

Comparative biology of three invasive species in the Pacific Northwest: Sulfur cinquefoil (*Potentilla recta*), yellow starthistle (*Centaurea solstitialis*), and spotted knapweed (*Centaurea maculosa*)

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Exotic invasive plants pose a critical threat to ecosystems throughout western North America. The economic costs of containing established populations are increasing and native biodiversity, community structure, and whole ecosystems are at risk (Elton 1958; Sakai et al. 2001; Simberloff and Von Holle 1999; Vitousek et al. 1996). Attempts to characterize the life history traits of successful invaders have met with mixed success (McIntyre et al. 1995; Perrins et al. 1992; Reichard and Hamilton 1997; Williamson and Fitter 1996). An effective strategy to understand invasiveness and develop management alternatives has come from basic biological studies of life history and demography, of key invasive species, which can then be used to predict habitat susceptibility to their invasion.

Three exotic invasive species that are prevalent throughout western North America are sulfur cinquefoil (*Potentilla recta*), yellow starthistle (*Centaurea solstitialis*), and spotted knapweed (*Centaurea maculosa*). There are many studies on the population biology of yellow starthistle and spotted knapweed (Benefield et al. 2001; Joley et al. 1997; Roché et al. 1997; Schirman 1981; Sheley et al. 1983; Watson and Renney 1974) but only a few studies on sulfur cinquefoil (Baskin and Baskin 1990; Powell 1996; Rice et al. 1994). Although *P. recta* has been considered an invasive plant in the United States for the last century, it has not received the level of attention that the *Centaurea* species have. The three species co-occur in some areas, but there is evidence that *P. recta* can replace *C. solstitialis* and *C. maculosa* on some sites (Rice 1991).

The objectives of this study are to: (1) determine germination responses of *P. recta*, *C. solstitialis* and *C. maculosa* to temperature, light and moisture, and (2) compare the early growth characteristics of *P. recta* with *C. solstitialis* and *C. maculosa* under controlled temperature, light, and moisture regimes.

Review

Potentilla recta. Sulfur cinquefoil, a member of the family Rosaceae, is a perennial plant native to Spain, France, Italy, Romania and Russia (Polunin 1969). It reproduces by seeds and possesses a woody taproot that enables the plant to sprout if shoots are damaged (Powell 1996). *P. recta* was introduced to the northeastern United States and southeastern Canada before 1900, and was well established in those regions by the 1950s (Werner and Soulé 1976). The species was first documented in Idaho in 1934, and most recently in Oregon in 1988 (Rice 1991). It is also present in Washington, Montana, and Wyoming. It is currently invading the dry meadows above the Hells Canyon National Monument, in northeastern Oregon.

Highly disturbed sites such as roadsides and abandoned fields are susceptible to early colonization by *P. recta*. Once established, it disperses to minimally disturbed areas such as natural grasslands and open canopy forests (Callihan 1991). The seed persist in soil for at least 4 years (Rice et al. 1994). Sulfur cinquefoil is not palatable and livestock are reported to prefer spotted knapweed in habitats where the two species coexist. Sulfur cinquefoil competes successfully with spotted knapweed, yellow starthistle, leafy spurge (*Euphorbia esula*), and most perennial grass species (Rice 1991). *P. recta* is also adapted to many soil types (except silty soils) and is found most often at altitudes of 1000–2000 m with less than 75% vegetative cover (Rice 1991). It is distributed in areas with 750–1250 mm mean annual precipitation and occurs in areas where less than one percent of the minimum daily temperature falls below 0° C in May and less than five percent falls below 10° C in July (Werner and Soulé 1976).

Under field conditions, *P. recta* produces about 1650 seeds per plant (Werner and Soulé 1976), and germination success is influenced by soil moisture. In controlled studies, 17.5% of *P. recta* seeds germinated when they were stored under moist conditions but minimal germination occurred when stored under dry conditions (Kelley 1953). In another study, *P. recta* seeds were buried and exhumed on a monthly basis for over two years and were exposed to various light and temperature regimes (Baskin and Baskin 1990). While buried, the seed were exposed to temperatures and moistures that would occur under field conditions. Results from subsequent photoperiod and temperature experiments after burial indicated that a high percentage of seed are dormant when fresh, mature over summer, and are non-dormant by autumn. When seed were exposed to light during the growing season they germinated if moisture was not limiting. An absolute light requirement was necessary for germination. The upper maximum temperature threshold for germination was between 20 and 35° C (alternating at 12 hour intervals), but was erratic, ranging from 2–71 percent (Baskin and Baskin 1990). Field studies of *P. recta* in Montana indicate that seedlings emerge by mid-March and basal rosettes are fully formed in April (Rice 1993). Plants produce an elongated flowering stalk in May and form flowers that bloom in June. Flower production continues depending on the availability of moisture. Seeds set in July and disperse by early August, when they senesce. However, new basal leaves often appear when fall rains begin. Growth ceases when plants are exposed to extended cold periods (Rice 1993).

