# *CENTAUREA* IN THE COLUMBIA BASIN ECOREGION:

# DISTURBANCE, INVASION, AND COMPETITION

By

JOEL ROBERT PANKEY

A dissertation submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

WASHINGTON STATE UNIVERSITY
School of Biological Sciences

MAY 2009

To the Faculty of Washington State University:

The members of the committee appointed to examine the dissertation of JOEL ROBERT PANKEY find it satisfactory and recommend that it be accepted.

R. Alan Black, Chair

Richard N. Mack

Mark F. Dybdahl

# *CENTAUREA* IN THE COLUMBIA BASIN ECOREGION: DISTURBANCE, INVASION, AND COMPETITION

## Abstract

By Joel Robert Pankey, Ph.D.
Washington State University

May 2009

Chair: R. Alan Black

To assess the potential role of biological soil crusts and native perennial grasses in the establishment and resource acquisition of three invasive species of *Centaurea* in the Columbia Basin Ecoregion, I conducted two different multi-year, multi-site, field-based investigations. In one study, *C. maculosa, C. diffusa,* and *C. solstitialis* were experimentally invaded into nine habitat types across three disturbance regimes. In another study, plot-level species removals allowed inference of the competitive effects of native bunchgrasses on *Centaurea* species and of *Centaurea* species on the native bunchgrasses.

Recruitment of *Centaurea* species was approximately 1-2% in non-disturbed (control) plots compared to 5-10% in the disturbance treatments. Regionally, within the disturbance treatments, there were no overall differences in establishment between plots where the soil crust was removed and plots where the plants and the soil crusts were removed although species and treatment differences did occur at some sites. Rates of establishment for all three *Centaurea* species were positively correlated with precipitation across years and sites.

Experimental removal of native bunchgrasses did not result in elevated leaf water potential of *Centaurea* species relative to control plots (grasses and *Centaurea* individuals present) at any sites for any of the *Centaurea* species tested. Midday leaf water potentials for *Centaurea* species decreased from -1.0 MPa in May to -2.5 MPa in July regardless of native bunchgrass presence. Midday leaf water potentials for native bunchgrasses decreased from -1.5 MPa in May to approximately -4.0 MPa in July. Native bunchgrasses maintained greater leaf water potentials in plots where *Centaurea* individuals had been removed compared to bunchgrasses in control plots early in the season (0.16 MPa mean difference, $p = 0.007$) and late in the growing season (0.70 MPa mean difference, $p < 0.0001$).

In a greenhouse study, *Festuca idahoensis* individuals grown with *Centaurea maculosa* produced 0.54 (+/- 0.1) grams of root mass in the 10-20 cm depth range compared to 1.02 (+/- 0.2) grams of root mass at the same depths, for *Festuca idahoensis* individuals grown with a conspecific. These data suggest that *Centaurea maculosa* achieves its competitive effect through negatively affecting the rooting depth of *Festuca idahoensis* individuals.

# TABLE OF CONTENTS

Page

CHAPTER

2. TESTING THE BIOTIC RESISTANCE HYPOTHESIS: EFFECTS OF COMMUNITY DISTURBANCE ON ESTABLISHMENT RATES OF *CENTAUREA*

3. ASSESSING RESOURCE COMPETITION THROUGH SPECIES REMOVALS: LEAF WATER POTENTIAL COMPARISONS BETWEEN *CENTAUREA* AND NATIVE GRASSES

4. DIFFERENTIAL RESPONSES OF *CENTAUREA* AND *FESTUCA* TO COMPETITION UNDER A VARIETY OF SOIL CONDITIONS

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER ONE

# INTRODUCTION

## The genus *Centaurea*

Biological invasions are a major component of global change (Hooper et al. 2005) and cause massive economic and ecologic damage, sometimes leading to the disassembly of entire communities (Sanders et al. 2003). The genus *Centaurea* is one of the most threatening group of invasive dicotyledonous plants in the United States (Skinner 2000, LeJeune and Seastedt 2001, Seastedt and Suding 2007) because of the ability of some *Centaurea* species to invade rangelands, influence soil moisture and nutrient availability (Gerlach and Rice 1996, Gerlach et al. 1998), increase surface water runoff and erosion (Lacey et al. 1989), alter the floristic (Tyser and Key 1988, Lesica and Sheley 1996) and microbial (Batten et al. 2006, Mummey and Rillig 2006) composition of a community, impact wildlife habitat and forage (Thompson 1996, Sheley et al. 1998, Ortega et al. 2006), increase transpiration (Dukes 2001), and alter rates of organic matter deposition on the soil surface (Olson 1999).

Fifteen species of *Centaurea* have naturalized in western rangeland (Roche and Roche 1991). Of these species, the three most abundant are *C. solstitialis* (winter annual), *C. maculosa* (perennial), and *C. diffusa* (annual to biennial). These species have established populations in more than 40 states nationwide and collectively they have invaded more than 10 million hectares (DiTomaso 2000). All three species are capable of rapid population growth (Whitson 1998).

*Centaurea solstitialis*, *C. maculosa*, and *C. diffusa* are all tap-rooted forbs native to Eastern Europe, the Middle East, and Western Asia and phenologically they behave similarly. All three species have a rosette-morphology in fall through early spring and begin to bolt and flower in late spring to early summer. They are relatively scattered and infrequent in their native range (Callaway and Aschehoug 2000) but are capable of forming dense monoculture stands in their invasive range. In the Columbia Basin Ecoregion, *Centaurea* species are most successful in the grass dominated steppe habitats (Talbot 1987) and the majority of these habitats have been modified for agricultural and urban purposes (Washington GAP, 1997). *Centaurea* species threaten the integrity of the increasingly rare stands of native vegetation in this region. In the remaining patches of native vegetation, the perennial bunchgrass *Festuca idahoensis* (Idaho Fescue) is often the dominant plant species (Daubenmire 1970). An understanding of the interaction between *Festuca idahoensis* and the invasive *Centaurea* species may aid land managers and biologists both in conserving these endangered plant associations and restoring *Centaurea*-invaded habitats.

Human activity is largely responsible for the initial introductions of alien plants, intentionally or accidentally, around the planet (Baker 1974). Although the majority of introductions fail to produce a sustaining population, some introductions lead to rapid population growth. The factors responsible for failed introductions are often simpler to determine than the factors contributing to an invasion (Williamson and Fitter 1996). The fate of an introduced population may be affected by demographic stochasticity (May 1973), environmental stochasticity (Fagerstrom and Agren 1979), or its competitive ability relative to the natives (Callaway and Aschehoug 2000). The outcome of an introduction may also be affected by the amount of niche overlap between the introduced species and members of the native community (Elton 1958, Jacobs and Sheley 1999, Levine and D'Antonio 1999, Dukes 2001, Mack 2003, Mwangi et al. 2007).

Every species has a finite range of environmental conditions within which it can persist, and an even narrower range of conditions within which it can thrive (Townsend et al. 2003). When an organism arrives at a location outside of its native range, it may be confronted with a set of environmental conditions that are generally different than the set of conditions under which it evolved. If the introduced species is not adequately adapted to the new conditions or if the competition with the natives is too great, then the immigrant population will not persist (Williamson and Fitter 1996). However, if the suite of environmental conditions at this new location falls within the range tolerable to the introduced species, then this species may persist. In some cases, the climate in the new range may be so similar to the climate in which the species evolved that establishment may occur quite readily. This was apparently the case for many Eurasian species that have become established in the Intermountain Region of western North America (Young et al. 1972) including several species of *Centaurea*.

When a species can tolerate the abiotic environment in a new location, competition typically determines how much, if any, of this fundamental niche will be realized (Connell 1961, Williamson and Fitter 1996) One possibility following an introduction is that the introduced species could fill an “empty” niche and utilize resources that were previously unused by the community (MacArthur 1972), which tends to occur when the introduced species represents a life form previously absent from the recipient community (Mack 2003). In this scenario there would be little or no competitive resistance from the community on the introduced species (Von-Holle 2004). Another possibility though, is that the introduced species interferes with the native community by capturing resources that were previously used by one or more of the natives (sensu Goldberg 1990). If the interference by the invader is strong, one or more native species may be competitively excluded from the community as the immigrant species dominates (Ortega 2005). In severe cases the invader may even establish a monoculture by competitively excluding all other species from the site (Schmitz et al. 1997). A third possibility is that the native community may provide enough competitive resistance to retard the spread of the recently established population (Levine et al. 2004).

In addition to the composition and competitive ability of the native community, the outcome of an introduction may also be affected by disturbance (Zavaleta and Hulvey 2004, Kneitel and Perrault 2006). In contrast to the intermountain region of western North America, many plants from the Mediterranean region have been subjected to intense grazing regimes for long periods of time (Mack and Thompson 1982). As a result, evolution has produced species with grazing resistant features such as spines, thorns, pungent leaf chemicals, toxins, and the ability to vigorously re-sprout. When a plant community that has not evolved to cope with high levels of grazing is suddenly subjected to cattle grazing, the cattle create a large disturbance which weakens the native community (Mack 1981) and may make it more susceptible to invasion by the grazing-tolerant Eurasian species (Sheley et al. 1997).

The establishment of non-indigenous species is often preceded by disturbance (Baker 1974, Mack 1986). This observation forms the basis of the biotic resistance hypothesis which will be addressed in chapter 2. Although a large disturbance may be necessary to remove the native plant community, smaller scale disturbances can damage the biological soil crust which can cover 70% of the soil surface in semi-arid environments (Belnap et al. 2006). Positive correlations have been found between soil crust disturbance and non-indigenous plant richness in the western United States (Kleiner and Harper 1977, Belnap and Lange 2001) suggesting that soil crust integrity plays a role in resisting establishment of non-indigenous species. Additionally, in the Columbia Basin Ecoregion (Washington DNR, 2003), a negative relationship has been found between *Centaurea* and native grass abundance (Ridenour and Callaway 2001) suggesting that native grass cover may also play a role in resisting establishment of non-indigenous species.

Although disturbances such as grazing and trampling by cattle often facilitate *Centaurea* invasion (Watson and Renney 1974, Mack 1986), disturbance is not a requisite for invasion. There are numerous accounts of *Centaurea* species growing in apparently undisturbed grasslands (Myers and Berube 1983, Morris and Bedunah 1984, Tyser and Key 1988, Lacey et al. 1990), although *Centaurea* invasion is most common on disturbed sites. In cases where disturbance was not involved with a species establishment in a community, the introduced species may have competed with the recipient community or avoided competition by representing a life form novel to the community (Mack 2003).

In the Columbia Basin Ecoregion, *Centaurea* species (commonly referred to as knapweeds and starthistles) are most often found in grasslands (Roche and Talbot 1986). These grasslands, or steppe communities (Daubenmire 1970), receive most of their 15 to 45 cm of annual precipitation in the winter and early spring. By late spring, most of the soil moisture has been depleted and water is likely to be the limiting resource (LeJeune and Seastedt 2001, LeJeune et al. 2006). With limited amounts of available water in the soil this should be the time at which competition for water is most intense, if competition is occurring.

## The Columbia Basin Ecoregion

Situated between the Cascade and Rocky Mountains in the western United States and Canada, the Columbia Basin Ecoregion, sometimes called the Columbia Plateau Ecoregion, is the largest and driest of Washington's nine ecoregions and occupies approximately one third of Washington (Washington DNR, 2003). Ecoregions are areas defined not by political boundaries but by climatic, geologic and hydrologic features. Bedrock in this region is almost entirely Columbia River basalt and most of the soils are derived from windblown silt and volcanic ash (Washington DNR, 2003). All rivers in the region flow into the Columbia River which ultimately drains into the Pacific Ocean. Elevations in the region range from 50 meters above sea level along the Columbia River to approximately 1200 meters above sea level in the upland areas. More than 50% of the Columbia Basin Ecoregion has been plowed, paved, or grazed (Washington GAP, 1997) and the remaining natural habitat is becoming increasingly fragmented and disturbed leading to losses of species from some areas (Washington DNR, 2003). Over the last few decades, non-native invasive plants have increased in abundance and native species abundance has declined (Klepeis 2001). Although conservation plans have been established for some areas, knowledge concerning the interactions between native and non-native species is limited.

Most native grasses in the Columbia Basin, and other arid environments, have relatively shallow, fibrous root systems (Caldwell and Richards 1986, Hook et al. 1994, Jackson et al. 1996) and actively grow from spring to early summer when water is most available in the upper portion of the soil (Daubenmire 1970). In arid and semi-arid environments community structure can be strongly affected by belowground interactions (Fowler 1986, Mahall and Callaway 1992). Root growth can account for 80 - 90% of the productivity in grasslands (Steinaker and Wilson 2008) demonstrating the evolutionary force that soil water limitation can have on a plant community. It is not uncommon for *Centaurea* species to grow for 6 or 8 weeks after the native grasses have gone dormant for the summer (personal observations). This extended growing season of knapweeds and starthistles relative to the grasses, strongly suggest that *Centaurea* roots more deeply than the native grasses and may therefore be less affected by competition for water than the grasses.

My dissertation research focused on understanding the nature of competition between three invasive *Centaurea* species and the dominant native grasses in the Columbia Basin Ecoregion. Chapter 2 explores the role of the native community in resisting the establishment of introduced species in both natural and disturbed habitats. I tested the effects of biological soil crust disturbance, native plant community removal, and habitat type, on recruitment of *Centaurea diffusa, C. maculosa, and C. solstitialis* throughout the Columbia Basin Ecoregion. Chapter 3 addresses the effect of the native perennial grasses on water acquisition by adult *Centaurea* plants and the effect of adult *Centaurea* plants on water acquisition by the native grasses. Chapter 4 focuses on the mechanisms involved with the observed patterns of competition between *Centaurea maculosa* (spotted knapweed) and the native grass *Festuca idahoensis* (Idaho fescue).

## Literature Cited

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics (1974):1-24.

Batten, K. M.; K. M. Scow; K. F. Davies; S. P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. Biological Invasions 8:217-230.

Belnap, J. S.; O. L. Lange (editors) 2001. Biological Soil Crusts: Structure, Function, and Management. Springer, New York, NY.

Belnap, J.; S. L. Phillips; T. Troxler. 2006. Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the exotic annual grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology 32:63-76.

Caldwell, M. M.; J. H. Richards. 1986. Competing root systems: morphology and models of absorption. In: Givnish, T. J. (editor) On the Economy of Plant Form and Function. Cambridge University Press. Cambridge. pp 251-273.

Callaway, R. M.; E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521-523.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42 (4):710-723.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. Weed Science 48:255-265.

Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia 126:563-568.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Chapman and Hall, New York, NY.

Fagerstrom, T.; G. I. Agren. 1979. Theory for coexistence of species differing in regeneration properties vegetation. Oikos 33 (1):1-10.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17:89-110.

Gerlach, J. D. Jr.; K. Rice. 1996. *Centaurea solstitialis* threatens California's ecosystems. Bulletin of the Ecological Society of America 77:160.

Gerlach, J.; A. Dyer; K. Rice. 1998. Grassland and foothill woodland ecosystems of the Central Valley. Fremontia 26(4): 39-43.

Goldberg, D. E. 1990. Components of resource competition in plant communities. In: Grace, J. B. and D. Tillman (editors) Perspectives on plant competition. Springer.

Hooper, D. U.; E. S. Chapin III; J. J. Ewel; A. Hector; P. Inchausti; S. Lavorel; J. H. Lawton; D. M. Lodge; M. Loreau; S. Naeem, B. Schmid; H. Setala; A. J. Symstad; J. Vandermeer; D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75 (1):3-35.

Hook, P. B.; W. K. Lauenroth; I. C. Burke. 1994. Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and regeneration gaps. Journal of Ecology 82:485-494.

Jackson, R. B.; J. Canadell; J. R. Ehleringer; H. A. Mooney; O. E. Sala; E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411.

Jacobs, J. S.; R. L. Sheley. 1999. Competition and niche partitioning among *Pseudorognaria spicata, Hedysarum boreale,* and *Centaurea maculosa*. Great Basin Naturalist 59:175-181.

Kleiner, E. F.; K. T. Harper. 1977. Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. J. of Range Management 30 (4):286-289.

Klepeis, D. M. 2001. Structure and susceptibility of steppe to biotic invasion: re-analysis of permanent plots. Thesis (M.S.) Washington State University.

Kneitel J. M.; D. Perrault. 2006. Disturbance-induced changes in community composition increase species invasion success. Community Ecology 7 (2):245-252.

Lacey, J. R.; C. B. Marlow; J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. Weed Technology 3:627-631.

Lacey, J.; P. Husby; G. Handl. 1990. Observations on spotted and diffuse knapweed invasion into ungrazed bunchgrass communities in western Montana. Rangelands 12:30-32.

LeJeune, K. D.; T. R. Seastedt. 2001. *Centaurea* species: the forb that won the west. Conservation Biology 15, No. 6: 1568-1574.

LeJeune, K. D.; K. N. Suding; T. R. Seastedt. 2006. Nutrient availability does not explain invasion and dominance of a mixed grass prairie by the exotic forb *Centaurea diffusa.* Applied Soil Ecology 32 (1):98-110.

Lesica, P.; J. S. Sheley. 1996. Competitive effects of *Centaurea maculosa* on the population dynamics of *Arabis fecunda*. Bulletin of the Torrey Botanical Club 123:111-121.

Levine, J.; C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. Oikos 87:1-12.

Levine, J. M.; P. B. Adler; S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7 (10):975-989.

MacArthur, R. H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York, NY.

Mack R. N. 1981. Invasion of *Bromus tectorum* in western North America: An ecological chronicle. Agro-Ecosystems 7:145-165.

Mack, R. N.; J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757-773.

Mack, R. N. 1986. Alien Plant Invasion into the Intermountain West: a case history. In: Mooney, H. A.; J. Drake (editors) Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York, NY:191-213.

Mack, R. N. 2003. Phylogenetic constraint, absent life forms, and pre-adapted alien plants: a prescription for biological invasions. International Journal of Plant Sciences 164 (3 supplement): S185-S196.

Mahall, B. E.; R. M. Callaway. 1992. Root communication mechanisms and intercommunity distributions of two Mojave Desert shrubs. Ecology 73:2145-2151.

May, R. M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ.

Morris, M. S.; D. Bedunah. 1984. Some observations on the abundance of spotted knapweed (*Centaurea maculosa* Lam.) in western Montana. Knapweed Symposium Proceedings, Plant and Soil Science Department and Cooperative Extension Service, Montana State University Bulletin 1315:77-81.

Mummey, D. L.; M. C. Rillig. 2006. The invasive plant species *Centaurea maculosa* alters arbuscular mycorrhizal communities in the field. Plant and Soil 288 (1-2):81-90.

Mwangi, P. N.; M. Schmitz; C. Scherber; C. Roscher; J. Schumacher; M. Scherer-Lorenzen; W. W. Weisser; B. Schmid. 2007. Niche pre-emption increases with species richness in experimental plant communities. Journal of Ecology 95 (1):65-78.

Myers, J. H.; D. E. Berube. 1983. Diffuse knapweed invasion into rangeland in the dry interior of British Columbia. Canadian Journal of Plant Science 63:981-987.

Olson, B. E. 1999. Impacts of noxious weeds on ecologic and economic systems. In: Sheley, R. L.; J. K. Petroff (editors) Biology and Management of Noxious Rangeland Weeds. Oregon State University Press, Corvallis, OR: 4-18.

Ortega, Y. K.; D. E. Pearson. 2005. Weak vs. strong invaders of natural plant communities: Assessing invasibility and impact. Ecological Applications 15 (2):651-661.

Ortega, Y. K.; K. S. McKelvey; D. L. Six. 2006. Invasion of an exotic forb impacts reproductive success and site fidelity of a migratory songbird. Oecologia 149:340-351.

Ridenour, W. M.; R. M. Callaway. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126:444-450.

Roche, B. F. Jr.; Talbott, C. J. 1986. The collection history of *Centaureas* found in Washington State. Research Bulletin XB 0978. Pullman, WA: Washington State University, College of Agriculture and Home Economics, Agriculture Research Center. 36 p.

Roche, B. F. Jr.; C. T. Roche. 1991. Identification, introduction, distribution, ecology, and economics of *Centaurea* species. In: James, L. F.; J. O. Evans; M. H. Ralphs; R. D. Child (editors) Noxious Range Weeds. Westview press, San Francisco, CA:274-291.

Sanders, N. J.; N. J. Gotelli; N. E. Heller; D. M. Gordon. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences of the USA 100 (5):2474-2477.

Schmitz, D. C.; D. Simberloff; R. H. Hofstetter; W. Haller; D. Sutton. 1997. The ecological impact of nonindigenous plants. In: Simberloff, D.; D. C. Schmitz; T. C. Brown (editors) Strangers in Paradise:39-61. Island Press, Washington D.C.

Seastedt, T. R.; K. N. Suding. 2007. Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. Oecologia 151 (4):626-636.

Sheley, R. L.; B. E. Olson; L. L. Larson. 1997. Effect of weed seed rate and grass defoliation level on diffuse knapweed. Journal of Range Management 50:39-43.

Sheley, R. L.; J. S. Jacobs; M. F. Carpinelli. 1998. Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technology 12:353-362.

Skinner, K.; L. Smith; P. Rice. 2000. Using noxious weed lists to prioritize targets for developing weed management strategies. Weed Science 48:640-644.

Steinaker D. F.; S. D. Wilson. 2008. Phenology of fine roots and leaves in forest and grassland. Journal of Ecology 96 (6): 1222-1229.

Talbott, C. J. 1987. Distribution and ecologic amplitude of selected *Centaurea* species in eastern Washington. Thesis (M.S) Pullman, WA: Washington State University.

Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. Northwest Science 70:10-19.

Thomsen, M. A.; C. M. D'Antonio. 2007. Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability and environmental gradients. Oikos 116 (1):17-30.

Townsend, C. R.; M. Begon; J. L. Harper. 2003. Essentials of Ecology 2nd Edition. Blackwell.

Tyser, R. W.; C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. Northwest Science 62:151-160.

Von Holle, B.; D. Simberloff. 2004. Testing Fox's assembly rule: does plant invasion depend on recipient community structure? Oikos 105 (3):551-563.

Washington Department of Natural Resources. 2003. State of Washington Natural Heritage Plan; 64 pp. Olympia, WA.

Washington GAP Analysis. 1997. Washington Department of Fish and Wildlife.

Watson, A. K.; A. J. Renney. 1974. The biology of Canadian weeds: *Centaurea diffusa* and *C. maculosa*. Canadian Journal of Plant Science 52:687-701.

Whitson, T. D. 1998. Integrated pest management systems for weed control. Proceedings of the Western Society of Weed Science 51:43.

Williamson, M; A. Fitter. 1996. The varying success of invaders. Ecology 77:1661-1666.

Young, J. A.; R. A. Evans; J. Major. 1972. Alien plants in the Great Basin. Journal of Range Management 25:194-201.

Zaveleta, E. S.; K. B. Hulvey. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. Science 306:1175-1177.

# CHAPTER TWO

# TESTING THE BIOTIC RESISTANCE HYPOTHESIS: EFFECTS OF COMMUNITY DISTURBANCE ON ESTABLISHMENT RATES OF *CENTAUREA*

## Introduction

The terms “ecological resistance” (Elton 1958) and “ecosystem integrity” (Leopold 1949) have been coined in the last century as a result of a phenomenon that humans have long observed and exploited: that disturbance and biologic invasions drive changes in plant communities (Kulmatiski 2006). This phenomenon has been observed on a large scale from natural occurrences such as flooding or wildfire and exploited on a large scale for agriculture for thousands of years (Watts and Bradbury 1982). An implication of these terms then is that a mature plant community without disturbance will resist changes (Levine et al. 2004). The biotic resistance hypothesis (D’Antonio and Thomsen 2004) is consistent with observations that introduced species occur most commonly in disturbed areas. After centuries of interest in finding ways to optimally disturb ecosystems to achieve particular goals, the growing threat of invasive species has created an interest in understanding factors that help to resist change in plant communities.

Globally, biological invasions are mediated by human intercontinental travel (Baker 1986), but locally, biological invasions are generally facilitated by some form of human disturbance (Mack and Thompson 1982). Once established, invasive species can decrease plant diversity both locally (Kleiner and Harper 1977, Tyser and Key 1988) and globally (Schofield 1989), as well as alter certain ecosystem functions (May 1977, Vitousek 1986) and disturbance regimes (Mack and D'Antonio 1998). The nature of the disturbance may provide some indication of which species or functional groups may flourish following the disturbance, but the attributes of the pre-disturbance community responsible for the maintenance of community composition are not as well understood. Community attributes conferring persistence and resilience frequently result from the additive effects of a single species (Emery and Gross 2007) or of functional groups (Pokorny et al. 2005, Rinella 2007) at a particular site, but community composition may be regulated in some habitats by the synergistic effects of the interactions within the community as a whole (Renne et al. 2006, Reinhart and Callaway 2006, Fridley et al. 2007).

Community resistance to invasion should be viewed as a probabilistic rather than a deterministic phenomenon (Crawley 1989), therefore the ultimate significance of biotic resistance is often the reduction in establishment probability for invaders, not the complete elimination of establishment (Levine et al. 2004). By experimentally introducing small populations of seeds across a range of habitat types or disturbance regimes, relative probabilities of establishment can be estimated for each species within different disturbance and habitat types so that differences in biotic resistance can be detected between treatments.

In the Intermountain West, *Centaurea* species (knapweeds and starthistles) are considered some of the worst non-grass invasive plants (LeJeune and Seastedt 2001). The role of the native steppe communities in the Columbia Basin Ecoregion to resist further spread of *Centaurea* species, the biotic resistance hypothesis was tested for the seedling establishment stage of the life-cycle for *Centaurea solstitialis, C. maculosa,* and *C. diffusa* in a stand nine throughout the Columbia Basin Ecoregion. The biotic resistance hypothesis predicts a negative relationship spatially between the native community and introduced *Centaurea* in grasslands. Two species co-occurring at a lower frequency than would be predicted by random is one indication that interspecific competition occurs or has occurred in the past (Connell 1980). Therefore, we predicted that the presence of the native community would reduce the probability of establishment for *Centaurea*.

By disturbing the biological soil crusts but not the plants, the biological soil crusts and the plants, or not disturbing the native community (control), I investigated the effect of plants and biological soil crusts on recruitment of three species of *Centaurea*. To clarify, biological soil crusts consists of a diversity of photosynthetic organisms such as lichens and mosses and is built up over several years eventually forming a thin barrier between the mineral soil and the air that acts to retain moisture and prevent erosion (Belnap et al. 2006). I tested the hypothesis that the greatest recruitment for all species of *Centaurea* would occur in plots of greatest disturbance, the ones where the crust and plants had both been removed, in all locations. I hypothesized that the lowest recruitment rates would occur in the control plots where there was no disturbance and I expected to see an intermediate level of recruitment in the disturbance treatment where the plants were left intact and only the soil crust was removed. Finally, since grasslands are chronically water limited, I expected precipitation and recruitment to be positively correlated.

## Methods

To assess the effect of disturbance on the potential for populations of three species of *Centaurea* to expand, recruitment was measured for each species in nine habitat types within the current range of each *Centaurea* species. Recruitment was measured for all 3 *Centaurea* species for 2 consecutive years across three disturbance regimes at each site. Comparisons were made between treatments to identify attributes of the native communities that contribute resistance to establishment by new populations. Additionally, comparisons were made between species on a site by site basis to provide finer scale resolution of each species potential for range expansion in specific habitat types.

Nine experimental sites were selected to represent a range of habitat types (Sensu Daubenmire 1970) that occur in the Columbia Basin Ecoregion including examples of steppe, shrub-steppe, and forest-steppe communities. Sites were selected in Idaho County (ID), Latah County (ID), Umatilla County (OR), Whitman County (WA), Walla Walla County (WA), Spokane County (WA) and two sites in Okanogan County (WA).

The nine habitat types represented in this study are *Festuca idahoensis / symphoricarpos albus, Agropyron spicatum / Festuca idahoensis, Agropyron spicatum / Poa secunda, Aristida longesita / Poa secunda, Artemisia tridentata / Stipa comata, Artemisia tridentata / Agropyron spicatum, Artemisia tripartita / Festuca idahoensis, Purshia tridentata / Festuca idahoensis, and Pinus ponderosa / Festuca idahoensis.* One site was selected within each habitat type and sites were selected where native plant associations and biological soil crusts were present and where disturbance appeared minimal.

Achenes (hereafter referred to as seeds) of *C. diffusa*, *C. maculosa*, and *C. solstitialis* were collected in the summers of 2002 and 2003 from a range of habitat types throughout the region. For *C. diffusa*, seeds were collected from multiple habitat types in Spokane County, Lincoln County, and Okanogan County in Washington. For *C. maculosa*, seeds were collected from several habitat types in Stevens County, Spokane County, and Whitman County in Washington. For *C. solstitialis*, seeds were collected from multiple habitat types in Whitman County in Washington and Nez Perce County and Idaho County in Idaho. For each species, seeds collected from different years and habitat types were bulked to reduce the potential influence of local adaptation or genetic bottlenecking. 3240 seeds of each species were sorted and counted by hand for each year of the study. Seeds were selected for the experiment that were filled and exhibited a complete seed coat without signs of insect damage. For *Centaurea solstitialis,* presence or absence of pappus on the seed was ignored as a factor for selection. Random sub-samples of seeds for each species were germinated on wet filter paper to ensure viability. Germination for seeds of all 3 species was greater than 95 percent.

Three experimental blocks were established at each of the nine sites for each year of the study. The blocks were two meters by three meters and contained three treatments: control, crust removal, and crust plus plant removal, with each treatment randomly assigned to one third of each block. Each treatment was divided into three subplots into which 40 seeds of one of the three *Centaurea* species were randomly sowed. The 40 seeds in each envelope were sprinkled by hand within a two decimeter by five decimeter plot to ensure equal seed density across treatments, sites, and species. Steel stakes were driven into the ground to mark the plots. Therefore each block contained nine subplots with each of three species across each of three treatments (9 sites x 3 blocks x 3 treatments x 3 species).

Disturbance treatments were applied to all experimental blocks at all sites during the winters of 2003-2004 and 2004-2005. The biological soil crusts were removed with a garden hoe by carefully scraping and lifting the soil crusts from the mineral soil. The plant plus crust removal treatment was accomplished by first removing the crust from the mineral soil and then removing the crowns of the perennial grasses while minimizing disturbance to the mineral soil. Roots of the grasses were left in place as to not alter the structure of the soil but were expected to have little effect on the water status of the soil because they lacked evaporative surfaces through which water might have been lost. Seeds were sowed in their respective plots immediately following treatment.

Plants were counted at all sites in June, and all plants were removed while in the rosette stage, before flowering. Since mortality rates are highest in the seed and seedling stages, survival until the rosette stage was used as an index of reproductive potential. Establishment rates were compared between species in each habitat type since species and treatment interact in some habitat types.

## Results

Recruitment of all three species of *Centaurea* in undisturbed plots at was very low (1-2%). Disturbance of soil crust increased establishment three-fold to five-fold compared to controls which is not significantly different from the treatment with crust and plant removal (figure 2.1, tables 2.2 and 2.4). Recruitment in control plots for all three species was approximately 1% in 2004 and 2% in 2005 whereas recruitment in plots with disturbance treatments was between 5% and 10% for 2004 and 2005. Recruitment in undisturbed plots for all three species of *Centaurea* was positively correlated with annual precipitation for the two years of the study.

Spatial variation in recruitment in disturbed plots also correlated positively with spring-time precipitation (figures 2.3-2.8). At the two wettest sites, *Purshia tridentata*/ *Festuca idahoensis* (figure 2.14) and *Pinus ponderosa*/ *Festuca idahoensis* (figure 2.15), mean recruitment in disturbance plots was greater than 10% (figure 2.2). *Centaurea maculosa* established at nearly double the rate of the other two species at the two wettest sites (20.2% compared to 11.8% and 12.4% for *C. diffusa* and *C. solstitialis* respectively) (figure 2.2). At all other sites, *C. maculosa* established at rates equal to or less than the other two species. At the three driest sites, *Agropyron spicatum/ Festuca idahoensis* (figure 2.10), *Agropyron/ Poa secunda* (figure 2.11), and *Artemisia tripartita/ Agropyron spicatum* (figure 2.12), recruitment in disturbance plots were less than 5%. *Centaurea solstitialis* established at nearly double the rate of the other two species at the three driest sites (3.3% compared to 1.8% for each of the other two species) (figure 2.2).

Overall, *Centaurea* recruitment in plots where the soil crust had been removed was not different than recruitment in plots where the soil crust and the plants had been removed (tables 2.3 and 2.5), but some species did not follow this general pattern at all sites. At the *Festuca idahoensis/ Symphoricarpos albus* site and the *Agropyron spicatum/ Poa secunda* site, in 2004 and 2005 *Centaurea solstitialis* recruitment was two to three times as great in plots where soil crust and plants were removed compared to plots where only soil crusts were removed (figures 2.9 and 2.11). At the *Artemisia tripartita/ Festuca idahoensis* site, *Centaurea maculosa* recruitment was three times greater where soil crust and plants were removed from plots compared to plots where only soil crust had been removed (figure 2.13). Finally, at the *Pinus ponderosa/ Festuca idahoensis* site, both *C. maculosa* and *C. solstitialis* recruitment was twice as great where soil crusts and plants were removed from plots compared to plots where only soil crusts were removed (figure 2.15). The only habitat types where recruitment was not greater in disturbed plots compared to control plots were *Artemisia tridentata/ Stipa comata* and *Aristida longiseta/ Poa secunda* and only during 2005, the wetter year (figures 2.16 and 2.17).

## Discussion

The 5-fold to 10-fold greater recruitment in disturbed versus undisturbed plots across species, sites, and years provides support for the biotic resistance hypothesis and supports the hypothesis that the lowest recruitment would occur in the undisturbed plots. Although I was not able to separate the effects of the plants and the soil crusts on the conferred resistance to *Centaurea* establishment, it was clear that the vegetation alone cannot resist *Centaurea* invasion. Species evolve in the context of the communities in which they occur rather than in isolation (Mack and Thompson 1982) so it is not surprising that few species will not provide the same integrity as an intact grassland community.

My data show that biological soil crusts play a surprisingly important role in providing resistance to *Centaurea* establishment. The sensitivity of biological soil crusts to disturbance (Lauenroth and Coffin 1992) and highly disturbed nature of the Columbia Basin Ecoregion (Washington DNR, 2003) emphasizes the importance of the interactions between the native perennial grasses and *Centaurea* species in disturbed areas.

Also apparent in the data is the difference in recruitment in the undisturbed plots between the two years of the study. Recruitment in undisturbed plots was twice as great in 2005 compared to 2004. The National Climatic Data Center (www.ncdc.noaa.gov) reported that spring rainfall totals in the Columbia Basin were approximately double in 2005 compared to 2004 and describes 2004 as a mild to moderate drought year and 2005 as an abnormally moist year. Davis and others (2000) argue that biotic resistance to invasion is a function of resource supply, and resource use by the established community so the least invasible community is one without unused resources. Increased resource availability has been experimentally shown to increase community invisibility (Davis and Pelsor 2001, Maron and Marler 2007) suggesting that biotic resistance in a community should fluctuate through time with resource availability. My data are consistent with this prediction and suggest that the probability of *Centaurea* invasion into undisturbed habitat should be greater during wet years than during dry years.

