

REPORT

Accelerated seedling emergence in interspecific competitive neighbourhoods

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Abstract

Seed dormancy models suggest that evaluation of environmental conditions should influence the decision to germinate and that waiting for more favourable conditions may increase potential fitness. However, because rapid emergence is often positively correlated with performance and survival, an alternative strategy to accelerate the rate of emergence may increase the potential for site pre-emption. This response is more likely to be found in seasonal environments with greater potential for rapid resource depletion in which early emergence may confer a competitive advantage. The experiments reported here found more rapid emergence in a perennial grass species when it was planted in potentially highly competitive interspecific neighbourhoods. This response suggests an inherent ability in seeds of this species to sense and respond to the competitive nature of the immediate neighbourhood.

Keywords

Competition, emergence, germination, grasses, *Nassella pulchra*, neighbourhood, seeds.

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INTRODUCTION

1 The rate at which seeds germinate and seedlings emerge from the soil has important consequences for subsequent survival and fitness in competitive situations (Ross & Harper 1972; Mack & Harper 1976; Abul-Fatih & Bazzaz 1979; Weiner 1985; Weiner & Thomas 1986.; Smith *et al.* 2000). This is particularly true for annual and herbaceous communities in which density and competition intensity are positively correlated and in which very short delays in emergence can be magnified into large differences in final biomass and reproduction (Ross & Harper 1972; Rabinowitz 1979; Kalisz 1986; Weiner & Thomas 1986; Rice 1990). One would predict strong selection for mechanisms that either increase the rapidity of seedling emergence in competitive environments or delay germination via seed dormancy until environmental conditions have improved. Indeed, seed dormancy has been modelled extensively as a bet-hedging strategy for annual species in unpredictable environments (Cohen 1966; Venable & Lawlor 1980; Brown & Venable 1986; Venable & Brown 1988; Philippi 1993; Pake & Venable 1996). However, little attention has been given to biotically influenced increase in germination rate as a potential competitive strategy for either annual or perennial species.

Germination models usually posit two opposing strategies: seeds can germinate and compete for space and resources immediately or remain dormant for some

period or until the following year (citations above). These strategies were modelled principally for annual species and characterize the option to remain dormant as a risk-spreading strategy for avoiding unfavourable growing conditions. As a third potential strategy, particularly for perennial species with low seed dormancy, seeds may use environmental stimuli to evaluate neighbourhood quality and to adjust the timing of first emergence, rate of germination or of seedling emergence, or total germinable fraction (Inouye 1980; Smith *et al.* 2000). There are physiological constraints to shortening the minimum time required for germination, but increased rates of emergence and total germinable fractions have been reported (Palmbad 1968; Linhart & Pickett 1973; Linhart 1976; Waite & Hutchings 1978; Bergelson & Perry 1989). However, no studies have been conducted that record changes in the mean time to germination or emergence while manipulating both intra- and interspecific neighbour density and using natural substrates and temperature regimes. In fact, few studies have closely analysed germination patterns under natural conditions, e.g. in natural soils with realistic temperature regimes (C. C. Baskin, pers. comm.).

In crowded or competitive conditions, early emergence may result in a priority effect in which the first seedlings to establish, through space pre-emption, have greater access to resources and therefore a higher probability of survival (Ross & Harper 1972; Harper 1977; Abul-Fatih

& Bazzaz 1979; Weiner 1985; Kalisz 1986). When interspecific competition is intense, especially for light, the importance of early establishment is likely to be of critical importance, particularly as seedling density increases (Miller *et al.* 1994). In Mediterranean and arid environments, an early growth advantage may be especially important for perennial species that must grow sufficiently large in the spring to endure 6–8 months of summer drought. However, because premature germination also may lead to increased exposure to extreme conditions and subsequent mortality (Rice 1990), it would be advantageous if germination decisions were mediated by specific biotically influenced environmental cues from the immediate environment in addition to abiotic factors such as water and temperature. It follows from the resource pre-emption arguments that particularly important biotic cues should include the potential seedling density of the immediate interspecific neighbourhood (e.g. Inouye 1980). If true, a plastic, environmentally influenced germination response is predicted as an important mechanism for competition and one that should be subject to reasonably strong selection (Kalisz 1986).