Centaurea solstitialis. Yellow starthistle is in the family Asteraceae, and native to the Mediterranean region. The species most likely came to North America via contaminated alfalfa seeds shipped to California in the early 1800s. By mid-1980, the species inhabited over 3.2 million ha in California and over 220,000 ha in Washington, Idaho, and Oregon. It is estimated that each year yellow starthistle infests an additional 2800–8000 ha (Sheley et al. 1999). This species is a facultative winter annual that usually germinates in the fall following rainfall (Joley et al. 1997; DiTomaso 2000). During the spring, yellow starthistle forms a rosette consisting of 6 to 28 leaves. The plant bolts during early to mid-summer and plant height ranges from 10 cm to 1.5 m depending on density, temperature, and light availability. The flowering stalk has many branches that produce spiny yellow flower heads (Roché et al. 1997; Sheley et al. 1999). The plants generally mature long after most other annuals have senesced and each mature plant can produce up to 150,000 seeds. Over 200 million seeds per hectare may be produced (Callihan et al. 1982). Yellow starthistle produces dimorphic achenes (plumed and nonplumed) that are dispersed at different times; plumed achenes initiate germination more rapidly (but, after 96 hours percent germination for both types of achenes is about equal) and generally have a higher

percent viability than nonplumed achenes (Joley et al. 1997; Sheley et al. 1993; Sheley and Larson 1994a). The majority of seeds are plumed and 92% of them disperse within 60 cm of the mother plant (Roché 1991). However, seeds may disperse up to 40 meters when they are on bare ground and exposed to high winds and birds may also carry them over much greater distances (Roché 1992).

Most yellow starthistle achenes (90%) germinate within one week after seed dispersal (Benefield et al. 2001; Joley et al. 1997; Sheley et al. 1993). Maximum germination of 95–100% occurs in the laboratory when seeds are exposed to light and constant temperatures of 10, 15, and 20° C or alternating temperatures of 15:5 or 20:10° C (Joley et al. 1997). Temperatures above 30° C dramatically reduce germination (Joley et al. 1997; Roche et al. 1997). In the field under optimum conditions (20° C) germination occurs rapidly, typically within 16 hours. This high germination rate can result in extremely dense seedling populations. Intraspecific competition is an important factor in juvenile and adult survivorship. The number of plants that survive to produce seeds is more important to total seed output than the number of seeds produced per plant (Sheley et al. 1993; Sheley and Larson 1994a). Ultimately, seed output is dependent on sufficient spring precipitation.

Yellow starthistle lacks a vernalization and photoperiod requirement (Roché et al. 1997). Since this plant germinates in the fall, winter, or spring, different stages of the plant are observed in the field at the same time. Following germination, yellow starthistle initially allocates environmental resources to root growth and subsequently to leaf expansion, stem development, and flower production. Root growth during the winter and early spring is rapid and can extend well beyond one meter in soil depth (Sheley et al. 1993). Roché et al. (1994) reported yellow starthistle roots grow a mean rate of 0.5 cm per day and as fast as 2.1 cm per day. In another study, root growth averaged 1.7 cm per day (Sheley et al. 1993). The deeper rooting depth enables yellow starthistle to coexist with more shallow rooted species, such as cheatgrass (*Bromus tectorum*). Interspecific competition between *B. tectorum* and yellow starthistle is limited by vertical and temporal partitioning and fields infested with both species can be difficult to revegetate with native species (Sheley and Larson 1994b).

