of both large and small seeds varied greatly among populations. However, linear regression indicated that the relationship between large and small seed mass was very consistent (Fig. 1). Large seeds were 2.5–3.0 times heavier than small seeds, and the slope of the relationship was consistently near 0.35. The range of seed mass was 9.4–25.8 mg for large seeds and 4.6–10.7 mg for small seeds. For 10 of 12 populations, the slope of the regression was 0.27–0.39 ($r > 0.69$, $P < 0.0001$) and the large seed was ca. 2.6–3.8 times larger than the small seed.

In the first watering period, emergence of small seeds varied greatly among populations, but ANOVA explained >65% of the variation in 10 of the 12 populations (Table 2). The main effect of the large seed on small seed emergence was significant for all 12 populations (Table 2; Fig. 2: e.g., Hopland-Foster). The main effect of spikelet washing on small seed emergence was significant for 9 of the 12 populations (Table 2; Fig. 2: e.g., Jepson Prairie). The interaction term between large seed presence and spikelet washing was significant in 6 of the 10 populations for which there were

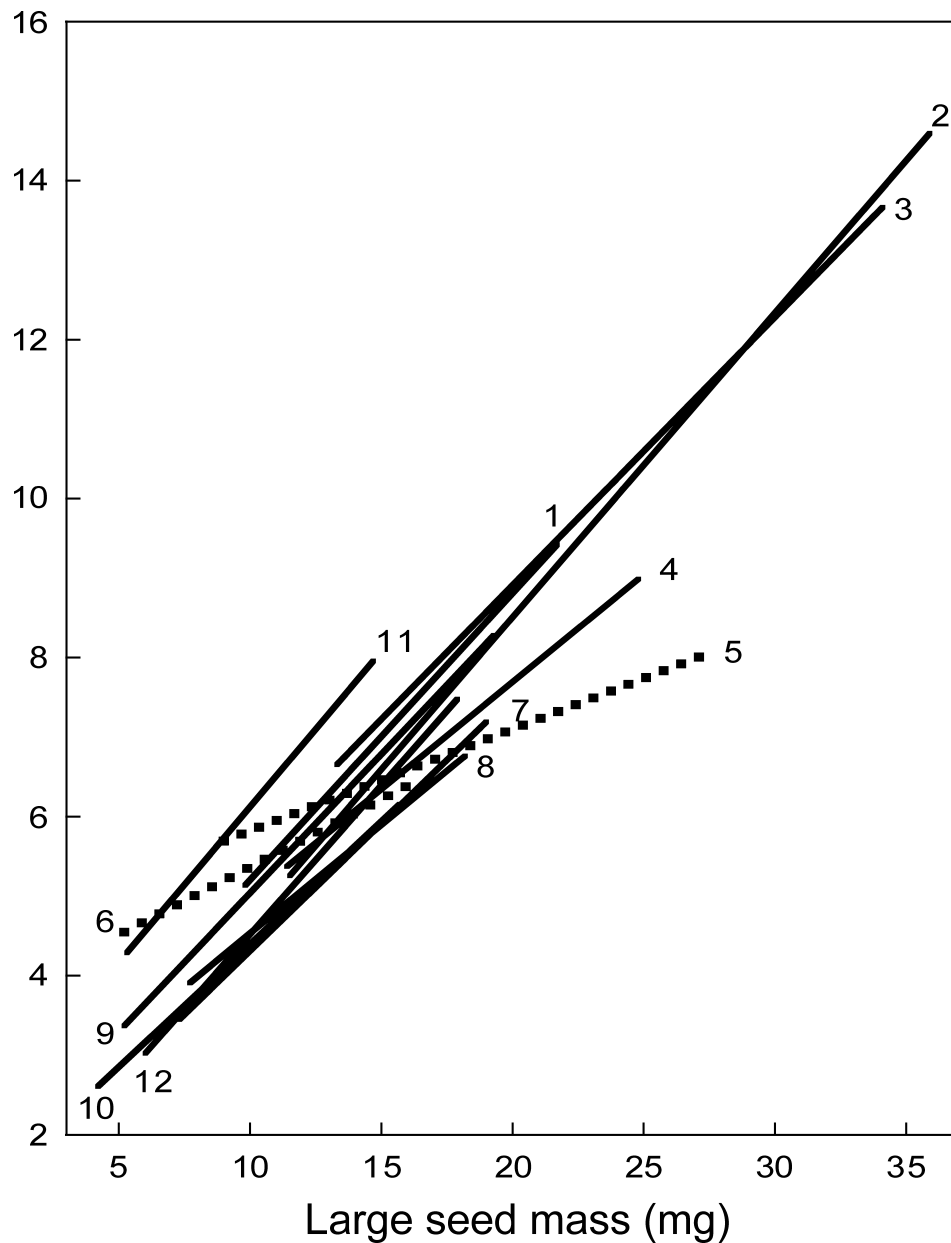


Fig. 1.—Linear regressions of small vs. large seed mass for 50 seed pairs from 12 populations of *Aegilops triuncialis*. All regressions were significant at $P < 0.001$. Numbers match the order of populations listed in Table 1. The slope of the regressions for 10 of the 12 populations fell between 0.27 and 0.39 (solid lines).

sufficient data. This indicated, usually, that emergence of the small seed was greatest when both influences were reduced, i.e., washing the spikelet and removing the large seed (Fig. 2: e.g., Bear Creek). In the second wet period, emergence of the previously dormant small seeds did not reflect a strong influence of the presence of the large seed (now a dead seedling) or maternal effects. While this is interpreted as the predictable weakening or loss of the dormancy-inducing factors, in some populations the absence of strong effects was also due in part to low numbers of remaining seeds.

