Observation: Comparative live-history of cheatgrass and yellow starthistle

ROGER L. SHELEY AND LARRY L. LARSON

Authors are graduate research assistant and associate professor Department of Rangeland Resources, Oregon State University, Corvallis, and are stationed at OSU-EOSC Agriculture Program, Eastern Oregon State College, La Grande, OR 97850.

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. The entire cheatgrass seed crop reached the soil surface, 41% of yellow starthistle's seed output was lost during seed rain. Frost heaving reduced winter seedling populations of cheatgrass (53%) more than yellow starthistle (40%). All cheatgrass seedlings surviving the frost heaving period became adults. Yellow starthistle density was reduced by 75% during the juvenile phase. Cheatgrass adults appeared about 6 weeks before yellow starthistle adults. Cheatgrass seed output remained about 7,000 m^{-2} with moist and dry spring conditions. Yellow starthistle seed output was about 21,600 m^{-2} and 5,200 m^{-2} with moist and dry spring conditions, respectively. Reduction of yellow starthistle seed output with dry spring conditions suggest oscillatory community dynamics. Key processes associated with life-history transitions were interference (competition), resource acquisition rates and duration, and reproductive allocation.

Key words: *Centaurea solstitialis, Bromus tectorum,* alien winter annuals, sensitivity analysis, demography, population dynamics

Cheatgrass (*Bromus tectorum* L.) and yellow starthistle (*Centaurea solstitialis* L.) are alien winter annual weeds which grow in association on the Grassland Steppe of the Pacific Northwest. Cheatgrass was introduced to N. America in the 1890's 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 10,000 ha per year

in Washington and Idaho alone (Talbott 1987, Callihan et al. 1989). Yellow starthistle is considered poor forage for all classes of livestock and causes nigropallidal encephalomalacia, a nervous disorder, in horses (Cordy 1954, Roché 1983).

Cheatgrass and yellow starthistle currently dominate over 250,000 ha throughout the Pacific Northwest. (Mack 1981, Maddox et al. 1985). Generally, it is 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 reduces resource value further.

Control and rehabilitation of these communities has been investigated, but have yielded limited success in small scale application (Evans et al. 1967, Eckert et al. 1974, Roché 1983, Sheley et al. 1983, Larson and McInnis 1989). The investigation of processes that control population and community dynamics appears essential to future regulation of species dominance and the establishment of functional communities on degraded grasslands (Cousens 1985, MacMahon 1987, Radosevich 1987, Allen 1988, 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 developed by Watson (1985) for leafy spurge (*Euphorbia esula* L.) to identify key processes regulating population dynamics. We used the Sager and Mortimer (1976) methodology to characterize the life-history of cheatgrass and yellow starthistle growing in association. Sensitivity analyses were 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, Wash. (NW 1/4, NW 1/4, Sec. 6, T.6 N., R. 35.; elev. 320 m) in bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith = *Pseudoroegneria spicata* (Pursh) Scribn. & Smith)-Idaho fescue (*Festuca idahoensis* Elmer) 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, (coarse-silty, mixed. mesic Calciorthidic Haploxeroll) had a 15-30% southeasterly

slope. Average annual precipitation approximated 380 mm with a bimodel distribution with peaks in winter and spring. Temperatures range from 45 to -34° C with a frost free season of 170 days.

Life cycles of cheatgrass and yellow starthistle were monitored during 1991 and 1992 in a 40 x 40-m area. Simple random sampling occurred at 2-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 m^{-2} 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 mm^3 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 wooden traps (37 x 300 mm) were coated with a smooth surface of lithium based grease and randomly placed flush on the soil surface. Traps were cleaned and grease reapplied at each visit. Seeds were counted by species and type (plumed and plumeless for yellow starthistle) 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. Densities of seedling, juveniles, and adults 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 15 March and ending 15 July 1992. Mean individual weights were determined. Individual weights were multiplied by the total population density at the time to provide a comparison of the changes in biomass during the spring growing season of 1992.