In addition to variation in rainfall, disturbance can also significantly affect resource availability. Several studies have found that disturbance in grasslands can have a large effect on establishment rates of introduced species (Kotanen 1997, Sheley et al. 1997, Renne et al. 2006, Kyle et al. 2007). This study is noteworthy however, because it is the first to separate the effects of disturbance to the biological soil crusts from the effects of disturbance to the resident grasses. The relatively high level of establishment observed in both disturbance treatments leads to the conclusion that the biological soil crusts may have a critical role in the maintenance of natural communities in the Columbia Basin. The establishment rates in this study emphasize the importance of conserving and restoring the soil crust communities to efforts aimed at conservation and restoration of native plant associations.

Although I did find support for the biotic resistance hypothesis, I did not observe significant differences in establishment in the plots with both the crust and plants removed compared to the plots with just the crust removed and the grasses remaining. Similarly, Thomsen and D'Antonio (2007) also found that resistance to invasion can sometimes be due to a subset of species in the native community.

The native perennial grasses were expected to play a larger role in controlling *Centaurea* because of their ability to rapidly capture limiting resources in shallow soil (Eissenstat and Caldwell 1988, Black et al. 1994). *Centaurea* appears to avoid competition from *Festuca* by rooting more deeply in the soil where water is more available (Hill et al. 2006, Kulmatiski et al. 2006). Since *Centaurea* taproot growth is reduced by about half when seedlings are shaded (DiTomaso et al. 2003), shading from established grasses was expected to increase the length of time over which competition between adult grasses and *Centaurea* seedlings could occur. However, in this study we found very little evidence that established native grasses without intact soil crust interfered with *Centaurea* establishment because seedling survivorship was not different between the disturbance treatment with grasses present and the disturbance treatment with the grasses removed for the majority of the habitat types.

These results are consistent with those from a study by Sheley and others (1997) who found that complete defoliation of the native grasses at one site in eastern Washington resulted in quadruple the number of *Centaurea* becoming established compared to non-defoliated plots nearby. That study however, involved only one

*Centaurea* species and two plots and did not consider biological soil crusts as a factor. It is likely that in the process of defoliating plots, biological soil crusts were damaged as the authors did not report controls for potential crust damage in the non-defoliated plots.

My results are also consistent with the findings of Seastedt and Suding (2007) who found that *Centaurea diffusa* established at a very low rate in undisturbed grassland plots. When they removed grass competitors from plots, *Centaurea diffusa* experienced 30-fold greater recruitment compared to the undisturbed plots.

In contrast to my data, Larson and McInnis (1989) noted that survivorship of *Centaurea* seedlings was several times greater in proximity to grasses than on bare soil suggesting facilitation of *Centaurea* by the grasses. They suggested soil moisture conservation as the mechanism. Callaway and others (2003) also found evidence for positive effects of grasses on *Centaurea* in a greenhouse experiment. The factors responsible for these spatial and temporal fluctuations between interference and facilitation for *Centaurea* and native grasses are not clear. Such variability was observed in this study as well; when data are compared between habitat types or between species within a habitat type it becomes clear that multiple factors may interact to determine the observed outcome at a given location for a given year.

Although there are differences in ecological amplitude between *Centaurea* species at a fine (slope, aspect, and soil depth) scale of resolution (Talbott 1987), all 3 *Centaurea* species in this study occur in virtually all eastern Washington counties (Talbott 1987). As seeds continue to be dispersed around the region and biological soil crusts are damaged from human activities, all *Centaurea* from this study have the potential to grow and compete in all surveyed counties.

### *Site and species specific observations*

In particular, the establishment rates of *C. solstitialis* in the *Purshia tridentata/ Festuca idahoensis* stand and both *C. solstitialis* and *C. maculosa* in the *Pinus ponderosa/ Festuca idahoensis* and *Artemisia tripartita/ Stipa comata* stands were surprisingly high considering the apparent scarcity of these species in the surrounding area. The grass dominated habitats with southern exposure in both of these counties appear to be highly suited for invasion by *C. solstitialis.* The largest factor working against the invasion of *C. solstitialis* (winter annual) in these counties may be the relatively late onset of spring compared to the lower latitude and lower elevation sites where it currently dominates. However, *C. solstitialis* often germinates in the fall and survives the winter as a rosette underneath the snow continuing growth anytime light is available and temperatures are favorable. As the weather continues to change and temperatures rise, the main limitation to growth of *C. solstitialis* in Spokane and Okanogan Counties may be alleviated.

There are several locations in Riverside State Park in Spokane County where *C. maculosa* and *C. diffusa* co-occur and there are reports of populations in that appear to be hybrids of the two species (Marrs et al. 2003). In Okanogan County however, *C. diffusa* is widespread and dominant whereas *C. maculosa* is much less common and generally occurs as a ruderal along roadsides. *C. maculosa* also lacks the dispersal capabilities of *C. diffusa* which produces a single-stalked inflorescence that detaches and “tumbles” in the wind and can be dragged by vehicles. As *C. maculosa* continues to establish new populations in Okanogan County, based on this study there is no apparent reason that *C.*

*maculosa* will not become as widespread and problematic in Okanogan County as *C. diffusa*.

Whitman County (WA) and Idaho County (ID) may be the two counties in which *C. diffusa* has the greatest potential to establish new populations. Some populations of *C. diffusa* have already been established in these counties but much suitable habitat remains. *C. diffusa* is capable of growth in xeric environments that are common in these counties and its establishment rates there are sufficient for it to persist where introduced. The hilly terrain in these counties may make the "tumbleweed-type" dispersal of *C. diffusa* less effective than it is in the flatter steppe habitats of Lincoln and Okanogan Counties. Although *C. diffusa* also commonly disperses along rivers by floating downriver, the major seed sources for *C. diffusa* are downriver from Whitman and Idaho Counties so dispersal limitation may be the major factor keeping *C. diffusa* from invading Whitman and Idaho Counties.

As the human population in the Columbia Basin Ecoregion continues to grow, disturbance to biological soil crusts may become more frequent and more intense. This disturbance appears to facilitate the establishment of new *Centaurea* populations regardless of the state of the co-occurring plant community. All three species of *Centaurea* in this study have the potential to establish new populations in virtually all grass-dominated habitat types in the Columbia Basin Ecoregion. Continued dispersal along roadways and rivers coupled with soil disturbance and time may lead to the establishment of populations of all three *Centaurea* species in almost all counties in Eastern Washington, Western Idaho, and Eastern Oregon.

Biological soil crusts are not the largest or most conspicuous organisms in the grasslands of the Columbia Basin but they are an integral part of the system. Biotic resistance in grasslands is a synergistic rather than an additive phenomenon (Foster et al. 2004, Renne 2006) so even though the plants use the vast majority of soil resources, preserving the integrity of our grasslands requires more than just preserving the plant species.

This study has illuminated an important role of biological soil crusts in maintaining the integrity of native plant communities in the Columbia Basin Ecoregion. Although further research is needed to identify the mechanism underlying the ability of biological soil crusts to reduce the probability of establishment and recruitment of *Centaurea diffusa*, *C. maculosa*, and *C. solstitialis*, restoration efforts in steppe habitats of the Columbia Basin Ecoregion may be more successful if biological soil crust communities are re-established as the native vegetation is restored.

## Literature Cited

Baker, H. G. 1986. Patterns of plant invasions in North America. In: H. A. Mooney; J. A. Drake (editors) Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York, NY:44-57.

Belnap, J.; S. L. Phillips; T. Troxler. 2006. Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the exotic annual grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology 32:63-76.

Black, R.A.; Richards, J.H.; Manwaring, J.H. 1994. Nutrient uptake from enriched soil microsites by three Great Basin perennials. Ecology 75:110-122.

Callaway, R.M., B.E. Mahall, C. Wicks, J. Pankey, and C. Zabinski. 2003. Soil fungi and the effects of a native forb on native versus naturalized grasses: neighbor identity matters. Ecology 84:129-135.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Crawley, M. J. 1989. Chance and timing in biological invasions. In: Drake, J. A.; H. A. Mooney; F. DiCastri; R. H. Groves; F, J. Kruger; M. Rejmanek; M. Williamson (editors) Biological Invasions: A Global Perspective. Jon Wiley & Sons Inc., Chichester, UK:407-423.

D’Antonio, C. M.; M. Thomsen. 2004. Ecological resistance in theory and practice. Weed Technology 18:1572-1577.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62.

Davis, M. A.; J. P. Grime; K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528-534.

Davis M. A.; M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421-428.

DiTomaso, J. M.; G. B. Kyser; C. B. Pirosko. 2003. Effect of light and density on yellow starthistle (*Centaurea solstitialis*) root growth and soil moisture use. Weed Technology 51(3):334-341.

Eissenstat, D. M.; M. M. Caldwell. 1988. Competitive ability is linked to rates of water extraction: a field study of two aridland tussock grasses. Oecologia 75:1-7.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Chapman and Hall, New York, NY.

Emery, S. M.; K. L. Gross. 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland communities. Ecology 88 (4):954-964.

Fridley, J. D.;J. J. Stachowicz; S. Naeem; D. F. Sax; E. W. Seabloom; M. D. Smith; T. J. Stohlgren; D. Tilman; B. Von Holle. 2007. The invasion paradox: Reconciling pattern and process in species invasions. Ecology 88 (1):3-17.

Hill, J. P.; M. J. Germino; J. M. Wraith; B. E. Olson; M. B. Swan. 2006. Advantages in water relations contribute to greater photosynthesis in *Centaurea maculosa* compared with established grasses. International Journal of Plant Sciences 167 (2):269-277.

Kleiner, E. F.; K. T. Harper. 1977. Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. J. of Range Management 30 (4):286-289.

Kotanen, P. M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal California meadows. Journal of Applied Ecology 34:631-644.

Kulmatiski, A. 2006. Exotic plants establish persistent communities. Plant Ecology 187 (2):261-275.

Kulmatiski, A.; K. H. Beard; J. M. Stark. 2006. Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. Plant and Soil 288 (1-2):271-284.

Kyle, G. P.; K. H. Beard; A. Kulmatiski. 2007. Reduced soil compaction enhances establishment of non-native plant species. Plant Ecology 193 (2):223-232.

Larson, L. L.; McInnis, M. L. 1989. Impact of grass seedlings on establishment and density of diffuse knapweed and yellow starthistle. Northwest Science. 63 (4):162-166.

Lauenroth, W. K.; D. P. Coffin. 1992. Belowground processes and the recovery of semiarid grasslands from disturbance. In: Wali, M. K. (editor) Ecosystem Rehabilitation: Ecosystem Analysis and Synthesis. SBP Academic, The Hague, the Netherlands: 131-150.

LeJeune, K. D.; T. R. Seastedt. 2001. *Centaurea* species: the forb that won the west. Conservation Biology 15, No. 6: 1568-1574.

Leopold, R.A. 1949. A Sand County Almanac and Sketches Here and There. Oxford University Press. 226 pp.

Levine, J. M.; P. B. Adler; S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7 (10):975-989.

Mack, M. C.; C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology and Evolution 13:195-198.

Mack, R. N.; J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757-773.

Maron J.; M. Marler, 2007. Native plant diversity resists invasion at both low and high resource levels. Ecology 88 (10):2651-2661.

Marrs, R.; R. Hufbauer; J. Vivanco; H. Bais. 2003. The effects of hybridization and introgression on allelopathy in invasive *Centaurea* species. Ecological Society of America, 88th annual meeting abstracts:218.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471-477.

Pokorny, M. L.; R. L. Sheley; C. A. Zabinski; R. E. Engel; T. J. Svejcar; J. J. Bokorski. 2005. Plant functional group diversity as a mechanism for invasion resistance. Restoration Ecology 13:448-459.

Reinhart, K. O.; R. M. Callaway. 2006. Soil biota and invasive plants. New Phytologist 170 (3):445-457.

Renne, I. J.;B. F. Tracy; I. A. Colonna. 2006. Shifts in grassland invasibility: Effects of soil resources, disturbance, composition, and invader size. Ecology 87 (9):2264-2277.

Rinella, M. J.; M. L. Pokorny; R. Rekaya. 2007. Grassland invader responses to realistic changes in native species richness. Ecological Applications 17 (6):1824-1831.

Schofield, E. K. 1989. Effects of introduced plants and animals on island vegetation: examples from the Galapagos Archipelago. Conservation Biology 3 (3):227-238.

Seastedt, T. R.; K. N. Suding. 2007. Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. Oecologia 151 (4):626-636.

Sheley, R. L.; B. E. Olson; L. L. Larson. 1997. Effect of weed seed rate and grass defoliation level on diffuse knapweed. Journal of Range Management 50:39-43.

Talbott, C. J. 1987. Distribution and ecologic amplitude of selected *Centaurea* species in eastern Washington. Thesis (M.S) Pullman, WA: Washington State University.

Thomsen, M. A.; C. M. D'Antonio. 2007. Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability and environmental gradients. Oikos 116 (1):17-30.

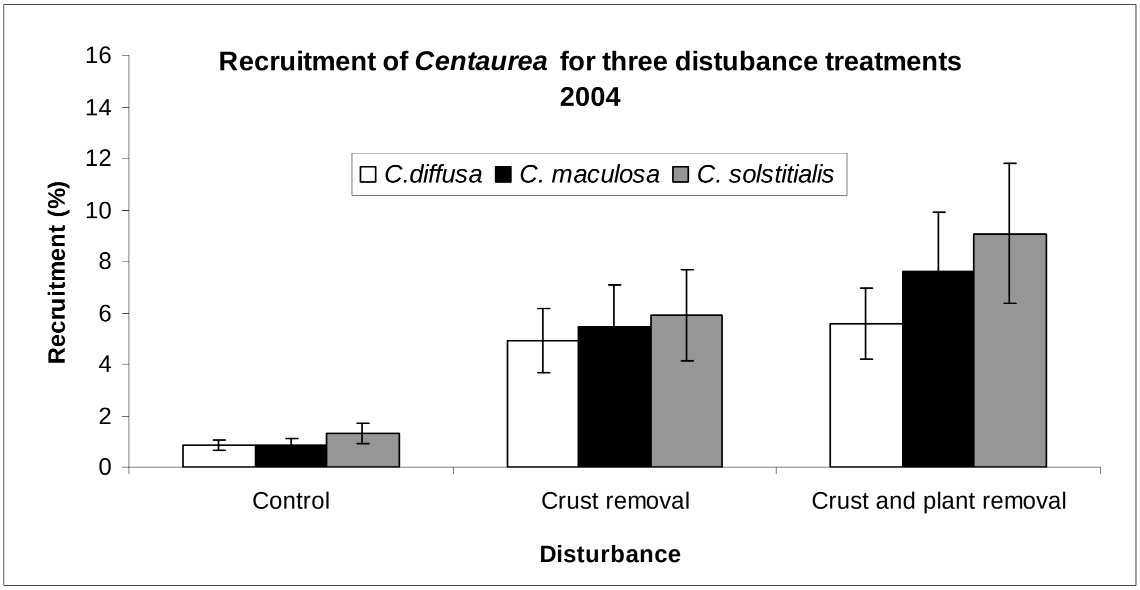
Tyser, R. W.; C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. Northwest Science 62:151-160.

Vitousek, P. M. 1986. Biological invasions and ecosystem properties: can species make a difference? In: H. A. Mooney; J. A. Drake (editors) Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York, NY:163-176.

Washington Department of Natural Resources. 2003. State of Washington Natural Heritage Plan; 64 pp. Olympia, WA.

Watts, W. A.; J. P. Bradbury. 1982. Paleo ecological studies at Lake Patzcuaro on the west central Mexican Plateau and at Chalco in the Basin of Mexico. Quaternary Research 17 (1):56-70.

**Figure 2.1.** Recruitment for three species of *Centaurea* across three disturbance regimes for 2004 and 2005. Bars represent means of a treatment for a species across nine habitat types. Habitat type means were from 3 plots for each species within a stand and each plot was sowed with 40 seeds. Error bars represent one standard error above and below the mean.


Recruitment of *Centaurea* for three distubance treatments
2004
☐ *C.diffusa* ■ *C. maculosa* ▨ *C. solstitialis*
Recruitment (%)
16
14
12
10
8
6
4
2
0
Control
Crust removal
Crust and plant removal
Disturbance

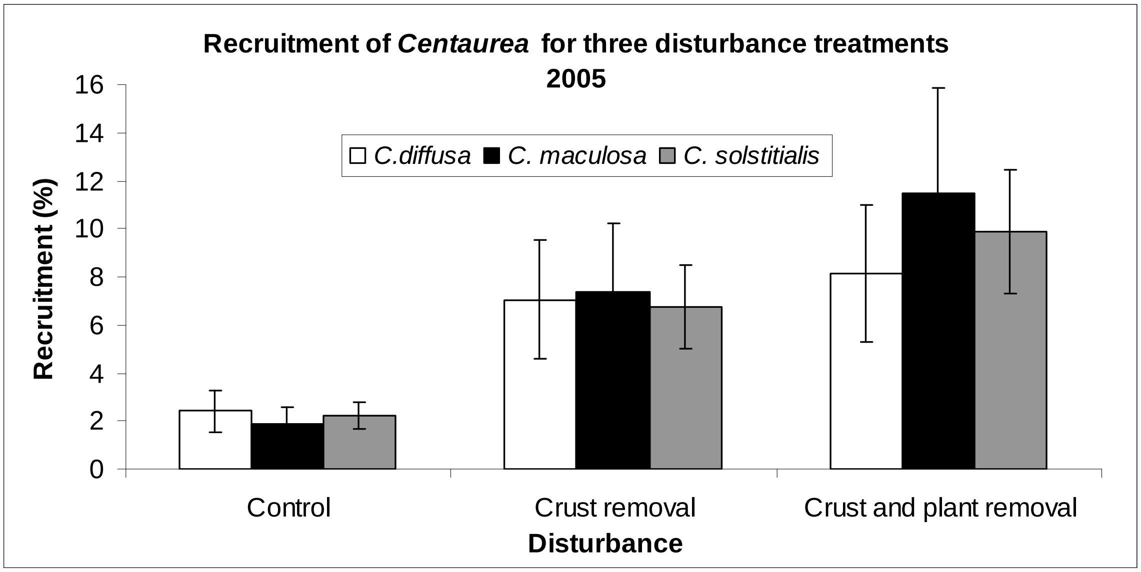
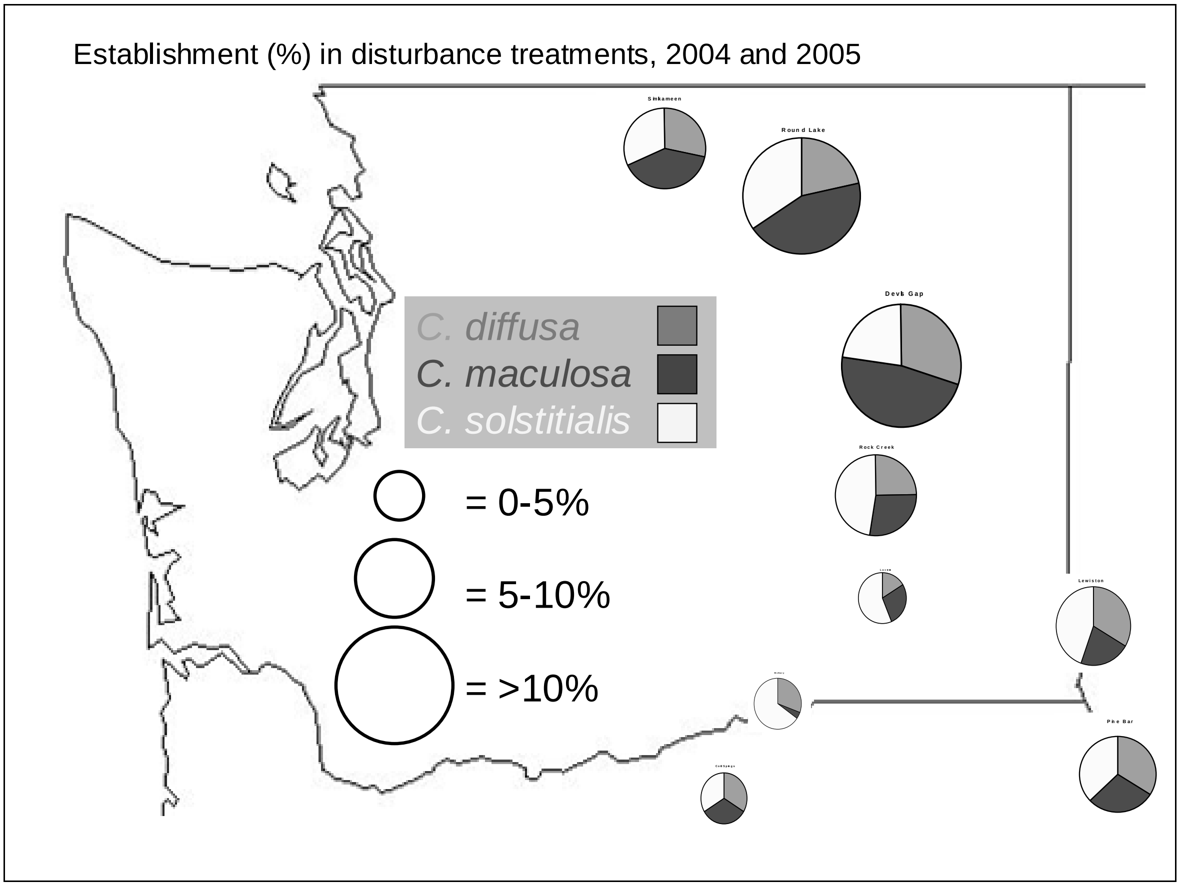

Recruitment of *Centaurea* for three disturbance treatments
2005
☐ *C.diffusa* ■ *C. maculosa* ▨ *C. solstitialis*
Recruitment (%)
16
14
12
10
8
6
4
2
0
Control
Crust removal
Crust and plant removal
Disturbance

**Figure 2.2.** Each pie chart represents data from a single stand. The three small pie charts represent stands where the mean establishment rate across both disturbance treatments and all three species was five percent or less. From top to bottom on the figure the small pie charts are from *Agropyron spicatum/ Festuca idahoensis, Agropyron spicatum/ Poa secunda,* and *Artemisia tridentata/ Agropyron spicatum* habitat types respectively. The four medium sized pie charts represent stands where the mean establishment rate across both disturbance treatments and all three species was between five and ten percent. From top to bottom on the figure the medium pie charts are from *Artemisia tridentata/ Stipa comata, Artemisia tripartita/ Festuca idahoensis, Festuca idahoensis/ Symphoricarpos albus,* and *Aristida longiseta/ Poa secunda* habitat types respectively. The two large pie charts represent stands where the mean establishment rate across both disturbance treatments and all three species was greater than ten percent. The upper large pie chart is from a *Pinus ponderosa/ Festuca idahoensis* habitat type and the lower large pie chart is from a *Purshia tridentata/ Festuca idahoensis* habitat type. Within each pie chart, the relative proportion of established plants from each species for that stand is represented by shading; the light grey represents *C. diffusa,* the dark grey represents *C. maculosa,* and the white represents *C. solstitialis.*



Establishment (%) in disturbance treatments, 2004 and 2005

**Figure 2.3.** Recruitment of *Centaurea diffusa* in 2004 plotted against mean April, May, and June accumulative precipitation. Data points are means of disturbance treatments within a stand for a habitat type. From left to right on the chart, data points are from the following habitat types respectively: 1) *Agropyron spicatum/ Poa secunda*, 2) *Artemisia tridentata/ Agropyron spicatum*, 3) *Agropyron spicatum/ Festuca idahoensis*, 4) *Artemisia tridentata/ Stipa comata*, 5) *Artemisia tripartita/ Festuca idahoensis*, 6) *Festuca idahoensis/ Symphoricarpos albus*, 7) *Purshia tridentata/ Festuca idahoensis*, 8) *Pinus ponderosa, Festuca idahoensis*, and 9) *Aristida longiseta/ Poa secunda*. Recruitment was positively correlated with precipitation ($r^2 = 0.34$). Each data point represents the mean recruitment percentage of 40 seeds in each of 6 plots.

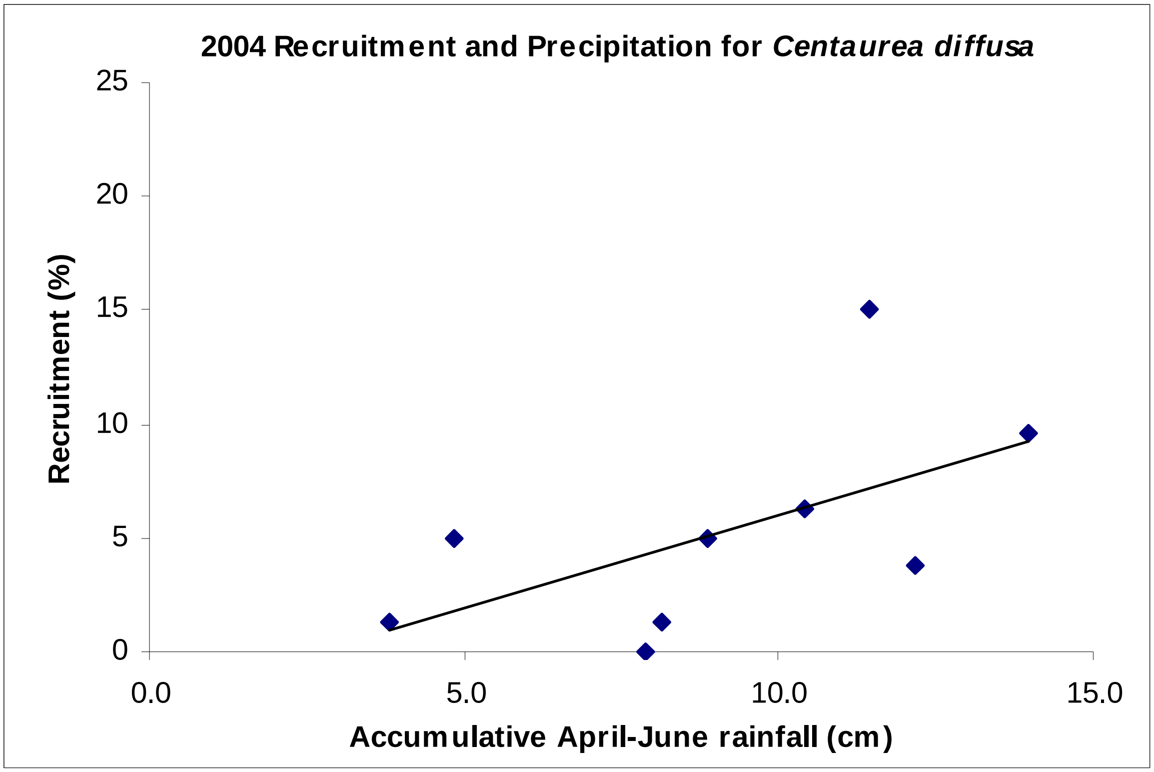

2004 Recruitment and Precipitation for *Centaurea diffusa*
Recruitment (%)
25
20
15
10
5
0
0.0
5.0
10.0
15.0
Accumulative April-June rainfall (cm)

**Figure 2.4.** Recruitment of *Centaurea diffusa* in 2005 plotted against mean April, May, and June accumulative precipitation. Data points are means of disturbance treatments within a stand for a habitat type. From left to right on the chart, data points are from the following habitat types respectively: 1) *Agropyron spicatum/ Poa secunda*, 2) *Artemisia tridentata/ Agropyron spicatum*, 3) *Agropyron spicatum/ Festuca idahoensis*, 4) *Artemisia tridentata/ Stipa comata*, 5) *Artemisia tripartita/ Festuca idahoensis*, 6) *Festuca idahoensis/ Symphoricarpos albus*, 7) *Purshia tridentata/ Festuca idahoensis*, 8) *Pinus ponderosa*, *Festuca idahoensis*, and 9) *Aristida longiseta/ Poa secunda*. Recruitment was positively correlated with precipitation ($r^2 = 0.55$). Each data point represents the mean recruitment percentage of 40 seeds in each of 6 plots.

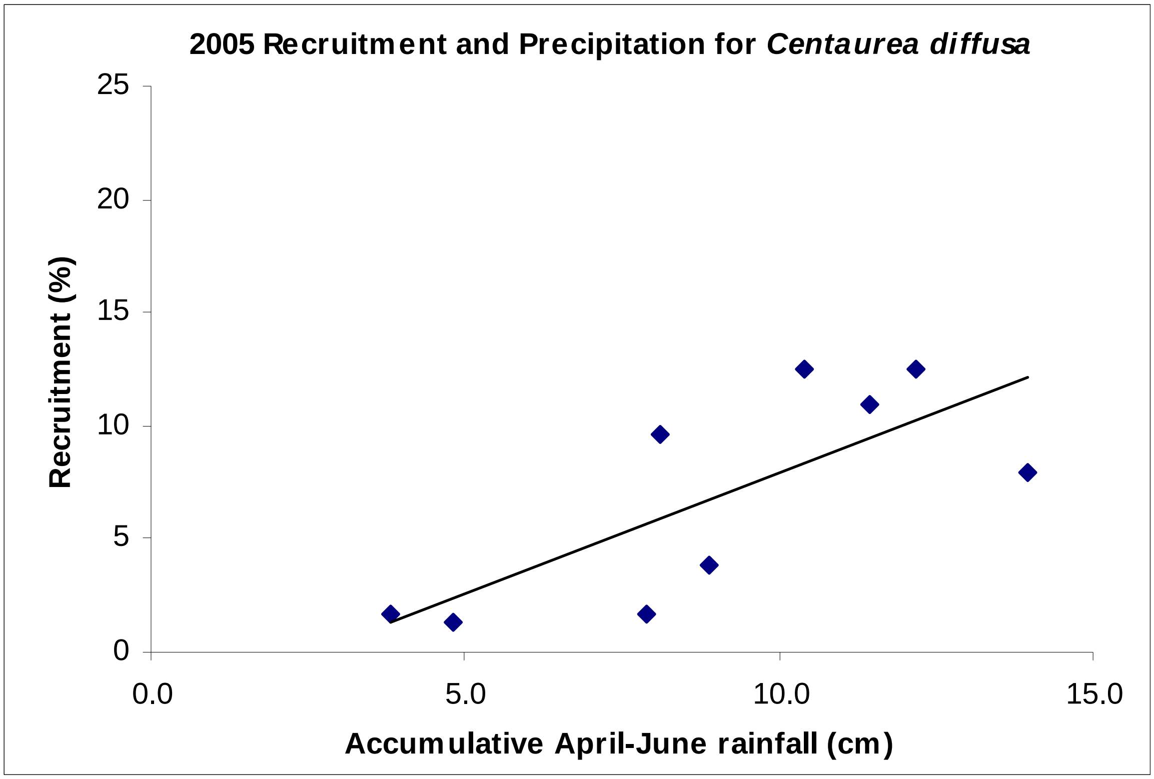
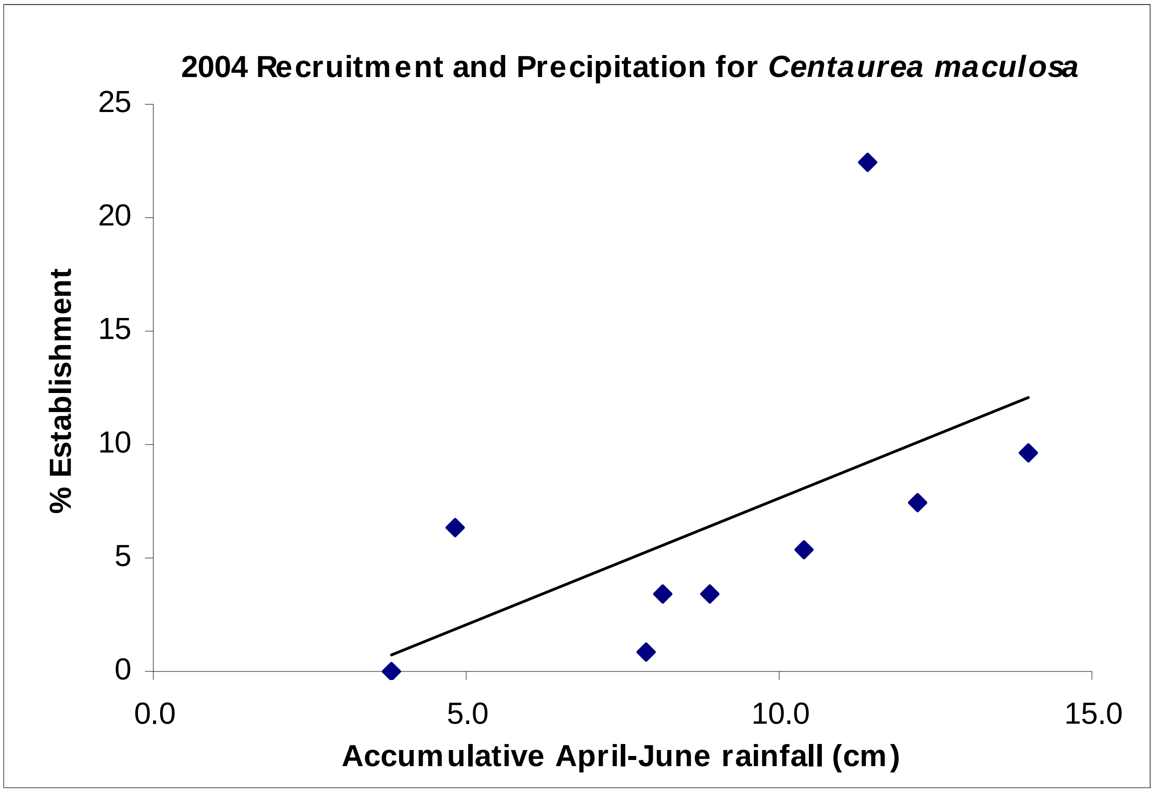

2005 Recruitment and Precipitation for *Centaurea diffusa*
Recruitment (%)
25
20
15
10
5
0
0.0
5.0
10.0
15.0
Accumulative April-June rainfall (cm)

**Figure 2.5.** Recruitment of *Centaurea maculosa* in 2004 plotted against mean April, May, and June accumulative precipitation. Data points are means of disturbance treatments within a stand for a habitat type. From left to right on the chart, data points are from the following habitat types respectively: 1) *Agropyron spicatum/ Poa secunda*, 2) *Artemisia tridentata/ Agropyron spicatum*, 3) *Agropyron spicatum/ Festuca idahoensis*, 4) *Artemisia tridentata/ Stipa comata*, 5) *Artemisia tripartita/ Festuca idahoensis*, 6) *Festuca idahoensis/ Symphoricarpos albus*, 7) *Purshia tridentata/ Festuca idahoensis*, 8) *Pinus ponderosa, Festuca idahoensis*, and 9) *Aristida longiseta/ Poa secunda*. Recruitment was positively correlated with precipitation ($r^2 = 0.31$). Each data point represents the mean recruitment percentage of 40 seeds in each of 6 plots.



2004 Recruitment and Precipitation for *Centaurea maculosa*
% Establishment
25
20
15
10
5
0
0.0
5.0
10.0
15.0
Accumulative April-June rainfall (cm)

**Figure 2.6.** Recruitment of *Centaurea maculosa* in 2005 plotted against mean April, May, and June accumulative precipitation. Data points are means of disturbance treatments within a stand for a habitat type. From left to right on the chart, data points are from the following habitat types respectively: 1) *Agropyron spicatum/ Poa secunda*, 2) *Artemisia tridentata/ Agropyron spicatum*, 3) *Agropyron spicatum/ Festuca idahoensis*, 4) *Artemisia tridentata/ Stipa comata*, 5) *Artemisia tripartita/ Festuca idahoensis*, 6) *Festuca idahoensis/ Symphoricarpos albus*, 7) *Purshia tridentata/ Festuca idahoensis*, 8) *Pinus ponderosa, Festuca idahoensis*, and 9) *Aristida longiseta/ Poa secunda*. Recruitment was positively correlated with precipitation ($r^2$ = 0.36). Each data point represents the mean recruitment percentage of 40 seeds in each of 6 plots.