We investigated the response of a native perennial bunchgrass, purple needlegrass (*Nassella pulchra* (Hitche.)-Barkworth), to the presence, at two densities, of interspecific neighbours by germinating seeds in a controlled environment, but under conditions as close to natural as possible. Because contemporary California grasslands are characterized by dense and widespread populations of many annual grasses of Mediterranean and Eurasian origin (Mack 1989), *N. pulchra* seeds were planted in low and high density interspecific neighbourhoods composed of 7 species of non-native annual grasses. Most germination studies report final germination or emergence values that reveal population-level responses to environmental conditions, but which can offer little information about germination dynamics or the responses of individual seeds. In this study, our objective was to investigate the influence of seed neighbourhoods on germination and this was done by closely observing the actual timing of *N. pulchra* seedling emergence both alone and in seven interspecific neighbourhoods through the entire period of active emergence.

METHODS

We collected caryopses (seeds) of seven species of non-native annual grasses commonly found in California grasslands and planted them as neighbourhoods around the seeds of a widespread native perennial grass (Table 1). *Nassella pulchra* seeds were planted awnless with five seeds in a circular arrangement (low density) and with 50 seeds planted haphazardly (high density) to determine the

germination pattern in the absence of interspecific neighbours. We tested the effect of neighbour presence on emergence with the low density arrangement of *N. pulchra* seeds and with neighbour seeds planted at low density (five seeds interspersed with the target seeds) or at a high density that varied with the neighbour species (Table 2). All neighbour densities are within the range normally observed in California grasslands. All seeds of all species except *B. hordeaceus* were individually planted by hand into the soil to the depth of the caryopsis. The small seeds of *B. hordeaceus* were buried horizontally. *A. triuncialis* and *H. murinum* seeds were not separated from their dispersal structures and were planted intact as spikelets. Toothpicks were placed near each *N. pulchra* seed to aid in seedling identification; the seeds of annuals were not marked but were easily located by vegetative characteristics such as awns that stuck out of the soil. All pots (Conetainers, Steuwe and Sons, Inc., Corvallis, Oregon, USA) contained local clay-loam topsoil. There were 10 replicates of all target–neighbour by density combinations.

The pots were watered daily with de-ionized water and allowed to germinate in a growth chamber set for day–night temperatures of 12 h at 20°C and 12 h at 10°C. Beginning 48 h after wetting of the soil, the first neighbour seedlings emerged and all pots were censused every 6 h for the next 72 h. Emergence was recorded when any evidence of a shoot tip was observed at the soil surface. To avoid bias, the same observer conducted all censuses.

To analyse these data, we took seedling counts from the five census periods following first emergence (84, 90, 96, 102 and 108 h after soil wetting) and calculated a single value to represent the average time to emergence of *N. pulchra* in each planting density by neighbour species treatment. The mean value was the sum of the products of the count of newly emerged seedlings at each census and the census number (1, 2, 3, 4 or 5) divided by the total number of seedlings emerged by the final census (≈ 50). This approach was more appropriate for these data than survival analysis (D. Pyke, pers. comm.). Using a two-factor ANOVA (planting density and neighbour species) we ran a series of linear contrasts comparing the emergence time of *N. pulchra* in control pots (intraspecific rate at low density) vs. all treatment plots within a density treatment (interspecific effect). We asked specifically whether there were differences in the mean time to emergence among all responses, between intra- and interspecific neighbourhood responses, and among only interspecific responses. We also asked whether there were differences among the interspecific treatments at low and high planting density. We did not make individual pairwise comparisons between the control and the responses to each interspecific neighbour because of low statistical power.

Table 1 Names and seed collection locations in California of the target species and the seven annual grass species used as neighbours.

Species	Common name	Collection
<i>Nassella pulchra</i> (Hitche.) Barkworth	Purple needlegrass	Grown at Hedgerow Farms, Yolo County from seed collected in Glenn County
<i>Aegilops triuncialis</i> L.	Barbed goatgrass	Dry pasture, Yolo County
<i>Avena barbata</i> Pott ex Link	Slender wild oat	Jepson Prairie, Solano County
<i>Avena fatua</i> L.	Wild oat	Old field, Yolo County
<i>Bromus diandrus</i> Roth.	Ripgut brome	Old field, Yolo County
<i>Bromus hordeaceus</i> L.	Softchess	Old field, Yolo County
<i>Hordeum murinum</i> L.	Hare barley	Old field, Yolo County
<i>Taeniatherum caput-medusae</i> (Sim.) Nevski	Medusahead	Dry pasture, Yolo County

Table 2 Seed mass (grams per 100 seed), target and neighbour planting density, and mean total emergence of *N. pulchra* and neighbour species (10 replicates). Mean total emergence (± 1 se) of *N. pulchra* is of the target seeds within the respective neighbourhoods. Intra-specific response of the neighbours compares emergence in low and high density neighbourhoods. Negative responses were significant at $P < 0.05$ (pairwise t -test); parentheses indicate a weakly significant effect ($P < 0.10$)

Species	Seed mass (g/100)	Planting density	<i>Nassella pulchra</i> Mean total emergence	<i>Neighbour species</i>	
				Mean total emergence % (se)	Intraspecific response % (se)
Target					
<i>N. pulchra</i>	0.639	5	0.98 (0.02)		
		50	0.91 (0.02)		
Neighbour					
<i>A. triuncialis</i>	3.897	5	0.90 (0.05)	0.66 (0.09)	
		15	0.98 (0.02)	0.59 (0.06)	none
<i>A. barbata</i>	1.455	5	0.94 (0.03)	1.00	
		25	0.96 (0.03)	0.90 (0.02)	negative
<i>A. fatua</i>	2.422	5	0.98 (0.02)	0.46 (0.07)	
		20	0.93 (0.03)	0.56 (0.03)	none
<i>B. diandrus</i>	1.592	5	0.96 (0.03)	0.80 (0.04)	
		30	0.90 (0.05)	0.70 (0.02)	negative
<i>B. hordeaceus</i>	0.205	5	0.94 (0.04)	1.00	
		50	0.94 (0.04)	0.93 (0.01)	negative
<i>H. murinum</i>	1.481	5	0.92 (0.03)	0.92 (0.04)	
		30	0.84 (0.10)	0.86 (0.02)	(negative)
<i>T. caput-medusae</i>	0.506	5	0.88 (0.04)	0.92 (0.03)	
		50	0.92 (0.02)	0.92 (0.02)	none

RESULTS

Mean total emergence (%) of *N. pulchra* seedlings after 108 h (fifth census period) was 90% or greater in 12 of the 14 interspecific neighbourhoods (Table 1). *Nassella pulchra* mean total emergence was not uniformly higher in either low or high density interspecific neighbourhoods, but may have been reduced in high density intraspecific neighbourhoods. However, the rate of emergence in low and high density intraspecific plots was nearly identical (Fig. 1).

The mean time to emergence of *N. pulchra* differed significantly among all treatments (Table 2, contrast 1)

and among the different interspecific neighbours (Table 2, contrast 3). The overall mean time to emergence of *N. pulchra* was shorter when interspecific neighbours were present (contrast 2 comparing the intraspecific and interspecific responses). When plotted (Fig. 2), mean responses to three of the neighbour species were noticeably faster than the intraspecific control in each density treatment although several means were equal to or slightly greater than the control. These results indicate strongly accelerated emergence in some neighbourhoods, but considerable variation overall.

Results from ANOVA (not shown) found a strong main effect of neighbour species, but not of neighbour density.

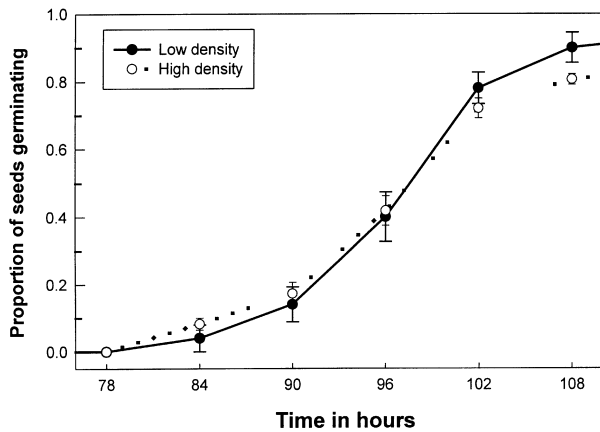


Figure 1 Cumulative emergence (mean \pm 1 se) of *Nassella pulchra* at low (5 seeds) and high (50 seeds) intraspecific density. Error estimates based on 10 replicates.

No correlation was found between mean seed mass or total seed mass per pot and the mean time to emergence. There was no correlation between the mean time to emergence of neighbour seedlings and of *N. pulchra* seedlings. The neighbour effect represented an apparent response to the presence of the interspecific neighbour seeds rather than to seed biomass or seed density.

Neighbour species varied in timing of emergence and, unlike *N. pulchra*, in total emergence and in response to density. *Aegilops triuncialis*, *A. barbata*, *B. hordeaceus*, *H. murinum* and *T. caput-medusae* all emerged rapidly and before *N. pulchra*. *B. diandrus* emergence was similar to *N. pulchra* and *A. fatua* was much slower. Total emergence was 50–80% in *A. triuncialis*, *A. fatua* and *B. diandrus*, all of which show some degree of dormancy associated with seed size and location within the spikelet. Four of the seven neighbour species had lower total emergence as density increased suggesting a density-dependent intraspecific effect (Table 1).

DISCUSSION

In this study, we found strong evidence for the ability of *N. pulchra* seeds to reduce their mean time to emergence in some interspecific neighbourhoods. Our results support the general prediction that the emergence response of a perennial grass should have an inherent plastic component and should vary with specific information obtained from the immediate vicinity of the propagule. Both increasing and decreasing the mean time to seedling emergence indicates a capacity for rapid evaluation of some measure of the quality of the seed neighbourhood. Although *N. pulchra* showed plasticity in the speed of emergence, no change in the minimum time to first emergence or in total germinability was observed, nor was

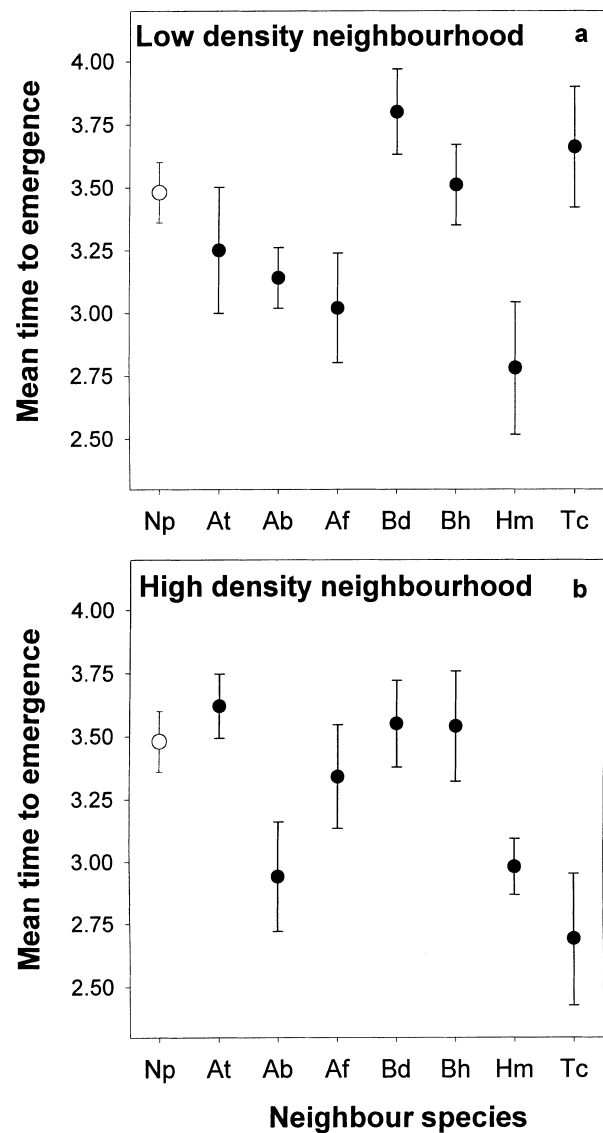


Figure 2 Time to emergence (mean census interval \pm 1 se) of *Nassella pulchra* seedlings planted at low density alone (open circles) and in seven annual grass neighbourhoods planted at two densities (filled circles). Neighbour species are listed in alphabetical order (see Table 1). Accelerated emergence (lower mean value) was found in three of the seven neighbourhoods at both low and high density. Error estimates based on 10 replicates.

the mean time to emergence of *N. pulchra* significantly reduced by any neighbour species. We interpret these results as evidence of selection for rapid germination response in *N. pulchra*, a perennial grass with low seed dormancy (Bartolome & Gemmill 1981), rather than bet-hedging via seed dormancy as would be predicted in annual species (see chapter 12 in Baskin & Baskin 1998).

When considered in the context of resource competition, accelerated emergence is a predicted outcome if fitness in highly competitive environments is correlated

Table 3 Linear contrasts testing whether *N. pulchra* emergence responses in low and high density treatments differ from the control and among the neighbourhoods.

Contrast tested	d.f.	SS	MS	F	P
Low density					
1. Equality of all responses	7	9.299	1.328	4.17	0.0003
2. Equality of intrav. interspecific responses	7	8.130	1.161	3.65	0.0012
3. Equality of interspecific responses	6	8.950	1.492	4.69	0.0002
Model error	134				
High density					
1. Equality of all responses	7	8.950	1.279	4.02	0.0005
2. Equality of intrav. interspecific responses	7	7.669	1.096	3.44	0.0020
3. Equality of interspecific responses	6	7.658	1.276	4.01	0.0010
Model error	134				

with early emergence and increased pre-emptive access to resources (Ross & Harper 1972; tables 12.2 in Baskin & Baskin 1998). Under such circumstances, early emergence (in the order of hours) can be compounded over time into a disproportional size and fecundity advantage and would therefore be under very strong selective pressure (Rabinowitz 1979; Weiner 1985; Miller 1987). In this study, the time required to reach equivalent proportional germination between treatments was as great as 10 h. Ross & Harper (1972), working with monospecific stands of another perennial bunchgrass, *Dactylis glomerata*, found that 95% of the variation in plant mass could be accounted for by time since emergence. An increased rate of emergence in plants can be interpreted as an adaptive mechanism for resource pre-emption in crowded neighbourhoods and therefore as a component of competitive ability.

Negative influences on seedling emergence also have been predicted, but often in terms of increased dormancy in the affected seeds. Differentiating whether seeds remain dormant as a response to neighbourhood quality or whether seed dormancy is chemically induced by neighbours is not easily tested. In this study, total emergence of *N. pulchra* was not reduced either by neighbour species or by neighbour density, suggesting no effect of neighbours on germinability. However, the mean time to seedling emergence was accelerated in some neighbourhoods and not in others implying possible species specific influences.

The results of this study suggest, first, that it was the presence of neighbouring seeds, rather than neighbour density, that affected the emergence of *N. pulchra* seedlings. Second, the effect on *N. pulchra* emergence, and presumably on germination, was an interspecific effect that may vary with the identity of the neighbour. For example, although we did not test the significance of all pairwise comparisons, the mean time to emergence was accelerated at both densities with *A. barbata* and *H. murinum* as neighbours, while *B. diandrus*, *B. hordeaceus*

and *A. triuncialis* had no apparent effect on emergence. Mixed results were seen for other species; *T. caput-medusae* had a strong effect at high, but not low, density and the effect of *A. fatua* was weaker at high density. The reason for the variation in response by *N. pulchra* to different neighbour species is unknown; however, further experiments are planned to quantify the differences in the interspecific effects using a wider range of seed density combinations and with other target species.

We have not determined whether the mechanism underlying the influence on *Nassella* emergence was related to increasing the total biomass in each experimental unit (i.e. a per gram effect), allelo-chemicals from the annual grass seed coats, changes in soil chemistry related to root or shoot growth, or to a combination of influences. Total neighbour seed biomass was not correlated with the mean time to *N. pulchra* emergence at either density nor overall. In contrast, germination experiments with species of *Aegilops* have shown very clear evidence of self-inhibition via hormones on the surface of the spikelets (Wurzburger & Leshem 1969; Lavie *et al.* 1974). Both reduced and accelerated interspecific germination resulting from seed leachate also has been reported (Lavie *et al.* 1974; Bergelson & Perry 1989; Murray 1998). Recent work with *A. triuncialis* revealed induced dormancy among dimorphic seeds within the same spikelet, suggesting the possibility of multiple cues negatively affecting germination (A. Dyer, unpublished data). Little is known about the general occurrence of these chemical cues in other annual grasses or the influence of such signals on germination of interspecific neighbours.

Positive density-dependent germination has been associated with species of highly restricted or specialized habitats (Linhart 1976), however, *N. pulchra* is widely distributed throughout California grasslands and woodlands and along elevation gradients (Bartolome & Gemmill 1981; Knapp & Rice 1998) and these results do not support this correlation. In contrast to the emergence

patterns of *N. pulchra*, four of the neighbour species used in these experiments showed negative density-dependent responses to increasing intraspecific density (mean final emergence) and no evidence of positive density-dependence in their rate of emergence. The latter finding supports the contention that negative density-dependence may be a characteristic of weedy species from open habitats (Linhart 1976; Waite & Hutchings 1978).

Our results imply an *apparent* adaptive response of a native species to the presence of several non-native annual species. However, although grasslands in California are highly invaded ecosystems (Mack 1989), the presettlement species composition was likely to have been predominantly annual species, especially dicots (reviewed in Hamilton 1997). Thus, the response seen in *N. pulchra* may be viewed as a result of a long history of coevolution with annual species rather than a recent adaptation to invasive annual grasses. Our recent work has demonstrated the poor competitive ability of *N. pulchra* and other perennial grasses in the growing conditions of contemporary California grasslands (Dyer & Rice 1997, 1999; Brown & Rice 2000). Invasive annuals may provide germination cues similar to those produced by native annuals, but the competitive superiority of the invading species may negate the adaptive value of the emergence responses of *N. pulchra* and this may be true for other native species growing in highly invaded habitats.

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