

Factors Affecting the Success of California Poppy (*Eschscholzia californica*) Introduced into Western Washington State

Abstract

California poppies (*Eschscholzia californica*), native to Californian grasslands, have been introduced to the south Puget Sound region and apparently persist along roadbanks and as volunteers in gardens, where the biomass of other vegetation is relatively low. Whether poppies can successfully invade other areas from these source populations may depend on the ability of poppies to withstand the abiotic environment and/or to compete with the established vegetation. To examine the potential for competition to limit California poppy success, I tested the effects of competition with perennial ryegrass (*Lolium perenne*), soil type, and wintering regime in a factorial experiment. Single poppy plants were grown outside in pots with from 0 to 32 ryegrass plants, either previously established or simultaneously seeded, in relatively dry or moist soil. Half these pots were harvested in the fall; the rest were overwintered outside or inside the greenhouse.

Competition with established ryegrass prevented successful establishment of almost all poppy plants. Competition with simultaneously-seeded ryegrass caused mortality of poppy plants only at the highest densities; however, vegetative biomass, fruit number, and seed mass all decreased with increasing ryegrass biomass. Poppies were bigger and produced more fruits and seeds in moist soil, but soil type did not alter the intensity of competition. Poppy winter survival outside depended heavily on ryegrass abundance; competition with ryegrass significantly decreased survival of the plants wintered outside. These results suggest that competition from existing vegetation may relegate California poppies to sites where vegetation is sparse because of drought, low nutrients, or disturbance.

Introduction

How important is interspecific competition in determining which species are present in a community? This question has been of central interest to ecologists for several decades. Much debate has focused on the role of interspecific competition in ecological processes such as assembling communities (Diamond 1975; Connor and Simberloff 1979, 1983; Diamond and Gilpin 1982; Simberloff and Connor 1982; Moulton and Pimm 1983), controlling species' abundances (Tilman 1982, numerous reviews in Diamond and Case 1986), and allowing or preventing invasions by non-native species (Bazzaz 1986, Moulton and Pimm 1986, Newsome and Noble 1986, Pimm 1989, 1991).

Though not native to the Puget Sound region, California poppy (*Eschscholzia californica* Cham. (Papaveraceae)) has been introduced to the region by local gardeners and in wildflower mixes seeded along highways, and it persists sporadically in gardens and roadsides. California poppy has a rather high invasive potential, as demonstrated by its successful invasions of other regions with Mediterranean climates such as central Chile (Frias et al. 1975). However, it presently persists only sporadically in the Puget Sound region. Given

its invasive potential, why has California poppy remained relatively sparse after its introduction to western Washington?

An introduced species may be limited in its spread either by physical and chemical conditions or by biological interactions (Pimm, 1991; Begon et al. 1996). The south Puget Sound region differs in both climatic conditions and species composition from the California grasslands to which California poppy is native. California poppies survive and reproduce in the Puget Sound region. However, they do so sporadically, indicating that one or more conditions limit their success in the region. This paper reports the results of a pot experiment designed to test the potential for interspecific competition to limit California poppy abundance.

One of the major differences in vegetation between the habitats occupied by California poppy in the south Puget Sound region and those of its native California grasslands is that the post-deforestation vegetation in south Puget Sound is dominated by perennial grasses rather than the annual grasses that now dominate the Californian grasslands. Competition with perennials may be more severe than with annuals because established perennials generally initiate growth earlier,

accumulate aboveground biomass more rapidly upon initiation of growth (Tilman 1988), and more quickly sequester limiting soil resources with their established root systems.

I investigated whether the success of California poppies is influenced by the biomass of surrounding vegetation, whether soil moisture influences their success, and whether poppies can survive the colder winter environment in the south Puget Sound region. I was interested in answering four specific questions regarding the success of California poppy in south Puget Sound: 1) Does neighboring vegetation decrease California poppy fitness (survival, vegetative biomass, fruit number, and seed biomass), and if so, how intense is that competition? 2) Does competition differ between seedling neighbors (more similar to annuals) and established neighbors (perennials)? 3) Is the intensity of competition from neighbors more severe in moist soil than in drier soil? and 4) Are poppies able to survive winter temperatures in the south Puget Sound region and is that survival influenced by competition?