Analysis

A confidence interval ($P = 0.05$) for each demographic 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 1 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. Transitions with the highest sensitivity values have the greatest effect on determining seed output. 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:

$$\text{Sensitivity value} = \frac{\Delta \text{ seed output}}{\text{seed output}} \Big/ \frac{\Delta \text{ transition parameter}}{\text{transition parameter}}$$

Results and Discussion

Life-history
Cheatgrass

The 1991 cheatgrass population produced 660 adults m^{-2}, with 10.7 seeds per individual for an approximate seed output of 7,000 seeds m^{-2} (Fig. 1). In 1992 the adult cheatgrass density was 4,000 individuals m^{-2}, with 1.75 seeds per individual for an approximate seed output of 7,000 seeds m^{-2}.

Cheatgrass seed bank size was 333 ± 140 and 267 ± 97 m^{-2} prior to the seed release in 1991 and 1992, respectively. The seed bank 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 was 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 15 November 1991, shortly after fall precipitation (10 mm) (Fig. 1). Mack and Pyke (1983) observed fall cheatgrass recruitment before 1 November in all sites and years studied. Seedling recruitment peaked at about 6,200 seedlings m^{-2} in late-January. Following a 2 week period of freezing and thawing, seedling densities were reduced to 2,900 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. Cheatgrass seedlings emerging in fall developed into juveniles in February. Juveniles were the dominant growth stage for 6 weeks with a maximum population of about 2,400 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 per individual for an approximate seed output of 21,600 seeds m^{-2} (Fig. 2). In 1992 the adult starthistle density was 236 individuals m^{-2}, with 22 seeds per individual for an approximate output of 5,200 seeds m^{-2}.

The size of the starthistle seed bank was 3,224 ± 987 in 1991 and 2,897 ± 99 m^{-2} in 1992. All seeds were plumeless and represented about 13% of total seed production (1991). This corresponds with observations by Larson and Kiemnec (1993 Unpublished data) suggesting lower field germination by plumeless seed following a November-March seed burial.

