Soil physical properties and soil water dynamics under spotted knapweed and native grasses
by Tamara Dawn Sperber

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Land Rehabilitation
Montana State University

Abstract:
Spotted knapweed (Centaurea maculosa Lam.) is an introduced perennial forb that has invaded disturbed and undisturbed semiarid grasslands in the western United States. In the past, success in controlling spotted knapweed and restoring invaded areas has been limited. I hypothesized that the persistence of spotted knapweed in semiarid rangelands might reflect an ability to alter site conditions or a superior ability to take up soil water. The objective of this study was to compare soil physical properties and soil water dynamics under spotted knapweed-dominated areas and native perennial grass-dominated areas on semiarid rangeland. I used six field sites in western Montana with blocks containing almost adjacent plots dominated by spotted knapweed and native perennial grasses. I estimated basal cover and measured plant density and leaf area index (LAI) in each vegetation type at three sites in 1999 and 2000. Basic soil physical properties including particle size fractions, bulk density, and organic carbon content of near-surface soil samples were measured for each vegetation type. I measured soil hydraulic properties in each vegetation type using tension disk infiltrometers. I measured thermal conductivity and calculated volumetric heat capacity and apparent thermal diffusivity of near-surface soils. Near-surface soil temperature regime in each vegetation type at three sites was characterized using buried thermocouples. Soil water dynamics were monitored using a neutron moisture meter at one site and time domain reflectometry at three sites. Total basal cover for spotted knapweed plots was similar to native grass plots at two sites, but basal cover was higher for spotted knapweed plots at one site. LAI was consistently greater in spotted knapweed plots than in native grass plots. Soil physical properties were highly variable and differences between vegetation types were inconsistent within and among sites. At my study sites, soils were not degraded in areas invaded by spotted knapweed. Spotted knapweed plots had lower net precipitation than native grass plots late in the growing season, likely the result of differences in rainfall interception of the two growth forms and litter. Spotted knapweed used more soil water at deeper depths and later in the growing season than native grasses. Soil water was reduced to lower absolute levels at some depths under spotted knapweed compared with native grasses. During this study, greater water use by spotted knapweed for longer periods of time resulted in less soil water for the subsequent growing season. Altering near-surface soil characteristics does not appear to be a mechanism for spotted knapweed's persistence. Rather, spotted knapweed may invade and persist in semiarid rangelands by taking up soil water unavailable to native grasses because of apparent differences in rooting characteristics and phenology and potentially leaving less soil water for native species during subsequent growing seasons.

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Tamara Dawn Sperber

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Jon M. Wraith J M Wraith 7-19-01
(Signature) Date

Approved for the Department of Land Resources and Environmental Sciences

Jeffrey S. Jacobsen Jeffrey S. Jacobsen 7/23/01
(Signature) Date

Approved for the College of Graduate Studies

Bruce R. McLeod Bruce R. McLeod 7-23-01
(Signature) Date

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ABSTRACT

Spotted knapweed (*Centaurea maculosa* Lam.) is an introduced perennial forb that has invaded disturbed and undisturbed semiarid grasslands in the western United States. In the past, success in controlling spotted knapweed and restoring invaded areas has been limited. I hypothesized that the persistence of spotted knapweed in semiarid rangelands might reflect an ability to alter site conditions or a superior ability to take up soil water. The objective of this study was to compare soil physical properties and soil water dynamics under spotted knapweed-dominated areas and native perennial grass-dominated areas on semiarid rangeland. I used six field sites in western Montana with blocks containing almost adjacent plots dominated by spotted knapweed and native perennial grasses. I estimated basal cover and measured plant density and leaf area index (LAI) in each vegetation type at three sites in 1999 and 2000. Basic soil physical properties including particle size fractions, bulk density, and organic carbon content of near-surface soil samples were measured for each vegetation type. I measured soil hydraulic properties in each vegetation type using tension disk infiltrometers. I measured thermal conductivity and calculated volumetric heat capacity and apparent thermal diffusivity of near-surface soils. Near-surface soil temperature regime in each vegetation type at three sites was characterized using buried thermocouples. Soil water dynamics were monitored using a neutron moisture meter at one site and time domain reflectometry at three sites. Total basal cover for spotted knapweed plots was similar to native grass plots at two sites, but basal cover was higher for spotted knapweed plots at one site. LAI was consistently greater in spotted knapweed plots than in native grass plots. Soil physical properties were highly variable and differences between vegetation types were inconsistent within and among sites. At my study sites, soils were not degraded in areas invaded by spotted knapweed. Spotted knapweed plots had lower net precipitation than native grass plots late in the growing season, likely the result of differences in rainfall interception of the two growth forms and litter. Spotted knapweed used more soil water at deeper depths and later in the growing season than native grasses. Soil water was reduced to lower absolute levels at some depths under spotted knapweed compared with native grasses. During this study, greater water use by spotted knapweed for longer periods of time resulted in less soil water for the subsequent growing season. Altering near-surface soil characteristics does not appear to be a mechanism for spotted knapweed's persistence. Rather, spotted knapweed may invade and persist in semiarid rangelands by taking up soil water unavailable to native grasses because of apparent differences in rooting characteristics and phenology and potentially leaving less soil water for native species during subsequent growing seasons.

CHAPTER 1

INTRODUCTION

Invasion of native grasslands by exotic forbs has become a substantial threat to native ecosystems in the western United States. Grazing and human disturbance have greatly increased the spread of exotic species (DiTomaso, 2000; Mack, 1989; Watson and Renney, 1974). Initially only invading disturbed areas, many invasive species are spreading to undisturbed habitats (Mooers and Willard, 1989; Tyser and Key, 1988). Exotic species control has become very important in wildland management. Success in controlling invasive plants in the western United States, with herbicides, grazing, or biological agents, has been limited (Lacey et al., 1986). Invasive species' may persist by altering site conditions or by having greater ability to take up soil water or other limiting resources. Several plant species alter soil physical and chemical properties, favoring their own growth and reproduction (van Breemen and Finzi, 1998). Altering site conditions and/or preempting soil water or other resources may inhibit restoring native species in areas invaded by exotic forbs, because some effects may last long after the forbs are eradicated.

Centaurea species likely pose the greatest threat of all invasive plants to wildland management in the northern intermountain region of the United States (DiTomaso, 2000). On western Montana rangelands, spotted knapweed (*Centaurea maculosa* Lam.) is the number one problem weed (Whitson et al., 1996). Spotted knapweed has invaded 326 counties in the northwestern United States, including every county in Montana, Idaho, Washington, and Wyoming (Sheley et al., 1998). Its invasion has degraded wildlife habitat and cost millions of dollars in livestock forage (Hirsh and Leitch, 1996; Spoon et al., 1983; Watson and Renney 1974). This species invades grasslands and open woodlands in arid and semiarid regions, forming dense infestations that inhibit growth of other species (Fletcher and Renney, 1963; Kelsey and Bedunah, 1989; Tyser and Key, 1988; Watson and Renney, 1974). The limited success in controlling spotted knapweed may partially be due to prolific seed production and seed longevity (Davis et al., 1993; Lacey et al., 1990).

Spotted knapweed may alter hydrology by increasing surface runoff and erosion (French and Lacey, 1983; Lacey et al., 1989) and is thought to degrade wildland soils. However, evidence that this actually occurs is largely anecdotal. Only one study assessed the impact of spotted knapweed on erosion potential (Lacey et al., 1989). Rainfall simulation resulted in greater surface runoff and sediment yield in areas invaded by spotted knapweed compared with areas dominated by native grasses. However, these effects were not significant after the vegetation was removed by clipping, implying that the effects were a result of differences in plant structure and canopy cover rather than a result of altered soil conditions.

Perennial bunchgrasses, common in the semiarid climate of western Montana, have fibrous root systems which are most densely distributed in the upper 30 cm of the soil profile (Frank et al., 1996). Many large tussock grasses, such as bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], have rooting depths that extend to about 1.5 m (Dobrowolski et al., 1990; Weaver, 1919) under favorable conditions. Other common native grasses, such as Idaho fescue (*Festuca idahoensis* Elmer), have root systems concentrated in the upper 0.5 m of soil (Dobrowolski et al., 1990; Weaver, 1919). In general, most native grasses begin to grow in April or May (Dobrowolski et al., 1990; Stubbendieck et al., 1997). These native species mature and become quiescent in mid- to late summer (Stubbendieck et al., 1997). Regrowth in fall may occur if soil water and temperature conditions are favorable (Stubbendieck et al., 1997).

In comparison, spotted knapweed is a tap-rooted perennial (Watson and Renney, 1974). This forb generally remains a rosette its first year (Boggs and Story, 1987; Watson and Renney, 1974). Spotted knapweed seeds germinate in the fall and early spring (Watson and Renney, 1974). Rosettes form in early spring, tend to bolt in early May, and produce flower buds in early June, which bloom from July until as late as September (Sheley et al., 1998).

Mechanisms of spotted knapweed's persistence need to be determined for successful management and control of spotted knapweed and for sustainable restoration of invaded areas. Some near-surface soil properties and temporal and spatial soil water dynamics might be modified by spotted knapweed because rooting characteristics, basal and canopy cover, and phenology between this species and native grasses may differ. Infiltration of water may be reduced and surface runoff and erosion increased because of changes in near-surface soil characteristics as a result of lower basal and canopy cover in areas invaded by spotted knapweed compared with native grasses. Soil thermal properties might be altered by changes in soil water content, soil organic matter content, or bulk density, which may result in more extreme temperature variations at the soil surface. This could be detrimental to seed germination of native species, seedling emergence and growth. Spotted knapweed might preempt soil water resources by taking up soil water at different times during the growing season than native grasses or by having access to soil water deeper in the soil profile via its taproot when surface soil is dry.

Altered site conditions by spotted knapweed could limit success in restoring native species by possibly inhibiting seed germination or growth of native species. Spotted knapweed could potentially have a greater ability to utilize soil resources, affecting native species growth and survival. Together or separately, these factors might allow spotted knapweed to persist on semiarid grasslands. Ultimately, to restore invaded areas it is necessary to understand the ecological role of spotted knapweed rather than merely eradicating the invasive forb (Hester, 1991).

Thesis Objective

The objective of this study was to determine if soil physical properties and temporal and spatial soil water dynamics differ under spotted knapweed and native grasses in semiarid grasslands. The potential effects of spotted knapweed on site conditions and soil water dynamics need to be understood to improve weed and land management. Whether simply eradicating spotted knapweed is enough to restore native species, or whether site conditions and/or soil water dynamics differ sufficiently to inhibit restoration in invaded areas needs to be determined.

In this study, I used six field sites to determine whether near-surface soil physical properties differed in areas dominated by spotted knapweed compared with areas dominated by native grasses. Near-surface soil properties included particle size fractions, bulk density, organic carbon content, soil hydraulic properties, and soil thermal properties. Potential differences in selected soil properties were assessed by sampling near-surface soils, measuring infiltration with tension infiltrometers to determine soil hydraulic properties, estimating thermal conductivity with a line-source heat sensor, calculating volumetric heat capacity and thermal diffusivity, and monitoring soil thermal regime with thermocouples. Soil water dynamics under spotted knapweed were compared with native grasses at three field sites. Temporal and spatial soil water dynamics and soil water storage under spotted knapweed and native grasses were monitored using a neutron moisture meter and automated time domain reflectometry (TDR). Soil water retention of near-surface soils collected from spotted knapweed and native grass plots at three sites was measured in the laboratory using a pressure chamber apparatus.

Spotted Knapweed

Spotted knapweed, an invasive forb, was introduced from Europe into the U.S. Pacific Northwest around 1900 (Boggs and Story, 1987; Chicoine et al., 1985; Fletcher and Renney, 1963). Using climate and soils maps, Chicoine et al. (1985) estimated that almost 40% (15 million ha) of Montana is at risk for possible invasion by spotted knapweed. Almost 3 million ha in the Pacific Northwest, with more than 1.9 million ha in Montana, had been infested by spotted knapweed as of 1989 (Lacey, 1989). Spotted knapweed has now invaded at least 326 counties in the northwestern United States, including every county in Montana, Idaho, Washington, and Wyoming (Sheley et al., 1998).

Spotted knapweed alters plant community composition by reducing species richness and species frequency (Tyser and Key, 1988). It also reduces wildlife habitat and costs millions of dollars in livestock forage (Hirsh and Leitch, 1996; Spoon et al., 1983; Watson and Renney 1974). Bluebunch wheatgrass (*P. spicata*)-rough fescue (*Festuca scabrella*) production was decreased by almost 88% in areas invaded by knapweed (Watson and Renney, 1974). The impacts of spotted knapweed in Montana have cost the livestock industry an estimated $11 million annually (Hirsh and Leitch, 1996).

Spotted knapweed is a tap-rooted perennial that can live as long as 5 to 9 years (Boggs and Story, 1987). Its seeds (up to 40,000 m^{-2}) germinate in early spring or fall (Watson and Renney, 1974). Spotted knapweed seeds may be viable for up to 8 years in soil (Davis et al., 1993). Spotted knapweed may over-winter as rosettes or seeds and can regenerate from old crowns for several years (Watson and Renney, 1974). Root growth is thought to be greatest when in the rosette form (Watson and Renney, 1974). Spotted knapweed infestations usually expand along boundaries of existing stands since seedfall usually occurs within 1 m of the parent plant (Tyser and Key, 1988; Watson and Renney, 1974). The plant contains the growth inhibitor cnicin and is considered to be allelopathic (Fletcher and Renney, 1963; Kelsey and Bedunah, 1989; Kelsey and Locken, 1987).

However, Kelsey and Bedunah (1989) did not consider cnicin's effects to be significant in most habitats.

Invasive Species

As the ecological effects of many plant invasions are becoming evident, more and more studies are being conducted on invasive species and their impact on the environment (Pyšek, 1995). However, research on ecosystem-level impacts of plant invasions has been limited (Ramakrishnan and Vitousek, 1989).

An invasive species can be defined as an exotic species which, regardless of the habitat, is increasing in abundance or distribution (Pyšek, 1995). Many invasive species pose threats to native ecosystems including replacing diverse communities with monotypic stands, threatening native fauna, leading to the extinction of other plant species, altering biogeochemical, geomorphological, or hydrologic processes, or altering disturbance regimes (Cronk and Fuller, 1995; Gordon, 1998). Invasions could change species composition, richness, and diversity, community physical structure, phenology, resource competition, or the trajectory of succession (Gordon, 1998, Walker and Smith, 1997; Woods, 1997). Effects on ecosystem properties are likely to be more substantial when the invading species differs in growth form or resource acquisition, or alters the pattern or frequency of disturbance events (Vitousek, 1986; Vitousek, 1990). However, one of the main catalysts of plant invasions is disturbance, thereby making it difficult to separate the disturbance effects from invasive species effects on an ecosystem (Ramakrishnan and Vitousek, 1989; Vitousek, 1986; Woods, 1997).

The potential of many invasive species to alter ecosystem properties is likely more widespread than initially imagined (Gordon, 1998). For example, at least half of the 31 most invasive, non-indigenous plants in Florida have the potential to alter ecosystem processes (Gordon, 1998). Sand dune formation is an example of a geomorphological effect of an invasive species (e.g., *Ammophila arenaria* L., *Casuarina equisetifolia* J.R. & G. Forst.; Macdonald et al., 1989). Biogeochemical processes, such as nutrient cycling, have been altered in areas invaded by the nitrogen-fixing species *Cytisus scoparius* L. in the Pacific Northwest (Vitousek, 1986), *Kochia scoparia* L. in Colorado (Vinton and Burke, 1995), and *Myrica faya* Ait. in Hawaii (Vitousek and Walker, 1989). These changes in nutrient cycling could potentially alter the trajectory of succession at invaded sites. In California, iceplant (*Mesembryanthemum crystallinum* L.) alters soil biogeochemistry by concentrating salt from the soil profile onto the soil surface (Vivrette and Muller, 1977). Hydrologic patterns have been altered by invasive species such as *Tamarix* spp. and *Andropogon virginicus* L. (Graf, 1978; Mueller-Dombois, 1973). In the southwestern United States and Australia, *Tamarix* spp. have dewatered streams and have altered streamflow and flooding regimes (Graf, 1978). In Hawaii, *A. virginicus* invasion has led to development of boggy areas because its phenology differs from native species (Mueller-Dombois, 1973).

Species Effects

Interest in the effects of individual species on ecosystem properties and processes has increased (Vitousek, 1986; Walker and Smith, 1997; Wardle et al., 1998). An individual species could have an impact at the ecosystem level if it could alter biogeochemical and hydrological processes, disturbance regimes, or the trajectory of succession.

Wardle et al. (1998) studied 20 herbaceous species from the same functional group to determine if plant ecophysiological traits could be used to predict the impact of a species at the ecosystem-level scale. They assessed relationships between plant traits and litter decomposition, competition and herbivory, and effects of these plants on soil properties including microbial biomass, pH, nitrate concentration, and total nitrogen. They concluded that different plant species have substantially different effects on soil properties and that some plant traits, such as flowering and growth rates, were good predictors of these effects. Combinations of multiple traits could be used to determine a plant species' ecosystem-level effects on soil properties, nutrient dynamics, and the path of succession (Wardle et al., 1998).

Individual species' effects on site conditions and resources may alter successional processes, thus impeding or complicating restoration efforts. The trajectory of succession can be determined by initial and successive seral conditions (Allen, 1988). When the trajectory is altered by initial conditions, restoring the area to a predisturbance state may be impossible (Allen, 1988). Succession may be "suspended" in a state when a highly competitive species dominates (Allen, 1988). According to the traditional range condition model of succession on grasslands, when a community is disturbed it will always return to the "climax" community (Laycock, 1991; Westoby et al., 1989). Changes in the plant community occur along a continuum and were considered reversible.

However, in the “state-and-transition” model, if a plant community is severely altered or disturbed to the extent that it crosses a “threshold,” the system may not return to its original state without intervention (Friedel, 1988; Laycock, 1991; Westoby et al., 1989). Instead, the community will maintain a different stable state.

Exotic species are one of the main factors in North America that may “push” a stable community across a threshold to another stable state community dominated by exotic species (Laycock, 1991). An invasive forb that preempts soil water resources might prevent a plant community from returning to its initial state. If an area is severely infested by an exotic species that has altered site conditions, restoring native species may require additional intervention to remediate the site environment.

Soil Physical Properties

Soil conditions altered by exotic species could be detrimental to western wildlands. Exotic species effects on soil properties have rarely been studied (Macdonald et al., 1989). Most studies in the literature examine the effects of exotic species on soil processes such as nutrient cycling (Blicker, 2000; Vitousek and Walker, 1989; Vivrette and Muller, 1977). Studies on the effects of native or exotic plant species on soil physical properties have seldom been published. Research on the effects of different agricultural practices and crops on soil physical properties, and of soil physical properties influencing crop growth, crop production, root growth, and water use is relatively common. However, agricultural systems substantially differ from semiarid grasslands.

Because many nonindigenous species differ in physical structure, phenology, and function compared with native species, the potential for nonindigenous species to alter soil physical properties seems high. The ability of a soil to be an effective growth medium for plants depends on several physical properties including soil structure, texture, organic matter content, bulk density, and porosity. These same attributes strongly influence soil thermal and hydraulic properties. In semiarid grasslands, water and nutrients are often the most limiting resources (Fowler, 1986). Any changes in soil physical properties may potentially affect soil water and nutrient dynamics of these ecosystems.

Soil Structure

Soil structure, the arrangement of soil particles and pore spaces, plays a key role in soil water and nutrient dynamics (Angers and Caron, 1998). Although soil structure is influenced by climate, human activities, and other factors, vegetation has a substantial impact. Vegetative effects on soil structure and structural stability are related to root penetration, soil water extraction, organic carbon turnover rates, persistence of carbon in the soil, microbial activity, root exudates, and amount of protection provided against precipitation (Angers and Caron, 1998; Goss, 1991; Kay 1990).

Fine roots stabilize soil aggregates (soil particles strongly bound to each other) by enmeshment, by increasing microbial activity, and by releasing binding materials (Angers and Caron, 1998; Oades, 1984; Tisdall and Oades, 1982). Soil aggregate stability tends to increase in areas with perennial grasses because of higher root length density near the soil surface (Kay, 1990). Roots penetrate the soil and enhance the formation of soil aggregates and pore sequences (Angers and Caron, 1998).

The arrangement of soil aggregates and pore spaces, integral components of soil structure, affect pore size distribution and pore continuity which are important to water flow and storage (Angers and Caron, 1998; Kay, 1990).

Particle Size Fractions

Soil particle size fractions, or texture, can influence soil properties such as bulk density, porosity, thermal properties, hydraulic properties, and water holding capacity. Surface soil in semiarid grasslands can be redistributed from openings between plants to areas surrounding individual plants (Hook et al., 1991). However, this contributes more to differences in soil organic matter content than to differences in soil texture.

Bulk Density

Bulk density of a soil, defined as mass of oven dry soil per unit bulk soil volume, is related to soil texture, soil structure, and the degree of soil compaction and affects soil aeration, root growth, microbial activity, and nutrient and water transport (Smith et al., 1987). Water holding capacity generally decreases with an increase in bulk density for a given soil texture. Although coarse-textured soils (e.g., sandy) have relatively larger pores, total porosity is lower and bulk density is higher than for finer soils or soils high in organic matter. Organic matter content, biological activity, and management practices also affect bulk density. Because the density of organic matter is about half that of soil minerals (Brutsaert, 1982), bulk density tends to increase with a decrease in organic matter content (Smith et al., 1987). However, organic matter content is typically less than 3-4% percent (mass basis) in most soils of semiarid grasslands.

In general, plant growth is optimal in soils of intermediate bulk density (Passioura, 1991; Stirzaker et al., 1996). In soils with very high bulk density, penetration by roots can be inhibited and access to soil water and nutrients can be limited. In mineral soils with very low bulk density, likely as a result of cultural practices, root-soil contact may be low enough to restrict extraction of soil water and nutrients.

Organic Matter

Organic matter is one of the most important factors affecting soil structure (Hamblin, 1985; Kay, 1990; Smith et al., 1987). In agricultural soils organic matter content, commonly estimated from organic carbon measurements, is the most important indicator of soil quality and productivity (Reeves, 1997). The amount of organic matter in a soil affects soil physical properties such as structure, bulk density, water holding capacity, and heat capacity. Organic matter can increase infiltration by increasing the water holding capacity of near-surface soil, reducing crust formation, and increasing soil aggregation (Oades, 1984; Smith et al., 1987). Lack of organic matter in surface soils can lead to crusting which can decrease infiltration rates by orders of magnitude (Hamblin, 1985). Cultivated soils with lower organic matter contents have lower water holding capacities and are more susceptible to compaction compared with soils with higher organic matter contents (Hamblin, 1985).

In many ecosystems, roots are the most important source of carbon in the soil because a substantial portion of the carbon fixed by plants is allocated belowground (Angers and Caron, 1998). Plant traits such as growth form, biomass allocation, lifespan, and litter quality affect the quantity and quality of organic matter that accumulates under a plant (Burke et al., 1998). In general, grasses are the most efficient at improving soil structure because they allocate about 50% of their photosynthate belowground (Oades, 1984). In addition, there is some evidence that thin roots, which predominate in grasses, have higher turnover rates than thicker roots (Caldwell and Richards, 1986). Tap-rooted plants might contribute less organic matter to near-surface soil layers due to lower root density and slower root turnover rates compared with grasses.

Soil Thermal Properties

Soil temperature is affected by soil color, surface roughness, surface residue, soil water content (Singh and Sainju, 1998), and vegetation. Most literature evaluating the effects of vegetation on soil thermal properties reflects cultivated agricultural systems. Although these systems differ from semiarid grasslands, some general principles can be used to understand these plant-soil interactions.

Many biological processes such as seed germination, seedling emergence, plant production, root growth, microbial activity, and organic matter decomposition and mineralization are affected by soil temperature (Hillel, 1982; Hillel, 1998; Jury et al., 1991; Singh and Sainju, 1998). Most of these processes have an optimum temperature range, with a decrease in rate at temperatures above and below this range (Jury et al., 1991; McMichael and Burke, 1998). Plant growth is affected by sub- and supra-optimal temperatures because they affect soil water and nutrient uptake (Jury et al., 1991). For example, soil water depletion increased with soil temperature for winter wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.; Wraith and Ferguson, 1994; Wraith and Hanks, 1992). Plants growing in warmer soils matured earlier than plants grown in cooler soils (Wraith and Hanks, 1992). Decomposition rates of organic matter are generally higher at higher temperatures and lower at lower temperatures (Hillel, 1998).

Vegetation can affect the soil surface energy balance by changing the reflectance or albedo of the soil surface, shading the soil surface from solar radiation, altering the soil water regime, removing latent heat by evapotranspiration, and insulating the soil surface (Hillel, 1998; Jury et al., 1991). These effects reduce the amplitude of daily temperature fluctuations at the soil surface relative to bare soil conditions.

Heat is transported in soil mainly through conduction by soil particles, but also occurs by latent heat transfer. Substantial quantities of latent heat may be conducted through soils by evaporation and condensation of water, and by convection with moving water (Hillel, 1982; Shiozawa and Campbell, 1990). Extreme temperature changes may occur at the soil surface because it is the point of radiant energy exchange (Campbell and Norman, 1998). Diurnal and annual temperature regimes are affected by climate, vegetation, and soil thermal properties (Hillel, 1982). The amplitude of the soil temperature oscillations, which approximate a sinusoidal pattern around an average temperature, decreases with depth because heat is absorbed and released by the soil (Campbell and Norman, 1998; Hillel, 1982).

Soil thermal properties are characterized by volumetric heat capacity, thermal conductivity, and thermal diffusivity, which depend on soil composition including organic matter, bulk density, and soil water content (Hillel, 1982; Jury et al., 1991; Shiozawa and Campbell, 1990).

Volumetric heat capacity is the heat required to raise a unit soil volume one degree Celsius and is calculated using the volume fractions of soil constituents, their densities and specific heat capacities (Hillel, 1982; Jury et al., 1991).

Thermal conductivity is the amount of heat transferred through a unit area over a unit time across a unit temperature gradient (Hillel, 1982). Thermal conductivity depends on soil water content, soil aggregation, and soil structure (Hillel, 1982; Jury et al., 1991). The arrangement of soil particles affects the thermal contact between the particles through which heat flows. Thermal conductivity of air is much lower than for water or solids, therefore a soil with a lower water content, higher porosity, or lower bulk density will have lower thermal conductivity (Hillel, 1982; van Wijk and de Vries, 1966). The influence of soil water content on thermal conductivity is much greater in magnitude than the effect of bulk density (Jury et al., 1991).

Thermal diffusivity is the ratio of thermal conductivity to volumetric heat capacity and is the "change in temperature produced in a unit volume by the quantity of heat flowing through the volume in unit time under a unit temperature gradient" (Hillel, 1982).

The effects of plant-soil interactions on ecosystem processes are potentially very important. Considering the marked differences in plant structure, rooting characteristics, and phenology between spotted knapweed and native grasses, it is reasonable to hypothesize that invasion by spotted knapweed may lead to differences in near-surface soil properties. Particle size fractions are not expected to differ under spotted knapweed and native grasses. In general, plants do not directly alter soil texture. However, different vegetation types could influence the manner in which water and wind redistribute soil particles. Changes in bulk density and organic matter content are possible because potential differences in plant canopy and basal cover, quality and quantity of plant litter, distribution of roots, and type of root structure. These possible changes could alter soil thermal properties and temperature regime, soil water holding capacity, and infiltration. Such changes in soil physical properties could persist after eradicating spotted knapweed and might limit the establishment and growth of native species.

Soil Water Infiltration and Dynamics

Several invasive species alter the hydrology or soil water dynamics of a plant community to the degree of inhibiting growth and survival of native species (Woods, 1997). Drastic effects include dewatering wetlands (*Iris pseudacorus*, *Mimosa pigra*; Woods, 1997), creating boggy areas (*A. virginicus*; Mueller-Dombois, 1973), and altering the hydrology of river systems (*Tamarix* spp.; Graf, 1978).

Invasive species can alter temporal and spatial soil water dynamics by several mechanisms. Invasive species can use more soil water than the native species (Walker and Smith, 1997), which would have a substantial impact in water-limited habitats such as semiarid grasslands. Invasive plants may differ in phenology and use water at different times in the growing season (Walker and Smith, 1997). Seasonal differences in physiological activities associated with canopy formation, flowering, and dormancy could affect competitive relationships between invasive and native plants. Invasive species that remove soil water earlier or later in the growing season compared with native species could have a substantial impact by reducing the initial amount of water available at the beginning of the current or subsequent growing season. Invasive species may have access to soil water resources which are not utilized by the native community (Walker and Smith, 1997). For example, deep-rooted invasive species may have access to water deeper in the soil profile that is not available to shallower-rooted natives.

Invasive species that differ in growth form from native species could alter surface soil characteristics (Walker and Smith, 1997) or could intercept more or less rainfall. Both of these could affect the overall water balance of a site. Changes in surface soil characteristics could affect infiltration of water into the soil (Branson et al., 1981). An invasive species intercepting different amounts of rainfall than native species would affect the amount of water that reaches the soil surface.

Soil water is often the most limiting resource in semiarid ecosystems (Fowler, 1986). Plant characteristics such as rooting density and depth can greatly influence spatial and temporal water dynamics. The rate at which plants can take up water is a function of soil properties, climatic conditions, and plant traits (Hillel, 1982). The principle soil properties affecting plant water uptake are hydraulic conductivity, matric potential distribution, and soil water retention (Hillel, 1982). Small differences in soil water content can be biologically important because of the nonlinear relationship between soil water content and soil water potential. Soil matric potential is a major factor affecting plant available water and is primarily affected (at a given soil wetness) by pore size distribution, soil texture, and soil structure (Hillel, 1982).

Soil properties that influence infiltration may affect the amount of water available to plants, in addition to the potential for surface runoff and erosion (Hillel, 1982). Infiltration depends on several factors, including initial soil water content, soil hydraulic conductivity, and conditions of the soil surface (Hillel, 1982). Vegetative growth form, density, and spatial distribution are important factors that may influence erosion by adding organic matter, detaining particles transported by wind and water, and their impacts on soil faunal activity which will alter surface soil characteristics (Blackburn and Pierson, 1994). Infiltration rates are nearly three times greater near the stems of some desert plants than for areas between plants (Lyford and Qashu, 1969). Soils in areas under plant cover may also have lower bulk densities and higher organic matter contents than soils in open areas (Lyford and Qashu, 1969).

Plant basal and canopy cover, soil structure, soil texture, organic matter content, bulk density, and rainfall intensity affect erosion and runoff (Branson et al., 1981; Gutierrez and Hernandez, 1996; Weltz et al., 1998). Vegetative cover affects erosion by intercepting or dispersing raindrops as well as by obstructing and dispersing overland flow (Rogers and Schumm, 1991). This decreases the velocity of runoff water and its capacity for erosion. Plant and litter cover are among the most influential site factors and organic matter content is one of the most important soil factors influencing erosion (Meeuwig, 1970).

Other factors being similar, as the amount of bare soil increases, erosion rate usually increases (Gutierrez and Hernandez, 1996; Weltz et al., 1998). Erosion and runoff usually increase as grasses are replaced by forbs because of reduced basal and aerial cover (Gutierrez and Hernandez, 1996). In areas with lower basal and canopy cover, less precipitation is intercepted and more bare soil is exposed to the impact of raindrops. The impact of raindrops on bare soil causes the breakdown of soil aggregates (Dobrowolski et al., 1990; Hillel, 1982; Oades, 1984). This can result in a 'sealing' or crusting of the soil surface, decreasing hydraulic conductivity and infiltration, and possibly increasing erosion and surface runoff (Dobrowolski et al., 1990; Hillel, 1982; Oades, 1984). In addition, seedling emergence and survival can be reduced by surface crusting (Hillel, 1982).

About 50 to 70% grass cover is needed to control surface runoff during the growing and dormant seasons on semiarid rangelands of northern Mexico (Gutierrez and Hernandez, 1996). The presence of a fibrous-rooted species decreased runoff by about 250% compared with tap-rooted species by creating more root channels near the soil surface for preferential flow of water into the soil (Pearse and Woolley, 1936). Soil porosity surrounding roots is reduced as a result of compression and the production of organic materials in the rhizosphere (Kay, 1990). However, root channels are created because the soil adjacent to a root has greater strength and stability than the surrounding soil. After the roots dies, these root channels are sites for preferential flow of soil water and new root growth (Kay, 1990).

Lacey et al. (1989) examined the effects of spotted knapweed on surface runoff and sediment yield. Using a rainfall simulator, they found that runoff and sediment yield from grass-dominated sites were significantly less than for spotted knapweed-dominated sites. However, there were no significant species effects on surface runoff and sediment yield after vegetation was clipped. This suggests that soil properties affecting surface runoff and sediment yield were not affected by any particular characteristic associated with spotted knapweed. The authors concluded that grasses protect the soil and enhance infiltration more than spotted knapweed.

Preempting soil water resources by using more water or using soil water earlier or later in the growing season may be a competitive mechanism of some invasive species. Semiarid regions characteristically have high potential evapotranspiration rates with most precipitation coming in small rainfall events (Sala et al., 1992). Therefore, the surface soils of these areas are usually dry. The upper layer of soil generally has the highest root density and is subject to extreme drying because of evaporation as well as water uptake by roots. The response times of plants to small rainfall events can influence which temporal and spatial water resources are available. Plants with quicker response times are more able to exploit small rainfall events than plants that have slower response times (Sala and Lauenroth, 1982; Wraith et al., 1995).

Root distribution also influences which soil water resources are available to plants (Sala et al., 1992). In general, root density decreases with depth (Singh and Sainju, 1998). Fibrous roots are relatively more dense near the soil surface than taproots which usually grow to deeper depths (Singh and Sainju, 1998). Plant species with deeper root systems may escape competition at certain times by having access to water deep in the soil during prolonged periods when evaporative demands are high (Dobrowolski et al., 1990). The deeper penetration of taproots may allow access to soil water deeper in the soil profile when the surface soil may be dry (Sala et al., 1992). In the shortgrass region of the U.S. Great Plains, deep taproots of shrubs and forbs provide an advantage during or following wetter years when soil deeper in the profile has been recharged (Sala et al., 1992). Extensive fibrous root systems may have greater overall root length and surface area, which may facilitate rapid access to the volume of soil in which water is most often present. However, in a case where growth form, root distribution, and root biomass were similar between two tussock grasses, Eissenstat and Caldwell (1988) found that other differences in the root systems (root thickness and season of root growth) affected the ability to compete for soil water and nutrients.

Early spring growth and/or delayed dormancy in late summer or fall could make spotted knapweed relatively effective at utilizing limited soil water resources and this could result in less soil water being available for growth of native species. The taproot of spotted knapweed could allow access to water stored deeper in the soil profile, which is relatively inaccessible by native grasses. However, in many semiarid regions presence of substantial soil water at depths below native plant roots is probably not common.

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CHAPTER 2

SOIL PHYSICAL PROPERTIES AND PROCESSES UNDER SPOTTED KNAPWEED AND NATIVE GRASSES

Introduction

In the western United States, native grassland ecosystems are being threatened by invasive plant species. Initially invading disturbed areas, many exotic species are spreading into undisturbed habitats (Lacey et al., 1990; Tyser and Key, 1988). Spotted knapweed (*Centaurea maculosa* Lam.), an invasive forb introduced from Europe (Boggs and Story, 1987; Chicoine et al., 1985), is an extensive noxious weed on western Montana rangelands (Whitson et al., 1996) and is a serious concern in the Pacific Northwest (Sheley et al., 1998) and Canada. Spotted knapweed invades grasslands and open woodlands in arid and semiarid regions, forming dense stands that inhibit the growth of other species (Fletcher and Renney, 1963; Tyser and Key, 1988; Watson and Renney, 1974). Wildlife habitat and millions of dollars in livestock forage have been lost as a result of its invasion (French and Lacey, 1983; Hirsh and Leitch, 1996).

Success in controlling spotted knapweed and restoring invaded areas to native species has been limited. Because of differences in plant and root structure, and phenology between spotted knapweed and native grasses, spotted knapweed may alter site conditions or may have a superior ability to utilize limited soil resources such as water or nutrients. Several plant species alter soil physical and chemical properties, favoring their own growth and reproduction (van Breemen and Finzi, 1998). The potential for nonindigenous species to alter soil physical properties may be related to differences in plant growth form, phenology, and function compared with native species. Native grasses in semiarid grasslands have fibrous root systems that are densely distributed in the upper soil profile (Dobrowolski et al., 1990; Weaver, 1919). Spotted knapweed is a tap-rooted perennial (Watson and Renney, 1974). This forb generally spends its first year as a rosette and bolts during subsequent years (Watson and Renney, 1974).

Soil physical properties including texture, structure, bulk density, and organic matter content influence plant germination and growth as well as soil thermal and hydraulic properties and processes. Changes in plant community structure might alter near-surface soil properties, which could impact root growth, soil water and nutrient uptake (Hamblin, 1985), water holding capacity, infiltration characteristics, or heat capacity (Oades, 1984; Smith et al., 1987). Altering properties such as soil water content, organic matter content, or bulk density would alter soil thermal properties, which could influence seedling emergence and growth. Substantial changes in soil physical properties could sufficiently alter site conditions to inhibit native species' growth or limit the success of restoring desired plant communities. Such changes might persist long after eradicating the invasive plant community. If so, suitable revegetation with native species would require amending these altered soils.

In semiarid grasslands, soil water and nutrients are frequently limiting resources for plant growth (Fowler, 1986). Changes in soil physical properties might alter soil water and nutrient dynamics of these ecosystems. As bare soil area increases, erosion and potential for surface runoff also generally increase (Gutierrez and Hernandez, 1996; Weltz et al., 1998). Areas dominated by species with fibrous root systems generally have less runoff than areas dominated by taproot species (Pearse and Woolley, 1936). Greater exposure to raindrop impact can cause surface soil crusting, reducing hydraulic conductivity and infiltration (Dobrowolski et al., 1990; Hillel, 1982; Oades ,1984). Surface crusting can also negatively affect seedling emergence and survival (Hillel, 1982).

Spotted knapweed might increase surface runoff and erosion (French and Lacey, 1983; Lacey et al., 1989) and is thought to degrade wildland soils, but evidence for this appears to be largely anecdotal. Only one study has assessed the impact of spotted knapweed on erosion potential (Lacey et al., 1989). Simulated rainfall resulted in greater surface runoff and sediment yield in areas dominated by spotted knapweed compared with areas dominated by native grasses. However, after clipping the vegetation and repeating the measurements, surface runoff and sediment yield were similar. This suggests the initial responses were a result of differences in plant structure and canopy cover rather than of altered soil properties. Therefore, if soil properties are not altered in spotted knapweed-dominated areas, to successfully restore these areas land managers would not need to physically ameliorate soils.

The objective of this study was to determine whether near-surface soil properties differed between adjacent areas dominated by spotted knapweed and native grasses. I measured selected soil physical properties including particle size fractions, bulk density, organic carbon content, soil hydraulic properties, and soil thermal properties for adjacent rangeland plots dominated by spotted knapweed or native perennial grasses.

Materials and Methods

Six field sites in western Montana were used in this study. At each site I established blocks consisting of two paired 2 m^2 plots. One site (Thiede) contained eight blocks of 1 m^2 plots. The paired plots included one plot dominated by spotted knapweed (>50% spotted knapweed canopy cover) and one plot dominated by native grasses (<10% spotted knapweed canopy cover). I selected plot locations to obtain paired plots close enough to minimize spatial heterogeneity of soil properties, physiography, and inherent site differences. I excavated soil pits in spotted knapweed and native grass-dominated areas at four sites (only one pit at Thiede in mixed vegetation) to confirm that soil profiles and soil classification were similar. I measured leaf area index (LAI; LAI-2000, LiCOR, Lincoln, NE) and estimated basal cover for spotted knapweed and native grasses by growth form: bunchgrass, rhizomatous grass, and annual grass, at three study sites on August 3-5, 1999 and July 28-August 4, 2000. Descriptive statistics were calculated to summarize these measurements.

Site history and measurement restrictions guided my selection of the six sites. Basic site selection criteria were as follows: 1) spotted knapweed reportedly present for at least 5-10 years; 2) spotted knapweed-dominated areas intermixed with or intergrading to areas dominated by native perennial grasses; 3) lack of known previous site disturbance that may have caused differences in soil properties; 4) little or no active grazing or herbicide use; 5) at least 10-15 cm of surface soil with low rock content; and 6) reasonably level terrain. The first four criteria defined the vegetation types and minimized potential for confounding of plant effects with site history. The remaining criteria related to measurement constraints. Stony soils prevented proper insertion of soil thermal conductivity probes, and tension infiltrometers required moderately level surfaces.

I removed five to ten spotted knapweed plants at each site, except at the Thiede Site, to estimate the age of spotted knapweed plants present. I selected larger plants to get an age estimate for the older plants at each site. Ages of spotted knapweed plants were determined by oven drying the taproot at 47°C for about 7 d, breaking the root in several places, and counting the rings of secondary xylem under a dissecting microscope. Each ring was presumed to represent one year's growth (Boggs and Story, 1987). The average age of spotted knapweed plants at each site does not indicate the time of invasion, but indicates a minimum number of years that spotted knapweed has been present on the site.

Study Sites

The Thiede Site was near the Red Bluff Research Ranch, 60 km west of Bozeman, Montana in Madison County. Soils at this site were Nesda loams (sandy-skeletal, mixed, frigid, Fluventic Haploborolls) with 3 to 5% slopes (Appendix). Average annual precipitation is 405 mm (Norris 3 ENE, Western Regional Climate Center [WRCC], 2000). Native grasses included Idaho fescue (*Festuca idahoensis* Elmer) and western wheatgrass [*Pascopyrum smithii* (Rydb.) Löve]. Some areas of the soil surface at this site were covered with club moss (*Selaginella* spp.), which was removed before the plots were measured. The area was grazed heavily until the 1980s.

The Helena Site was 21 km southeast of East Helena, Montana in Broadwater County. Soils at this site were Rothiemay loams (fine-loamy, mixed, superactive, frigid Aridic Calciustolls) with 1 to 2% slopes (Appendix). Average annual precipitation is 305 mm (Helena WSO, WRCC, 2000). Dominant native grasses were bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve] and needle-and-thread (*Stipa comata* Trin. & Rupr.). The site had not been grazed, leading to large amounts of litter present in spotted knapweed and native grass dominated areas. The spotted knapweed areas had large amounts of fallen 'stalk' litter compared with the finer, leaf litter characteristic of the native grass dominated areas.

The Belgrade Site was 6 km west of Belgrade, Montana in Gallatin County. Soils were Kassler gravelly coarse sandy loams (sandy-skeletal, mixed, frigid Torriorthentic Haplustolls) with 0 to 1% slopes. (Appendix). Average annual precipitation is 360 mm (Belgrade Airport, WRCC, 2000). *Pascopyrum smithii* was the dominant native grass. This site had also been invaded by annual cheatgrass (*Bromus tectorum* L.) and had a history of light grazing by horses. Plots were fenced to prevent grazing in the study area.

The Hyalite Site was 12 km southwest of Bozeman, Montana in Gallatin County. Average annual precipitation is about 465 mm (Bozeman Montana State University, WRCC, 2000). Soils were Hyalite loams (fine-loamy, mixed, superactive, frigid Typic Argiustolls) with 0 to 1% slopes (Appendix). Native grasses included *F. idahoensis* and *P. smithii*. The site had not been grazed since the 1970s.

The Loch Leven Site was 29 km south of Livingston, Montana in Park County. Annual precipitation averages 424 mm (Livingston 12S, WRCC, 2000). This site included a mixture of Beaverell gravelly loam (loamy-skeletal over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls) and Attewan loam (fine-loamy over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls) soils with 0 to 1% slopes (Amy Miller, Natural Resources Conservation Service [NRCS], pers. comm., 2000). Dominant native grasses included *S. comata*, *P. spicata*, and *P. smithii*. Junegrass (*Koeleria cristata* Pers.) and blue grama [*Bouteloua gracilis* (H.B.K.) Lag.] were also present. Club moss was present at the soil surface and was removed before areas were measured. Sheep grazed the area until the 1980s.

The Cottonwood Site was 20 km southwest of Bozeman, Montana in Gallatin County. Annual precipitation averages 575 mm (Gallatin Gateway 10SSW, WRCC, 2000). Soils at this site were Beaverton gravelly loams (loamy-skeletal over sandy or sandy-skeletal, mixed, superactive, frigid Aridic Argiustolls) with 0 to 1% slopes (Amy Miller, NRCS, pers. comm., 2000). Dominant native grasses included *S. comata*, *F. idahoensis*, and *P. smithii*. Club moss was present on the soil surface in a few plots and was removed before sampling. This site had recently been grazed lightly by cattle.

Basic Soil Properties

I measured near-surface soil properties including United States Department of Agriculture (USDA) particle size fractions (soil texture), bulk density, and total organic carbon content. I sampled soils and measured soil properties in plot areas that were not continuously monitored for temperature and soil water status. I collected 4.76-cm diameter soil cores at the 0-6 cm depth for particle size fractions at Helena, Belgrade and Hyalite, and at the 0-5 cm depth for all remaining measurements for all sites.

Soils were oven-dried (105 °C) and sieved (2 mm) before processing. I measured particle size fractions using the modified Day hydrometer method (Gee and Bauder, 1986). Volumetric soil cores were used to determine bulk density (Blake and Hartge, 1986), which I calculated as the ratio of oven dry soil mass to bulk soil volume. Total organic carbon content was estimated by combustion using a LECO analyzer (CNS-2000, LECO Corp., St. Joseph, MI).

During the 1999 field season, I collected four soil cores in each plot at Helena, Belgrade, and Hyalite to determine particle size fractions. Two soil cores were collected and composited from areas where hydraulic properties were measured. I also collected and composited two additional cores from other locations within the plot that had not been disturbed for measuring hydraulic properties, for a total of two soil samples per plot. During the 2000 field season, I collected four soil cores in all plots, two wetted samples (to measure soil thermal conductivity) and two ambient soil samples. I calculated bulk density from these soil cores and measured organic carbon content on two composite samples, one wetted and one ambient.

In 2000 at Loch Leven and Cottonwood, I collected and composited two soil cores at four sample locations, resulting in four soil samples from each plot. At Thiede, two soil samples were collected from each plot. I calculated particle size fractions, bulk density, and organic carbon content using these soil cores. Soil properties for each plot within each site were compared between vegetation types using analysis of variance (ANOVA; SAS, 2000).

Soil Hydraulic Properties

The saturated and unsaturated soil hydraulic conductivity relationship within each plot was characterized using tension disk permeameters (Soil Measurement Systems, Tucson, AZ; Perroux and White, 1988). I measured steady state infiltration rates at supply pressures (i.e., matric potentials) of -3, -6, -9, and -15 cm at the same soil locations at Thiede in the fall of 1998. Steady infiltration rates at supply pressures of -3, -6, and -15 cm were measured at Helena, Belgrade, and Hyalite during the 1999 field season. I used supply pressures of -2, -4, -6, and -15 cm at Loch Leven and Cottonwood during the 2000 field season. A pressure transducer connected to a datalogger (CR23X, Campbell Scientific, Inc., Logan, UT) measured water outflow from the infiltrometers at 2 s intervals during early stages of infiltration (approximately 5 min) and every 10 s for the remainder of the 30 to 45 min runs.

I estimated infiltration rates using linear regression of measured cumulative infiltration (cm) vs. time (s) for the last 5 min at each supply pressure. Best-fit estimates of saturated hydraulic conductivity (K_s; cm s^{-1}) and the variable α (cm^{-1}) in Gardner's (1958) hydraulic conductivity model (Logsdon and Jaynes, 1993) were determined using nonlinear least-squares optimization (Wraith and Or, 1998) of infiltration rates to Wooding's (1968) solution of three-dimensional infiltration from shallow circular ponds:

$$\frac{q}{\pi r^2} = K_s e^{\alpha h}\left(1 + \frac{4}{\pi \alpha r}\right) \qquad [1]$$

where q is the final infiltration rate ($cm^3\ s^{-1}$), r is radius (cm) of fine sand contact material between the infiltrometer disk and the soil surface, and *h* is the water supply potential (cm),.

I estimated time to ponding using sorptivity, a soil hydraulic property that dominates the initial infiltration process. Sorptivity was estimated using linear regression of cumulative infiltration (cm) vs. the square root of time ($s^{0.5}$) during initial infiltration (the initial 1-2 min; Philip, 1969) at the -5 cm supply pressure. Sorptivity and hence time to ponding were not measured at Loch Leven, Cottonwood, or Thiede. For a given water application (e.g., rainfall) rate, I predicted when infiltration capacity will be exceeded and surface runoff will begin by calculating time to ponding using the relationship proposed by Philip (1969), including a time compression correction:

$$t_p = \frac{S^2(2P - A)}{4P(P - A)^2} \qquad [2]$$

where t_p is the estimated time (s) to surface water ponding, *S* is the sorptivity ($cm\ s^{-0.5}$), P is the precipitation intensity ($cm\ s^{-1}$), and *A* ($cm\ s^{-1}$) is a parameter that depends on soil properties and soil water content (Kim et al., 1996). *A* was estimated as $K_s/2$ (Philip, 1969), where K_s is the saturated hydraulic conductivity calculated using Eq. [1].

I measured infiltration at two locations in each plot at all field sites except Thiede. At Thiede, infiltration was measured in five blocks of paired plots, with one measurement location per plot. Mean K_s and α values were compared between native grass and spotted knapweed plots within sites using ANOVA. I transformed Loch Leven K_s values and

Belgrade α values using the natural log because of unequal variances as indicated by residual plots.

Soil Thermal Properties

I measured three soil thermal properties to characterize the soil thermal regime: volumetric heat capacity (c_v), thermal conductivity (λ), and thermal diffusivity (D_h) (Campbell and Norman, 1998; Hillel, 1982). Volumetric heat capacity was calculated as the sum of the heat capacities of the mineral, water, and organic matter soil components multiplied by their respective volume fractions:

$$c_v = \rho_m \varphi_m c_m + \rho_w \varphi_w c_w + \rho_a \varphi_a c_a + \rho_{om} \varphi_{om} c_{om} \qquad [4]$$

where ρ_i is the density of soil constituents (m=mineral, w=water, a=air, and om=organic matter), φ_i is the volume fraction, and c_i is the specific heat per unit mass (Campbell and Norman, 1998; Hillel, 1982). I converted organic carbon contents of surface soil samples to organic matter contents by multiplying by 1.7 (Nelson and Sommers, 1982). Values of specific heat and the densities used in these calculations were 733 J kg^{-1} K^{-1} and 2650 kg m^{-3} for soil minerals, 1926 J kg^{-1} K^{-1} and 1300 kg m^{-3} for soil organic matter, and 4182 J kg^{-1} K^{-1} and 1000 kg m^{-3} for water (Brutsaert, 1982).

Thermal conductivity of near-surface soils (0-6 cm) was estimated using a line-source heat sensor (Soiltronics, Burlington, WA; Shiozawa and Campbell, 1990). Before inserting the heat sensor, sample areas were cleared of litter or moss (if present). Thermal conductivity depends on soil water content and is sensitive to thermal gradients, thus half of the sample locations were wetted by ponding water within a 22 cm diameter ring then covered with 3.8 cm thick styrofoam boards and allowed to drain for about 1 d. Sample locations that I did not wet were also covered with styrofoam boards to equilibrate temperatures for about 1 d before I measured thermal conductivity.

Volumetric water content (m^3 m^{-3}), bulk density (g cm^{-3}), and total organic carbon content (g kg^{-1}) were determined by coring the soil (spanning the 0-5 cm depth) where the heat sensor had been inserted. These soil cores were also used to determine particle size fractions at Loch Leven, Cottonwood, and Thiede. Thermal conductivity was calculated for the heating period using Shiozawa and Campbell (1990):

$$T - T_0 = \frac{q}{4\pi\lambda}\left[\ln(t) + d\right], \text{ for } t < t_1 \qquad [3]$$

where T is sensor temperature (°C), T_0 is the initial temperature, q is the heat production per unit time per unit length of the source (W m^{-1}), λ is thermal conductivity (W m^{-1} K^{-1}), t is time (s), d is a constant, and t_1 is the time when heating is stopped. I estimated apparent thermal diffusivity as the ratio of thermal conductivity to volumetric heat capacity (Campbell and Norman, 1998).

To characterize the near-surface soil temperature regime, I buried copper-constantan thermocouples at Helena, Belgrade, and Hyalite in May 1999. Thermocouples were installed in two blocks at each site (i.e., two spotted knapweed and two native grass plots). A datalogger connected to signal multiplexers (21X and AM416, Campbell Scientific, Inc., Logan, UT) monitored soil temperatures at 2.5, 5, and 15 cm depths at 0600, 1200, 1800, and 2400 h. With two datalogger systems servicing the three sites, each site was monitored for variable lengths of time during the 1999 field season. I only monitored Helena and Hyalite during the 2000 field season.

Soil temperatures at 2.5, 5, and 15 cm depths were fitted to a sinusoidal heat flow model to estimate the thermal damping depths, mean daily surface temperatures, and daily amplitudes of surface soil temperature variation (Campbell and Norman, 1998):

$$T(z,t) = \overline{T} + A_0 e^{\frac{-z}{d}} \sin\left[\omega\,(t-8) + \frac{-z}{d}\right] \qquad [5]$$

where T is temperature (°C) of the soil as a function of depth (z; cm) below the surface and time (t; h), $\overline{T}$ is the mean daily soil surface temperature, A_0 is the amplitude (°C) of surface soil temperature fluctuations, d is the characteristic damping depth (cm), ω is the angular frequency (h^{-1}) equal to $2\pi/P$, and P is the temperature oscillation period of 24 h. Consecutive days with stable weather conditions were used to estimate d, $\overline{T}$, and A_0.

Mean plot values of volumetric heat capacity, thermal conductivity, and apparent thermal diffusivity for each vegetation type and wetted or ambient soil conditions were compared within sites using split plot ANOVA (SAS, 2000). I omitted one thermal conductivity measurement outlier for Helena. Thermal diffusivity data for Thiede were natural log transformed due to unequal variances as indicated by residual plots. Analysis of covariance was used to compare mean damping depth between vegetation types using mean soil water content as a covariate (SAS, 2000), with one damping depth outlier omitted for Helena. I compared the amplitude of surface soil temperature fluctuations using ANOVA. I conducted a nonparametric rank F test on mean daily surface soil temperatures because the distribution was not normal (Neter et al., 1996). Because of the high inherent degree of spatial variability associated with soil properties and processes (Mulla and McBratney, 2000), a significance level of $P \leq 0.10$ was selected for all statistical comparisons.

Results

Soil Profiles

Soil pits excavated at Helena, Belgrade, and Hyalite confirmed similar soil profiles and soil taxonomy in spotted knapweed and native grass dominated areas (Appendix). The only observed differences between soils in the two vegetation types were slight and non-systematic variations in soil horizon thickness as expected due to natural spatial heterogeneity.

Vegetation

Total basal cover was greater in spotted knapweed plots than in native grass plots at Belgrade in 1999 and 2000 (Table 2.1; Fig. 2.1). While total basal cover at Belgrade was similar for both seasons, total basal cover at Helena and Hyalite was notably lower in 2000 than in 1999 (Table 2.1). Spotted knapweed plots at Hyalite had greater grass cover and lower spotted knapweed cover compared with the other sites. Overall, native grass cover was lower in spotted knapweed plots than in native grass plots.

LAI for both species includes living and standing dead culms and stems ≥3 cm above ground surface. LAI in spotted knapweed plots was higher than in native grass plots at all three sites (Fig. 2.2).

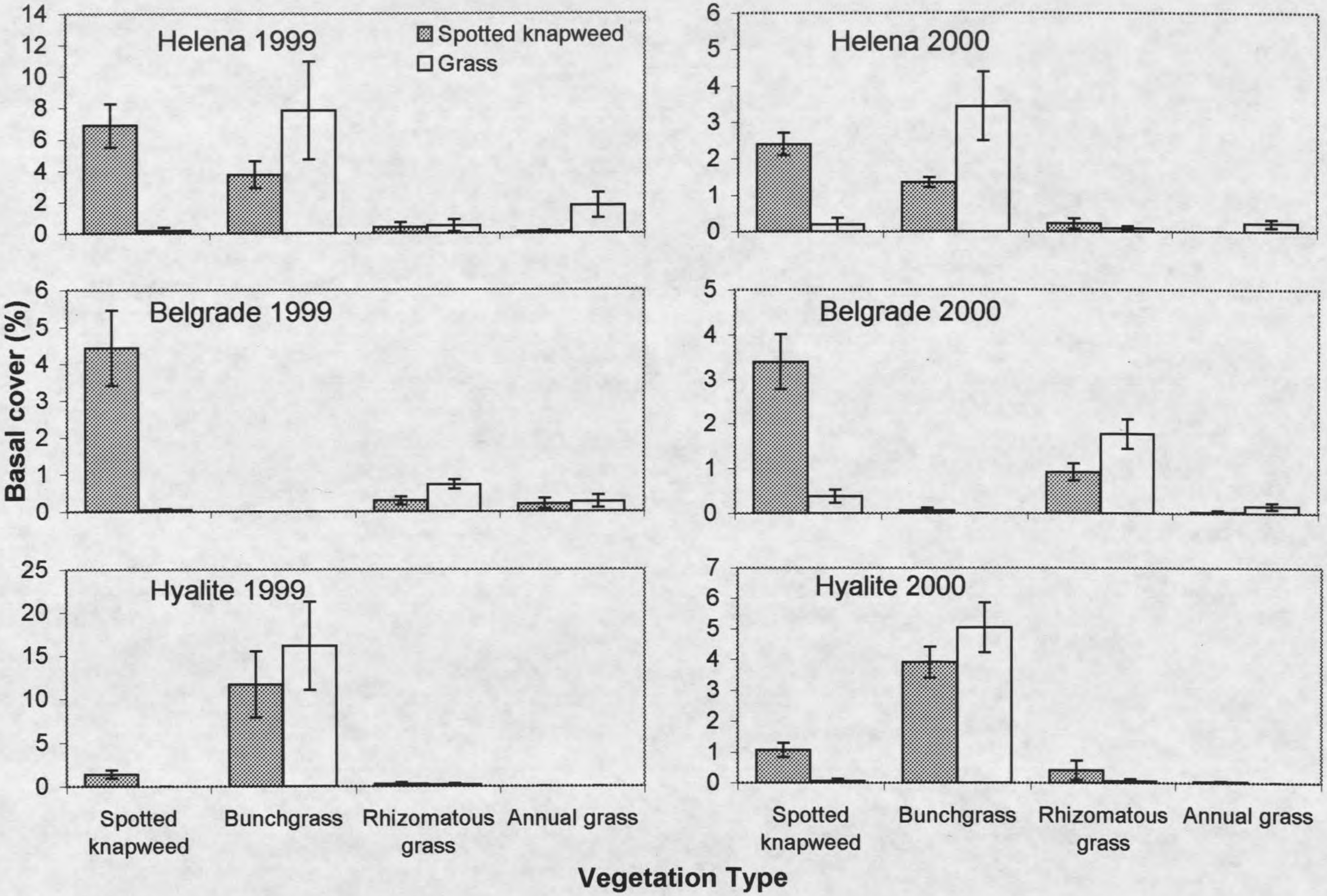

Fig. 2.1. Basal cover (mean ± SE; n=4) of spotted knapweed and grasses in spotted knapweed and native grass plots.

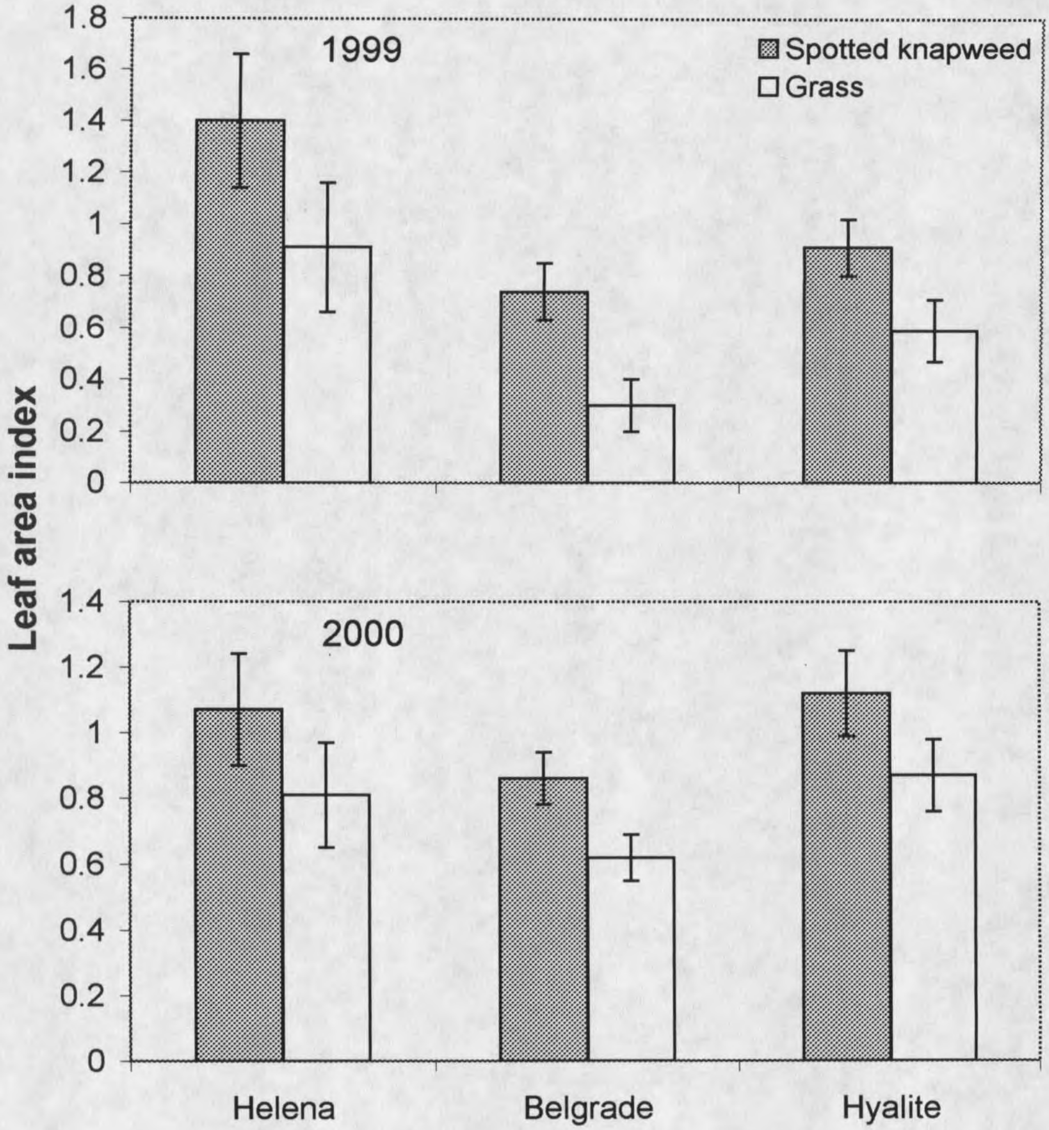

Fig. 2.2. Total leaf area index (mean ± SE; n=4) for spotted knapweed and native grass plots in 1999 and 2000. This measurement includes everything that intercepts diffuse solar radiation > 3 cm height above the soil surface.

The average age of sampled spotted knapweed plants was 4 to 5 years at each site, although spotted knapweed was not aged at Thiede. In many cases, observations by landowners or county weed supervisors indicated that spotted knapweed had been present for more than a decade.

Table 2.1. Total basal cover (mean ± SE; n=4) of spotted knapweed and native grass plots in 1999 and 2000 for the three measured sites.

		Total basal cover (%)	
Site	Year	Spotted knapweed	Grass
Helena	1999	11.3 ± 1.0	10.3 ± 2.9
	2000	4.0 ± 0.2	3.9 ± 1.0
Belgrade	1999	4.9 ± 0.9	1.0 ± 0.2
	2000	4.4 ± 0.5	2.3 ± 0.4
Hyalite	1999	13.3 ± 3.1	16.3 ± 5.0
	2000	5.4 ± 0.4	5.2 ± 0.7

Basic Soil Properties

Particle Size Fractions Spotted knapweed and native grass plots had similar near-surface soil particle size fractions at most sites (Fig. 2.3). Helena and Belgrade had greater (by 4 to 5%) sand fraction in spotted knapweed plots than in native grass plots (Table 2.2). This difference was consistent among all the plots at these sites. Silt and clay size soil fractions were similar between vegetation types at all sites.

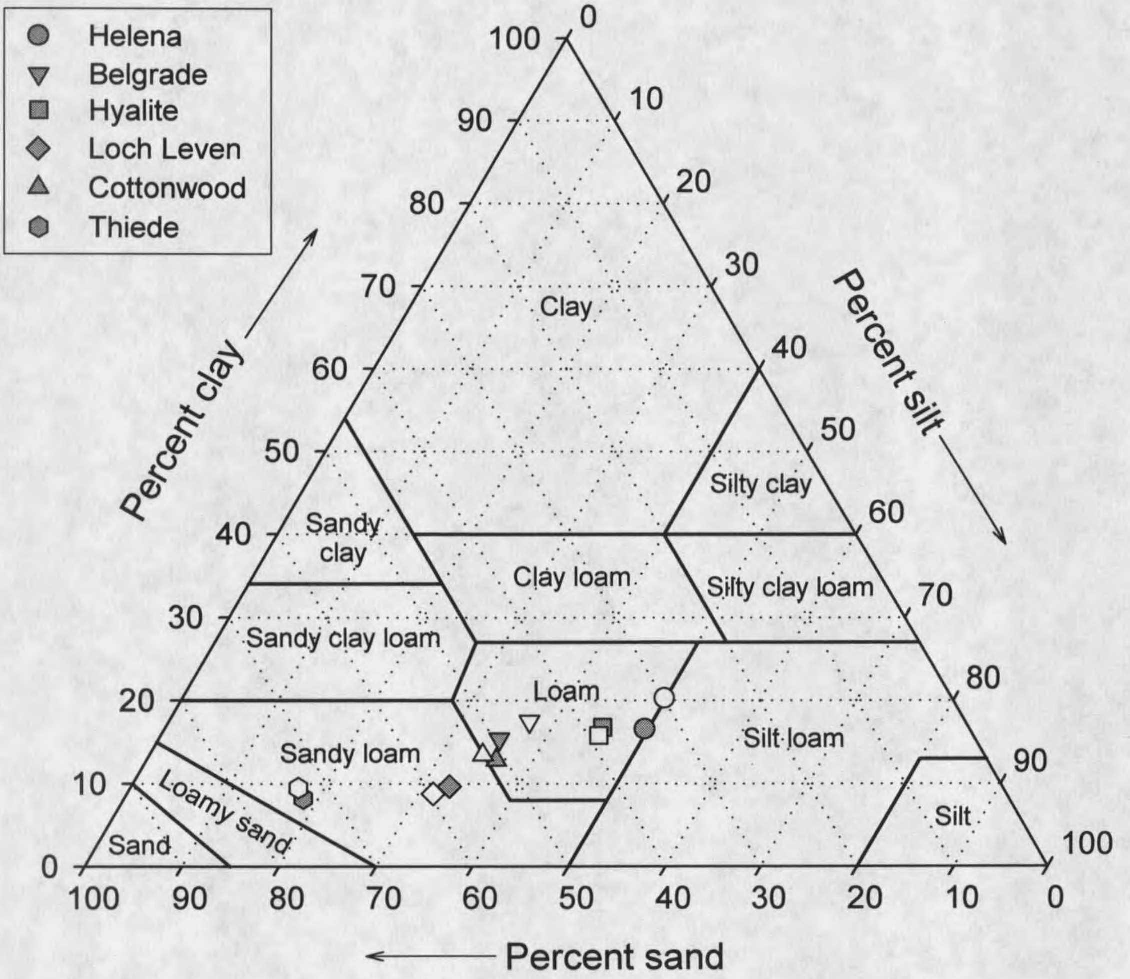

Figure 2.3. Soil textural triangle showing USDA particle size fractions (mean ± SE; n=4; Thiede n=8) of spotted knapweed plots (closed symbols) and native grass plots (open symbols). Error bars are smaller than symbols in all cases.

Table 2.2. ANOVA P-values (n=4; Thiede n=8) for the difference between spotted knapweed and native grass plots for mean USDA primary particle size fractions of near-surface soil at each site.

Site	Sand	Silt	Clay
Helena	0.07	0.92	0.14
Belgrade	0.10	0.16	0.53
Hyalite	0.18	0.88	0.33
Loch Leven	0.22	0.34	0.27
Cottonwood	0.57	0.40	0.44
Thiede	0.92	0.43	0.18

Bulk Density Native grass plots had higher near-surface soil bulk densities than spotted knapweed plots at Helena (Table 2.3). Trends between vegetation types were inconsistent among the blocks for the remaining sites and inconsistent across all sites.

Table 2.3. Near-surface soil bulk density (mean ± SE; n=4; Thiede n=8) and ANOVA P-values for the difference between spotted knapweed and native grass plots for each site.

	Bulk density (g cm^{-3})		
Site	Spotted knapweed	Grass	P-value
Helena	0.88 ± 0.02	0.99 ± 0.03	0.02
Belgrade	1.08 ± 0.03	1.06 ± 0.02	0.72
Hyalite	0.97 ± 0.04	0.98 ± 0.02	0.87
Loch Leven	1.09 ± 0.03	1.18 ± 0.02	0.28
Cottonwood	0.94 ± 0.02	1.03 ± 0.02	0.14
Thiede	1.06 ± 0.04	1.04 ± 0.04	0.76

Organic Carbon At Loch Leven, spotted knapweed plots had higher total organic carbon contents than native grass plots (Table 2.4). However, differences between vegetation types at all other sites were inconsistent among blocks.

Table 2.4. Near-surface soil total organic carbon content (mean ± SE; n=4; Thiede n=8) and ANOVA P-values for the difference between spotted knapweed and native grass plots for each site.

	Soil organic carbon (g kg^{-1})		
Site	Spotted knapweed	Grass	P-value
Helena	70.4 ± 9.02	69.8 ± 5.87	0.95
Belgrade	25.2 ± 1.25	27.9 ± 1.82	0.30
Hyalite	38.8 ± 1.37	41.7 ± 1.26	0.30
Loch Leven	18.6 ± 0.77	16.7 ± 0.92	0.09
Cottonwood	43.3 ± 1.44	39.3 ± 1.48	0.39
Thiede	32.1 ± 1.97	32.3 ± 0.98	0.94

Soil Hydraulic Properties

Saturated hydraulic conductivity (K_s) and the α coefficient, which is related to the range in water conducting pore sizes, were similar between vegetation types at all sites (Table 2.5). The measured soil hydraulic properties were highly variable (Fig. 2.4; Fig. 2.5) as expected. Variation of K_s and α between vegetation types was inconsistent among blocks at most sites as well as among sites.

Sorptivity, a soil hydraulic property used to estimate time to ponding, differed between vegetation types only at Helena (Table 2.6). At Helena, spotted knapweed plots

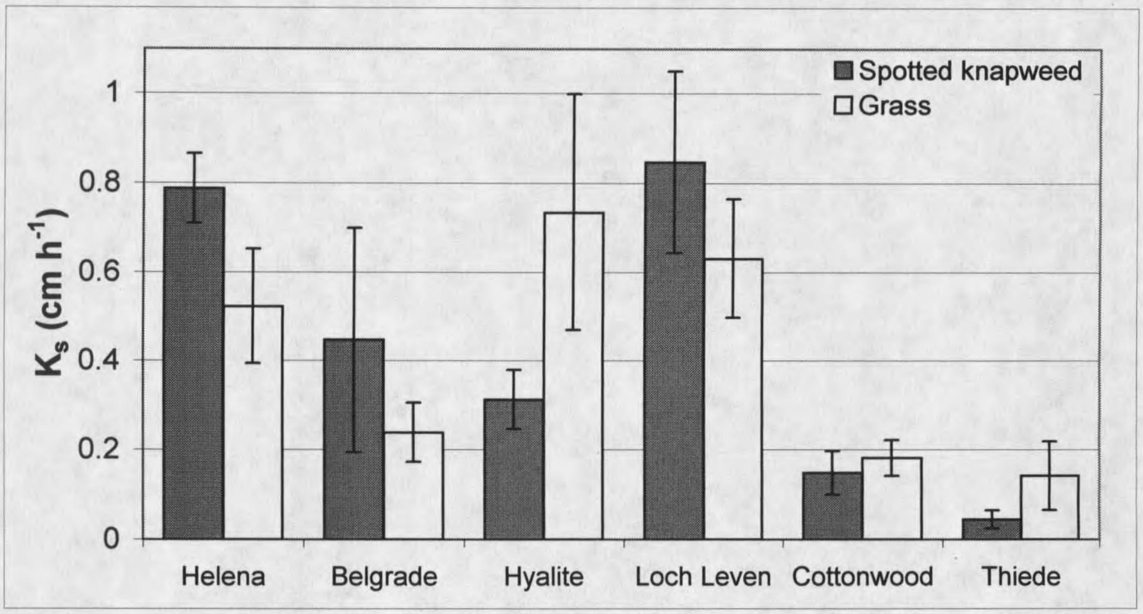

Figure 2.4. Saturated hydraulic conductivity (K_s; mean ± SE; n=4; Thiede n=5) for spotted knapweed and native grass plots.

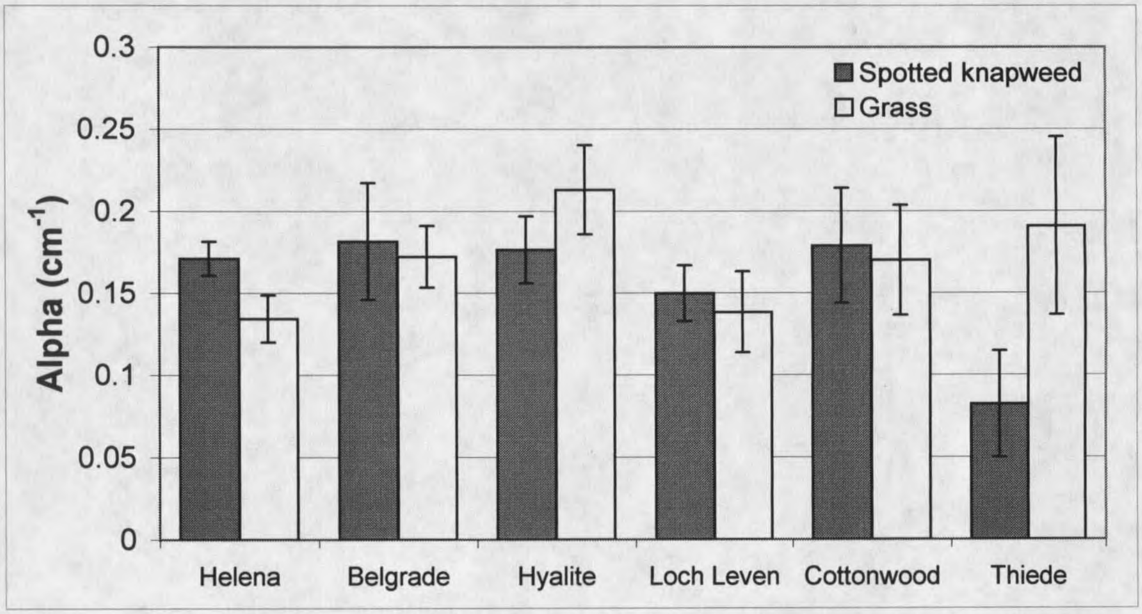

Figure 2.5. Alpha (mean ± SE; n=4; Thiede n=5) for spotted knapweed and native grass plots.

had higher sorptivity than native grass plots. Differences in sorptivity between vegetation types were not consistent among blocks at the two remaining sites.

Table 2.5. ANOVA P-values (n=4; Loch Leven n=8; Thiede n=5) for the difference between spotted knapweed and native grass plots for mean saturated hydraulic conductivity (K_s) and mean α, a hydraulic model coefficient related to the range in water conducting pore sizes.

Site	P (K_s)	P (α)
Helena	0.16	0.17
Belgrade	0.38	0.61
Hyalite	0.27	0.40
Loch Leven	0.12	0.69
Cottonwood	0.67	0.86
Thiede	0.30	0.11

Table 2.6. Sorptivity (mean ± SE; n=4) for spotted knapweed and native grass plots and ANOVA P-values for the three measured sites.

	Sorptivity (m $s^{-0.5}$ × 10^5)		
Site	Spotted knapweed	Grass	P-value
Helena	5.4 ± 0.4	4.6 ± 0.6	0.03
Belgrade	3.0 ± 0.2	3.4 ± 0.5	0.20
Hyalite	4.4 ± 0.4	4.3 ± 0.3	0.80

Trends in estimated time to ponding at a given precipitation intensity were inconsistent for the vegetation types (Fig. 2.6). Time to ponding curves for Helena and Hyalite are plotted in Figure 2.6. The results for Belgrade were similar to Helena, except that calculated time to ponding for Belgrade occurred at precipitation intensities about 0.2

cm h^{-1} lower than for Helena. At Helena and Belgrade, calculated time to ponding for native grass plots started at lower precipitation intensities than for spotted knapweed plots. The trend was opposite at Hyalite (Fig. 2.6).

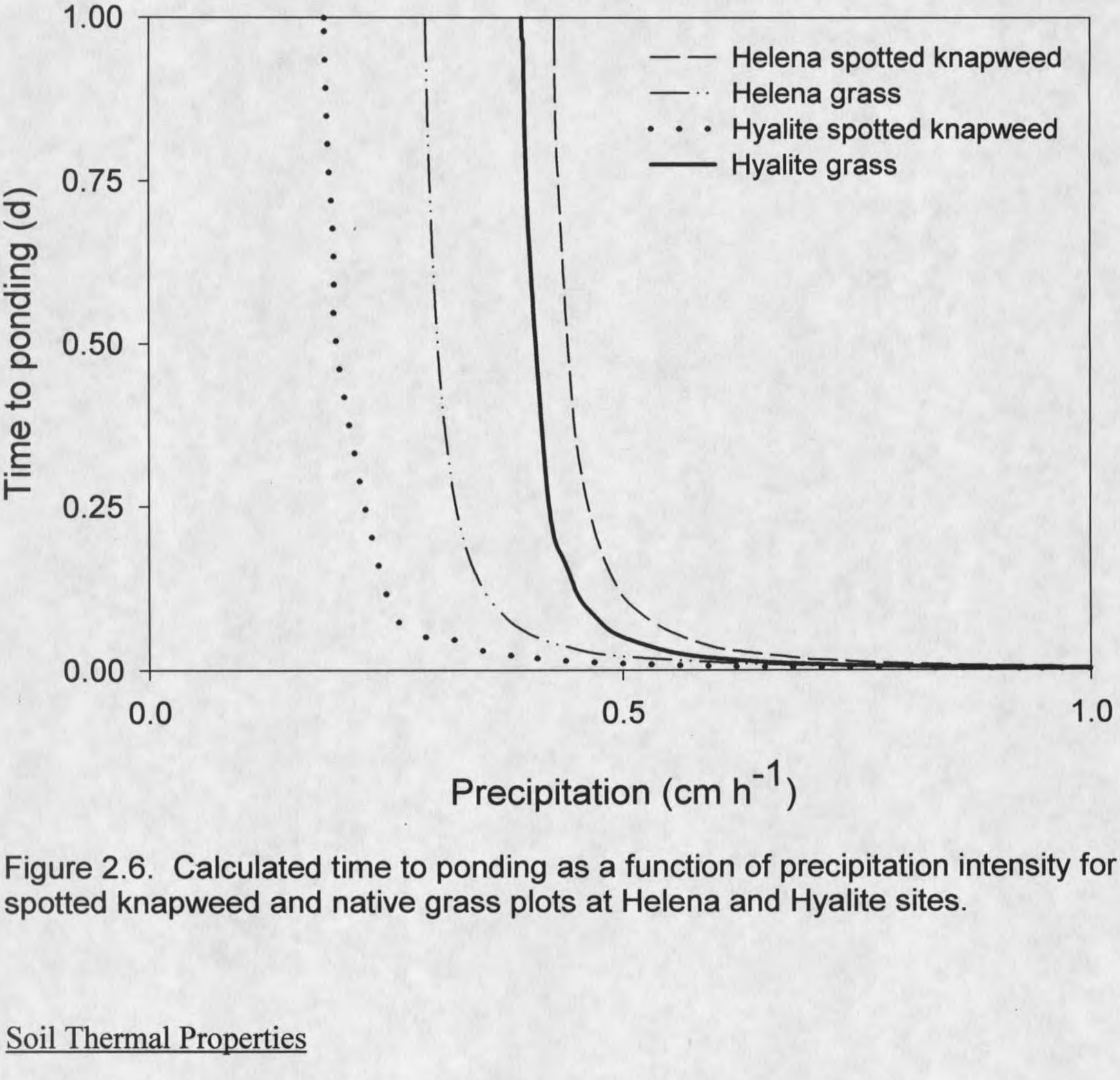

Figure 2.6. Calculated time to ponding as a function of precipitation intensity for spotted knapweed and native grass plots at Helena and Hyalite sites.

Soil Thermal Properties

Near-surface soil volumetric heat capacity did not differ between vegetation types at any of the six sites (Table 2.7; Fig. 2.7). Differences in soil thermal conductivity (λ) between vegetation types were inconsistent among sites (Fig. 2.8). At Helena, native grass plots had higher near-surface soil thermal conductivity than spotted knapweed plots (Table 2.7; Fig. 2.8). At Thiede, soils in spotted knapweed plots had greater thermal conductivity than native grass plots (Table 2.7; Fig. 2.8). Native grass plots tended to have greater thermal conductivity than spotted knapweed plots at Cottonwood (P=0.13) but the trend was opposite at Belgrade (P=0.12; Table 2.7; Fig. 2.8).

Table 2.7. ANOVA P-values (n=4; Thiede n=8) for the difference between spotted knapweed and native grass plots for the soil thermal properties volumetric heat capacity (c_v), thermal conductivity (λ), and thermal diffusivity (D_h) for all sites.

Site	P (c_v)	P (λ)	P (D_h)
Helena	0.16	0.06	0.11
Belgrade	0.61	0.12	0.25
Hyalite	0.73	0.65	0.62
Loch Leven	0.28	0.33	0.45
Cottonwood	0.83	0.13	0.10
Thiede	0.99	0.07	0.09

Apparent soil thermal diffusivity differed between vegetation types only at Cottonwood and Thiede (Table 2.7). At Cottonwood, native grass plots had greater thermal diffusivity than spotted knapweed plots (Fig. 2.9), whereas at Thiede spotted knapweed plots had greater thermal diffusivity than native grass plots. At Helena, thermal diffusivity in native grass plots tended to be greater than in spotted knapweed plots (P=0.11; Table 2.7).

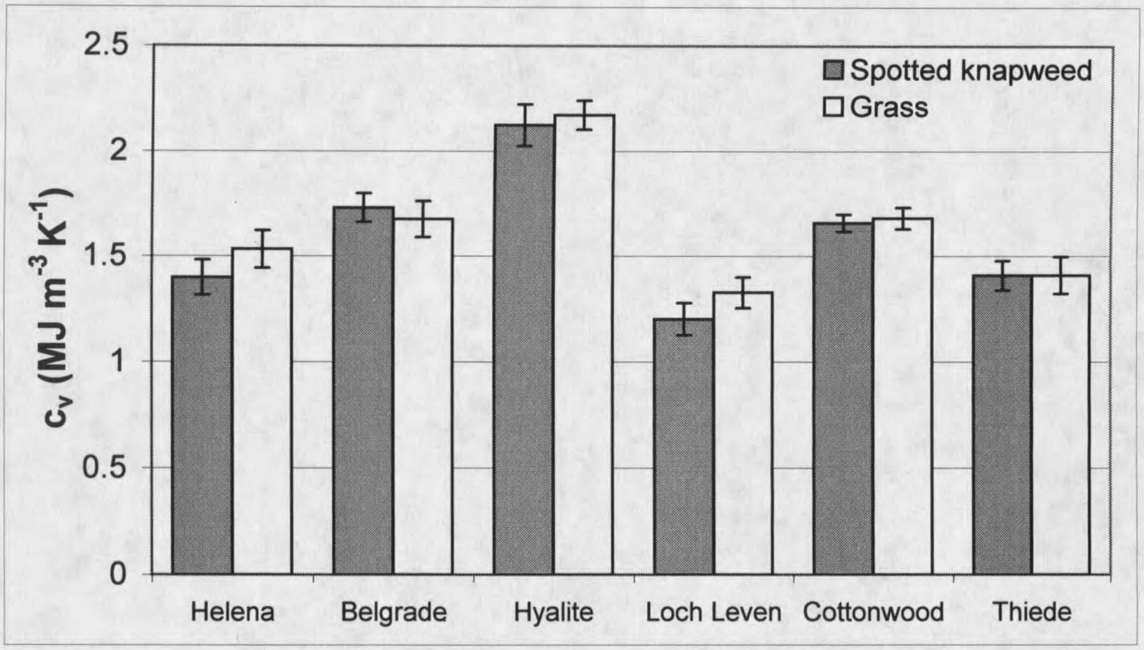

Figure 2.7. Near-surface soil volumetric heat capacity (c_v; mean ± SE; n=4; Thiede n=8) for spotted knapweed and native grass plots.

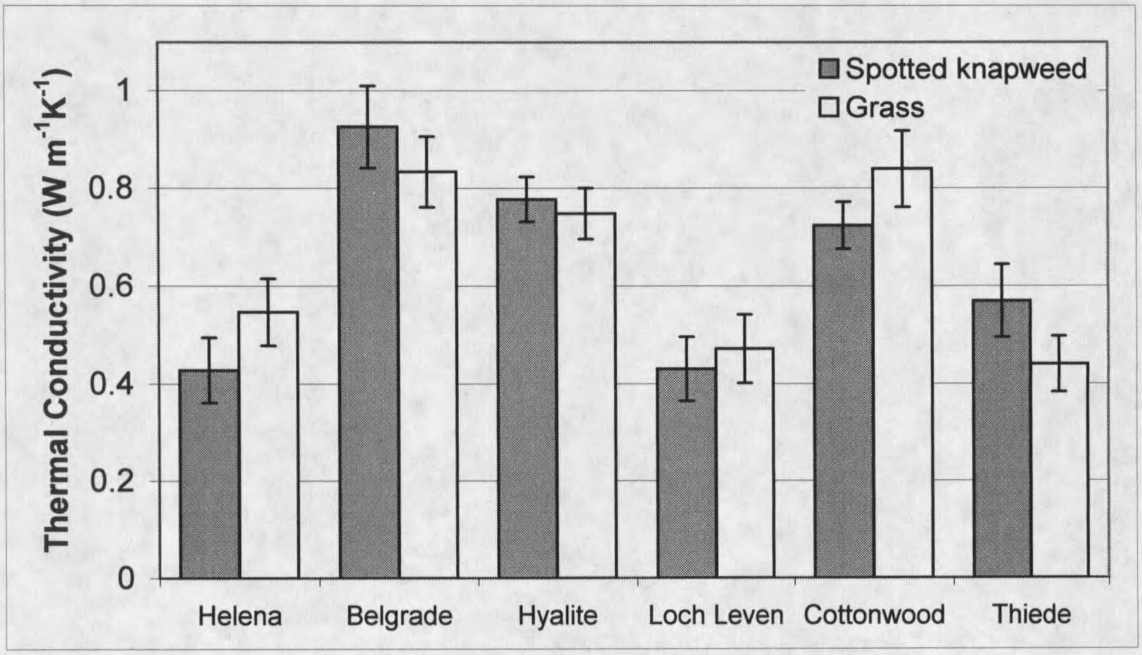

Figure 2.8. Near-surface soil thermal conductivity (mean ± SE; n=4; Thiede n=8) for spotted knapweed and native grass plots.

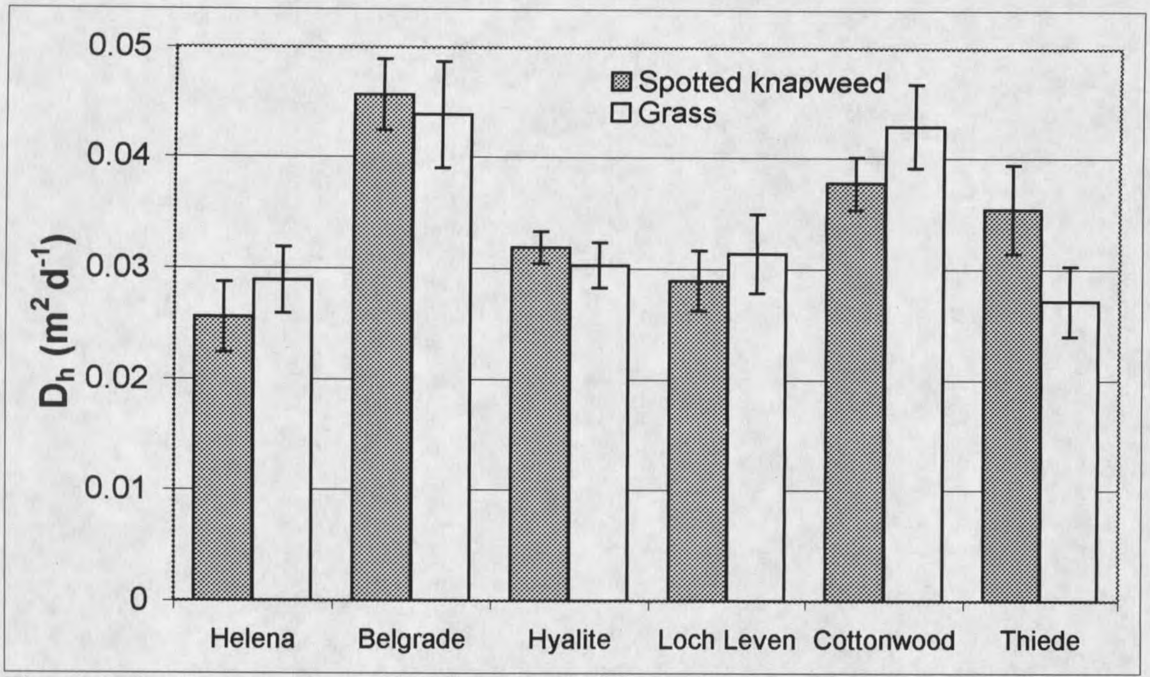

Figure 2.9. Near-surface soil thermal diffusivity (D_h; mean ± SE; n=4; Thiede n=8) for spotted knapweed and native grass plots.

Thermal damping depths differed between native grass and spotted knapweed plots at Helena and Belgrade (Table 2.8). Native grass plots at Belgrade had greater damping depths than spotted knapweed plots, but the trend was opposite at Helena. Damping depth is strongly influenced by soil water content, which was used as a covariate to determine statistical significance. Therefore, the damping depths in Table 2.8 are averaged over a range of soil water contents, and differences between these means may not necessarily represent solely differences in vegetation.

Table 2.8. Thermal damping depths (mean ± SE; n=2) for spotted knapweed and native grass plots and ANOVA P-values for the three sites where soil temperature was monitored.

	Damping depth (m)		
Site	Spotted knapweed	Grass	P-value
Helena	0.07 ± 0.004	0.07 ± 0.003	0.01
Belgrade	0.05 ± 0.002	0.08 ± 0.005	< 0.0001
Hyalite	0.06 ± 0.003	0.07 ± 0.005	0.35

At Belgrade and Hyalite, native grass plots had higher mean daily soil surface temperatures than spotted knapweed plots (Table 2.9; Fig. 2.10). At Hyalite, the amplitude of soil surface temperature fluctuations (A_0) was greater for native grass plots than spotted knapweed plots (Table 2.9). Differences in A_0 between vegetation types were inconsistent among sites (Fig. 2.11).

Table 2.9. ANOVA P-values (n=2) for the difference between spotted knapweed and native grass plots for average soil surface temperatures ($\bar{T}$) and amplitude of soil surface temperature fluctuations (A_0) for the three monitored sites.

Site	$\bar{T}$	A_0
Helena	0.27	0.16
Belgrade	0.05	0.67
Hyalite	0.01	0.003

Discussion

Differences in soil particle size fractions, bulk density, total organic carbon content, saturated hydraulic conductivity, the range in water conducting pore sizes (α), and soil thermal properties between vegetation types were inconsistent among blocks at

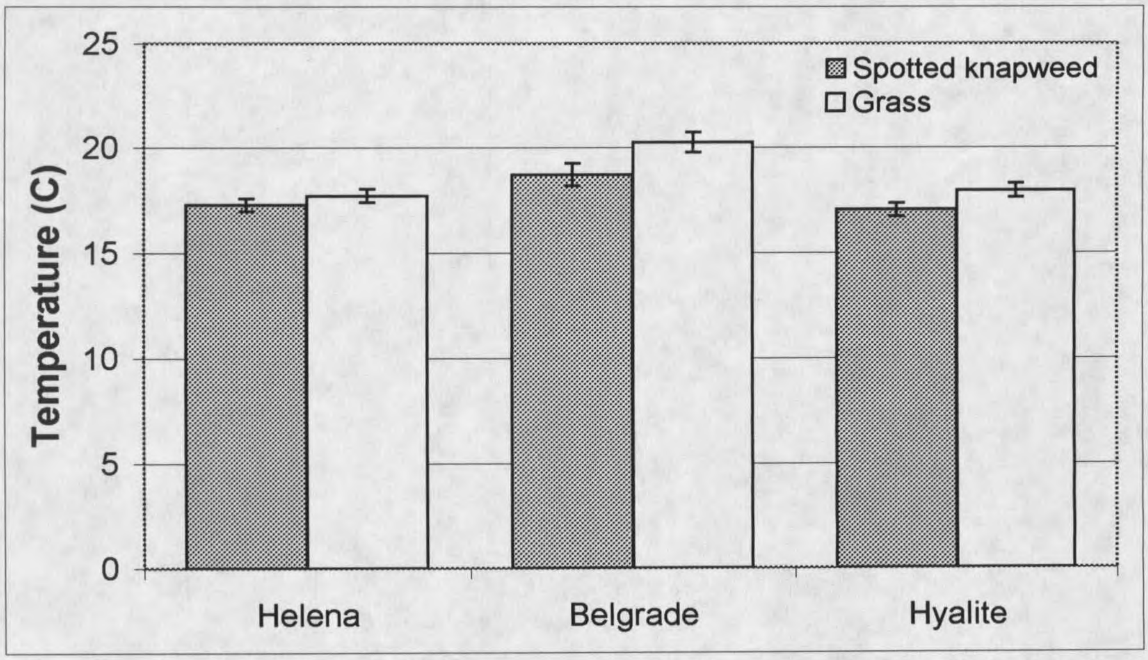

Figure 2.10. Fitted daily soil surface temperature (mean ± SE; n=2) for spotted knapweed and native grass plots.

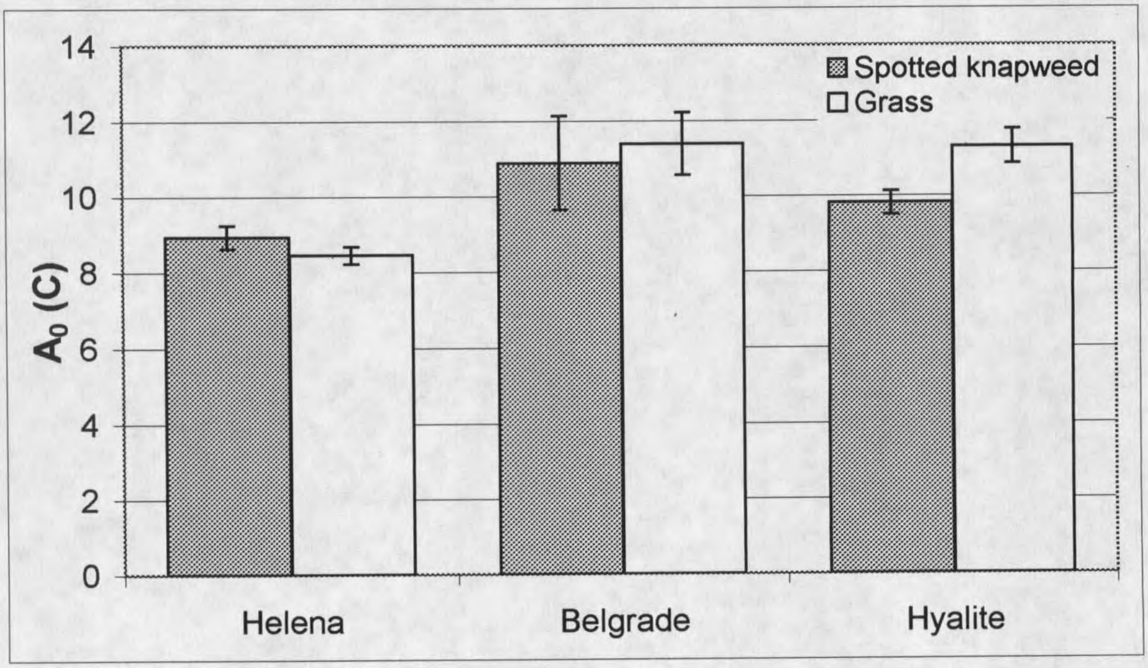

Figure 2.11. Amplitude of fitted soil surface temperature fluctuations (A_0; mean ± SE; n=2) for spotted knapweed and native grass plots.

most sites and across sites. Presumably, this inconsistency reflects the inherently high spatial variability of these properties, the relatively negligible or weak effects of vegetation type, or the numerous interactions between plant structure, canopy cover, and soil. Primary particle size fractions of surface soils did not differ substantially between the two vegetation types. The slightly greater sand fractions at Helena and Belgrade might indicate redistribution of surface soil by wind or water at these sites. However, if surface soil is redistributed, organic carbon content of surface soil should also differ (Hook et al., 1991), but organic carbon content was similar on spotted knapweed and native grass plots at each site.

Lower bulk density in spotted knapweed plots at Helena was not expected because these plots had a greater sand fraction, which would likely result in higher bulk density. Overall, bulk density values were lower than typical values for mineral soils of similar texture. This could be the result of large amounts of organic matter in the near-surface soil, frost heaving, or sampling bias.

Small differences in bulk density, which may develop at the soil surface in response to differences in rainfall impact or other vegetative influences, may not be detectable using the 0-5 cm depth. Soil hydraulic and thermal properties were generally similar for native grass and spotted knapweed plots which indicates that the soil characteristics immediately at the soil surface that influence these properties (including bulk density) were similar.

Saturated hydraulic conductivity is strongly influenced by soil pore size distribution and pore continuity, which can be affected by plant root characteristics. Any differences between the tap-rooted spotted knapweed and the fibrous-rooted native grasses did not result in consistent differences in saturated hydraulic conductivity or the α coefficient in the Gardner (1958) hydraulic conductivity model. The low estimated K_s at Thiede may reflect apparent hydrophobicity of that site's soil surface. Differences in calculated time to surface water ponding were relatively small and inconsistent and not likely to differentially influence erosion or surface runoff at my sites. For the Bozeman and Helena areas, a precipitation intensity of 0.5 cm h^{-1} has a return time of less than 2 years (Miller et al., 1973). This short of a return time could be significant for surface runoff and erosion.

Measuring soil hydraulic properties using tension infiltrometers created some disturbance at the soil surface. This disturbance could have masked differences in soil hydraulic properties between vegetation types. However, other techniques used to measure attributes related to soil infiltration capacity, such as infiltrometer rings or rainfall simulators, have other disadvantages that make them less appropriate to directly evaluate vegetative impacts on soil properties.

Soil thermal properties were also highly variable and inconsistent. Because air has low thermal conductance, thermal conductivity increases with bulk density and also depends on soil water content (Hillel, 1998). At most sites, differences in thermal conductivity were generally consistent with differences in bulk density. The influence of soil water content, bulk density, organic matter content, and their possible synergistic effects on thermal properties makes it difficult to isolate vegetative impacts. My study does not suggest that areas dominated by spotted knapweed have a more extreme near-surface soil thermal environment because the amplitude of surface soil temperature fluctuations was similar between vegetation types, and native grass plots had higher mean daily surface soil temperatures than spotted knapweed plots. The greater mean daily surface soil temperatures in native grass plots may reflect the lower LAI in these areas.

Because I did not have definitive knowledge or control of long-term site histories, my ability to determine cause and effect is constrained. I cannot claim that changes in plant community are responsible for any measured differences in soil properties without having characterized site properties before spotted knapweed invasion. Certain soil or site characteristics may favor spotted knapweed invasion. However I minimized the potential for confounding cause and effect by measuring replicated, intermixed spotted knapweed and native grass plots at six different field sites. Because I found few systematic differences between vegetation types in soil physical properties, either there were no pre-existing differences in soils prior to spotted knapweed invasion between the two vegetation types or spotted knapweed ameliorated these differences.

My results suggest that spotted knapweed did not alter near-surface soil properties in a consistent direction at the six sites. This agrees with Lacey et al.'s (1989) interpretation that differences in plant structure and canopy cover were responsible for greater surface runoff and sediment yield in spotted knapweed-dominated areas compared with native grass-dominated areas. Infiltration can be influenced by differences in canopy structure associated with native grasses, forbs, and shrubs (e.g., Gutierrez and Hernandez, 1996; Meeuwig, 1970; Pearse and Woolley, 1936).

With rainfall simulators, the variability associated with infiltration on 'homogeneous' semiarid rangeland soils is influenced greatly by vegetative cover and related soil properties (Devaurs and Gifford, 1984). Short-term effects of plant canopy removal suggest that rangeland vegetative canopy cover has less of an impact on surface runoff and erosion than the indirect effects of plant canopy cover on soil structure, organic matter, and litter (Simanton et al., 1990).

The specific vegetative impacts on soil properties are difficult to determine because of the intricate relationships between these properties and their unknown rates of change in wildland soils. In some cases, synergistic effects (Hillel, 1998) of small differences in some soil properties may result in significant influences on other related properties. Because I did not measure consistent differences in most of the selected soil properties measured, I presume that seed germination or seedling growth of the dominant native species would not be affected.

I could not determine the exact duration or histories of the spotted knapweed invasions at the sites. However, organic carbon content and bulk density can differ following tree and shrub removal after only 55 months (Albaladejo et al., 1998). It is possible that spotted knapweed might ultimately alter surface soil properties relative to native grass vegetation, but it may take many years for these changes to become detectable.

The sites used in this study do not represent the entire spectrum of spotted knapweed invasion of native grasslands. Results might differ on sites with stonier soils, steeper slopes, or concurrent grazing. To develop a more comprehensive analysis of the impacts of spotted knapweed on soil properties and processes, I recommend that a "garden" research facility with extensively pre-characterized (and preferably homogeneous) soils be planted with intermixed plots of spotted knapweed and native perennial grass monocultures and mixtures. Sampling soil and vegetation through time would provide invaluable insights concerning plant-soil interactions. However, long-term studies of this sort require administrative and financial commitment that is beyond the scope of typical research grant funding.

Summary and Conclusions

Presence of spotted knapweed for at least five years did not alter surface soil characteristics of wildland soils at six sites. A few soil properties differed between spotted knapweed and native grass plots, but these were inconsistent within and among sites. The high spatial variability associated with soil physical properties, and the complex interactions among different soil properties, makes it difficult to directly assess plant species' impacts on soil properties or processes. However, results from this study do not support assertions that spotted knapweed degrades soils. If such effects occur, they are relatively weak or require longer periods of time to develop.

The demonstrated success of spotted knapweed in colonizing disturbed (and increasingly undisturbed) areas of western North America might therefore be a result of it being: 1) opportunistic in capturing resources through functional flexibility, 2) plastic in modifying form to enhance resource capture in different environments or when competing with different neighbors, 3) efficient in using captured resources, or 4) some combination of these different strategies. Further, these findings suggest that eradicating spotted knapweed should be sufficient to prepare sites for restoring native perennial grasslands; i.e., soils in invaded areas similar to those studied would not need to have physical attributes ameliorated.

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CHAPTER 3

SOIL WATER DYNAMICS UNDER SPOTTED KNAPWEED AND NATIVE GRASSES ON SEMIARID RANGELANDS

Introduction

Spotted knapweed (*Centaurea maculosa* Lam.) was introduced to the Pacific Northwest from Europe in the early 1900s (Boggs and Story, 1987; Chicoine et al., 1985), and has become a serious threat to native grassland ecosystems. In the past this forb invaded disturbed areas, but more recently spotted knapweed has spread to undisturbed habitats (Lacey et al., 1990; Tyser and Key, 1988). Spotted knapweed tends to form dense, monotypic stands (Fletcher and Renney, 1963) thereby altering the structure of many plant communities. Spotted knapweed has invaded 326 counties in the northwestern United States, including every county in Montana, Idaho, Washington, and Wyoming (Sheley et al., 1998). Extensive wildlife habitat and millions of dollars in livestock forage have been lost due to spotted knapweed invasion (French and Lacey, 1983; Hirsh and Leitch, 1996).

Because success in controlling spotted knapweed and restoring invaded areas to native species has been limited, mechanisms that enable it to be such a successful invader of semiarid grasslands need to be determined. In semiarid ecosystems, belowground plant competition is generally more important than aboveground competition (Wilson, 1988). A species that uses more of a critical soil resource or preempts that resource, leaving less for its neighbors, could have a competitive advantage. Soil water is often a limiting resource for plant growth in semiarid ecosystems (Fowler, 1986). Species that have a competitive advantage over neighboring species for soil water could decrease the growth and survival of their neighbors. Potential mechanisms responsible for spotted knapweed's success include altering spatial or temporal soil water dynamics, or having a superior ability to take up water.

Several invasive plant species may alter soil water dynamics of a vegetation community, often inhibiting native species (Woods, 1997). Some impacts include dewatering wetlands (*Iris pseudacorus*, *Mimosa pigra*; Woods, 1997), generating boggy areas (*A. virginicus*; Mueller-Dombois, 1973), and modifying the hydrology of river systems (*Tamarix* spp.; Graf, 1978). Invasive species can potentially alter soil water status via: 1) greater water use than native species; 2) access to water sources not utilized by the native plant community via different rooting or root function; 3) physiological differences resulting in water use at different times; and 4) altered soil surface characteristics as a result of different canopy structure or production of hydrophobic litter layers, influencing infiltration and perhaps the overall water balance of the site (Walker and Smith, 1997).

Plant characteristics such as root phenology, root distribution, and root density can greatly influence temporal and spatial soil water dynamics by determining when and at what depths roots can take up soil water (Dobrowolski et al., 1990; Sala et al., 1992). In general, root density decreases with depth (Singh and Sainju, 1998). Fibrous roots are generally more dense at shallow depths (Dobrowolski et al., 1990; Singh and Sainju, 1998). Taproots usually grow to deep depths (Dobrowolski et al., 1990; Singh and Sainju, 1998).

Perennial bunchgrasses in semiarid grasslands of southwestern Montana have fibrous root systems which are generally distributed in the upper 1.5 m of the soil profile (Dobrowolski et al., 1990; Weaver, 1919) but are most dense in the upper 30 cm (Frank et al., 1996), depending on species and soil conditions. In general, most of these native grasses begin to grow in April or May (Dobrowolski et al., 1990; Stubbendieck et al., 1997). These native species mature and become quiescent in mid- to late summer (Stubbendieck et al., 1997). Regrowth in fall may occur if soil moisture and temperature conditions are favorable (Stubbendieck et al., 1997).

Spotted knapweed is a tap-rooted perennial (Watson and Renney, 1974). It generally spends its first year as a rosette and bolts during subsequent years (Boggs and Story, 1987; Watson and Renney, 1974). Spotted knapweed seeds germinate in the fall and early spring (Watson and Renney, 1974). Rosettes form in early spring, tend to bolt in early May, and produce flower buds in early June that bloom from July until as late as September (Sheley et al., 1998).

Plant species with deep taproots might escape competition by having access to soil water deeper in the soil profile when surface soil may be dry for prolonged periods because of evaporation and water extraction by roots (Dobrowolski et al., 1990; Singh and Sainju, 1998). However, extensive fibrous root systems may have greater overall root length and surface area which may facilitate access to a greater total volume of soil and possibly more soil water than a taproot system, depending on soil water distribution.

Even when growth form, root distribution, and root biomass are similar, other root system differences such as root thickness and season of root growth can affect the ability to compete for water (Eissenstat and Caldwell, 1988). Growth in early spring and/or late summer may allow spotted knapweed to utilize soil water not available to quiescent native grasses. This could result in less soil water being available for growth of native species during the current or following growing season under some climatic conditions.

Small precipitation events may be another soil water source potentially not utilized by some native species but possibly utilized by spotted knapweed (Sala et al., 1992). Surface soils of semiarid areas are usually dry because of high evaporation rates which may make small precipitation events very important for potential biomass production and survival (Sala and Lauenroth, 1982). A quicker physiological response time to small rainfall events may allow access to soil water not physiologically available to other species (Sala and Lauenroth, 1982; Wraith et al., 1995).

Near-surface soil properties or soil water dynamics might be modified by spotted knapweed because root characteristics or basal and canopy cover differ relative to native grasses. Spotted knapweed might simply use more soil water than native grasses, use soil water earlier or later during the growing season than native grasses, have access to deeper soil water unavailable to native grasses, or have quicker response times for soil water uptake after soil drying. Together or separately, these factors might inhibit the restoration and growth of native species in areas where spotted knapweed has invaded. Understanding the mechanisms of persistence of spotted knapweed rather than simply attempting to eradicate it will be needed to successfully restore invaded areas.

The objective of this study was to compare the growing season soil water dynamics under spotted knapweed and native perennial grasses in adjacent rangeland plots. Vegetative influences on temporal and spatial soil water dynamics and soil water storage were evaluated by monitoring soil water content using a neutron moisture meter and automated time domain reflectometry (TDR).

Materials and Methods

I periodically monitored soil water content throughout the soil profile (0-100 cm) in four blocks at one site (Helena) in western Montana using a neutron moisture meter. In addition, I continuously monitored near-surface soil water content using time domain reflectometry (TDR) in two blocks at the Helena Site and two additional sites in western Montana. Each block contained a pair of 2 m^2 plots, with one plot dominated by spotted knapweed (>50% spotted knapweed canopy cover) and one plot dominated by native grasses (<10% spotted knapweed canopy cover). I selected plots close to one another to minimize potential influences of soil property spatial heterogeneity, physiography, and inherent site differences.

I excavated soil pits in spotted knapweed- and native grass-dominated areas at each study site to confirm that soil profiles and soil classification were similar. I measured soil water retention of near-surface soils (0-5 cm) for spotted knapweed and native grass plots using a pressure chamber apparatus (SoilMoisture Equipment Co., Santa Barbara, CA; Klute, 1986). I filled a 25 cm diameter ring with about 4 cm of sieved (2 mm) soil on a 1.5-MPa bubbling pressure porous ceramic pressure plate.

Pressure was measured using a mercury manometer for pressures ≤ 0.1 MPa and a pressure regulator for pressures > 0.1 MPa. Volumetric water content was measured at about 0.01, 0.02, 0.05, 0.1, 0.2, 0.5, 0.8, and 1.3 MPa using two TDR probes buried in the soil.

I estimated basal cover of spotted knapweed and grasses by growth form: bunchgrass, rhizomatous grass, and annual grass. Leaf area index (LAI; LAI-2000, Lincoln, NE) and density of spotted knapweed by growth stage (seedling, rosette, and adult) and grasses by growth form were measured. Basal cover, LAI, and density were determined at the three sites on August 3-5, 1999 and July 28-August 4, 2000.

I removed five to ten spotted knapweed plants at each site to estimate the minimum age of invasion. Larger plants were chosen to estimate the age of the oldest plants. Ages of the spotted knapweed plants were determined by drying the taproot in an oven at 47°C for about 7 d, breaking the root in several places, and counting the rings of secondary xylem under a dissecting microscope. Each ring represented one year's growth (Boggs and Story, 1987). The average age of spotted knapweed plants at each site does not indicate the time of invasion, but indicates a minimum number of years spotted knapweed has been present on the site.

Site history and measurement constraints guided my selection of study sites. Basic site criteria were as follows: 1) spotted knapweed reportedly present for at least 5-10 years; 2) spotted knapweed-dominated areas adjacent to or interspersed with areas dominated by native perennial grasses; 3) lack of known previous site disturbance that may have caused differences in soil properties; 4) little or no active grazing or herbicide use; and 5) at least 10-15 cm of surface soil with low rock content. The first four criteria describe the vegetative types and minimized potential for confounding of plant effects and site history. Stony soils prevented proper insertion of TDR probes to desired depths and indicated different water holding capacities among plots.

Study Sites

The Helena site was 21 km southeast of East Helena, Montana in Broadwater County. Soils at this site are Rothiemay loams (fine-loamy, mixed, superactive, frigid Aridic Calciustolls) with 1 to 2% slopes (Appendix). Average annual precipitation ranges from 305 mm (Helena WSO, Western Regional Climate Center [WRCC], 2000). Native grasses include bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Löve) and needle-and-thread (*Stipa comata* Trin. & Rupr.). This site had not been grazed and large amounts of litter were present in the spotted knapweed- and grass-dominated areas. The spotted knapweed areas had large amounts of "stem" litter compared with the finer, leaf litter characteristic of native grass-dominated areas.

The Belgrade site is 6 km west of Belgrade, Montana in Gallatin County. Soils were Kassler gravelly coarse sandy loams (sandy-skeletal, mixed, frigid Torriorthentic Haplustolls) with 0 to 1% slopes are present at this site (Appendix). Average annual precipitation is 360 mm (Belgrade Airport, WRCC, 2000). *Pascopyrum smithii* (Rydb.) Löve (western wheatgrass) is the dominant native grass at this site. This site had also been invaded by annual cheatgrass (*Bromus tectorum* L.) and had a history of light horse grazing. Plots were fenced to prevent grazing in the study area.

The Hyalite site is 12 km southwest of Bozeman, Montana in Gallatin County. Average annual precipitation is about 465 mm (Bozeman Montana State University, WRCC, 2000). Soils at this site are Hyalite loams (fine-loamy, mixed, superactive, frigid Typic Argiustolls) with 0 to 1% slopes (Appendix). Native grasses include Idaho fescue (*Festuca idahoensis* Elmer) and western wheatgrass. The site had not been grazed since the 1970s.

Soil Water Dynamics

I monitored soil water status using a neutron moisture meter (Model 503DR, CPN, Martinez, CA; Schmugge et al., 1980) and TDR (Model 1502C, Tektronix, Beaverton, OR; Topp et al., 1980). The neutron moisture meter measured soil water content at deeper depths than TDR because high amounts of coarse fragments in subsoils prevented inserting TDR probes at deeper depths. TDR measurements provided greater spatial and temporal resolution of near-surface soil water dynamics.

Neutron moisture meter access tubes were installed only at Helena in May 1999, because of very cobbly (10 to 15 cm diameter) subsoils at the other two sites. Thin-wall polyvinyl chloride (PVC) access tubes 5.5 cm in diameter were installed up to 100 cm deep in four blocks (four spotted knapweed, four native grass plots). The neutron moisture meter was field-calibrated by collecting volumetric soil cores using a Giddings hydraulic corer and determining the linear relationship between the slow neutron count ratios and measured volumetric water contents.

With the neutron moisture meter, I measured soil water content at 20 cm depth increments from 20 to 100 cm. In 1999, soil water content was measured approximately weekly from mid-May to mid-August and once in mid-September. In 2000, soil water content was measured approximately biweekly from late April to mid-September and once in mid-October. I assumed that all plots at the same study site received the same amount of precipitation as they were within a radius of about 40 m. For neutron probe measurements, I calculated cumulative changes in soil water storage as the difference between each measurement and the initial soil water content measurement for the growing season, multiplied by 20 cm to obtain depth equivalent water.

I used repeated measures analysis of variance (SAS, 2000) to test for vegetation type effects (spotted knapweed vs native grass), time-within-year effects, and the interaction of the effect of vegetation type with time on soil water content at each depth, using a significance level of $P \leq 0.10$. Vegetation effects on linear and quadratic trends over time are only reported when significant. Each year was analyzed separately. For 1999, I analyzed drying curves rather than the entire growing season to assess vegetation effects on drying rates and degree of soil drying. For 2000, the entire growing season was analyzed because of the general lack of precipitation (Table 3.1), and therefore lack of drying curves.

I buried TDR probes in two blocks at each study site (two spotted knapweed, two native grass plots). Depths of TDR probes varied by site because of depth constraints of rocky soil: 5, 15, and 30 cm at Helena; 5, 10, and 15 cm at Belgrade; and 5 and 10 cm at Hyalite. The automated measurement system included a datalogger (21X, Campbell

Scientific, Inc., Logan, UT), TDR cable tester, and coaxial multiplexers (SDMX50, Campbell Scientific, Inc.). Soil water content was measured with TDR at 0600, 1200, 1800, and 2400 h each day. Using two automated systems, all three sites were continuously monitored for various lengths of time during the 1999 field season. The Helena and Hyalite sites were monitored continuously during the 2000 field season. I calculated cumulative changes in soil water content as the differences between each year's initial and subsequent soil water content. Descriptive statistics were calculated to convey mean soil water content and cumulative changes in soil water storage.

Results

Soils and Climate

Spotted knapweed had been present for at least 4 to 5 years at each site. Soil profiles and soil taxonomy in spotted knapweed- and native grass-dominated areas were similar at Helena, Belgrade, and Hyalite (Appendix). The only observed differences between soil pits in the two vegetation types were slight, non-systematic variations in soil horizon thicknesses. Soil water retention of near-surface soils (0-5 cm) for spotted knapweed and native grass plots differed at the wet end (>-0.05 MPa for Helena and Belgrade, >0.8 MPa for Hyalite), but were similar at the dry end for Helena and Hyalite (< 0.05 MPa for Helena, < 0.8 MPa for Hyalite; Fig. 3.1). Soil water retention for Belgrade surface soils differed between vegetation type at the dry end (< 0.5 MPa; Fig. 3.1).

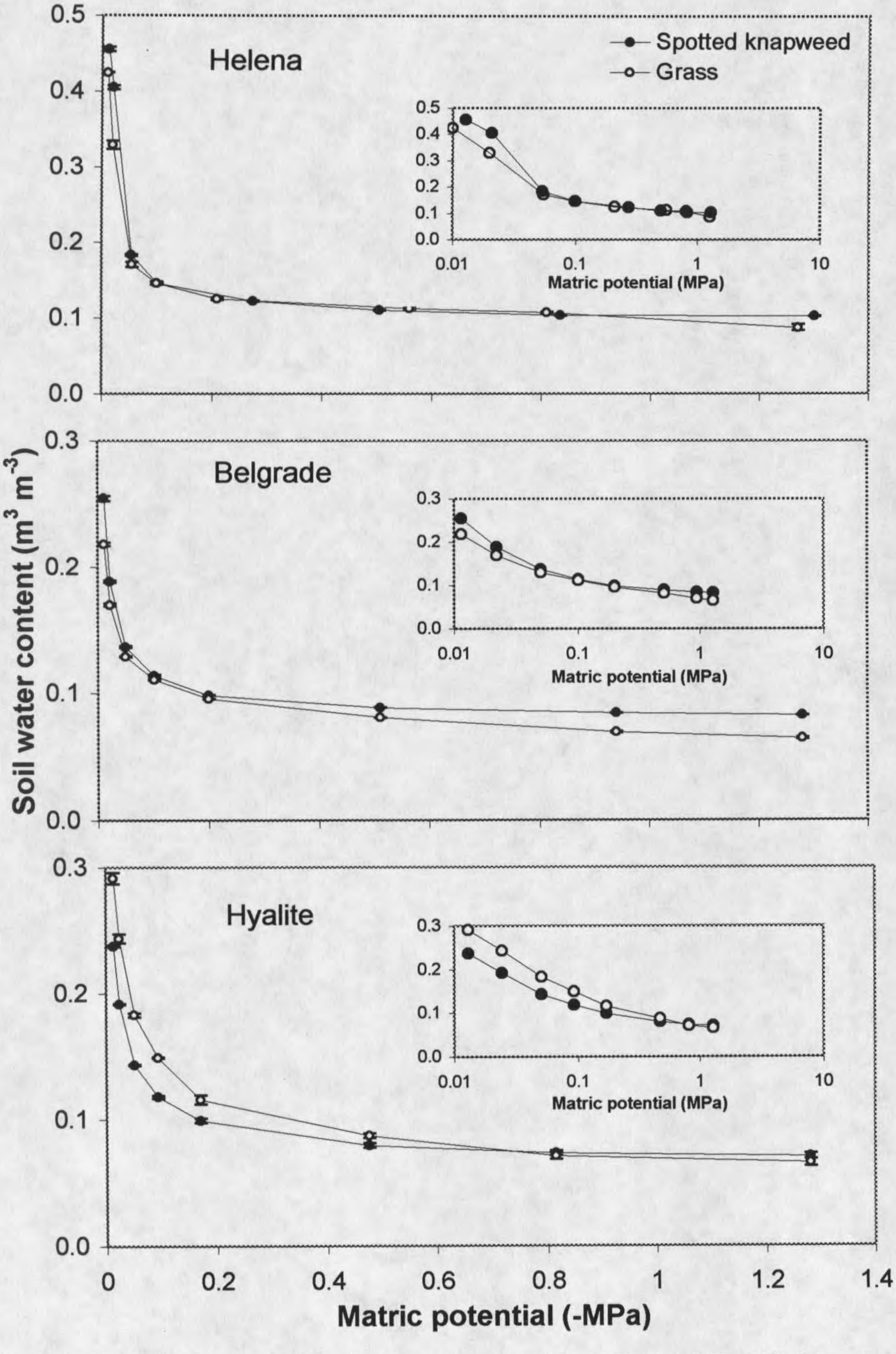

Fig. 3.1. Soil water retention curves (mean soil water content ± SE; n=2) for near-surface soil (0-5 cm) in spotted knapweed and native grass plots. Insets are matric potential (MPa) plotted on a log scale.

Calibration of the neutron moisture meter provided a linear relationship (R^2=0.87) between volumetric water content and slow neutron count ratios. A single calibration relationship was appropriate for all depths.

The amount of precipitation during the 2000 field season was low relative to long-term averages (Table 3.1). Most of the monthly precipitation totals for the Helena, Montana area during 2000 were below 1999 monthly totals and well below long-term mean monthly totals (Table 3.1). At Bozeman, precipitation differences between years varied among months (Table 3.1). However, both years were lower than the long-term mean precipitation totals for Helena and Bozeman (Table 3.1).

Table 3.1. Monthly and annual total precipitation during the growing season for the Helena, MT and Bozeman, MT areas. The mean monthly and annual total precipitation data are based on the past 96 to 108 years. These data were not collected at my field sites but at the nearest weather station (WRCC, 2000).

		Precipitation (cm)							
	Year	**Apr.**	**May**	**Jun.**	**Jul.**	**Aug.**	**Sept.**	**Oct.**	**Annual**
Helena	1999	2.67	5.56	5.46	1.04	4.88	1.37	0.99	24.23
	2000	1.85	2.49	3.61	1.85	1.09	1.37	5.64	21.59
	Mean	2.44	4.88	5.31	2.87	2.51	2.79	1.88	30.45
Bozeman	1999	5.49	6.40	6.48	0.25	8.71	1.60	0.79	39.85
	2000	4.04	7.82	6.48	1.19	2.24	3.53	5.61	41.91
	Mean	4.60	7.32	7.24	3.48	3.18	4.47	3.81	46.79

Vegetation

Total basal cover was greater in spotted knapweed plots than native grass plots at Belgrade in 1999 and 2000 (Table 2.1). In general, total basal cover was lower in 2000 than in 1999, except for Belgrade where it was similar both years (Fig. 2.1; Table 2.1). Spotted knapweed plots at Hyalite had lower spotted knapweed basal cover and higher bunchgrass basal cover compared with the other two sites (Fig. 2.1). Overall, grass cover was lower in spotted knapweed plots than in native grass plots (Fig. 2.1).

Density of spotted knapweed seedlings and annual grasses was lower in 2000 compared with 1999 at Helena and Belgrade (Fig. 3.2). Spotted knapweed seedling density was higher in 2000 than 1999 at Hyalite (Fig. 3.2). At Helena, density of spotted knapweed adults and rosettes were higher in 2000 than 1999 (Fig. 3.2).

LAI was higher in spotted knapweed plots than in native grass plots (Fig. 2.2). LAI remained constant or was slightly higher in 2000 than 1999 (Fig. 2.2).

Soil Water Dynamics

Helena Site At Helena in 1999, initial soil water contents at depths from 20 to 60 cm were similar for spotted knapweed and native grass plots (Fig. 3.3). Towards the end of the growing season at these depths, spotted knapweed plots had less water than native grass plots. Overall soil water content and trends in soil water content during drawdown at depths 20 to 60 cm were similar for both vegetation types (Table 3.2).

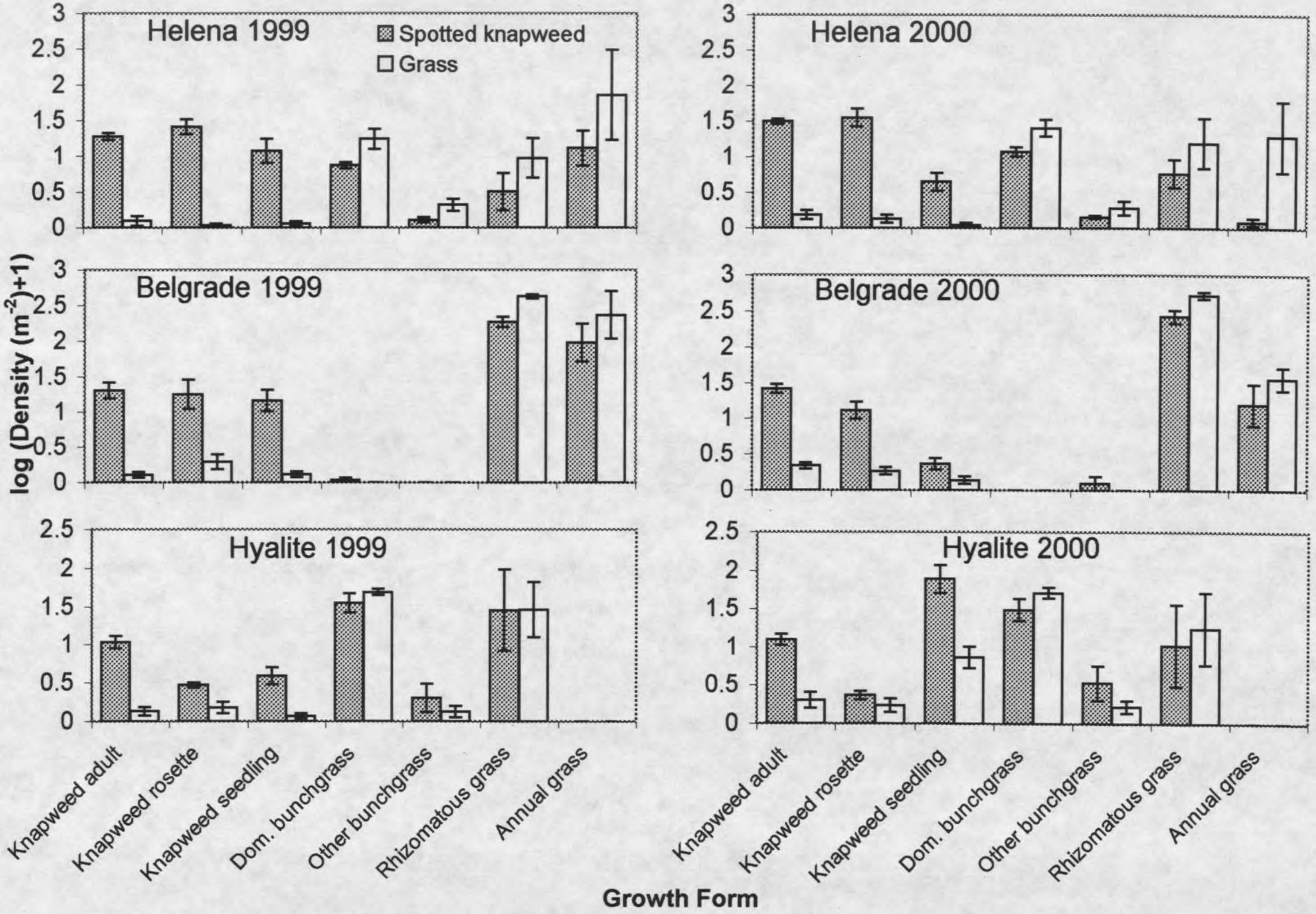

Fig. 3.2. Growth form density (mean ± SE; n=4) for spotted knapweed and native grass plots in 1999 and 2000. Dominant bunchgrasses were: bluebunch wheatgrass at Helena and Idaho fescue at Hyalite.

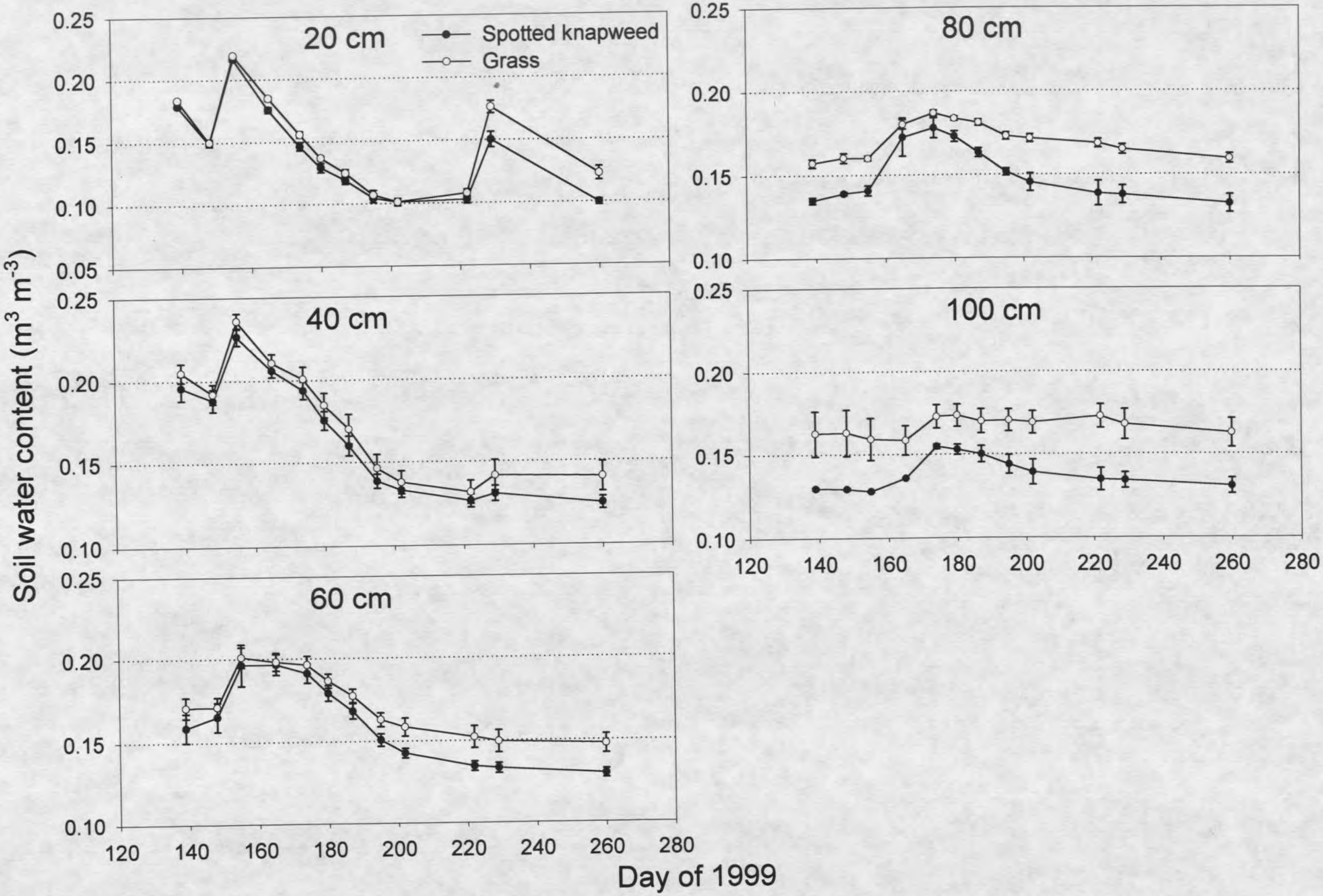

Fig. 3.3. Soil water content (mean ± SE; n=4) for Helena during 1999 using the neutron moisture meter.

At 80 and 100 cm, initial and final soil water contents for spotted knapweed plots were lower than for native grass plots. Similarly, spotted knapweed plots remained lower in soil water content than native grass plots throughout most of the growing season. At these depths, overall soil water content during drawdown differed between vegetation type (Table 3.2). The linear trend of soil water content through time at 100 cm differed between vegetation types (P=0.03). At 100 cm, spotted knapweed plots had a steeper decline in soil water content between Day 174 and Day 202 than native grass plots (Fig. 3.3).

Table 3.2. Repeated measures ANOVA P-values for vegetation type effects, time effects, and the interaction between vegetation type and time for Helena soil water content during drawdown for 1999 and entire growing season for 2000.

			P-values		
Depth (cm)		Days of year	Vegetation type	Time	Vegetation x Time
1999	20	155-222	0.13	<0.0001	0.21
	40	155-260	0.35	<0.0001	0.37
	60	155-260	0.15	<0.0001	0.23
	80	174-260	0.001	0.0008	0.17
	100	174-260	0.09	<0.0001	<0.0001
2000	20	118-287	0.07	<0.0001	0.03
	40	118-287	0.42	<0.0001	0.16
	60	118-287	0.02	<0.0001	0.64
	80	118-287	0.009	0.0067	0.51
	100	118-287	0.10	0.0011	0.06

During the drier 2000 season, soil water content changed noticeably only at the 20 cm depth (Fig. 3.4). Soil water contents during the 2000 growing season were similar between vegetation types at 40 cm (Table 3.2). At 20 cm and 60 to 100 cm depths, spotted knapweed plots had less soil water than native grass plots (Table 3.2). Initial and final soil water contents in spotted knapweed plots were lower than native grass plots at 60 to 100 cm depths. Linear trends of soil water content through time at 40 cm (P=0.05) and 100 cm (P=0.02) differed between vegetation types. Time affected soil water content at all depths for both years (Table 3.2).

Cumulative changes in soil water storage reflect overall vegetation influences. Negative cumulative changes in soil water storage indicate a net loss of soil water, whereas positive changes reflect a net gain of soil water. A net gain in soil water for both vegetation types was evident early in 1999 at Helena due to precipitation (Fig. 3.5; Table 3.1). Cumulative effects of the two vegetation types were similar during most of the 1999 growing season for most depths. However, spotted knapweed plots had a larger net loss of soil water than native grass plots at 20 cm depth near the end of the growing season (Fig. 3.5). Native grass plots gained less soil water at 60 to 100 cm than spotted knapweed plots early in the growing season (Fig. 3.5).

Similar to soil water content, most cumulative changes in soil water storage during the 2000 season were of lesser magnitude than during the 1999 season (Fig. 3.6). Prominent changes in soil water storage at 20 cm corresponded to periods of greater precipitation (Fig.6; Table 3.1). Spotted knapweed plots had a larger net loss of soil water than native grass plots at 100 cm near the end of the growing season.

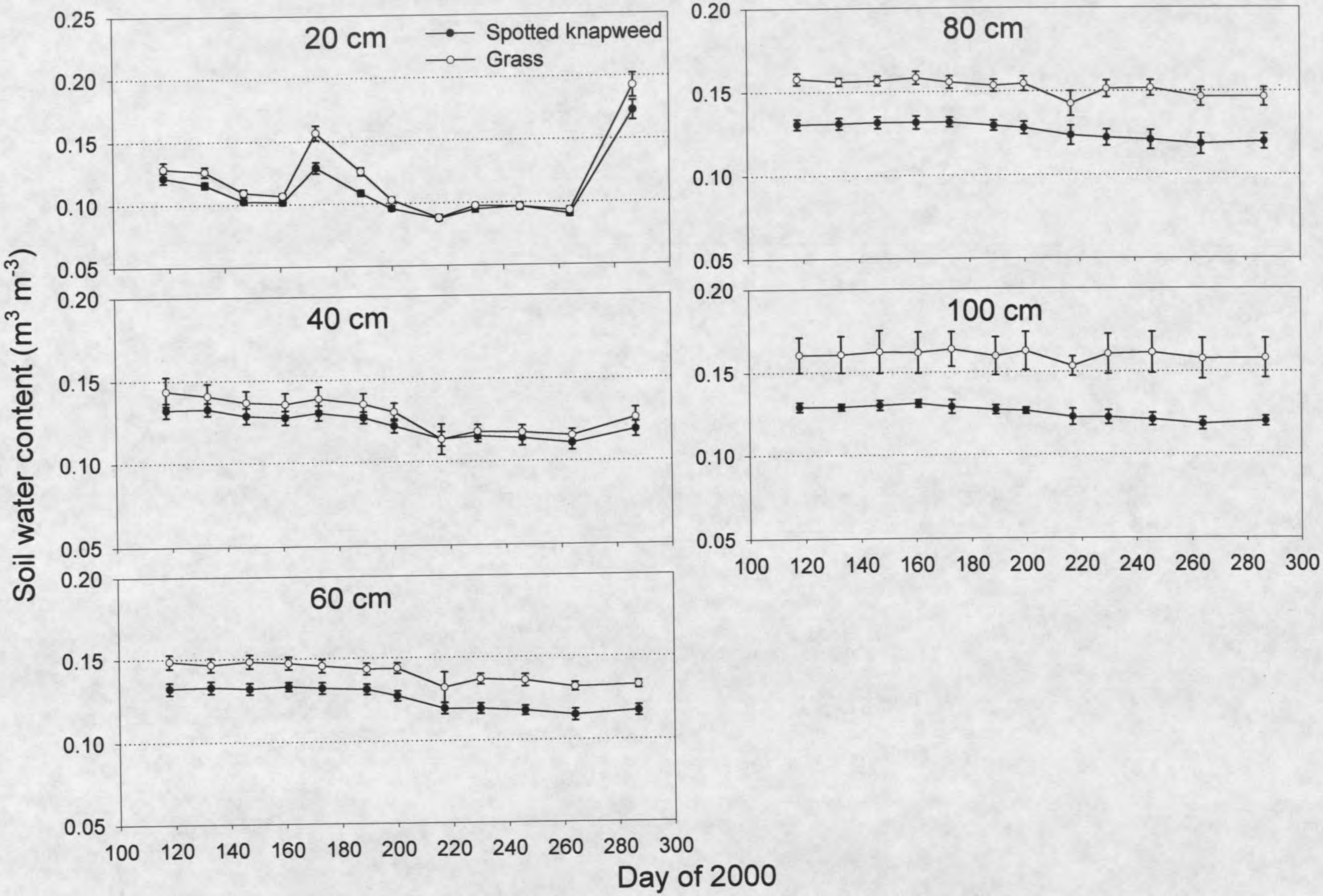

Fig. 3.4. Soil water content (mean ± SE; n=4) for Helena during 2000 using the neutron moisture meter.

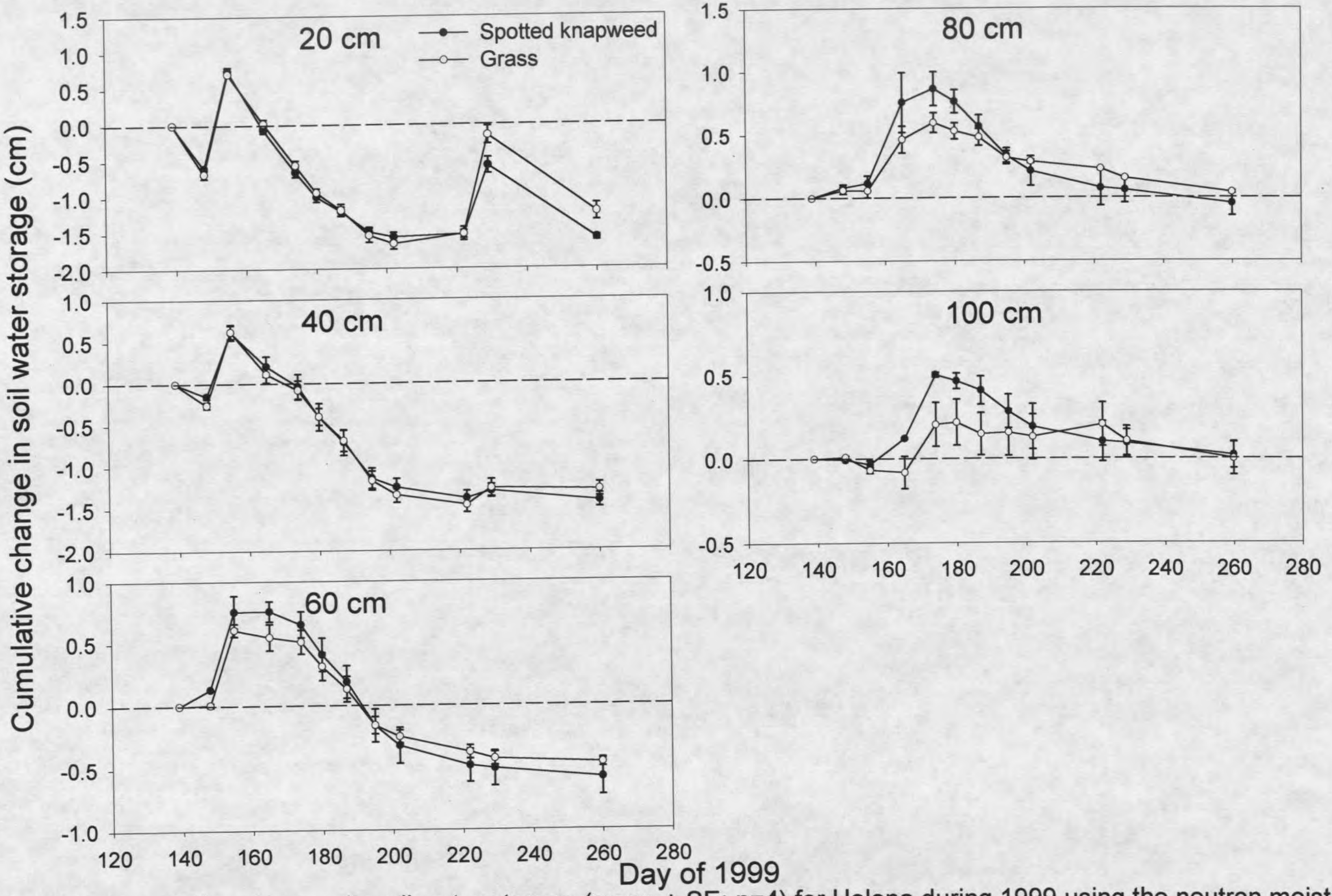

Fig. 3.5. Cumulative changes in soil water storage (mean ± SE; n=4) for Helena during 1999 using the neutron moisture meter.

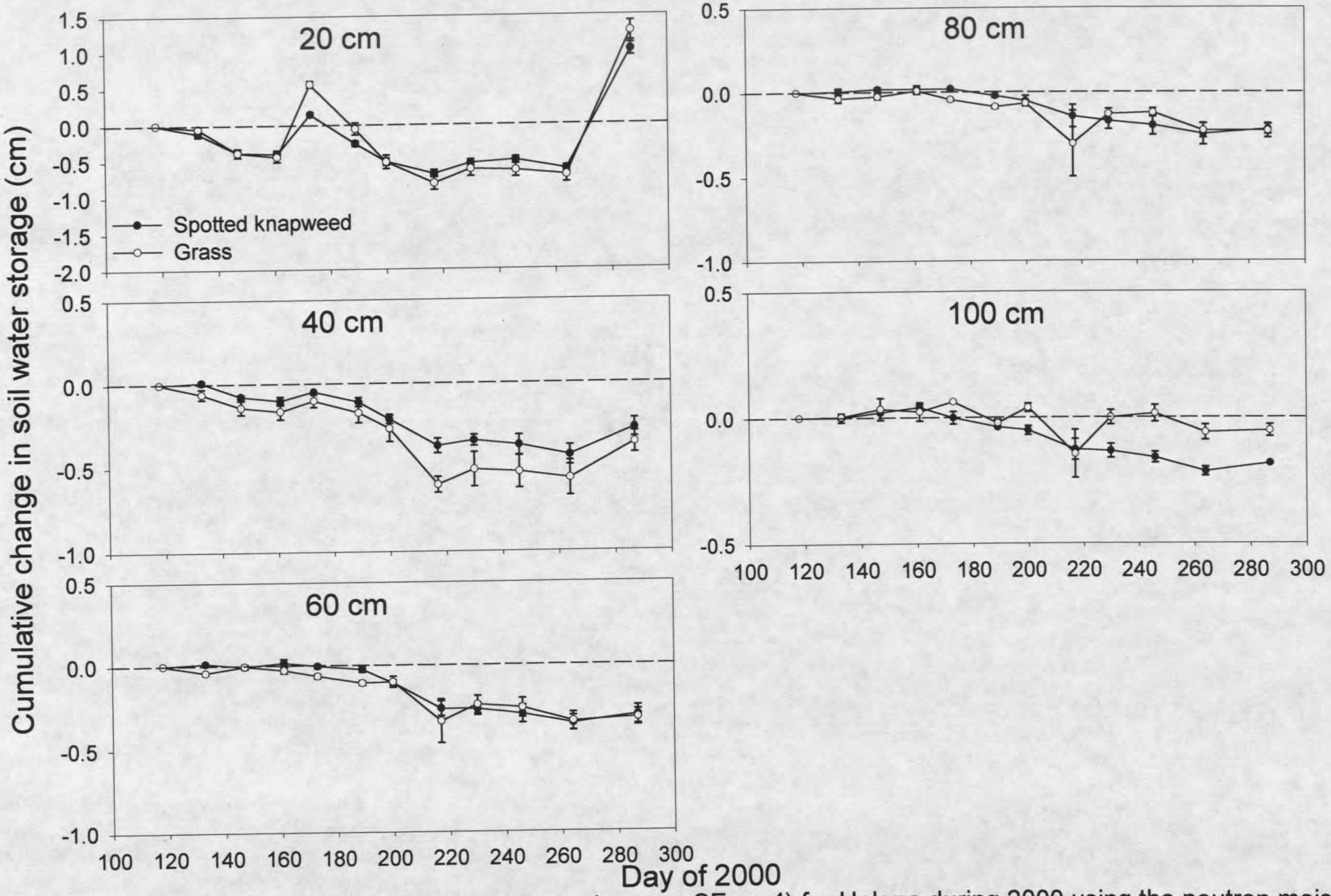

Fig. 3.6. Cumulative changes in soil water storage (mean ± SE; n=4) for Helena during 2000 using the neutron moisture meter.

In 1999 in Helena, near-surface soil water contents measured with TDR did not differ between vegetation types until late in the growing season (Fig. 3.7). Initial soil water contents at 5, 15, and 30 cm depths for spotted knapweed and native grass plots were similar. Later in the growing season at 5 and 15 cm depths, spotted knapweed plots had lower soil water content than native grass plots (Fig. 3.7). This difference remained at 15 cm but not at 5 cm until monitoring ended in early October. In the upper 15 cm near the end of the growing season, spotted knapweed plots did not gain as much water after precipitation events as native grass plots (Fig. 3.7). Soil water at 30 cm was only recharged early in the growing season (Fig. 3.7).

In 2000, spotted knapweed and native grass plots initially had similar soil water contents at shallow depths. At 5 cm, soil water content of spotted knapweed plots increased less than in native grass plots after mid- and late season precipitation events (Fig. 3.8). Soil water contents under spotted knapweed plots were lower than native grass plots at 15 cm mid-season and remained lower through the rest of the growing season (Fig. 3.8). Soil water content at 30 cm did not differ between vegetation types. Little or no soil water recharge was evident at 15 and 30 cm (Fig. 3.8).

In 1999, spotted knapweed had a greater net loss of soil water near the end of the growing season than native grasses for all three depths (Fig. 3.9). Spotted knapweed plots also had lower net gain of soil water than native grass plots after late season precipitation events at 5 and 15 cm in 1999 and at 5 cm in 2000 (Fig. 3.9; Fig. 3.10). In 2000, native grass plots had a greater net loss of soil water at 5 cm than spotted knapweed plots during mid-season that persisted until late season (Fig. 3.10).

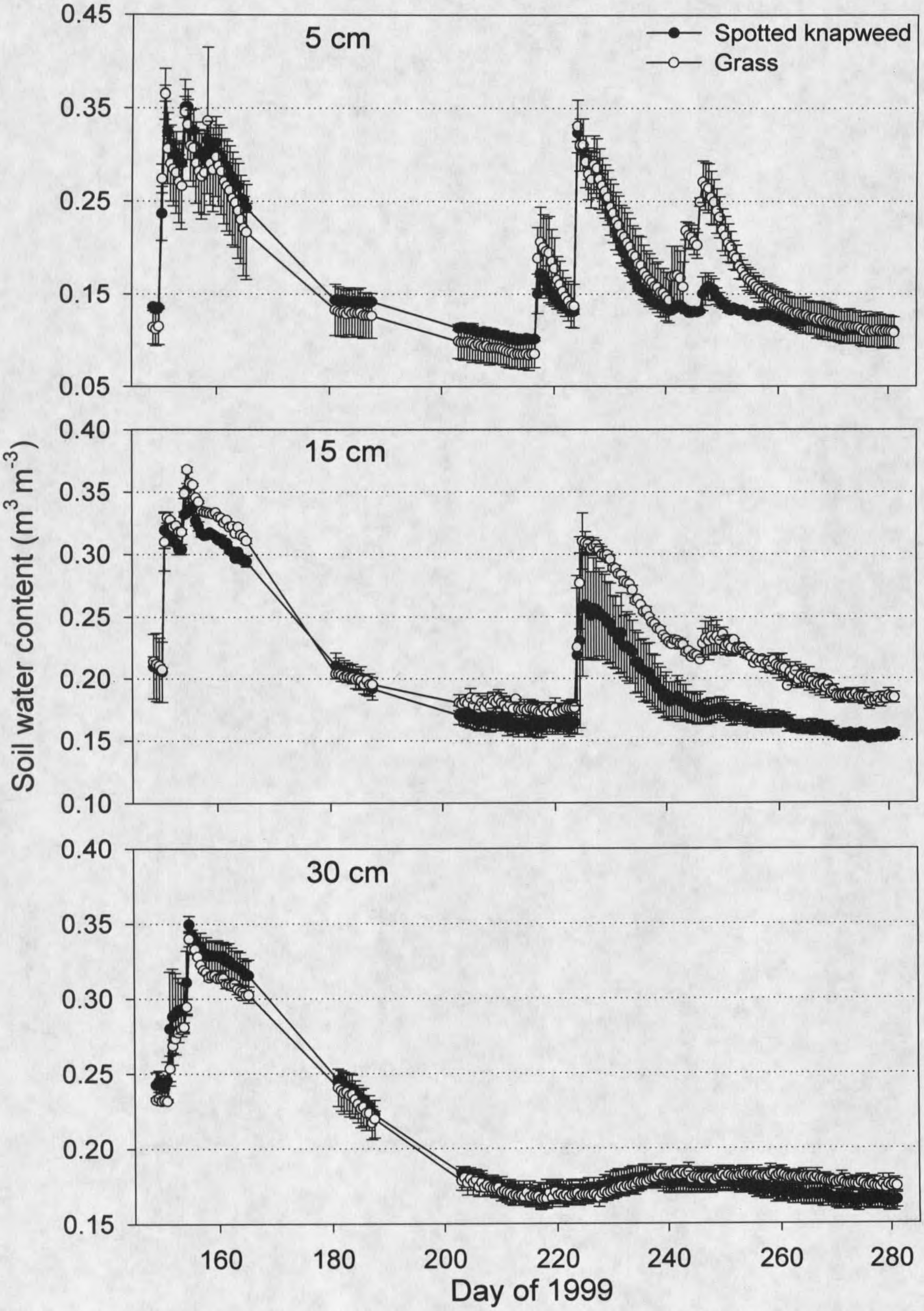

Fig. 3.7. Soil water content (mean ± SE; n=2) time series at 5, 15, and 30 cm depths for Helena during 1999 using TDR. Every second data point is plotted.

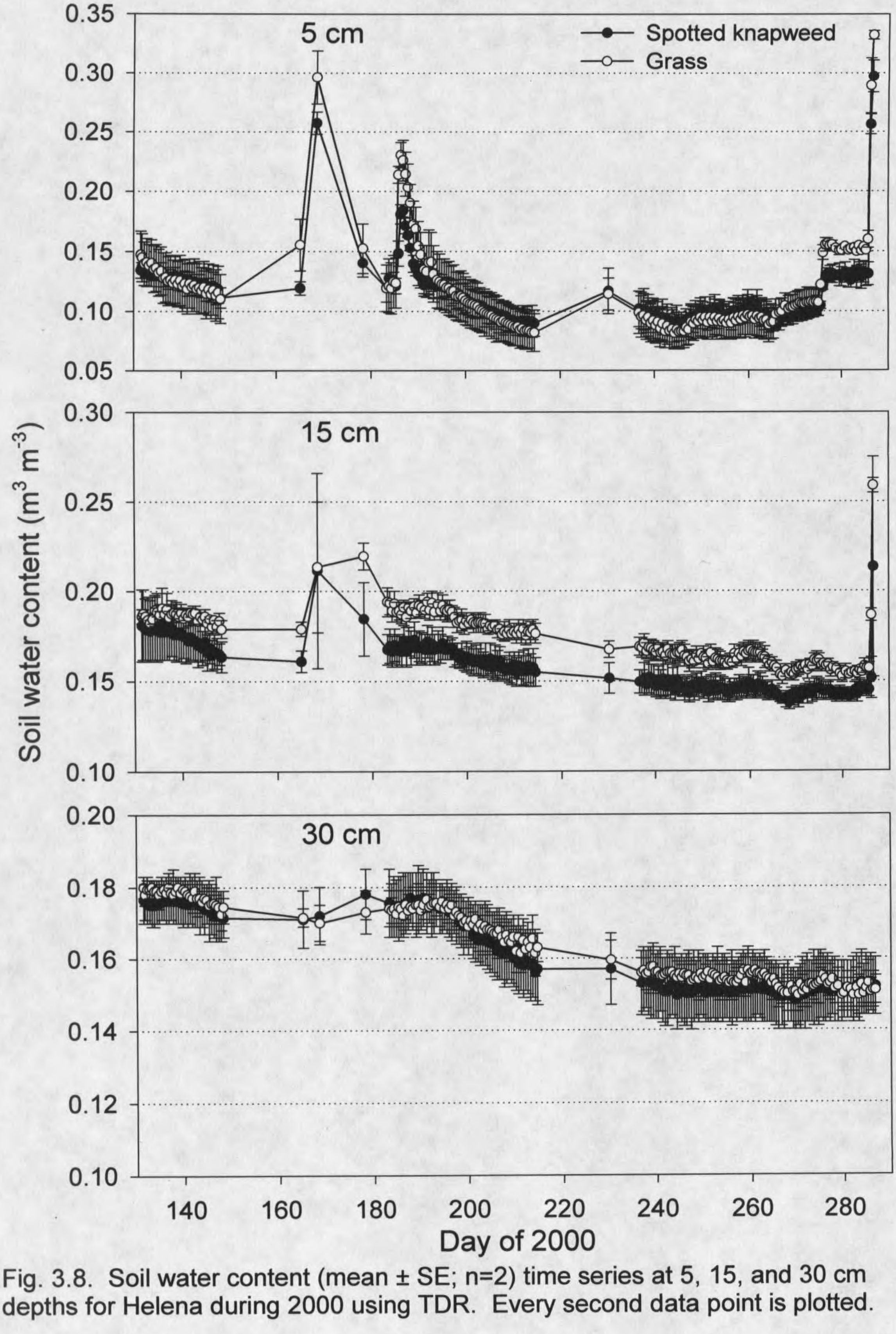

Fig. 3.8. Soil water content (mean ± SE; n=2) time series at 5, 15, and 30 cm depths for Helena during 2000 using TDR. Every second data point is plotted.

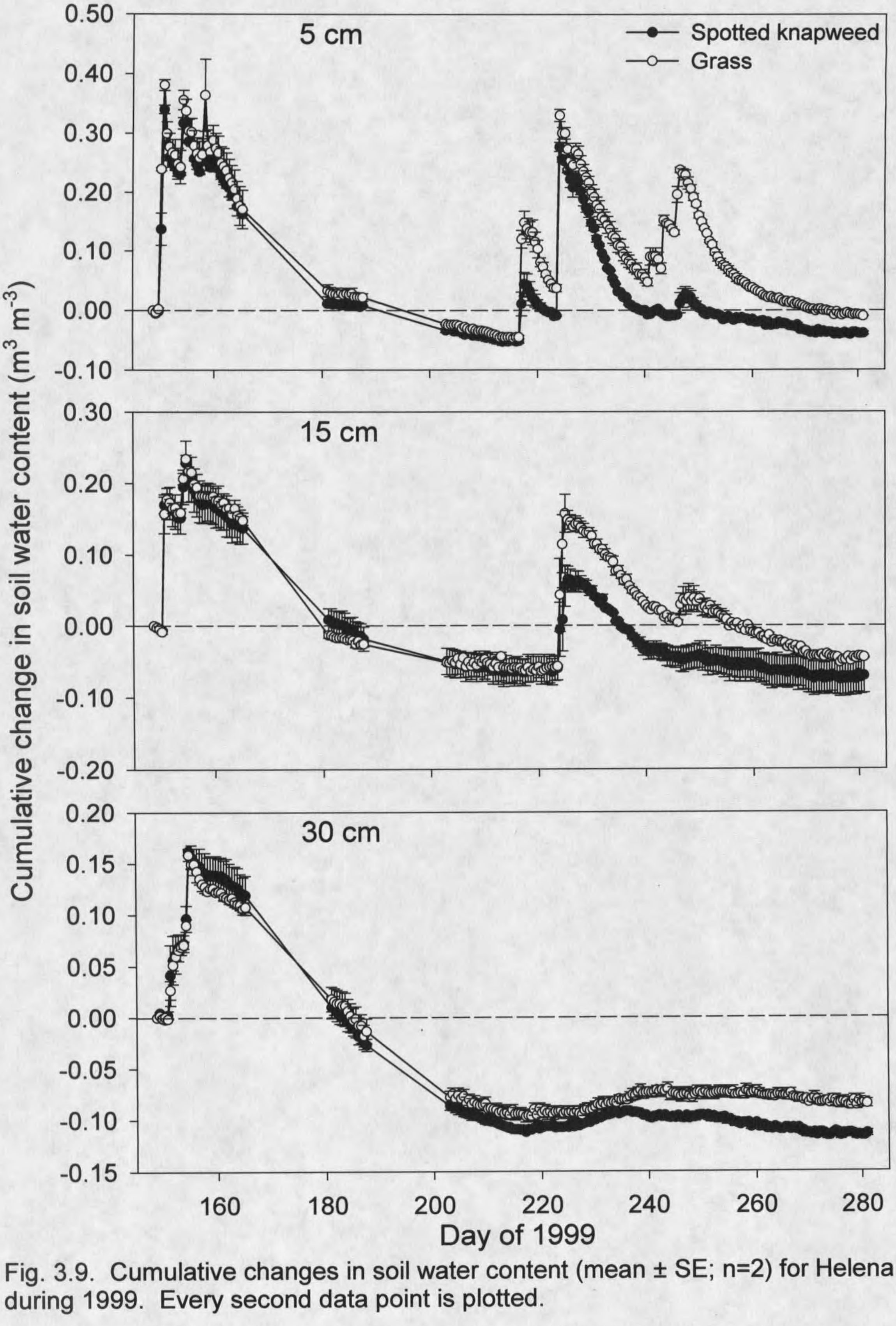

Fig. 3.9. Cumulative changes in soil water content (mean ± SE; n=2) for Helena during 1999. Every second data point is plotted.

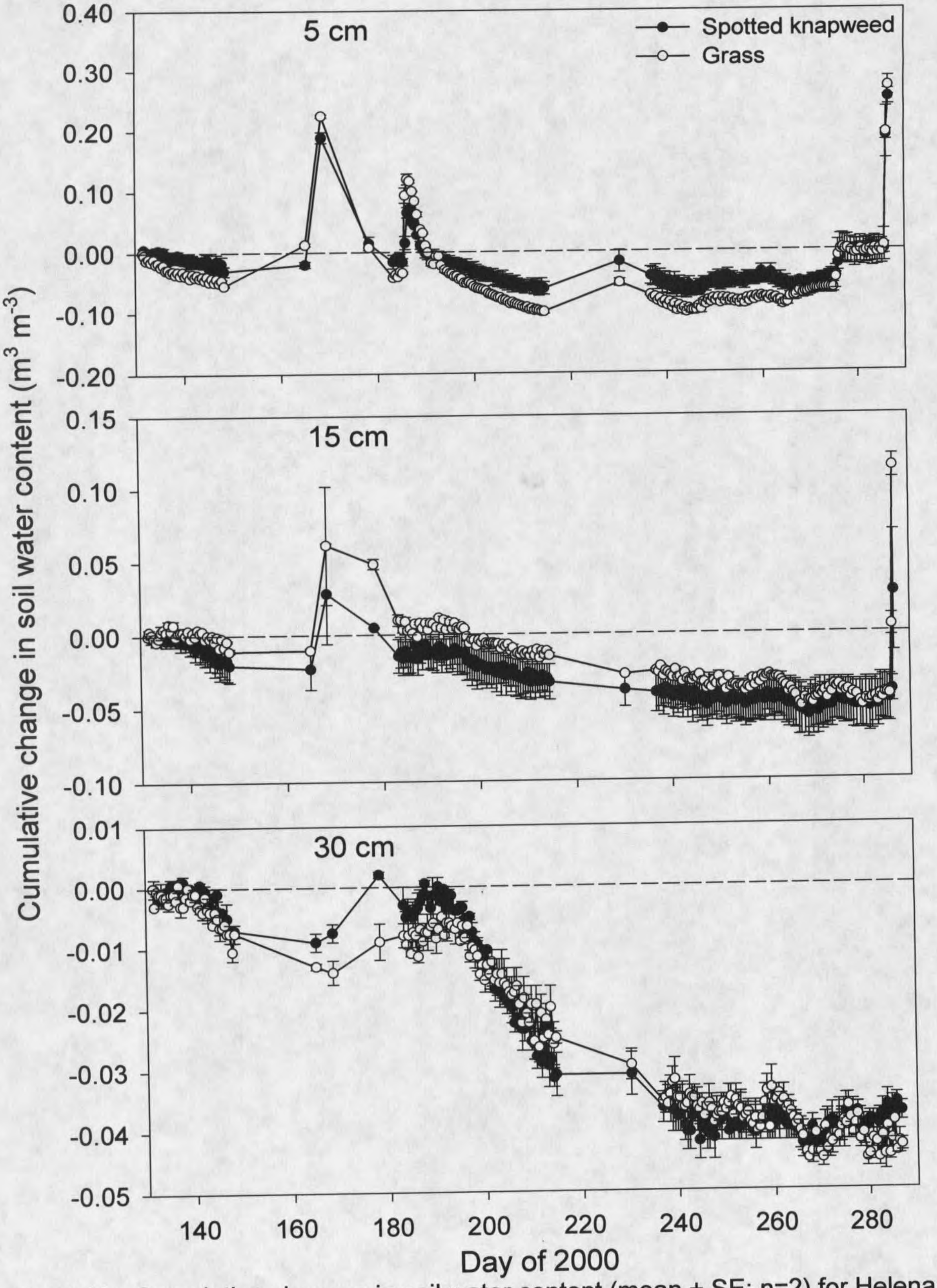

Fig. 3.10. Cumulative changes in soil water content (mean ± SE; n=2) for Helena during 2000. Every second data point is plotted.

Belgrade Site At Belgrade during 1999, soil water contents varied among the two blocks resulting in large error bars (Fig. 3.11). Spotted knapweed plots initially had lower soil water contents than native grass plots at 5, 10, and 15 cm depths (Fig. 3.11). At 10 cm, spotted knapweed plots had less soil water than native grass plots later in the growing season (Fig. 3.11). At 5 cm, soil water content decreased more under native grasses than spotted knapweed late in the growing season (Fig. 3.12).

Hyalite Site During 1999 at Hyalite, soil water contents at 5 cm in spotted knapweed and native grass plots were similar at the beginning and end of the monitoring period (Fig. 3.13). In late summer at 5 cm depth, spotted knapweed plots had less water than native grass plots. At 10 cm, soil water content was lower under native grass plots than spotted knapweed plots early to mid-growing season and at the end in 1999 (Fig. 3.13). During 2000, soil water contents were similar for spotted knapweed and native grass plots at 5 cm during most of the growing season (Fig. 3.14). Similar to 1999, native grass plots had less water at 10 cm during some periods of the 2000 growing season (Fig. 3.13; Fig. 3.14). Increases in soil water content after precipitation at the end of the 2000 growing season were smaller under native grass plots than spotted knapweed plots at both depths (Fig. 3.14).

Spotted knapweed appeared to use more soil water than native grasses at 5 and 10 cm during 1999 (Fig. 3.15), although this is not evident in the 10-cm soil water content data (Fig. 3.13). Cumulative changes in soil water content were similar between vegetation types during 2000 (Fig. 3.16), except at both depths in late summer when

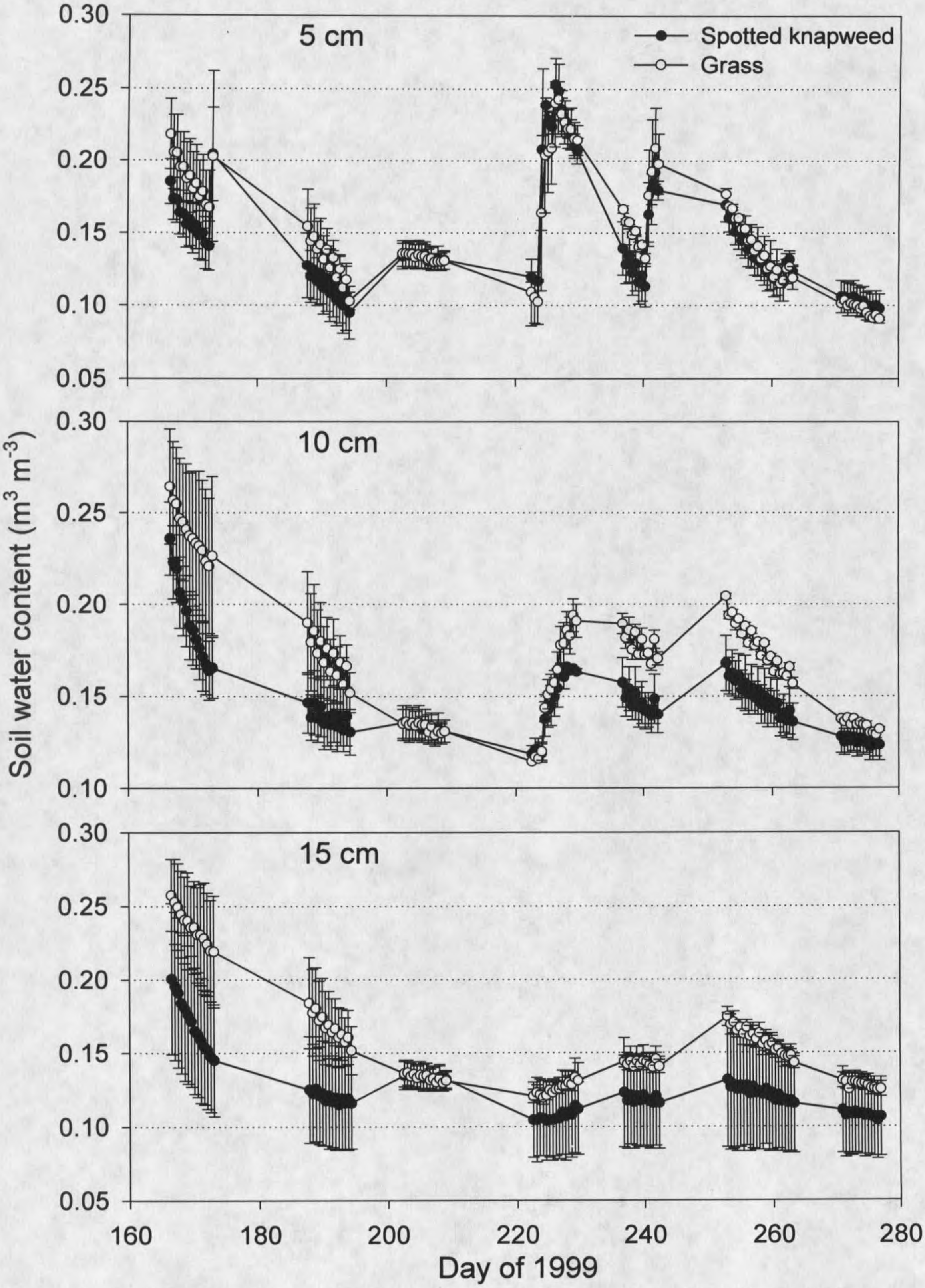

Fig. 3.11. Soil water content (mean ± SE; n=2) time series at 5, 10, and 15 cm depths for Belgrade during 1999 using TDR. Every second data point is plotted.

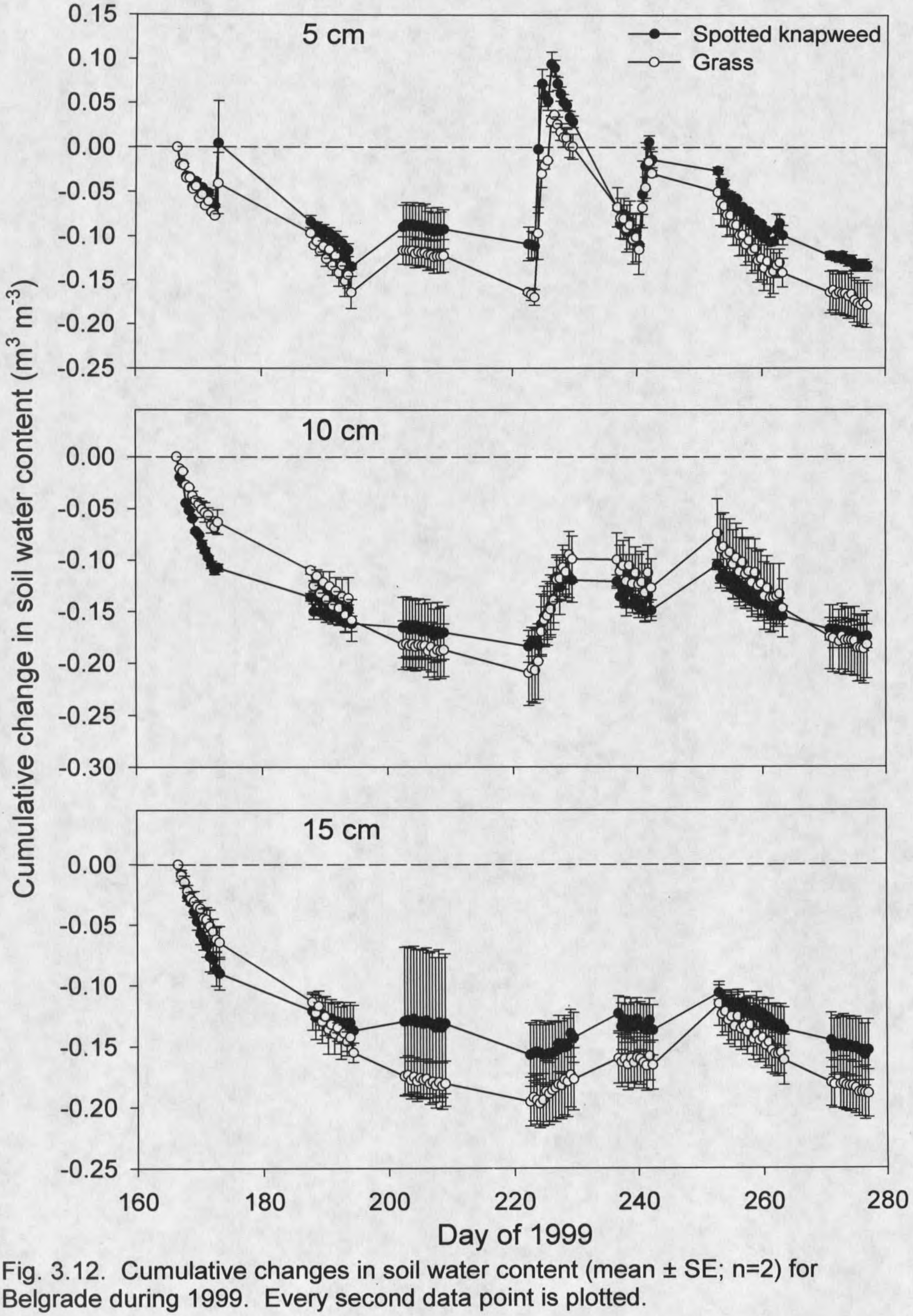

Fig. 3.12. Cumulative changes in soil water content (mean ± SE; n=2) for Belgrade during 1999. Every second data point is plotted.

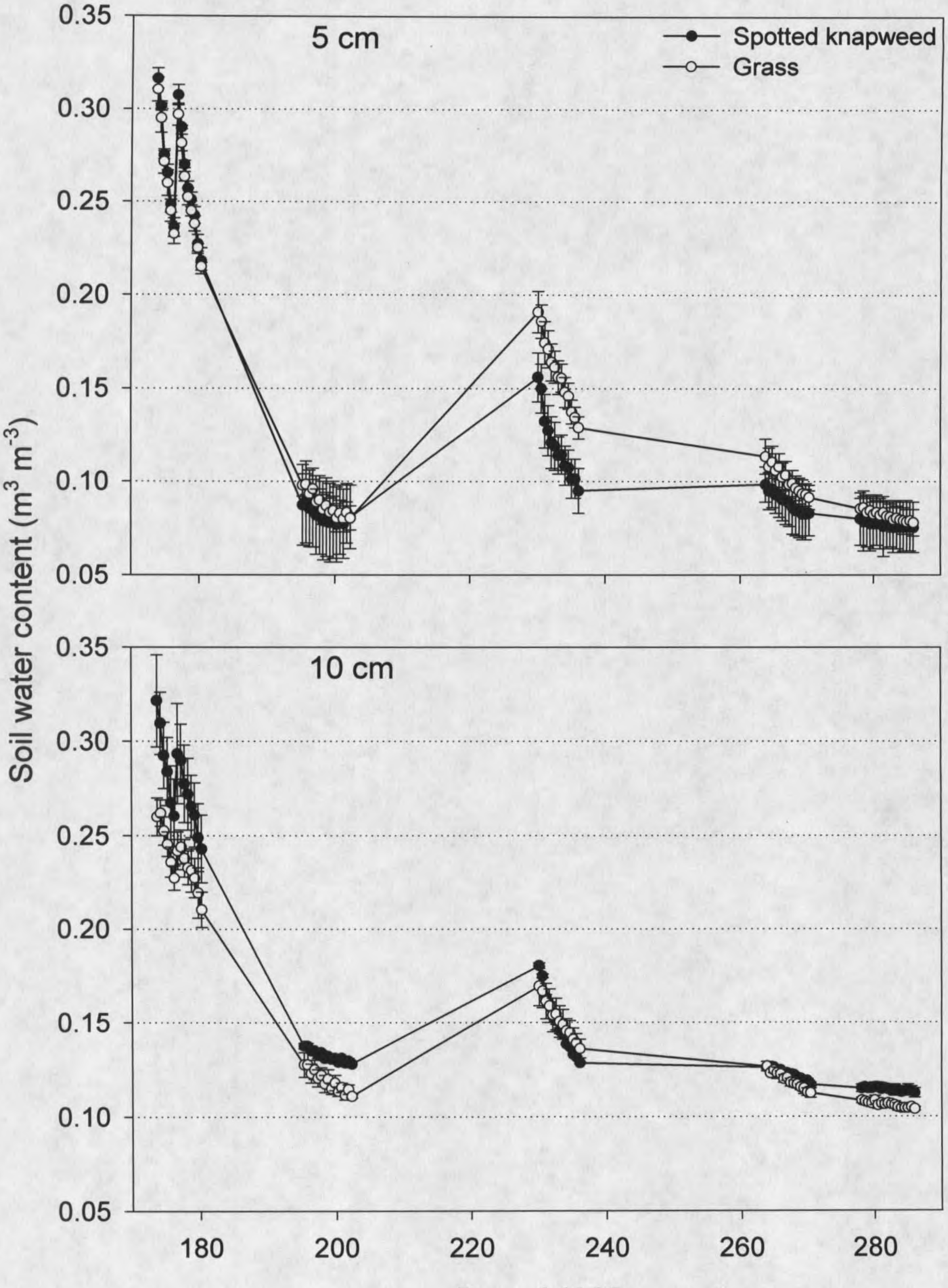

Fig. 3.13. Soil water content (mean ± SE; n=2) time series at 5 and 10 cm depths for Hyalite during 1999 using TDR. Every second data point is plotted.

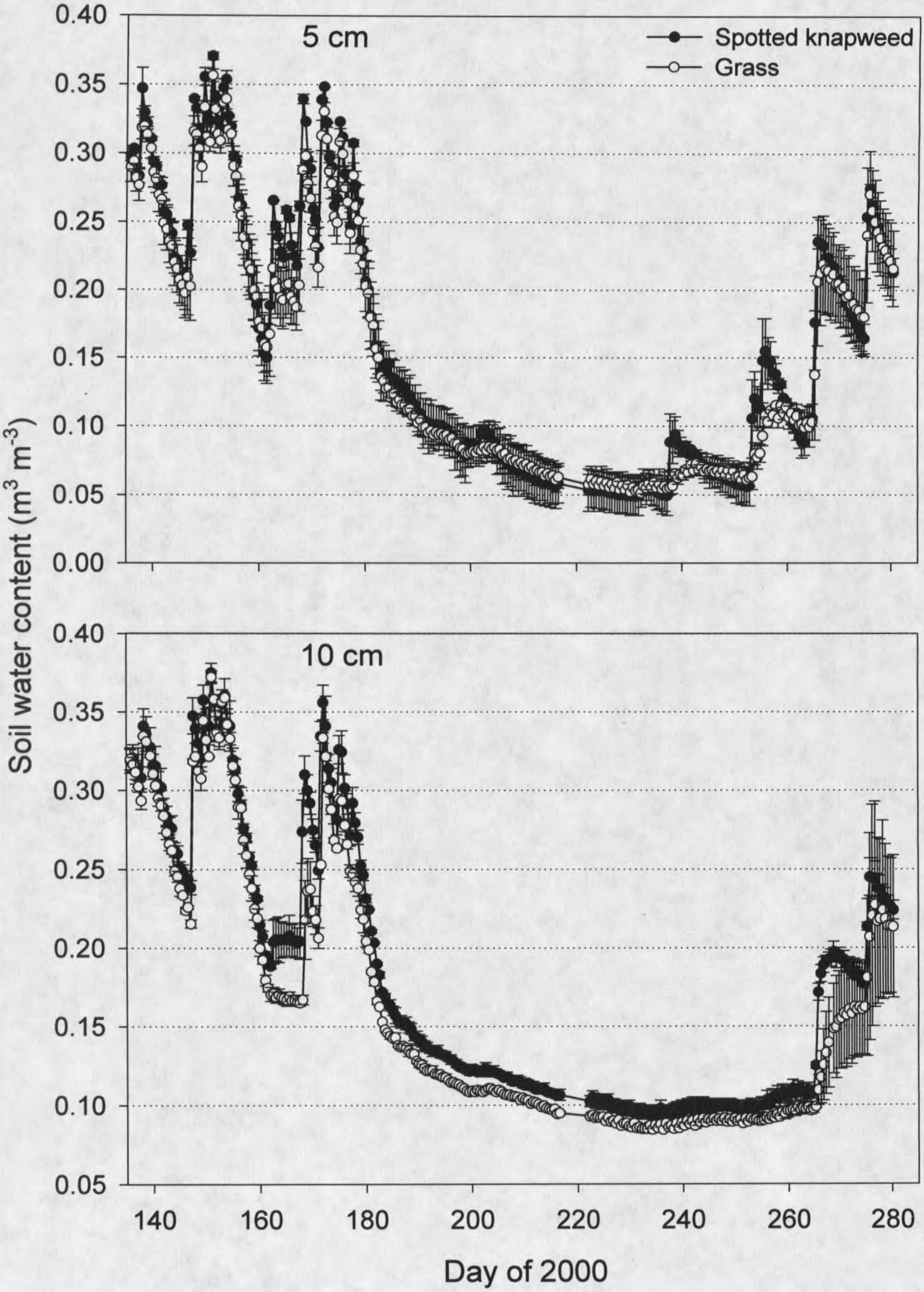

Fig. 3.14. Soil water content (mean ± SE; n=2) time series at 5 and 10 cm depths for Hyalite during 2000 using TDR. Every second data point is plotted.

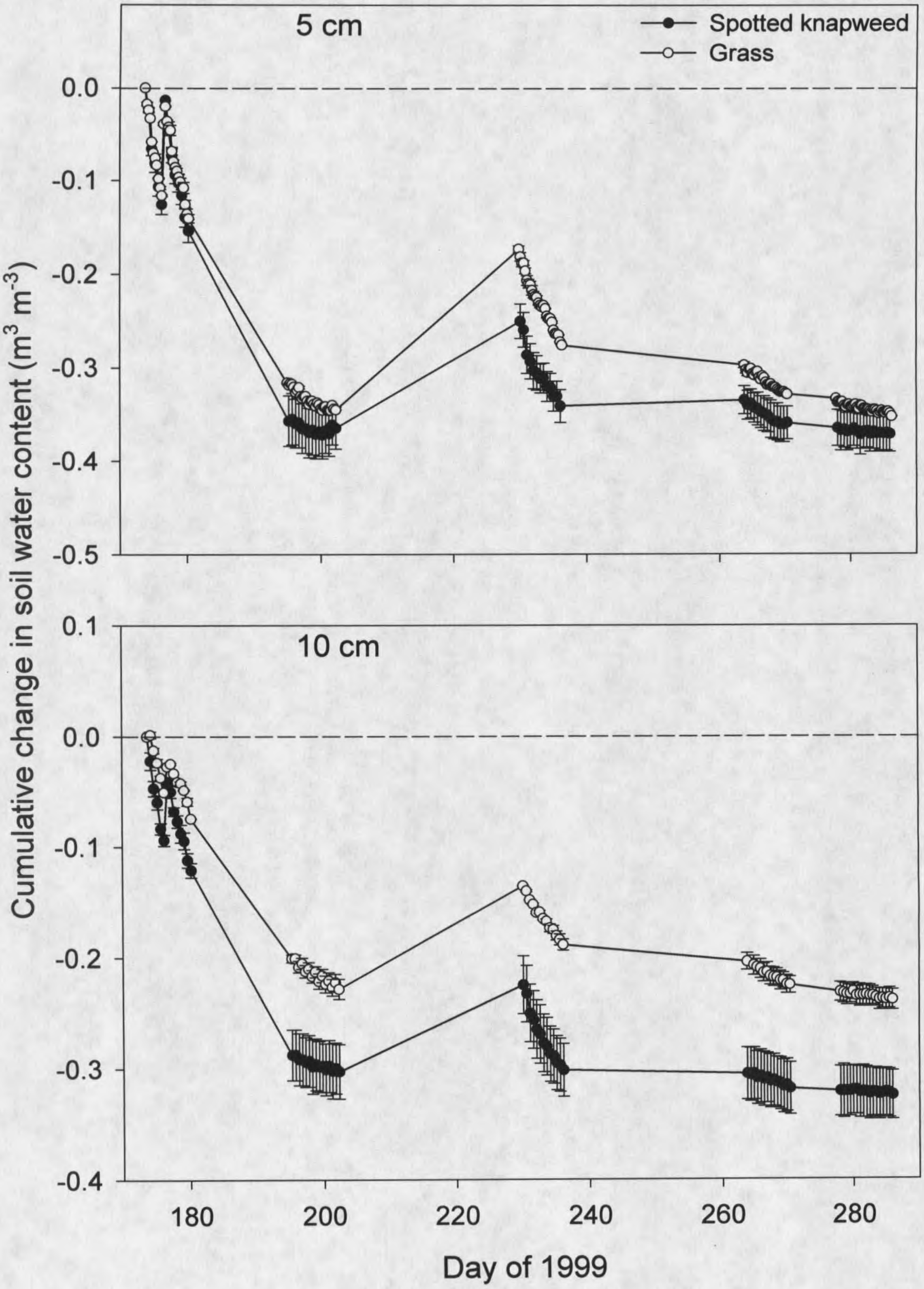

Fig. 3.15. Cumulative changes in soil water content (mean ± SE; n=2) for Hyalite during 1999. Every second data point is plotted.

native grass plots gained less soil water after precipitation events than spotted knapweed plots (Fig. 3.16).

Discussion

Soils

Small differences in soil water content can be biologically important because of the nonlinear relationship between soil water content and soil water potential. Soil matric potential is a major factor affecting plant available soil water (Hillel, 1982). Disturbance of my soil samples likely altered soil water retention for matric potentials greater than -0.1 MPa (Or and Wraith, 2000). The water retention relationship is strongly influenced by pore size distribution at matric potentials greater than about -0.1 MPa (Or and Wraith, 2000). Pore size distribution is related to the degree of aggregation, presence of biopores, and other factors. The retention characteristics measured on disturbed field soil may not reflect field conditions at the 'wet end.' Measuring soil matric potential *in-situ* would more accurately characterize soil water retention of soils from the different vegetation types. Differences in near-surface soil particle size fractions may have influenced soil water retention at matric potentials less than about -0.1 MPa (Or and Wraith, 2000). Near-surface soils of spotted knapweed plots at Helena and Belgrade had greater sand fractions than native grass plots (Table 2.2). At potentials less than about -0.1 MPa, soil water retention is mainly related to wettable surface area of soil solids (Or and Wraith, 2000).

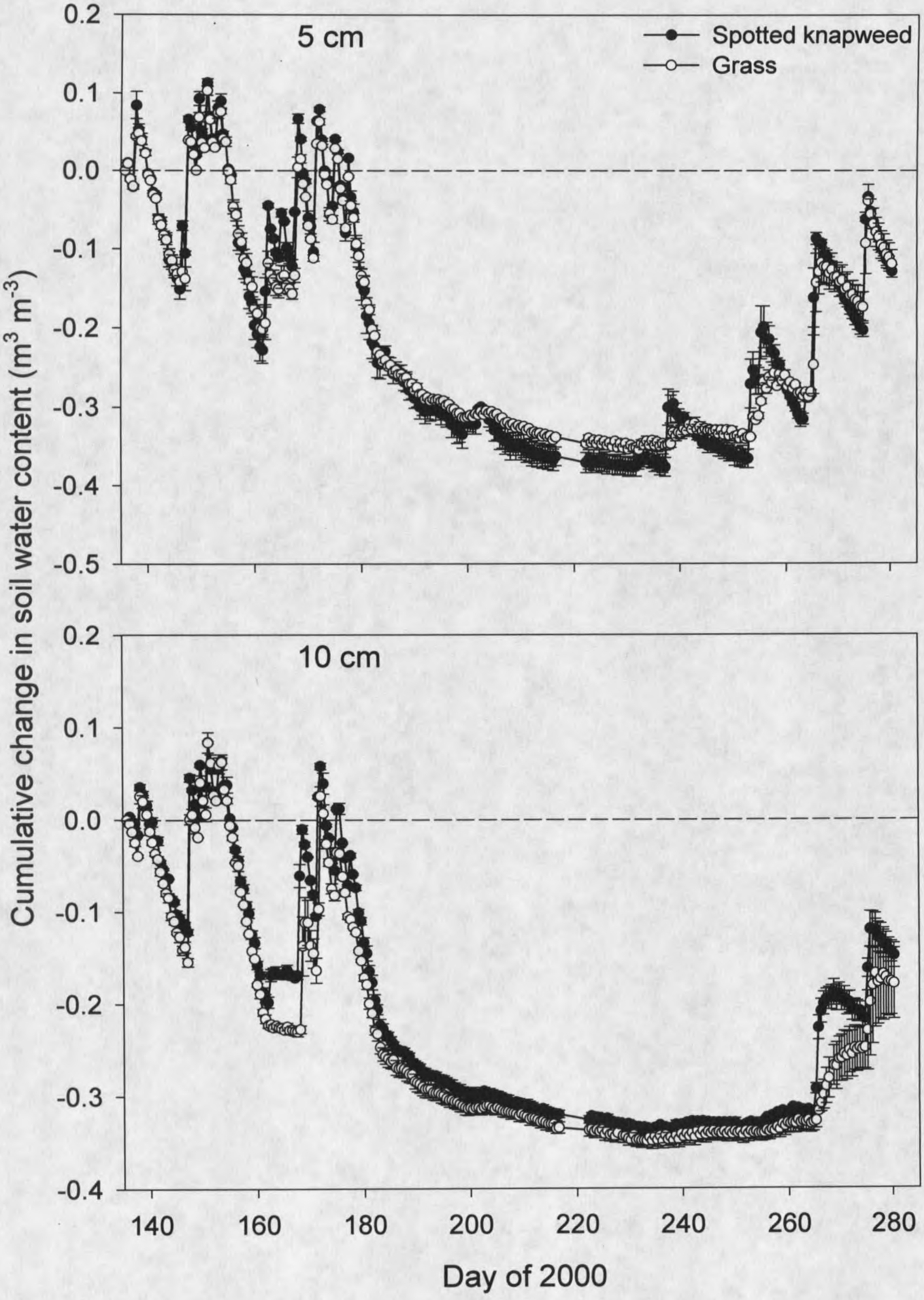

Fig. 3.16. Cumulative changes in soil water content (mean ± SE; n=2) for Hyalite during 2000. Every second data point is plotted.

Vegetation

The lower spotted knapweed seedling and annual grass densities in 2000 compared with 1999 were likely the result of low precipitation during the 2000 growing season. The overall lower total basal cover could also be due to less precipitation. The lower spotted knapweed cover and high bunchgrass cover in spotted knapweed plots at Hyalite reflect a lesser degree of infestation at this site. Spotted knapweed plots consistently had higher LAI than native grass. This trend might change with soils, climate, and degree of infestation.

Soil Water Dynamics

Several introduced and exotic species alter soil water dynamics in grasslands. Introduced and exotic grasses with earlier spring growth preempt soil water resources before native species (Borman et al., 1992; Clausnitzer et al., 1999; Eissenstat and Caldwell, 1988; Harris, 1967). Soil water dynamics are also altered by species able to extract soil water at different depths than native (Holmes and Rice 1996) or crop (Jacobsen et al., 1994) species. Consistent with phenological differences, spotted knapweed used more soil water than native grasses later in the growing season, when native grasses were quiescent. This was most evident at the deeper depths (60 to 100 cm). Spotted knapweed adults have greater water use efficiency during mid- and late summer (Blicker, 2000), which may facilitate a longer growing season compared with native grasses.

Spotted knapweed plots also had less soil water than native grass plots at depths greater than about 60 cm throughout most of the growing season, indicating soil water was depleted to lower absolute levels under spotted knapweed than native grasses. The ability to continue soil water uptake at lower matric potentials could be linked to differences in phenology, physiology, or rooting characteristics between spotted knapweed and native grasses. Native grasses may not have root densities as great as spotted knapweed at deeper depths and native grasses appeared quiescent during at least part of the period when spotted knapweed reduced soil water to lower levels. In some cases, plants can adjust their osmotic potential to more negative values to allow for water uptake in drier soils (Lafolie et al., 1999). Heavily suberized roots allowed medusahead to transport water deep in the profile up through dry soil (Clausnitzer et al., 1999). Spotted knapweed may possess these traits, but this has not been studied.

Areas invaded by spotted knapweed may not start the subsequent growing season with soil water levels equal to noninvaded areas, especially when the soil profile is not fully recharged by winter and spring precipitation. Late in the season in 1999, less soil water at these deeper depths carried over to the 2000 growing season. The growing seasons of 1999 and 2000 were drier than usual, and whether these patterns might hold for wetter years or coarser soils is not known.

The differential net recharge of the native grass plots compared with the spotted knapweed plots at 60 to 100 cm depths at Helena during mid-growing season of 1999 could be the result of differences in water use rather than net precipitation (total precipitation minus interception by plant structures and litter). At Helena by sample Day

150, both native grass and spotted knapweed plots were recharged to similar water contents above 60 cm (Fig. 3.5; Fig. 3.7). During subsequent weeks, some of this water drained downward to 80 and 100 cm. Native grasses could have utilized more soil water as it moved downward, leaving less soil water to recharge deeper depths. Most native grasses were flowering during this time (June) and spotted knapweed was forming flower buds. Vegetation and litter in native grass plots could have intercepted and stored more precipitation than spotted knapweed plots, but this is not consistent with LAI measurements, or with differences in near-surface soil wetting later in the growing season at Helena.

Precipitation can be intercepted by plant canopies or litter. The amount of precipitation lost to interception is relatively more important for small precipitation events than for larger events (Branson et al., 1981). Water stored in plant litter can range from 0.1 to 0.7 cm (Branson et al., 1981). The amount of potential interception storage depends on the moisture-holding capacity of the litter and on environmental conditions. Water intercepted and stored by canopies of grasses can range from 0.01 to 0.51 cm (Branson et al., 1981).

At Helena on Day 223 in 1999, near-surface soils (5 cm) were again recharged close to field capacity (Fig. 3.7). However less soil water recharged the 15 cm depth for spotted knapweed plots than native grass plots, indicating spotted knapweed was either using more soil water or was intercepting more precipitation than native grasses. Greater interception is the likely explanation because of the almost immediate difference in recharge between the vegetation types as measured using automated TDR. Most native grasses were quiescent at this time (mid-August) and spotted knapweed was flowering or forming seed.

The effects of apparent greater interception in spotted knapweed plots is also evident starting about Day 240 at Helena in 1999 (Fig. 3.7). Several precipitation events increased soil water content to higher levels in native grass plots than spotted knapweed plots. Because these precipitation events were smaller, interception likely had a greater effect on net precipitation (Branson et al., 1981). Similar trends were apparent at Helena in 2000 at 5 cm depth.

The opposite trend was visible at Hyalite in 1999 and 2000 (Fig. 3.13; Fig. 3.14). Native grass plots had lower net precipitation than spotted knapweed plots, most evident mid-season of 1999 and near the end of the 2000 season. The difference in net precipitation is likely related to precipitation interception, especially since native grasses were visibly quiescent in mid- to late season. The difference in trends between Helena and Hyalite could be species specific. The dominant native grass at Helena was bluebunch wheatgrass, whereas the dominant native grass at Hyalite was Idaho fescue. These grasses may differ in water use or canopy storage. I cannot conclude that spotted knapweed used more soil water than native grasses at Hyalite in 1999 because monitoring did not begin until mid-June and cumulative impacts would have been relative to mid-growing season when soil water levels may have already differed from early season soil water levels.

The variability of soil water contents at Belgrade was possibly a result of partial shading or water use by nearby cottonwood trees. Spotted knapweed at Belgrade reduced soil water to lower levels than native grasses, but relative to mid-season soil water levels grasses appeared to use more near-surface soil water. If native grass plots used more soil water, it may reflect differences in grass species, rooting patterns, and soil type compared with the other sites. The dominant native grass at Belgrade is western wheatgrass, which is rhizomatous and differs in rooting characteristics compared with the bunchgrasses dominant at the other two sites. Rhizomatous grasses spread laterally by underground stems which results in more evenly distributed plants and roots in the upper soil profile. Bunchgrasses are generally spaced farther apart than rhizomatous grasses and their fibrous root systems are generally deeper. Although roots are still dense in the upper soil profile, their lateral distribution is not as homogeneous.

The soil at Belgrade was more coarse and shallow than the other sites (Appendix). This would have influenced spatial and temporal dynamics of soil water availability and reduced total quantity of soil water held in the Belgrade soil. The fibrous root system of native grasses might exploit water in the upper soil profile more than spotted knapweed, which may rely more on water held in the stony subsoil.

Although spatial and temporal rooting patterns are major factors affecting belowground competition, little is known about the rooting characteristics of spotted knapweed in general or at different life stages. Temporal and spatial dynamics of spotted knapweed root systems have only been reported in one study (Marler et al., 1999). Fine root densities of spotted knapweed and bluebunch wheatgrass were similar when averaged over the upper 60 cm, but their densities differed with depth (Marler et al., 1999). Spotted knapweed had greater fine root densities from 30 to 60 cm and generally developed fine roots earlier than bluebunch wheatgrass (Marler et al., 1999). Spotted knapweed's root system response to differences in soil water status is unknown.

Invasibility of grasslands is strongly correlated with soil water availability (Dukes, 2001). Communities are considered less resistant to invasion if they lack deep-rooted species that are active throughout the summer (Dukes, 2001). Spotted knapweed may also be successful because it may fill unoccupied niches, depending on its life stage (Sheley et al., 1996) and on site conditions. The sites used in my study may be at a successional stage where the niche typically filled by deep-rooted species, such as sagebrush, is open thereby allowing spotted knapweed to invade and take advantage of unused soil resource.

Soil water is often the most important factor for the growth and survival of native cool-season grasses in semiarid grasslands because spring growth depends on stored soil water (Frank et al., 1996). During periods of low water availability, populations of native grasses are more likely to decrease when growing with more drought-resistant species (Frank et al., 1996). Because spotted knapweed is such a successful invader of western semiarid grasslands, it has become very important to understand the mechanisms of its success. Identifying these traits could increase opportunities for control and management of this species.

Summary and Conclusions

My results from one study site suggest that spotted knapweed used more soil water at deeper depths and later in the growing season than native grasses. Spotted knapweed also lowered soil water to lower absolute levels than native grasses at this site, where I was able to measure water content to deeper depths than for the remaining locations. Greater water use in spotted knapweed plots may have partially reflected higher LAI than in native grass plots, rather than inherent species differences. The canopy of spotted knapweed may intercept and store more precipitation than native grasses, but this effect might differ depending on the species of native grass.

In this study, greater water use by spotted knapweed at some depths and its prolonged growing season resulted in less soil water than for native grass plots during the subsequent growing season. These traits may be critical to spotted knapweed's success, especially in years when the soil profile is not fully recharged by winter and spring precipitation. Detailed knowledge of spotted knapweed spatial and temporal root dynamics at different life stages and under different soil water regimes may be key to identifying spotted knapweed's competitive strategies.

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CHAPTER 4

SUMMARY

The objectives of this study were to compare near-surface soil physical properties and soil water dynamics under spotted knapweed and native perennial grasses on semiarid rangelands. We hypothesized that the persistence of spotted knapweed may be the result of it altering site soil conditions or having a superior ability to utilize soil water. We used six field sites in western Montana with blocks of spotted knapweed and native grass plots. Basal cover was estimated and plant density and leaf area index (LAI) were measured. We measured near-surface soil physical properties and monitored soil temperature regime and soil water dynamics. Without knowing the long-term history of our field sites and not having characterized soils prior to spotted knapweed invasion, our ability to determine cause and effect was potentially constrained. However, the general lack of consistent differences in soil physical properties indicates that either there were no pre-existing systematic differences prior to spotted knapweed invasion or that spotted knapweed ameliorated these if they were already present.

Spotted knapweed plots consistently had greater LAI than native grass plots. Surface soil characteristics of semiarid rangeland soils were similar under both vegetation types. Although a few soil properties differed, these were highly variable and inconsistent among plots and among sites. No systematic relationships between vegetation type and measured soil properties were found. The results of this study indicate that presence of spotted knapweed did not alter near-surface soil properties on semiarid grasslands.

In addition, this study also suggests that spotted knapweed is a strong competitor for soil water in semiarid grasslands. Spotted knapweed had similar soil water use patterns at shallow depths where we anticipated that the fibrous root system of the native grasses would confer advantage. Spotted knapweed used more water at deeper depths than native grasses and continued to use soil water later in the growing season. However, greater water use in spotted knapweed plots may have reflected higher LAI compared with native grass plots, and not inherent species differences.

Spotted knapweed apparently intercepted more precipitation than native grasses, leading to less net precipitation in spotted knapweed plots. Soil water was depleted to lower absolute levels under spotted knapweed compared with native grasses. During this study, less soil water in spotted knapweed plots at the end of the 1999 growing season resulted in less soil water than for grass plots at the beginning of the 2000 growing season.

Spotted knapweed might be successful because it may fill unoccupied niches, depending on its life stage. Some grassland communities are more susceptible to invasion if they lack deep-rooted species that are active throughout the summer. Spotted knapweed may persist in these systems because of its prolonged growing season, access to deeper soil water, and ability to deplete soil water to lower levels compared with native grasses. Separately or combined, these traits can potentially affect water availability in current and subsequent growing seasons.

Determining the spatial and temporal dynamics of spotted knapweed's rooting characteristics under different soil water regimes appears key to understanding its successful invasion of semiarid grasslands. Conditions were unusually dry during this study. Spotted knapweed may have a competitive advantage over native grasses during dry years, but may not be as successful during wetter years. This study suggests that eradicating spotted knapweed should be sufficient in restoring invaded native, perennial grasslands; i.e., soils in invaded areas similar to those in our study would not need to have physical attributes ameliorated.

APPENDIX A

SOIL PROFILE DESCRIPTIONS AND CLASSIFICATIONS

Site Name: Thiede
Site Location: 60 km west of Bozeman, Montana in Madison County

Elevation: 1426 m Latitude: 45° 35' 5" Longitude: 111° 36' 35"
Slope: 5% Aspect: northwest

Vegetation: Idaho fescue, Kentucky bluegrass, spotted knapweed, hairy mullein

Depth of Soil Pits: 140 cm

Depth (cm)	Horizon Classification	Horizon Description
0-11	A1	10YR 4/2 dry; 10YR 3/2 moist sand; medium granular structure; 4% coarse fragments; pH 5.9
11-40	A2	10YR 4/2 dry; 10YR 3/2 moist sand; fine granular structure; 10% coarse fragments; pH 6.1
40-56	C1	7.5YR 5/2 dry; 7.5YR 3/2 moist sand; massive structure; 15% coarse fragments; pH 6.4
56-83	C2	10YR 5/4 dry; 10YR 4/3 moist sand; structureless; 50% coarse fragments; pH 6.2
83-103	C3	10YR 5/3 dry; 10YR 4/2 moist sand; massive structure; 8% coarse fragments; pH 6.7
103-127	C4	10YR 5/3 dry; 10YR 4/2 loamy sand; massive structure; 15% coarse fragments; pH 6.8
127-134	C5	10YR 4/2 dry; 10YR 3/2 moist sand; massive structure; 3% coarse fragments; pH 6.8
134-140	C6	2.5YR 6/3 dry; 2.5YR 4/3 moist sand; structureless; 30% coarse fragments; pH 6.9

Series: Nesda

Taxonomic Class: Sandy-skeletal, mixed, frigid, Fluventic Haploboroll

Notes: soil pit was dug in mixed vegetation

Site Name: Helena
Site Location: 21 km southeast of East Helena, Montana in Broadwater County

Elevation: 1285 m Latitude: 46° 33' 1" Longitude: 111° 45' 38"
Slope: less than 1% Aspect: northeast

Vegetation: bluebunch wheatgrass, needle-and-thread grass, Kentucky bluegrass, smooth brome, Japanese brome, sagebrush, spotted knapweed, and goats beard

Depth of Soil Pits: approximately 120 cm

Depth (cm)			
Spotted knapweed	**Grass**	**Horizon Classification**	**Horizon Description**
0-5	0-5	A	7.5YR 4/2 dry, 7.5YR 2.5/2 moist silt loam; granular structure; 2 % coarse fragments; pH 7
5-14	5-14.5	Bw	7.5YR 4/3 dry, 7.5YR 2.5/2 moist clay loam/silt loam; blocky structure; 5% coarse fragments; pH 7, slight HCl reaction
14-30.5	14.5-31.75	Bk1	7.5YR 7/2 dry, 7.5YR 6/3 moist clay; massive structure, powdery; pH 8, violent HCl reaction
30.5-122	31.75-120	Bk2	5YR 8/1 dry, 5YR 7/2 moist clay; massive structure, powdery; pH 8.7, violent HCl reaction

Series: Rothiemay

Taxonomic Class: Fine-loamy, mixed, superactive, frigid Aridic Calciustolls

Notes: the true texture of the Bk1 and Bk2 horizons is likely clay loam since clay-sized carbonates were not burnt off prior to particle size analysis

Site Name: Belgrade
Site Location: 6 km west of Belgrade, Montana in Gallatin County

Elevation: 1330 m Latitude: 45° 48' 18" Longitude: 111° 13' 36"
Slope: less than 1% Aspect: northwest

Vegetation: western wheatgrass, cheat grass, spotted knapweed, sulfur cinquefoil

Depth of Soil Pits: approximately 71 cm

Depth (cm)			
Spotted knapweed	**Grass**	**Horizon Classification**	**Horizon Description**
0-4.5	0-4	A1	7.5YR 4/3 dry, 7.5YR 2.5/2 moist loam; fine granular structure, some areas platy; 2% coarse fragments; pH 6.8
4.5-21.5	4-15	A2	10YR 5/3 dry, 10YR 3/3 moist loam; blocky to coarse granular structure; 5% coarse fragments; pH 7.2
21.5-78.75	15-71	C	sandy gravel with cobbles; 80% coarse fragments

Series: Kassler

Taxonomic Class: Sandy-skeletal, mixed, frigid Torriorthentic Haplustolls

Notes: some cobbles within the profile were coated with calcareous material; classified as Kassler series although parent material was not arkose deposits

Site Name: Hyalite
Site Location: 12 km southwest of Bozeman, Montana in Gallatin County

Elevation: 1620 m Latitude: 45° 35' 36" Longitude: 111° 5' 24"
Slope: less than 1% Aspect: northwest

Vegetation: Idaho fescue, western wheatgrass, lupine, timothy, spotted knapweed

Depth of Soil Pits: 102 cm

Depth (cm)			
Spotted knapweed	**Grass**	**Horizon Classification**	**Horizon Description**
0-12.5	0-11.5	A	2.5YR 3/3 dry, 10YR 2/2 moist loam; granular structure; 5% coarse fragments
12.5-33	11.5-28	Bt	10YR 4/2 dry, 10YR 2.2 moist loam; granular to small blocky structure; 10% coarse fragments
33-58.5	28-58.5	C1	2.5YR 4/3 dry sandy loam; massive structure; 80% coarse fragments
58.5-99	58.5-101.5	C2	loamy sand; 80% coarse fragments

Series: Hyalite

Taxonomic Class: Fine-loamy, mixed, superactive, frigid Typic Argiustolls

Notes: some cobbles and boulders had calcareous coatings