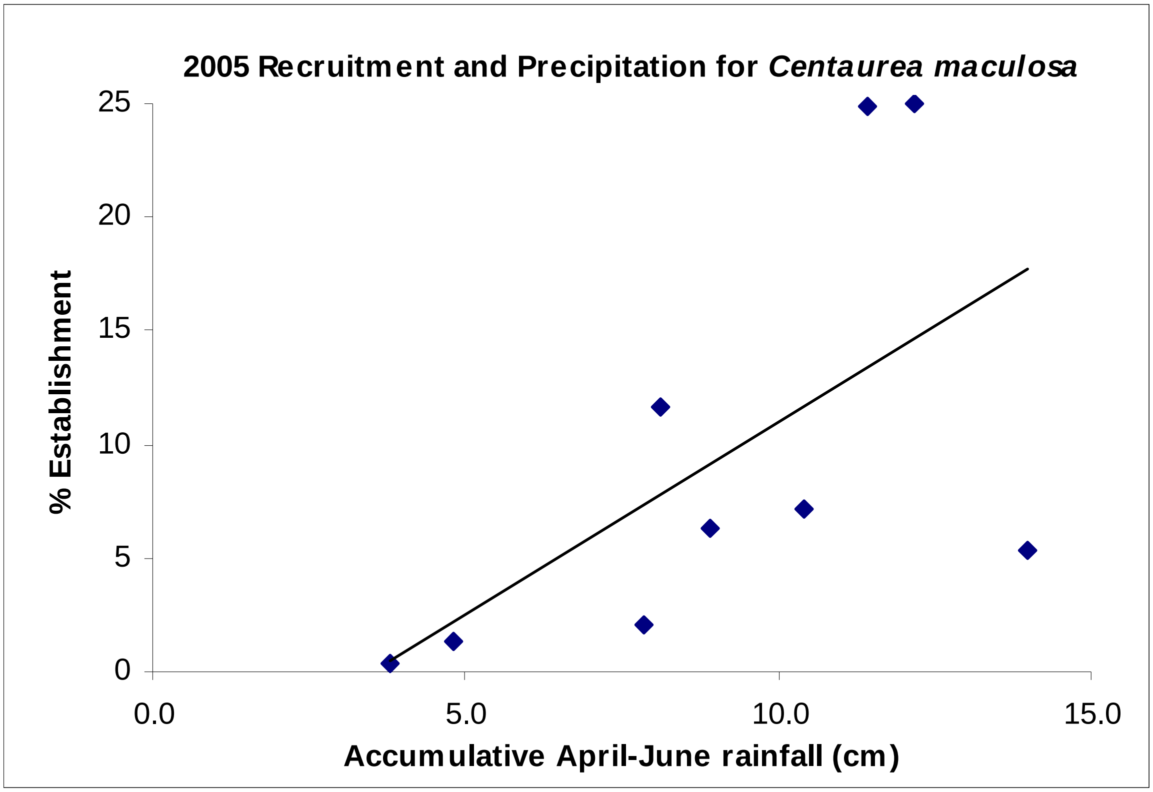

2005 Recruitment and Precipitation for *Centaurea maculosa*
% Establishment
25
20
15
10
5
0
0.0
5.0
10.0
15.0
Accumulative April-June rainfall (cm)

**Figure 2.7.** Recruitment of *Centaurea solstitialis* in 2004 plotted against mean April, May, and June accumulative precipitation. Data points are means of disturbance treatments within a stand for a habitat type. From left to right on the chart, data points are from the following habitat types respectively: 1) *Agropyron spicatum/ Poa secunda*, 2) *Artemisia tridentata/ Agropyron spicatum*, 3) *Agropyron spicatum/ Festuca idahoensis*, 4) *Artemisia tridentata/ Stipa comata*, 5) *Artemisia tripartita/ Festuca idahoensis*, 6) *Festuca idahoensis/ Symphoricarpos albus*, 7) *Purshia tridentata/ Festuca idahoensis*, 8) *Pinus ponderosa, Festuca idahoensis*, and 9) *Aristida longiseta/ Poa secunda*. Recruitment was positively correlated with precipitation ($r^2 = 0.49$). Each data point represents the mean recruitment percentage of 40 seeds in each of 6 plots.

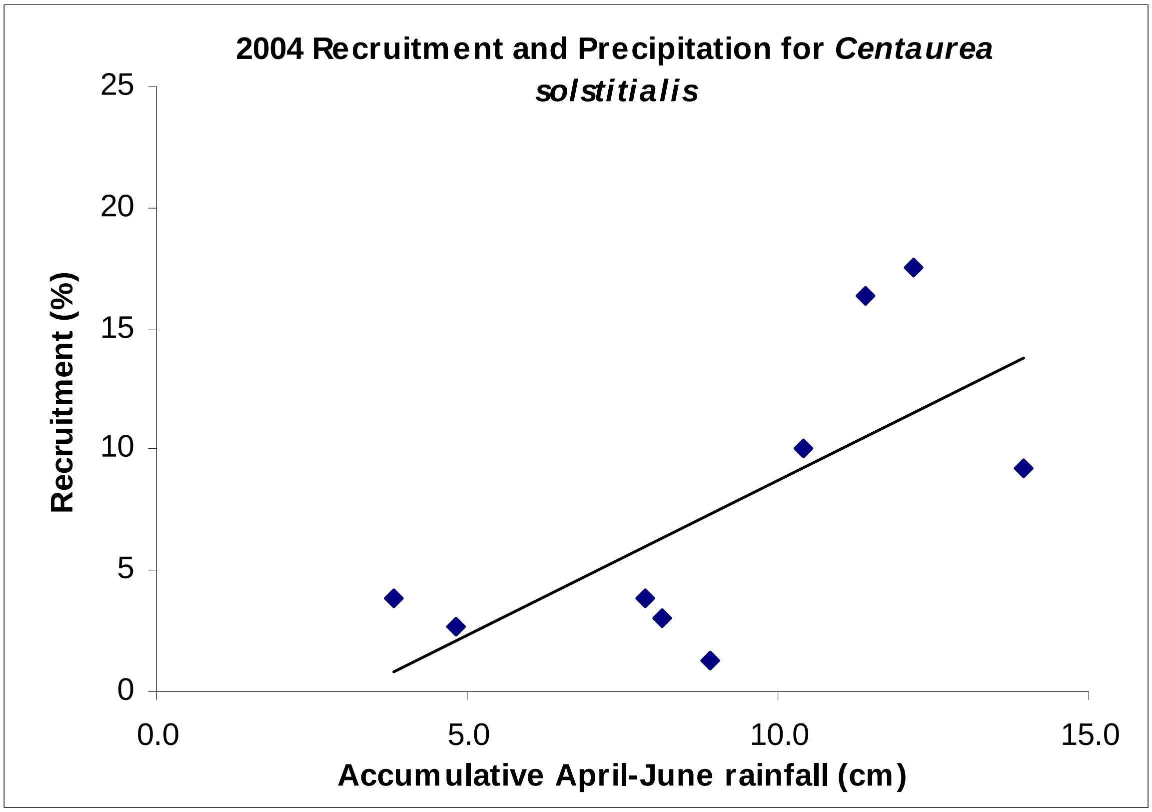

2004 Recruitment and Precipitation for *Centaurea solstitialis*
Recruitment (%)
0
5
10
15
20
25
0.0
5.0
10.0
15.0
Accumulative April-June rainfall (cm)

**Figure 2.8.** Recruitment of *Centaurea solstitialis* in 2005 plotted against mean April, May, and June accumulative precipitation. Data points are means of disturbance treatments within a stand for a habitat type. From left to right on the chart, data points are from the following habitat types respectively: 1) *Agropyron spicatum/ Poa secunda*, 2) *Artemisia tridentata/ Agropyron spicatum*, 3) *Agropyron spicatum/ Festuca idahoensis*, 4) *Artemisia tridentata/ Stipa comata*, 5) *Artemisia tripartita/ Festuca idahoensis*, 6) *Festuca idahoensis/ Symphoricarpos albus*, 7) *Purshia tridentata/ Festuca idahoensis*, 8) *Pinus ponderosa, Festuca idahoensis*, and 9) *Aristida longiseta/ Poa secunda*. Recruitment was positively correlated with precipitation ($r^2 = 0.26$). Each data point represents the mean recruitment percentage of 40 seeds in each of 6 plots.

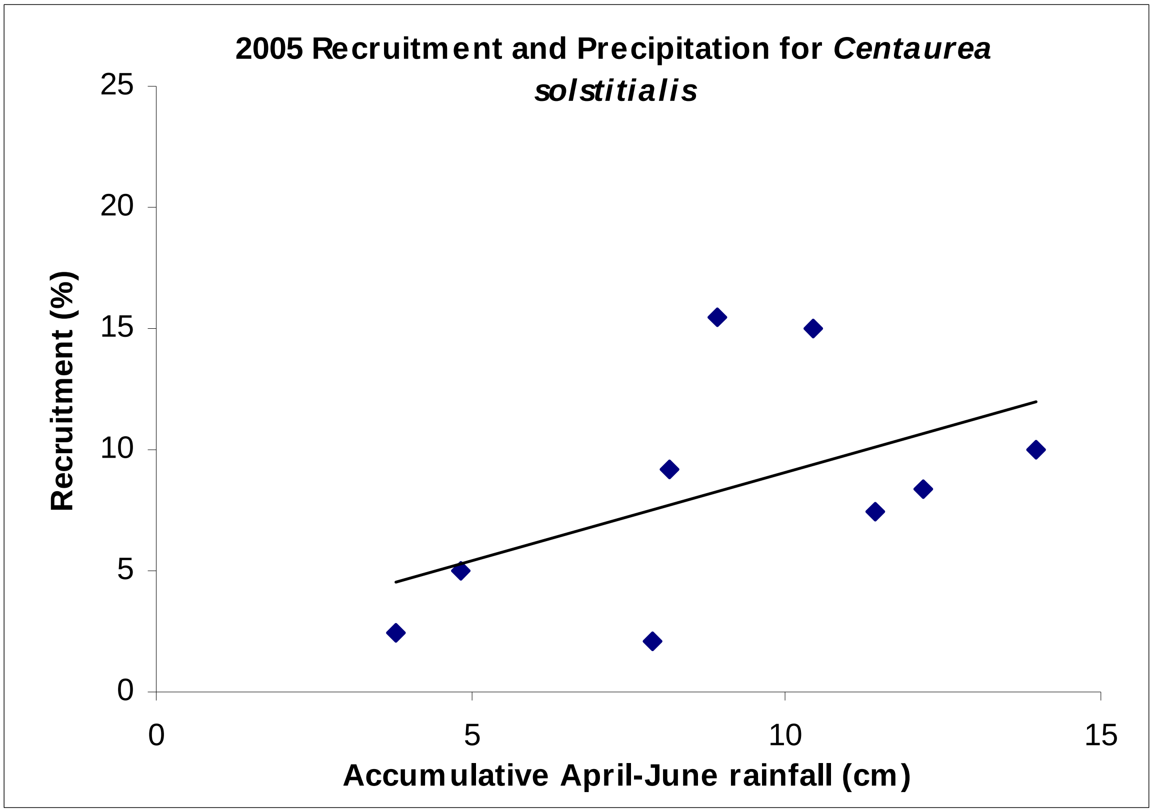

2005 Recruitment and Precipitation for *Centaurea solstitialis*
Recruitment (%)
25
20
15
10
5
0
0
5
10
15
Accumulative April-June rainfall (cm)

**Figure 2.9.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Festuca idahoensis/ Symphoricarpos albus* south of Uniontown, WA. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

*Festuca idahoensis/ Symphoricarpos albus* habitat type

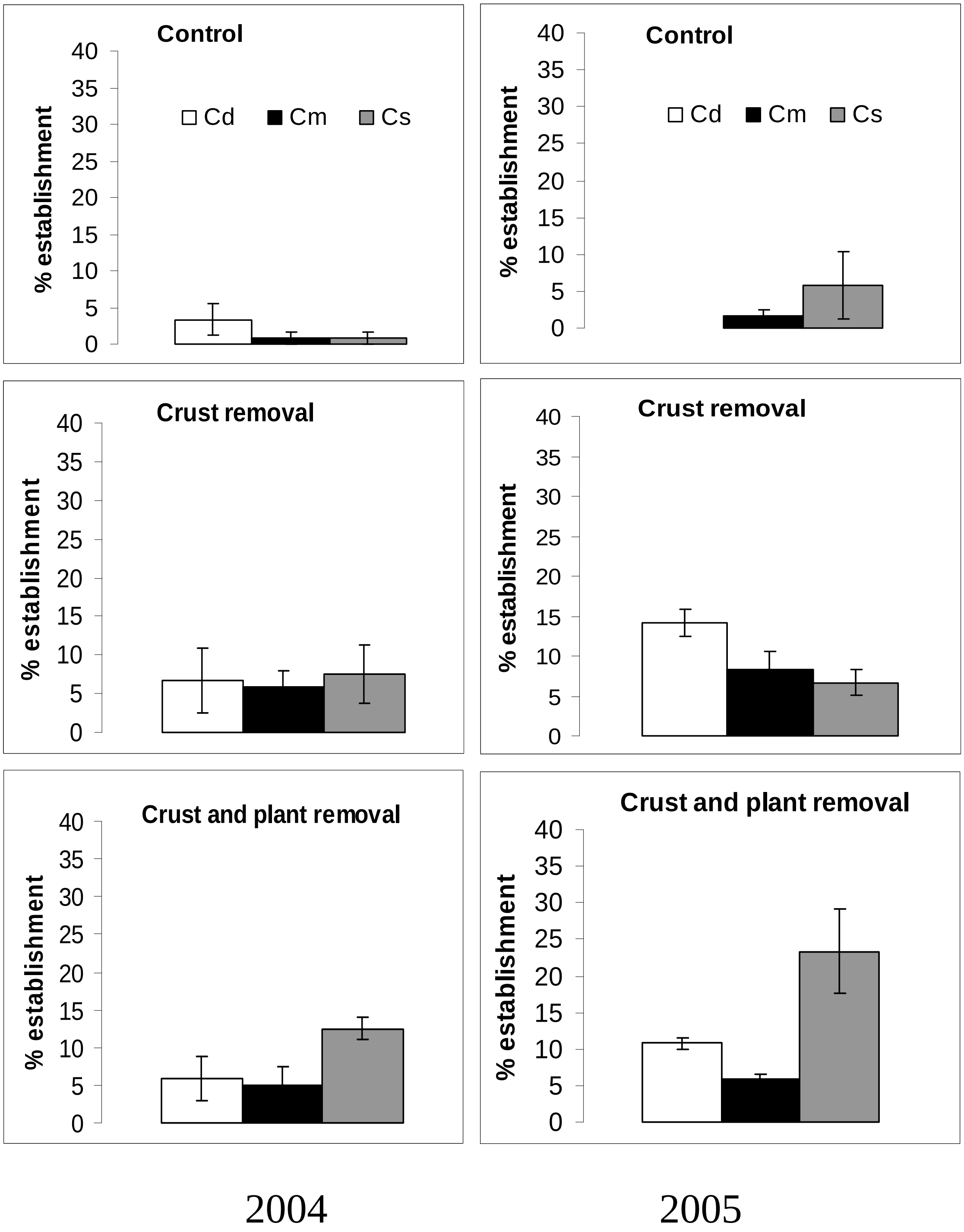


**Figure 2.10.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Agropyron spicatum/ Festuca idahoensis* near La Crosse, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

## *Agropyron spicatum/ Festuca idahoensis* habitat type

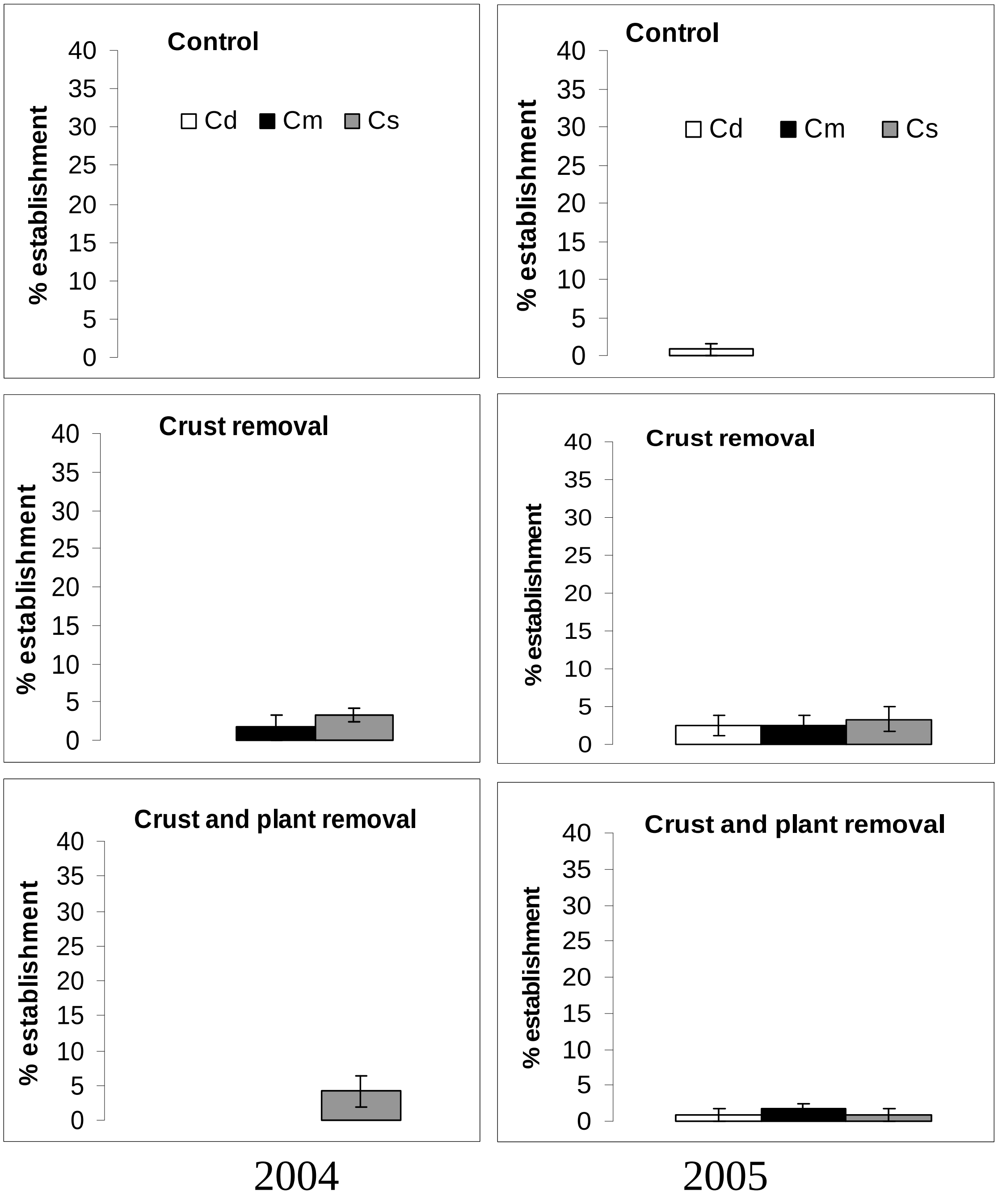


**Figure 2.11.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Agropyron spicatum/ Poa secunda* at McNary National Wildlife Refuge near Wallula, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

## *Agropyron spicatum/ Poa secunda* habitat type

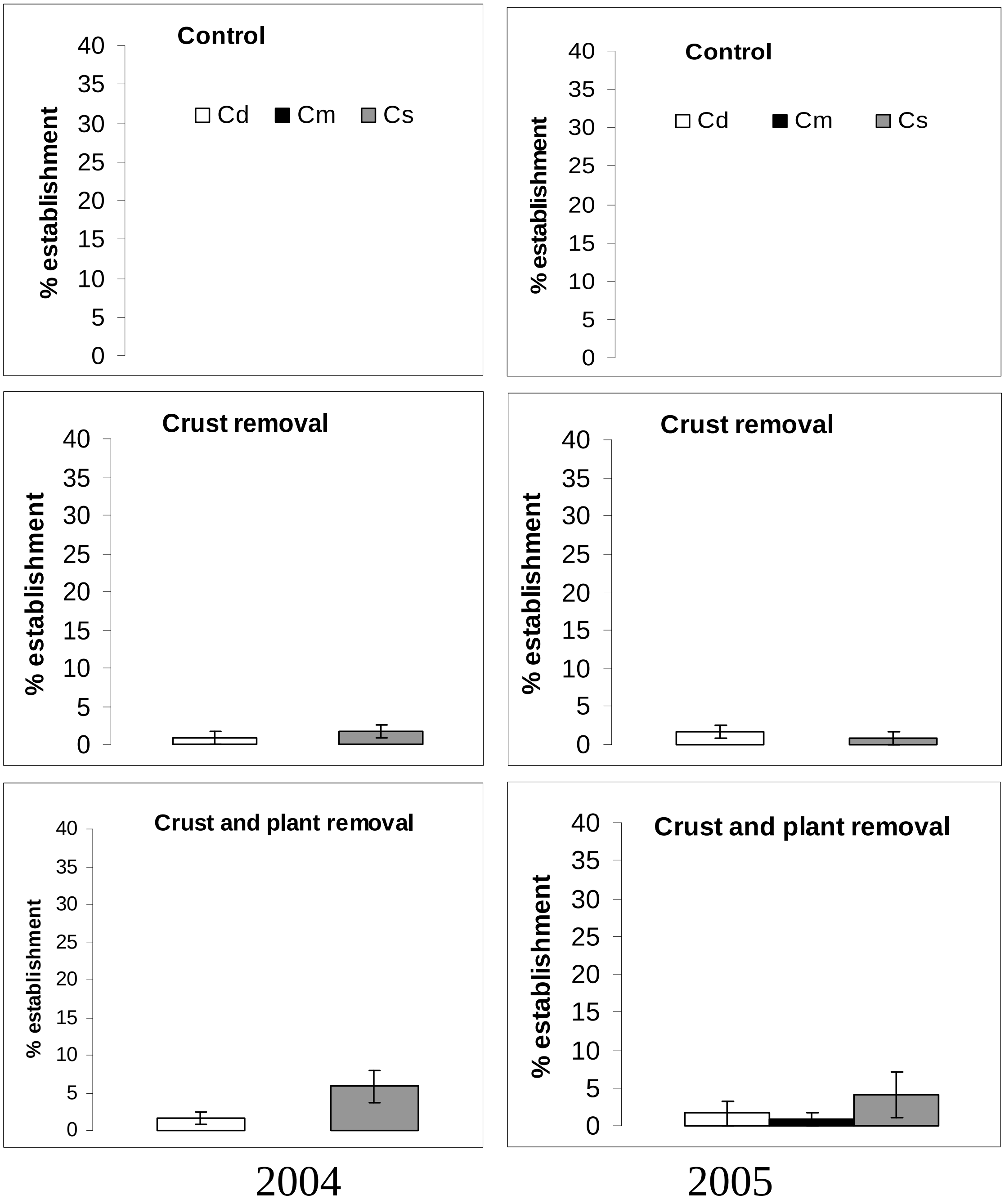


**Figure 2.12.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Artemisia tridentata/ Agropyron spicatum* at Cold Springs National Wildlife Refuge east of Hermiston, OR. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

*Artemisia tridentata/ Agropyron spicatum* habitat type

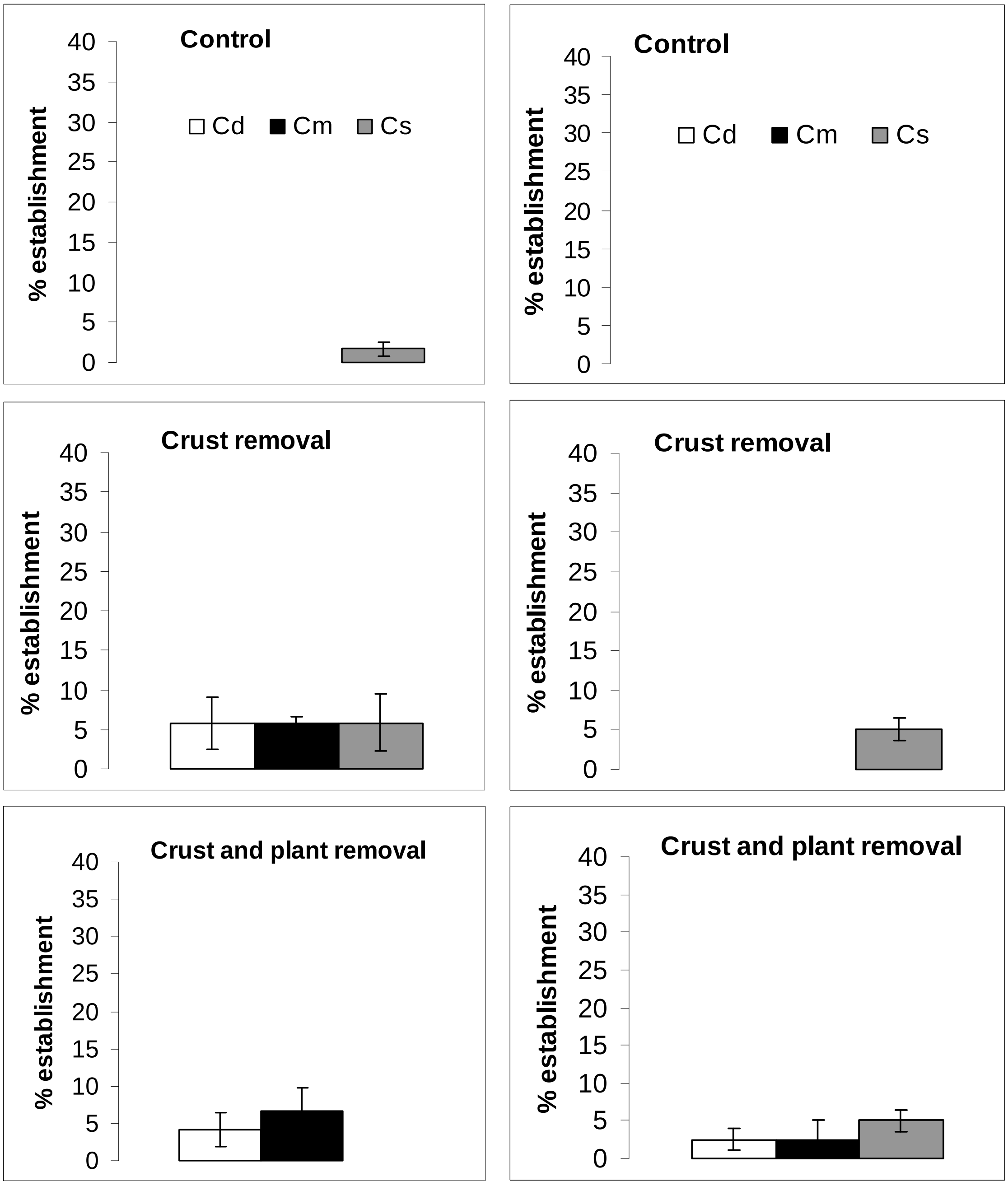


**Figure 2.13.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Artemisia tripartita/ Festuca idahoensis* near Rock Creek west of Winona, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

*Artemisia tripartita/ Festuca idahoensis* habitat type

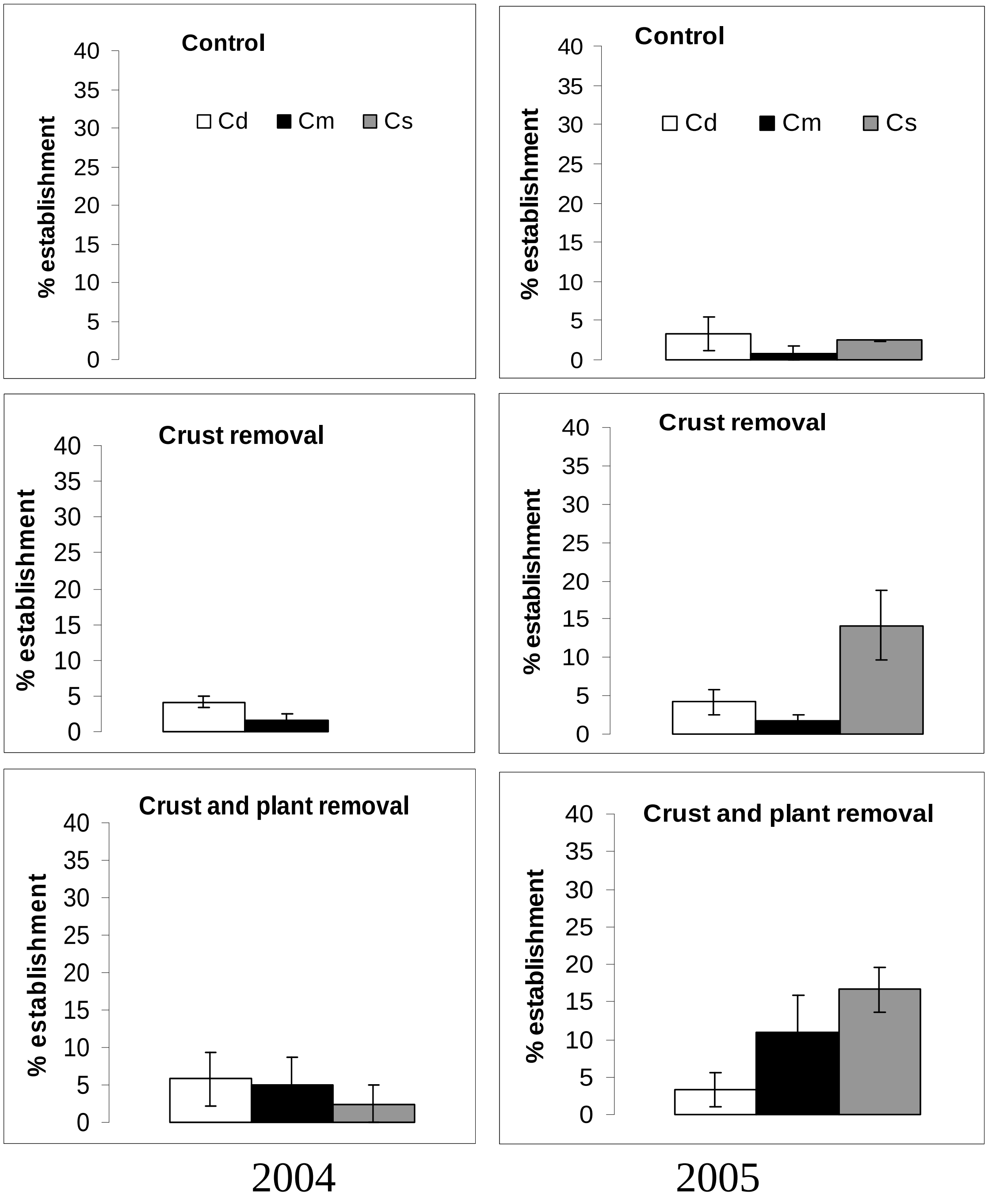


**Figure 2.14.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Purshia tridentata/ Festuca idahoensis* at Devil's Gap Recreation Area south of Long Lake, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

*Purshia tridentata/ Festuca idahoensis* habitat type

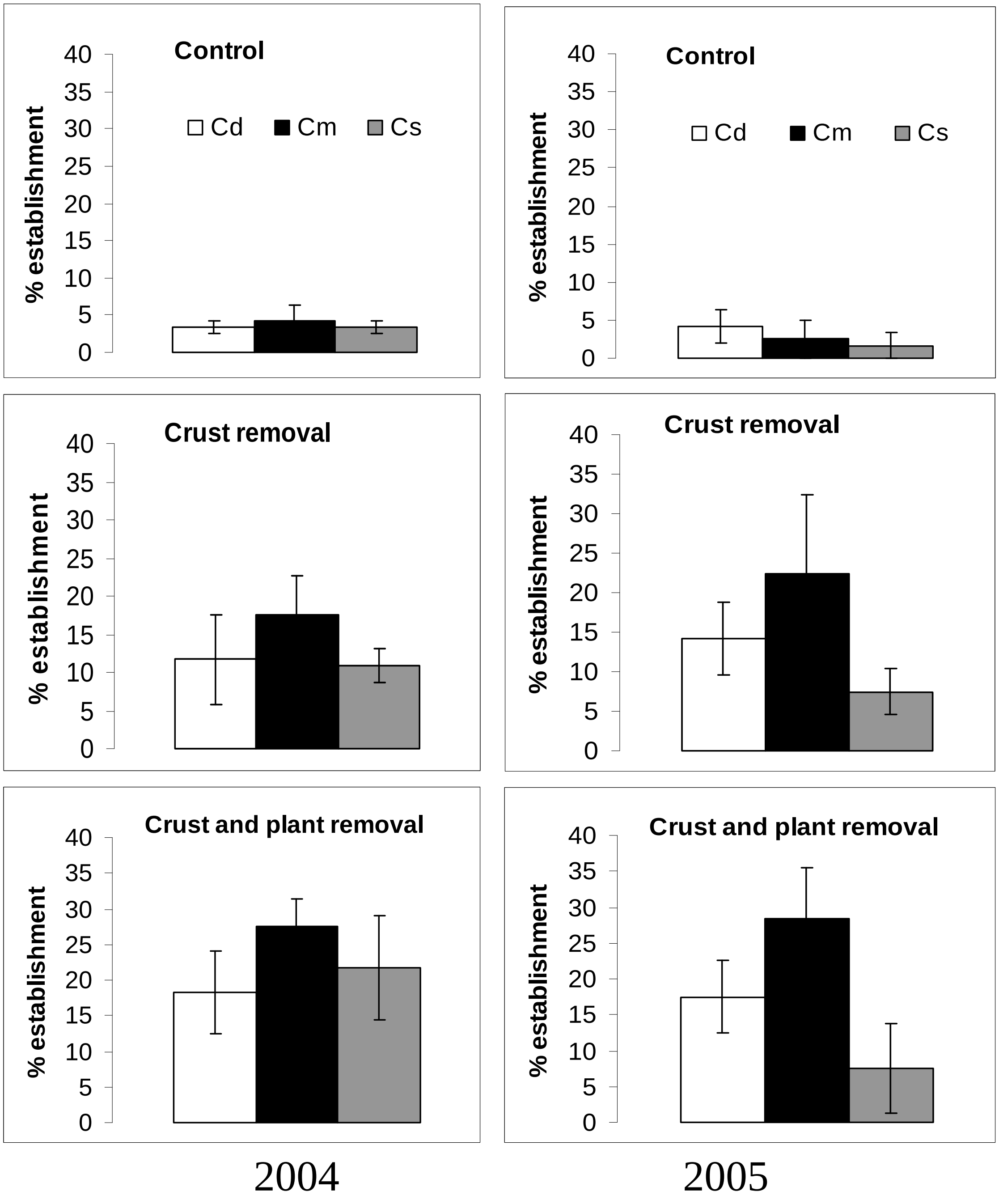


**Figure 2.15.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Pinus ponderosa/ Festuca idahoensis* near Round Lake, east of Tonasket, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