Seed rain represented 59% of the total seed output. 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
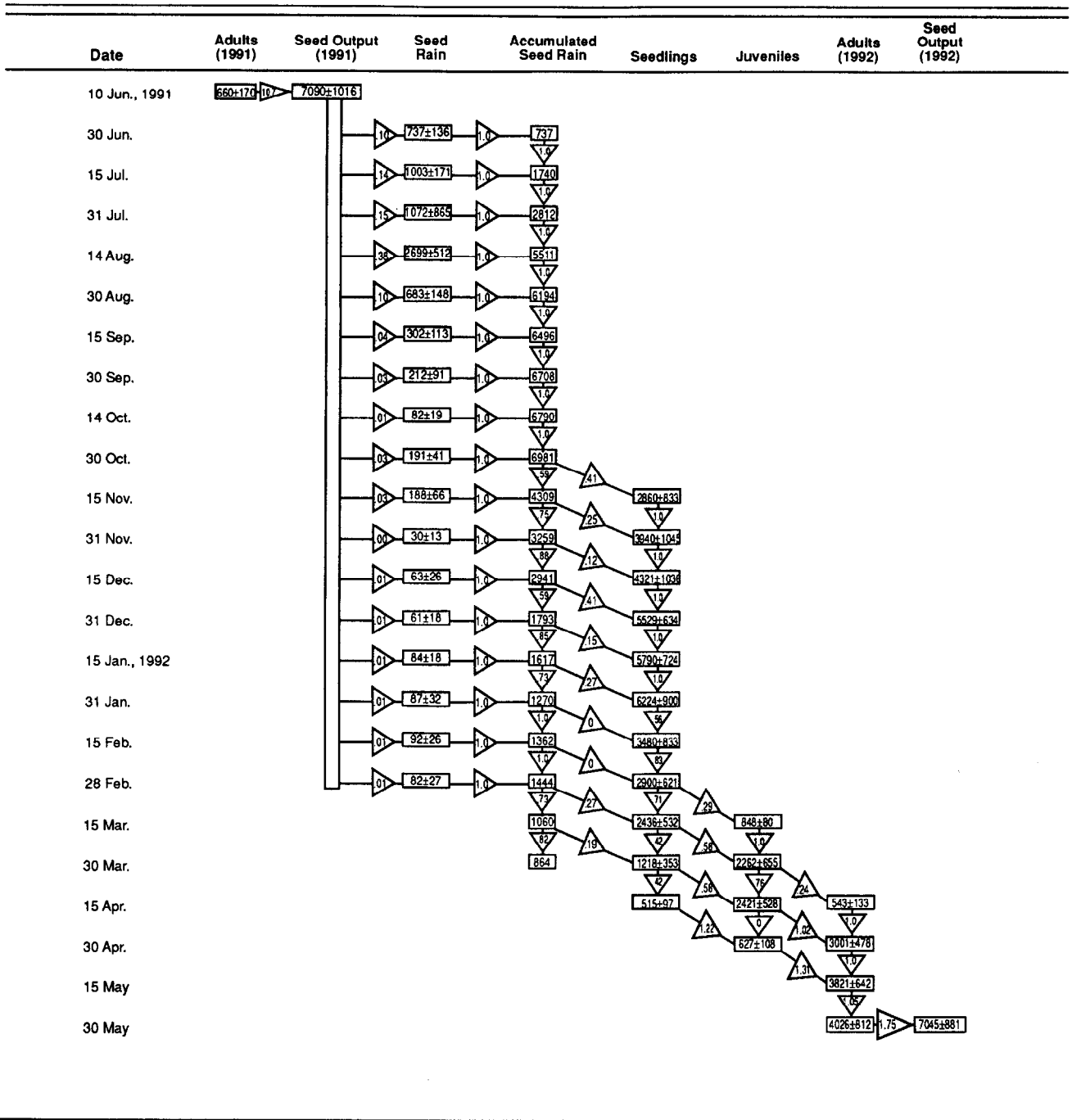
Fig. 1. Life-history of cheatgrass (June 1991-May 1992). Boxes represent life-history stages (population m⁻²) at a sample date. Vertical arrows indicate the population fraction remaining in the life-history stage at the next sample date. Horizontal and diagonal arrows indicate the population fraction transferred to the next life history stage (left to right). Population fractions are rounded and estimate actual population values.

(November-February) seed rain (Table 1).

Fall seedling recruitment of yellow starthistle was observed in mid-November with about 4,000 seedlings m⁻² (Fig. 2). Recruitment increased at the rate of 1,000 individuals m⁻² per sampling date for 6 weeks. Starthistle seedlings peaked at about 7,600 individuals m⁻² in late-January decreasing to 4,700 seedling m⁻² by mid-March. Spring

seedling recruitment was 410 individuals m⁻².

By 30 March, starthistle plants were beginning to achieve juvenile status. The transition from seedling to juvenile increased the juvenile population to 4,560 individuals m⁻² by mid-May. Juvenile mortality began in late-May and reached 75% by mid-June. Roché (1965) observed a 58% reduction in starthistle density from April to July.

Table 1. Distribution of yellow starthistle seed rain by type.

Date	Seed type	
	Plumed	Plumeless
	--------(seeds m⁻²)--------	
30 Jun. 1991	97±21[1]	5±3
15 Jul.	483±70	13±7
31 Jul.	2469±316	0
14 Aug.	5377±643	5±3
30 Aug.	935±142	11±6
15 Sep.	320±83	45±16
30 Sep.	258±42	88±36
14 Oct.	145±17	0
30 Oct.	200±39	59±26
15 Nov.	95±14	93±22
31 Nov.	45±18	637±37
15 Dec.	53±17	214±21
31 Dec.	32±15	285±28
15 Jan. 1992	43±21	45±20
31 Jan.	72±23	208±27
15. Feb	68±22	161±30
28 Feb.	74±18	81+19

[1]Confidence interval at P = 0.05.

Starthistle adults were observed in mid-June. Mortality however, reduced the adult population 75% by mid-July.