DISCUSSION

Adaptive variation in seed germination within a species is very likely to contribute to successful invasion into new hab-

itats. These results suggest that patterns of germination in *Aegilops triuncialis* demonstrate both fixed seed-production traits and more plastic traits governing the germinability of small seeds from dimorphic seed pairs. I found consistent patterns of seed mass allocation and of germination across populations and regions. Large seeds from dimorphic pairs were consistently 2.5–3.0 times larger than small seeds across the range of seed mass, reflecting a relatively fixed maternal resource allocation pattern in this species. One or both of the maternal and sibling seed effects found in Dyer (2004) were significant in all populations tested; however, there was also a high degree of variation in the strength of the effects. In some populations the maternal effect appeared dominant, but in others the sibling effect was stronger.

Table 2. Results of two-way ANOVA on emergence (arcsine [square root %]) of small seeds for each of 12 populations of *Aegilops triuncialis*. In some cases, very high initial emergence resulted in insufficient data (i.d.) for testing treatment interactions or main effects in the second watering period. Significant values are indicated by * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; ns = not significant.

Population	Year	First watering period				Second watering period				
		r^2	Effect of large seed	Effect of washing	Treatment interaction	r^2	Effect of large seed	Effect of washing	Treatment interaction	
Sacramento Valley										
1. Jepson Prairie	2000	0.86	***	***	**	0.46	**	ns	ns	
2. Mather Field	2001	0.86	*	***	*	0.12	ns	ns	ns	
Northern Sierra Nevada Foothills										
3. Bear Creek	2000	0.89	**	***	**	0.33	ns	ns	*	
4. Sierra AD	2001	0.66	***	***	ns	0.25	ns	ns	*	
5. Sierra Shubert	2001	0.54	***	ns	i.d.	—	—	—	—	
Northern Coast Range										
6. Hopland-Foster	2001	0.81	***	ns	ns	0.00	i.d.	ns	i.d.	
7. Hopland-BA	2001	0.94	***	***	***	0.44	ns	ns	**	
8. Hopland-WSII	2001	0.71	***	**	ns	0.10	ns	ns	ns	
Central Coast Range (inland)										
9. Bear Valley	2000	0.85	***	***	***	0.25	ns	ns	ns	
10. Bear Valley	2001	0.46	**	*	ns	0.00	i.d.	*	i.d.	
11. McLaughlin	2001	0.68	**	**	***	0.94	***	ns	ns	
12. Snell Valley	2001	0.93	***	ns	i.d.	—	—	—	—	

Whether or not these patterns are maintained across years within a population is under investigation.

In this study, differential allocation to large and small seeds showed little variation among populations and appears not to be a highly plastic trait. This result is not unexpected: annual species from highly variable environments are predicted to show distinct seed production strategies that enhance the potential for survival in such habitats. The classic “bet-hedging” seed strategy (Cohen 1967) holds that seeds should show variation in dormancy characteristics such that a soil seed bank is maintained. The production of dimorphic seeds, one dormant and one nondormant, fits this model for long-term survival well and is likely to be a seed production strategy maintained by strong selection pressure.

The amount of energy devoted to seed production and the size and number of seeds produced by each plant will be greatly influenced by the growing conditions within a given season (Roach and Wulff 1987). More and larger seeds may be produced in high resource and high productivity years; however, the long-term importance of dimorphic seed production will not change with short-term resource variation. Thus, plasticity in traits related to seed quality is expected to be very low (Weiner et al. 1997).

In contrast, the germination characteristics of seeds should be influenced by the maternal environment because they represent the ability of the plant to respond to short-term, seasonal growing conditions. In the dimorphic seed pairs of this species, large seeds are never dormant and germinate rapidly whenever conditions are appropriate (Dyer 2004). The small seeds from dimorphic pairs also are not inherently dormant, but do show germination responses governed by both the maternal tissues and by the presence of the large seed.

The data presented here indicate that both the maternal and sibling influences governing germination of the small

seed vary significantly across populations and regions. Coupled with nonplastic allocation patterns to seeds, this suggests genetically fixed seed production strategies, but high response plasticity associated with the production of dimorphic seed pairs.

For species such as *Aegilops triuncialis*, plasticity in germination patterns that are conditioned by the growing environment of the parent and the neighborhood of the seed can provide greater opportunities for successful establishment. If temporal variation in emergence can reduce neighborhood competition intensity, a mechanism is provided for reducing the competition experienced by any plant attempting to colonize a new habitat. In particular, seeds that are more sensitive to the conditions in the immediate neighborhood can modify their response time (Dyer et al. 2000) and optimize early growth and reproductive potential (Bergelson and Perry 1989).