*Pinus ponderosa/ Festuca idahoensis* habitat type

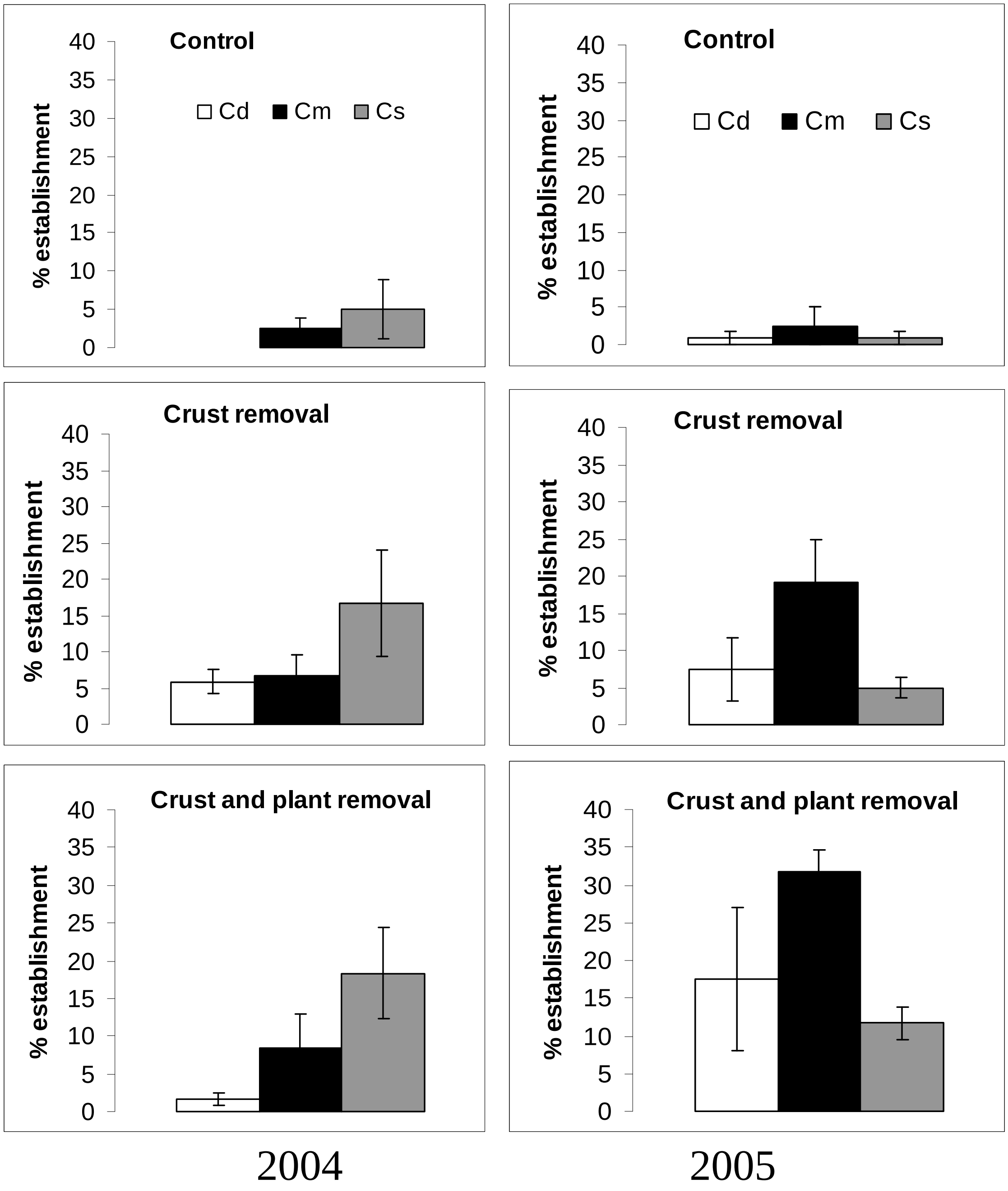


**Figure 2.16.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Artemisia tridentata/ Stipa comata* near the Similkameen River, northwest of Oroville, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

*Artemisia tridentata/ Stipa comata* habitat type

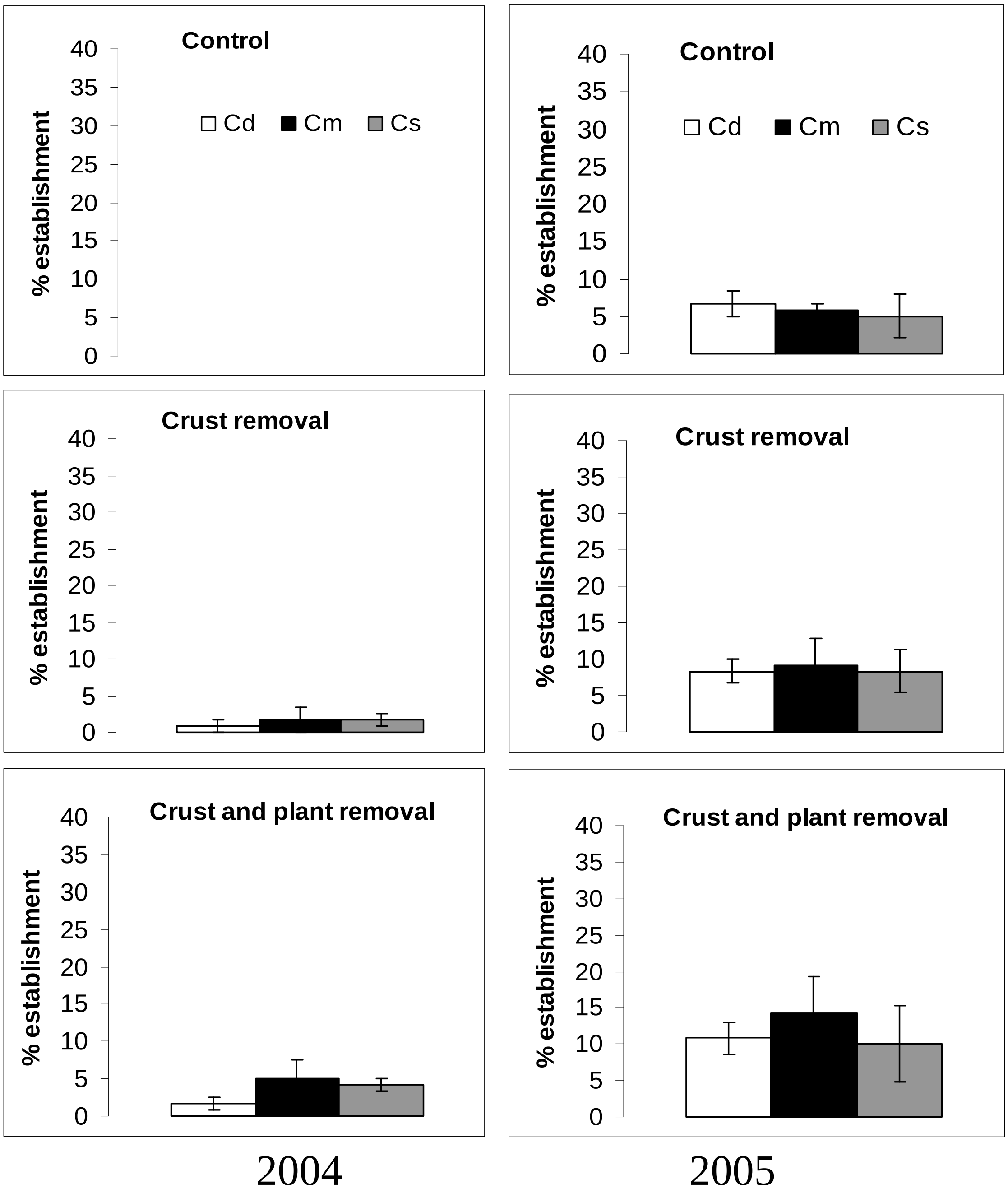
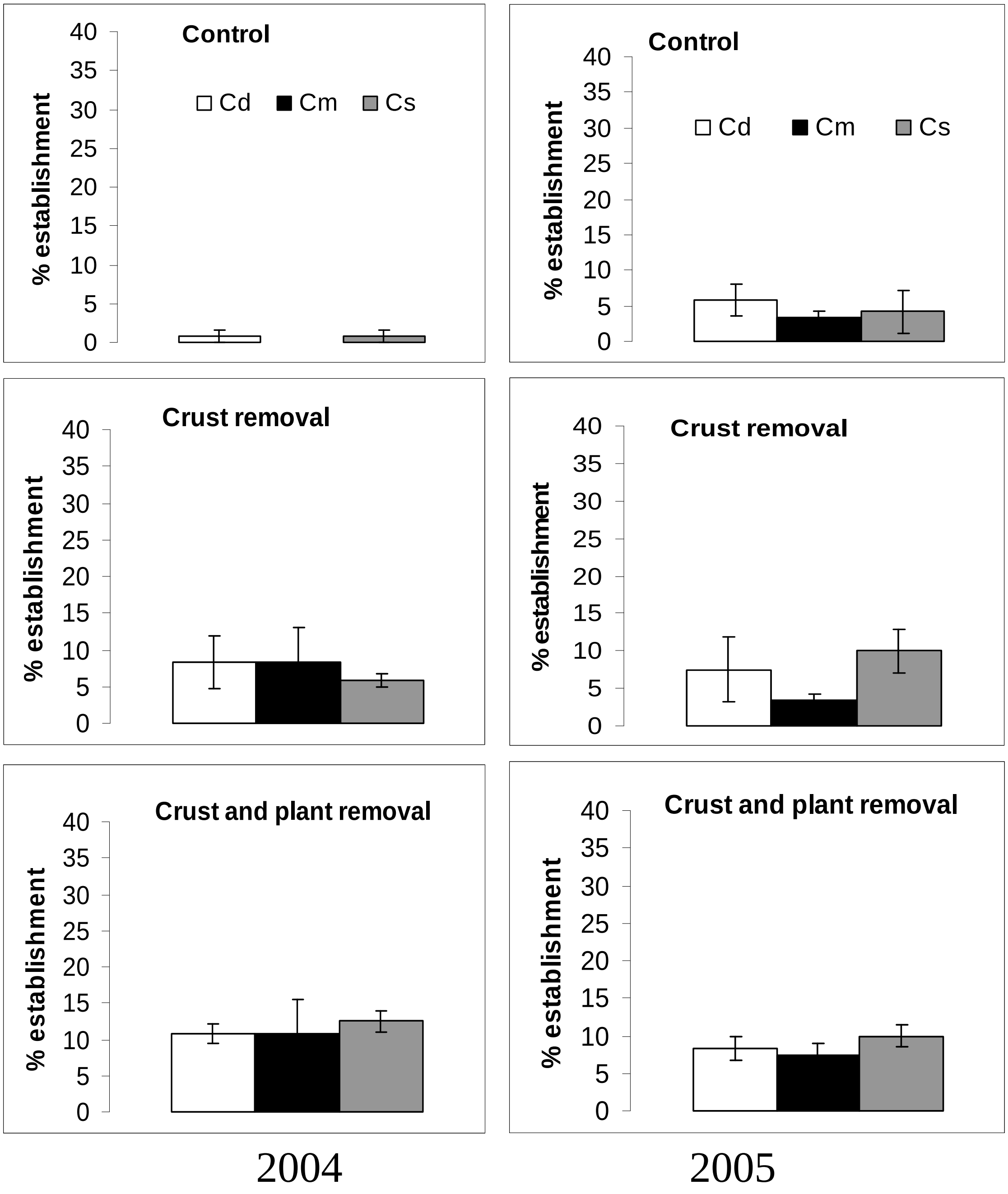


**Figure 2.17.** Recruitment of *Centaurea diffusa* (Cd, open bars), *Centaurea maculosa* (Cm, black bars), and *Centaurea solstitialis* (Cs, grey bars) in a stand of *Aristida longiseta/ Poa secunda* at Pine Bar near Lucile, WA. Bars are absent where recruitment was zero. Bars represent percent recruitment out of 120 seeds. Stands were sub-sampled by sowing 40 seeds in each of 3 replicate plots per treatment per species for each year. Germination and survival through the seedling stage was considered an establishment event. Error bars are one standard error above and below the mean.

## *Aristida longiseta/ Poa secunda* habitat type



## Site Descriptions

| Habitat type | Location | Soil Type | Mean Annual Precipitation |
|---|---|---|---|
| *Agropyron spicatum / Festuca idahoensis* | 46° 47' 20" N, 117° 55' 00" W | Typic Haploxeroll | 36.2 cm |
| *Agropyron spicatum / Poa secunda* | 45° 53' 30" N, 119° 19' 40" W | Xeric Torriorthent | 19.8 cm |
| *Aristida longiseta / Poa secunda* | 46° 54' 30" N, 116° 22' 00" W | Lithic Haploxeroll | 50.8 cm |
| *Artemisia tridentata / Agropyron spicatum* | 45° 50' 50" N, 119° 10' 00" W | Xeric Torriorthent | 22.5 cm |
| *Artemisia tridentata / Stipa comata* | 48° 59' 10" N, 119° 35' 00" W | Lithic Haploxeroll | 28.9 cm |
| *Artemisia tripartita / Festuca idahoensis* | 47° 04' 30" N, 117° 56' 00" W | Lithic Haploxeroll | 39.0 cm |
| *Festuca idahoensis / Symphoricarpos albus* | 46° 28' 30" N, 117° 02' 10" W | Lithic Haploxeroll | 45.7 cm |
| *Pinus ponderosa / Festuca idahoensis* | 48° 36' 30" N, 119° 07' 20" W | Typic Haploxeroll | 36.3 cm |
| *Purshia tridentata / Festuca idahoensis* | 47° 49' 40" N, 117° 51' 00" W | Vitrandic Haploxeroll | 48.1 cm |

**Table 2.1.** Habitat type, location, soil type, and mean annual precipitation for field sites

## ANOVA for 2004

| Factor | DF | SS | Mean Square | F-value | P-value |
|---|---|---|---|---|---|
| Disturbance | 2 | 583.8 | 291.9 | 11.1 | < 0.0001 |
| Species | 2 | 37.52 | 18.76 | 0.713 | 0.4934 |
| Disturbance * Species | 4 | 24.62 | 6.16 | 0.234 | 0.9183 |

**Table 2.2.** Analysis of variance for the effects of experimental factors on recruitment of three species of *Centaurea* in 2004. Disturbance positively affected the probability of recruitment for all three species. *Centaurea* species did not differ in their response to disturbance nor did species interact with treatment.

### Fisher's PLSD for 2004

**Effect: Disturbance**

| Treatment | Mean Difference | Critical Difference | P-value |
|---|---|---|---|
| Control, Crust Removal | -4.44 | 2.78 | 0.0021 |
| Control, Crust and Plant Removal | -6.42 | 2.78 | < 0.0001 |
| Crust Removal, Crust and Plant Removal | -1.98 | 2.78 | 0.1613 |

**Table 2.3.** Fisher's protected Least Significant Difference for disturbance treatments in 2004. Both disturbance treatments positively affected probability of recruitment for all three *Centaurea* species. The effect of the crust removal treatment did not differ from the effect of the crust and plant removal treatment.

### ANOVA for 2005

| Factor | DF | SS | Mean Square | F-value | P-value |
|---|---|---|---|---|---|
| Disturbance | 2 | 817.7 | 408.9 | 10.8 | < 0.0001 |
| Species | 2 | 15.02 | 7.51 | 0.198 | 0.8207 |
| Disturbance * Species | 4 | 38.37 | 9.59 | 0.253 | 0.9069 |

**Table 2.4.** Analysis of variance for the effects of experimental factors on recruitment of three species of *Centaurea* in 2005. Disturbance positively affected the probability of recruitment for all three species. *Centaurea* species did not differ in their response to disturbance nor did species interact with treatment.

## Fisher's PLSD for 2005

**Effect: Disturbance**

| Treatment | Mean Difference | Critical Difference | P-value |
|---|---|---|---|
| Control, Crust Removal | -4.91 | 3.34 | 0.0046 |
| Control, Crust and Plant Removal | -7.69 | 3.34 | < 0.0001 |
| Crust Removal, Crust and Plant Removal | -2.78 | 3.34 | 0.1017 |

**Table 2.5.** Fisher's protected Least Significant Difference for disturbance treatments in 2005. Both disturbance treatments positively affected probability of recruitment for all three *Centaurea* species. The effect of the crust removal treatment did not differ from the effect of the crust and plant removal treatment.

# CHAPTER THREE

# ASSESSING RESOURCE COMPETITION THROUGH SPECIES REMOVALS: LEAF WATER POTENTIAL COMPARISONS BETWEEN *CENTAUREA* AND NATIVE GRASSES

## Introduction

As the Law of the Minimum (Sprengel 1837, Liebig 1840) predicts, the resource that limits growth for a plant community also is generally the limiting resource for individuals in that particular community. Consequently, interspecific competition for a common limiting resource often influences community composition (Casper and Jackson 1997) and the best competitor is the dominant species (Tilman 1987). A species that is not the superior competitor for the resource most limiting to community productivity may still dominate the plant community if it can utilize a resource supply that is inaccessible to the other members of the community (Hill et al. 2006, Kulmatiski et al. 2006).

Grasslands, and biomes dominated by grasses, including savannah, steppe and prairie, occupy almost 20 percent of Earth's terrestrial surface (Whittaker and Likens 1973, White et al. 2000) and occur where the timing and quantity of rainfall is unsuitable for tree seedling establishment (Daubenmire 1943). Perennial bunchgrasses, with the capacity for quiescence in times of drought or unfavorable conditions and a clumped growth habit, are highly adapted to arid and semi-arid environments because of their ability to survive intense radiation even when water is not available (Ryel et al. 1993).

Perennial grasses in the Columbia Basin Ecoregion complete their annual growth and reproduction in approximately 3 to 4 months but are physically present on the soil surface year round. Forbs are present in the native flora of Columbia Basin but never dominate resource use in upland plant associations (Daubenmire 1970). Also, native forbs are generally only active each year for the same amount of time as the native grasses which suggests they too are limited by water availability and either exhibit an annual habit or become dormant each year when soil water is not available to them. Grasses are generally the dominant species in the semiarid habitats of the Columbia Basin (Daubenmire 1970).

Biological soil crusts may cover half or more of the soil surface in grassland and steppe habitats (Kleiner and Harper 1977, Belnap and Lange 2001). Communities with less than 100% coverage by plants are generally limited in growth by water (Fowler 1986). *Centaurea* invasion into grass dominated communities often increases the leaf-area-index (LAI) of the community sometimes to the extent that *Centaurea* achieves 100% cover (Ridenour and Callaway 2001). The strong positive relationship between evapotranspiration and LAI in a community indicates that if invasion of *Centaurea* species leads to an increase in evapotranspiration then *Centaurea* species access water sources that are not accessed by the native community. Through experimental removal, biological soil crusts have been shown to provide resistance to establishment by *Centaurea* species in grass-dominated habitats of the Columbia Basin Ecoregion (Pankey, chapter 2). This lower rate of recruitment for *Centaurea* species on soils with undisturbed biological crusts may contribute to the relative scarcity of tap-rooted dominant species in the grasslands of the Columbia Basin. Grasslands in the

Intermountain Region of western North America are primarily composed of shallow rooted species (Jackson et al. 1996) so crust disturbance in these communities may remove the greatest impedance to establishment for drought avoiding (deep rooted) species like *Centaurea*.

The factors that affect the probability of establishment for *Centaurea* seedlings are not necessarily the same factors that affect the competitive ability of *Centaurea* adults (Seastedt and Suding 2007). *Centaurea diffusa*, *C. maculosa*, and *C. solstitialis* have persisted and have expanded their range in the Columbia Basin Ecoregion during the last three decades (Roche and Roche 1991) so the persistence and expansion of these populations should be affected more by their interactions with the perennial grasses (Williamson and Fitter 1996).

The consequences of competition for water include more negative leaf water potential and lower stomatal conductance (Fonteyn and Mahall 1978, Ehleringer 1993, Kirkham 2005). Stomatal conductance (G) and leaf water potential are positively correlated as are G and photosynthesis (Pugnaire and Haase 1996, Garcia et al. 2002), therefore measurement of a plant's leaf water potential can provide information about its current capacity for photosynthesis and growth.

The objectives of this study were to clarify the nature of resource competition between three non-indigenous *Centaurea* species and two native perennial grass species and to estimate mean rooting depths for each of these species. By selectively removing species from plots we quantified the effects of native grasses on the leaf water potential of *Centaurea* and of *Centaurea* on the leaf water potential of the native grasses.

I tested the hypotheses that 1) Native perennial grasses would not provide resistance to water acquisition by *Centaurea* species, and 2) that *Centaurea* would negatively affect the grasses leaf water potential compared to grasses growing where *Centaurea* had been experimentally removed.

## Methods

Three habitat types were selected in 2001 and 2002 within the Columbia Basin for examination of *Centaurea*. Three criteria were used for stand selection within each habitat type. First, stands were selected that contained the native plant associations found within that habitat type. Secondly, the sites were selected that were adjacent to *Centaurea* infestations and individuals of *Centaurea* occurred within the nearby native plant assemblages. Finally, stands were selected where the native perennial grasses occurred at similar density to stands nearby without *Centaurea* species present.

In three stands within each of three habitat types, twelve 3x3 meter plots were established and marked with unobtrusive pins. Four plots in each stand had all *Centaurea* removed, four plots in each stand had all native perennial grasses removed, and four plots in each stand contained both *Centaurea* and the native grasses which served as controls. Plants were carefully removed in the fall of each year. Perennial grass crowns were removed with a shovel taking care to minimize disturbance to the soil and adult *Centaurea* were either pulled by hand or the above ground tissue was clipped and the remaining taproots pulled. Sites were revisited in the winter and spring to hand-remove new seedlings that germinated. Three treatments were assigned to plots randomly.

In three of the nine stands (one stand within each habitat type), 24 individually calibrated screen-caged thermocouple psychrometers were installed in the soil during the fall prior to the spring data collection.  Twelve psychrometers were installed in soil that contained both *Centaurea* species and native grasses, and twelve were installed where *Centaurea* had been removed.  Eight cylindrical holes were dug at each site using a power auger and a six inch diameter bit.  Three 7-mm diameter holes were hand drilled into the side of each hole at the appropriate depths in the soil.  At the stand in the *Aristida longiseta/ Poa secunda* habitat type and at the stand in the *Artemisia tripartita/ Festuca idahoensis* habitat type the psychrometers were installed at 25-cm, 35-cm and 50-cm deep in the soil.  At the stand in the *Pinus ponderosa/ Festuca idahoensis* habitat type, psychrometers were installed at 30-cm, 50-cm, and 70-cm.  As suggested by Brown and Bartos (1982) the psychrometers were installed with a horizontal orientation in the soil rather than a vertical orientation to minimize the effects of thermal disequilibria in the soil due to diurnal solar heating.  Before backfilling each pit, 50 to 100 cm of each psychrometer's lead wire was coiled and buried to further reduce thermal disequilibria at the sensing junctions and so that the same length of wire was underground for each psychrometer.  Psychrometers were read using a Campbell Scientific CR-7 datalogger with cooling current modules attached.

The habitat types were visited in an order determined by the timing of the growing season, that is, *Pinus ponderosa/ Festuca idahoensis* was sampled earliest, followed by *Artemisia tripartita/ Festuca idahoensis* and then *Aristida longiseta/ Poa secunda*.  Leaf water potential measurements and stomatal conductance measurements were taken at each stand in a particular habitat type for three to four days before moving to the next habitat type. All stands were visited for two 3 to 4 day periods during May, June, and July each year with one period occurring early in the growing season and the other occurring later in the growing season. When possible, mid-day leaf water potentials were measured at 2 or 3 stands within a habitat type on a single day.

Leaf water potentials were measured at each time period for 3 plants of each species being examined within each plot using a Scholander-style pressure chamber using standard techniques (Tyree and Hammel 1972). Stomatal conductance was measured using a LICOR-1600 steady-state porometer (LiCOR Instruments, Lincoln, NE) with a closed, two square-centimeter leaf attachment. Comparisons of predawn leaf water potential and predawn soil water potential allow inference of the importance of different soil depths for water acquisition of each species. Comparisons of midday stomatal conductance (G) and predawn leaf water potential allowed us to assess differences between species in stomatal response to varying levels of water availability.

Treatment effects for each species were assessed through comparisons of midday leaf water potentials of each *Centaurea* species with and without grass competitors, and for the native grasses with and without the *Centaurea* competitors. ANOVA was performed for each site and for each year. Additionally, treatments are compared collectively (ANOVA) across species, sites, and years for both early growing season and late growing season.

## Results

*Centaurea* species maintained greater leaf water potentials than *Festuca idahoensis* and *Aristida longiseta* throughout the entire growing season (figures 3.1-3.3).

Midday leaf water potentials for *Centaurea* species ranged from -0.9 to -1.5 MPa before Julian day 160 (June 9) and from -1.0 to -2.7 MPa after Julian day 160 in 2004 and 2005. Midday leaf water potentials for native grasses ranged from -1.0 to -2.5 MPa before Julian day 160 (June 9) and from -1.1 to -4.5 MPa after Julian day 160.

Midday leaf water potentials for all three species of *Centaurea* growing with native grasses were not different than for the *Centaurea* in plots where grasses had been removed at any sample date for any site (figure 3.1-3.3, top panels). *Centaurea* species had a small effect on the midday leaf water potential of native grasses in the early part of the growing season (0.16 MPa mean difference, $p = 0.007$) but in the latter part of the growing season, midday leaf water potentials of native grasses growing with *Centaurea* were 0.70 MPa lower when compared to grasses in plots where *Centaurea* individuals had been removed ($p < 0.0001$) (figures 3.1-3.3, lower panels).

Native grasses experienced a greater range of midday leaf water potentials than *Centaurea* species both temporally and spatially (figures 3.1-3.3). This variability was more pronounced in the latter half of the growing season compared to the first half of the growing season.

*Centaurea* species maintained greater leaf water potentials despite greater transpiration rates than the grasses (figure 3.4). Predawn leaf water potentials for *Centaurea* ranged from -0.1 to -0.8 MPa (figure 3.5) whereas predawn leaf water potentials for native grasses (*Festuca idahoensis* and *Aristida longesita*) decreased from -0.1 to -1.6 MPa (figure 3.7) throughout the growing season. Midday stomatal conductance to water vapor for *Centaurea* ranged from 30 to 190 µmol $m^{-2}s^{-1}$ and midday stomatal conductance to water vapor for native grasses ranged from 15 to 70 µmol $m^{-2}s^{-1}$

(figure 3.4). The slope of the 90th percent quantile regression line for stomatal conductance plotted against predawn leaf water potential for *Centaurea* species is 250 µmol $m^{-2}s^{-1}$ per MPa increase in predawn leaf water potential compared to 35 µmol $m^{-2}s^{-1}$ per MPa for native grasses (figure 3.4).

The predawn leaf water potential of *Centaurea* was approximately equal to or less than the soil predawn water potential at all measured depths (figure 3.5). For the grasses growing in plots where *Centaurea* had been removed, predawn leaf water potential was below the 1:1 line at all 3 measured soil depths. The predawn leaf water potential of grasses growing without *Centaurea* was approximately equal to the predawn soil water potential at the 3 measured depths (figure 3.6). For the grasses growing with *Centaurea,* predawn leaf water potentials were lower and more variable than grass predawn leaf water potentials where *Centaurea* had been removed, for all but the shallowest soil depth (figure 3.7).

*Centaurea diffusa* had no measurable effect on predawn soil water potential at any soil depth throughout the growing season (Table 3.1). Plants of *Centaurea maculosa* lowered the predawn soil water potential at 30-cm depth (p=0.001, table 3.1) but had no measurable effect on soil water potential at 50-cm (p=0.187, table 3.1) or 70-cm (p=0.608, table 3.1) early in the season. However, *Centaurea maculosa* plants lowered predawn soil water potential at all measured soil depths in the latter half of the growing season (p<0.001, table 3.1). *Centaurea solstitialis* plants decreased the soil water potential at 25 and 35-cm depths early and late in the growing season (p<0.001, table 3.1), but had no measurable effect on soil water potential at 50-cm soil depth early (p=0.291, table 3.1) or late in the growing season (p=0.593, table 3.1).

Nocturnal patterns of hydraulic redistribution (Richards and Caldwell 1987, Caldwell et al. 1998) were evident late in the growing season where *C. maculosa* was present (figure A2, top panel). Hydraulic redistribution also occurred early and late in the growing season where *C. solstitialis* was removed (figures A3 and A4, lower panels ) but occurred 2-3x more where *C. solstitialis* was present (figures A3 and A4, top panels). Finally, hydraulic redistribution was evident at only the most shallow soil depth early in the growing season both where *C. diffusa* was present and where *C. diffusa* had been removed (figure A5), but was evident at all measured soil depths late in the growing season regardless of *C. diffusa* presence although *C. diffusa* plants doubled the magnitude of the hydraulic redistribution at 35-cm and 50-cm soil depths (figure A6).

## Discussion

A significant competitive effect of *Centaurea* on native grasses was detected in support of hypothesis 2 and the established adult native grasses (*Festuca idahoensis* and *Aristida longiseta*) failed to limit soil resource use by *Centaurea* which is consistent with hypothesis 1. Asymmetric competition between plant species is not rare (Bauer et al. 2004). However, it is rare for the dominant species of the community (in this case grasses) to have no competitive effect on plants of other species as was observed in these experiments. Stomatal conductance and leaf and soil water potentials support the hypothesis that all 3 species of *Centaurea* root more deeply in the soil than the native grasses with which they occur. By rooting deeper than the grasses, *Centaurea* species may reduce the water limitation to growth and therefore have a competitive advantage over the dominant native species. In hindsight it is not surprising that the native grasses did not provide competition for water with *Centaurea* species, because of the deeper-rooting habit of *Centaurea* species relative to the grasses (Hill et al. 2006, Kulmatiski et al. 2006). Water availability in grasslands varies spatially with soil depth so the deepest-rooting plants in grasslands should not experience competition for deep water sources.

Although asymmetry in intraspecific competition generally results from individuals growing earlier than nearby competitors (Harper 1977, De Luis *et al.* 2008), asymmetry in interspecific competition may result simply from differences in phenology or morphology between species (Schwinning and Weiner 1998). Asymmetric competition in mesic environments often results from limited light availability (Wayne and Bazzaz 1997), whereas asymmetric competition in xeric environments may occur due to limited water availability (Fowler 1986).

Although individuals of *Centaurea* apparently experience no competition for water as a result of rooting deeper than the native grasses, they also produce fine roots in the shallow soil within the rooting zone of the grasses (Sheley and Larson 1995) and have the potential to reduce water available to the grasses. Since water availability increases with depth, anything that reduces the rooting depth of the grasses would further reduce available water for the grasses. Plots of predawn leaf water potential against predawn soil water potential (figures 3.5-3.7) allow inference of the importance of different soil depths for water acquisition of each species. The soil depth at which the predawn leaf water potential matches the predawn soil water potential should approximate the mean rooting depth for that species (Yu et al. 2007).

Predawn disequilibria (Donovan et al. 1999, Donovan et al. 2001), that is, the failure of a plant to become isotonic with the surrounding soil at night, may confound interpretation of these data. Predawn disequilibria between leaf and the wettest soil in which the plant is rooted may be due to nighttime transpiration (Snyder et al. 2003, Caird et al. 2007), osmotically active solutes in the plant (James et al. 2006), or the rooting system spanning a moisture gradient (Hultine et al. 2003). The magnitude of predawn disequilibria however, may be estimated by the difference between predawn leaf water potential and predawn soil water potential when the soil is at field capacity (Donovan *et al.* 2003). Graphically, on plots of leaf versus soil predawn water potentials, predawn disequilibria may be estimated by the difference between predawn water potential of the leaves and predawn water potential of the soil in which the plant is rooted. For both *Centaurea* species and the native grasses, predawn disequilibria are approximately 0.3 to 0.4 MPa. After shifting leaf predawn water potentials up by 0.3 to 0.4 MPa to account for predawn disequilibria, better estimates of mean rooting depths can be made for each species. The mean rooting depth for all *Centaurea* species is equal to or greater than the deepest measured soil depth (50 to 70-cm). The native grasses growing where *Centaurea* individuals had been removed, have mean rooting depths between 35 and 50-cm (figure 3.6) and the grasses growing with *Centaurea* individuals have a mean rooting depths of approximately 25 to 35-cm (figure 3.7).

The difference in mean rooting depth estimates for the native grasses growing with *Centaurea* individuals relative to the mean rooting depth of native grasses growing where *Centaurea* individuals had been removed is approximately 10-cm (40-cm mean rooting depth for grasses without *Centaurea* compared to 30-cm mean rooting depth for grasses growing with *Centaurea*). This pattern is consistent with the difference in mean late-season midday leaf water potential between the native grasses growing with and without *Centaurea* competition (-3.0 MPa for grasses with *Centaurea* compared to -2.3 MPa for grasses where *Centaurea* had been removed) (figures 3.1-3.3).

In contrast to the native grasses, *Centaurea* species experienced very little change in midday leaf water potential between early and late in the growing season (figures 3.1-3.3). This pattern also supports the conclusion that *Centaurea* has access to deeper, more persistent sources of water. Moreover, the differences between *Centaurea* species and native grasses in the relationship between predawn leaf water potential and midday stomatal conductance (figure 3.4) are consistent with the idea that *Centaurea* species are drought-avoiding species and native grasses are drought-tolerating species. Although grasses may conduct gas exchange at predawn leaf water potentials as low as -1.8 MPa (Pugnaire and Haase 1996, Garcia et al. 2002), stomatal conductance for grasses when soils are at field capacity are less than half of the maximum rates for *Centaurea* (figure 3.4). The grasses were more conservative than *Centaurea* in their water-use throughout the growing season.

Finally, hydraulic redistribution is evidence that roots span a gradient of water potentials in the soil and the magnitude of hydraulic redistribution should be positively related to the range of water potentials over which the root system occurs. The greater magnitude of hydraulic redistribution in plots where *Centaurea* occurs is further evidence that *Centaurea* is accessing deeper, wetter soil than the native bunchgrasses.

Native grasses did not provide detectable resistance to water acquisition by adult *Centaurea* (figures 3.1-3.3). Since *Centaurea* reduces the water available to native grasses, drier than average years may be especially detrimental to the persistence of native bunchgrass populations in the Columbia Basin Ecoregion. Multiple consecutive dry years may result in competitive exclusion of native grasses from high-density *Centaurea* populations which may in part explain the observed negative relationship between *Centaurea* and native grass abundance.

Since competition for water with *Centaurea* species negatively impacts native perennial grasses, soil water additions may reduce the negative effects of *Centaurea* species on the native perennial grasses.  The final chapter of this dissertation consequently, explores the hypothesis that soil resource additions may affect the outcome of competition between *Centaurea maculosa*, the most abundant *Centaurea* species in the Columbia Basin, and *Festuca idahoensis*, one of the most abundant perennial grasses in the Columbia Basin Ecoregion.

## Literature Cited

Bauer, S.; T. Wyszomirski; U. Berger; H. Hildenbrandt; V. Grimm. 2004. Asymmetric competition as a natural outcome of neighbor interactions among plants: results from the field-of-neighborhood modeling. Plant Ecology 170 (1):135-145.

Belnap, J. S.; O. L. Lange (editors) 2001. Biological Soil Crusts: Structure, Function, and Management. Springer, New York, NY.

Brown R. W.; D. L. Bartos. 1982. A calibration model for screen caged Peltier thermocouple psychrometers. USDA Forest Service Research Paper INT-293, Ogden, p 155.

Caird, M. A.; J. H. Richards; L. A. Donovan. 2007. Nighttime stomatal conductance and transpiration in C3 and C4 plants. Plant Physiology 143:4-10.