Individual weights of both species were similar at the first 2 sampling dates (Table 2). Total biomass of yellow starthistle was greater than cheatgrass because of higher densities. Individual weight and total biomass was greater for yellow starthistle on the 15 May sampling date. From 15 May to the end of the growing period, cheatgrass exceeded yellow starthistle in total biomass, whereas the individual weight of yellow starthistle remained greater. Yellow starthistle total

Table 2. Individual weight and total biomass of cheatgrass and yellow starthistle during 1992.

Date	Individual weight		Total biomass	
	Cheatgrass	Starthistle	Cheatgrass	Starthistle
	-----(mg/plant)-----		----(gm m⁻²)----	
15 Mar.	3.3±0.5[1]	3.6±0.5	107[2]	168
15 Apr.	4.0±0.8	4.3±0.5	139	214
15 May	4.9±0.5	11.4±1.8	189	575
15 Jun.	7.2±1.1	21.9±6.5	290	251
15 Jul.	7.5+1.3	80.9+39.5	304	191

[1]Confidence intervals at P=0.05.
[2]Mean individual weight multiplied by mean population density.

biomass was less because density was reduced during the transition from juvenile to adult. These data suggest 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 3). 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 reaching the juvenile growth stage decreased seed output by about 600 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 3). A 10% reduction in either adult survivorship (15-30 May) or seed output per individual decreased seed production by 700 m⁻².

Table 3. Sensitivity values[1] 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%)------------------------------								
10 Jun. 1991									1.111
30 Jun.	0.097								
15 Jul.	0.130	0.097							
31 Jul.	0.142	0.233							
14 Aug.	0.366	0.382							
30 Aug.	0.096	0.777							
15 Sep.	0.040	0.882							
30 Sep.	0.028	0.929							
14 Oct.	0.011	0.962							
30 Oct.	0.025	0.975							
15 Nov.	0.025	0.565	0.393						
31 Nov.	0.004	0.435	0.103	0.393					
15 Dec.	0.008	0.384	0.050	0.500					
31 Dec.	0.008	0.223	0.162	0.606					
15 Jan. 1992	0.011	0.195	0.034	0.789					
31 Jan.	0.011	0.147	0.058	0.829					
15. Feb	0.011	0.158	0.0	0.897					
28 Feb.	0.011	0.169	0.0	0.897					
15 Mar.		0.065	0.133	0.637	0.229				
30 Mar.		0.0	0.065	0.348	0.338	0.229			
15 Apr.				0.219	0.190	0.478	0.144		
30 Apr.				0.0	0.219	0.0	0.687	0.144	
15 May.							0.219	0.852	
30 May.								1.111	1.111