Materials and Methods

Species Description

California poppy is a short-lived perennial or facultative annual native to grasslands of California and Oregon. It is generally outcrossed (Cook 1961), with bumblebees as the main pollinators. The showy flowers develop into elongated capsules that burst at maturity, ejecting seeds approximately 1 m (Robinson et al. 1995). The recognized native range of California poppy is described as California north to the Columbia river (Hitchcock and Cronquist 1973). In the central valley of California, California poppies are one of the few native species that still occur abundantly within the introduced annual grasslands (Robbins et al. 1951, Munz and Keck 1959, Cook, 1965). These introduced grasses are Mediterranean in origin and have been very successful in California's Mediterranean climate. Prior to the invasion by these annual grasses, the California grasslands were occupied by perennial grass species. Presently, most species of the California grasslands, including California poppy, germinate in the cool, wet winter and flower and set seed during the spring and summer (Robinson et al. 1995). In contrast, poppies in the south Puget Sound region germinate in the spring (March-April) or fall (October-November). Spring-germinated

seedlings can reproduce their first year, generally blooming from August until frost. Perenniating plants bloom much earlier, from late March until frost, and mature seed is produced starting in late June.

Poppies in the south Puget Sound region usually occupy treeless habitats with a wide variety of soil types. Naturally-occurring seedlings are found most often where other herbaceous cover is sparse (personal observation). Such sites are commonly steep, south- or west-facing hillsides with relatively poor, dry soils or disturbed areas such as graveled roadsides that may have richer soils. Individual poppy plants are typically surrounded by a mixture of introduced, largely annual, grasses (e.g., *Bromus mollis*, *B. rigidus*, *B. tectorum*, *Festuca myuros*), but including some perennial grasses (e.g., *Dactylis glomerata*, *Lolium perenne*, *Holcus lanatus*, *Agrostis alba*), and several introduced forbs (e.g., *Cytisus scoparius*, *Hypericum perforatum*, *Rumex acetosella*, *Sonchus oleraceus*, *S. asper*). In some of the dry soil habitats, poppy populations are apparently persistent (personal observation), but have not spread beyond a small area.

Experimental Design

To compare the effects of competition between established and seedling perennial grasses, between moist and dry soil, and on winter survival, I set up a three-way factorial additive experiment. An additive experiment is more appropriate than a substitutive experiment to the question of poppy establishment in surrounding vegetation and for measuring the intensity of competition (Goldberg and Scheiner 1993). To quantify the intensity of competition, I grew individual poppy plants with perennial ryegrass (*Lolium perenne*). Single poppy targets were grown with ryegrass at one of seven densities (0, 1, 2, 4, 8, 16, or 32 grass plants per 12.5 cm diameter pot). I grew poppies with ryegrass planted at two different times to compare the effects on poppies of simultaneously-sown ryegrass with those of established ryegrass. In half of the pots of each density treatment, ryegrass seeds were planted two months before poppy seeds to allow ryegrass to establish; in the high neighbor density treatments, ryegrass covered roughly 75% of the surface area of the pot when the poppy seeds were planted. In the other half of the pots, ryegrass seeds were planted simultaneously with poppy seeds. To examine the effects of variation in soil type, two different soil mixes [100% Sunshine® potting mix (moist soil) and 50% potting mix and

50% Perlite® (dry soil)] were compared. These different soil types induced documented differences in water availability (see below) and presumed differences in nutrient availability. Thus, a treatment combination is defined by one of seven ryegrass densities, one of two ryegrass planting times, and one of two soil types. Finally, to test winter survival of poppies, I overwintered half the surviving poppies in each treatment combination outside and the other half inside a greenhouse.

Each treatment combination was replicated 8 times for a total of 224 pots. These pots were placed on greenhouse benches outside on a roof terrace at the University of Puget Sound campus in Tacoma, WA, USA (47°15' N, 122°30' W), during the summer of 1994. For all pots, I used commercially available seeds of California poppy and perennial ryegrass. Although I would have preferred using seeds produced by the locally adapted poppy populations, they were unavailable until much later than the necessary initiation date.

Poppies were planted 26 May 1994 and thinned to one poppy target individual per pot after germination. All pots were kept watered to field capacity during seedling establishment. Seedlings became established in all pots, and then I watered (to field capacity) only when natural rainfall was insufficient to keep grasses from showing signs of water stress.

In mid-July, I weighed each pot before and after watering to assess differences in total water held between the two soil types: the pots with the Perlite/potting soil mix held significantly less water than the pots with 100% potting soil (means of 70 pots per group were 506.0 and 666.1 g water per pot, respectively; $t = 10.94$, $P < 0.0001$).

I collected mature fruits from each poppy target daily, cutting the stem just below the swollen receptacle to collect all tissue dedicated to reproductive activity. On 12 September, 1994, I collected remaining fruits from all plants and recorded the survival of all poppy target individuals. Then, from each treatment combination, I randomly selected for harvest half the pots with a living poppy. Harvesting a pot consisted of cutting the ryegrass plants at soil level and extracting the poppy target from the soil by washing the soil away from the orange roots of the poppy target. The ryegrass shoots, the poppy shoot, and the poppy root from each pot were wrapped in separate newspaper envelopes, labeled, and dried for 5 days at 50°C. I weighed each dried poppy component as one

measure of performance and weighed the ryegrass shoots as a more precise measure of neighbor abundance than density class. Ryegrass roots were too difficult to extract from the soil to be harvested. I also dried and weighed reproductive components (receptacles, fruits, and seeds). Because all of these reproductive biomass measures gave qualitatively similar results, data are presented only for seed biomass.

The pots I did not harvest were randomly assigned within treatment combination to winter inside the greenhouse or outside on the terrace. Pots inside the greenhouse were watered to capacity when necessary to prevent signs of wilting in the ryegrass. Outside pots were watered with natural rainfall. The following spring (May 1995), I recorded the survival status of all overwintered poppy target individuals.

Data Analysis

Survival data, both for the growing season and for the winter, were analyzed using Chi-square goodness of fit tests for the main effects and Chi-square tests of independence for interactions between treatment factors. Poppy vegetative biomass, number of fruits, and seed biomass were analyzed both on an absolute and on a relative basis. To convert absolute biomass to relative biomass, each biomass within a timing x soil type treatment combination was divided by the mean biomass for poppy targets with no ryegrass neighbors in that treatment combination. These measures were analyzed using ANCOVAs, with ryegrass biomass as a covariate. All statistical analyses were carried out using SYSTAT 5.2 statistical software (Wilkinson et al., 1992).

Results

Poppy Survival

Almost no poppy target individuals survived in the established ryegrass whereas many survived in the simultaneously-seeded ryegrass (Table 1, planting time main effect). Of the 96 poppy individuals that germinated in pots with established ryegrass, only 2 survived the summer, and these were in pots with only a single ryegrass plant in the drier soil (Figure 1a). In contrast, where no ryegrass neighbors were present, all eight poppy target individuals survived in each soil type. Ryegrass density decreased the survival of poppies (Table 1, ryegrass density main effect; Figure 1), with established

TABLE 1. Chi-square test results for poppy summer survival. Each treatment combination began with eight replicates. Main effect tests of planting time and ryegrass density used all cells; the planting time x density interaction pooled the three lowest density classes to minimize cells with expected numbers less than five.

Comparison	df	X ²	P
Planting time	1	42.7	< 0.0001
Ryegrass density	6	44.5	< 0.0001
Planting time x density	4	33.3	< 0.0001

ryegrass neighbors having a much greater negative effect on survival than simultaneously-seeded ryegrass neighbors (pooling the last three ryegrass densities to minimize cells with expected numbers less than five; Table 1, timing x density interaction). In simultaneously-seeded ryegrass, all poppy target individuals survived except in the two highest density ryegrass treatments (16 and 32 neighbors; Figure 1b). With 16 ryegrass neighbors, 25% of poppy targets survived; with 32 ryegrass neighbors, no poppy target individuals survived. Soil type had no significant effect on survival in either established ryegrass or in simultaneously-seeded ryegrass (df = 1, P = 0.593 and P = 0.913, respectively).

Poppy Vegetative Biomass

Because so few poppies survived in the established ryegrass treatment, I analyzed poppy vegetative biomass only for the simultaneously-seeded ryegrass treatment. The results of analyses on absolute and relative bases were similar for two effects: ryegrass biomass reduced total poppy vegetative biomass markedly (Table 2, ryegrass biomass main effect; Figure 2a), and the negative effect of ryegrass was similar between the two soil types (Table 2: absolute

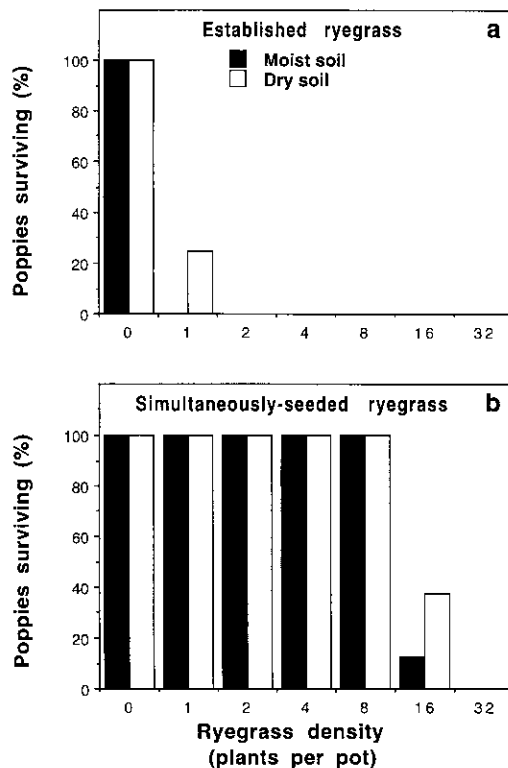


Figure 1. Poppy survival during summer in (a) established ryegrass and (b) simultaneously-seeded ryegrass. Each treatment combination started with eight replicates. Survival was much worse in established ryegrass than in simultaneously-seeded ryegrass (P < 0.0001) and with higher ryegrass densities (P < 0.0001). Density had a more severe effect in established ryegrass than in simultaneously-seeded ryegrass (using only the lowest three density categories, P = 0.0002).

TABLE 2. ANCOVA results (P-values, sample sizes, and R²) from analysis of poppy fitness measures. Relative measures were adjusted by dividing each value by the mean biomass in the zero neighbor control (each soil type calculated separately).

	Ryegrass biomass	Soil type	Ryegrass x soil interaction	N	R ²
Absolute measures					
Vegetative biomass	<0.0001	0.003	0.724	39	0.824
Fruit number	<0.0001	0.013	0.694	20	0.719
Seed biomass	<0.0001	<0.0001	0.127	21	0.814
Relative measures					
Vegetative biomass	<0.0001	0.386	0.240	39	0.802
Fruit number	0.0002	0.407	0.202	20	0.655
Seed biomass	<0.0001	0.670	0.662	21	0.767

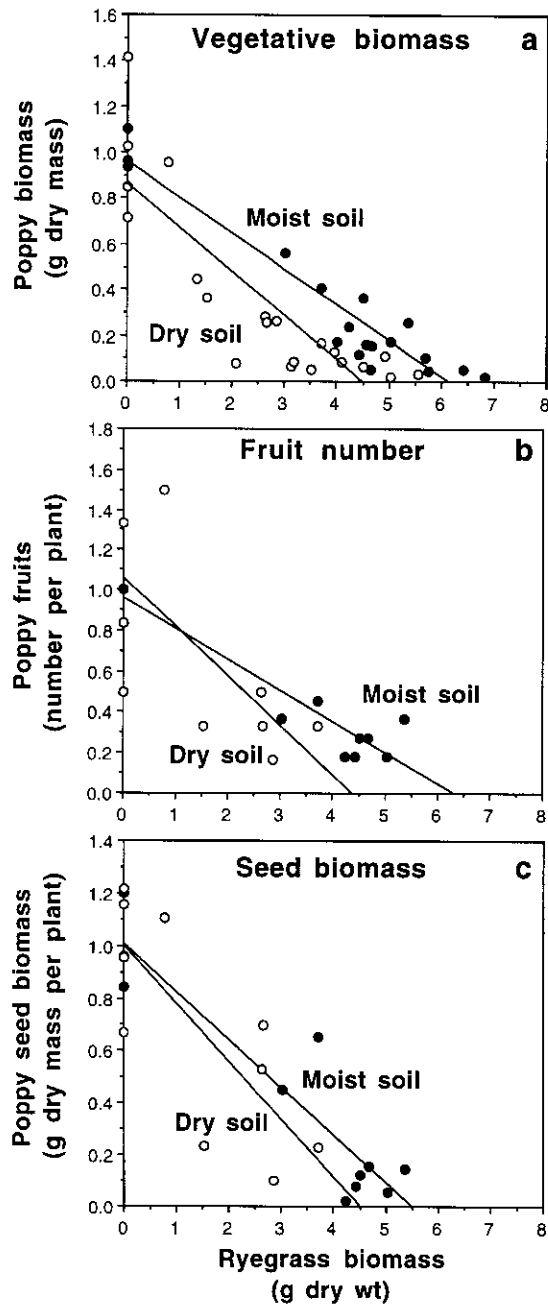


Figure 2. Effects of ryegrass competitors on (a) vegetative biomass, (b) fruit number, and (c) seed biomass of California poppy in moist and dry soils. All poppy measures are presented on a relative basis wherein each poppy biomass with ryegrass neighbors was divided by mean poppy biomass when no ryegrass neighbors were present. Only data from the simultaneously-seeded treatment were analyzed. Increasing ryegrass biomass decreased all measures of poppy performance, and in no case did the intensity of that competition differ between moist and dry soils. When measured on an absolute basis, all measures of poppy performance were higher on moist soils than on dry soils. (a) Increasing ryegrass biomass decreased poppy biomass ($P < 0.0001$; moist soil: $Y = 0.959 - 0.156X$, $R^2 = 0.908$; dry soil: $Y = 0.860 - 0.191X$, $R^2 = 0.735$). (b) Increasing ryegrass biomass decreased fruit number ($P = 0.0002$; moist soil: $Y = 0.810 - 0.128X$, $R^2 = 0.883$; dry soil: $Y = 0.987 - 0.226X$, $R^2 = 0.495$). (c) Increasing ryegrass biomass decreased seed biomass ($P < 0.0001$; moist soil: $Y = 1.066 - 0.193X$, $R^2 = 0.860$; dry soil: $Y = 1.00 - 0.221X$, $R^2 = 0.601$).