Centuaria maculosa. Spotted knapweed, also in the family Asteraceae, is native to Europe and was introduced to North America in the late 1800's as a seed grain contaminant (Muller et al. 1988). It is rapidly spreading throughout the western U.S. and is present in 14 western states (Sheley et al. 1999). Overgrazing and road construction have been correlated with rapid expansion of populations (Watson and Renney 1974). Spotted knapweed is a perennial that has an average life span of 3 years, but it can live up to nine years (Boggs and Story 1987). Seed production varies considerably (400–25,000 seeds/plant) and, is dependent on moisture availability (Jacobs and Sheley 1998; Watson and Renney 1974). Over 80 percent germination occurs between 10–28° C. In the laboratory, seeds germinate under alternating light and dark conditions (12:12 h), but they also germinate under constant light or constant dark conditions (Watson and Renney 1974). Germination occurs in the fall or early spring in the field and seedlings develop into rosettes that allocate resources to root growth. Overwintering plants bolt in early May and produce 1–6 stems; perennial plants can have 15 or more stems (Watson and Renney 1974). Flowering occurs in July and August and seeds mature in August. If moisture is adequate, seeds will germinate by fall. In one study, Jacobs and Sheley (1998) found that less than 6 percent of the seeds on the ground germinated in the fall, and recruitment peaked (20%–36%) in the spring and early summer. Spotted knapweed also reproduces vegetatively. Lateral

shoots beneath the soil surface grow horizontally and produce rosettes that mature the following season (Watson and Renney 1974). The critical life history stages for *C. maculosa* are juvenile and adult survivorship and the transition from juvenile to adult (Jacobs and Sheley 1998). This finding is comparable to the critical life history stages for yellow starthistle (Sheley and Larson 1994a).

Materials and Methods

Effects of temperature, light, and moisture stress on seed germination of *P. recta*

Three experiments were conducted to determine the comparative effects of temperature, light, and moisture on seed germination of sulfur cinquefoil, yellow starthistle, and spotted knapweed.

Experiment 1: Temperature responses. Seven temperatures, ranging between 5-35° C, were selected to determine germination responses of the three species. Temperatures of 5, 10, 15, 20, 25, 30, and 35° C were maintained on a thermogradient plate. Three replicates of 50 seeds of each species were subjected to each temperature regime. Seeds were placed on a moist filter paper in separate petri dishes. Temperatures along the gradient bar and moisture were monitored daily throughout the experiment. Photoperiod was maintained at 14L/8D (L = light; D= dark) using fluorescent lights. Light intensity at the gradient bar was a constant 300 $\mu\text{mole m}^{-2} \text{s}^{-1}$.

A seed was considered germinated when the radicle protruded from the seed coat. Germinated seeds were counted, recorded, and removed from petri dishes daily. However, the first five germinated seeds in each petri dish were not removed until the end of the experiment when their shoot and root lengths were measured as indicators of seedling vigor.

Experiment 2: Light responses. An experiment was designed to investigate the effects of light on seed germination, using only the optimum germination temperature determined from Experiment 1. Three replicates of each species were used. In this experiment, all petri dishes were completely wrapped in aluminum foil to exclude light, and after 6 days the aluminum foil was removed (light exposure). Rates of germination were determined following the light exclusion period and were monitored for the following 5 days of light exposure. As in Experiment 2, the first five germinated seeds in each petri dish were not removed until the end of the experiment when their shoot and root lengths were measured as indicators of seedling vigor.

Experiment 3: Osmotic potential. The third experiment in this series examined the effects of moisture stress, using polyethylene glycol (PEG) 6000 was used to alter water potential levels (Michael and Kaufman 1973), on seed germination. Six treatments (0, -3, -6,-9,-12 and -15 bars) were used, and the treatments were replicated three times. Photoperiod and temperature were kept at 14L/10D and 20° C, respectively. Subsequent procedures followed the same protocol as in Experiments 1 and 2.

Effects of temperature on early root and shoot growth

Pre-germinated seeds of the three species were planted in 16 x 80 mm test tubes containing mixtures of peat and vermiculite. Small holes were cut into the test tubes for water drainage and all treatments were maintained at the optimum temperature for each species as determined from Experiment 1 and until cotyledons emerged from the soil. After cotyledon emergence, the lower half of each test tube was placed in one of seven temperature regimes (5, 10, 15, 20, 25, 30, 35° C) in the thermogradient plate. Shoots growing from the upper portion of the test tubes were

exposed to a 14h photoperiod and an ambient temperature of $25^{\circ} \pm 2^{\circ}$ C. Shoot and root biomass were recorded at the end of the experiment.

Phenology and growth analysis experiment

Five seeds of each species were planted in separate 0.5 liter greenhouse pots and thinned to one per pot after one week. The plants were maintained in a growth cabinet with an alternating temperature regime of $25/15^{\circ}$ C (day/night temperatures, respectively) and 14h photoperiod. Height, number of leaves, and the appearance of flower buds were recorded for each plant throughout the experiment. Four plants of each species were randomly selected and destructively harvested at four-day intervals. Leaf area was measured for each plant using a Li-Cor leaf area meter. Leaf dry weight and stem dry weight were measured. Growth parameters calculated from these data included Relative Growth Rate (RGR), Absolute Growth Rate (GR), Root-Shoot Ratio (R:S), Leaf Area Per Plant (LAP), Leaf Area Ratio (LAR), Specific Leaf Area (SLA), and Leaf Area Expansion Rate (LAER). The experiment lasted for 65 days.

Results and Discussion

Effects of temperature, light, and moisture stress on seed germination

All three species responded to similar temperatures for seed germination with over 95 percent germination occurring between 15° and 30° C. However, nearly 40 percent of yellow starthistle seeds germinated at 38° C while no seeds of spotted knapweed or sulfur cinquefoil germinated at that temperature. These results suggest that yellow starthistle has a higher temperature tolerance for seed germination than the other species and that maximum percent germination of yellow starthistle occurs within a broader temperature range than the other two species.

Percent germination of seed over a 12-day period varied among species and temperatures. Over 90 percent of yellow starthistle seed germinated at temperatures between 13 – 33° C. Highest germination rates of spotted knapweed seed occurred between 13 – 28° C. Germination of sulfur cinquefoil never exceeded 70 percent at any temperature, but highest germination occurred between 13 – 28° C. No seed of any species germinated at the lowest temperature (3° C), while all species germinated to some degree at 8° C. Both spotted knapweed and sulfur cinquefoil germination significantly declined at 33° C and higher.

All three species germinated when light conditions were constant. Some germination also occurred when seeds were subjected to total darkness, which ranged from 80 percent for *C. maculosa* seed, but only 8 percent of *P. recta*. Percent germination for each of the species was not significantly different whether received by light or alternating light/dark treatments.

Water potential below -6 bars precluded germination of *P. recta*, while germination of *C. solstitialis* (below 10 percent) and *C. maculosa* (37 percent) germinated at that water potential. Highest germination occurred when no water stress was present.

Effects of temperature on early root and shoot growth

Root to shoot ration (R:S) varied among the three species according to different temperature treatments. Maximum root and shoot growth generally occurred near 20° C for all species, but resource allocation to root development was much less for *P. recta* than the other species. R:S ratios ranged from 0.7 and 0.6 for *C. solstitialis* and *C. maculosa*, respectively, to only 0.3 for *P.*

recta. Maximum R:S ratios were attained at 10° C for *P. recta*, 15° C for *C. maculosa*, and 20° C for *C. solstitialis*.

Phenology and growth analysis

P. recta, *C. solstitialis*, and *C. maculosa* exist for part of their lifecycle as a rosette. Each species then bolts, develops secondary branches, and produces flower buds. *C. solstitialis* bolted 21 days after emergence, while both *P. recta* and *C. maculosa* required 41 days. Maximum height obtained for both *Centaurea* species was about 50 cm, although height was attained earlier for *C. solstitialis* (43 days) than either *C. maculosa* or *P. recta* (60 days). *P. recta* was significantly shorter than the two *Centaurea* species, reaching a maximum height of 28 cm.

Although *P. recta* was shorter than the other two species, it produced the most leaf area per plant. Maximum leaf area for *P. recta* was attained at 55 days after emergence, whereas *C. solstitialis* attained maximum leaf area after 33 days. *C. maculosa* grew more leaf area per plant than *P. recta* until day 37, when *P. recta* surpassed it. Although *P. recta* produced about twice the leaf area per plant as *C. maculosa*, total dry mass (TDM) differences were not as disparate. *C. maculosa* has thicker leaves than *P. recta* and both *Centaurea* species had greater stem lengths than *P. recta*, which increased in TDM.

Conclusion

This study elucidated biological characteristics of *P. recta*, *C. solstitialis*, and *C. maculosa*. *P. recta* does not appear to be more competitive than either *Centaurea* species. Both *Centaurea* species germinated faster and maintained higher seedling growth rates than *P. recta*. However, but *P. recta* produced more leaf area per plant, and total dry matter production. These laboratory studies contribute to an understanding of the effects of environmental factors on germination and growth of the species. It is a first step to understanding how their life histories and strategies differ, which ultimately should influence population distribution.

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