[1]Sensitivity values are the relatives effects of a 10% reduction in each transition parameter on seed output.
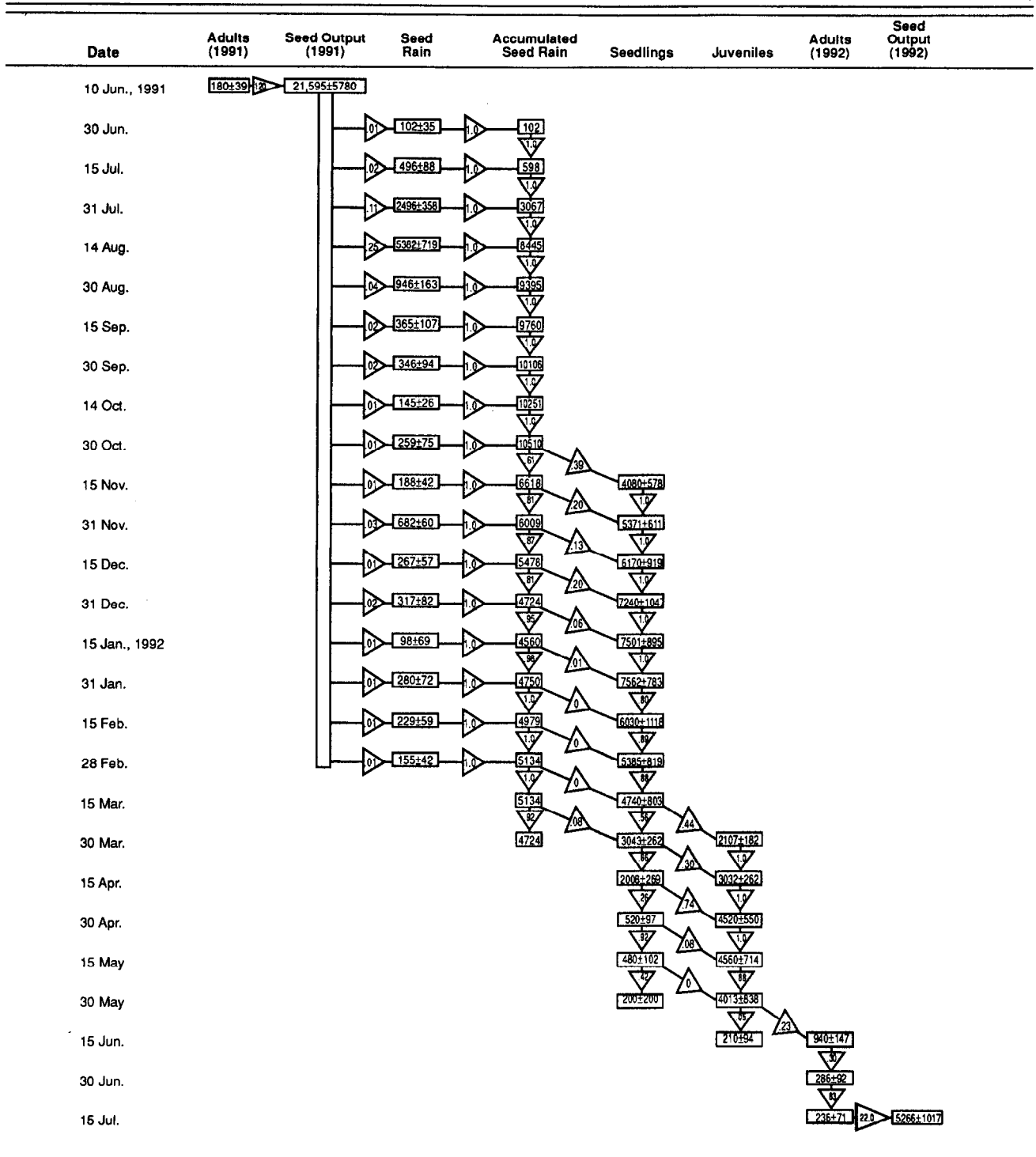
Fig. 2. Life-history of yellow starthistle (June 1991-July 1992). Boxes represent life-history stages (population m-2) at a sample date. Vertical arrows indicate the population fraction remaining in the life-history stage at the next sample date. Horizontal and diagonal arrows indicate the population fraction transferred to the next life-history stage (left to right). Population fractions are rounded and estimate actual population values.

Yellow Starthistle

Maximum sensitivity values for starthistle occurred with reductions in juvenile and adult survivorship, juvenile transition to adult, and seed production (Table 4). 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 (30 May-15 June) decreased production by 1,000

seeds m-2. A similar reduction in the seed production phase reduced seeds by about 500 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 reduction in accumulated seed rain

Table 4. Sensitivity values[1] 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%)				
10 Jun. 1991									1.111
30 Jun.	0.009								
15 Jul.	0.044	0.009							
31 Jul.	0.222	0.053							
14 Aug.	0.496	0.277							
30 Aug.	0.084	0.802							
15 Sep.	0.032	0.900							
31 Sep.	0.031	0.938							
14 Oct.	0.013	0.975							
30 Oct.	0.023	0.990							
15 Nov.	0.012	0.442	0.527						
31 Nov.	0.036	0.285	0.161	0.527					
15 Dec.	0.011	0.219	0.099	0.705					
31 Dec.	0.007	0.095	0.133	0.819					
15 Jan. 1992	0.002	0.070	0.032	0.974					
30 Jan.	0.004	0.064	0.008	1.010					
15 Feb.	0.003	0.068	0.0	1.020					
28 Feb.	0.002	0.071	0.0	1.020					
15 Mar.		0.073	0.0	1.020					
30 Mar.		0.0	0.073	0.488	0.484				
15 Apr.				0.347	0.207	0.484			
30 Apr.				0.009	0.667	0.712			
15 May				0.0	0.009	1.100			
30 May				0.0		1.111			
15 Jun.						0.0	1.111		
30 Jun.								1.111	
15 Jul.								1.111	1.111