and relative soil x ryegrass interactions). However, on an absolute basis, poppy targets accumulated higher biomass in the moist soil than in the dry soil (Table 2, absolute soil type main effect), whereas on a relative basis, that difference was eliminated by the relativizing process (Table 2, relative soil type main effect). In an analysis of root/shoot ratio, one very small target individual in the dry soil was recognized as an outlier and removed [residual was tested after regression against ryegrass biomass using Grubb's test (Rohlf and Sokal 1981; statistic = 4.25, $n = 21$, $P < 0.005$)]. Root/shoot ratio increased as ryegrass biomass increased ($F_{1,34} = 4.96$, $P = 0.033$), but did not differ with soil type ($F_{1,34} = 0.023$, $P = 0.880$).

Poppy Fruit Number and Reproductive Biomass

Of the 102 poppy target individuals surviving, only 59 set fruit. One of these fruiting plants in the simultaneously-seeded ryegrass treatment had been infested with aphids and set 66% more fruits than any other plant. This individual was removed from the fruit number variable as an outlier by Grubb's test (statistic = 4.27, $n = 59$, $P < 0.005$). However, because this individual's many fruits were small, it was not an outlier and was included in the analyses of the reproductive biomass variables. Excluding this plant, 47 surviving poppy target individuals from the simultaneously-planted ryegrass treatment were harvested, and of these, 29 set fruit. Fruit number decreased significantly with increasing ryegrass biomass (Table 2, Figure 2b). Mean fruit number in moist soils (10.6 fruits/plant) was almost double that in dry soils (6.0 fruits/plant, Table 2, absolute soil type main effect). The decrease in fruit number with higher ryegrass biomass was similar between the two soil types, whether measured on an absolute or relative basis (Table 2, absolute and relative soil x ryegrass interactions).

Seed biomass of poppies in the simultaneously-seeded ryegrass treatment decreased with ryegrass biomass (Table 2, ryegrass biomass main effect; Figure 2c), and was higher in moist soils than in dry soils (Table 2, absolute soil type main effect). The effects of ryegrass biomass on seed biomass did not differ between soil types whether measured on an absolute or relative basis (Table 2: absolute and relative soil x ryegrass interactions).

However, another measure of reproductive success, fruit biomass, did differ in its response to ryegrass biomass between soil types depending on whether they were measured on an absolute or relative basis. On an absolute basis, fruit biomass decreased more per gram of ryegrass in moist soil than in dry soil ($P = 0.046$, $r^2 = 0.874$). On a relative basis, however, fruit biomass did not differ in its response to ryegrass biomass between soil types.

Poppy Winter Survival

Whereas half the poppies with no ryegrass neighbors survived outside the greenhouse, no poppies in competition with ryegrass survived the winter outside (Figure 3a). Poppy plants wintered inside the greenhouse survived much better than those wintered outside the greenhouse (Table 3, wintering location main effect). Ryegrass density reduced poppy survival much more severely outside the greenhouse than inside (Table 3, location x density interaction): 19 of 24 poppy target individuals survived inside the greenhouse, with survival unrelated to soil type ($X^2_{1,df} = 1.00$, $P = 0.371$) or ryegrass density ($X^2_{2,df} = 1.37$, $P = 0.504$).

Discussion

The south Puget Sound region (Olympia and Tacoma area) is slightly warmer and drier than much of the rest of the Puget Trough Province (Franklin and Dyrness 1973). Other such pockets of warm and dry conditions occur on the northeast coast of the Olympic Peninsula and on southwest exposures in the San Juan Islands. Lyons and Merilees (1995) also indicate similarly warm and dry conditions may occur on southeastern Vancouver Island and the Gulf Islands in British Columbia. As such, these areas may be more favorable for California poppy to persist than other sites within the Puget Sound region. The pre-European northern range limit of poppies was just north of the Columbia River (Hitchcock and Cronquist 1973), suggesting that the cooler winter temperatures of the Puget Trough limited the northward expansion of poppies. After being artificially introduced to the warmer microclimate of the south Puget Sound region, poppies might now be persisting near the limits of their physiological tolerance. As such, small variations in environmental factors such as soil moisture or

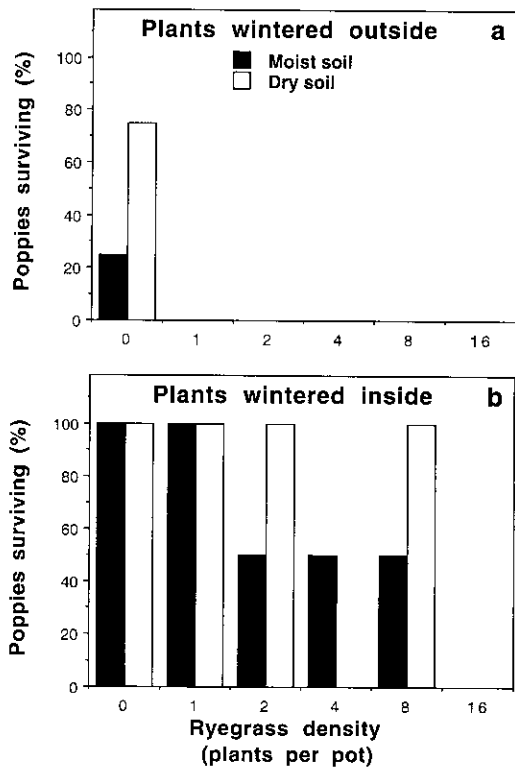


Figure 3. Poppy survival when wintered (a) outside and (b) inside the greenhouse. Sample sizes were four pots in each treatment combination (density x soil type). Ryegrass density had a much more severe negative effect on winter survival outside than inside ($P = 0.0008$) and poppies wintered inside survived much better than those wintered outside ($P = 0.002$). Winter survival inside was unrelated to soil type ($P = 0.683$) or ryegrass density ($P = 0.129$).

winter temperature may be critical, either alone or in conjunction with competition, to poppy establishment and survival. Results from the present experiment suggest that higher soil moisture increases poppy growth independently of competition, but that winter temperatures decrease poppy survival more drastically with competition than without. Moreover, competition has the potential to severely limit poppy success.

Established ryegrass precluded essentially all poppy survival whereas simultaneously-seeded ryegrass allowed poppy survival in all but the highest densities. This priority effect was so strong that even a single ryegrass plant established two months prior to poppy seeding excluded the poppy target in 14 of 16 pots. In contrast, densities of

TABLE 3. Chi-square test results for poppy winter survival. Cells were pooled over soil type and ryegrass densities (pots with two and four ryegrass neighbors were pooled and pots with eight and 16 ryegrass neighbors were pooled) so that each treatment combination began with 8 replicates. Wintering location and ryegrass density were tested as main effects and location x density was tested as an interaction.

Comparison	df	χ^2	P
Wintering location	1	9.78	0.002
Ryegrass density	2	4.26	0.129
Location x density	2	9.78	0.0008

16 or more simultaneously-seeded ryegrass plants per pot were necessary to exclude any poppy target plants. These results are consistent with previous work on California poppies that showed that a simultaneously-seeded annual grass (*Avena fatua*) decreased poppy survival, growth and reproduction (Cook 1965). Cook compared poppy growth and reproduction with and without a single high density of *Avena* (seeded at approx. 2 plants/cm²) in two large outdoor planter boxes. Unfortunately, because Cook used only a single *Avena* density, a comparison of the intensity of competition from the annual *Avena* with that from simultaneously-seeded perennial ryegrass is not possible.

Established perennials have previously been shown to have stronger competitive effects than annuals on the establishment of seedlings (Perth and Foin 1985). When five species of grasses were sown into plots with either mixed annuals or a single dominant perennial, all five successfully established in the annual plots, and none established in the perennial plots. These authors attributed the difference in success to the quantity of above-ground biomass, and they confirmed this hypothesis by finding establishment success similar to that in the annual plots when the perennial plots were partially defoliated to match the biomass of the annual plots. Although the simultaneously-seeded perennials used in the present study are not annuals, their accumulation of biomass and pre-emption of resources in the first season is likely more similar to annuals than to established perennials. This interpretation leads to conclusions in the present study consistent with those of Perth and Foin, except for the increasing root:shoot ratio shown by the poppies as ryegrass biomass increased. However, in contrast to Perth

and Foin's result, higher allocation to roots under competition suggests that soil resources were more limiting than above-ground resources (Harper 1977, Chapin et al. 1987, Crick and Grime 1987, Tilman 1988, Wilson and Tilman 1995, but cf. Gedroc et al. 1996). This difference may result from growing the plants in pots rather than in the field, thus restricting their rooting volume. Alternatively, perhaps the perennial ryegrass seedlings allocated more assimilate to root tissue than an annual would have, thus increasing their capture of below-ground resources.

The effect of priority is likely to be based on both total biomass and biomass distribution. If a competing plant has roots infiltrating much of the available soil volume, then a new seedling will have a difficult time procuring soil resources. Similarly, existing shoot biomass positioned above the seedling will pre-empt light. Therefore, the establishment success of California poppy may well depend on the existing biomass at the potential establishment site. Robinson et al. (1995) tested the establishment and reproductive success of California poppies in the annual grasslands of California. They added poppy seeds to experimental plots that previously had no poppies present, and followed the success of these poppies as a function of species richness, disturbance, and dominance of a single species. They found that poppies were unable to establish in plots dominated by *Bromus diandrus*, an annual grass. They attributed this effect to the sequestration of limiting resources or the physical exclusion of poppies by the grass. Robinson et al. also found that small scale vegetation disturbance increased the germination success of poppies. Because they conducted a census every 10 days, their germination index included both actual germination and early seedling survival. Such early seedling survival might well have benefited from small scale animal disturbances that removed or trampled immediately adjacent biomass. However, because the focus of their study was on characteristics that affected invasibility of the plots, rather than on the causes of success or failure of poppy establishment, they did not manipulate or measure biomass of existing vegetation, and could not quantitatively assess the role of competition.

The intensity of the competitive effect of ryegrass can be compared between moist soil and dry soil on both an absolute and a relative basis. Comparing relative effects is probably a more

accurate representation of long-term outcome (Goldberg and Scheiner 1993, Grace 1995). In the present experiment, on an absolute basis, poppies gained more biomass in moist soil across the entire ryegrass biomass range, but this effect was eliminated by the relativizing process (setting both intercepts to 1). Other than this soil moisture effect, vegetative biomass, fruit number, and seed biomass results did not differ between absolute and relative analyses. In contrast, fruit biomass did differ between absolute and relative analyses: on an absolute basis, fruit biomass was reduced more per gram of ryegrass biomass (i. e., greater competitive intensity) in moist soil than in dry soil, but on a relative basis, the competitive effect of ryegrass on poppy did not differ between soil types. This result is consistent with that of Campbell and Grime (1992), who found greater competitive intensity in higher resource conditions when measured on an absolute basis but equal competitive intensities when measured on a relative basis. Wilson and Tilman (1991, 1995) also found no difference in competitive intensity with increasing resource conditions when measured on a relative basis. This is not a consistent result among all studies, however. Kadmon (1995) found a higher competitive intensity in higher resource conditions using both absolute and relative measures. Kadmon suggested that inconsistency among studies sometimes may be explained by the range of competitor density or the range of resource levels used in studies. Kadmon's data (regression slopes in his Table 5) also apparently suggested that competitive intensity increased from low to moderate resource levels but then stayed constant or decreased from moderate to higher resource levels. This pattern holds whether using his absolute or relative competitive intensity measures.

Winter survival in pots may have underestimated survival rates in the ground, but the strong interaction between survival and competitive intensity is probably robust and has been observed previously (Woodward and Jones 1984). The dependence of winter survival on competitive intensity is likely to be mediated by carbohydrate storage. Larger stores of carbohydrate at the onset of winter, as evidenced by larger plants, have been positively correlated with winter survival in both foxglove (*Digitalis purpurea*) and ironweed (*Eupatorium cannabinum*, Woodward and Jones 1984). Because competition decreases plant size

and carbohydrate stores, it is also likely to decrease winter survival.

Populations of California poppies in temporarily disturbed habitats may encounter problems different from populations in sites where competing vegetation is chronically sparse. A single disturbance can temporarily reduce competing biomass, allowing poppy seedlings to establish a population. But as the surrounding vegetation regains biomass, it will compete more intensely with new seedlings. Even if those seedlings survive the summer, they may not have gained enough biomass to survive the winter. Because seedlings are typically much more susceptible to competition than adults (Harper 1977), poppy populations in which individuals must function as facultative annuals are more at risk of extinction than perennial populations. At sites where recurrent disturbance or low soil resources cause competing vegetation to remain sparse, populations may be fully capable of maintaining their presence. This interpretation suggests the hypothesis that populations of California poppies in the south Puget Sound region may be of two types: permanent populations—established and able to maintain themselves, or temporary—germinating, flowering, and reseeding only as long as the biomass of competing

vegetation remains low. Greater disturbance introduced into the landscape by human expansion may allow poppies a higher frequency of temporarily favorable sites.

It is possible that cold hardiness or invasive ability may have been selected for in locally adapted populations. If so, winter survival or the ability of poppies to compete with established grasses may have been underestimated in this experiment because of the commercial origin of the seeds. Seeds produced by locally successful populations would have produced a more robust result, but were unavailable at the start of the experiment. Similarly, field tests of local soil and climatic factors, alone and in competition with naturally-occurring vegetation are imperative to assess the robustness of the results. Such field studies, using locally-collected seeds, are presently underway.

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Literature Cited

- Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic and physiological factors. In H. A. Mooney and J. A. Drake (eds.) *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York. Pp. 96-110.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology: Individuals, Populations and Communities*, 3rd ed. Blackwell Science, Cambridge, MA.
- Campbell, B. D. and J. P. Grime. 1992. An experimental test of plant strategy theory. *Ecology* 73:15-29.
- Chapin III, F. S., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience* 37: 49-57.
- Connor, E. F., and D. Simberloff. 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132-1140.
- . 1983. Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. *Oikos* 41:455-465.
- Cook, S. A. 1961. Genetic systems, variation, and adaptation in *Eschscholzia californica*. *Evolution* 16: 278-299.
- . 1965. Population regulation of *Eschscholzia californica* by competition and edaphic conditions. *Journal of Ecology* 53:759-769.
- Crick, J. C., and J. P. Grime. 1987. Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *The New Phytologist* 107:403-414.
- Diamond, J. M. 1975. Assembly of species communities. In M. L. Cody and J. M. Diamond (eds.) *Ecology and Evolution of Communities*, Harvard University Press, Cambridge, MA. Pp. 342-444.
- Diamond, J. M., and T. J. Case (eds.). 1986. *Community Ecology*. Harper and Row, New York.
- Diamond, J. M., and M. E. Gilpin. 1982. Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. *Oecologia* 52:64-74.
- Franklin, J. F., and C. T. Dyrness. 1973. *Natural vegetation of Oregon and Washington*. U.S.D.A. Forest Service General Technical Report PNW-8.
- Frias, D. L., R. Godoy, P. Iturra, S. Koref-Santibáñez, J. Navarro, N. Pacheco, and G. L. Stebbins. 1975. Polymorphism and geographic variation of flower color in Chilean populations of *Eschscholzia californica*. *Plant Systematics and Evolution* 123:185-198.

- Gedroc, J. J., K. D. M. McConnaughay, and J. S. Coleman. 1996. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? *Functional Ecology* 10:44-50.
- Goldberg, D. E., and S. M. Scheiner. 1993. ANOVA and ANCOVA: Field competition experiments. In S. M. Scheiner and J. Gurevitch (eds.) *Design and Analysis of Ecological Experiments*, Chapman and Hall, New York. Pp. 69-93.
- Grace, J. B. 1995. On the measurement of plant competition intensity. *Ecology* 76:305-308.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press, New York.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle.
- Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology* 83:253-262.
- Lyons, C. P., and B. Merilees. 1995. *Trees, shrubs and flowers to know in Washington and British Columbia*. Lone Pine Publishing, Redmond, WA.
- Moulton, M. P., and S. L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. *American Naturalist* 121:669-690.
- _____. 1986. The extent of competition in shaping an introduced avifauna. In J. Diamond and T. J. Case (eds.) *Community Ecology*, Harper and Row, New York. Pp. 80-97.
- Munz, P. A., and D. D. Keck. 1959. *A California flora*. University of California Press, Berkeley.
- Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. In R. H. Groves and J. J. Burdon (eds.) *Ecology of Biological Invasions: an Australian Perspective*, Australian Academy of Science, Canberra. Pp. 1-20.
- Pearth, D. R., and T. C. Foin. 1985. Analysis and prediction of population and community change: a grassland case study. In J. White (ed.) *The Population Structure of Vegetation*, Dr. W. Junk, Dordrecht, The Netherlands. Pp. 312-339.
- Pimm, S. L. 1989. Theories of predicting success and impact of introduced species. In J. A. Drake, F. DiCastrì, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmánek, and M. H. Williamson (eds.) *Biological Invasions: A Global Perspective*, Wiley, New York. Pp. 351-367.
- _____. 1991. *The Balance of Nature?* University of Chicago Press, Chicago.
- Robbins, W. W., M. K. Bellue, and W. S. Ball. 1951. *Weeds of California*. State of California Printing Division, Sacramento, CA, USA.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76:786-794.
- Rohlf, F. J., and R. R. Sokal. 1981. *Statistical tables*. W. H. Freeman and Co. New York.
- Simberloff, D., and E. F. Connor. 1982. Missing species combinations. *American Naturalist* 118:215-239.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- _____. 1988. *Plant Strategies and the Dynamics and Structures of Plant Communities*. Princeton University Press, Princeton.
- Wilkinson, L., M. Hill, and E. Vang. 1992. *SYSTAT: The system for statistics*. Version 5.2. Systat, Inc., Evanston, IL, USA.
- Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72:1050-1065.
- _____. 1995. Competitive responses of eight old-field plant species in four environments. *Ecology* 76:1169-1180.
- Woodward, F. I. and N. Jones. 1984. Growth studies of selected plant species with well-defined European distributions. I. Field observations and computer simulations on plant life-cycles at two altitudes. *Journal of Ecology* 72:1019-1030.

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