These data, in combination with previous experiments, suggest that plasticity in timing of emergence and fixed strategies for survival in highly seasonal environments provide a mechanism to explain how some species, especially annual grasses in the western USA, have been able to establish, colonize and ultimately spread throughout habitats to which they were not previously adapted. The “lag phase” typical of many invasive species, therefore, may be interpreted as a period of establishment strongly influenced by germination plasticity that facilitates the survival of the population during the period of genetic adaptation to the new environment.

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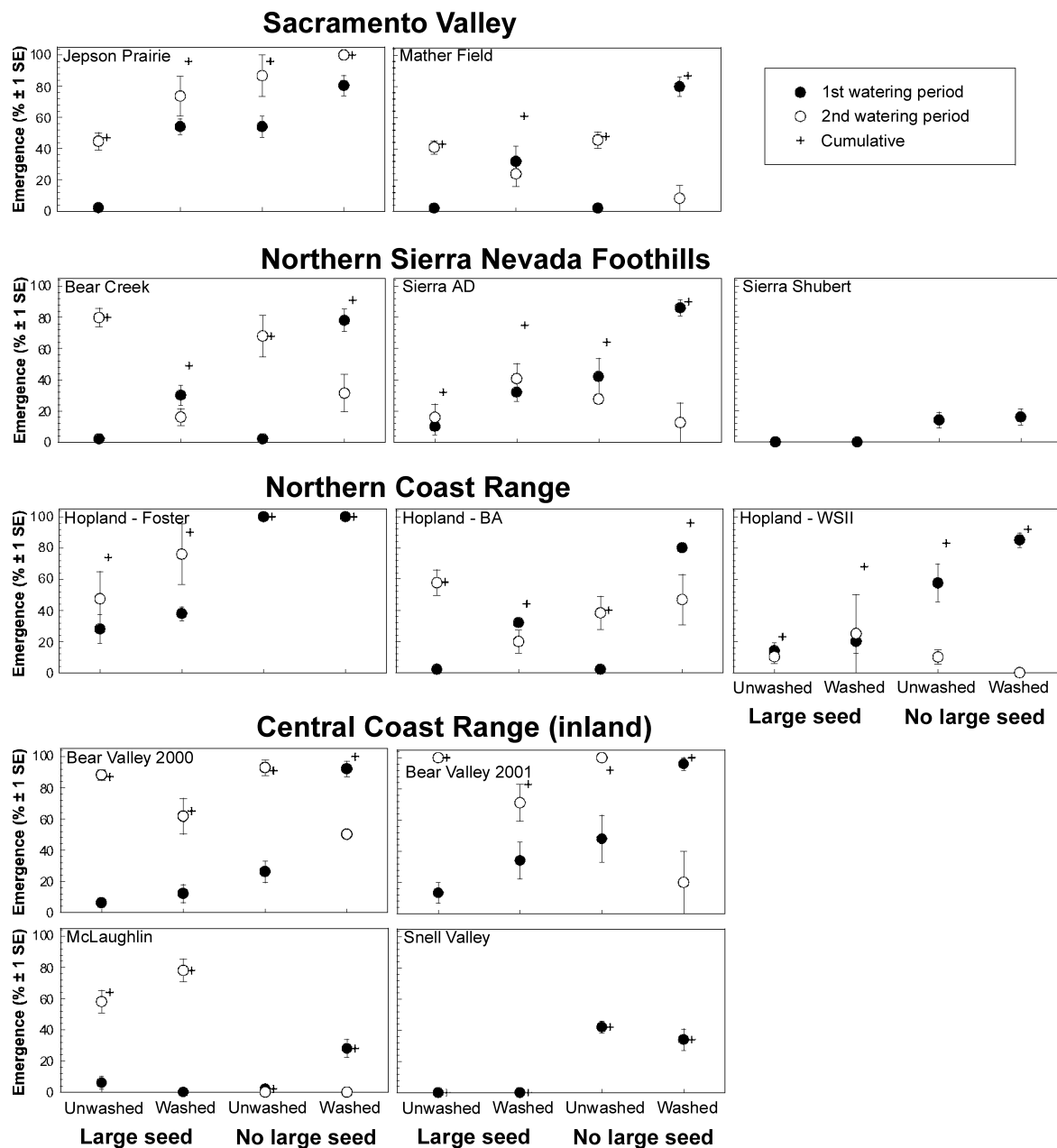


Fig. 2.—Effects of washing of spikelets and the presence of large seeds on the emergence ($\% \pm 1$ SE) of small seeds of *Aegilops triuncialis* for 12 populations representing four sampled regions. The first wet period stimulated complete germination of the large seeds (when present). Maternal and sibling effects were predicted to be strongest in the first watering period (filled circles) and weaker in the second period (open circles). Although washing and large seed removal treatments did have significant effects on emergence, the responses varied strongly among populations (see Table 2).

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