[1]Sensitivity values are the relative effects of a 10% reduction in each transition parameter on seed output.

and seedling survivorship reduced seeds by about 450 and 500 m^{-2} respectively.

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 1994). In contrast, the later maturing starthistle populations declined during the transition from juvenile to adult.

Life-history models indicate cheatgrass and yellow starthistle populations are reduced naturally 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 used resources made available as a result of density-independent seedling mortality (frost heaving) to increase seed output of the remaining survivors. Young et al. (1976) observed a similar cheatgrass response following fire disturbance. In that case, adjustments in individual seed output within the cheatgrass population also maintained near-predisturbance levels of seed production.

In this study, cheatgrass density increased 6 times with below average spring (May-June 1992) precipitation, while maintaining a seed output equal to that of 1991 (Table 5). Population dynamics in 1992 were comparable to the drier big sagebrush (*Artemisia tridentata* Nutt.)-bluebunch wheatgrass habitat type investigated by Mack and Pyke (1983).

Our data support the conclusion of Palmbald (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

Table 5. Monthly precipitation totals (mm) for study site near Walla Walla, Wash. during 1991 and 1992.[1]

Month	Year	
	1991	1992
	(mm)	
Jan.	26	19
Feb.	16	27
Mar.	42	8
Apr.	14	32
May	111	8
Jun.	51	24
Jul.	8	40
Aug.	7	34
Sep.	0	24
Oct.	25	22
Nov.	80	41
Dec.	16	28
Total[2]	395	310

[1]Average annual precipitation = 380 mm
[2]Totals may vary from monthly values as a result of rounding.

high densities of aggressive individuals exhaust resources prior to the completion of their life cycle. Our data also suggest that below average spring precipitation limits the growth potential of cheatgrass and the density-dependent mortality observed with average spring precipitation. The early maturation characteristic of cheatgrass appeared to increase the probability that high population densities would mature but with a reduced 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 per m²), however seed output was about 21,600 m² in 1991 and 5,200 m² 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 roots permits later maturation and increased seed production. In this study, the dry spring in 1992 eliminated yellow starthistle's seed production advantage. 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 seeds. 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 result in oscillatory patterns of community dynamics. ·

Literature Cited

Allen, M.F. 1988. Belowground structure: A key to reconstructing a productive arid ecosystem 113-135. In: E.B. Allen (ed.), The reconstruction of disturbed arid lands: An ecological approach. Westview Press, Boulder, Colo.

Call, C.A., and B.A. Roundy. 1991. Perspectives and processes in revegetation of arid and semi arid rangelands. J. Range Manage. 44:543-549.

Callihan, R.H., F.E. Northham, J.B. Johnson, E.L. Michalson, and T.S. Prather. 1989. Yellow starthistle biology and management in pasture and rangeland. University of Idaho. CIS No. 634. Moscow, Ida.

Cordy, D.R. 1954. Nigropallidal encephalomalacia in horses associated with ingestion of yellow starthistle. J. Neuropathology and Exp. Neurology. 13:330-342.

Cousens, R. 1985. A simple model relating yield loss to weed density. Ann. Appl. Biol. 107:239-252.

Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agr. Exp. Sta. Tech. Bull. No. 62.

Eckert, R.E., Jr., J.E. Asher, M.D. Christensen, and R.A. Evans. 1974. Evaluation of the atrazine-fallow technique for weed control and seedling establishment. J. Range Manage. 27:288-292.

Emmerich, F.L., F.H. Tipton, and J.A. Young 1993. Cheatgrass: changing perspectives and management strategies. Rangelands 15:37-40.

Evans, R.A., R.E. Eckert, Jr., and B.L. Kay. 1967. Wheatgrass establishment with paraquat and tillage on downy brome ranges. Weed. Sci. 15:50-55.

Huenneke, L.A., and C. Graham. 1987. A new sticky trap for monitoring seed rain in grasslands. J. Range Manage. 40:370-372.

Hull, A.C., Jr., and J.F. Pechanec. 1947. Cheatgrass: A challenge to range research. J. For. 45:555-564.

Klemmedson, J.O., and J.G. Smith. 1964. Cheatgrass (Bromus tectorum L.). Bot Rev. 30:226-262.

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

Mack, R.N. 1981. Invasion of Bromus tectorum L. into western North America: an ecological chronicle. Agro-ecosystems. 7:145-165.

Mack, R.N., and D.A. Pyke. 1983. The demography of Bromus tectorum: variation in time and space. J. Ecol. 71:69-93.

MacMahon, J.A. 1987. Disturbed lands and ecological theory: an essay about a mutualistic association 221-237. In: W.R. Jordan, M.E. Gilpin, and

J.D. Aber (eds.), Restoration ecology: A synthetic approach to ecological research. Cambridge Univ. Press. New York, N.Y.

Maddox, D.M., A. Mayfield, and N.H. Portiz. 1985. Distribution of yellow starthistle (Centaurea solstitialis) and Russian Knapweed (Centaurea repens). Weed Sci. 33:315-327.

Maxwell, B.D., M.V. Wilson, and S.R. Radosevich. 1988. A population modeling approach to studying leafy spurge (Euphorbia esula). Weed Technol. 2:132-138.

Morrow, L.A., and P.W. Stahlman. 1984. The history and distribution of downy brome (Bromus tectorum) in North America. Weed Sci. 32:2-6.

Palmblad, I.G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecology. 49:26-34.

Pyke, D.A., and S. Archer. 1991. Plant-plant interactions affecting establishment and persistence on revegetated rangeland. J. Range Manage. 44:550-557.

Radosevich, S.R., and J.S. Holt. 1984. Weed ecology, implications for vegetation management, first edition. John Wiley and Sons, New York, N.Y.

Radosevich, S.R. 1987. Methods to study interactions among crops and weeds. Weed Technol. 1:190-198.

Radosevich, S.R., and M.L. Roush. 1990. The role of competition in agriculture, 341-363. In: Grace, J. and Tilman, D. (eds.). Perspectives on plant competition. Academic Press, London.

Roché, B.F., Jr. 1965. Ecological studies of yellow starthistle (Centaurea solstitialis L.) Ph.D. Thesis, Univ. Idaho, Moscow, Ida.

Roché, B.F., Jr., 1983. Range plants: their identification, usefulness, and management. Washington State University. Pullman, Wash.

Roché, B.F. Jr. 1991. Achene dispersal in yellow starthistle (Centaurea solstitialis L.). Northwest Sci. 66:62-65.

Sagar, G.R., and A.M. Mortimer. 1976. An approach to the study of the population dynamics of plants with special reference to weeds. Ann. Appl. Biol. 1:1-47.

Sheley, R.L., R.H. Callihan, and D.C. Thill. 1983. Effects of burning, seeding, fertilization, and herbicide application on yellow starthistle infested rangeland one year after application, p. 45. In: W. Soc. Weed Sci. Res. Prog. Rep.

Sheley, R.L., and L.L. Larson. 1994. Comparative growth and interference between cheatgrass and yellow starthistle seedlings. J. Range Manage. 47:470-474.

Sheley, R.L., L.L. Larson, and D.E. Johnson. 1993. Germination and root dynamics of three range weeds and two forage species. Weed Technol. 7:234-237.

Talbott, C.J. 1987. Distribution and ecological amplitude of selected Centaurea species in eastern Washington. M.S. Thesis, Washington State University, Pullman, Wash.

Thill, D.C. 1979. The influence of certain environmental and edaphic factors on the germination of Bromus tectorum L., Ph.D. Thesis, Oregon State University, Corvallis, