

AN ABSTRACT OF THE THESIS OF

Roger L. Sheley for the degree of Doctor of Philosophy in Rangeland

Resources presented on June 18, 1993.

Title: Life-History, Growth, and Interference of Cheatgrass (*Bromus tectorum* L.) and Yellow Starthistle (*Centaurea solstitialis* L.).

Abstract approved: Signature redacted for privacy.

Dr. Larry L. Larson

Cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) have invaded over 3 million ha of grasslands in the western U.S. Future management will require an understanding of the conditions, mechanisms, and processes which control species dominance, community dynamics, and desirable plant establishment in these alien dominated annual rangelands. Life-history models of cheatgrass and yellow starthistle were developed. Sensitivity analysis indicated that cheatgrass and yellow starthistle seed output was most sensitive to population reductions during the transition from juvenile to adult and adult survivorship phase of their life history. Key processes associated with these transition phases are interference (competition), growth rates and duration, and reproductive allocation. The objective of this research was to investigate those key processes.

Several addition series experiments, with total densities ranging from 20-20000 plants m^{-2} , were conducted to quantify the intensity of interference between cheatgrass and yellow starthistle. In unrestricted soil depths,

intraspecific interference was approximately twice as important as interspecific interference for both species with respect to predicting plant weight throughout the growing season and seed production. Resource partitioning via rooting depth was evident. The ecological importance of strong intraspecific interference was associated with being strong competitors, the advantages of self-thinning, and regulating community composition. Decreasing soil depth altered the competitive balance toward the relatively shallow and fibrous rooted cheatgrass.

In a growth chamber study, isolated seedling growth rates of both species were similar, however yellow starthistle roots grew more geotropically than those of cheatgrass. In field experiments, yellow starthistle grew more rapidly than cheatgrass after the seedling stage. We believe that rapid and geotropic growth allowed deeper soil penetration, continued growth and increased seed output of yellow starthistle over that of cheatgrass. As densities increased and/or soil depth decreased, the growth rates and maturation dates of cheatgrass and yellow starthistle became increasingly similar and lower.

**Life-history, Growth, and Interference
of Cheatgrass (*Bromus tectorum* L.) and
Yellow Starthistle (*Centaurea solstitialis* L.)**

by

Roger L. Sheley

A THESIS

submitted to

Oregon State University

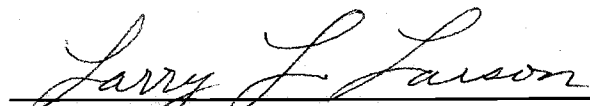
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the requirements for
the degree of


Doctor of Philosophy

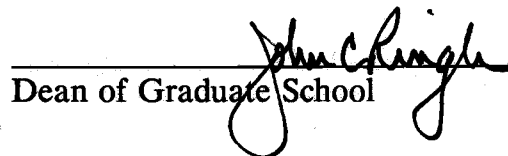
Completed June 18, 1993

Commencement June 1994

Approved:


Associate Professor of Rangeland Resources, in charge of major


Head of Department of Rangeland Resources


Dean of Graduate School

Date dissertation is presented June 18, 1993

Typed by Chris Presley for Roger L. Sheley

ACKNOWLEDGEMENTS

I am deeply indebted to Dr. Larry Larson, my major professor and friend, for his encouragement, inspiration, direction, and help during my studies. I always felt that Larry and I were a team working toward the same goals. I appreciated his constant availability and valuable advice. His insight and foresight helped me in my intellectual and professional development. I am especially grateful to Larry for his unwavering commitment, solid and reliable support, and personal sacrifice in my quest for the "green card." I also appreciate Pat Larson for her technical help.

I am thankful to Dr. Steven Radosevich for his advisement and inspiration, especially early in the development of my study plan. Dr. Radosevich was a constant source of current and valuable information and kindly made himself readily available to me. I was inspired and stimulated by his ecological approach to weed science.

I am grateful to Drs. William Krueger, Richard Miller, and Gary Kiemnec for serving as members of my committee. Dr. Krueger forced me to discover the underlying theory of my research, which helped me realize the significance of my work, and added to my enjoyment of the process of scientific discovery. Dr. Krueger also provided me the opportunity to teach Arid Land Plants, a valuable and rewarding experience. I appreciate Dr. Miller for his careful and constructive review of my study plan and manuscripts. His suggestions regarding using pre-split PVC tubes for my growth chamber studies were very helpful. Dr. Kiemnec was a solid and positive member of my

committee. I am especially grateful to him for his helpfulness and timely review of each draft manuscript, when time was of the essence.

I would like to give special thanks to the Rangeland Resources faculty for making my experience at O.S.U. a great one. Dr. Douglas Johnson acted as an on-campus research advisor and friend. Dr. Paul Doescher was an excellent teacher. I owe him special thanks for his advice towards shortening the length of my last term of coursework. At the same time, I thank Jeff Rose for his ability to endure pain. Dr. John Buckhouse was a teaching inspiration to me. I enjoyed Dr. Steve Sharrow.

Several fellow graduate students were helpful. Mohammed Nasri and John Bates and I had the opportunity to become close friends.

Most importantly I thank my family for whom my work is to benefit. My wife, Mindy, provided enthusiastic support while suffering many days and evenings alone amusing our two beautiful children, Jordan and Melissa. Tony Wooldridge, essentially a family member, has helped me throughout my studies, as a technician, friend and "son". Their love, patience, respect, and well-being is my guiding light. They are an endless source of pride and happiness to me.

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**LIFE-HISTORY, GROWTH, AND INTERFERENCE OF CHEATGRASS
(*BROMUS TECTORUM* L.) AND YELLOW STARThISTLE
(*CENTAUREA SOLSTITIALIS* L.)**

CHAPTER 1

**CHEATGRASS AND YELLOW STARThISTLE PERFORMANCE
AND COMMUNITY DYNAMICS: AN INTRODUCTION
AND LITERATURE REVIEW**

INTRODUCTION

The decline of native perennial vegetation on North American grasslands has been accompanied by increases in alien annual weeds (Hulbert 1955, Hironaka 1961, Roché 1965, Mack 1981). In the grasslands of the Pacific Northwest and the California Annual Grasslands, the decline of perennial grass species, such as bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith) populations were accompanied by dramatic increases in annual grasses, such as cheatgrass (*Bromus tectorum* L.) (Mack 1981). This was followed by increases in yellow starthistle (*Centaurea solstitialis* L), which began to invade around 1920 (Callihan et al. 1982, Talbot 1987, Hironaka 1989, Sheley et al. 1993). These events altered successional dynamics within these rangelands (Harris 1967, Hironaka 1989, Sheley et al. 1993) and subsequent rehabilitation has yielded limited success (Callihan et al. 1982, Sheley et al. 1983, Huston et al. 1984, Larson and McInnis 1989).

The research presented in this document aims to identify and understand the conditions, mechanisms, and key processes which control plant community dynamics and plant establishment to aid development of alternative rehabilitation methods for cheatgrass and yellow starthistle dominated ecosystems. The purpose of this chapter is to provide a summary of the literature regarding cheatgrass and yellow starthistle performance characteristics and to categorize this information into a logical resource management framework. Research in chapter 2 characterizes the life-histories of cheatgrass and yellow starthistle growing in association. Sensitivity analysis was performed on life-history models to determine transitions and associated processes important to seed output. The objectives of the research presented in chapters 3 and 4 were to utilize addition series methodology to quantify the effects of interference between cheatgrass and yellow starthistle. Chapter 3 focuses on seedling interactions, and the relative growth rates and soil depth penetration of isolated seedlings of these species. Chapter 4 discusses the effects of interference between cheatgrass and yellow starthistle throughout the growing period and upon seed output, and the effects of soil depth upon cheatgrass and yellow starthistle and the interaction between the two species. Finally, in chapter 5, the effects of density, species proportions, and soil depth upon the growth rates and duration of cheatgrass and yellow starthistle are investigated using functional growth analysis techniques.

LITERATURE REVIEW

Historical Framework

Traditional models of rangeland succession were derived from Clementsian plant ecology (Clements 1916, Weaver and Clements 1938, Ellison 1960), which consisted of single equilibrium communities and deterministic successional pathways. The Clementsian model has proven inadequate to explain vegetation changes where mechanisms produce complex ecosystem dynamics (Westoby et al. 1989). Many alternative theories have been proposed (Drury and Nisbet 1973, Connell and Slayter 1977, May 1977, Wiens 1977, Price et al. 1984, Strong et al. 1984, Krebs 1985, and Westoby et al. 1989). Laycock (1991) reviewed these concepts and concluded that much theoretical work needs to be done before these models can be incorporated into range condition standards.

A detailed understanding of the causes of succession, contributing processes, and modifying factors are required for the ecological manipulation of community dynamics (Pickett et al. 1987, Radosevich and Roush 1990). One approach to understanding the processes directing community dynamics has been to focus on individual species (Nobel and Slayter 1980, Pickett 1976, Radosevich and Roush 1990). Nobel and Slayter (1980) and Pickett et al. (1987) developed a three component successional model for management based upon site availability, species availability, and species performance (Table 1.1). The three components of this model are: designed disturbance (perturbation),

controlled colonization, and controlled species performance. Designed disturbance includes activities aimed at creating or eliminating site availability. Controlled colonization includes methods of decreasing or enhancing availability and establishment of specific plant species. Controlled species performance includes procedures used to decrease or enhance growth and reproduction of specific plants species.

The purpose of this literature review is to summarize research on yellow starthistle and cheatgrass performance. A conceptional life-history model developed by Radosevich and Roush (1990) for annuals, was modified and used to organize species performance information (Figure 1.1). This review will: 1) categorize current knowledge into a logical resource management framework and allow the categorization of future research results; 2) identify information gaps; 3) provide insight and direction for future research; and 4) allow evaluation of the importance and success of current research toward contributing to the successional model. Clearly, more information is available on cheatgrass than on yellow starthistle. Therefore, many discussions do not include the latter species.

Life Cycle

Cheatgrass and yellow starthistle are facultative winter annuals (Finnerty and Kingman 1962, Klemmedson and Smith 1964, Roché 1965). A typical life cycle for both species is initiated with fall germination, followed by a semi-

dormant overwintering period, with the completion of the life cycle occurring during the next growing season. Both species can germinate in the spring.

Cheatgrass may exhibit biennial growth characteristics if germination occurs in late spring (Stewart and Hull 1949, Hulbert, 1955, Finnerty and Kingman 1962).

The main difference between the life cycle of cheatgrass and yellow starthistle is that cheatgrass typically reaches maturity a few weeks earlier than yellow starthistle (Klemmedson and Smith 1964, Callihan et al. 1982). Sheley et al. (1993) suggested that this difference was due to the root growth pattern of yellow starthistle which allows the extraction of moisture and nutrients from greater soil depths.

Seed Characteristics

Cheatgrass and yellow starthistle survive from year to year as viable seed on the soil surface, in litter on the soil surface or buried in the soil (Young et al. 1969, Callihan et al. 1982). Cheatgrass seed has been reported to be viable at several stages of development, exhibiting little or no dormancy. Hulbert (1955) and Finnerty and Kingman (1962) germinated cheatgrass seed at the premilk and dough stages. Hulbert (1955) found cheatgrass seed to be 90% viable in the later developmental stages. This report is in agreement with other reports of the time (Stewart and Hull 1949, Steinbauer and Grigsby 1957) and suggests that cheatgrass seed readily germinate when presented with favorable conditions.

Young and Evans (1982) germinated cheatgrass seed in 55 different (constant and alternating) temperature regimes and concluded the germinability of cheatgrass was very high. Mean germination across all temperature regimes tested was 81%. Roughly one quarter of the tested regimes proved optimal, with an average of 96% germination. Three quarters of the regimes resulted in a germination percentage of 75 or greater.

Several researchers have shown that cheatgrass seed remain viable in the soil for more than one year (Beddows 1931, Young et al. 1969, Wicks et al. 1971). Young et al. (1969) reported the acquisition of winter dormancy in cheatgrass seed near the soil surface, and proposed an environmentally-induced dormancy. In contrast, Thill et al. (1979) found that all cheatgrass seed germinated, deteriorated or lacked embryos and endosperm by 85 days after burial. Mack (1989) proposed that germination pulses may be influenced by the different rates at which seed fall through the straw of plants produced the previous year and land on a safe site. Chepil (1946) and Hulbert (1955) report that few cheatgrass seed remain viable beyond 2 to 3 years. Wicks et al. (1971) reported the occurrence of viable cheatgrass seed after 5 years of burial.

Under favorable conditions, yellow starthistle seed can germinate within 24 to 30 hours (Sheley et al. 1993, Larson and Kiemnec 1993). Sheley et al. (1993) compared germination rates of yellow starthistle with hedgehog dogtail (*Cynosurus echinatus* L.) and medusahead (*Taeniatherum asperum* Nevski).

They found plumed yellow starthistle germination to be most rapid, and hedgehog dogtail to be slowest.

Callihan et al. (1989) reported that about 95% of yellow starthistle seeds are viable, and that 10% remained in a dormant state for more than 10 years. Huston et al. (1983) conducted an experiment testing seed viability at 3 soil depths (20 mm, 80 mm, 130 mm) over a year. They found no difference between soil depths, and reported less than 35% germination after 3 months, 45% germination at 6 months, and 65% germination after 12 months of burial. Unplumed seed buried at 20 mm had significantly greater viability than plumed seed. Larson and Kiemnec (1993) determined that field germination (first year) of plumed seed was greater than unplumed seed. More recently, Callihan et al. (1993) reported that the average longevity of plumeless and plumed achenes was 6 and 10 yr., respectively.

Cheatgrass dormancy appears to be temperature dependent. At maturity, cheatgrass seed readily germinate at temperatures of 10 to 15 C. (Hulbert 1955, Steinbauer and Grigsby 1957). Newly developed seed germinate poorly at temperatures above 15 C and germination increases with after-ripening (Laude 1956). After-ripening can occur while cheatgrass seed lie in litter or on the soil surface, and the time period for after-ripening decreases with temperature fluctuation (Steinbauer and Grigsby 1957, Thill et al. 1980). Following post-harvest dormancy, cheatgrass germinates rapidly under a wide variety of alternating temperature regimes (Evans and Young 1972). The

optimum temperature for cheatgrass germination after 7 weeks of after-ripening is 20 C. (Hulbert 1955).

Steinbauer and Grigsby (1957) found that light had no effect on the germination of cheatgrass. Hulbert (1955) reported the interactive effects of light and temperature upon cheatgrass dormancy to be complex. At optimum temperatures, light had little effect on germination, however it inhibited germination at low temperatures and stimulated germination at high temperatures (Hulbert 1955).

Water matric potential and soil texture also effect germination. Evans and Young (1972) found that cheatgrass seed did not germinate in any soil texture if the water matric potential was greater than -1.0 MPa. However, germination was better in loamy soils than clay or sand at matric potentials from 0 to -0.8 MPa. Hinds (1975) reported that cheatgrass seed osmotically adjust internal matrix potential to -1.6 MPa between 20 and 60 hours after the initial imbibition to complete the germination process. Under osmotic stress (0 to -1.5 MPa), yellow starthistle germination was reduced by half between 0 to -0.5 MPa, and halted at osmotic potentials below -1.0 MPa (Larson and Kiemnec 1993). Under salt stress (0 to 12 ds m⁻¹), yellow starthistle seed germination was reduced from 77 to 61 percent (Larson and Kiemnec 1993).

Seedlings

The most widely studied factor affecting seedling emergence is depth of planting. Hulbert (1955) found nearly 100% emergence of cheatgrass from depths of 50 mm or less. In field studies, most cheatgrass emerged from soil depths of 25 mm or less, and little emergence was found at planting depth of 100 mm (Wicks et al. 1971). Wicks et al. (1971) also reported that emergence from silt loam and silty clay loam soils was greater at shallow depths (<12 mm), while emergence was best in sandy soil at depths near 50 mm.

Timing of emergence can be very important in determining the outcome of competition (Ross and Harper 1972, Harper 1977) and seed output. When cheatgrass emerged 1 week after winter wheat, wheat yields were depressed 20 to 30% (Wicks 1966). However, Wicks (1966) found wheat yields to be unaffected if cheatgrass emerged 2 or more weeks after wheat.

Thill et al. (1979) studied the effects of water matric potential and temperature on emergence of cheatgrass. They found that at high matric potentials, emergence was greater in warmer soils (20 C), while at low matric potentials, emergence was greater in cooler soils (15 C).

Thill et al. (1979) found that compaction of the soil inhibited cheatgrass emergence. Increased bulk densities progressively decreased emergence.

Juveniles

Establishment and resource preemption by a seedling is dependent upon autotrophism. Autotrophism in grass seedlings requires the formation of adventitious roots for sufficient water and nutrient transfer (Hyder et al. 1971, Ries and Svejcar 1991). Aguirre and Johnson (1991), in a greenhouse study (28 to 38 C) using sandy loam soil, determined that adventitious roots appeared in cheatgrass after 17 days of growth.

Sheley et al. (1993), in a greenhouse study (15 C nights, 20-25 C days) using standard potting mixture, determined that yellow starthistle began lateral root spread after 2 days of growth, and developed 1134 mm² of lateral root spread in 10 days. Radicle elongation and root growth by yellow starthistle, during the first 18 days of growth, was more rapid than that of annual grasses growing in association in southwestern Oregon.

Mature Adults

Interference:

Interference is a collective term for the general interactions among species or populations. The term includes competition, amensalism (allelopathy), and trophic level interactions (Burkholder 1952, Archer and Pyke 1991).

Competition:

Competition studies involving cheatgrass or yellow starthistle have focused upon competition intensity (Evans 1961, Roché 1965, Harris 1967, Borman et al. 1990, Svejcar 1990, Aguirre and Johnson 1991, Prather and Callihan 1991, Sheley et al. 1993). Substantial literature relates cheatgrass competition to native and introduced perennial grasses (Eckert and Evans 1963, Kay and Evans 1965, Harris 1967, Harris and Wilson 1970, Buman et al. 1988, Svejcar 1990, Aguirre and Johnson 1991, and Melgoza and Nowak 1991). In general, these studies indicate that cheatgrass seedlings are more competitive than perennial grass seedlings because of their rapid growth rates. Established perennial grasses appear to be more competitive than seedling cheatgrass, however, cheatgrass tends to reduce perennial grass production. Competition studies aimed at determining the effects of density and timing on the control of cheatgrass indicate that early control benefit competing plants (Rydrych and Muzik 1968, Rydrych 1974). Much of this literature has also been reviewed by Thill et al. (1984) and Morrow and Stahlman (1984).

Prather and Callihan (1991) found yellow starthistle to be more competitive than pubescent wheatgrass after 7 weeks of growth. Borman et al. (1991) reported that established perennial grasses that initiate growth early, maintain some growth through the winter months, and mature early, can limit reinvasion by yellow starthistle.

Dakheel (1986) investigated cheatgrass and medusahead interference. He found cheatgrass interference on medusahead weight, in adequate moisture environments, to be greater than intraspecific interference. In contrast, cheatgrass intraspecific interference was greater than medusahead influence on cheatgrass weight. In a moisture-stressed environment, relative total yield indicated a slight degree of mutual antagonism.

Medusahead is probably most successful in competing with cheatgrass under high moisture environments (Dakheel 1986). Under these conditions, medusahead, with a longer life cycle, produces a greater number of seed than cheatgrass and dominates the site (Dakheel 1986). In contrast, cheatgrass produces relatively constant seed numbers under a variety of environments, and is more likely to dominate more arid environments with its early maturing characteristic (Kay and Evans 1965, Rydrych 1974).

Amundson (1980) and Talbott (1987) found yellow starthistle associated with deep soils, and cheatgrass with shallow soils. Sheley et al. (1993) suggested that yellow starthistle may be competitive with annual grasses due to its rapid root growth and soil penetration.

Amensalism:

Yellow starthistle has been reported to contain alkaloids (Mamedor 1956), polyphenols (Masso et al. 1979), terpenoids (Buttery et al. 1986), sesquiterpene lactones (Merrill and Stevens 1985), and two chromenes (Merrill 1989).

Zamora et al. (1983) conducted a series of investigations aimed at elucidating the allelopathic potential of yellow starthistle. They found that aqueous extracts of fresh yellow starthistle leaves decreased yellow starthistle germination, but had no effect on cheatgrass. Radicle length inhibition was greatest in cheatgrass and yellow starthistle with extracts from ground senesced leaves. Increasing soil-incorporated yellow starthistle foliage and root residue decreased indicator plant weight. A greenhouse plantback study indicated that 15 weeks of growth by yellow starthistle, cheatgrass, or yellow starthistle plus cheatgrass, reduced the shoot height of cheatgrass but had no effect on germination or shoot weight by either species.

Trophic level interactions:

Several authors have reported smut (*Ustilago bromiuara* Tul Fisch von Waldh.) infestations on cheatgrass populations (U.S. Forest Service 1937, Daubenmire 1940, Young et al. 1969). In Nevada, oscillations in Basidiomycete populations reduced cheatgrass seed production in moist summer environments (Young et al. 1969).

Kreitlow and Bleak (1964) reported the soil borne pathogen *Podosporiella verticillata* O'Gara. to commonly infect cheatgrass. Young et al. (1969) found protruding fungal synnemata closely resembling this species in litter samples of cheatgrass which rendered the caryopsis non-viable.

Yellow starthistle produces viable seed when pollinated by insects (Roché, 1992). About 20 insects utilize the heads of yellow starthistle in the Mediterranean region (Sobhian and Zwolfer 1985). Some species are potentially damaging (e.g. *Carthamus tinctorius* L., *Urophora sirunaseva* (Hering) and *Chaetorellia hexachaeta* (Loew)), and are being considered as biological control agents (Roché et al. 1993). However, the most important interactions between insects and yellow starthistle are probably in inter-population hybridization (Roché et al. 1993).

Both species appear to have evolved under intense grazing pressure. Herbivores graze cheatgrass early in the spring (Harris 1967), but the species avoids prolonged grazing through early maturation. The protein content of green forage is as high as that of many perennial grasses, but decreases to approximately 3% upon maturity (Carter et al. 1957). Roché (1983) reports the potential for mechanical injury to livestock following cheatgrass maturity.

In early spring, livestock will graze yellow starthistle where solid stands occur (Callihan et al. 1982, Thompson et al. 1990); however, nutrient quality is poor (Callihan et al. 1982). Yellow starthistle is responsible for nigropallidal encephalomalacia ('chewing disease') in horses (Kingsbury 1964).

Growth Analysis:

A number of studies have been conducted on the growth of cheatgrass compared to perennial grass species (Hull 1963, Harris 1967, Svejcar 1990,

Melgoza and Nowak 1991, Aguirre and Johnson 1991). In summary, Svejcar (1990) found cheatgrass an efficient producer of leaf area and root length, which benefited establishment and the exploitation of soil nutrient and moisture reserves. No growth analysis of yellow starthistle has been performed.

Dakheel (1986) compared the growth rates of medusahead and cheatgrass, and determined that cheatgrass had a growth potential in mixtures equal to or higher than medusahead. He concluded that genetic and phenotypic plasticity were major contributors to the success of cheatgrass.

Reproductive Biomass and Seed Output

Cheatgrass and yellow starthistle are generally facultative monocarpic winter annuals. However, cheatgrass individuals can be ephemeral monocarpic annuals as well (Callihan et al. 1982, Mack and Pyke 1983).

Cheatgrass produce seed prior to yellow starthistle (Mack and Pyke 1983, Hironaka 1989). This characteristic may be advantageous to cheatgrass during periods of moisture stress, when seed production in later maturing species would be limited (Harris 1967, Dakheel 1986, Hironaka 1989).

Under optimum conditions, cheatgrass produced over 45,000 seeds per square meter (Hull and Pechanec 1947). Mack and Pyke (1983) showed that individual seed output for cheatgrass is more closely associated with year to year variation in environment than the intrinsic differences among three habitats (dry, mesic, moist). They report that most cheatgrass plants surviving into June

produce at least one seed. The number of non-reproducing members in the cheatgrass population was as high as 23%. More than half the individuals produced six seeds or fewer regardless of site condition (Mack and Pyke 1983).

Mack and Pyke (1983) found considerable year-to-year and site-to-site variation in seed production by fall- and spring-emerged plants. In most populations, plants emerging in the fall produced 50-75% of the seed harvested in June. Few seeds were produced by plants emerging during December and January. Spring emerged individuals occasionally dominated seed output.

Young and Evans (1976) found cheatgrass a uniparental reproducer (self-pollinator) with occasional genetic recombination (cross-breeder). In degraded *Artemisia* communities, cheatgrass was predominantly a self-pollinator. When the community was burned, cross-pollination increased and new genotypes appeared (Young and Evans 1976). Dakheel (1986) suggests that cheatgrass has a high degree of phenotypic plasticity allowing this species to optimize out-crossing and maximize its fitness to a site.

Palmblad (1968) studied the effects of density upon reproduction of cheatgrass. Seed output per unit area remained relatively constant over a wide range of densities indicating that mortality and growth plasticity tended to maintain a reliable seed output from the population.

Little is known about the breeding system of yellow starthistle. Roché et al. (1993) provide evidence that this species is cross-pollinated by insects. Of 34

populations collected from the Pacific Northwest and California, all appeared genetically different with regard to phenological development, growth, and reproduction.

Dispersal

Mack (1981) indicates that cheatgrass arrived in the 1890's and by 1930 dominated nearly all disturbed areas in the intermountain grasslands. Hulbert (1955) reported that animals and humans are important long distance dispersal agents of cheatgrass seed. Viable cheatgrass seed can be dispersed through physical attachment to fur and clothing or ingested by ruminants. Mack (1989) concluded that animals as cheatgrass seed vectors is overstated and that much of the spread associated with livestock was initiated with bedstraw discarded along railroad sidings.

Hulbert (1955) studied the effect of wind on the dispersal of several annual grasses, including cheatgrass. He concluded that wind typically did not disseminate their seeds over a couple of meters. Hulbert (1955) also showed that cheatgrass seeds were blown along a smooth soil surface more frequently than they were carried through the air.

The earliest indications of yellow starthistle in N. America came from analysis of flora associated with the adobe brick from the post-mission period after 1824 (Roché 1965). Herbarium records indicate that yellow starthistle was present in the mid to late 1800's (Howell 1959). Talbott (1987) suggests that

yellow starthistle will reach its ecological boundaries in the late 1900's because this species does not appear to survive in latitudes north of its current existence. Long distance dispersal mechanisms for yellow starthistle are human-mediated through crop seed, clothing, and vehicles.

Yellow starthistle has two types of seeds, with and without plumes. Plumeless seeds fall directly below the parent for site reoccupation, while plumed seeds are transported greater distances for colonization (Callihan et al. 1982). Roché (1991) trapped 92% of wind-blown yellow starthistle achenes within 0.6 m of the source. About 50% of the plumed seeds fell within 0.3 m of the parent source (Roché 1991). Dispersal distance was associated with the daily saturation deficit and maximum wind gusts.

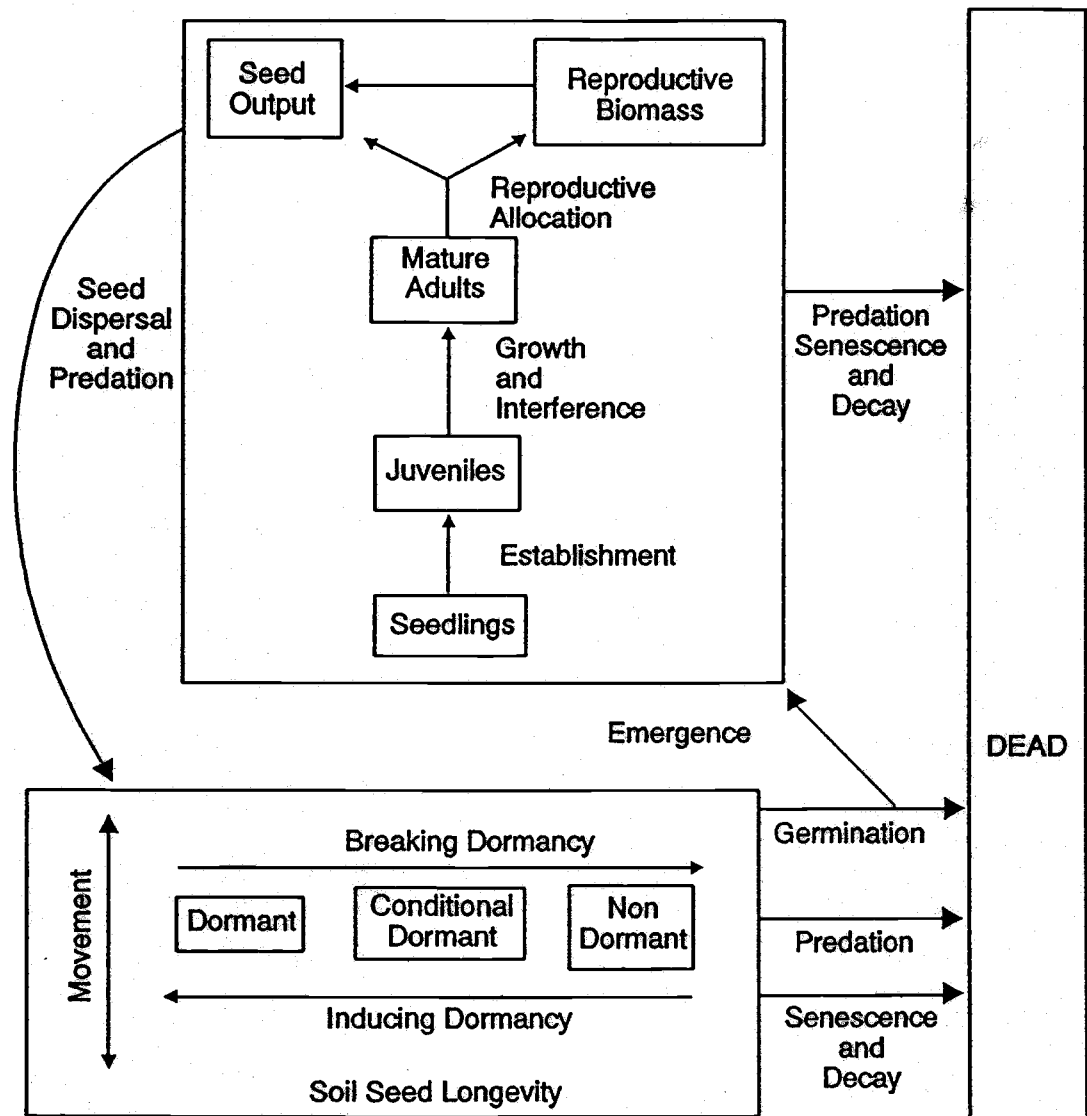


Figure 1.1. A conceptual model of an annual plant life cycle. Boxes represent life-history stages, arrows represent processes that regulate species performance among the life-history phases (modified from Radosevich and Roush 1990).

Table 1.1. Three components of successional management corresponding to three general causes of succession.

<i>Three components of succession management</i>	<i>Three general causes of succession</i>
1. Designed disturbance	1. Site availability
2. Controlled colonization	2. Differential species availability
3. Controlled species performance	3. Differential species performance

From Lukan (1990) Modified from Pickett et al. (1987).

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CHAPTER 2
COMPARATIVE LIFE-HISTORIES OF CHEATGRASS
AND YELLOW STARHISTLE

ABSTRACT

The objective of this research was to characterize the life-histories of cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) growing in association. Biweekly demographic attributes were monitored during 1991 (moist spring) and 1992 (dry spring). Data were arranged into life-history tables, and sensitivity analysis was performed to determine key transition phases. Cheatgrass and yellow starthistle seed banks were 4 and 13.5% of their total seed output, respectively. The entire cheatgrass seed crop reached the soil surface, 41% of yellow starthistle's seed output was lost during seed rain. Frost heaving reduced cheatgrass (79%) winter seedling populations more than yellow starthistle (55%). All cheatgrass surviving the frost heaving period became an adult. Yellow starthistle density was reduced by 75% during the juvenile phase. Cheatgrass adults appeared about 6 weeks prior to yellow starthistle adults. Cheatgrass seed output remained a constant 7000 m⁻² during both years. Yellow starthistle seed output was 21595 m⁻² (1991) and 5226 m⁻² (1992). Key processes associated with transition phases were interference (competition), resource acquisition rates and duration, and reproductive allocation. Cheatgrass matured

early in dry spring conditions. Dry spring conditions reduced yellow starthistle seed output suggesting community dynamics may be oscillatory and determined by spring precipitation.

INTRODUCTION

Cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) are alien winter annual weeds which grow in association on the California Annual Grasslands and the Grassland Steppe of the Pacific Northwest. Cheatgrass was introduced to N. America in the 1890s and could be found in most grassland steppe communities of the Intermountain West by 1930 (Mack 1981). Cheatgrass, although less desirable than perennial grass, provides early spring forage on millions of hectares of grassland throughout this region (Hull and Pechanec 1947, Klemmedson and Smith 1964, Morrow and Stahlman 1984, Emmerich et al. 1993).

Yellow starthistle, a noxious weed, began invading perennial grass and cheatgrass dominated rangelands in N. America around 1920, and is estimated to be increasing at a rate of about 10000 ha per year in Washington and Idaho alone (Talbot 1987, Callihan et al. 1989). Yellow starthistle is considered poor forage for all classes of livestock and causes nigropallidal encephalomalacia in horses (Cordy 1954, Roché 1983).

Cheatgrass and yellow starthistle currently dominate millions of ha throughout western U.S. (Mack 1981, Maddox et al. 1985). It is generally accepted by land managers that conversion of perennial grasslands to cheatgrass has reduced resource values (forage, watershed, ecological processes) and that the invasion of cheatgrass-dominated rangeland by yellow starthistle further reduces resource value.

Control and rehabilitation of these communities have been researched, but have yielded limited success in small scale application (Evans et al. 1967, Eckert et al. 1974, Roché 1983, Sheley et al. 1983, Huston et al. 1984, Larson and McInnis 1989). The investigation of processes that control population and community dynamics is essential to future regulation of species dominance and the establishment of functional communities on degraded grasslands (Cousens 1985, MacMahon 1987, Radosевич 1987, Allen 1988, El-Tayeb 1989, Call and Roundy 1991, Pyke and Archer 1991).

Sager and Mortimer (1976) proposed examining the life-history of weeds and the interphases within their life-history as a means of identifying vulnerable periods and population regulating processes. Maxwell et al. (1988) conducted sensitivity analyses on a life-history model of leafy spurge (*Euphorbia esula* L.) developed by Watson (1985) to identify key processes regulating population dynamics. We utilized the Sager and Mortimer (1976) methodology to characterize the life-history of cheatgrass and yellow starthistle growing in association. Sensitivity analyses was conducted on life-history models to determine key processes related to seed output and population and community regulation.

MATERIALS AND METHODS

Study site and sampling procedures

The study was conducted 14 km west of Walla Walla, WA (elev. 320 m) in a bluebunch wheatgrass (*Agropyron spicatum*)-Idaho fescue (*Festuca idahoensis*) habitat type (Daubenmire 1970). The study area was co-dominated by cheatgrass and yellow starthistle. Neither bluebunch wheatgrass nor Idaho fescue were represented. The soil, a deep upland Ellisforde very fine sandy loam, had a 15-30% southeasterly slope. Average annual precipitation approximated 380 mm with a bimodal distribution which peaks in winter and spring. Temperatures range from 45 to -34° C with a frost free season of 170 days.

The life cycles of cheatgrass and yellow starthistle were monitored during 1991 and 1992 in a 40 x 40 m² area. Simple random sampling occurred at two week intervals beginning in mid-June 1991 and continued through 2 seed-producing generations. At each sampling date, data were collected and characterized as seed output m⁻², seed rain m⁻² upon the soil surface, accumulated seed rain upon the soil surface, seedlings m⁻² (1-5 leaves for yellow starthistle and 1 or 2 leaves for cheatgrass), juveniles m⁻² (6 and 3 leaves for yellow starthistle and cheatgrass, respectively, to initiation of flower head), and adults m⁻² (initiation of flower head to maturity).

The soil seed bank m⁻² was determined by sifting (2 mm sieve) 30 randomly located soil samples before seed drop each year. Each sample

contained 686 mm³ of soil, from the top 80 mm of the soil profile. All intact cheatgrass and yellow starthistle seeds were counted. Deteriorated and unfilled caryopsis and achenes were noted.

Seed rain on the soil surface was estimated using a variation of the sticky trap discussed by Huenneke and Graham (1987). Forty 37 X 300 mm wooden traps were coated with a smooth surface of lithium based grease, and randomly placed flush on the soil surface. Traps were cleaned and regreased at each visit. Seeds were counted by species and type at each sampling to estimate seed rain. Accumulated seed rain was calculated by summing prior seed rain estimates.

Density of individuals was determined by counting plants in 30 randomly located 20 X 50 cm plots. Seedling, juvenile, and adult densities were determined by counting individuals in 5, 50, and 100% of the plots, respectively.

Twenty mature (seed set) cheatgrass individuals were harvested at each plot location to determine seed output. Yellow starthistle seed output was determined by counting the number of seed heads on 10 plants at each plot location. A single seedhead was randomly harvested from each of the 10 plants and the number of seeds were counted. Seeds were separated by species and type to obtain seed output.

Fifty randomly selected individuals of each species were harvested, dried and weighed on monthly intervals beginning March 15 and ending July 15, 1992.

Mean individual weights were determined. Individual weights were multiplied by the total population density at the time to provide a comparison of the change in biomass during the spring growing season of 1992.

Analysis

A confidence interval ($\alpha = .05$) for each parameter at each sampling date was calculated. Models were developed by arranging demographic data into life-history tables (Sager and Mortimer 1976). Each transition parameter was calculated as the percent change from one sample date and/or life-history stage to the next. Life-history models of cheatgrass and starthistle were generated using Quattro Pro spreadsheets (Borland International 1990). It was assumed that during periods of population decline, transitions from one growth stage to the next did not occur, and that mortality constituted the decline. Conversely, it was assumed that during periods of population increase that all individuals within a stage survived to the next sampling date. These assumptions are supported by the observations of Mack and Pyke (1983) for cheatgrass populations.

A 10% sensitivity analysis (Maxwell et al. 1988) was conducted on life-history models. The processes associated with the transition parameters with the highest sensitivity values were considered most important. The relative effect of 10% reductions on seed output was determined as:

$$\text{Sensitivity value} = \frac{\frac{\Delta \text{ seed output}}{\text{seed output}}}{\frac{\Delta \text{ trans. prob.}}{\text{trans. prob.}}}$$

Life-history models and sensitivity values are presented.

RESULTS

Life-history

Cheatgrass

The 1991 cheatgrass population produced 660 adults m^{-2} , with 10.7 seeds individual⁻¹ for an approximate seed output of 7000 seeds m^{-2} (Table 2.1).

Cheatgrass seedbank size was 333 ± 140 and 267 ± 97 m^{-2} prior to the seed release in 1991 and 1992, respectively. The seedbank was similar between years and represented about 4% of the total seed produced. A majority of the seed in the seed bank appeared partially deteriorated or unfilled. Our observations are comparable to those by Thill (1979) and Mack and Pyke (1983) who found that the bulk of the cheatgrass seed bank were germinated, deteriorated, or lacked endosperm following the first growing season. The entire cheatgrass seed crop reached the soil surface. Peak seed rain occurred in July and August, however seed input to the soil surface continued until the end of February. Nine percent of the total seed rain reached the soil surface after the initiation of fall seedling recruitment.

Fall seedling recruitment was observed on November 15, 1991, shortly after fall precipitation (10 mm)(Table 2.1). Mack and Pyke (1983) observed fall cheatgrass recruitment prior to November 1 in all sites and years studied. Seedling recruitment peaked at 6224 seedlings m^{-2} in late January. Following a 2 wk period of freezing and thawing, seedling densities were reduced to 2900 seedlings m^{-2} by the end of February. Spring seedling recruitment was 12% of

the total seedling population, and occurred during late February and early March. The majority of the cheatgrass seed germinated by early March and spring seedling recruitment was most likely limited by availability of viable seeds.

Fall cheatgrass seedlings developed into juveniles in February. Juveniles were the dominate growth stage for 6 wks with a maximum population of 2421 individuals m^{-2} in mid-April. All individuals that survived to the juvenile stage lived to produce an inflorescence. Cheatgrass adults appeared in mid-April. Representatives of all growth stages were present in the community at that time.

Yellow Starthistle

The 1991 starthistle population produced 180 adults m^{-2} , with 120 seeds individual⁻¹ for an approximate seed output of 21600 seeds m^{-2} (Table 2.2). In 1992 the adult starthistle density was 236 individuals m^{-2} , with 22 seeds individual⁻¹ for an approximate output of 5000 seeds m^{-2} .

The size of the starthistle seed bank was 3224 ± 987 in 1991 and 2897 ± 992 in 1992. All seeds were plumeless and represented approximately 13% of total seed production. This corresponds with observations by Larson and Kiemnec (1993) suggesting lower field germination by plumeless seed following a November-March seed burial.

Seed rain represented 59% of the total seed output (Table 2.2). Roché (1991) identified birds as a primary seed predator for starthistle during seed

dispersal, but suggested they play a minor role in long distance dispersal. Peak seed rain occurred between late-July and early-August. Seed rain continued into February and 16% of the seed rain occurred after the initiation of fall seedling recruitment. Plumeless starthistle seed comprised 25% of the total seed rain and 76% of late (November-February) seed rain (Table 2.3).

Fall seedling recruitment was observed in mid-November with 4080 seedlings m^{-2} (Table 2.2). Recruitment increased at the rate of 1000 individuals m^{-2} sampling date⁻¹ for 6 wk. Starthistle seedlings peaked at 7563 individuals m^{-2} in mid-January decreasing to 4740 seedling m^{-2} by mid-February. Spring seedling recruitment was 410 individuals m^{-2} .

Juvenile starthistle first appeared March 30, 1992 (2107 individuals m^{-2}). The transition from seedling to juvenile increased the juvenile population to 4560 individual m^{-2} by mid-May. Juvenile mortality began in late-April and reached 75% by mid-June. Roché (1965) observed a 58% reduction in starthistle density from April to July.

Starthistle adults were observed in mid-June. Approximately 940 juveniles m^{-2} made the transition to adult, however mortality reduced the adult population to 236 plants m^{-2} by mid-July.

Individual weights of both species were similar at the first two sampling dates (Table 2.4). Yellow starthistle had greater total biomass than cheatgrass due to higher densities. Yellow starthistle had the highest individual weight and total biomass on the May 15 sampling date. From May 15 to the end of the

growing period cheatgrass exceeded yellow starthistle in total biomass, while the individual weight of yellow starthistle was greatest. Yellow starthistle total biomass was lower due to a large reduction in density during the transition from juvenile to adult. These data suggests that yellow starthistle populations are sensitive to May precipitation.

Sensitivity analysis

Cheatgrass

Reductions in accumulated cheatgrass seed rain and seedling survivorship resulted in high sensitivity values (Table 2.5). A 10% reduction in seed rain (14-30 October) reduced the number of seed producing adults by 400 individuals m^{-2} and seed output by 600 seeds m^{-2} . Similarly, a 10% reduction in the number of cheatgrass seedlings transitioning to the juvenile growth stage resulted in a seed output decrease of 580 seeds m^{-2} . This later reduction corresponded with an observed population decline during a period of frost heaving.

The highest sensitivity values were associated with adult cheatgrass survivorship and seed production (Table 2.5). A 10% reduction in either adult survivorship (15-30 May) or seed output per individual resulted in decreases of 700 seeds m^{-2} .

Yellow Starthistle Maximum sensitivity values for starthistle occurred with reductions in juvenile and adult survivorship, juvenile transition to adult, and seed production (Table 2.6).

Juvenile and adult survivorship as well as the transition from juvenile to adult are critical stages for starthistle populations. A 10% reduction during the transition from juvenile to adult (May 30 - June 15) resulted in a decrease of 1000 seeds m^{-2} . A similar reduction in the seed production phase resulted in a reduction of 526 seeds m^{-2} . This suggests that the number of individual plants surviving to produce seed was more important to total seed output than a comparable reduction in the number of seeds produced per plant.

Seed rain and seedling survivorship yielded large sensitivity values at maximum density. Ten percent reductions in accumulated seed rain and seedling survivorship resulted in a 474 and 512 seeds m^{-2} reduction, respectively.

DISCUSSION

The life-history models indicate that cheatgrass and yellow starthistle populations are naturally reduced at the seedling stage, and seed output is sensitive to these reductions. Winter seedling reductions appear to be associated with periods of frost heaving. However, empirical life-history models do not address population adjustments associated with species plasticity and the ability to capture newly available resources. We believe that cheatgrass utilized newly available resources after density-independent seedling mortality (frost heaving), increasing the seed output of the remaining survivors. Young et al. (1976) observed a similar cheatgrass response following fire disturbance. In that case adjustments of individual seed output within the cheatgrass population also maintained near-predisturbance levels of seed production.

Sensitivity analysis identified transitions from juvenile to adult and adult survivorship as critical to seed output reductions for both cheatgrass and yellow starthistle. Key processes associated with this phase are competition, growth rates and duration, and reproductive allocation (Radosevich and Roush 1990). We did not observe cheatgrass mortality during this life-history phase and believe that cheatgrass avoided mortality by partitioning resources through differential rooting zones and early maturation (Sheley and Larson 1993). In contrast, the later maturing starthistle populations declined dramatically during the transition from juvenile to adult.

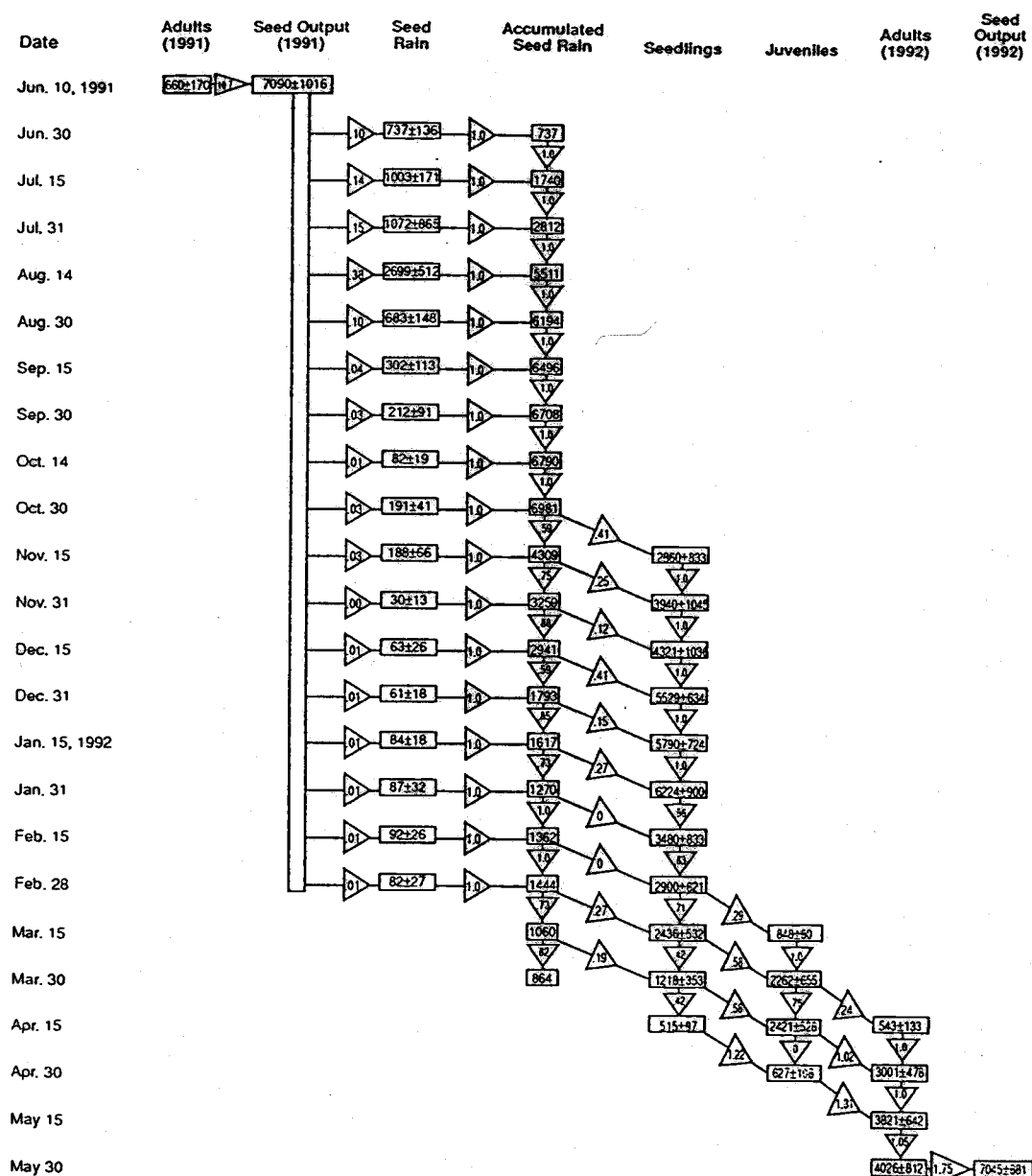
In this study, the cheatgrass population increased from 660 to over 4000 adults m^{-2} while maintaining a seed output of 7000 seeds m^{-2} in near average (1991) and below average (1992) spring (May-June) precipitation, respectively (Table 2.7). Cheatgrass adult density and seed output was comparable to a 3 yr study by Mack and Pyke (1983) on a similar habitat type in WA. Population dynamics in 1992 were comparable to the drier big sagebrush (*Artemisia tridentata*) - bluebunch wheatgrass habitat type (Mack and Pyke 1983).

Our data supports the conclusion of Palmblad (1968) that cheatgrass uses the process of self thinning along with plasticity to maintain a constant and reliable seed output. Life-history tables suggest that a conspecific hierarchy of size classes is established as a result of differential seedling emergence. We speculate that with average spring moisture, density-dependent mortality was enhanced because the dominant plants in the hierarchy of size classes continued to capture most of the resources, suppressing and thinning smaller plants (Radosevich and Holt 1984). This may prevent a situation where high densities of aggressive individuals exhaust resources prior to the completion of their life cycle. In abnormally moist years, the process of self thinning may result in greater reproductive output than in years with average moisture (Harper 1977, Pyke and Archer 1991). Link et al. (1990) observed that when soil water was not limiting, cheatgrass senescence was delayed for only 10 days. Intrinsic early maturation regulates growth and seed production during moist years. In dry years, the early maturing characteristics of cheatgrass regulates growth and seed

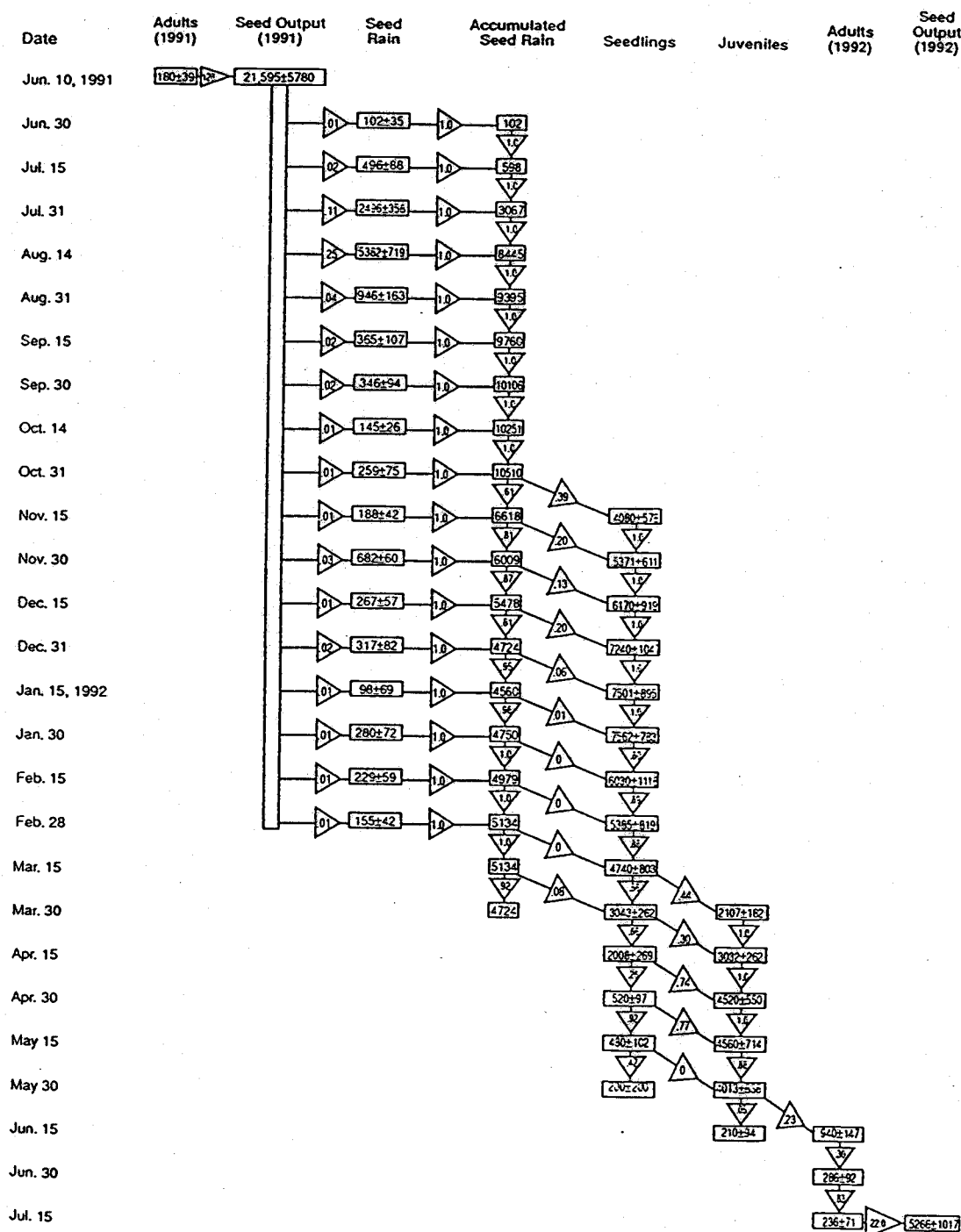
production. Our data suggest that the early maturing characteristic of cheatgrass allows this species to avoid drought during years without spring precipitation. Limited moisture availability may not provide cheatgrass the growth potential to allow dominant individuals to suppress subordinate individuals, resulting in high population densities with low individual seed output. This hypothesis is supported by the demographic analysis of Mack and Pyke (1983) for cheatgrass along an environmental gradient from dry to moist sites.

Yellow starthistle adult populations remained constant between years (about 200 adults m^{-2}), however seed output was 21600 seed m^{-2} in 1991 and 5000 seed m^{-2} in 1992. This suggests that adequate spring precipitation and self-thinning enhance yellow starthistle seed production. Sheley et al. (1993) speculate that rapid root growth and soil penetration by yellow starthistle permits later maturation and increased seed production. In this study yellow starthistle's seed production advantage was removed in 1992. Less than 25% of the juveniles reached the adult stage, and only 25% of the individuals reaching the adult stage survived to produce a limited number of seed. We believe that only dominant individuals possessed enough root system for continued resource uptake and completion of their life cycle under dry conditions.

Our study suggests that variations in seed output by yellow starthistle is dependent upon the availability of spring precipitation. Variations in yellow starthistle seed output will likely result in oscillatory patterns of community dynamics.

Table 2.1. Life-history of cheatgrass (June 1991-May 1992).¹

¹ Boxes represent life-history stages (m^2), arrows represent the fractional change from one stage to the next.

Table 2.2. Life-history of yellow starthistle (June 1991-July 1992).¹

¹ Boxes represent life-history stages (m^2), arrows represent the fractional change from one stage to the next.

Table 2.3. Distribution of yellow starthistle seed rain by type.

Date	SEED TYPE	
	Plumed	Plumeless
	----- (seeds m ⁻²) -----	
June 30, 1991	97 ± 21 ¹	05 ± 03
July 15	483 ± 70	13 ± 07
July 31	2469 ± 316	0
August 14	5377 ± 643	05 ± 03
August 31	935 ± 142	11 ± 06
September 15	320 ± 83	45 ± 16
September 30	258 ± 42	88 ± 36
October 14	145 ± 17	0
October 31	200 ± 39	59 ± 26
November 15	95 ± 14	93 ± 22
November 30	45 ± 18	637 ± 37
December 15	53 ± 17	214 ± 21
December 31	32 ± 15	285 ± 28
January 15, 1992	43 ± 21	45 ± 20
January 30	72 ± 23	208 ± 27
February 15	68 ± 22	161 ± 30
February 28	74 ± 18	81 ± 19

¹ confidence interval at $\alpha = .05$.

Table 2.4. Individual weight and total biomass of cheatgrass and yellow starthistle during 1992.

Date	Individual weight		Total Biomass	
	<u>cheatgrass</u> ----- (mg plant ⁻¹)	<u>yellow starthistle</u> ----- (mg plant ⁻¹)	<u>cheatgrass</u> ----- (gm m ⁻²)	<u>yellow starthistle</u> ----- (gm m ⁻²)
March 15	3.25 ± .50 ¹	3.55 ± .50	106.7 ²	168.3
April 15	4.00 ± .84	4.25 ± .50	139.2	214.2
May 15	4.94 ± .50	11.41 ± 1.84	188.8	575.1
June 15	7.19 ± 1.12	21.85 ± 6.51	289.5	251.3
July 15	7.54 ± 1.25	80.86 ± 39.51	303.6	190.8

¹ Confidence intervals at $\alpha = .05$

² Mean individual weight multiplied by mean population density

Table 2.5. Sensitivity values calculated for cheatgrass life-history transitions.

Date	Seed Rain	Accumulated Seed rain	Seedling Recruitment	Seedling Survivorship	Seedling to Juvenile	Juvenile Survivorship	Juvenile to Adult	Adult Survivorship	Seed Output
Sensitivity Values (-10%)									
June 10, 1991									1.111
June 30	.097								
July 15	.130	.097							
July 31	.142	.233							
August 15	.366	.382							
August 31	.096	.777							
September 15	.040	.882							
September 31	.028	.929							
October 15	.011	.962							
October 31	.025	.975							
November 15	.025	.565	.393						
November 30	.004	.435	.103	.393					
December 15	.008	.384	.050	.500					
December 31	.008	.223	.162	.606					
January 15, 1992	.011	.195	.034	.789					
January 31	.011	.147	.058	.829					
February 15	.011	.158	0	.897					
February 28	.011	.169	0	.897					
March 15		.065	.113	.637	.229				
March 30		0	.065	.348	.338	.229			
April 15				.219	.190	.478	.144		
April 31				0	.219	0	.687	.144	
May 15							.219	.852	
May 30								1.111	1.111

Table 2.6. Sensitivity values calculated for yellow starthistle life-history transitions.

Date	Seed Rain	Accumulated Seed rain	Seedling Recruitment	Seedling Survivorship	Seedling to Juvenile	Juvenile Survivorship	Juvenile to Adult	Adult Survivorship	Seed Output
Sensitivity Values (-10%)									
June 10, 1991									1.111
June 30	.009								
July 15	.044	.009							
July 31	.222	.053							
August 15	.496	.277							
August 31	.084	.802							
September 15	.032	.900							
September 31	.031	.938							
October 15	.013	.975							
October 31	.023	.990							
November 15	.012	.442	.527						
November 30	.036	.285	.161	.527					
December 15	.011	.219	.099	.705					
December 31	.007	.095	.133	.819					
January 15, 1992	.002	.070	.032	.974					
January 31	.004	.064	.008	1.010					
February 15	.003	.068	0	1.020					
February 28	.002	.071	0	1.020					
March 15		.073	0	1.020					
March 30		0	.073	.488	.484				
April 15				.347	.207	.484			
April 31				.009	.667	.712			
May 15				0	.009	1.100			
May 30				0		1.111			
June 15						0	1.111		
June 30								1.111	
July 15								1.111	1.111

Table 2.7. Monthly precipitation totals (mm) for study site near Walla Walla, WA during 1991 and 1992.¹

Month	Year	
	1991	1992
	----- (mm) -----	
January	26	19
February	16	27
March	42	8
April	14	32
May	111	8
June	51	24
July	8	40
August	7	34
September	0	24
October	25	22
November	80	41
December	16	28
Total ²	395	310

¹ Average annual precipitation = 380 mm.

² Totals may vary from monthly values due to rounding.

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CHAPTER 3

**COMPARATIVE GROWTH AND INTERFERENCE BETWEEN
CHEATGRASS AND YELLOW STARHISTLE SEEDLINGS**

ABSTRACT

Annual grasslands in California and the Pacific Northwest are being invaded by Eurasian weeds, such as yellow starthistle (*Centaurea solstitialis* L.). Plant-plant interactions influence community dynamics and plant establishment. The objectives of this study were to quantify the effects of interference between seedlings of cheatgrass (*Bromus tectorum* L.) and yellow starthistle and to compare growth of isolated individuals of these species. Isolated individuals and addition series mixtures with total stand densities ranging from 20-20000 plants m⁻² were grown in environmental chambers (10 C, 12 hr day length). Individuals were harvested on 4 d intervals for 46 d, and mixtures were harvested 37 d after planting. Shoot weight, root weight, leaf area, and total root length of isolated individuals were similar. Yellow starthistle soil penetration was deeper than cheatgrass after 22 d from planting. Intraspecific interference was greater than interspecific interference for both species, and resource partitioning via rooting depth was evident. The yellow starthistle root:shoot ratio and the cheatgrass lower (below 200 mm):upper (above 200 mm) root ratio increased with increasing densities. Yellow starthistle and cheatgrass minimize interspecific interference as seedlings through differential

periods of growth and rooting depth. Invasion of cheatgrass rangelands by yellow starthistle increase resource partitioning and reduce our ability to revegetate rangelands by conventional means.

INTRODUCTION

The loss of native perennial vegetation on North American rangelands has been accompanied by invasions of aggressive alien annual weeds. The grassland steppe of the Pacific Northwest and the California Annual Grasslands, once dominated by native perennial grasses (e.g. bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith), now contain extensive areas dominated by annual grasses (e.g. cheatgrass (*Bromus tectorum* L.)) (Mack 1981, Young et al. 1987).

Cheatgrass, an early maturing winter annual, arrived from Eurasia preadapted (Grant 1977) and expanded its range to include most grasslands in the Intermountain West (Mack 1981, Morrow and Stahlman 1984). Much of the success of cheatgrass has been attributed to rapid germination and growth rate (Hulbert 1955, Hull 1963, Harris 1967, Svejcar 1990, Aguirre and Johnson 1991) at low soil temperatures and moisture availability (Harris 1967, Aguirre and Johnson 1991, Johnson and Aguirre 1991). Cheatgrass, although less desirable than perennial grass, provides early spring forage on millions of ha of grazing lands (Hull and Pechanec 1947, Klemmedson and Smith 1964).

Ecologists are concerned that these annual grass communities are in jeopardy of site occupation by less desirable Eurasian weeds, such as yellow starthistle (*Centaurea solstitialis* L.) (Hironaka 1961, Roché and Roché 1988, Callihan et al. 1989, Harris 1989, Hironaka 1989, Sheley et al. 1993). Yellow starthistle is currently spreading onto grasslands in Washington and Idaho at an

estimated rate of 7,800 and 2,800 ha per year, respectively (Talbott 1987, Callihan et al. 1989). Hironaka (1989) proposed that the sequence of species replacement among winter annuals in the Pacific Northwest would be from early maturing species to later maturing ones. In this scenario, cheatgrass would be replaced by later maturing medusahead (*Taeniatherum asperum* Nevski) or yellow starthistle. In either case the replacement species would be considered poor forage for all classes of livestock (Roché 1983).

Attempts to convert yellow starthistle and cheatgrass dominated rangelands into functioning perennial grasslands have yielded differing results due to ecological and economic reasons (Evans et al. 1967, Eckart et al. 1974, Young et al. 1976, Roché 1983, Sheley et al. 1983, Huston et al. 1984, Buman and Abernathy 1988, Larson and McInnis 1989, Prather and Callihan 1991). Successional management systems may offer an alternative solution for revegetating degraded rangelands (Slayter 1977, Rosenberg and Freedman 1984, Lukan 1990). The transition from vegetation management to successional management requires an understanding of mechanisms regulating ecosystem function and community dynamics (MacMahon 1987, Allen 1988, El-Tayeb 1989, Call and Roundy 1991, Archer and Pyke 1991, Pyke and Archer 1991). Investigations aimed at plant-plant interactions and the relationships which affect dominance, community dynamics, and plant establishment are critical to the development of successful management systems.

This study was conducted to develop an initial understanding of cheatgrass-yellow starthistle interactions. The specific objectives were to: 1) quantify the effects of interference between seedling cheatgrass and yellow starthistle, and 2) compare the weight, leaf area, root length, and soil depth penetration of isolated individuals of these species.

MATERIALS AND METHODS

Interference

Monocultures and mixtures of seedling cheatgrass and yellow starthistle were grown to assess interaction between the two species. Densities of cheatgrass and yellow starthistle were arranged to provide an addition series (Spitters 1983, Radosevich 1987). The cheatgrass:yellow starthistle densities were 10:10, 10:100, 10:1000, 10:10000, 100:10, 100:100, 100:1000, 100:10000, 1000:10, 1000:100, 1000:1000, 1000:10000, 10000:10, 10000:100, 10000:1000, 10000:10000 plants m⁻².

Seeds of cheatgrass and yellow starthistle were sown in 1824 mm² (surface area) X 400 mm (depth) poly vinyl chloride (PVC) tubes (split vertically and taped to facilitate root removal). Tubes were filled with sterilized Walla Walla silt loam (coarse-silty, mixed, mesic Typic Haploxeroll; A horizon) soil. Moisture was added to the soil and allowed to equilibrate to field capacity. No additional watering took place during the study. Seeds were broadcast then manually arranged until a uniform seed distribution was achieved. A small amount (<2 mm depth) of dry soil was used to cover the seeds. Tubes were arranged in a randomized complete block design with 4 replications and 16 tubes per block in an environmental chamber (10 C, 12 h daylength). Sampling occurred 37 d after planting.

Sampling involved manually rinsing soil from roots and measuring primary root penetration. Five individual root systems for each species (2 root

systems at lowest density) were extracted from each tube, separated from shoots, divided into upper (0-200 mm penetration) and lower (>200 mm penetration) portions, and measured for total length (cm) using a root length scanner (Comair Corp., Melbourne, Australia), and dried to a constant weight (48 h, 60 C) and weighed (mg). Leaf material was scanned for surface area (cm²)(Licor-3100 with conveyor belt, LI-COR, Inc., Lincoln, Nebraska), dried to a constant weight (48 h, 60 C) and weighed (mg).

Addition series data were incorporated into multiple linear stepwise regression models (least squares) using SPSSPC+ procedures (SPSS., Chicago, IL) of the form:

$$V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$$

$$V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$$

where V_c and V_y were the average per plant growth response for cheatgrass and starthistle, respectively, and N_c and N_y were their density. Regression coefficients B_{co} and B_{yo} estimate the maximum response of each variable for an isolated individual. Negative and/or nonsignificant intercepts are reported. They are considered to be estimates of values outside the range of the regression plane (Spitters 1983, Rejmanek et al. 1989), or random errors (Pantone and Baker 1991).

The regression coefficients B_{cc} and B_{yy} estimate intraspecific interaction, and B_{cy} and B_{yc} estimate interspecific interaction. The ratios $B_{cc}:B_{cy}$ and $B_{yy}:B_{yc}$ determine the relative influence of each species on the variable response. For

example, a $B_{cc}:B_{cy}$ ratio of 2 suggests that cheatgrass has twice the influence upon itself in determining the variable response when compared to yellow starthistle. Zero was used for all non-significant coefficients in the regression model, and a constant of .0001 was used for ratio calculations (Roush 1988).

The $[B_{cc}/B_{cy}:B_{yc}/B_{yy}]$ double ratio was used to determine the partitioning of resources between species (Spitters 1983, Connolly 1986, Joliffe 1988). Deviations from unity indicate increased resource partitioning (niche separation). The coefficient of determination (R^2) values were calculated to indicate the proportion of the variability associated with the dependent variable (V_c or V_y) that was accounted for by plant density (N_c and N_y).

Scatterplots of the residuals vs. standardized predicted values were used to determine the homogeneity of variances and the degree of model fit. The t -tests ($P \leq .05$) were used to determine significance of regression coefficients.

Individual Growth of Isolated Plants

Seeds of cheatgrass and yellow starthistle were pre-germinated and four seedlings were transplanted into PVC tubes for each of 10 harvest dates (46 d duration, 4 d harvest interval initiated on day 10). Tube surface area was increased with harvest date to insure minimal restriction of root growth (Table 3.1). Tube length was a constant 800 mm. Tubes were prepared following procedures described in the interference study. Tubes were arranged in a randomized complete block design with 5 replications and 10 tubes of each

species per block, and placed into an environmental chamber (10 C, 12 h daylength). Plants were transplanted on day 1 of the experiment and thinned to a single individual on day 5. Sampling procedures followed those described for the interference study, with the exception that upper and lower root portions were not separated. Data were analyzed using ANOVA (SPSS., Chicago, IL); Fisher's protected ($P \leq .05$) LSD mean comparisons are presented (Peterson 1985).

RESULTS

Interference

Intraspecific interference was more important than interspecific interference for the prediction of plant weight (Figure 2; Tables 3.2 and 3.3). The influence of cheatgrass density on total cheatgrass weight was 2 times greater than the influence of yellow starthistle density. Similarly, yellow starthistle density was twice as important as cheatgrass density in the prediction of total yellow starthistle weight. Shoot weight and leaf area had a similar interference pattern (Table 3.3 and 3.4). In both cases, cheatgrass density was about 1.5 times more important than yellow starthistle density in the prediction of cheatgrass response, and yellow starthistle density was about twice as important as cheatgrass density in predicting yellow starthistle response.

Increasing plant densities were associated with decreasing root weight for both species in the upper portion of the soil profile (Tables 3.2 and 3.3). Cheatgrass density had 5 times the influence of yellow starthistle density on cheatgrass root weight (0-200 mm depth). In contrast, yellow starthistle density was 1.37 times greater than cheatgrass density in influencing yellow starthistle root weight (0-200 mm depth). At soil depths below 200 mm, root weight was not associated with plant density for either species.

The prediction of cheatgrass root length suggests that intraspecific interference was greatest in the upper rooting zone (3.97) (Table 3.5). Decreasing root length (total and upper) was associated with increased

cheatgrass density. Intraspecific interference decreased yellow starthistle root length (Table 3.5). Cheatgrass density decreased yellow starthistle upper root length.

Increasing cheatgrass density was associated with increases in the cheatgrass root length:leaf area and lower:upper root length ratios (Table 3.6). However, increasing yellow starthistle density was associated with a decrease in cheatgrass root:shoot ratios. Mean comparisons ($P \leq .05$) of cheatgrass root length:leaf area ratios showed that cheatgrass densities of 10000 plants m^{-2} were necessary to achieve a significant ratio increase (data not shown).

Yellow starthistle root length:leaf area ratio was influenced by intraspecific and interspecific interference (Table 3.6). Increases in yellow starthistle density decreased the root length:leaf area ratio of yellow starthistle. Whereas, increasing cheatgrass density increased the yellow starthistle root length:leaf area ratio. Lower:upper root length ratios for yellow starthistle were not associated with either yellow starthistle or cheatgrass density.

The increases in root:shoot and lower:upper root ratios described above were associated with detectable increases in soil depth penetration (SDP). The model fit for predicting SDP was poor. The effect of density on SDP by yellow starthistle suggests a trend of decreasing penetration with increasing yellow starthistle density ($SDP_y = 420.9 - 9.71 \log N_y$; $R^2 = .10$). In contrast, SDP by cheatgrass increased with density increases in either species ($SDP_c = 219.53 + 23.51 \log N_c + 16.31 \log N_y$; $R^2 = .20$).

R^2 values ranged from .56 to .71 for each dependent variable involving weight (Tables 3.2 and 3.3). The double ratio [$B_{cc}/B_{cy} : B_{yc}/B_{yy}$] analysis indicate that resource partitioning occurred with respect to total plant, shoot, total root, and upper root weight (Table 3.7). Ratio values ranged from 3.10 to 32,691.

Individual Growth of Isolated Plants

Shoot weight, root weight, leaf area, and total root length were similar for both species (Table 3.8). The t-tests ($P \leq .05$) at each harvest date failed to show differences between species. Each parameter increased as days from planting increased, with the exception of total root length:leaf area ratio which declined. The range of the total root length:leaf area ratios are similar to those observed by Svejcar (1990) for cheatgrass; however, he reported a general increase in the ratio as days from planting increased.

Yellow starthistle had a low or initial root:shoot ratio (.16) than cheatgrass (.55) (Table 3.9). Individual t-tests at other harvest dates failed to reveal significant differences. These results are similar to root:shoot ratios observed by Svejcar (1990) for cheatgrass after 14 days from planting. Yellow starthistle roots grew deeper into the soil than cheatgrass after 22 d, and penetrated twice as deep as cheatgrass by 46 d.

DISCUSSION

Seedling cheatgrass and yellow starthistle populations are primarily influenced by intraspecific rather than interspecific interference. The ecological importance of intraspecific interference is associated with the process of self-thinning and being a strong competitor (Aarssen 1983, Pyke and Archer 1991). Palmbald (1968) studied intraspecific density effects upon several weeds, including cheatgrass. He concluded that cheatgrass used the process of self-thinning along with plasticity to ensure a reliable seed source. The ability of cheatgrass seedlings to suppress perennial grass seedlings has been attributed to rapid growth rate and the development of a root system adapted to declining soil moisture profiles (Evans 1961, Harris 1967, Harris and Wilson 1970, Svejcar 1990, Aquirre and Johnson 1991, Johnson and Aquirre 1991). Similarly, yellow starthistle was found to be a stronger competitor than pubescent wheatgrass (*Thinopyrum intermedium* spp. *barbulatum* (Schur) Bark, W. & D. R. Dewey) (Prather and Callihan 1991). Yellow starthistle possesses seedling growth rates similar to cheatgrass in terms of root and shoot weight, leaf area, and root length.

Our results suggest that cheatgrass and yellow starthistle seedlings reduce interspecific interaction by partitioning resources and that the mechanism for this partitioning is related to rooting depth (Table 3.9). Functional niche differentiation between plant populations and the ability of species coexistence based on rooting depth has a strong theoretical basis (Berendse 1979, Berendse

1981, Berendse 1982). Yellow starthistle roots grew to a greater soil depth than cheatgrass roots, suggesting vertical resource partitioning (e.g. soil moisture) between populations. Furthermore, yellow starthistle populations typically mature after cheatgrass (Sheley et al. 1993, Sheley and Larson 1993). We believe that interspecific interference between cheatgrass and yellow starthistle is limited by vertical and temporal resource partitioning.

Density related plasticity was associated with increased root resource allocation. Yellow starthistle root:shoot ratio increased with increasing densities. Similar trends have been reported for other species (Berendse 1981) and for cheatgrass (Dakheel 1986). Increasing cheatgrass densities were also associated with increased cheatgrass and yellow starthistle root length:leaf area ratios. Resource allocation to lower root portions (below 200 mm depth) increased in cheatgrass as densities increased. This characteristic should serve to stabilize populations and reduce the number of non-reproducing individuals during drought conditions.

Knowledge of resource partitioning can enhance efforts to revegetate degraded rangelands (Pyke and Archer 1991). Selection of plants having contrasting above and below ground allocation patterns, in particular at seedling and juvenile stages, augment resource partitioning, and enhance the probability of successional management. The invasion by yellow starthistle into cheatgrass dominated rangelands also represents resource partitioning. However, in this

case, resource partitioning in conjunction with population plasticity will likely decrease our ability to revegetate rangelands by conventional means.

Figure 3.1 Effects of density on total plant weight of: a) cheatgrass (Brte) and b) yellow starthistle (Ceso). Solid lines are predicted from multiple linear regression equations in Tables 3.2 and 3.3. Log transformed densities of cheatgrass and yellow starthistle indicated on abscissa or in key.

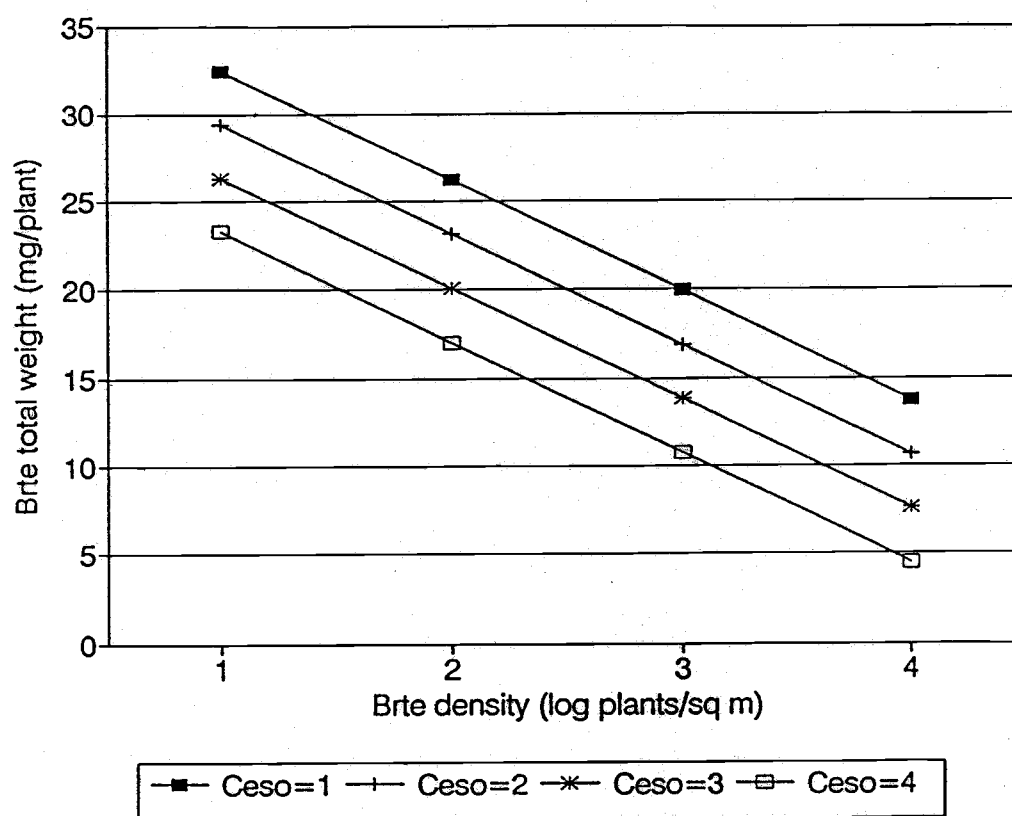


Figure 3.1a

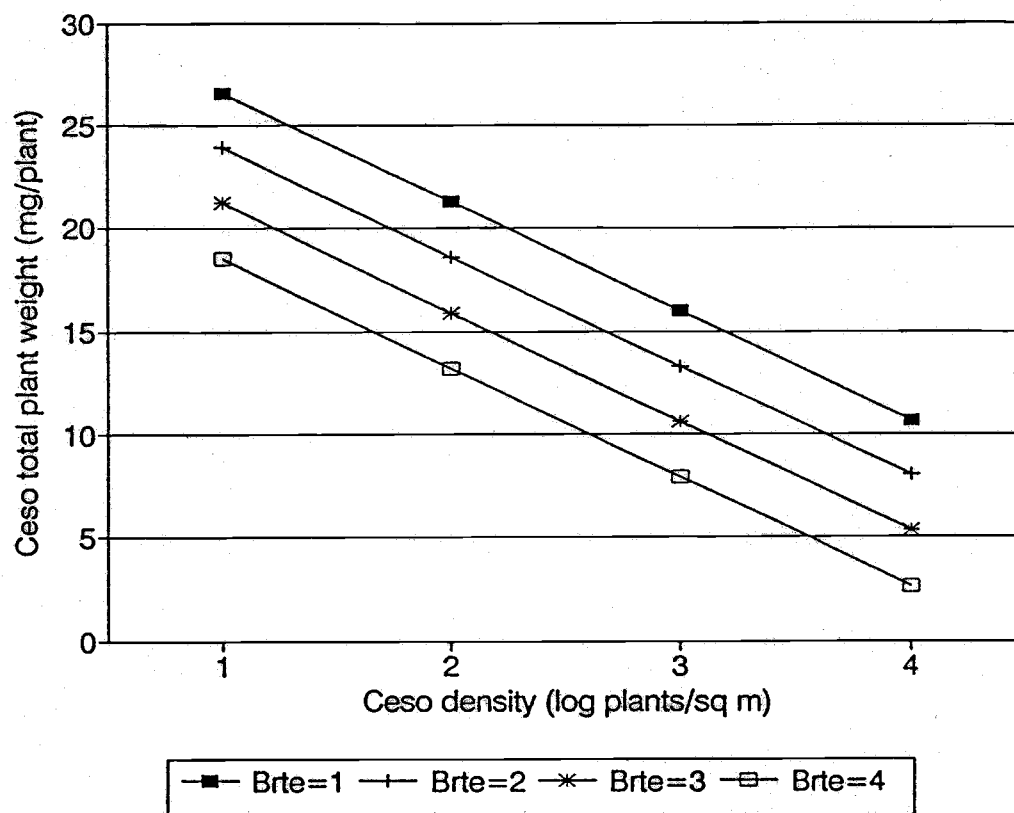


Figure 3.1b

Table 3.1. Surface area of PVC tubes¹ at each harvest.

Days from planting	Tube surface area -----mm ² -----
10	50.6
14	50.6
18	202.7
22	202.7
26	456.0
30	810.7
34	1266.7
38	1824.1
42	1824.1
46	1824.1

¹ Tube length was 800 mm.

Table 3.2. Multiple regression analysis¹ for the prediction of cheatgrass total plant weight (mg), shoot weight, and root weight using plant densities.²

Dependent variable (mg)	B _{co}	B _{cc}	B _{cy}	B _{cc} /B _{cy}	R ²
Total plant weight	41.82 (3.01)	-6.26 (.82)	-3.07 (.60)	2.04	.69
Shoot weight	28.49 (2.60)	-4.07 (.72)	-2.90 (.52)	1.40	.58
Root weight	12.96 (.89)	-2.19 (.28)	0 (NS)	21900	.56
Upper root weight (0-200 mm)	12.73 (.800)	-2.24 (.228)	-.44 (.162)	5.08	.71
Lower root weight (>200 mm)	No significant variables				

$$^1 V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$$

² The intercept B_{co} estimated the weight of an isolated cheatgrass seedling. Intraspecific interference for cheatgrass is measured by the regression coefficient B_{cc} and interspecific interference with yellow starthistle by B_{cy}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 3.3. Multiple regression analysis¹ for the prediction of yellow starthistle total plant weight (mg), shoot weight, and root weight using plant densities.²

Dependent variable (mg)	B_{y_0}	B_{yy}	B_{yc}	B_{yy}/B_{yc}	R^2
Total plant weight	34.56 (2.69)	-5.30 (.75)	-2.69 (.55)	1.97	.62
Shoot weight	25.45 (2.33)	-4.27 (.65)	-2.00 (.47)	2.14	.58
Root weight	9.11 (.67)	-1.03 (.19)	-.69 (1.37)	1.49	.55
Upper root weight (0-200 mm)	7.29 (.60)	-.89 (.17)	-.65 (.12)	1.37	.56
Lower root weight (>200 mm)	No Significant Variables				

$$^1 V_y = B_{y_0} + B_{yy} \log N_y + B_{yc} \log N_c$$

² The intercept B_{y_0} estimated the weight of an isolated yellow starthistle seedling. Intraspecific interference for yellow starthistle is measured by B_{yy} and interspecific interference with cheatgrass by B_{yc} . Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 3.4. Multiple regression analysis¹ for the prediction of cheatgrass and yellow starthistle leaf surface area (cm²) using plant densities.²

Dependent variable (cm ²)	B _{co}	B _{cc}	B _{cy}	B _{cc} /B _{cy}	R ²
Cheatgrass leaf surface area	6.53 (.62)	-.97 (.17)	-.66 (.13)	1.48	.57
Dependent variable (cm ²)	B _{yo}	B _{yy}	B _{yc}	B _{yy} /B _{yc}	R ²
Yellow starthistle leaf surface area	8.69 (.89)	-1.46 (.25)	-.78 (.18)	1.87	.55

¹ Cheatgrass $V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$
 Yellow starthistle $V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$

² The intercept B_{co} and B_{yo} estimate the leaf surface area of an isolated cheat grass and yellow starthistle seedling. Intraspecific interference is measured by B_{cc} and B_{yy} and interspecific interactions by B_{cy} and B_{yc}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 3.5. Multiple regression analysis¹ for the prediction of cheatgrass and yellow starthistle on the total root length (cm), upper root length, and lower root length using plant densities.²

Dependent variable (cm)	B _{co}	B _{cc}	B _{cy}	B _{cc} /B _{cy}	R ²
Cheatgrass					
Total root length	502.24 (44.47)	-47.27 (12.42)	-53.92 (9.00)	.88	.53
Upper root length	507.30 (41.45)	-89.34 (11.53)	-22.52 (8.40)	3.97	.60
Lower root length (> 200 mm)	0 (NS)	8.58 (3.55)	7.80 (2.63)	1.10	.24
Dependent variable (cm)	B _{yo}	B _{yy}	B _{yc}	B _{yy} /B _{yc}	R ²
Yellow starthistle					
Total root length	509.02 (55.92)	-89.67 (18.02)	0 (NS)	8970	.35
Upper root length (0-200 mm)	45.42 (55.29)	-72.02 (15.34)	-28.27 (11.19)	2.54	.39
Lower root length (> 200 mm)	12.45 (21.27)	-17.82 (6.87)	0 (NS)	1780	.13

¹ Cheatgrass $V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$
 Yellow starthistle $V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$

² The intercepts B_{co} and B_{yo} estimated the root length of an isolated individual. Intraspecific interactions for cheatgrass and yellow starthistle are measured by the B_{cc} and B_{yy} regression coefficients, and the interspecific interactions by the B_{cy} and B_{yc} regression coefficients, respectively. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 3.6. Multiple regression analysis¹ for the prediction of cheatgrass and yellow starthistle root:shoot (mg mg^{-1}), root length:leaf surface area (cm cm^{-2}), and lower:upper root length ratios (cm cm^{-2}) using plant densities.²

Dependent variable	B_{co}	B_{cc}	B_{cy}	B_{cc}/B_{cy}	R^2
Cheatgrass					
Root:shoot	0 (NS)	0 (NS)	-.26 (.06)	3.9×10^{-3}	.32
Root length:leaf area	0 (NS)	49.29 (18.93)	0 (NS)	4.9×10^5	.13
Lower:upper	-.47 (.11)	.22 (.03)	.06 (.02)	3.81	.55
Dependent variable	B_{yo}	B_{yy}	B_{yc}	B_{yy}/B_{yc}	R^2
Yellow starthistle					
Root:shoot	0 (NS)	.19 (.04)	0 (NS)	1920	.31
Root length:leaf area	392.4 (207.33) ³	-109.48 (57.50) ³	178.29 (42.00)	-.61	.33
Lower:upper	No Significant Variables				

¹ Cheatgrass $V_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$

Yellow starthistle $V_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$

² The intercepts B_{co} and B_{yo} estimated the root length of an isolated individual. Intraspecific interactions for cheatgrass and yellow starthistle are measured by the B_{cc} and B_{yy} regression coefficients, and the interspecific interactions by the B_{cy} and B_{yc} regression coefficients, respectively. Numbers in parentheses are standard errors for coefficients significantly different from zero.

³ $P = .06$

Table 3.7. Double ratio ($B_{cc}/B_{cy} : B_{yc}/B_{yy}$) assessing the resource partitioning based on cheatgrass and yellow starthistle weight (mg).¹

Dependent variable	$B_{cc}/B_{cy} : B_{yc}/B_{yy}$
Total weight	4.86
Shoot weight	3.10
Root weight	32691.00
Root weight (0-200 mm)	6.98

¹ Ratio other than unity indicate occurrence of resource partitioning.

Table 3.8. Mean shoot weight, root weight, leaf area, total root length, and root length/leaf area ratio for cheatgrass and yellow starthistle grown in isolation.

Days from Planting	Shoot weight/ plant	Root weight/ plant	Leaf area/ plant	Total Root length/ plant	Root length: leaf area ratio
	-----mg-----		---cm ² ---	---cm---	--cm cm ⁻² --
10	1.12	.36	.27	41	164
14	2.43	1.24	.55	131	232
18	3.59	2.62	.87	257	299
22	7.85	3.15	1.61	317	203
26	13.19	5.46	3.23	437	140
30	27.65	12.85	5.77	970	177
34	45.00	22.85	9.11	1233	133
38	107.48	42.00	16.64	1652	113
42	143.38	56.93	22.25	2017	94
46	327.71	137.81	41.34	3858	95
LSD (.05)	53.36	13.22	4.51	363	68

Table 3.9. Root:shoot ratios and soil depth penetration for cheatgrass and yellow starthistle grown in isolation.¹

Days from planting	Root:shoot ratio		Soil depth penetration	
	cheatgrass	yellow starthistle	cheatgrass	yellow starthistle
	-----mg mg ⁻¹ -----		-----mm-----	
10	.55	.16	81	93
14	.65	.51	120	150
18	.85	.69	114	184
22	.38	.57	150	260
26	.38	.50	166	325
30	.52	.52	209	427
34	.54	.42	265	521
38	.47	.32	335	567
42	.50	.34	382	715
46	.43	.63	404	767
	LSD (.05) = 22		LSD (.05) = 88	

¹ Mean comparisons may be made within columns or along rows.

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CHAPTER 4

INTERFERENCE BETWEEN CHEATGRASS AND YELLOW
STARTHISTLE AT THREE SOIL DEPTHS

ABSTRACT

Cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) have invaded over 3 million ha throughout the western U.S. Future management of rangelands dominated by these species will require an understanding of the plant-plant interactions which contribute to the regulation of community dynamics and desirable plant establishment. Addition series experiments, with total stand densities ranging from 20-20000 plants m⁻², were used to quantify the interference between cheatgrass and yellow starthistle in unrestricted soil depths on 12 d intervals throughout the growing season and under soil depths restricted to .2 and .5 m. In unrestricted soil, intraspecific interference was nearly twice as important as interspecific interference, for both species, with respect to the prediction of shoot weight throughout the growing season and seed output. Resource partitioning was evident. In soil restricted to .5 m, resource partitioning associated with variable rooting depth was removed and intra- and inter- specific interference were similar for both species. In soil restricted to .2 m, cheatgrass density was 2 times more important than yellow starthistle in the prediction of yellow starthistle shoot weight, while cheatgrass shoot weight was not associated with yellow starthistle density. Cheatgrass has a

competitive advantage over yellow starthistle in shallow soils. During moist years, yellow starthistle rooting depth may yield a seed production advantage over cheatgrass in deep soil.

INTRODUCTION

Yellow starthistle (*Centaurea solstitialis* L.) is a noxious weed that has been rapidly spreading in the California Annual Grasslands and the steppe regions of the Pacific Northwest (Maddox and Mayfield 1985, Talbott 1987, Sheley et al. 1993). Much of the rangeland under invasion was dominated by cheatgrass (*Bromus tectorum* L.), an undesirable, but forage yielding annual grass (Talbott 1987, Mack 1989, Hironaka 1989, Sheley and Larson 1993c). Both winter annual species arrived from Eurasia before the turn of the century, however the range of cheatgrass expanded so rapidly that this species became dominant in most disturbed grassland steppe communities of the Intermountain West by 1930 (Mack 1981). Yellow starthistle has been invading these annual grasslands since 1920 (Sheley et al. 1993). Currently, yellow starthistle and annual grasses co-dominate over 3 million ha, and infestations of yellow starthistle are estimated to be increasing at a rate of 7800 and 2800 ha per year in Washington and Idaho, respectively (Maddox and Mayfield 1985, Talbott 1987, Prather and Callihan 1991).

Conventional methods of rehabilitating cheatgrass and yellow starthistle infested rangeland have shown limited success (Eckert et al. 1974, Sheley et al. 1983, Roché 1983, Huston et al. 1984, Larson and McInnis 1989, Prather and Callihan 1991) and application due to topographic, economic, and environmental reasons (Buman et al. 1988, Sheley and Larson 1993b). Development of alternative control and rehabilitation methods for rangeland

dominated by these species is limited by the paucity of knowledge describing conditions, processes, and plant relationships affecting cheatgrass and yellow starthistle community dominance and dynamics.

Sheley and Larson (1993a) found that cheatgrass and yellow starthistle seed output was sensitive to population reductions during the transition from juvenile to adult and adult survivorship phase of their life history. Key processes associated with these phases are interference (competition), growth rates and duration, and reproductive allocation (Radosevich and Roush 1990, Sheley and Larson 1993a). In companion studies, we investigated the effects of density, species proportion, and soil depth upon the growth rates and duration of cheatgrass and yellow starthistle (Sheley and Larson 1993b, 1993c), and the interference between seedlings of these species (Sheley and Larson 1993b). The current study was aimed at understanding interference, resource partitioning, and edaphic relationships which affect dominance, community dynamics, and plant establishment in cheatgrass and yellow starthistle dominated ecosystems.

The specific objectives of this study were to: 1) quantify the effects of interference between cheatgrass and yellow starthistle during the growing season and upon seed output, and 2) determine the effect of soil depth upon cheatgrass and yellow starthistle, and the interaction between the two species.

MATERIALS AND METHODS

Field studies were conducted during 1992 in southeastern WA to evaluate the interference between cheatgrass and yellow starthistle at various harvest dates and soil depths. The study site lies on a bluebunch wheatgrass (*Agropyron spicatum*)-Idaho fescue (*Festuca idahoensis*) habitat type (Daubenmire 1970). The soil was a Walla Walla silt loam (course-silty, mixed, mesic Typic Haploxeroll). The elevation of the site is approximately 320 m. Temperatures for the study area range from 45 C to -34 C, with an average frost free season of 170 days. Average annual precipitation is about 380 mm with a bimodal distribution pattern which peaks during the winter and spring. Precipitation during May and June (1992) was below average.

Interference Without Rooting Depth Restriction

Mixtures of cheatgrass and yellow starthistle were grown to assess the interaction between the two species under unlimited rooting depth conditions. Densities of cheatgrass and yellow starthistle were arranged to provide an addition series (Spitters 1983, Radosevich 1987). The cheatgrass:yellow starthistle densities were 10:10, 10:100, 10:1000, 10:10000, 100:10, 1000:10, 10000:10, 100:100, 100:1000, 100:10000, 1000:100, 1000:1000, 1000:10000, 10000:100, 10000:1000, 10000:10000 plants m⁻². Seeds of cheatgrass and yellow starthistle were collected during August and September, 1991 from the study site and sown on February 29 and March 1, 1992 in .5 m² circular plots. Seeds

were randomly broadcast, then manually separated until a uniform distance between seed was achieved, and lightly (< 2 mm) covered with soil. Plots were thinned to the proper densities 1 wk after emergence. In unrestricted soil depths, the lowest density was thinned over time to provide samples for each harvest date. Plots with densities of 10000 plants m^{-2} did not require thinning. Treatments were replicated 4 times in a randomized complete block design (16 densities, 4 blocks). An individual shoot of each species was harvested from each plot on 12 d intervals beginning 24 d after planting. Six individual shoots (1 at lowest density) of each species were harvested at the final harvest, which was 96 and 120 d after planting for cheatgrass and yellow starthistle, respectively. Total seed production per plant was counted. Shoots were dried to a constant weight (48 h, 60 C) and weighed (g).

Interference With Rooting Depth Restriction

In two experiments, monocultures and mixtures of cheatgrass and yellow starthistle were grown to assess the effects of soil depth upon each species and the interaction between the two species. Monoculture densities were 10, 100, 1000, and 10000 plants m^{-2} for each species. Densities of cheatgrass and yellow starthistle mixtures 100:100, 100:1000, 100:10,000, 1000:100, 1000:1000, 1000:10000, 10000:100, 10000:1000, 10000:10000 plants m^{-2} were arranged to provide an addition series (Spitters 1983, Radosevich 1987). Monocultures and mixtures were established with the rooting depth restricted to .2 m and .5 m by

placing an 8 mil impermeable plastic liner below the soil surface. All monoculture densities and addition series were replicated 4 times in a split-plot design with soil depth as whole plots and plant density as subplots (Monocultures: 2 species, 2 depths, 4 densities, 4 blocks; Mixtures: 2 depths, 9 densities, 4 blocks). Seeds were collected, broadcast, and plants were thinned as described above. Six individual shoots (4 at lowest density) of each species from each subplot were harvested 72 days after planting. Shoots were dried to a constant weight (48 h, 60 C) and weighed (g).

Analysis

Addition series data were incorporated into multiple linear models using SPSSPC+ least squares stepwise regression procedures (SPSS., Chicago, Illinois.) of the form:

$$\text{In monocultures: } W_c = B_{co} + B_{cc} \log N_c + B_{cd} D$$

$$W_y = B_{yo} + B_{yy} \log N_y + B_{yd} D, \text{ and}$$

$$\text{In mixtures: } W_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y + B_{cd} D$$

$$W_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c + B_{yd} D$$

where W_c and W_y were the average per plant shoot weight or average number of seeds per plant for cheatgrass and yellow starthistle, respectively, N_c and N_y were their density, and D was the soil depth. Scatterplots of the residual vs. the standardized predicted values were used to determine the homogeneity of

variances and degree of model fit. T-tests ($P \leq .05$) were used to determine significance of the regression coefficients.

B_{cc} and B_{yy} estimate the maximum shoot weight or seed output of an isolated individual. The regression coefficients B_{cc} and B_{yy} estimate the intraspecific interaction, B_{cy} and B_{yc} estimate the interspecific interaction, and B_d estimate the importance of soil depth on the prediction of shoot weight. The model of interference without soil depth restriction did not include the B_d regression coefficient. The ratio of $B_{cc}:B_{cy}$ and $B_{yy}:B_{yc}$ were used to determine the relative abilities of the species on determining shoot weight. For example, a $B_{cc}:B_{cy}$ ratio of 2 indicated that cheatgrass has twice the impact upon itself in determining weight or seed output than yellow starthistle. A depth importance ratio was calculated by dividing the Beta coefficients corresponding to intra- and inter-specific interference by B_d for each equation.

The $[B_{cc}/B_{cy}:B_{yc}/B_{yy}]$ double ratio was used to assess the partitioning of resources between the two species (Spitters 1983, Connolly 1986, Joliffe 1988). The further the double ratio deviated from unity, the greater the degree of resource partitioning. The coefficient of determination (R^2) values were calculated to indicate the proportion of variability associated with W_c and W_y , which could be accounted for by N_c , N_y , and D .

RESULTS

Interference without rooting depth restriction

Intraspecific interference was about 2 times more important than interspecific interference for the prediction of shoot weight at all harvest dates when grown without rooting depth restriction (Figure 3; Table 4.1 and 4.2). An inverse association ($R^2 = .29$) between plant density and cheatgrass shoot weight was detected 48 d after planting (Table 4.1). The $B_{cc}:B_{cy}$ ratio ranged from 1.55 to 2.50 after 48 d of the experiment, indicating that the intraspecific effects were dominant throughout the growing season. Cheatgrass growth ceased 96 d after planting with the predicted maximum weight of a isolated cheatgrass individual being 1.83 g. At this time, a 10-fold increase in cheatgrass and yellow starthistle density resulted in a .323 g and .192 g reduction in predicted cheatgrass shoot weight, respectively.

An inverse association ($R^2 = .22$) between yellow starthistle shoot weight and plant density was detected 36 d after planting (Figure 3; Table 4.2). After 36 d from planting, the $B_{yy}:B_{yc}$ ratio ranged from 1.50 to 2.77, thus indicating that the intraspecific effects of yellow starthistle were dominant during the growing period. Yellow starthistle growth ceased after 120 d with the predicted maximum size of an isolated individual being 17.18 g. At 120 d, a 10-fold increase in yellow starthistle and cheatgrass density resulted in a 3.57 and 1.46 g reduction in the predicted yellow starthistle shoot weight, respectively. The $B_{yy}:B_{yc}$ ratio at the 108 and 120 d after planting was 2.77 and 2.44 respectively,

reflecting the fact that yellow starthistle intraspecific interference remained high after cheatgrass growth ceased.

Intraspecific interference had greatest importance on seed output (Figure 4; Table 4.3). The maximum predicted seed output of an isolated cheatgrass and yellow starthistle individual was approximately 22 and 1446, respectively. The regression model predicts a reduction of 4.0 and 2.3 cheatgrass seeds per individual with 10-fold increases in cheatgrass and yellow starthistle density, respectively. The same increase in cheatgrass and yellow starthistle density resulted in a reduction of about 99 and 311 yellow starthistle seeds per individual, respectively.

The $[B_{cc}/B_{cy}:B_{yc}/B_{yy}]$ double ratio was 5.39 based on seed output and ranged from 2.94 to 4.78 with respect to shoot weight (Table 4.4). These results indicate that resource partitioning between cheatgrass and yellow starthistle occurs throughout the growing season. The coefficient of determination (R^2) was .56 and .43 for cheatgrass and yellow starthistle, respectively at their final harvest dates (Table 4.2 and 4.3).

Interference With Rooting Depth Restriction

Monocultures

Regression analysis for both species indicate that soil depth was nearly 5 times more important than intraspecific interference in the prediction of shoot weight (72 d after planting) (Table 4.5). Density increases reduced predicted

shoot weight, while additional soil depth increased shoot weight. About 70% of the variation in yellow starthistle shoot weight was accounted for by soil depth and density variables.

Mixtures

The overall regression models ($W_c = .570 - .122 \log N_c - .095 \log N_y + .612D$, $R^2 = .44$; $W_y = .456 - .091 \log N_y - .102 \log N_c + .778D$, $R^2 = .38$) indicate that cheatgrass density was more important than yellow starthistle density in the prediction of shoot weight, when grown under restricted soil depth conditions (Table 4.6 and 4.7). Soil depth had 5 and 7 times the effect of density on the prediction of cheatgrass and yellow starthistle shoot weight, respectively.

An analysis of variance (shoot weight) indicated a significant three-way interaction (depth X cheatgrass density X yellow starthistle density) for both species at 72 d after planting (analysis not shown). At .5 m soil depth, intraspecific interference was slightly more important than interspecific interference with respect to the prediction of cheatgrass shoot weight (Figure 5; Table 4.6 and 4.7). Intraspecific and interspecific interference were equally important in the prediction of yellow starthistle shoot weight at this soil depth.

At .2 m soil depth, the maximum predicted shoot weight of isolated cheatgrass and yellow starthistle individuals were .110 g and .148 g, respectively (Figure 6; Table 4.6 and 4.7). A 10-fold increase in cheatgrass density reduced the predicted cheatgrass and yellow starthistle shoot weight by .023 g and .025 g, respectively. The same increase yellow starthistle density reduced the predicted starthistle shoot weight by .013 g. In contrast, cheatgrass shoot weight was not associated with yellow starthistle density grown under the most restricted soil depth.

At all density combinations, the importance of soil depth on the prediction of either species shoot weight was greater than that of plant density (Table 4.6 and 4.7). In general, as the density of cheatgrass increased, the relative importance of soil depth increased. Cheatgrass importance ratio ranged from 5.3 to 20.4.

When yellow starthistle was held constant at 100 plants m^{-2} , the importance of soil depth was about 6.6 times greater than the effects of interference in predicting shoot weight for both species (Table 4.6 and 4.7). The importance of soil depth decreased to about 5.5 times the effects of interference in predicting shoot weight of both species when yellow starthistle was held at a constant 1000 plants m^{-2} . At either a constant cheatgrass or yellow starthistle density of 10000 plants m^{-2} , soil depth was the only significant parameter associated with either cheatgrass or yellow starthistle shoot weight.

DISCUSSION

Yellow starthistle and cheatgrass populations are influenced by intraspecific rather than interspecific interference when edaphic conditions provide unrestricted rooting depth. These results are consistent with those found by Sheley and Larson (1993b) for cheatgrass and yellow starthistle seedlings.

The potential for intraspecific interference to influence community composition is important. Regression models of seed output (Table 4.3) indicate that a community dominated by 10000 yellow starthistle and 100 cheatgrass individuals m^{-2} result in a seed output of about 5 seeds per individual of cheatgrass, and a yellow starthistle seed output that would approach zero. If the densities were reversed, yellow starthistle predicted seed output would be 424 per individual, and cheatgrass predicted seed output would approach zero. These results indicate that shifts in community dominance can result from intraspecific interference in dense stands of either cheatgrass or yellow starthistle.

The relationship between cheatgrass and yellow starthistle is dynamic depending upon the soil depth. On deep soils intraspecific interference was 2 times greater than interspecific interference for both species. On soils restricted to .5 m, the intensity of intraspecific and interspecific interference were nearly equal for both species. On shallow soils, restricted to .2 m, cheatgrass interference was 2 times greater than intraspecific interference in determining

yellow starthistle shoot weight. However, interference from yellow starthistle did not effect cheatgrass shoot weight. These results support the hypothesis that differential rooting depth is the mechanism for vertical and temporal resource partitioning between cheatgrass and yellow starthistle. Cheatgrass has an advantage over yellow starthistle on shallow soils, due to it's relatively shallow and fibrous rooting system. Conversely, yellow starthistle has an advantage over cheatgrass in deep soils where taproot development enables continued resource uptake (e.g. soil moisture) and increased seed output during seasons with adequate moisture availability (Sheley et al. 1993, Sheley and Larson 1993a, Sheley and Larson 1993b, Sheley and Larson 1993c).

Figure 4.1 Effects of density on shoot weight of: a) cheatgrass (Brte) and b) yellow starthistle (Ceso) grown in unrestricted soil depth for 96 and 120 d, respectively. Solid lines are predicted from multiple linear regression equations in Tables 4.1 and 4.2. Log transformed densities of cheatgrass and yellow starthistle indicated on abscissa or in key.

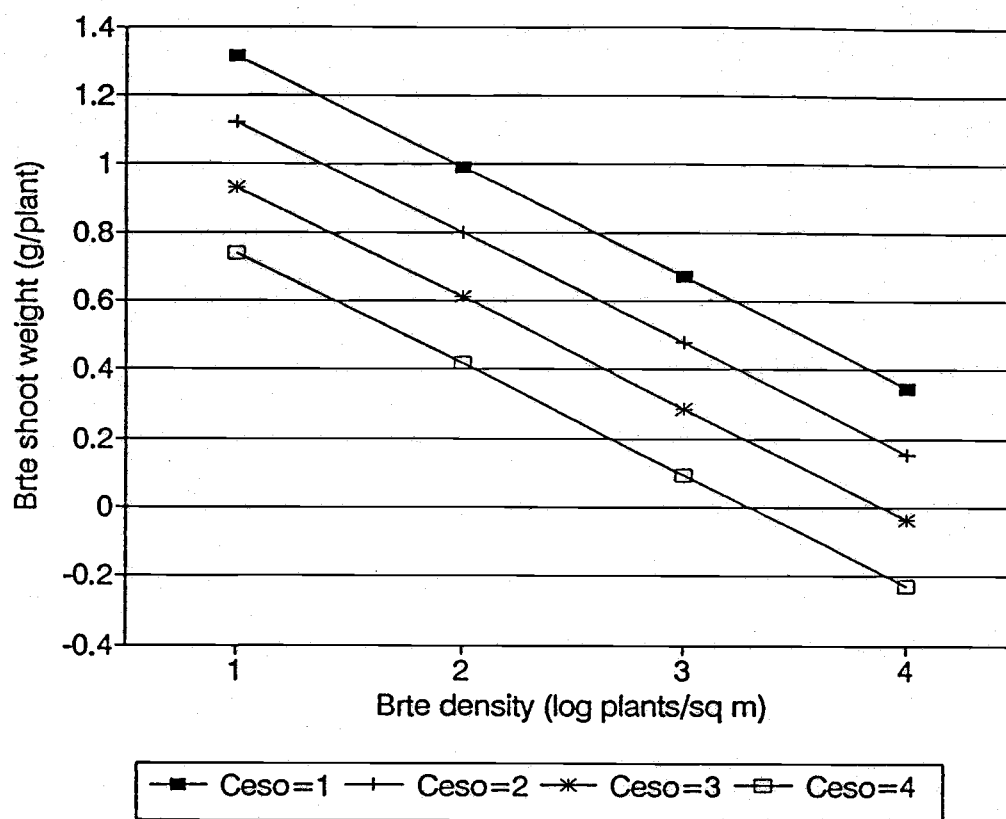


Figure 4.1a

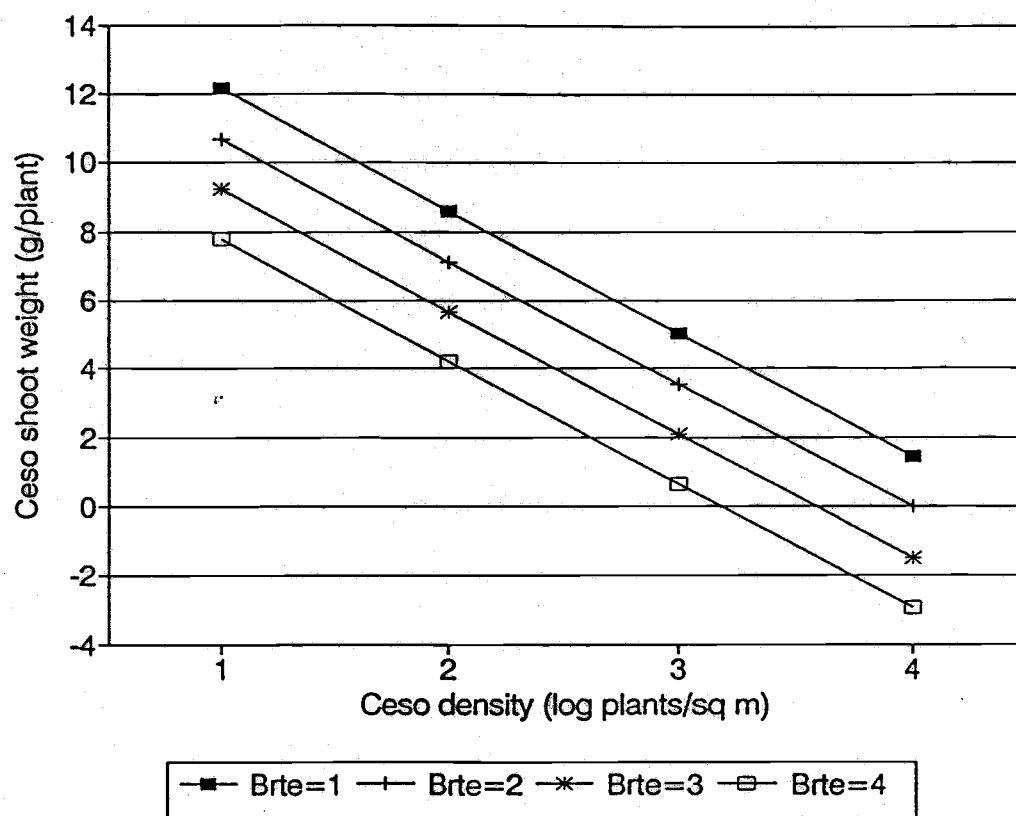


Figure 4.1b

Figure 4.2 Effects of density on seed production of: a) cheatgrass (Brte) and b) yellow starthistle (Ceso) grown in unrestricted soil depth for 96 and 120 d, respectively. Solid lines are predicted from multiple linear regression equations in Table 4.3. Log transformed densities of cheatgrass and yellow starthistle indicated on abscissa or in key.

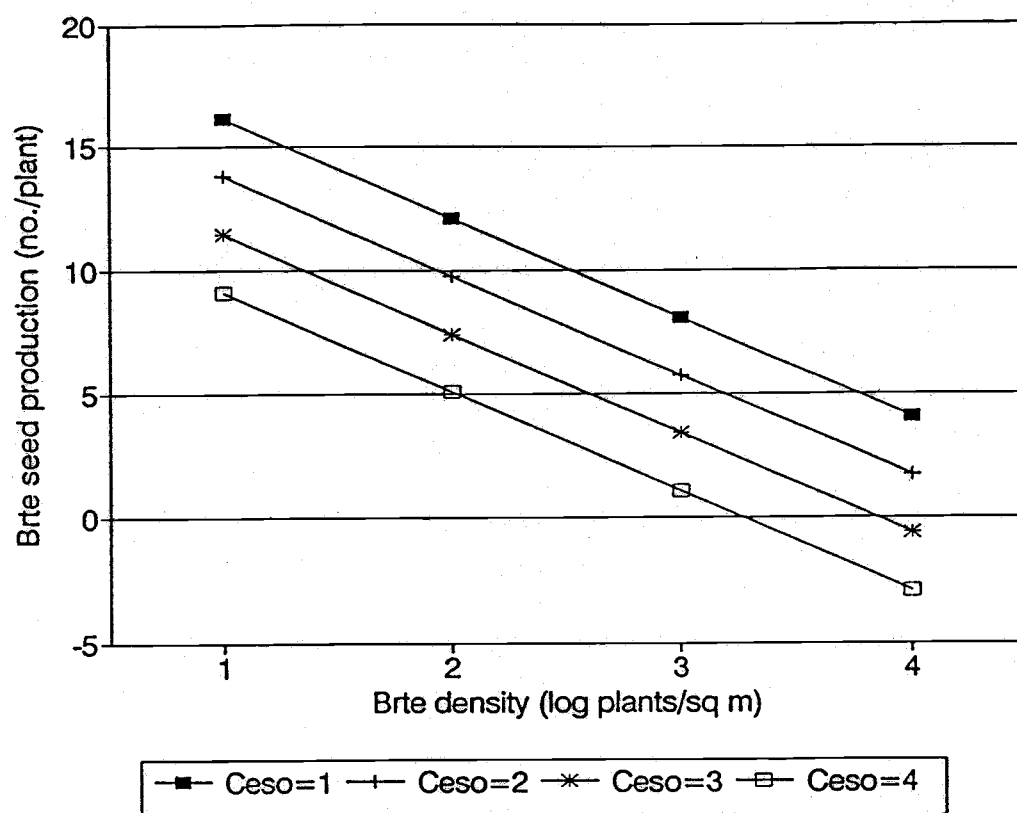


Figure 4.2a

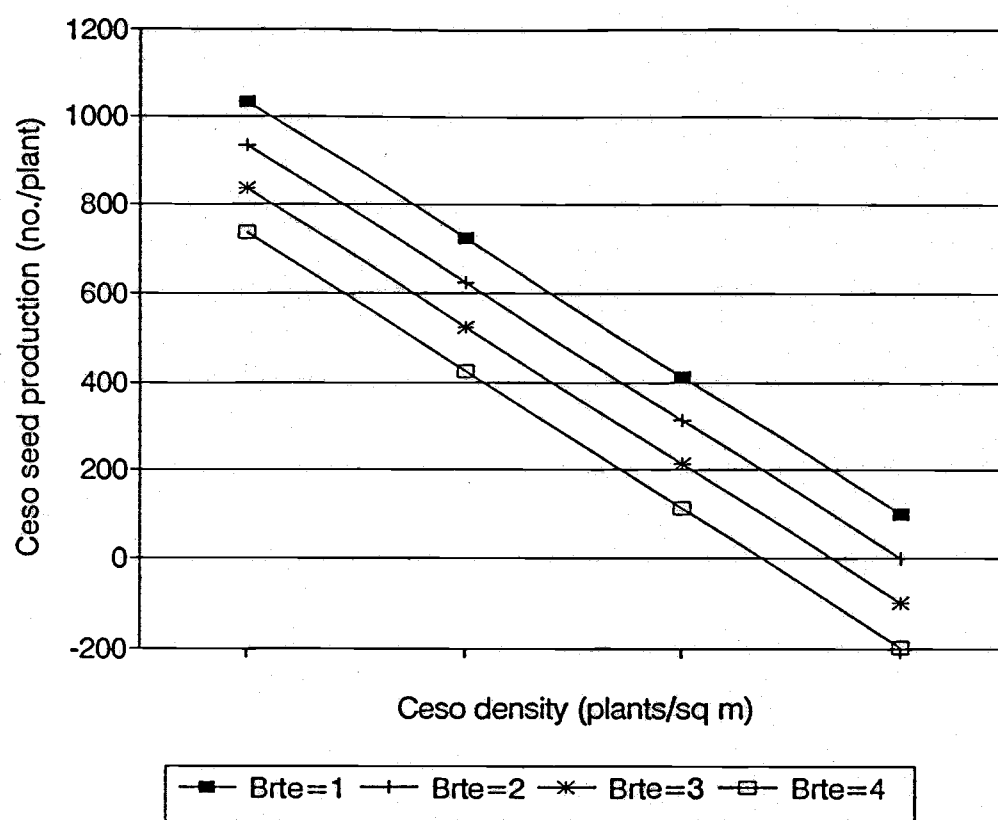


Figure 4.2b

Figure 4.3 Effects of density on shoot weight of: a) cheatgrass (Brte) and b) yellow starthistle (Ceso) grown in soil depths restricted to .5 m for 72 d. Solid lines are predicted from multiple linear regression equations in Tables 4.6 and 4.7. Log transformed densities of cheatgrass and yellow starthistle indicated on abscissa or in key.

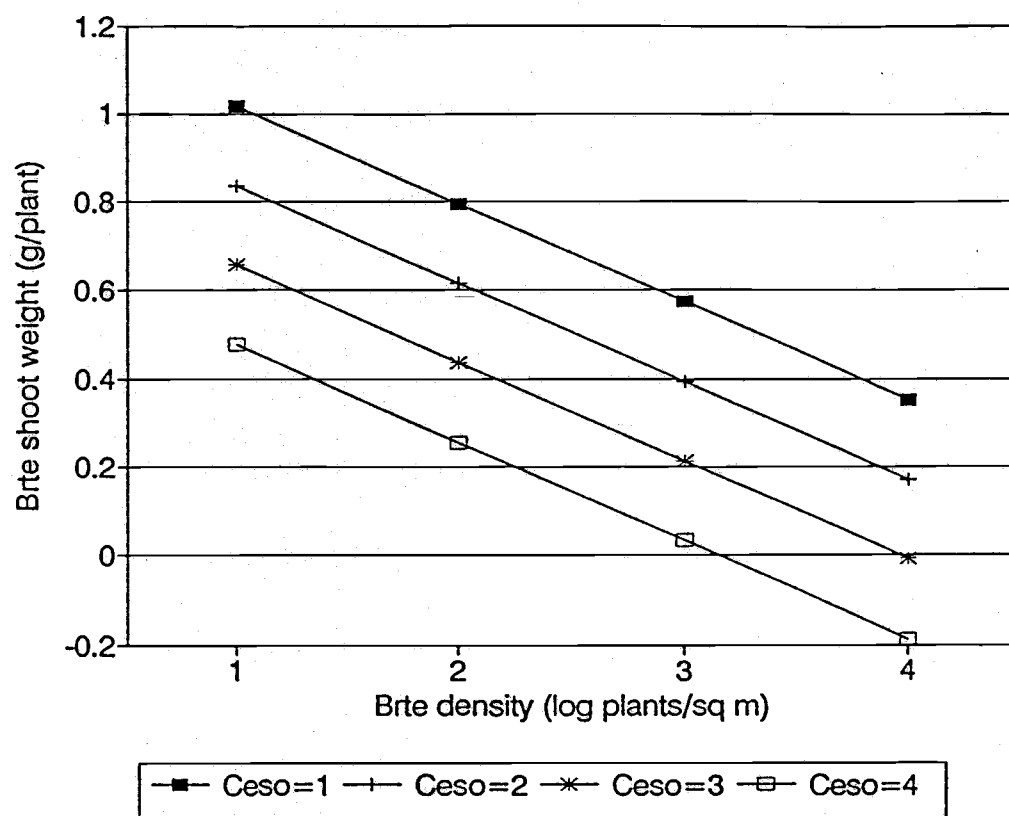


Figure 4.3a

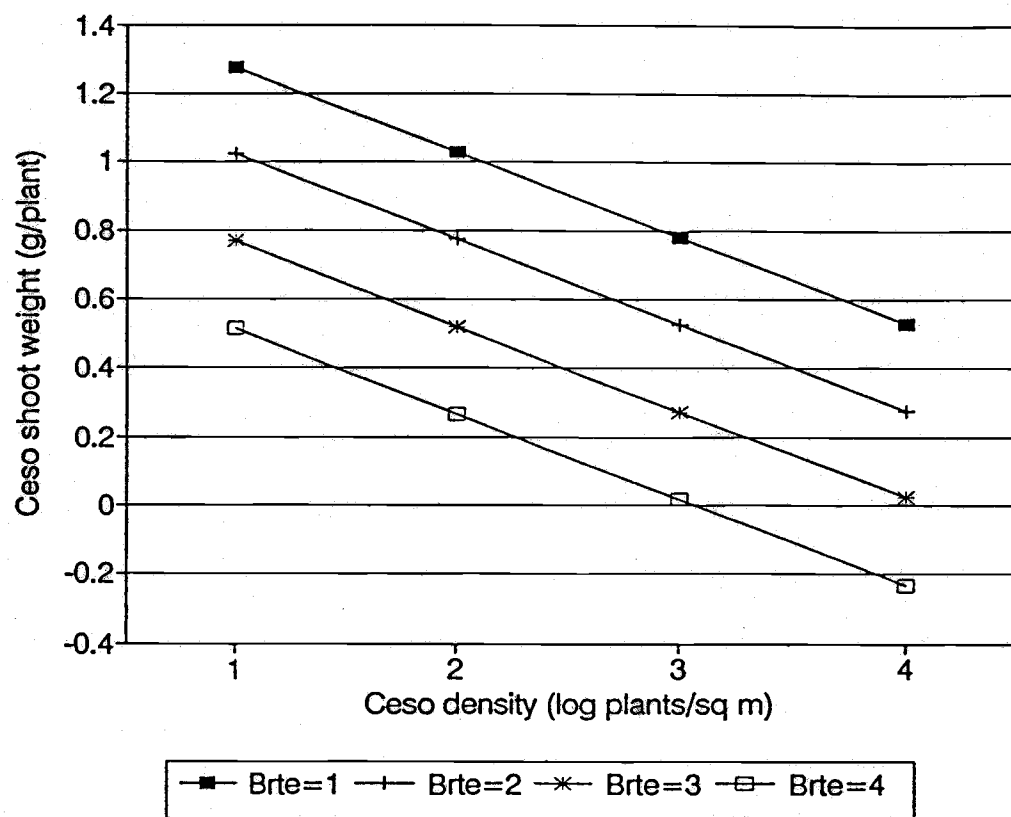


Figure 4.3b

Figure 4.4 Effects of density on shoot weight of: a) cheatgrass (Brte) and b) yellow starthistle (Ceso) grown in soil depths restricted to .2 m for 72 d. Solid lines are predicted from multiple linear regression equation in Tables 4.6 and 4.7. Log transformed densities of cheatgrass and yellow starthistle indicated on abscissa or in key.

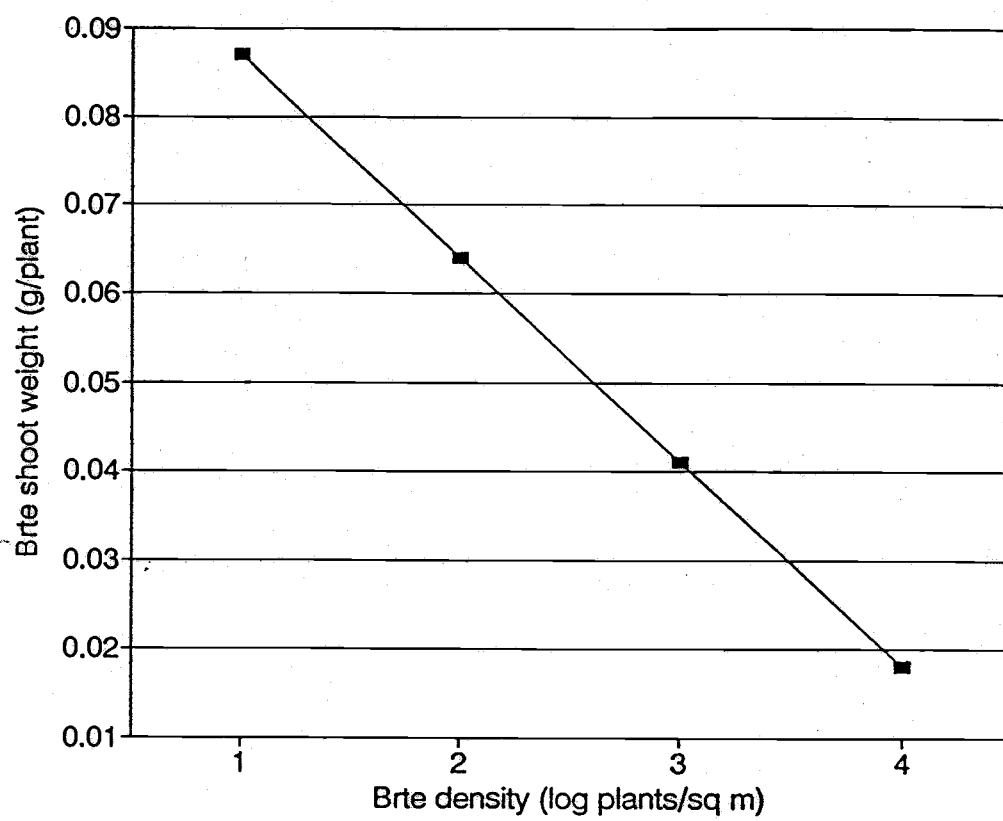


Figure 4.4a

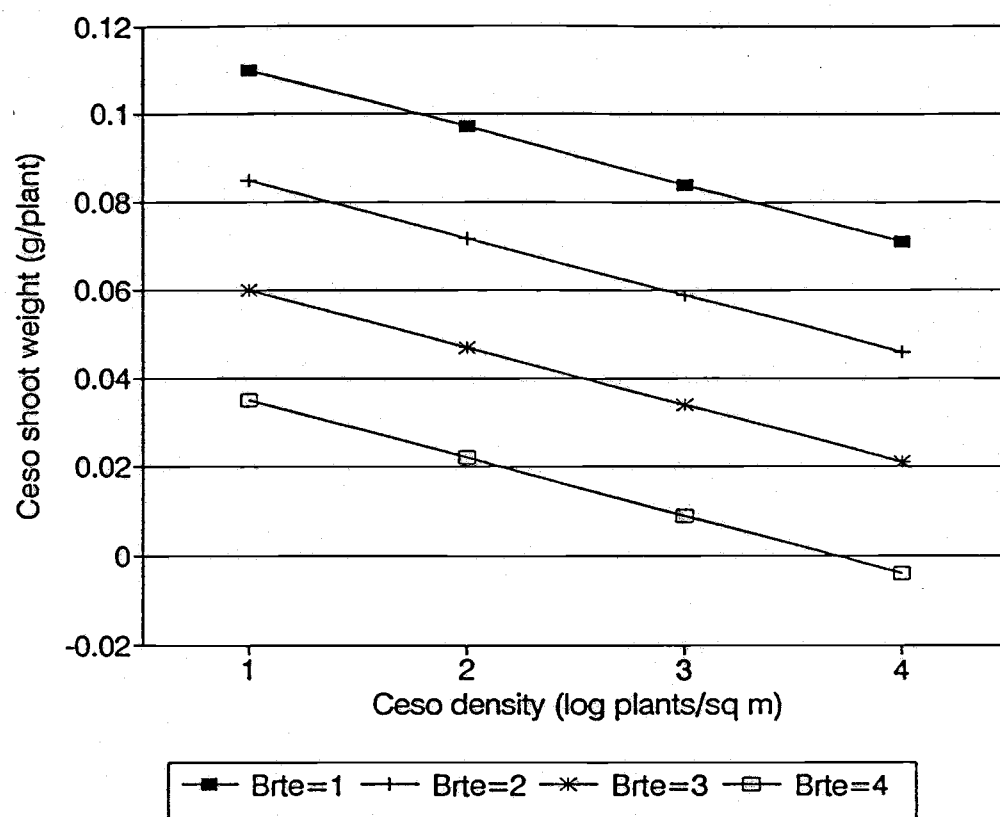


Figure 4.4b

Table 4.1. Multiple regression analysis¹ for the prediction of cheatgrass shoot weight (g) using plant densities without soil depth restriction.²

Days After Planting	B_{co}	B_{cc}	B_{cy}	B_{cc}/B_{cy}	R^2
24	No	Significant	Variables		
36	No	Significant	Variables		
48	.308 (.054)	-.053 (.015)	-.027 (.011)	1.96	.29
60	.688 (.075)	-.136 (.021)	-.054 (.015)	2.50	.55
72	.900 (.086)	-.153 (.024)	-.099 (.017)	1.55	.62
84	1.60 (.179)	-.309 (.050)	-.143 (.036)	2.16	.55
96	1.83 (.198)	-.323 (.055)	-.192 (.040)	1.68	.56

$$^1 W_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$$

² The intercept B_{co} estimated the shoot weight of an isolated cheatgrass plant. Intraspecific interference for cheatgrass is measured by the regression coefficient B_{cc} and interspecific interference by B_{cy} . Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 4.2. Multiple regression analysis¹ for the prediction of yellow starthistle shoot weight (g) using plant densities without soil depth restriction.²

Days After Planting	B_{y_0}	B_{yy}	B_{yc}	B_{yy}/B_{yc}	R^2
24	No Significant Variables				
36	.025 (.004)	-.003 (.001)	-.002 (.001)	1.50	.22
48	.372 (.096)	-.087 (.031)	0 (NS)	-----	.15
60	.611 (.085)	-.103 (.023)	-.063 (.017)	1.63	.42
72	1.91 (.328)	-.378 (.091)	-.174 (.066)	2.18	.35
84	4.64 (.671)	-.943 (.186)	-.426 (.136)	2.21	.44
96	5.53 (.736)	-1.05 (.204)	-.558 (.149)	1.88	.47
108	7.35 (1.45)	-1.56 (.403)	-.563 (.294) ³	2.77	.29
120	17.18 (2.52)	-3.57 (.698)	-1.46 (.509)	2.44	.43

$$^1 W_y = B_{y_0} + B_{yy} \log N_y + B_{yc} \log N_c$$

² The intercept B_{y_0} estimated the shoot weight of an isolated yellow starthistle plant. Intraspecific interference for yellow starthistle is measured by the regression coefficient B_{yy} and interspecific interference by B_{yc} . Numbers in parentheses are standard errors for coefficients significantly different from zero.

$$^3 P = .061$$

Table 4.3. Multiple regression analysis¹ for the prediction cheatgrass (SP_c) and yellow starthistle (SP_y) seed production using plant densities, without soil depth restriction.²

Dependent Variable	B_{co}	B_{cc}	B_{cy}	B_{cc}/B_{cy}	R^2
SP_c	22.50 (3.78)	-4.02 (1.05)	-2.34 (.77)	1.72	.35

Dependent Variable	B_{yo}	B_{yy}	B_{yc}	B_{yy}/B_{yc}	R^2
SP_y	1445.67 (215.72)	-311.63 (59.83)	-99.45 (43.69)	3.13	.42

$$^1 SP_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y$$

$$SP_y = B_{yo} + B_{yy} \log N_y + B_{yc} \log N_c$$

² The intercept B_{co} and B_{yo} estimated the shoot weight of an isolated plant. Intraspecific interference is measured by the regression coefficient B_{cc} and B_{yy} interspecific interference by B_{cy} and B_{yc} . Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 4.4. Double ratio [$B_{cc}/B_{cy} : B_{yc}/B_{yy}$] assessing the resource partitioning¹ between cheatgrass and yellow starthistle based on weight and seed production when grown without soil depth restriction.

Days after planting	Resource Partitioning Ratio
24 (weight)	-----
36 (weight)	-----
48 (weight)	2.94
60 (weight)	4.09
72 (weight)	3.37
84 (weight)	4.78
96 (weight)	3.16
108 (weight)	----- ²
120 (weight)	----- ²
120 (Seed Production)	5.39

¹ Resource partitioning were only calculated when B coefficients were significant. Ratios other than unity indicate the occurrence of resource partitioning.

² Growth of yellow starthistle after cheatgrass matured.

Table 4.5. Multiple regression analysis¹ for the prediction cheatgrass (c) and yellow starthistle (y) shoot weight using monocultural plant densities and soil depth restriction.²

Cheatgrass	B_{co}	B_{cc}	B_{cd}	Importance ratio	R^2
$W_c =$.586 (3.78)	-.270 (1.05)	1.39 (.77)	1.72	.35

Yellow starthistle	B_{yo}	B_{yy}	B_{yd}	Importance ratio	R^2
$W_y =$.855 (3.78)	-.388 (1.05)	1.97 (.77)	5.1	.72

$$^1 W_c = B_{co} + B_{cc} \log N_c + B_{cd} D$$

$$W_y = B_{yo} + B_{yy} \log N_y + B_{yd} D$$

² The intercepts B_{co} and B_{yo} estimate the shoot weight of an isolated individual. Intraspecific interference for cheatgrass and yellow starthistle are measured by the B_{cc} and B_{yy} coefficients. The impact of soil depth is expressed by the B_{cd} and B_{yd} coefficients. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 4.6. Multiple regression analysis¹ for the prediction cheatgrass shoot weight (g) using cheatgrass and yellow starthistle densities and soil depth restriction.²

Independent variable held constant	B _{co}	B _{cc}	B _{cy}	depth	Importance ratio	R ²
Depth (.2m)	.110 (.016)	-.023 (.005)	NS	—	----	.38
Depth (.5m)	1.42 (.182)	-.222 (.042)	-.180	—	1.23	.58
Brte 100 plants m ⁻²	.317 (.151)	—	-.175 (.042)	1.35 (.245)	7.7	.59
Brte 1000 plants m ⁻²	.024 (.020)	—	-.023 (.006)	.469 (.033)	20.4	.87
Brte 10000 plants m ⁻²	.012 (.003)	—	NS	.021 (.008)	----	.16
Ceso 100 plants m ⁻²	.363 (.156)	-.188 (.044)	—	1.26 (.253)	6.7	.57
Ceso 1000 plants m ⁻²	.202 (.054)	-.084 (.015)	—	.448 (.080)	5.3	.75
Ceso 10000 plants m ⁻²	.008 (.002)	NS	—	.125 (.054)	----	.20

$$^1 W_c = B_{co} + B_{cc} \log N_c + B_{cy} \log N_y + B_{cd} D$$

² The intercept B_{co} estimates the weight of an isolated individual. Intraspecific interference by cheatgrass was measured by B_{cc} and interspecific interference by yellow starthistle by B_{cy}. The impact of soil depth restriction was estimated by B_{cd}. Numbers in parentheses are standard errors for coefficients significantly different from zero.

Table 4.7. Multiple regression analysis¹ for the prediction of yellow starthistle shoot weight using plant densities and soil depth restriction.²

Independent variable held constant	B_{y_0}	B_{yy}	B_{yc}	depth	Importance ratio	R^2
Depth (.2m)	.148 (.022)	-.013 (.005)	-.025 (.005)	—	.52	.48
Depth (.5m)	1.78 (.248)	-.249 (.057)	-.254 (.057)	—	.98	.54
Ceso 100 plants m^{-2}	.463 (NS)	—	-.286 (.078)	1.89 (.461)	6.6	.56
Ceso 1000 plants m^{-2}	.204 (.075)	—	-.089 (.020)	.521 (.112)	5.85	.66
Ceso 10000 plants m^{-2}	.039 (.017)	—	-.016 (.005)	.117 (.026)	7.3	.60
Brte 100 plants m^{-2}	.650 (.308)	-.302 (.084)	—	1.59 (.460)	5.3	.54
Brte 1000 plants m^{-2}	.153 (.069)	-.087 (.019)	—	.669 (.103)	7.7	.75
Brte 10000 plants m^{-2}	NS	NS	—	.070 (.012)	-----	.62

$$^1 W_y = B_{y_0} + B_{yy} \log N_y + B_{yc} \log N_c + B_{yd} D$$

² The intercept B_{y_0} estimates the weight of an isolated individual. Intraspecific interference by yellow starthistle was measured by B_{yy} and interspecific interference by cheatgrass by B_{yc} . The impact of soil depth restriction was estimated by B_{yd} . Numbers in parentheses are standard errors for coefficients significantly different from zero.

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CHAPTER 5

**EFFECTS OF DENSITY, SPECIES PROPORTION, AND SOIL DEPTH
ON THE GROWTH OF CHEATGRASS AND YELLOW STARThISTLE**

ABSTRACT

Community dynamics and dominance on cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) infested rangeland were influenced by resource acquisition rates and duration which changes with changing environments. We studied the growth rates and duration of these species at various densities, proportions, and soil depths during the 1992 growing season. In 6 experiments isolated individuals, monocultures (100, 1000, 10000 plants m⁻²), and mixtures (same densities arranged factorially) were grown with unrestricted and restricted (.2 and .5 m) soil depths near Walla Walla, WA. Shoot weights were determined on 12 d intervals beginning d 24 and ending d 72 for plants grown with restricted soil depth and d 96 and 108 for cheatgrass and yellow starthistle, respectively, grown in unrestricted soil. Quadratic growth curves were fit for each treatment in each experiment. ANOVA was performed on time of inflection, point of inflection, relative growth rates at d 36, 60 and 84 and absolute growth rates at 3 growth periods (early, middle, late). Yellow starthistle growth parameters were greater than those of cheatgrass when grown in isolation without rooting depth restriction. The addition of soil depth restriction masked species differences and deeper soil allowed greater growth

and later maturation for both species. The effect of depth restriction was dependent upon the density. The time of inflection was later for yellow starthistle than cheatgrass at low densities in unrestricted soil. Under restricted soil depth time of inflection was earlier and similar for both species. Our data suggests that yellow starthistle has greater growth rates and later maturation than cheatgrass. However, density, soil depth, and soil moisture interact to dictate dominance and community dynamics in cheatgrass and yellow starthistle dominated rangeland.

INTRODUCTION

Cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) co-dominate millions of ha in the western United States. These winter annuals species arrived into N. America near the turn of the century from the steppes of Eurasia. Cheatgrass, an early maturing spring forage, dominated most disturbed steppe communities in the Intermountain West by 1930 (Mack 1981). Since 1920, yellow starthistle, a noxious weed, has rapidly joined cheatgrass (Maddox and Mayfield 1985, Sheley et al. 1993). In many areas these species have replaced perennial grass communities and resource values have been reduced (Roche 1983, Callihan et al. 1989). Moreover, the invasion of cheatgrass rangeland by yellow starthistle may increase niche occupancy and reduce revegetation and grazing potential (Callihan et al. 1982, Sheley and Larson 1993b). From an ecological and forage standpoint, it is important to understand the mechanisms governing dominance, community dynamics, and desirable plant establishment and persistence on alien annual dominated rangelands (Sheley and Larson 1993a, 1993b).

Community dynamics and dominance in winter annual dominated ecosystems have been explained based upon differences in resource acquisition rates and duration (Hironaka 1990, Sheley et al. 1993). Hironaka (1990) suggested that among winter annuals, early maturing species would be replaced by later maturing ones. Yellow starthistle germination, radicle elongation, and seedling root growth was faster than medusahead (*Taeniatherum caput-medusae*

L.) and hedgehog dogtail (*Cynosurus echinatus* L.), and allows preemptive resource use and deeper soil penetration (Sheley et al. 1993). Deeper soil depth penetration should extend the period of growth and increase seed production (success) in annual dominated foothills of southwestern Oregon (Sheley et al. 1993).

Competitive dominance in cheatgrass and yellow starthistle communities appear oscillatory and based primarily upon the ability for continued growth and increased seed production by yellow starthistle over that of cheatgrass (Sheley and Larson 1993a). Although seedling growth rates were similar, greater geotrophic root growth by yellow starthistle may provide the mechanism for continued resource acquisition over that of cheatgrass (Sheley and Larson 1993a, Sheley and Larson 1993b), similar to that proposed by Sheley et al. (1993). In support of this conclusion, Sheley and Larson (1993c) found edapic conditions which limit soil depth penetration by yellow starthistle roots alters the competitive advantage in favor of cheatgrass.

Community dynamics and dominance of cheatgrass and yellow starthistle infested rangeland appear influenced by resource acquisition rates and duration, which change with changing conditions. The objective of this study was to compare the relative and absolute growth rates, as well as the point and time of inflection of cheatgrass and yellow starthistle growth, throughout the growing season at various densities, species proportions, and soil depths.

MATERIALS AND METHODS

Field studies were conducted during 1992 near Walla Walla, WA to compare the growth of cheatgrass and yellow starthistle at various densities, species proportions, and soil depths. The study site lies on a bluebunch wheatgrass (*Agropyron spicatum*)-Idaho fescue (*Festuca idahoensis*) habitat type (Daubenmire 1970). Vegetation of the study area was dominated by cheatgrass and yellow starthistle. The soil was a Walla Walla silt loam (course-silty, mixed, mesic Typic Hapoxeroll). Soils have developed from thick loess redeposited with glacial outwash material over basalt. The elevation is about 320 m. Average annual precipitation is about 380 mm with a bimodal distribution pattern which peaks during the winter and spring. Temperatures range from 45 C to -34 C. The average frost free season is 170 d.

Growth without rooting depth restriction

Isolated individuals, monocultures, and mixtures of cheatgrass and yellow starthistle were grown to assess their growth under unlimited rooting depth conditions. Isolated ($.25 \text{ m}^2 \text{ plant}^{-1}$) individuals of cheatgrass and yellow starthistle were grown for each of 8 harvest dates (2 species, 4 replications). Monocultural plant densities were 100, 1000, and 10000 plants m^{-2} for each species (2 species, 3 densities, 4 replications). In mixtures these densities were factorially arranged (9 densities combinations, 4 replications). Each experiment was replicated 4 times in a randomized complete block design.

Growth with rooting depth restriction

In a similar series of experiments, cheatgrass and yellow starthistle were grown to assess their growth under limited rooting depth conditions. The above described experiments were repeated with the rooting zone restricted to .2 m (shallow soil) and .5 (moderate soil) m by placing an 8 mil impermeable plastic liner below the soil surface. The experiments were replicated 4 times in a split-plot design with soil depth as whole plots and plant density (isolated, monocultures, mixtures) as sub-plots.

Procedures

Seeds for all experiments were collected from the study site during 1991 and sown on February 29 and March 1, 1992 in .25m² (isolated) and .5 m² (monocultures and mixtures) plots. Seeds were randomly broadcast, then manually separated until a uniform distance between seed was achieved, and lightly covered with soil (<2 mm). Plots were thinned to the appropriate density 1 wk after emergence, densities of 10000 plants m⁻² did not require thinning. An individual of each species was collected from each plot on 12 d intervals beginning 24 d after planting. Experiments without rooting depth restriction had final harvest dates of 96 and 108 d for cheatgrass and yellow starthistle, respectively. Final harvests for experiments with rooting depth restrictions, occurred 72 d after planting for both species. Shoots were dried to a constant weight (48h, 60 C) and weighed (g).

Analysis

Regression analysis was used to describe the relationship between shoot weight and time after planting (SAS Institute 1985). A curve-fitting procedure utilizing the coefficient of determination, residual mean squares, sum of squares and residuals was used to determine the most suitable model for the prediction of accumulated shoot weight over time (Hunt 1982, France and Thornley 1984). A quadratic model ($\hat{y} = B_0 + B_1 X_1 + B_2 X_1^2$) was selected, and growth curves were determined for each treatment in each replication for each experiment.

The time of inflection (T), point of inflection (P) and relative growth rates (RGR) were calculated using the linear and quadratic regression coefficients derived from the growth curves. T is the date at which the absolute growth rate began to decrease with increasing time, and P is the shoot weight at T. Relative growth rate, an index of growth efficiency, was calculated at 36 (RGR36), 60 (RGR60) and 84 (RGR84) d after planting. Absolute growth rates (AGR) were determined for the early (AGRE=24-48 d after planting), middle (AGRM=48-72 d after planting) and late (AGRL=72-96 d after planting) growth periods. RGR84 and AGRL were only calculated for treatments without rooting depth restriction. The calculation of these parameters were as follows:

$$T = \frac{B_1}{2B_2} - \frac{1}{(-2B_2)^{1/2}}$$

$$P = \exp (B_1(B_2T) + B_2T^2)$$

$$RGR = B_1 + 2B_2t$$

$$AGR = \frac{W_2 - W_1}{t_2 - t_1}$$

where B_1 and B_2 are the linear and quadratic regression coefficients, respectively, t is time, and W_1 and W_2 are the initial and final plant weight, corresponding to t_1 and t_2 .

Differences among mean T , P , RGR_{36} , RGR_{60} , RGR_{84} , $AGRE$, $AGRM$, and $AGRL$ were tested by analysis of variance. P values are provided when means separations are required between significant main effects having 2 levels. Other mean separations were achieved using Fisher's protected LSD comparison at $P \leq .05$ unless stated otherwise (Peterson 1985).

RESULTS

Growth without rooting depth restriction.

Yellow starthistle shoot growth exceeded that of cheatgrass for all growth parameters ($P \leq .10$) except AGRE when grown in isolation without rooting depth restriction (Table 5.1). AGRE was similar for both species under these conditions.

With the exception of cheatgrass RGR36, AGRE, and P, increasing monoculture densities (for both species) decreased growth parameters when grown without rooting depth restriction (Table 5.2). Under these conditions, P, T, RGR60, RGR84, AGRM, and AGRL were greater for yellow starthistle than for cheatgrass at 100 plants m^{-2} . At 1000 plants m^{-2} , cheatgrass had later T, and greater RGR84, and AGRL than yellow starthistle. Cheatgrass and yellow starthistle had similar RGR36 and AGRE at all densities and all growth characteristics were similar at 10000 plant m^{-2} in monocultures grown without rooting depth restrictions.

In general, density combinations of 100 plants m^{-2} of cheatgrass (called Brte when referring to density) and yellow starthistle (called Ces0 when referring to density) resulted in the highest growth parameters for both species when grown without rooting depth restrictions (Table 5.3 and 5.4). Cheatgrass P decreased with increasing Brte density ($P = .0494$). The second latest yellow starthistle P resulted from the 1000:100 Brte:Ces0 density combination (Table 5.4). Yellow starthistle P was similar at all other density combinations.

Cheatgrass T decreased with increasing Brte ($P = .0007$) and Ceso ($P = .0788$) densities. Yellow starthistle T was greatest at 100:100 plants m^{-2} density combination, and decreased with increasing Brte density (Table 5.4). An increase in Ceso density above the lowest density combination decreased T.

Yellow starthistle and cheatgrass relative growth rates had similar trends for all time periods when grown in mixtures without soil depth restriction. The trend was toward lower relative growth rates as the season progressed (Table 5.3 and 5.4). At background densities of 10000 plants m^{-2} , RGR36 was unaffected when the other species density was maintained at 100 or 1000 plants m^{-2} . The lowest RGR36 was observed with a density combination of 10000:10000 plants m^{-2} . Brte:Ceso densities of 100:100 and 100:1000 plants m^{-2} resulted in the highest RGR60 for both species (Table 5.3 and 5.4). When Ceso density was 1000 and 10000 plants m^{-2} , an increase in Brte density to 1000 and 10000, reduced cheatgrass RGR60. The lowest RGR60 occurred when density combinations included 10000 plants m^{-2} .

Increased Ceso or Brte densities reduced cheatgrass RGR84. Increasing Brte density, while maintaining Ceso density at 100 plants m^{-2} , decreased yellow starthistle RGR84 (Table 5.4). Yellow starthistle RGR84 was similar at Brte:Ceso density combinations 100:1000, 100:10000, 1000:1000, and 1000:10000. The RGR84 of yellow starthistle decreased with increasing Ceso densities when Brte densities were held at 100 plants m^{-2} .

In general, cheatgrass and yellow starthistle absolute growth rates decreased with increasing densities (Tables 5.3 and 5.4). The absolute growth rates of cheatgrass increased through the early (24-48 d) to mid (48-72) growth period; however a decline in cheatgrass absolute growth rate was observed in the late period (72-84 d) (Table 5.3). Negative absolute growth rates were associated with leaf drop during maturation. Yellow starthistle absolute growth rates increased throughout the growing season (Table 5.4).

Cheatgrass AGRE was highest when Brte density was highest ($P = .0040$). This suggests a potential positive effect of cheatgrass upon itself during the early stages of growth when grown without rooting depth restriction. There was no difference in cheatgrass AGRE when Brte densities were maintained at 100 or 1000 plants m^{-2} , at any Ceso density.

Growth with rooting depth restriction.

Restricting rooting depth from .5 to .2 m reduced all growth parameters when plants were grown in isolation (Table 5.5). RGR36 ($P = .075$) and RGR60 ($P = .026$) were greater for yellow starthistle than for cheatgrass (data not shown).

An analysis of variance revealed a species main effect and a depth X density interaction for most parameters when cheatgrass and yellow starthistle were grown in monocultures with rooting depth restriction (Tables 5.6 and 5.7).

With the exception of T and RGR60, yellow starthistle growth parameters were greater than those of cheatgrass under these conditions (Table 5.6).

In general, restricting rooting depth and increasing densities decreased all cheatgrass and yellow starthistle growth parameters when grown in monocultures, except on shallow soil where a density increase from 1000 to 10000 plants m^{-2} had little effect (Table 5.7). Growth rates were greater at 100 and 1000 plants m^{-2} at a moderate soil depth when compared to shallow soil. Shallow soil had an earlier T at 1000 plants m^{-2} compared to a moderate soil depth restriction. At 10000 plants m^{-2} , most growth parameters were similar, regardless of soil depth.

Similarly, decreasing soil depth and/or increasing densities generally reduced growth parameters when grown in mixtures (Tables 5.8 and 5.9). For both species, .5 m soil depth and 100 plants m^{-2} had greatest P, relative growth rates, and absolute growth rates when grown in mixtures. Under these conditions, cheatgrass and yellow starthistle P was 14 and 7.5 times, greater than any other density combination, respectively.

Soil depth did not significantly affect T for either species, however a tendency toward a later yellow starthistle T was evident in the deeper soil treatments (Table 5.8 and 5.9). Increasing the densities of either species ($P=.0021$) decreased yellow starthistle T. An analysis of variance indicated that Brte density interacted with Ces0 density to affect ($P=.0001$) cheatgrass T. At 1000 Ces0 plants m^{-2} , cheatgrass T occurred later at 100 than at 1000 plants per

m^{-2} . Cheatgrass T was lowest at the highest density, regardless of the density of Ceso (data not shown).

At each density, cheatgrass relative growth rates were higher in moderate soil depth than in shallow soil, with the exception of Brte:Ceso density of 100:10000 plants m^{-2} , where the RGR60 were similar (Table 5.8). In moderately deep soil, at a Ceso density of 10000, an increase in Brte density from 100 to 1000 plants m^{-2} increased cheatgrass relative growth rates.

An analysis of variance of yellow starthistle relative growth rates indicated significant Ceso density X Brte density (RGR36, $P=.0004$; RGR60, $P=.0192$), depth X ceso density (RGR36, $P=.0314$) and depth X Brte density (RGR36, $P=.0328$) interactions. The lowest density combination resulted in the highest yellow starthistle relative growth rates (RGR36=.12, RGR60=.09 gm^{-1}). Density (Brte:Ceso) combinations of 100:1000 and 1000:1000 plants m^{-2} yielded similar relative growth rates. An increase in either species density to 10000 plants m^{-2} reduced the relative growth rates of yellow starthistle. Lowest yellow starthistle relative growth rates occurred when the Brte density was 10000 plants m^{-2} . At that density, changes in Ceso density did not alter the relative growth rate of yellow starthistle. At low densities starthistle RGR36 was greater at moderate soil depth, but at high densities soil depth did not effect RGR36 (data not shown). Shallow soil depth decreased yellow starthistle RGR60, regardless of plant density ($P=.0068$).

Density combinations of 100 plants m^{-2} resulted in highest absolute growth rates, and both species appeared to decrease similarly with increasing density (Tables 5.8 and 5.9). Cheatgrass and yellow starthistle absolute growth rates were lowest when grown in shallow soils and moderate depth soils at the highest densities, with the exception of cheatgrass AGRE, which remained high at the highest yellow starthistle density (Brte density = 100 and 1000 plants m^{-2}).

DISCUSSION

Isolated individuals of cheatgrass and yellow starthistle have similar absolute growth rates during the early stages of growth. The results are consistent with the observations of Sheley and Larson (1993b). The absolute growth rates of yellow starthistle exceeds cheatgrass in the middle and later growth stages when grown in isolation without rooting depth restriction. Under these conditions, the predicted time and weight at which the absolute growth rate begins to decline were greater for yellow starthistle than for cheatgrass. The addition of soil depth restriction (.5 and .2 m) masked the species differences. However, a soil depth restriction of .5 m did yield greater growth and later maturation compared to a .2 m soil depth restriction. These results support the conclusions of Sheley et al. (1993) that rapid growth of isolated yellow starthistle allow deeper soil penetration and continue growth later into the season than cheatgrass under deep soil conditions.

Using similar densities as in this study, Sheley and Larson (1993b, 1993c) found that on deep soil, intraspecific interaction had twice the influence of interspecific interaction (cheatgrass vs. yellow starthistle) in predicting plant weight. Our results indicate that on deep soil growth rates and duration are regulated by density. At low densities when monocultures and mixtures were grown without rooting depth restriction, the relationship between growth characteristics was similar to the growth of isolated individuals. Under these conditions, yellow starthistle appeared to grow more rapidly and mature later

than cheatgrass. This suggests that under low densities the mechanism for resource competition and competitive dominance is resource preemption (Harper 1977, Grime 1979, Keddy 1990, Grace 1990, Sheley et al. 1993), or asymmetric competition (Weiner 1986, 1990, Wilson 1988). As densities increase the preemptive advantage of yellow starthistle was reduced.

Amundson (1983) and Talbott (1987) found yellow starthistle dominated deep soils, while cheatgrass dominated shallow soils. In shallow soils, cheatgrass density had twice the impact of yellow starthistle density on the prediction of yellow starthistle plant weight. In contrast, yellow starthistle had no effect upon cheatgrass (Sheley and Larson 1993c). In this study we found that low densities and greater soil depth resulted in greatest growth rates. As densities increased and soil depth decreased, growth rates decreased. In monocultures and mixtures, cheatgrass maturation was not affected by soil depth restriction (.2 or .5 m). A non-significant tendency of later maturation in moderately deep (.5 m) soil was apparent for yellow starthistle, and the time of inflection of yellow starthistle appeared later in deep (unrestricted) soil treatments.

Our results suggest that the mechanism controlling community dynamics and competitive dominance in cheatgrass and yellow starthistle ecosystems is related to differences in rooting depth which affects resource acquisition rates and durations, and ultimately resource preemption.

Table 5.1. Growth of cheatgrass and yellow starthistle grown in isolation without rooting depth restrictions.

	Growth Parameters							
Species	P	T	RGR36	RGR60	RGR84	AGRE	AGRM	AGRL
	(g)	(d)	-----	$\text{g} \cdot \text{d}^{-1} \cdot \text{g}^{-1}$	-----	-----	$\text{g} \cdot \text{d}^{-1}$	-----
Cheatgrass	.73	75	.131	.078	.025	.004	.020	.024
Yellow starthistle	11.78	100	.141	.104	.067	.004	.047	.223
P value	.089	.069	.0004	.037	.062	.439	.001	.052

Table 5.2. Effects of density upon the growth of cheatgrass and yellow starthistle grown in monocultures without rooting depth restriction.

Density (plants m ⁻²)	Species	Growth Parameters							
		P (g)	T (d)	RGR36	RGR60	RGR84	AGRE	AGRM	AGRL
				-----g•d ⁻¹ •g ⁻¹ -----			-----g•d ⁻¹ -----		
100	Cheatgrass	.85	81	.130	.083	.037	1.14	1.09	1.04
	Yellow starthistle	9.80	108	.138	.105	.072	1.15	1.11	1.07
1000	Cheatgrass	.62	84	.118	.077	.037	1.12	1.08	1.04
	Yellow starthistle	.29	69	.122	.067	.012	1.13	1.07	1.01
10000	Cheatgrass	.04	57	.098	.040	-.017	1.10	1.04	.98
	Yellow starthistle	.07	62	.104	.049	-.005	1.11	1.05	.99
LSD (.05)		2.4	10.8	NS	.012	.022	NS	.013	.022

Table 5.3. Effects of cheatgrass and yellow starthistle density upon the growth of cheatgrass grown in mixtures without rooting depth restrictions.

Density		Cheatgrass Growth Parameters							
Cheatgrass	Yellow starthistle	P	T	RGR36	RGR60	RGR84	AGRE	AGRM	AGRL
-----Plants m ⁻² -----		(g)	(d)	-----g•d ⁻¹ •g ⁻¹ -----			-----g•d ⁻¹ -----		
100	100	1.27	72	.128	.081	.035	.003	.016	-.017
100	1000	.26	67	.122	.064	.006	.002	.010	-.056
100	10000	.10	69	.106	.061	.015	.009	.003	-.087
1000	100	.28	69	.120	.065	.009	.003	.010	-.060
1000	1000	.13	64	.114	.057	.000	.002	.005	-.083
1000	10000	.048	60	.102	.046	-.009	.001	.002	-.124
10000	100	.031	56	.096	.046	-.015	.007	.001	-.145
10000	1000	.032	60	.096	.046	.005	.0005	.001	-.134
10000	10000	.025	60	.093	.043	-.006	.0005	.001	-.145
LSD (.05)		NS	9.5 ¹	.005	.010	NS	NS	.003	.013

¹ P = .068

Table 5.4. Effects of cheatgrass and yellow starthistle density upon the growth of yellow starthistle grown in mixtures without rooting depth restriction.

Density		Yellow Starthistle Growth Parameters							
Cheatgrass	Yellow starthistle	P	T	RGR36	RGR60	RGR84	AGRE	AGRM	AGRL
-----Plants m ⁻² -----		(g)	(d)	-----g•d ⁻¹ •g ⁻¹ -----			-----g•d ⁻¹ -----		
100	100	2.70	84	.14	.094	.048	.005	.044	.105
100	1000	.41	73	.12	.070	.018	.002	.010	.019*
100	10000	.08	71	.10	.057	.012	.001	.003	.001
1000	100	.86	77	.13	.080	.030	.003	.021	.030
1000	1000	.19	69	.12	.066	.015	.002	.007	.004
1000	10000	.07	67	.10	.054	.006	.0001	.002	.001
10000	100	.06	60	.10	.049	-.007	.001	.003	-.001
10000	1000	.04	65	.10	.052	.006	.001	.002	.001
10000	10000	.03	67	.09	.052	.012	.000	.001	.001
LSD (.05)		.44	9.5 ¹	.006	.02	.013	.001	.007	.018

¹ P = .069

Table 5.5. Effect of rooting depth restriction upon growth of cheatgrass and yellow starthistle grown in isolation.

Soil depth (m)	Growth Parameter					
	P (g)	T (d)	RGR36 -----g•d ⁻¹ •g ⁻¹ -----	RGR60 -----g•d ⁻¹ •g ⁻¹ -----	AGRE -----g•d ⁻¹ -----	AGRM -----g•d ⁻¹ -----
.2	.07	63	.103	.062	.0007	.005
.5	2.64	82	.140	.094	.005	.043
P value	.0325	.0065	.0028	.031	.010	.008

Table 5.6. Growth of cheatgrass and yellow starthistle grown in monocultures with rooting depth restriction.

Species	Growth Parameter					
	P (g)	T (d)	RGR36 -----g•d ⁻¹ •g ⁻¹ -----	RGR60 -----g•d ⁻¹ •g ⁻¹ -----	AGRE -----g•d ⁻¹ -----	AGRM -----g•d ⁻¹ -----
Cheatgrass	.70	66	.103	.052	.001	.010
Yellow starthistle	1.11	66	.110	.061	.002	.016
P value	.034	.762	.001	.109	.021	.001

Table 5.7. Effect of depth and density upon the growth of cheatgrass and yellow starthistle grown in monocultures.

Soil depth (m)	Density (plants m ⁻²)	Growth Parameter					
		P (g)	T (d)	RGR36 -----g•d ⁻¹ •g ⁻¹ -----	RGR60 -----g•d ⁻¹ •g ⁻¹ -----	AGRE -----g•d ⁻¹ -----	AGRM -----g•d ⁻¹ -----
.2	100	.257	80	.108	.075	.0007	.004
	1000	.015	53	.087	.031	.0004	.0005
	10000	.013	57	.077	.022	.0002	.0003
.5	100	4.08	84	.143	.110	.004	.053
	1000	1.08	73	.129	.078	.003	.018
	10000	.033	49	.097	.021	.001	.0008
LSD (.05) ¹		.80	9.0	.004	.017	.0006	.005
LSD (.05) ²		.77	11.3	.006	.023	.0007	.005

¹ comparing depth at any density

² comparing density at a constant depth

Table 5.8. Effects of soil depth restriction and cheatgrass and yellow starthistle density upon cheatgrass growth.

Depth (m)	Plant Density		Cheatgrass Growth Parameters					
	Cheatgrass	Yellow starthistle	P	T	RGR36	RGR60	AGRE	AGRM
	-----Plants m ⁻² -----		(g)	(d)	-----g•d ⁻¹ •g ⁻¹ -----		-----g•d ⁻¹ -----	
.2	100	100	.096	70	.098	.056	.0006	.0020
	100	1000	.097	70	.099	.060	.0006	.0019
	100	10000	.021	58	.089	.038	.0004	.0007
	1000	100	.100	76	.098	.059	.0005	.0021
	1000	1000	.030	58	.088	.031	.0005	.0006
	1000	10000	.033	66	.089	.048	.0003	.0009
	10000	100	.007	47	.074	.017	.0003	.0002
	10000	1000	.007	42	.072	.000	.0003	.0000
	10000	10000	.009	49	.075	.016	.0003	.0002
.5	100	100	3.13	70	.140	.108	.0033	.0430
	100	1000	.400	71	.123	.064	.0030	.0110
	100	10000	.040	51	.097	.020	.0011	.0011
	1000	100	.153	59	.118	.049	.0029	.0065
	1000	1000	.212	63	.115	.053	.0022	.0056
	1000	10000	.069	56	.108	.041	.0028	.0028
	10000	100	.017	42	.083	-.005	.0008	.0000
	10000	1000	.017	44	.083	-.004	.0008	-.0001
	10000	10000	.012	42	.079	-.006	.0006	-.0001
LSD (.05) ¹			.28	NS	.007	.021	.0006	.0027
LSD (.05) ²			.28	NS	.008	.021	.0005	.0027

¹ Comparing depth at any density.

² Comparing densities at a constant depth.

Table 5.9. Effects of soil depth restriction and cheatgrass and yellow starthistle density upon yellow starthistle growth.

Depth (m)	Plant Density		Yellow starthistle Growth Parameters					
	Cheatgrass	Yellow starthistle	P	T	RGR36	RGR60	AGRE	AGRM
	Plants m ⁻²		(g)	(d)	g•d ⁻¹ •g ⁻¹		g•d ⁻¹	
.2	100	100	.12	73	.10	.06	.0006	.0026
	100	1000	.07	74	.10	.06	.0005	.0017
	100	10000	.03	53	.08	.011	.0003	.0004
	1000	100	.02	56	.09	.03	.0005	.0007
	1000	1000	.02	55	.09	.03	.0005	.0004
	1000	10000	.01	52	.08	.03	.0003	.0004
	10000	100	.01	45	.08	.01	.0003	.0001
	10000	1000	.01	54	.07	.02	.0002	.0002
	10000	10000	.01	39	.07	-.01	.0002	.0000
.5	100	100	4.40	84	.14	.12	.0036	.0554
	100	1000	.59	69	.12	.06	.0030	.0125
	100	10000	.06	57	.10	.03	.0011	.0018
	1000	100	.27	66	.12	.06	.0030	.0108
	1000	1000	.14	59	.12	.05	.0027	.0027
	1000	10000	.04	50	.10	.02	.0014	.0009
	10000	100	.03	47	.10	.01	.0011	.0005
	10000	1000	.02	48	.09	.01	.0008	.0008
	10000	10000	.02	44	.09	.00	.0009	.0001
LSD (.05) ¹			.36	12.56	.008	.027	.0005	.0050
LSD (.05) ²			.36	12.33	.008	.025	.0004	.0050

¹ Comparing depth at any density.

² Comparing densities at a constant depth.

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CHAPTER 6

SUMMARY

The loss of native perennial vegetation on North American rangelands has been accompanied by invasions of alien annual weeds. The grassland steppe of the Pacific Northwest and the California Annual Grasslands, once dominated by native perennial grasses, such as bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Scribn and Smith), now contain extensive areas dominated by annual grasses, such as cheatgrass (*Bromus tectorum* L.). These annual grasslands are being joined by less desirable Eurasian weeds, such as yellow starthistle (*Centaurea solstitialis* L.).

Attempts to convert yellow starthistle and cheatgrass dominated rangelands into functioning perennial grasslands have yielded poor results due to ecological and economical reasons. Successional management systems may offer an alternative solution for revegetating degraded rangelands. The transition from vegetation management to successional management requires and understanding of mechanism, processes, and conditions which regulate species dominance, community dynamics, and desirable plant establishment. The objectives of our research were to: 1) characterize the life histories of cheatgrass and yellow starthistle growing in association; 2) determine key community regulating processes and mechanisms; 3) investigate the intensity of interference between cheatgrass and yellow starthistle at various soil depths;

and 4) compare the growth of cheatgrass and yellow starthistle at various densities, species proportions, and soil depths.

Biweekly cheatgrass and yellow starthistle demographic attributes were monitored during 1991 (moist spring) and 1992 (dry spring), and arranged into life history tables. Sensitivity analysis was performed to determine key transition phases. The entire cheatgrass seed crop reached the soil surface, 41% of yellow starthistle's seed output was lost during seed rain. Frost heaving reduced cheatgrass winter seedling populations more than yellow starthistle. All cheatgrass surviving the frost heaving period became an adult. Cheatgrass seed output was a constant 7000 m^{-2} during both years. Yellow starthistle seed output was 21595 m^{-2} (1991) and 5226 m^{-2} (1992). Community dynamics appears oscillatory based upon the variation of yellow starthistle seed output around a constant cheatgrass seed output. Adequate spring precipitation allows continued growth, later maturation, and increased seed production by yellow starthistle. The early maturing characteristic of cheatgrass allows this species an advantage by escaping dry conditions. Key processes associated with transition phases were interference (competition), resource acquisition rates, and reproductive allocation.

Isolated individuals and addition series mixtures with total stand densities ranging from 20-20000 plants m^{-2} were grown in environmental chambers (10 C, 12 hr day length). Individuals were harvested on 4 d intervals for 46 d, and mixtures were harvested 37 d after planting. Shoot weight, root weight, leaf

area, and total root length of isolated was similar. Yellow starthistle soil depth penetration was deeper than cheatgrass after 22 d from planting. Intraspecific interference was greater than interference for both species, and resource partitioning via rooting depth was evident. Invasion of cheatgrass rangeland increases niche occupancy and reduces revegetation potential.

Addition series mixtures, with total stand densities ranging from 20-20000, were used to quantify the intensity of interference between cheatgrass and yellow starthistle in unrestricted soils depths on 12 d intervals throughout the growing season and under soil depths restricted to .2 and .5 m. In unrestricted soil, intraspecific interference was nearly twice as important as interspecific interference, for both species, with respect to the prediction of shoot weight throughout the growing season and seed output. Regression equations predicting seed output based upon plant density indicates that shifts in community dominance can result from intraspecific interference in dense stands of either cheatgrass or yellow starthistle. On soils restricted to .5 m, the intensity of intraspecific and interspecific interference were nearly equal for both species. On shallow soils, restricted to .2 m, cheatgrass interference was 2 times greater than intraspecific interference in determining yellow starthistle shoot weight. Cheatgrass has an advantage over yellow starthistle on shallow soils, due to it's relatively shallow and fibrous rooting system. Conversely, yellow starthistle has an advantage over cheatgrass in deep soils where taproot

development enables continued resource uptake and increased seed output during seasons with adequate moisture availability.

In 6 experiments, isolated individuals, monocultures (100, 1000, 10000 plants m^{-2}), and mixtures (same densities arranged factorially) were grown with unrestricted and restricted (.2 and .5 m) to compare the growth of cheatgrass and yellow starthistle. Quadratic growth curves were fit for each treatment in each experiment. ANOVA was performed on time of inflection, point of inflection, relative growth rates at d 36, 60, and 84 and absolute growth rates at 3 growth periods (early, middle, late). Yellow starthistle growth parameters were greater than those of cheatgrass when grown in isolation without rooting depth restriction. Rapid and geotropic yellow starthistle root growth allows deeper soil penetration and continued growth later into the season than cheatgrass. The addition of soil depth restriction and increasing densities masked the species growth differences and reduces yellow starthistle's growth advantage.

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