Caldwell, M. M.; T. E. Dawson; J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113 (2):151-161.

Casper, B. B.; R. B. Jackson. 1997. Plant competition underground. Annual Review of Ecology and Systematics 28:545-570.

Daubenmire, R. F. 1943. Soil Temperature versus Drought as a Factor Determining the Lower Altitudinal Limits of Trees in the Rocky Mountains. Botanical Gazette 105 (1):1-43.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62.

Donovan, L. A.; D. J. Grise; J. B. West; R. A. Pappert; N. N. Alder; J. H. Richards. 1999. Predawn disequilibrium between plant and soil water potentials. Oecologia 120 (2):209-217.

Donovan L. A.; M. J. Linton; J. H. Richards. 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. Oecologia 129:328-333.

Donovan L. A.; J. H. Richards; M. J. Linton. 2003. Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. Ecology 84 (2):463-470.

Ehleringer, J. R. 1993. Stable isotopes and plant carbon-water relations. Academic Press. San Diego, CA.

Fonteyn, P. J.; B. E. Mahall. 1978. Competition among desert perennials. Nature 275 (5680):544-545.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17:89-110.

Garcia, M. G.; C. A. Busso; P. Polci; G. N. L. Garcia; V. Echenique. 2002. Water relations and leaf growth rate of three *Agropyron* genotypes under water stress. Biocell 26 (3):309-317.

Hill, J. P.; M. J. Germino; J. M. Wraith; B. E. Olson; M. B. Swan. 2006. Advantages in water relations contribute to greater photosynthesis in *Centaurea maculosa* compared with established grasses. International Journal of Plant Sciences 167 (2):269-277.

Hultine, K. R.; W. L. Cable; S. S. O. Burgess, D. G. Williams. 2003. Hydraulic redistribution by deeps roots of a Chihuahuan Desert phreatophyte. Tree Physiology 23 (5):353-360.

Jackson, R. B.; J. Canadell; J. R. Ehleringer; H. A. Mooney; O. E. Sala; E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389-411.

James, J. J.; N.N. Alder; K. H. Muhling; A. E. Lauchli; K. A. Shackel; L. A. Donovan; J. H. Richards. 2006. High apoplastic solute concentrations in leaves alter water relations of the halophytic shrub, *Sarcobatus vermiculatus*. Journal of Experimental Botany 57:139-147.

Kirkham, M. B. 2005. Principles of soil and plant water relations. Elsevier Academic Press, New York, NY.

Kleiner, E. F.; K. T. Harper. 1977. Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. Journal of Range Management 30 (4):286-289.

Kulmatiski, A.; K. H. Beard; J. M. Stark. 2006. Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. Plant and Soil 288 (1-2):271-284.

Liebig, J. 1840. Organic chemistry in its applications to agriculture and physiology. Friedrich Viewig and Sons Publishing Company. Brunswig, Germany.

Pugnaire, F. I.; P. Haase. 1996. Comparative physiology and growth of two perennial tussock grass species in a semi-arid environment. Annals of Botany 77 (1):81-86.

Richards, J. h.; M. M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73 (4):486-489.

Ridenour, W. M.; R. M. Callaway. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126:444-450.

Roche, B. F. Jr.; C. T. Roche. 1991. Identification, introduction, distribution, ecology, and economics of *Centaurea* species. In: James, L. F.; J. O. Evans; M. H. Ralphs; R. D. Child (editors) Noxious Range Weeds. Westview press, San Francisco, CA: 274-291.

Ryel, R. I.; M. M. Caldwell; W. Beyschlag. 1993. Light field heterogeneity among tussock grasses: Theoretical considerations of light harvesting and seedling establishment in tussocks and uniform tiller distributions. Oecologia 98:241-246.

Schwinning, S.; J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113 (4):447-455.

Seastedt, T. R.; K. N. Suding. 2007. Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. Oecologia 151 (4):626-636.

Sheley, R. L.; L. L. Larson. 1995. Interference between cheatgrass and yellow starthistle at 3 soil depths. Journal of Range Management 48:392–397.

Snyder, K. A.; J. H. Richards, L. A. Donovan. 2003. Night-time conductance in C3 and C4 species: do plants lose water at night? Journal of Experimental Botany 54 (383):861-865.

Sprengel, C. 1837. Soil science and its doctrines. Immanuel Muller Publishing Company, Leipzig, Germany.

Tilman, D. 1987. On the meaning of competition and the mechanisms of community superiority. Functional Ecology 1:304-315.

Tyree, M. T.; H. T. Hammel. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. Journal of Experimental Botany 23:267-282.

Wayne, P. M. and F. A. Bazzaz. 1997. Light acquisition and growth by competing individuals in $CO_2$-enriched atmospheres: consequences for size structure in regenerating birch stands. The Journal of Ecology 85 (1):29-42.

White, A.; M. G. R. Cannell; A. D. Friend. 2000. The high latitude terrestrial carbon sink: a model analysis. Global Change Biology 6:227-245.

Whittaker, R.; G. Likens. 1973. Primary Productivity of the Biosphere. In: Lieth, H.; R. Whittaker (editors). Springer-Verlag, New York, NY.

Williamson, M; A. Fitter. 1996. The varying success of invaders. Ecology 77:1661-1666.

Yu, G. R.; J. Zhuang, K. Nakayama, Y. Jin. 2007. Root water uptake and profile soil water as affected by vertical root distribution. Plant Ecology 189 (1):15-30.

**Table 3.1.** Comparisons of predawn soil water potentials at three depths early and late in the growing season at sites where *Centaurea diffusa* (*Artemisia tripartita/ Festuca idahoensis* habitat type), *Centaurea maculosa* (*Pinus ponderosa/ Festuca idahoensis* habitat type), and *Centaurea solstitialis* (*Aristida longespica/ Poa secunda* habitat type) have been removed or are present. T-tests were performed to generate the p-values.

## Predawn soil water potentials (Mpa)

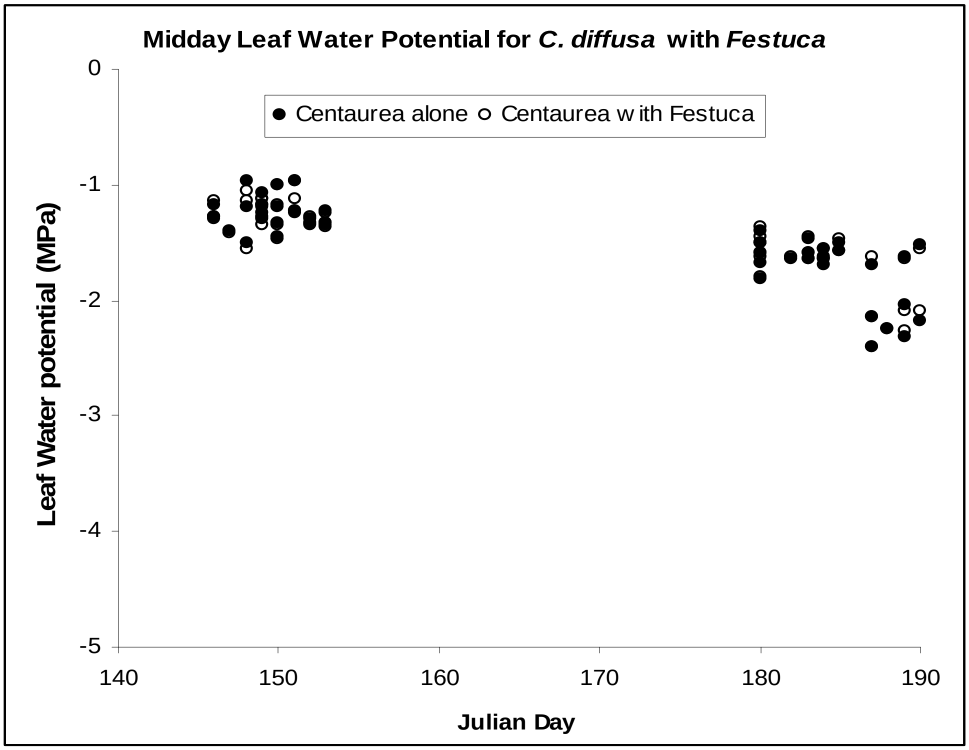
### EARLY SEASON

| | | *Centaurea* REMOVED | | *Centaurea* PRESENT | | |
|---|---|---|---|---|---|---|
| Habitat type | Depth | Mean | SE | Mean | SE | p-value |
| *Artemesia tripartita/ Festuca idahoensis* | 25-cm | **-0.109** | 0.020 | **-0.117** | 0.020 | 0.797 |
| | 35-cm | **-0.119** | 0.016 | **-0.087** | 0.012 | 0.109 |
| | 50-cm | **-0.073** | 0.040 | **-0.068** | 0.012 | 0.881 |
| *Pinus ponderosa/ Festuca idahoensis* | 30-cm | **-0.040** | 0.003 | **-0.080** | 0.014 | 0.001 |
| | 50-cm | **-0.025** | 0.002 | **-0.031** | 0.004 | 0.187 |
| | 70-cm | **-0.017** | 0.003 | **-0.020** | 0.006 | 0.608 |
| *Aristida longespica/ Poa secunda* | 25-cm | **-0.156** | 0.017 | **-0.432** | 0.057 | <0.001 |
| | 35-cm | **-0.092** | 0.009 | **-0.250** | 0.039 | <0.001 |
| | 50-cm | **-0.076** | 0.009 | **-0.059** | 0.010 | 0.291 |

### LATE SEASON

| | | *Centaurea* REMOVED | | *Centaurea* PRESENT | | |
|---|---|---|---|---|---|---|
| Habitat type | Depth | Mean | SE | Mean | SE | p-value |
| *Artemesia tripartita/ Festuca idahoensis* | 25-cm | **-2.394** | 0.075 | **-2.365** | 0.061 | 0.752 |
| | 35-cm | **-2.128** | 0.074 | **-1.997** | 0.066 | 0.189 |
| | 50-cm | **-1.455** | 0.165 | **-1.462** | 0.143 | 0.974 |
| *Pinus ponderosa/ Festuca idahoensis* | 30-cm | **-0.087** | 0.011 | **-0.249** | 0.015 | <0.001 |
| | 50-cm | **-0.037** | 0.007 | **-0.191** | 0.021 | <0.001 |
| | 70-cm | **-0.016** | 0.003 | **-0.120** | 0.026 | <0.001 |
| *Aristida longespica/ Poa secunda* | 25-cm | **-0.376** | 0.021 | **-1.616** | 0.048 | <0.001 |
| | 35-cm | **-0.205** | 0.010 | **-1.064** | 0.093 | <0.001 |
| | 50-cm | **-0.153** | 0.010 | **-0.138** | 0.033 | 0.593 |

**Figure 3.1.** Midday leaf water potential for *Centaurea diffusa* (top panel) and *Festuca idahoensis* (lower panel) plotted against day of year for May, June, and July of 2003 and 2004. Filled data points represent means of 12 individuals in plots where competitors are removed and open data points represent means of 12 individuals in plots where both *Centaurea diffusa* and *Festuca* are present.


Midday Leaf Water Potential for C. diffusa with Festuca
● Centaurea alone ○ Centaurea with Festuca
Leaf Water potential (MPa)
0
-1
-2
-3
-4
-5
140
150
160
170
180
190
Julian Day

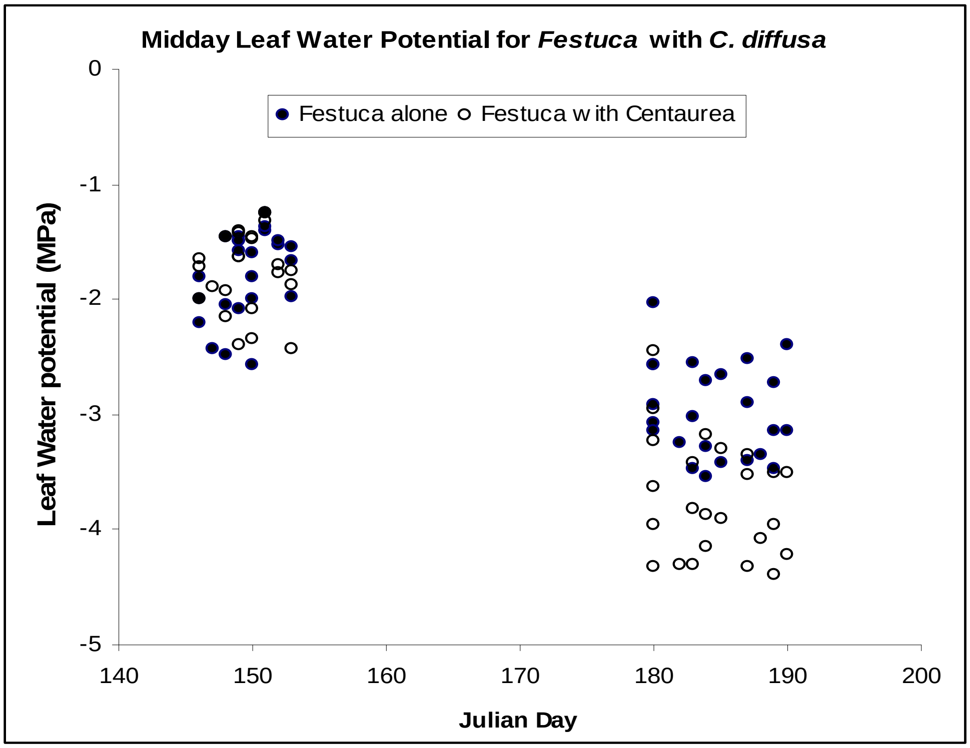
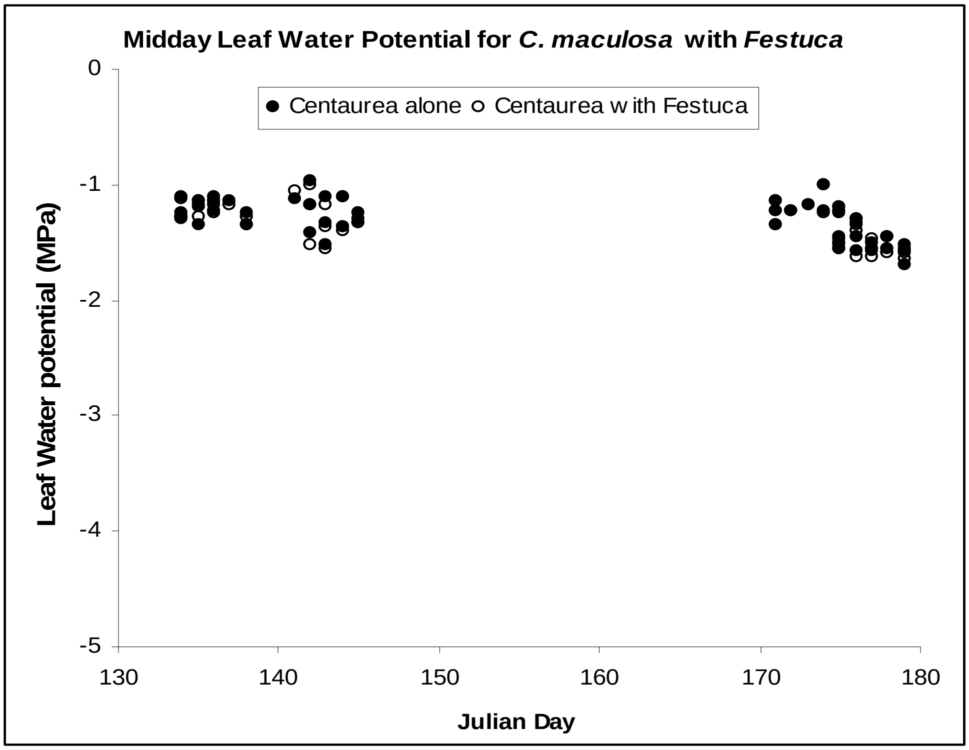

Midday Leaf Water Potential for Festuca with C. diffusa
● Festuca alone ○ Festuca with Centaurea
Leaf Water potential (MPa)
0
-1
-2
-3
-4
-5
140
150
160
170
180
190
200
Julian Day

**Figure 3.2.** Midday leaf water potential for *Centaurea maculosa* (top panel) and *Festuca idahoensis* (lower panel) plotted against day of year for May, June, and July of 2003 and 2004. Filled data points represent means of 12 individuals in plots where competitors are removed and open data points represent means of 12 individuals in plots where both *Centaurea maculosa* and *Festuca* are present.


Midday Leaf Water Potential for *C. maculosa* with *Festuca*
● Centaurea alone ○ Centaurea w ith Festuca
Leaf Water potential (MPa)
0
-1
-2
-3
-4
-5
130
140
150
160
170
180
Julian Day

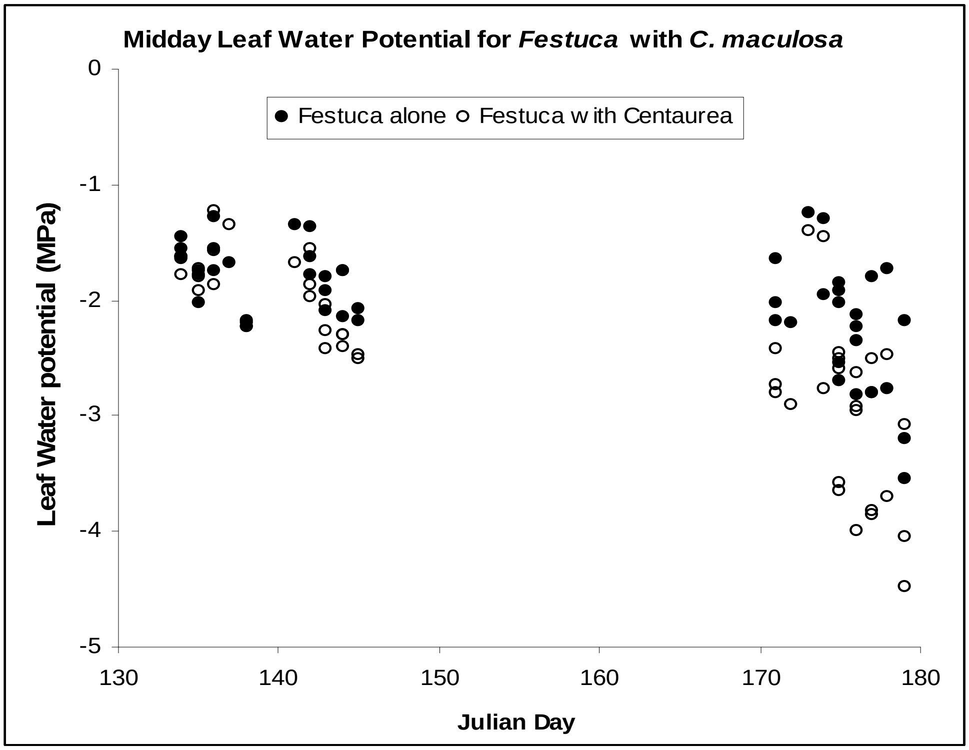
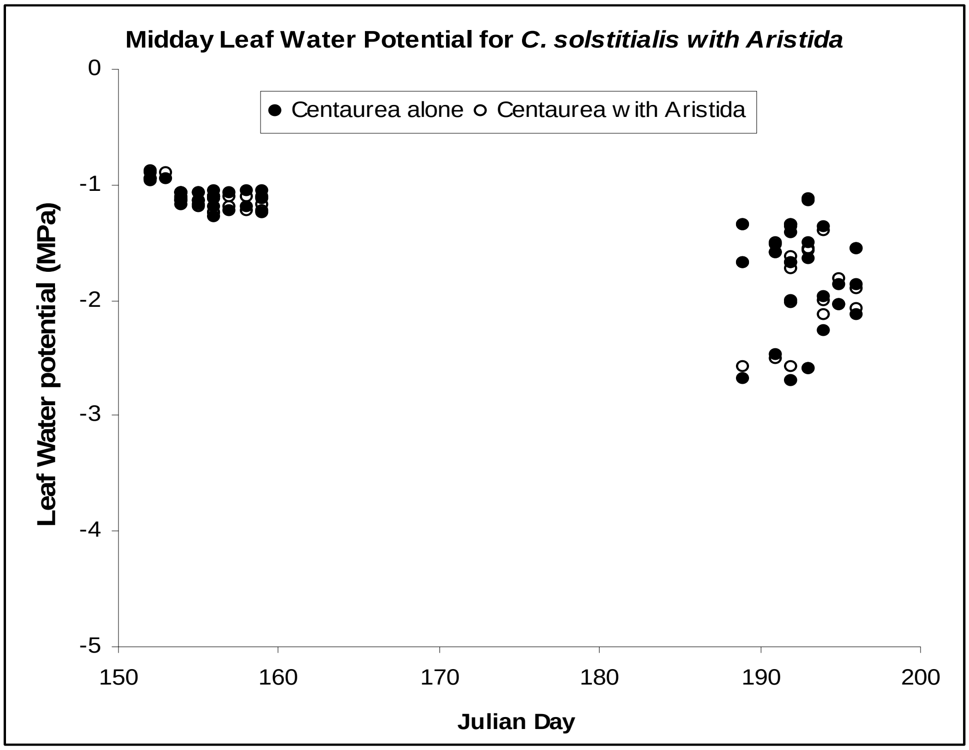

Midday Leaf Water Potential for *Festuca* with *C. maculosa*
● Festuca alone ○ Festuca w ith Centaurea
Leaf Water potential (MPa)
0
-1
-2
-3
-4
-5
130
140
150
160
170
180
Julian Day

**Figure 3.3.** Midday leaf water potential for *Centaurea solstitialis* (top panel) and *Aristida longiseta* (lower panel) plotted against day of year for May, June, and July of 2003 and 2004. Filled data points represent means of 12 individuals in plots where competitors are removed and open data points represent means of 12 individuals in plots where both *Centaurea solstitialis* and *Aristida* are present.


Midday Leaf Water Potential for C. solstitialis with Aristida
● Centaurea alone ○ Centaurea with Aristida
Leaf Water potential (MPa)
0
-1
-2
-3
-4
-5
150
160
170
180
190
200
Julian Day

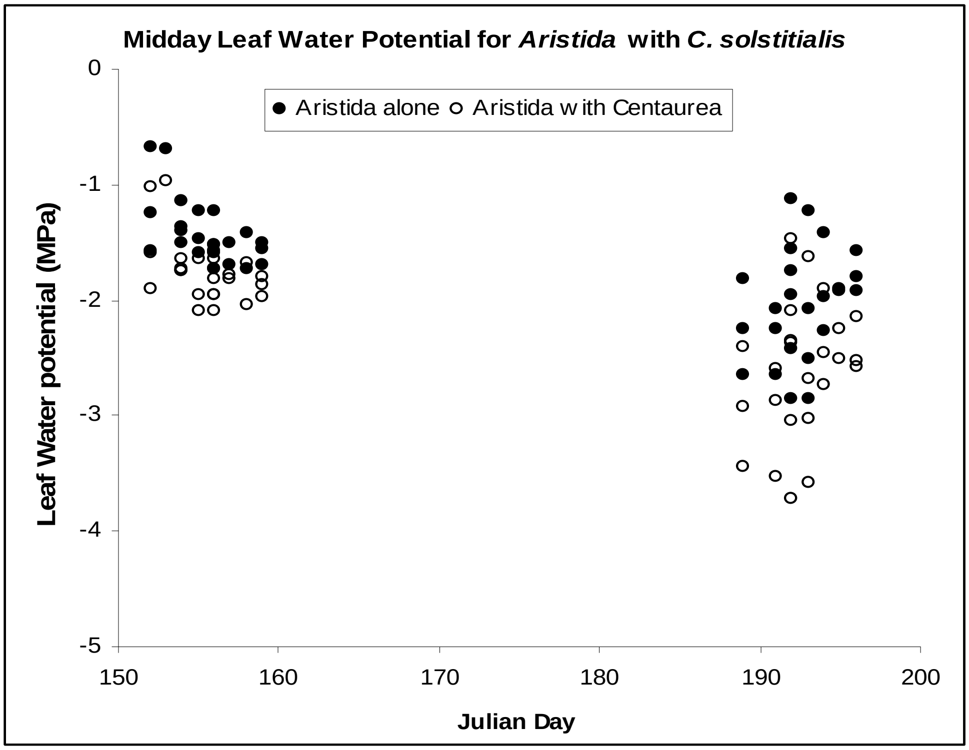
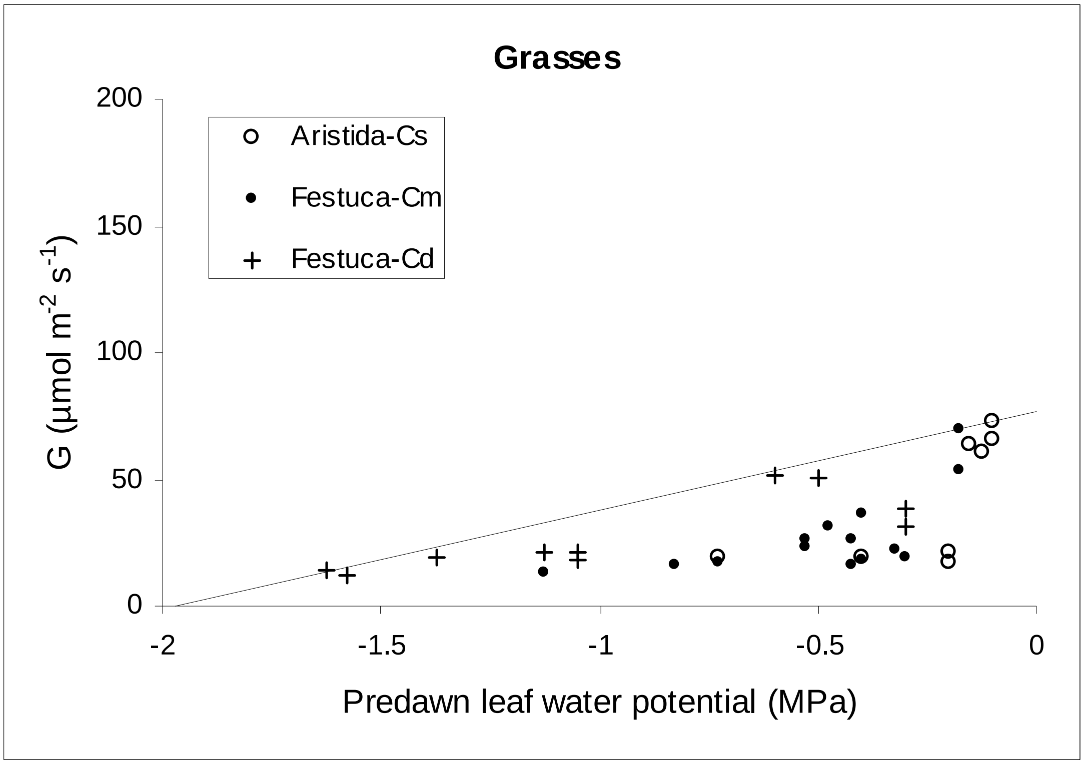

Midday Leaf Water Potential for Aristida with C. solstitialis
● Aristida alone ○ Aristida with Centaurea
Leaf Water potential (MPa)
0
-1
-2
-3
-4
-5
150
160
170
180
190
200
Julian Day

**Figure 3.4.** Stomatal conductance (G) plotted against pre-dawn leaf water potential for grasses (top panel) and *Centaurea* (lower panel). Stomatal conductance (G) values are means of 8 replicate measurements within a treatment in a stand of *Aristida longiseta/ Poa secunda* (for *Centaurea solstitialis* and *Aristida* with *Centaurea solstitialis*, open circles), a stand of *Pinus ponderosa/ Festuca idahoensis* (for *Centaurea maculosa* and *Festuca* with *Centaurea maculosa,* closed circles), and a stand of *Artemisia tripartita/ Festuca idahoensis* (for *Centaurea diffusa* and *Festuca* with *Centaurea diffusa*, crosses). Predawn leaf water potential values are means of 12 replicate measurements within a treatment at a site. Lines are 90th percentile quantile regression which represent theoretical maxima in the absence of limitation.


Grasses
200
150
100
50
0
G (µmol m-2 s-1)
Aristida-Cs
Festuca-Cm
Festuca-Cd
-2
-1.5
-1
-0.5
0
Predawn leaf water potential (MPa)

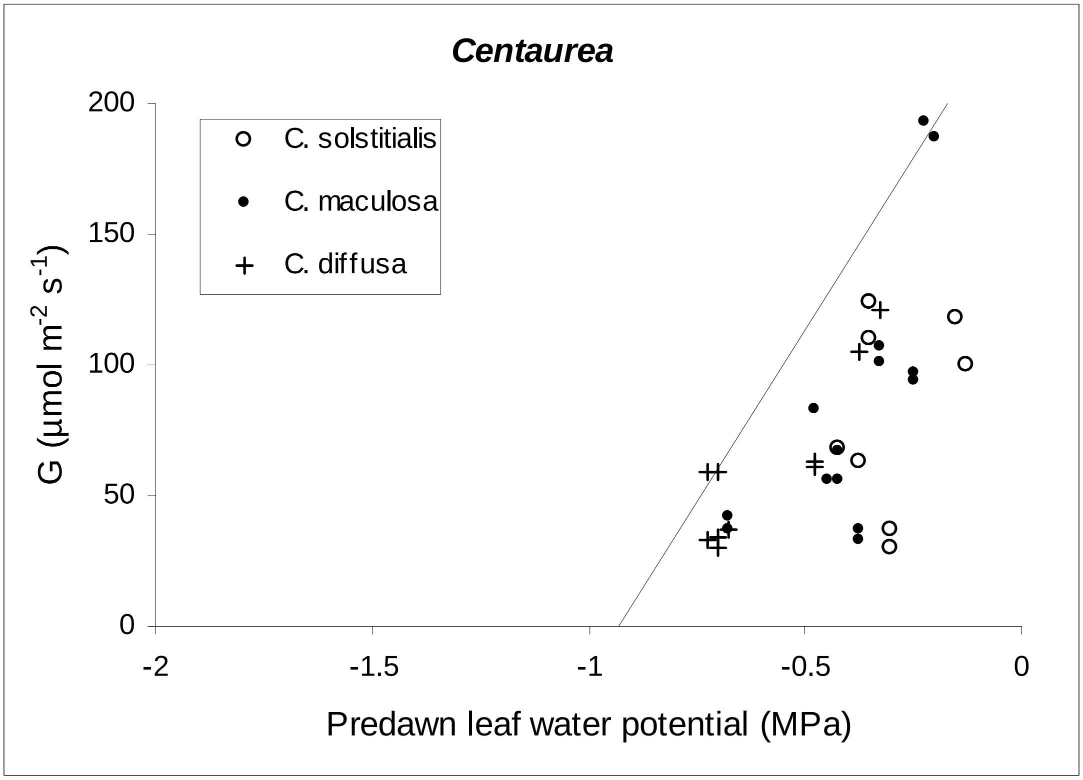
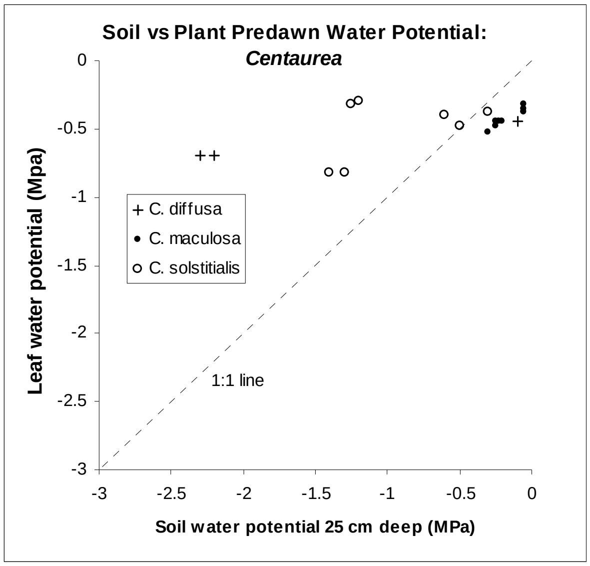
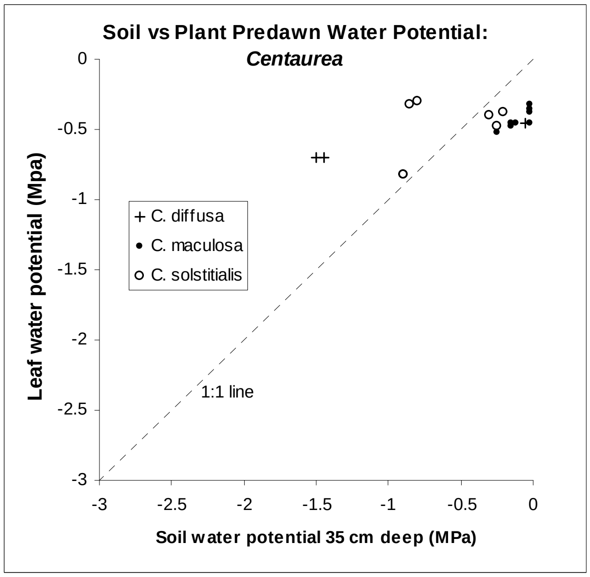

Centaurea
200
150
100
50
0
G (µmol m-2 s-1)
C. solstitialis
C. maculosa
C. diffusa
-2
-1.5
-1
-0.5
0
Predawn leaf water potential (MPa)

**Figure 3.5.** Predawn leaf water potential for *Centaurea diffusa* (crosses), *Centaurea maculosa* (closed circles), and *Centaurea solstitialis* (open circles) plotted against predawn soil water potential at 25-cm depth (top panel), 35-cm depth (center panel), and 50-cm depth (lower panel). Predawn leaf water potential values are means of 12 replicate measurements within a treatment in a stand of *Aristida longespica/ Poa secunda* (for *Centaurea solstitialis*), a stand of *Pinus ponderosa/ Festuca idahoensis* (for *Centaurea maculosa*), and a stand of *Artemisia tripartita/ Festuca idahoensis* (for *Centaurea diffusa*). Soil water potential values are the mean of 2 to 4 replicate measurements within a treatment in a stand. The 1:1 line is where leaf water potential equals soil water potential. Predawn disequilibria may be estimated by the difference between leaf and soil water potential when soils are at field capacity (0.1 MPa).


Soil vs Plant Predawn Water Potential:
Centaurea
Leaf water potential (Mpa)
0
-0.5
-1
-1.5
-2
-2.5
-3
+ C. diffusa
● C. maculosa
○ C. solstitialis
1:1 line
-3
-2.5
-2
-1.5
-1
-0.5
0
Soil water potential 25 cm deep (MPa)


Soil vs Plant Predawn Water Potential:
Centaurea
Leaf water potential (Mpa)
0
-0.5
-1
-1.5
-2
-2.5
-3
+ C. diffusa
● C. maculosa
○ C. solstitialis
1:1 line
-3
-2.5
-2
-1.5
-1
-0.5
0
Soil water potential 35 cm deep (MPa)

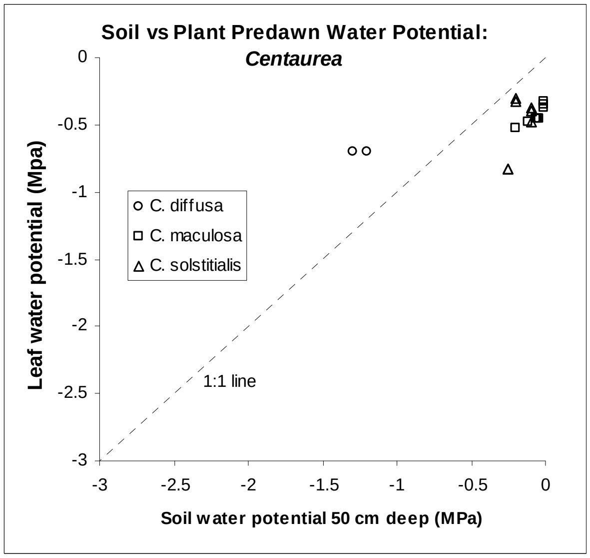
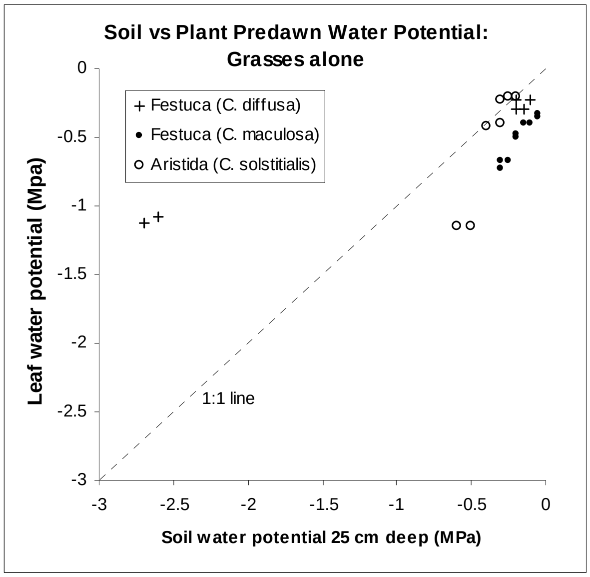
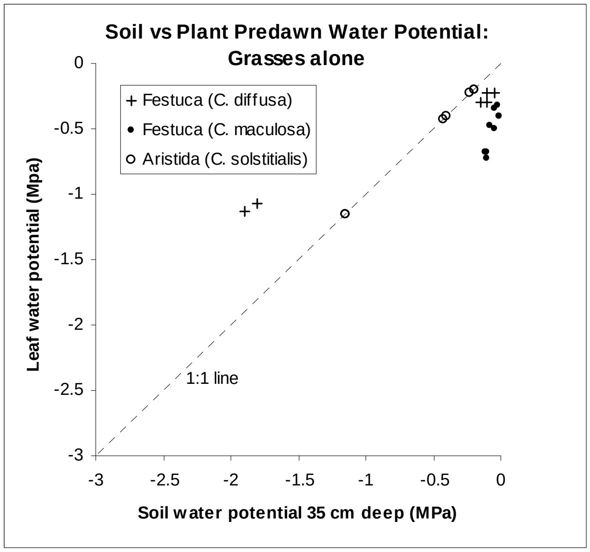

Soil vs Plant Predawn Water Potential:
Centaurea
Leaf water potential (Mpa)
0
-0.5
-1
-1.5
-2
-2.5
-3
○ C. diffusa
□ C. maculosa
△ C. solstitialis
1:1 line
-3
-2.5
-2
-1.5
-1
-0.5
0
Soil water potential 50 cm deep (MPa)

**Figure 3.6.** Predawn leaf water potential for *Festuca idahoensis* growing where *Centaurea diffusa* has been removed (crosses), *Festuca idahoensis* growing where *Centaurea maculosa* has been removed (closed circles), and *Aristida longespica* growing where *Centaurea solstitialis* has been removed plotted against predawn soil water potential at 25-cm depth (top panel), 35-cm depth (center panel), and 50-cm depth (lower panel). Predawn leaf water potential values are means of 12 replicate measurements within a treatment in a stand of *Aristida longespica/ Poa secunda* (for *Aristida*), a stand of *Pinus ponderosa/ Festuca idahoensis* (for *Festuca* with *Centaurea maculosa* removed), and a stand of *Artemisia tripartita/ Festuca idahoensis* (for *Festuca* with *Centaurea diffusa* removed). Soil water potential values are the mean of 2 to 4 replicate measurements within a treatment in a stand. The 1:1 line is where leaf water potential equals soil water potential. Predawn disequilibria may be estimated by the difference between leaf and soil water potential when soils are at field capacity (0.1 MPa).


Soil vs Plant Predawn Water Potential:
Grasses alone
Festuca (C. diffusa)
Festuca (C. maculosa)
Aristida (C. solstitialis)
Leaf water potential (Mpa)
Soil water potential 25 cm deep (MPa)
1:1 line
0
-0.5
-1
-1.5
-2
-2.5
-3


Soil vs Plant Predawn Water Potential:
Grasses alone
Festuca (C. diffusa)
Festuca (C. maculosa)
Aristida (C. solstitialis)
Leaf water potential (Mpa)
Soil water potential 35 cm deep (MPa)
1:1 line
0
-0.5
-1
-1.5
-2
-2.5
-3

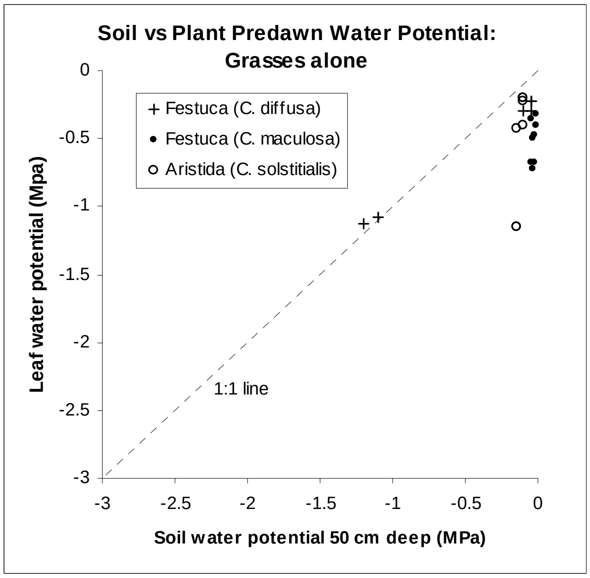
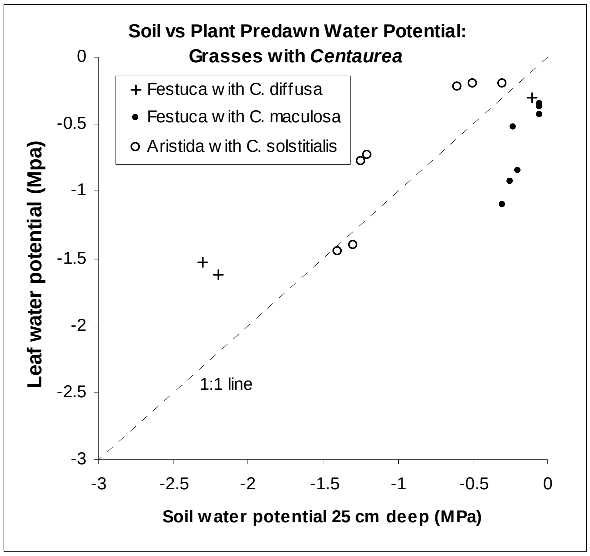
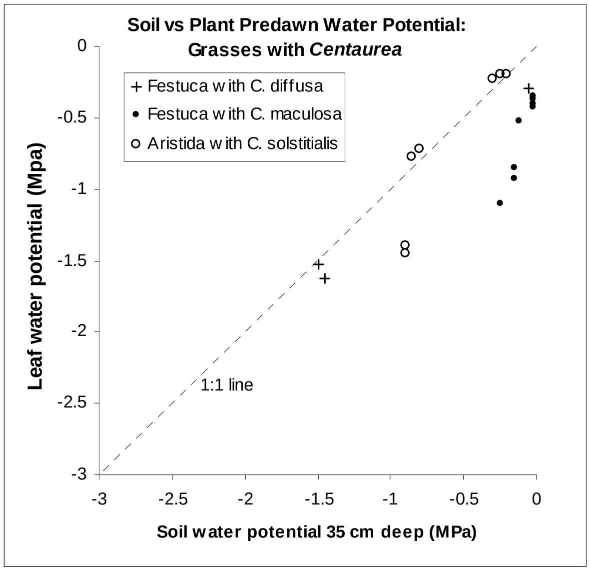
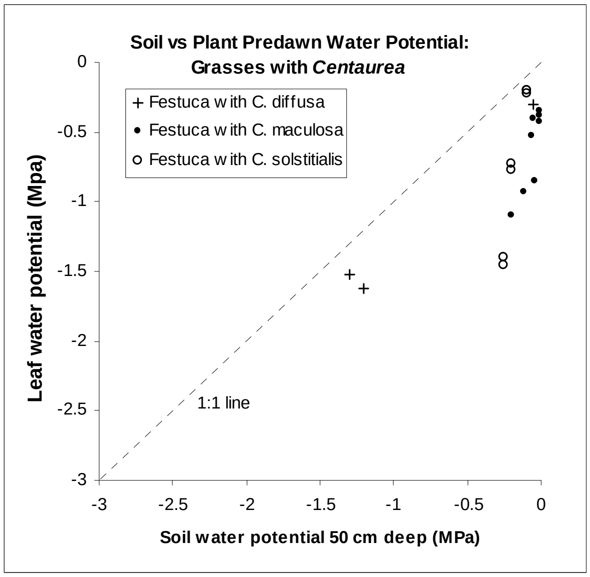

Soil vs Plant Predawn Water Potential:
Grasses alone
Festuca (C. diffusa)
Festuca (C. maculosa)
Aristida (C. solstitialis)
Leaf water potential (Mpa)
Soil water potential 50 cm deep (MPa)
1:1 line
0
-0.5
-1
-1.5
-2
-2.5
-3

**Figure 3.7.** Predawn leaf water potential for *Festuca idahoensis* growing with *Centaurea diffusa* (crosses), *Festuca idahoensis* growing with *Centaurea maculosa* (closed circles), and *Aristida longespica* growing with *Centaurea solstitialis* plotted against predawn soil water potential at 25-cm depth (top panel), 35-cm depth (center panel), and 50-cm depth (lower panel). Predawn leaf water potential values are means of 12 replicate measurements within a treatment in a stand of *Aristida longespica/ Poa secunda* (for *Aristida*), a stand of *Pinus ponderosa/ Festuca idahoensis* (for *Festuca* with *Centaurea maculosa*), and a stand of *Artemisia tripartita/ Festuca idahoensis* (for *Festuca* with *Centaurea diffusa*). Soil water potential values are the mean of 2 to 4 replicate measurements within a treatment in a stand. The 1:1 line is where leaf water potential equals soil water potential. Predawn disequilibria may be estimated by the difference between leaf and soil water potential when soils are at field capacity (0.1 MPa).


Soil vs Plant Predawn Water Potential: Grasses with *Centaurea*
+ Festuca with C. diffusa
• Festuca with C. maculosa
○ Aristida with C. solstitialis
1:1 line
Leaf water potential (Mpa)
Soil water potential 25 cm deep (MPa)
0
-0.5
-1
-1.5
-2
-2.5
-3


Soil vs Plant Predawn Water Potential: Grasses with *Centaurea*
+ Festuca with C. diffusa
• Festuca with C. maculosa
○ Aristida with C. solstitialis
1:1 line
Leaf water potential (Mpa)
Soil water potential 35 cm deep (MPa)
0
-0.5
-1
-1.5
-2
-2.5
-3


Soil vs Plant Predawn Water Potential: Grasses with *Centaurea*
+ Festuca with C. diffusa
• Festuca with C. maculosa
○ Festuca with C. solstitialis
1:1 line
Leaf water potential (Mpa)
Soil water potential 50 cm deep (MPa)
0
-0.5
-1
-1.5
-2
-2.5
-3

# APPENDIX

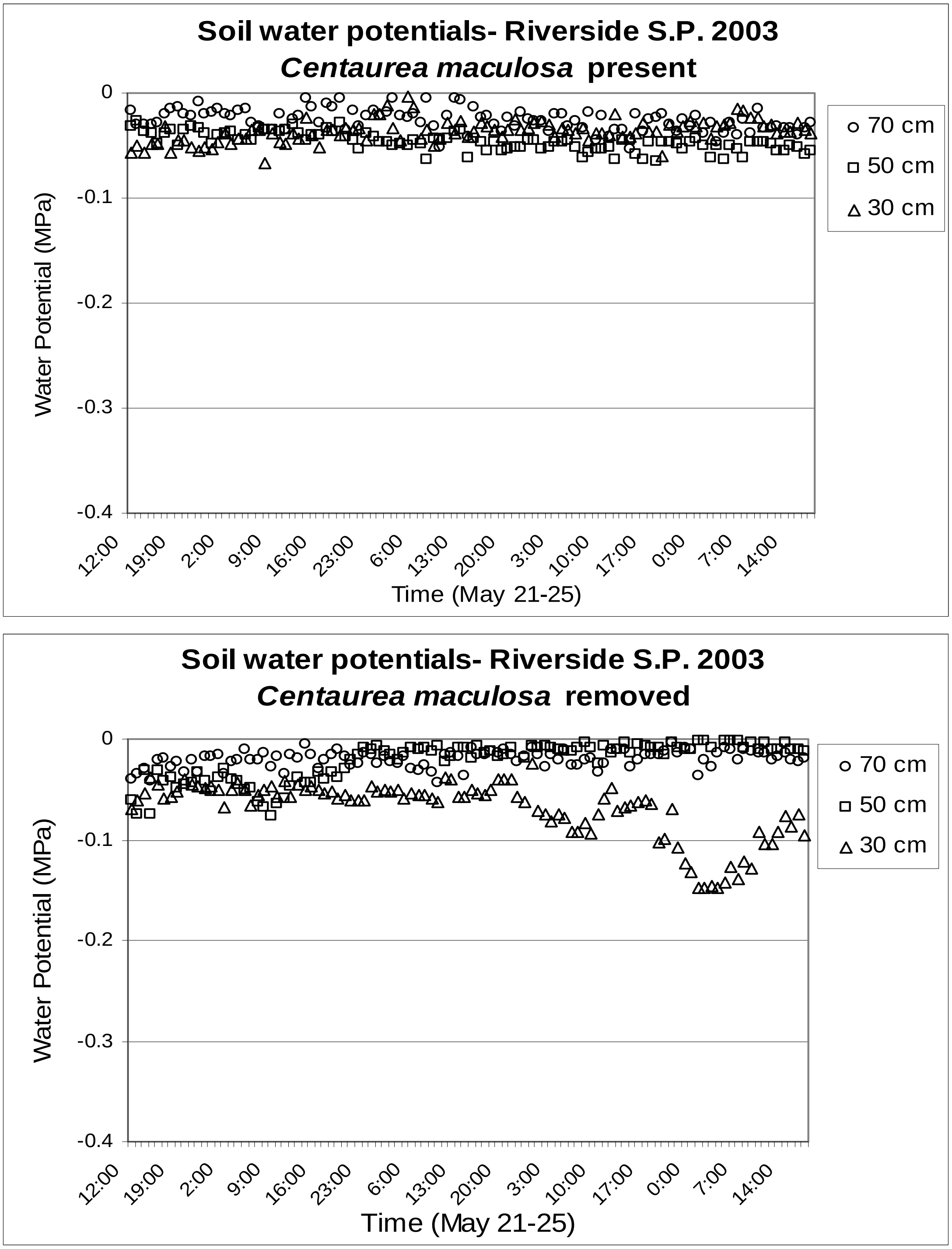


**Figure A1.** Soil water potential at 3 depths early in the growing season where *Centaurea maculosa* and *Festuca idahoensis* co-occur (top panel) and where *Centaurea maculosa* has been removed (lower panel) in a stand of *Pinus ponderosa/ Festuca idahoensis* in Riverside State Park west of Spokane, WA.

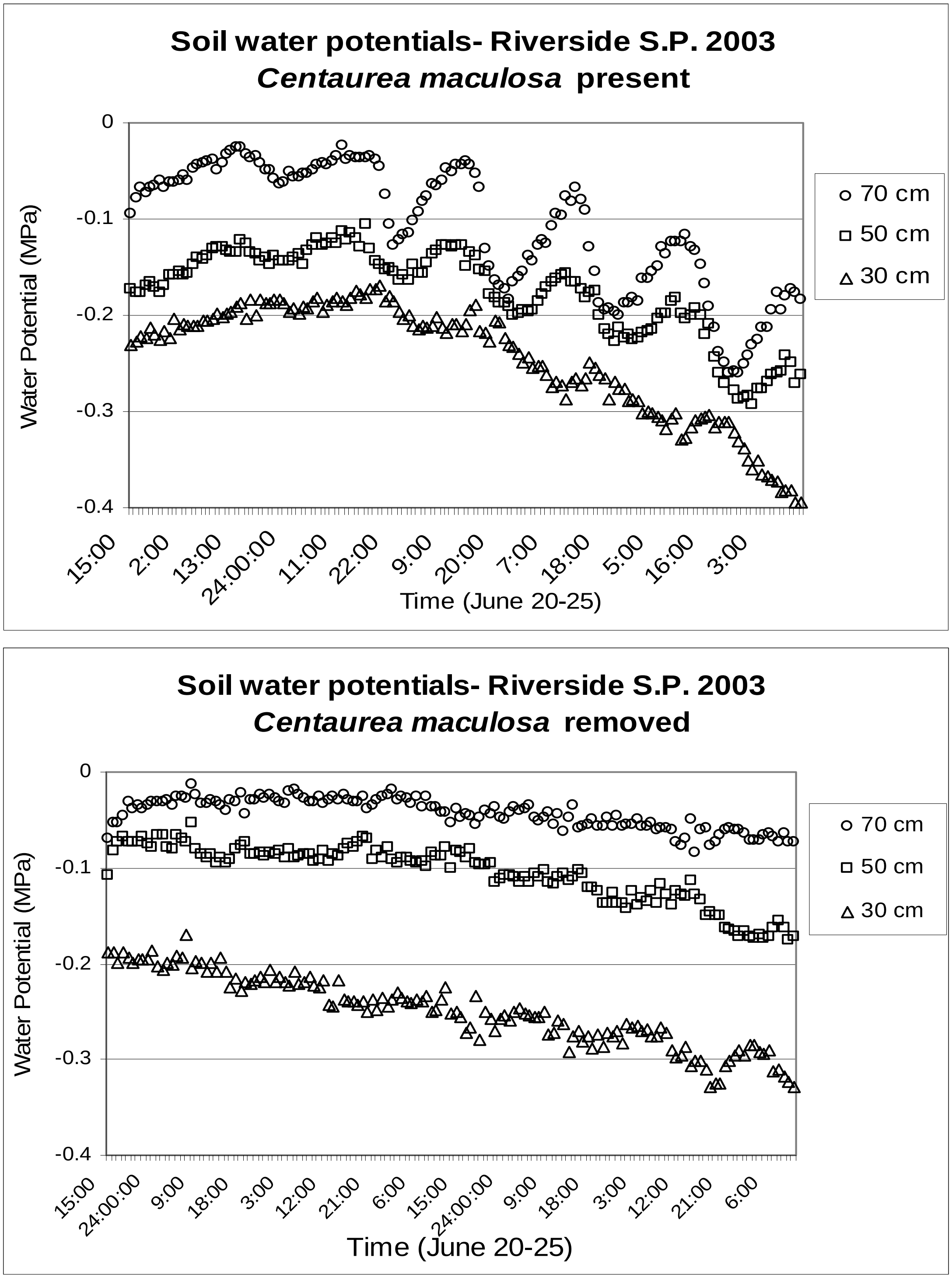


**Figure A2.** Soil water potential at 3 depths late in the growing season where *Centaurea maculosa* and *Festuca idahoensis* co-occur (top panel) and where *Centaurea maculosa* has been removed (lower panel) in a stand of *Pinus ponderosa/ Festuca idahoensis* in Riverside State Park west of Spokane, WA.

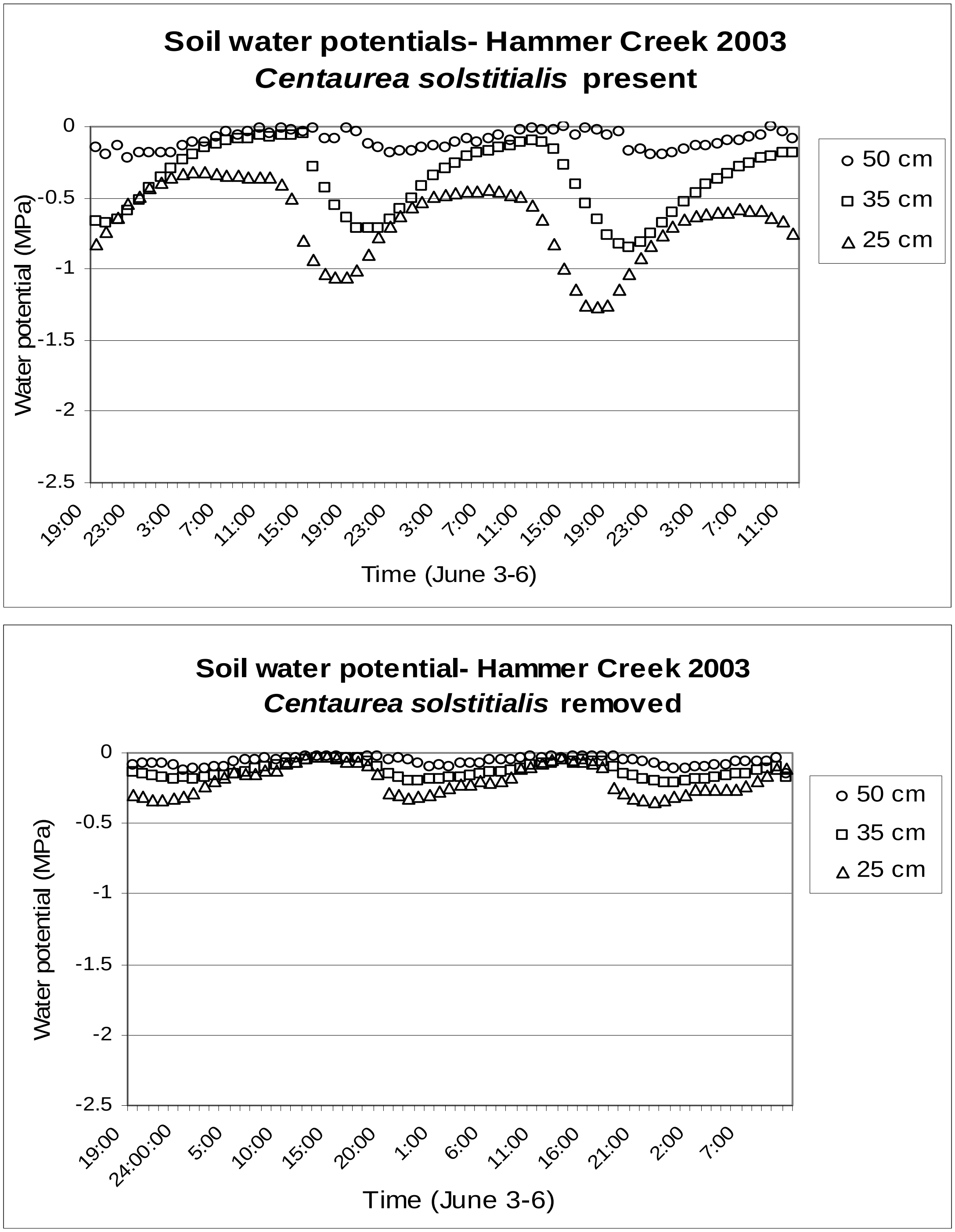


**Figure A3.** Soil water potential at 3 depths early in the growing season where *Centaurea solstitialis* and *Aristida longespica* co-occur (top panel) and where *Centaurea solstitialis* has been removed (lower panel) in a stand of *Aristida longespica/ Poa secunda* near Hammer Creek Recreation Site west of White Bird, ID.

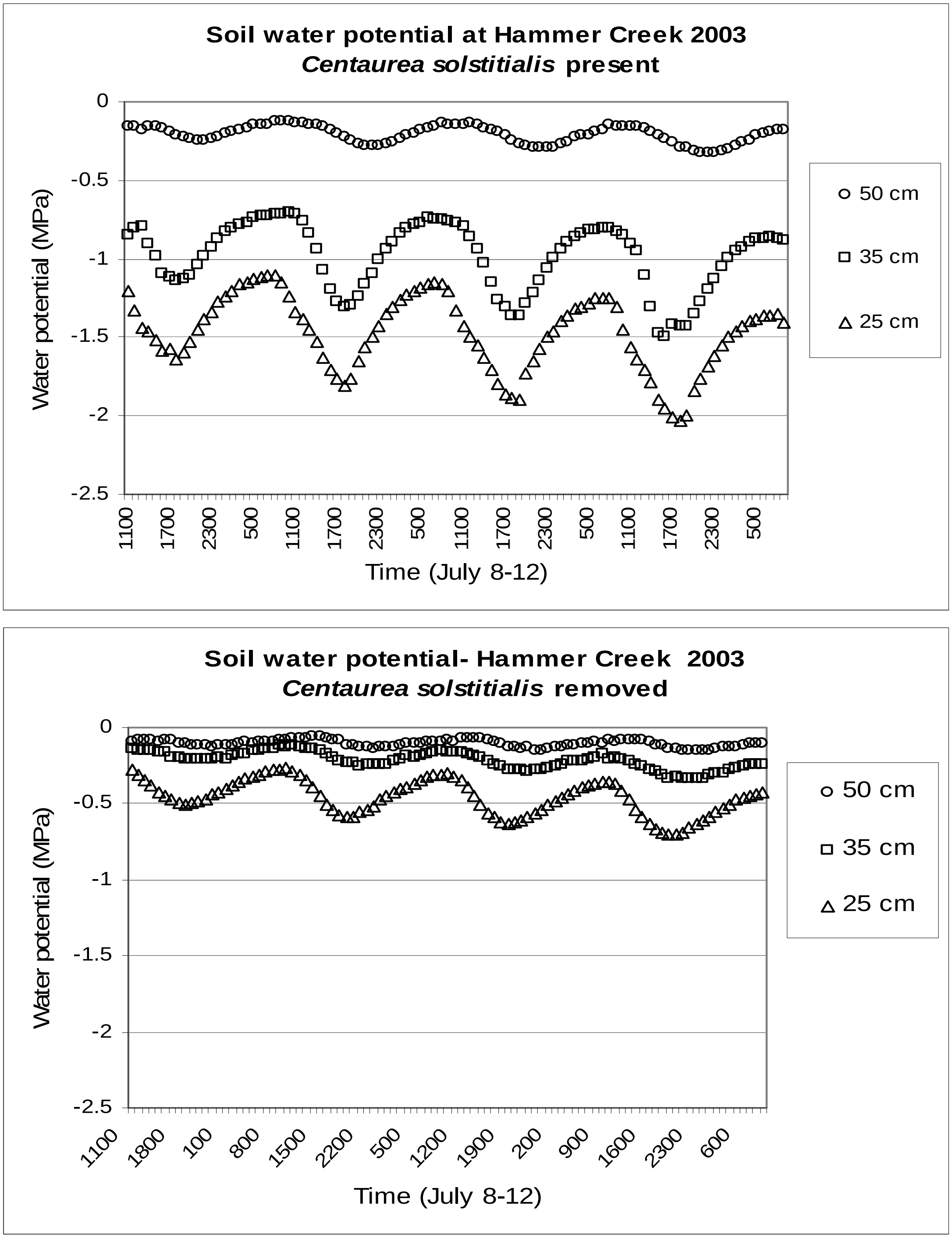
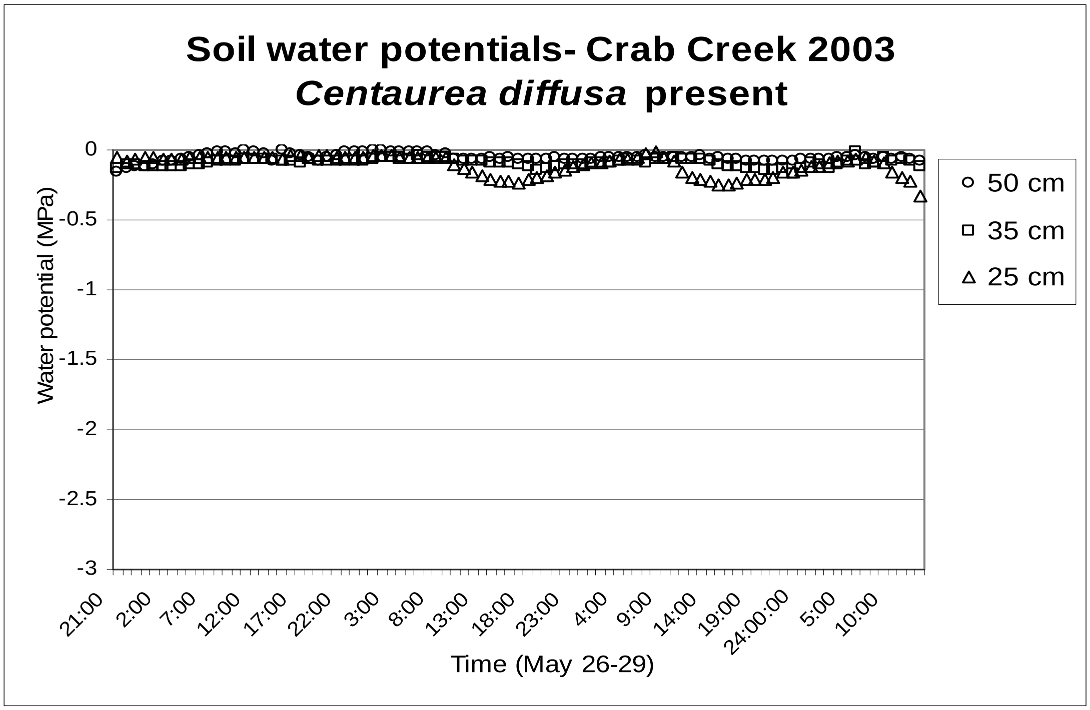


**Figure A4.** Soil water potential at 3 depths late in the growing season where *Centaurea solstitialis* and *Aristida longespica* co-occur (top panel) and where *Centaurea solstitialis* has been removed (lower panel) in a stand of *Aristida longespica/ Poa secunda* near Hammer Creek Recreation Site west of White Bird, ID.



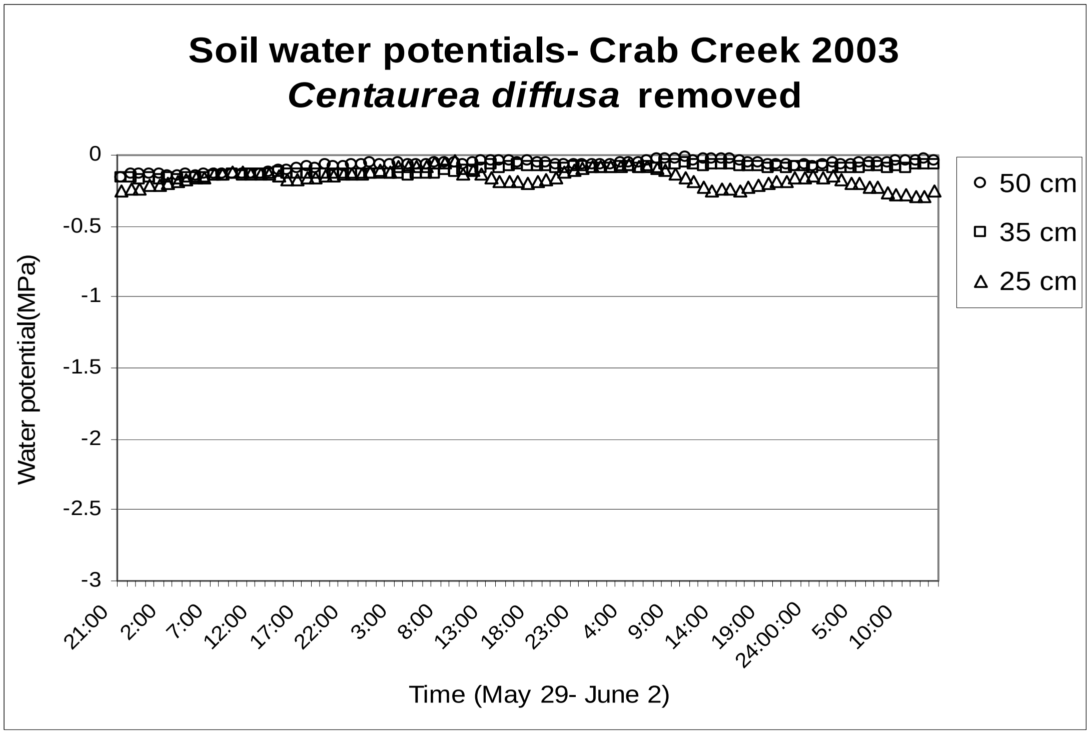
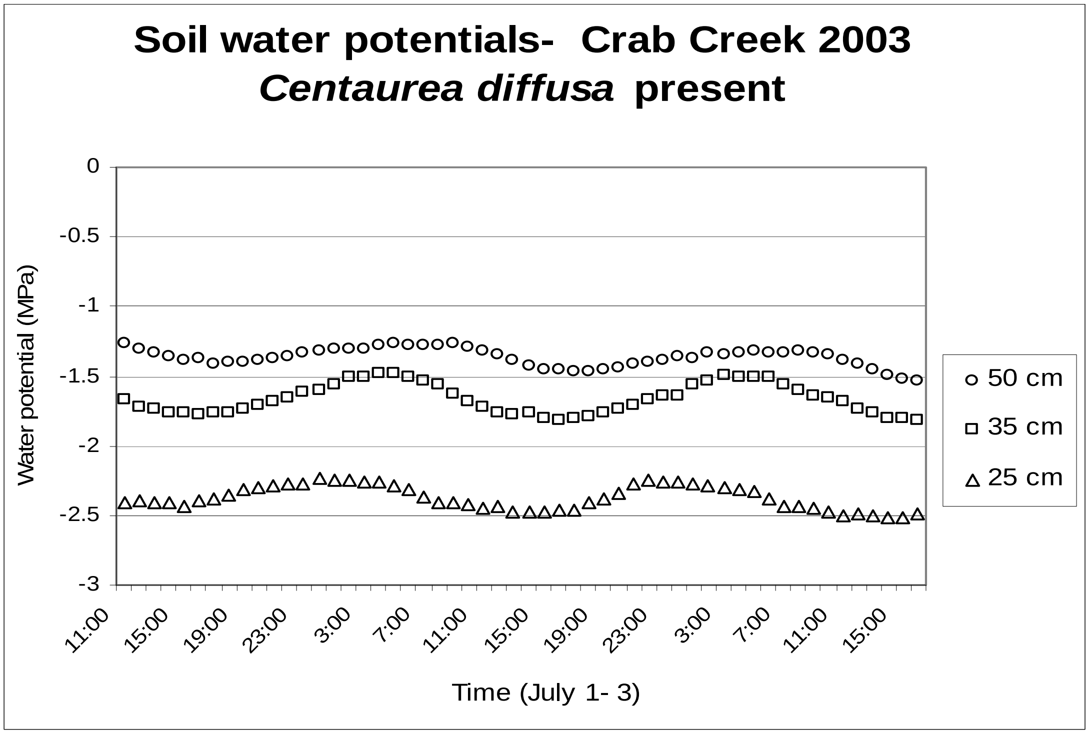


**Figure A5.** Soil water potential at 3 depths early in the growing season where *Centaurea diffusa* and *Festuca idahoensis* co-occur (top panel) and where *Centaurea diffusa* has been removed (lower panel) in a stand of *Artemisia tripartita/ Festuca idahoensis* near Crab Creek west of Sprague, WA.



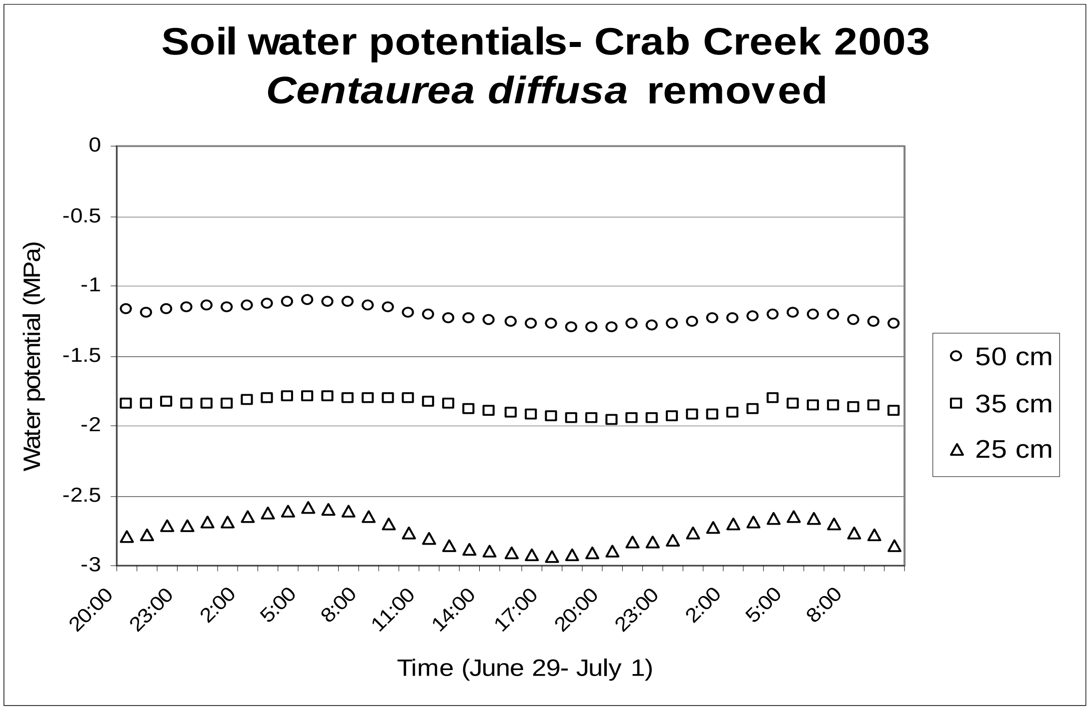


**Figure A6.** Soil water potential at 3 depths early in the growing season where *Centaurea diffusa* and *Festuca idahoensis* co-occur (top panel) and where *Centaurea diffusa* has been removed (lower panel) in a stand of *Artemisia tripartita/ Festuca idahoensis* near Crab Creek west of Sprague, WA.

# Midday leaf water potentials for *Centaurea solstitialis*

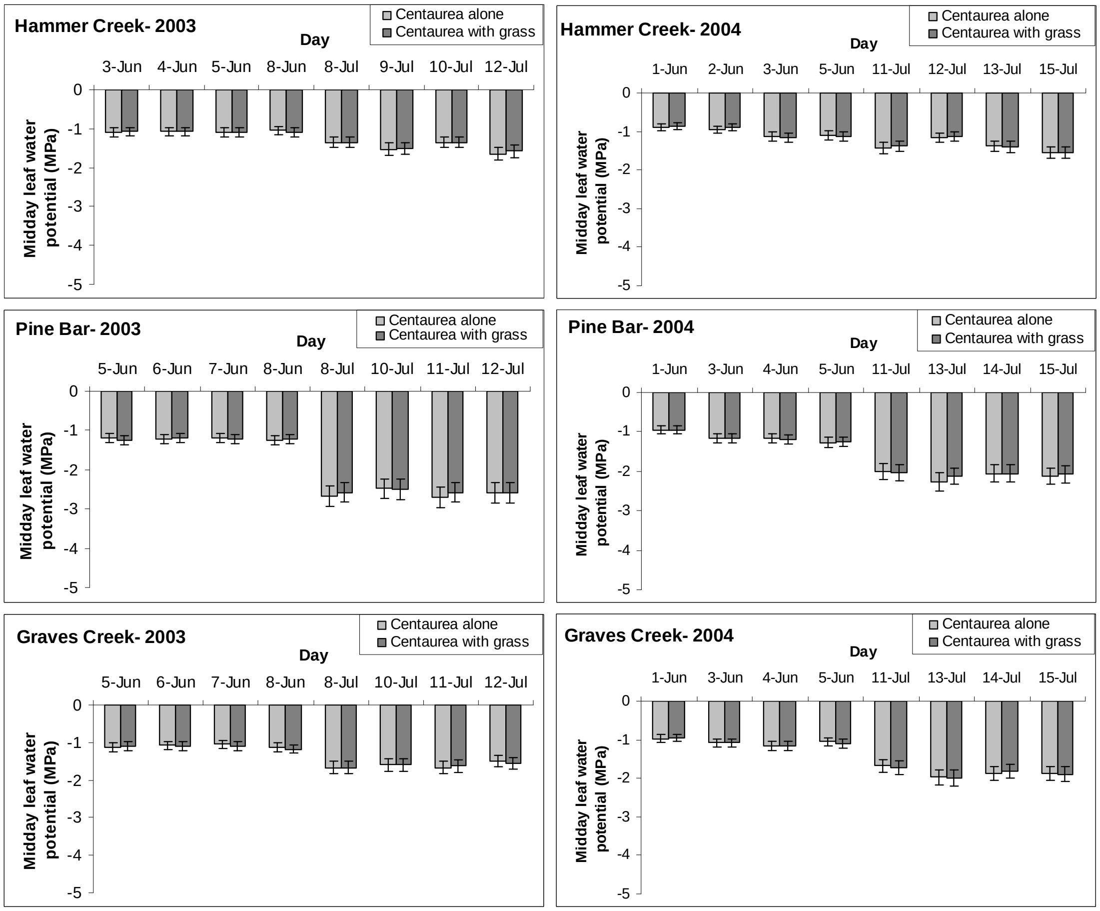


**Figure A7.** Midday leaf water potentials for *Centaurea solstitialis* in a stand of *Aristida longespica/ Poa secunda* where grasses have been removed (light bars) and where *Centaurea solstitialis* and grasses co-occur (dark bars). Leaf water potential values are means of 12 replicate measurements within a treatment in a stand. Error bars represent one standard error above and below the mean.

## Midday leaf water potentials for *Centaurea maculosa*

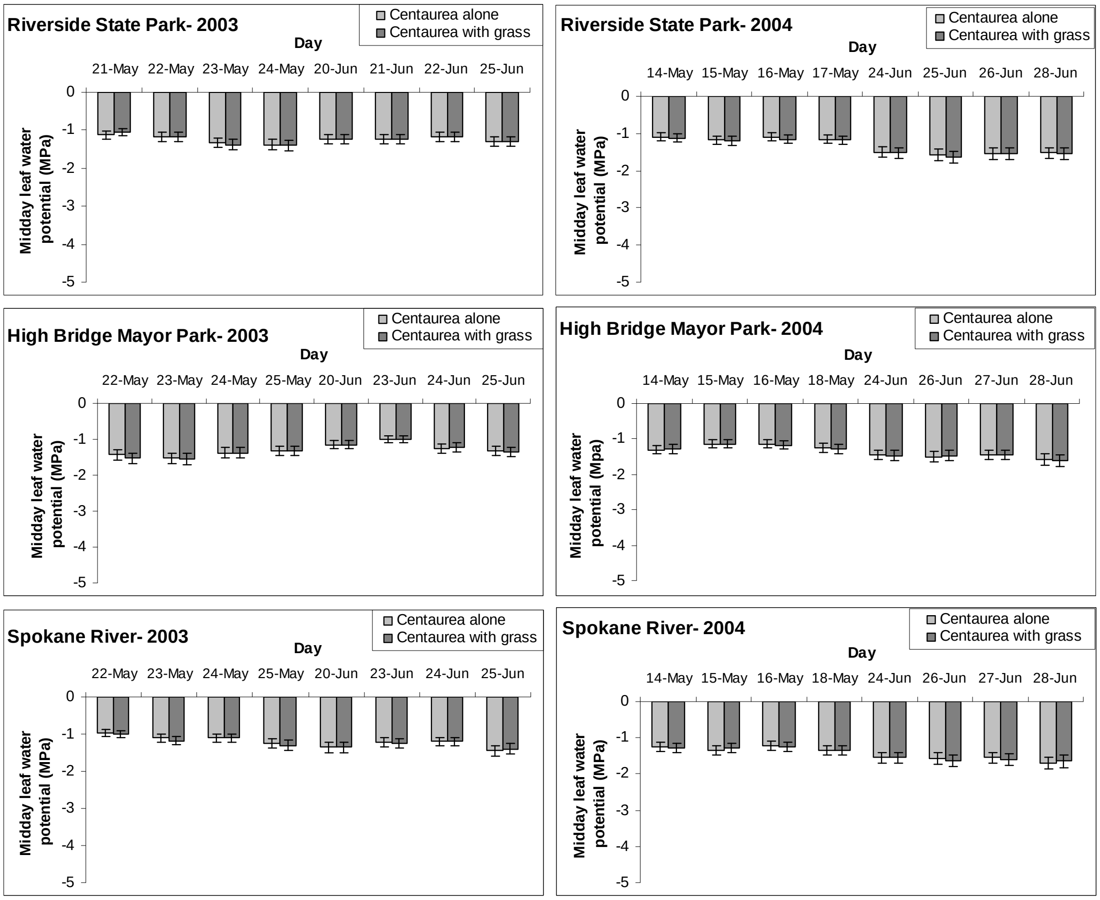


**Figure A8.** Midday leaf water potentials for *Centaurea maculosa* in a stand of *Pinus ponderosa/ Festuca idahoensis* where grasses have been removed (light bars) and where *Centaurea maculosa* and grasses co-occur (dark bars). Leaf water potential values are means of 12 replicate measurements within a treatment in a stand. Error bars represent one standard error above and below the mean.

# Midday leaf water potentials for *Centaurea diffusa*

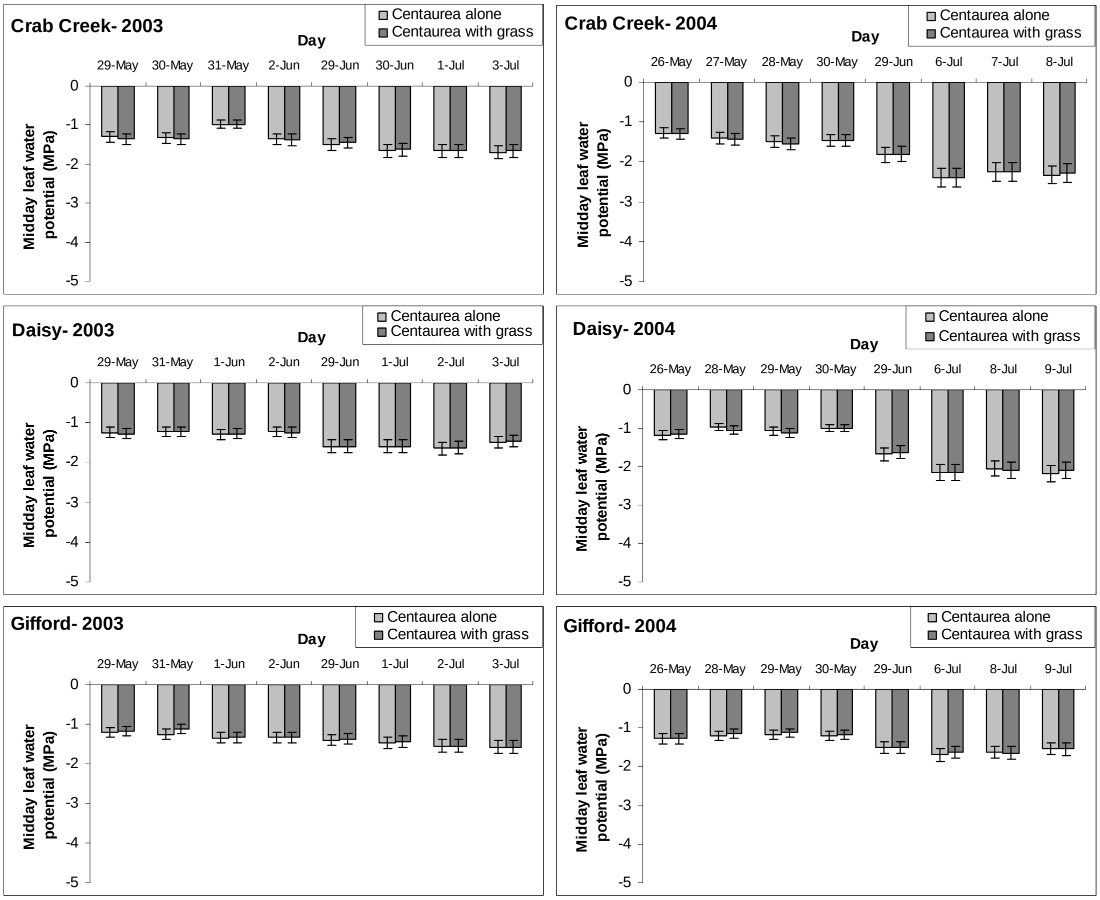


**Figure A9.** Midday leaf water potentials for *Centaurea diffusa* in a stand of *Artemisia tripartita/ Festuca idahoensis* where grasses have been removed (light bars) and where *Centaurea diffusa* and grasses co-occur (dark bars). Leaf water potential values are means of 12 replicate measurements within a treatment in a stand. Error bars represent one standard error above and below the mean.

## Midday leaf water potentials for *Aristida longesita*

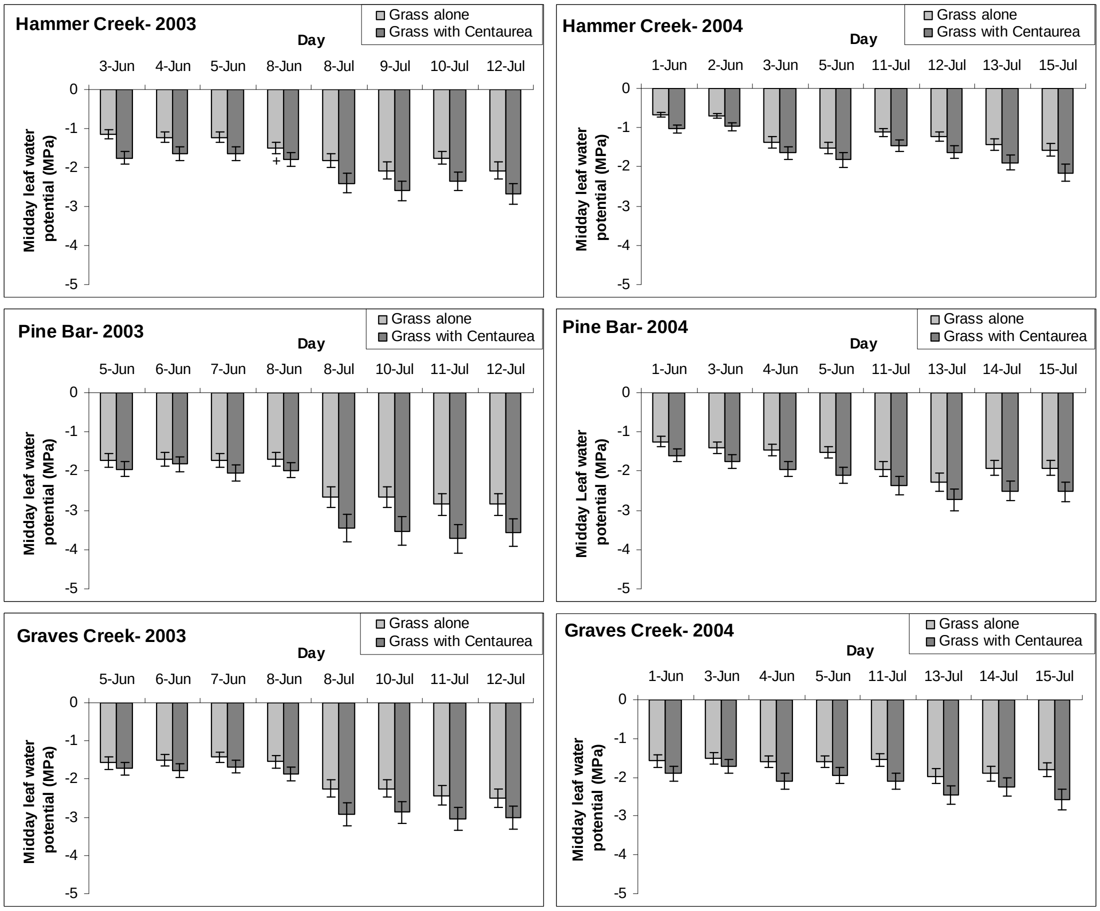


**Figure A10.** Midday leaf water potentials for *Aristida longespica* in a stand of *Aristida longespica/ Poa secunda* where *Centaurea solstitialis* has been removed (light bars) and where *Centaurea solstitialis* and grasses co-occur (dark bars). Leaf water potential values are means of 12 replicate measurements within a treatment in a stand. Error bars represent one standard error above and below the mean.

# Midday leaf water potentials for *Festuca idahoensis*

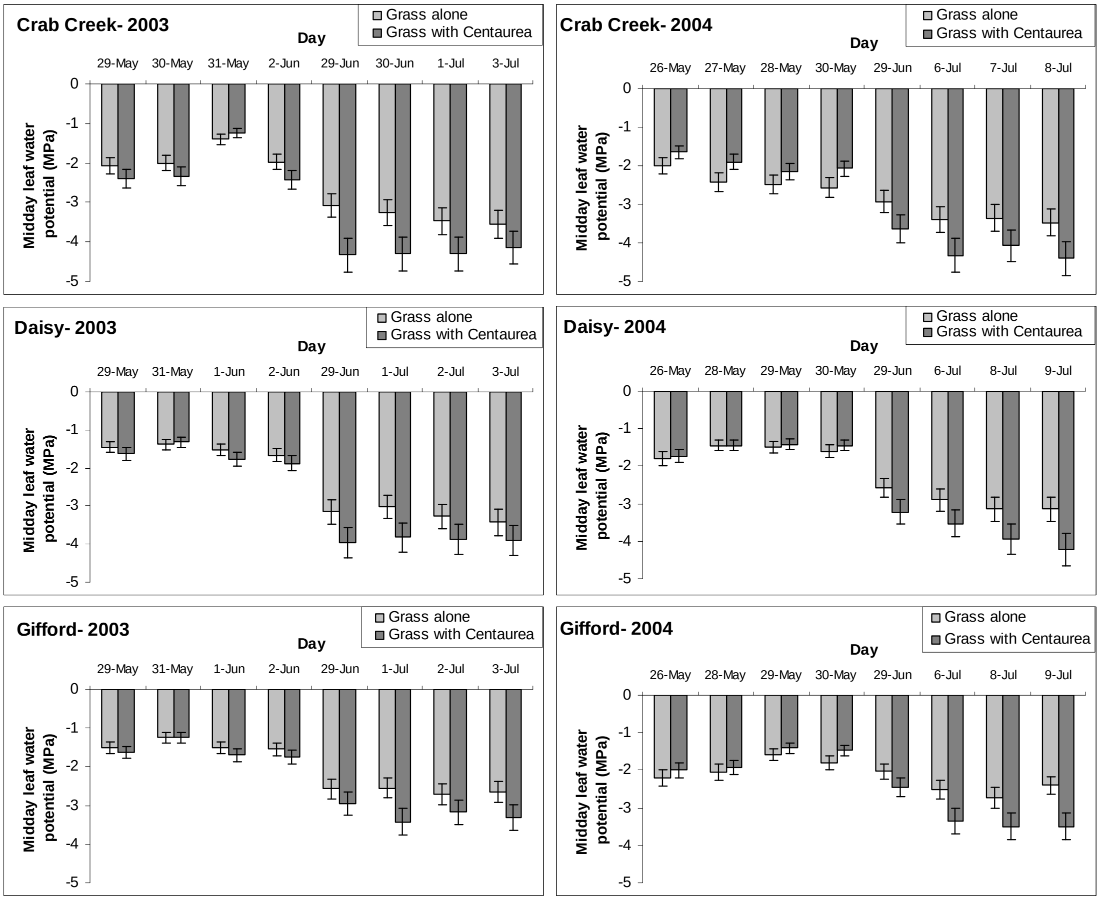


**Figure A11.** Midday leaf water potentials for *Festuca idahoensis* in a stand of *Artemisia tripartita/ Festuca idahoensis* where *Centaurea diffusa* has been removed (light bars) and where *Centaurea diffusa* and grasses co-occur (dark bars). Leaf water potential values are means of 12 replicate measurements within a treatment in a stand. Error bars represent one standard error above and below the mean.

# Midday leaf water potentials for *Festuca idahoensis*

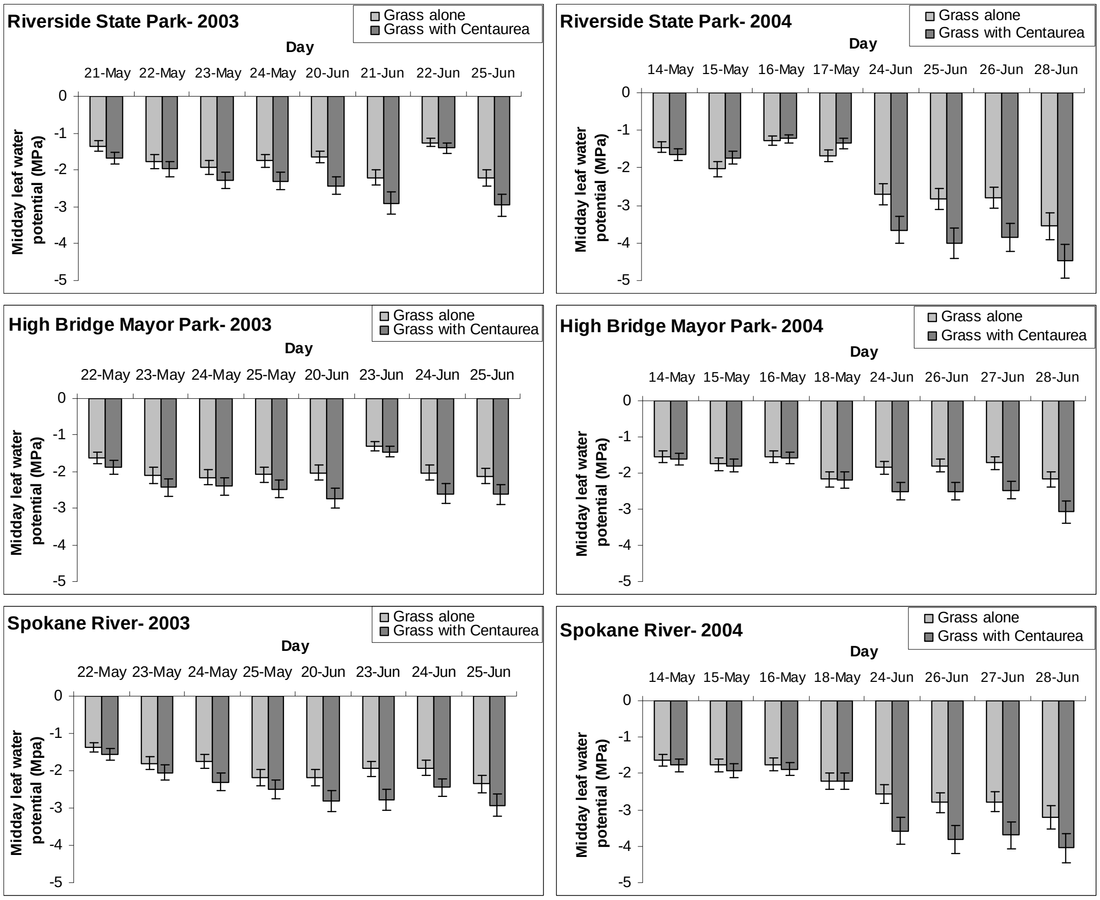


**Figure A12.** Midday leaf water potentials for *Festuca idahoensis* in a stand of *Pinus ponderosa/ Festuca idahoensis* where *Centaurea maculosa* has been removed (light bars) and where *Centaurea maculosa* and grasses co-occur (dark bars). Leaf water potential values are means of 12 replicate measurements within a treatment in a stand. Error bars represent one standard error above and below the mean.

# CHAPTER FOUR

# DIFFERENTIAL RESPONSES OF *CENTAUREA* AND *FESTUCA* TO COMPETITION UNDER A VARIETY OF SOIL CONDITIONS

## Introduction

Research has attempted to identify attributes of species that contribute to their invasive potential and to identify characteristics of environments and communities that make them susceptible to invasion by non-native species (Hooper et al. 2005). Generalizations have been elusive due to the varying nature of limiting resources through space and time (Renne et al. 2006, Thomsen and D'Antonio 2007) and the effects of resource availability on competitive interactions (Davis and Pelsor 2001, Maron and Marler 2007). Heretofore the only general conclusions are that species attributes which confer competitive success are highly dependent upon the environment, and that characteristics of communities that enhance resistance to invasion depend on the invading species (Mack 2003, Pokorney et al. 2005, Emery and Gross 2007) and on the spatial scale of the study(Fridley et al. 2004). Therefore investigative studies on attributes of invasive species are most meaningful when they involve a particular species or group of species in a specific environment.

*Centaurea* species have expanded their ranges in the semiarid parts of Western North America (DiTomaso 2000) and we are beginning to understand some of the factors underlying *Centaurea's* competitive success in this region (Marler *et al.* 1999, Hill et al. 2006, Kulmatiski et al. 2006). Once established, *Centaurea* species reduce the vigor of neighboring native grasses as a result of asymmetric competition for water favoring

*Centaurea* (Pankey chapter 3). Water is typically the limiting resource to plant growth in the Columbia Basin Ecoregion (LeJeune and Seastedt 2001). Although soils are generally at field capacity in April, they begin to dry from the top down as the summer drought approaches and by July water is generally only available in the deeper soil (Pankey chapter 3). Seasonally-dry shallow soil in this region accentuates the importance of deep roots. With a basal rosette and tap-root growth habit, *Centaurea* species access deeper water sources compared to the native grasses and do not experience competition for water from the native grasses (Pankey chapter 3). Since there are no upland plant associations in the region dominated by native forbs (Daubenmire 1970), *Centaurea* is a forb with a unique growth habit in this region and is also unique for its ability to dominate in grasslands.

Unlike the native forbs, such as *Balsamorhiza* species *and Lupinus* species, *Centaurea* can occur at high density whether grasses are present or not (Ridenour and Callaway 2001). These observations are consistent with our data that show the presence of native grasses having no measurable effect on the acquisition of water by *Centaurea* species (Pankey chapter 3). Earlier studies of grasses in the Columbia Basin Ecoregion suggest that downward root growth rate may be a single-factor determinant of success in semiarid regions (Harris 1967). Although rapid downward root growth may help to explain why *Centaurea* species are successful in western grasslands, it does not explain why native grasses, which primarily use shallow-soil water resources, would suffer as a result of *Centaurea* presence.

Studies examining the effects of variation in nutrient availability have found no relationship between nutrient availability and the outcome of competition between

*Centaurea* species and native grasses (Suding et al. 2004, Seastedt and Suding 2007) nor do *Centaurea* species appear to be better competitors for nutrients than native grasses (Olson and Blicker 2003, LeJeune et al. 2006). However, competitive interactions between *Centaurea* species and native grasses can be affected by altering soil chemistry through autoclaving native soils (Meiman et al. 2006), through charcoal additions to the soil (Ridenour and Callaway 2001), and through mid-spring burning (MacDonald *et al*. 2007), however the mechanisms responsible for these effects are elusive.

Fire has played an important role in the evolution of grasslands (Brown *et al*. 2005) and charcoal is one of the most significant byproducts of fire (DeLuca *et al.* 2006). One proposed hypothesis concerning the effect of charcoal on the competitive interactions between *Centaurea maculosa* and *Festuca idahoensis* proposes that charcoal immobilizes (±)-catechin, a secondary compound produced by *Centaurea maculosa* (Bais *et al*. 2002) which at high concentrations will inhibit growth by *Festuca idahoensis* (Callaway and Ridenour 2004). However, recent field investigations have revealed little or no (±)-catechin to be present in native soils where *Centaurea maculosa* occurs (Blair *et al*. 2005, Perry *et al.* 2007).

The first objective of this study was to characterize the root growth patterns of both *Centaurea maculosa* and the *Festuca idahoensis* and to measure potential shifts in root growth distribution resulting from interspecific competition for both water and nutrients. Secondly, my goal was to quantify the effect of charcoal on *Centaurea maculosa* and *Festuca idahoensis* and to investigate the importance of (±)-catechin on interspecific competition between these two species. After examination of each species' rooting pattern, I conducted a common garden competition experiment with a fully factorial arrangement of nutrients, water, and charcoal as soil additions, to test the hypotheses that 1) *Centaurea maculosa* competition results in a reduced rooting depth of *Festuca idahoensis* and 2) that the negative effects of *Centaurea maculosa* on *Festuca idahoensis* result from resource competition and are reduced by charcoal additions to the soil.

## Methods

Two separate experiments generated the data for this chapter. The goals of each experiment will first be presented and the descriptions of the materials and methods for each experiment will follow. The first experiment was conducted to allow direct measurement of each species relative rooting depths. The goals were to examine the depth distribution of root mass for *Festuca idahoensis* when grown with a conspecific competitor in pulverized soil and to determine whether competition with *Centaurea maculosa* caused a change in the root depth distribution of *Festuca idahoensis*. Second, the goal of the common garden experiment was to determine the relative importance of water, nutrients, and charcoal in the soil in controlling the competitive interactions between *Centaurea maculosa* and *Festuca idahoensis*.

### *Examination of rooting patterns*

*Festuca idahoensis* and *Centaurea maculosa* plants were grown from seed in a greenhouse with in the spring of 2003. Two 500-watt incandescent lamps were hung above each bench and provided supplemental lighting. Throughout the entire experiment, the locations of pots were randomized on a weekly basis to minimize the effect of environmental heterogeneity.  Several seeds were germinated in each pot and were then thinned as leaves emerged.  Plants remaining in the pots were selected to leave competing plants as similar in size as possible.  Plants were watered once weekly with one liter of water applied to each pot.  No additional nutrients were provided.  The treatments included growing one *Festuca idahoensis* individual with either a conspecific (as a control) or with a *Centaurea maculosa* individual (treatment).  The plants were grown in tall narrow pots (15 cm diameter, 40 cm height) filled with a 50:50 mixture of native soil and sand.  Native soil was sieved to remove rocks larger than 1 cm in diameter.  Nylon mesh (3 mm) was placed in the pots at 10-cm depth intervals to divide the pots into 4 layers and allow quantification of rooting depth upon harvesting.  After 4 months the plants were harvested.  Roots were separated at the nylon dividers, washed, oven dried at 60 °C, and weighed.

### *Common garden experiment*

*Festuca idahoensis* and *Centaurea maculosa* plants were grown from seed in a greenhouse beginning in early winter of 2005.  The greenhouse contained two 500-watt incandescent lamps above each bench.  The greenhouse temperature was maintained at approximately 5 °C during the night and 15 °C to 20 °C during the day.  Several seeds of one species or the other were germinated in each pot and were then thinned to one plant per pot as leaves emerged.  The plant nearest the center of the pot was left and all others were removed.  The plants were grown in small plastic pots (8 cm wide, 10 cm tall) filled with commercial potting mix.  The locations of the pots on the greenhouse bench were randomized each week.  In late April after 3 months of growth, the plants were removed from the greenhouse and transported to the common garden where they were randomly assigned to treatments.

The common garden plot was located on WSU property at the “Airport Garden” and contained native soil for the region and was hand cleared of vegetation. A randomized complete block design with ten experimental blocks was established. Within each block, nine holes (15 cm wide, 40 cm deep) were dug in a three by three arrangement using a power auger and leaving 30 cm between each hole and then the holes were lined with plastic tubes. The plastic tubes confined each replicate to a soil volume to facilitate harvesting of the roots. Each of the nine treatments was represented in each block. The location of each treatment was randomly assigned in each block. One of the nine treatments involved growing a *Festuca idahoensis* individual with a conspecific to serve as a control. The remaining eight treatments all involved one *Festuca idahoensis* individual growing with one *Centaurea maculosa* individual in soil with a unique combination of amendments (Table 4.2).

The charcoal and the nutrient treatments were applied to the soil only one time; the water treatment (described below) was applied weekly. The soil that had been removed from the ground when the holes were dug was bulked for each experimental block and then mixed with either finely ground charcoal, Osmocote® brand time-release plant fertilizer, both charcoal and Osmocote®, or neither soil amendment. Charcoal was added at a rate of 20 grams per liter of soil volume (Ridenour and Callaway 2001) and nutrients were added at the rate recommended by the manufacturer. The plastic-lined holes were then filled with the appropriate soil for the treatment and watered with one liter of water for each hole. Blocks and treatments were labeled with stakes and the young plants were then transplanted into their respective treatment locations randomly. Treatments that were to receive supplemental water were provided one additional liter of water weekly, added at the base of the plants, for the remainder of the experiment. No other treatments received supplemental water.

After ten weeks, in early July 2005, the plants were harvested, separated into roots and shoots, washed, oven dried at 60 °C and weighed. After weighing, plant material was combusted in a muffle furnace at 500° C to attain ash-free dry weight for each sample. When harvested, each plant was separated into 3 portions: aboveground, belowground shallow (< 20 cm deep), and belowground deep (> 20 cm deep) for processing. Soil samples were submitted to the lab of J. Vivanco at Colorado State University for analysis of (±)-catechin by gas chromatography.

### Data Analysis

ANOVA was conducted using SAS to detect the effects of *Centaurea maculosa*, water additions, nutrient addition, and charcoal on root biomass of *Festuca idahoensis*. We tested for significant variance of *Festuca idahoensis* biomass in the interaction of water additions, nutrient additions, and charcoal. Main effects of soil addition treatments were compared since no significant interactions were detected.

## Results

### Examination of rooting patterns

*Centaurea maculosa* strongly influenced total *Festuca idahoensis* biomass production ($p < 0.001$) and *Festuca* leaf production ($p < 0.05$). *Centaurea maculosa* also affected *Festuca idahoensis* root growth at 10-20 cm depth ($p < 0.05$), 20-30 cm depth ($p < 0.01$), and 30-40 cm depth ($p < 0.001$) (figure 4.1).

The *Festuca idahoensis* plants grown with *Centaurea maculosa* individuals produced 54% less biomass and did not root as deeply as the *Festuca idahoensis* plants grown with intraspecific competitors (figure 4.1). Aboveground biomass of *Festuca idahoensis* individuals grown with a conspecific were more than double the biomass of *Festuca idahoensis* individuals grown with *Centaurea maculosa,* 1.06 (±0.21) grams and 0.50 (±0.09) grams respectively (figure 4.1). *Festuca idahoensis* root mass per individual in the top 10 cm of soil was not different whether grown with a conspecific or with *Centaurea maculosa,* but *Festuca idahoensis* root mass per individual at all other soil depths was less when grown with *Centaurea maculosa* compared to growth with a conspecific. At the 10 to 20 cm soil depth, root mass was almost double for the *Festuca idahoensis* individuals grown with a conspecific compared to growth with a *Centaurea maculosa* individual (1.02 (±0.20) and 0.54 (±0.10) grams respectively) (figure 4.1). At the 20 to 30 cm depth *Festuca idahoensis* grown with a conspecific and *Festuca idahoensis* grown with a *Centaurea maculosa* individual produced 0.99 (±0.21) and 0.10 (±0.03) grams of biomass respectively, and at a depth greater than 30 cm, *Festuca idahoensis* individuals produced 0.59 (±0.13) grams of biomass with a conspecific compared to 0.00 grams with a *Centaurea maculosa* competitor (figure 4.1).

### *Common garden experiment*

In all treatments, *Centaurea maculosa* produced more biomass than *Festuca idahoensis*. Mean total biomass for the plants grown in the standard soil mix were 36.2

(±4.5) grams for *Centaurea maculosa* grown with *Festuca idahoensis* (figure 4.4) and 12.8 (±1.5) grams for *Festuca idahoensis* grown with a conspecific (figure 4.2). The *Festuca* grown with *Centaurea* however, were 31% smaller and produced only 8.8 (±1.2) grams of total biomass (figure 4.2). *Festuca idahoensis* individuals growing with *Centaurea maculosa* individuals produced less total root mass than *Festuca idahoensis* individuals growing with a conspecific ($p < 0.05$) (figure 4.3) but aboveground biomass of *Festuca idahoensis* was unaffected by the presence of *Centaurea maculosa* (figure 4.2).

Total root mass of *Festuca idahoensis* was significantly affected by all three soil amendments: charcoal, nutrients, and water (Table 4.1). However, no significant variance in biomass was detected for the interaction of the charcoal, nutrient or water treatments. Charcoal increased the biomass of *Festuca idahoensis* in the presence of *Centaurea maculosa* ($p < 0.05$) (figure 4.5), but charcoal had no effect on the biomass of *Centaurea maculosa* (figure 4.4) except when supplemental water was provided (figure 4.6). Total biomass of *Festuca idahoensis* was unaffected by the watering treatment but root fraction was reduced in response to the water additions. Total biomass of *Festuca idahoensis* was significantly greater in the nutrient and charcoal addition treatment compared to the nutrient addition treatment ($p < 0.05$) (figure 4.5).

*Centaurea maculosa* biomass was not significantly affected by the nutrient treatment ($p = 0.17$) and was positively affected by the watering treatment ($p < 0.01$) (figure 4.6). All soils tested negative for (±)-catechin.

## Discussion

Results from the common garden experiment support the hypothesis that young *Festuca idahoensis* plants produce less root mass and a shallower root system in the presence of *Centaurea maculosa* compared to young *Festuca idahoensis* plants growing with a *Festuca idahoensis* competitor. The *Festuca idahoensis* individuals grown with *Centaurea maculosa* competitors produced less total biomass ($p < 0.05$) (table 4.1) and less root biomass than *Festuca idahoensis* individuals grown with conspecific competitors (figure 4.2). These data are consistent with previously published data for the effect of *Centaurea maculosa* on growth of *Festuca idahoensis* plants (Maron and Marler 2008). Altered rooting patterns of *Festuca* in competition with *Centaurea* indicate that the 0-10 cm depth in the soil is proportionally twice as important (65% of total root mass compared to 33% of total root mass) for *Festuca idahoensis* growing with *Centaurea maculosa* relative to *Festuca idahoensis* growing with a conspecific (figure 4.1). Confinement of roots to shallower and drier soil, results in reduced water acquisition and growth for *Festuca idahoensis*.

If nutrient depletion by *Centaurea maculosa* plays an important role in the competitive effect of *C. maculosa* on *Festuca idahoensis,* the nutrient addition treatment should have positively affected *F. idahoensis* biomass. In contrast to this prediction, *Festuca idahoensis* individuals competing with *Centaurea maculosa* that received the nutrient addition treatment produced 33% less biomass than *F. idahoensis* individuals that did not receive nutrient additions. Nutrient additions lead to a small but insignificant ($p = 0.17$) increase in *Centaurea maculosa* biomass suggesting that *C. maculosa* growth was not limited by nutrients. Consistent with our results, Olson and Blicker (2003) also found that *Centaurea maculosa* was a better competitor against adult bunchgrasses in nutrient addition experiments. Western grasslands have historically been nutrient poor ecosystems so traits that confer nutrient retention should be favored over traits enabling precocious nutrient acquisition (Aerts 1999, Funk 2008).

If water is the growth-limiting resource then we should see an enhancement in growth only when water is added. Growth by *Centaurea maculosa* in the water-addition treatment was nearly 50% greater than in the control treatment indicating that water and not nutrients was the limiting resource for *C. maculosa*. Despite the significantly larger size of the *C. maculosa* competitors in the water-addition treatment, growth of the *Festuca idahoensis* individuals was unaffected and so the competitive relationship between species was unchanged suggesting that competition for water was an important factor contributing to the competitive effect of *C. maculosa* on *F. idahoensis* in our experiment. These data are consistent with data from an experiment by Maron and Marler (2008) who found that water additions did not change the competitive effect of *Centaurea maculosa* on *Festuca idahoensis* but instead resulted in two times greater growth by *C. maculosa*.

(±)-Catechin, a secondary compound produced by the roots of *Centaurea maculosa* (Bais *et al*. 2002) has also been reported to reduce growth of native grasses (Bais *et al*. 2003, Weir *et al*. 2003, Callaway and Ridenour 2004, but see Blair *et al*. 2005, Perry *et al*. 2007). Charcoal decreases the solution concentration of plant secondary compounds in the soil (DeLuca *et al*. 2006) but all soil analyses from the common garden experiment were negative for (±)-catechin which minimizes the possibility that (±)-catechin was responsible for the competitive effect we observed of *Centaurea maculosa* on *Festuca idahoensis*.

In my experiment, charcoal additions to the soil reduced the competitive effect of *Centaurea maculosa* on *Festuca idahoensis* and eliminated the effect of water or nutrient additions on this competitive interaction. Previous greenhouse experiments examining competition between grasses and *C. maculosa* have also found a relaxation of the competitive effect of *C. maculosa* individuals on grasses when charcoal is added to the soil (Ridenour and Callaway 2001). Similarly, field-based experiments in grasslands have found increased grass productivity following fires (MacDonald *et* al. 2007, Zimmerman *et al.* 2008) which may result from many factors including charcoal addition to the soil. Many field studies have found little or no effect of charcoal addition on soil resource availability in grasslands however (Bennett *et* al. 2002, DeLuca *et al.* 2006, Veen *et al*. 2008), so charcoal's stimulation of grass growth may be due to alleviation of some other limitation to growth.

Charcoal in the soil reduced the competitive effect of *Centaurea maculosa* on *Festuca idahoensis* (figure 4.5) indicating that fire may be a factor that reduces the success of *C. maculosa* when competing with native grasses. The deep-rooting habit of *Centaurea* and its ability to increase growth in response to resource additions are factors that increase the competitive ability of *Centaurea maculosa* relative to native grasses.

Soil water and nutrient additions did not affect the competitive outcome between *Centaurea maculosa* and *Festuca idahoensis* indicating that resource competition between *Festuca* and *Centaurea* is not likely to retard the growth of *Centaurea* populations. Resource competition negatively affects *Festuca* so the competitive success of *Centaurea* in steppe habitats of the Columbia Basin Ecoregion may be due in part to the reduction in growth of the dominant native grass species that results from the presence of *Centaurea* competitors. *Centaurea maculosa* is an invasive species because it detrimental to the native plant community where it establishes and spreads across the community. The superior competitive ability of *C. maculosa* relative to *F. idahoensis* across a range of soil resource levels suggests that the best way to control future *Centaurea* invasions is to prevent the establishment of new populations.

## Literature Cited

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs, and plant-soil feedbacks. Journal of Experimental Botany 50 (330):29-37.

Bais, H. P.; T. S. Walker; F. R. Stermitz; R. A. Hufbauer; J. M. Vivanco. 2002. Enantiomeric-dependent phytotoxic and antimicrobial activity of (+/-)-catechin. A rhizosecreted racemic mixture from spotted knapweed. Plant Physiology 128:1173-1179.

Bais, H. P.; R. Vepachedu; S. Gilroy; R. M. Callaway; J. M. Vivanco. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Science 301:1377-1380.

Bennett, L. T.; T. S. Judd; M. A. Adams. 2002. Growth and nutrient content of perennial grasslands following burning in semi-arid sub-tropical Australia. Plant Ecology 164:185-199.

Blair, A. C.; B. D. Hanson; G. R. Brunk; R. A. Marrs; P. Westra; S. J. Nissen; R. A. Hufbauer. 2005. New techniques and findings in the study of a candidate allelochemical implicated in invasion success. Ecology Letters 8:1039-1047.

Brown, K. J.; J. S. Clark; E. C. Grimm; J. J. Donovan; P. G. Mueller; B. C. S. Hansen; I. Stefanova. 2005. Fire cycles in North American interior grasslands and their relation to prairie drought. Proceedings of the National Academy of Science 102 (25):8865-8870.

Callaway, R. M.; W. M. Ridenour. 2004. Novel weapons: invasion success and the evolution of increased competitive ability. Frontiers in Ecology and Environment 2:436-443.

Daubenmire, R. 1970. Steppe Vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62.

Davis M. A.; M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421-428.

DeLuca, T. H.; M. D. MacKenzie; M. J. Gundale; W. E. Holben. 2006. Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. Soil Science of America Journal 70:448-453.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: Species, impacts, and management. Weed Science 48:255-265.

Emery, S. M.; K. L. Gross. 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland communities. Ecology 88 (4):954-964.

Fridley, J. D.; R. L. Brown; J. E. Bruno. 2004. Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. Ecology 85 (12):3215-3222.

Funk, J. L. 2008. Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96: 1162-1173.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecological Monographs 37 (2): 89-111.

Hill, J. P.; M. J. Germino; J. M. Wraith; B. E. Olson; M. B. Swan. 2006. Advantages in water relations contribute to greater photosynthesis in *Centaurea maculosa* compared with established grasses. International Journal of Plant Sciences 167 (2):269-277.

Hooper, D. U.; E. S. Chapin III; J. J. Ewel; A. Hector; P. Inchausti; S. Lavorel; J. H. Lawton; D. M. Lodge; M. Loreau; S. Naeem, B. Schmid; H. Setala; A. J. Symstad; J. Vandermeer; D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75 (1):3-35.

Kulmatiski, A.; K. H. Beard; J. M. Stark. 2006. Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. Plant and Soil 288 (1-2):271-284.

LeJeune, K. D.; T. R. Seastedt. 2001. *Centaurea* species: the forb that won the west. Conservation Biology 15, No. 6: 1568-1574.

LeJeune, K. D.; K. N. Suding; T. R. Seastedt. 2006. Nutrient availability does not explain invasion and dominance of a mixed grass prairie by the exotic forb *Centaurea diffusa.* Applied Soil Ecology 32 (1):98-110.

MacDonald, N. W.; B. T. Scull; S. R. Abella. 2007. Mid-spring burning reduces spotted knapweed and increases native grasses during a Michigan experimental grassland establishment. Restoration Ecology 15 (1):118-128.

Mack, R. N. 2003. Phylogenetic constraint, absent life forms, and pre-adapted alien plants: a prescription for biological invasions. International Journal of Plant Sciences 164 (3 supplement): S185-S196.

Marler, M. J.; C. A. Zabinski; T. Wojtowicz; R. M. Callaway. 1999. Mycorrhizae and fine root dynamics of *Centaurea maculosa* and native bunchgrasses in western Montana. Northwest Science 73 (3):217-224.

Maron J.; M. Marler. 2007. Native plant diversity resists invasion at both low and high resource levels. Ecology 88 (10):2651-2661.

Maron J. L.; M. Marler. 2008. Field-based competitive impacts between invaders and natives at varying resource supply. Journal of Ecology 96:1187-1197.

Meiman, P. J.; E. F. Redente; M. W. Paschke. 2006. The role of the native soil community in the invasion ecology of spotted and diffuse knapweed. Applied Soil Ecology 32 (1):77-88.

Olson, B. E.; P. S. Blicker. 2003. Response of the invasive *Centaurea maculosa* and two native grasses to N-pulses. Plant and Soil 254: 457-467.

Perry, L. G.; G. C. Thelen; W. M. Ridenour; R. M. Callaway; M. W. Paschke; J. M. Vivanco. 2007. Concentrations of the allelochemical catechin in *Centaurea maculosa* soils. Journal of Chemical Ecology 33 (12):2337-2344.

Pokorny, M. L.; R. L. Sheley; C. A. Zabinski; R. E. Engel; T. J. Svejcar; J. J. Bokorski. 2005. Plant functional group diversity as a mechanism for invasion resistance. Restoration Ecology 13:448-459.

Renne, I. J.; B. F. Tracy; I. A. Colonna. 2006. Shifts in grassland invasibility: Effects of soil resources, disturbance, composition, and invader size. Ecology 87 (9):2264-2277.

Ridenour, W. M.; R. M. Callaway. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126:444-450.

Seastedt, T. R.; K. N. Suding. 2007. Biotic constraints on the invasion of diffuse knapweed (*Centaurea diffusa*) in North American grasslands. Oecologia 151 (4):626-636.

Suding, K. N.; K. D. LeJeune; T. R. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. Oecologia 145:526-535.

Thomsen, M. A.; C. M. D'Antonio. 2007. Mechanisms of resistance to invasion in a California grassland: the roles of competitor identity, resource availability and environmental gradients. Oikos 116 (1):17-30.

Veen, G. F.; J. M. Blair; M. D. Smith; S. L. Collins. 2008. Influence of grazing and fire frequency on small-scale plant community structure and resource variability in native tallgrass prairie. Oikos 117:859-866.

Weir, T. L.; H. P. Bais; J. M. Vivanco. 2003. Intraspecific and interspecific interactions mediated by a phytotoxin, (-)-catechin, secreted by the roots of *Centaurea maculosa* (spotted knapweed). J. Chem. Ecol 29:2397-2412.

Zimmerman, J; S. I. Higgins; V. Grimm; J. Hoffman; T. Munkenmuller; A. Linstadter. 2008. Recruitment filters in a perennial grassland: the interactive roles of fire, competitors, moisture and seed availability. Journal of Ecology 96:1033-1044.

**Table 4.1.** Analysis of variance for the effects of experimental factors on ash-free dry weight of *Festuca idahoensis* roots. The effect of charcoal was positive and the effects of water, nutrients, and *Centaurea maculosa* were negative. Factors did not significantly interact.

| **Factor** | **DF** | **Type 1 SS** | **Mean Square** | **F Value** | **P Value** |
|---|---|---|---|---|---|
| Charcoal | 1 | 0.679 | 0.679 | 3.89 | 0.05 |
| Water | 1 | 2.086 | 2.086 | 11.93 | <0.001 |
| Nutrients | 1 | 2.987 | 2.987 | 17.08 | <0.001 |
| *Centaurea* | 1 | 1.056 | 1.056 | 6.04 | 0.02 |
| Charcoal * Water * Nutrients | 3 | 0.903 | 0.301 | 1.72 | 0.17 |
| Block | 9 | 8.353 | 0.928 | 5.31 | <0.001 |

**Table 4.2.** Descriptions of the nine experimental treatments including treatment number, species grown in each treatment, and soil amendments for each treatment.

| Treatment # | Species | Soil Amendments |
|---|---|---|
| 1. | *Festuca* with *Festuca* | Standard mix |
| 2. | *Festuca* with *C. maculosa* | Standard mix |
| 3. | *Festuca* with *C. maculosa* | Water |
| 4. | *Festuca* with *C. maculosa* | Nutrients |
| 5. | *Festuca* with *C. maculosa* | Charcoal |
| 6. | *Festuca* with *C. maculosa* | Water + Nutrients |
| 7. | *Festuca* with *C. maculosa* | Water + Charcoal |
| 8. | *Festuca* with *C. maculosa* | Nutrients + Charcoal |
| 9. | *Festuca* with *C. maculosa* | Water + Nutrients + Charcoal |

**Figure 4.1.** Shoot and root biomass produced by *Festuca idahoensis* target plants when grown with a *Centaurea maculosa* or a *Festuca idahoensis* competitor (test plant). Bars represent means of 6 replicate plants. Error bars represent one standard error above and below the mean. Differences between treatments are significant ($p < 0.05$) for all but root biomass at 0-10 cm depth.

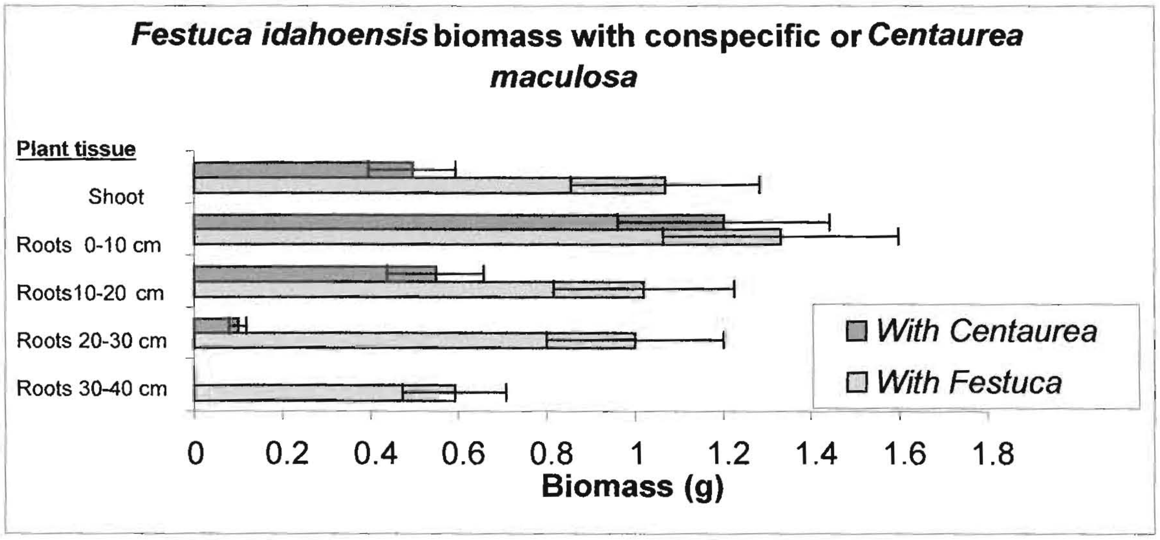

Festuca idahoensis biomass with conspecific or Centaurea maculosa
Plant tissue
Shoot
Roots 0-10 cm
Roots10-20 cm
Roots 20-30 cm
Roots 30-40 cm
▨ With Centaurea
☐ With Festuca
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
Biomass (g)

**Figure 4.2.** Ash-free dry weight for shoot and roots of *Festuca idahoensis* individuals grown with either a *Centaurea maculosa* competitor (dark bars) or a *Festuca idahoensis* competitor (light bars). Shoot production was not different between treatments but competitor identity significantly affected root growth at both soil depths ($p < 0.05$). Bars represent means of 10 replicate plants within a treatment. Error bars represent one standard error above and below the mean.

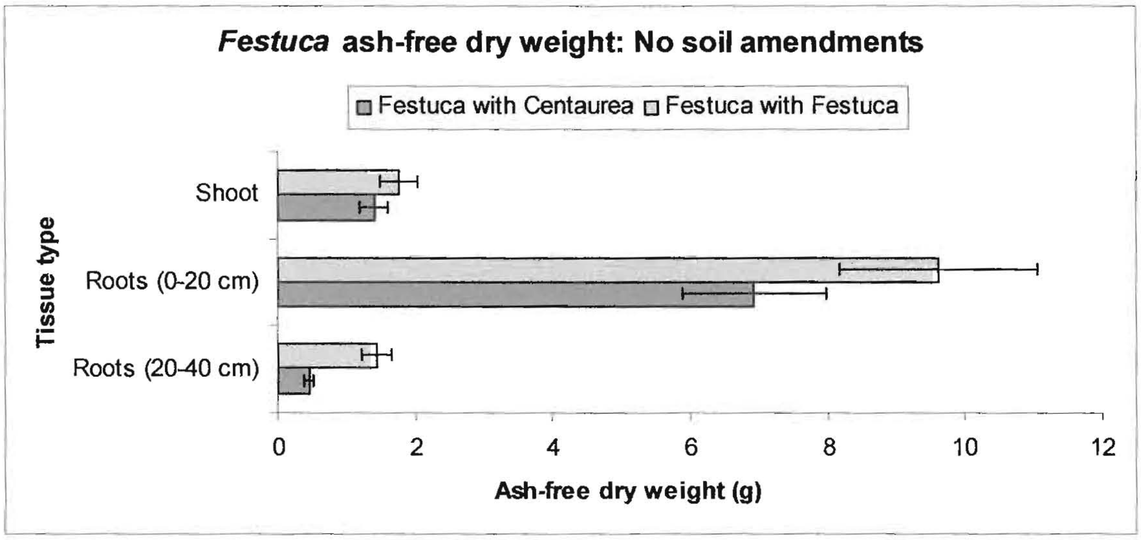

*Festuca* ash-free dry weight: No soil amendments
▨ Festuca with Centaurea
☐ Festuca with Festuca
Tissue type
Shoot
Roots (0-20 cm)
Roots (20-40 cm)
0
2
4
6
8
10
12
Ash-free dry weight (g)

**Figure 4.3.** Ash-free root mass of *Festuca idahoensis* individuals grown with a *Festuca idahoensis* competitor (left bar), with a *Centaurea maculosa* competitor (center bar) and with a *Centaurea* competitor and charcoal in the soil (right bar). The light portion of each bar represents the amount of *Festuca* root biomass from less than 20-cm deep and the dark portion of each bar represents the amount of *Festuca* root biomass from greater than 20-cm deep. Bars represent means of 10 replicate plants within a treatment. Error bars represent one standard error above and below the mean. *Centaurea* negatively affected *Festuca* total root mass ($p = 0.02$). The charcoal addition treatment positively affected *Festuca* root mass when grown with *Centaurea* as a competitor ($p = 0.05$).

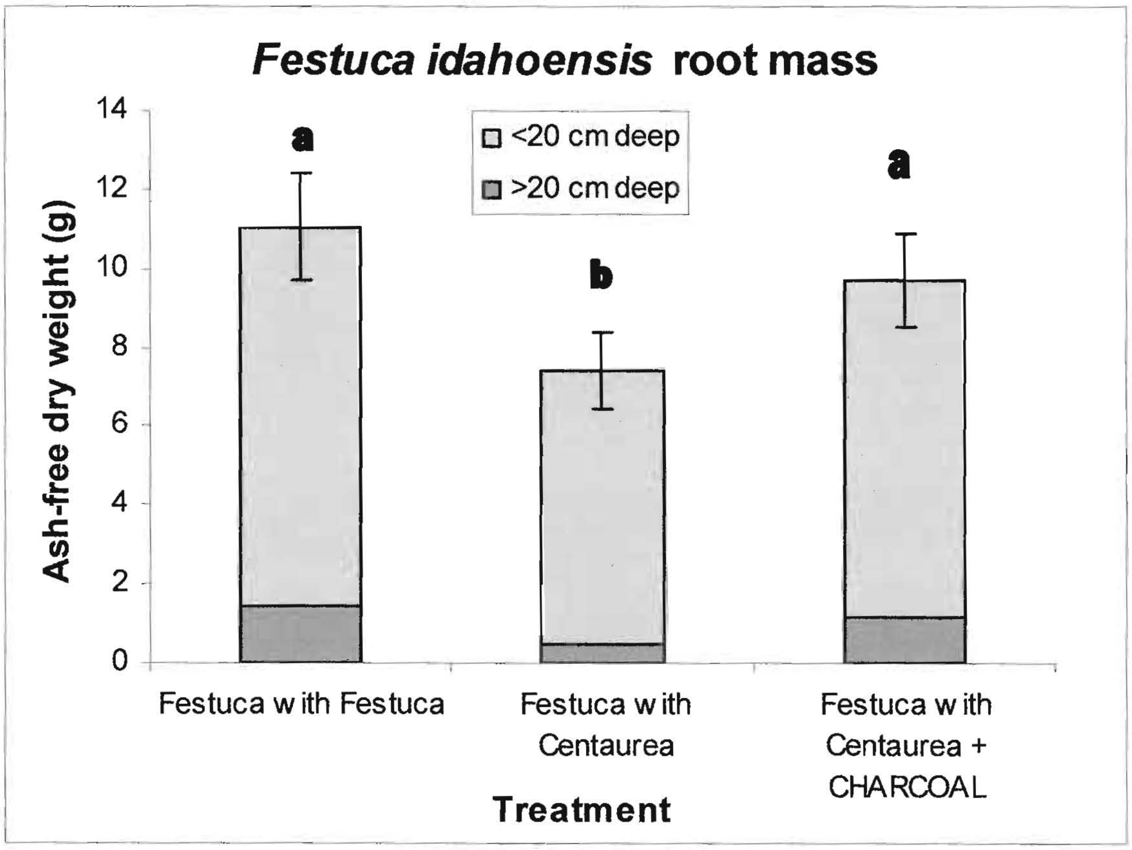
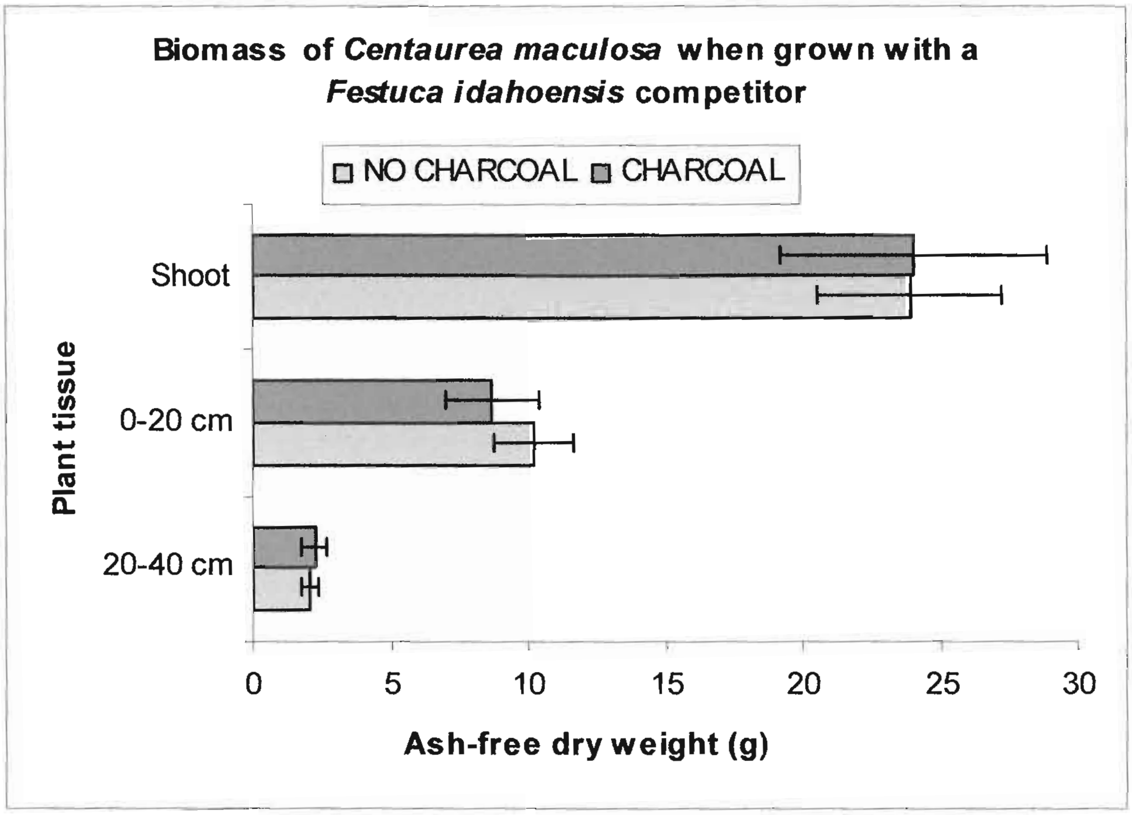

*Festuca idahoensis* root mass
14
12
10
8
6
4
2
0
Ash-free dry weight (g)
a
b
a
□ <20 cm deep
▨ >20 cm deep
Festuca with Festuca
Festuca with Centaurea
Festuca with Centaurea + CHARCOAL
Treatment

**Figure 4.4.** Ash-free dry weight for shoot and roots of *Centaurea maculosa* plants grown with a *Festuca idahoensis* competitor and no soil additions (light bars) or with charcoal added to the soil (dark bars). Bars represent means of 10 replicate plants within a treatment. Error bars represent one standard error above and below the mean.



**Biomass of *Centaurea maculosa* when grown with a *Festuca idahoensis* competitor**

**Figure 4.5.** Ash-free dry weight of *Festuca idahoensis* plants when grown with a *Centaurea maculosa* competitor without charcoal added to the soil (light bars) and with charcoal added to the soil (dark bars); with no additional water or nutrients (left bars), with additional nutrients (center bars), and with additional water (right bars). Nutrient additions had a negative effect on total biomass of *Festuca* ($p < 0.05$). Charcoal additions positively affected *Festuca* biomass ($p < 0.05$) in the nutrient addition, water addition, and control treatments. Bars represent means of 10 replicate plants within a treatment. Error bars represent one standard error above and below the mean.

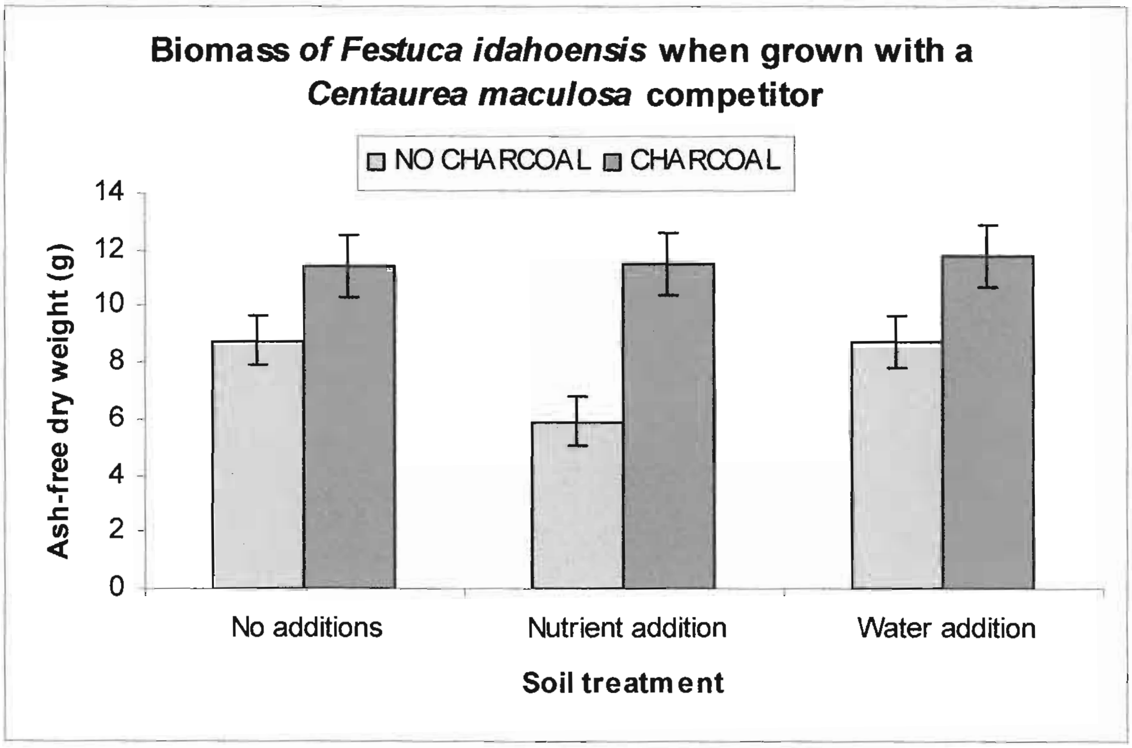
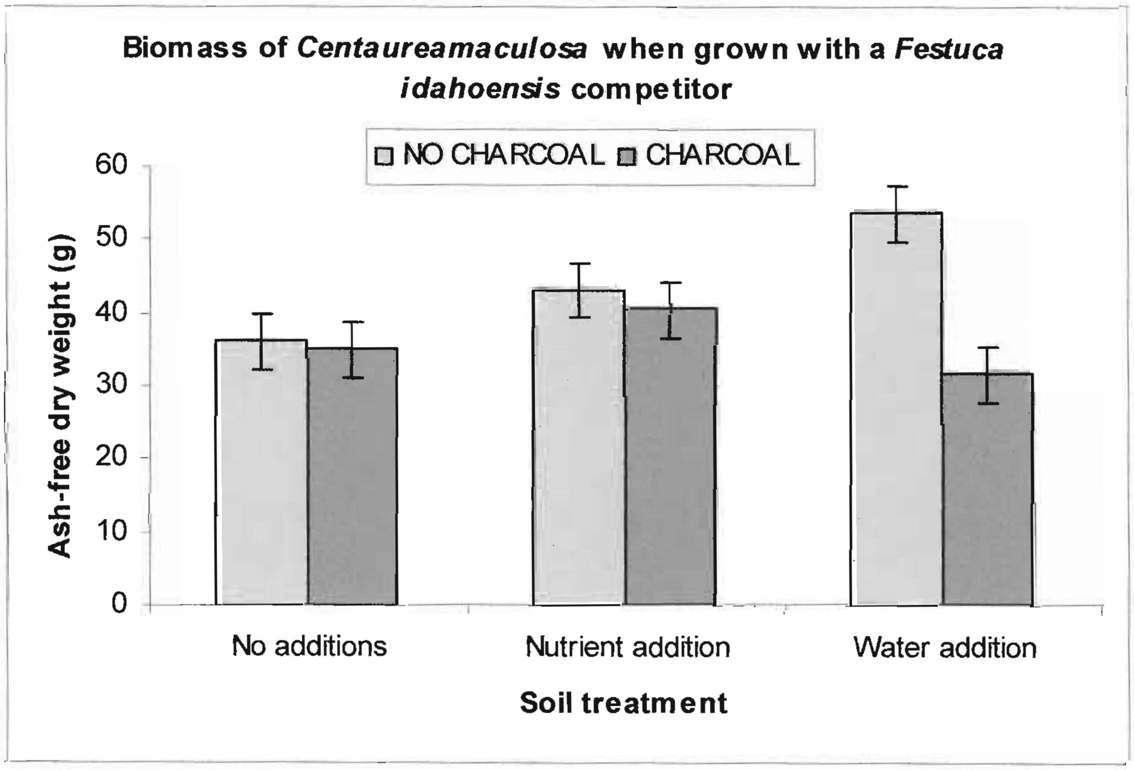

Biomass of Festuca idahoensis when grown with a Centaurea maculosa competitor
NO CHARCOAL
CHARCOAL
Ash-free dry weight (g)
0
2
4
6
8
10
12
14
No additions
Nutrient addition
Water addition
Soil treatment

**Figure 4.6.** Ash-free dry weight of *Centaurea maculosa* plants when grown with *Festuca idahoensis* competitors without charcoal added to the soil (light bars) and with charcoal added to the soil (dark bars); with no additional water or nutrients (left bars), with additional nutrients (center bars), and with additional water (right bars). *Centaurea* responded positively to the water addition treatment ($p < 0.05$). Bars represent means of 10 replicate plants within a treatment. Error bars represent one standard error above and below the mean.


Biomass of *Centaureamaculosa* when grown with a *Festuca idahoensis* competitor
☐ NO CHARCOAL ▨ CHARCOAL
Ash-free dry weight (g)
60
50
40
30
20
10
0
No additions
Nutrient addition
Water addition
Soil treatment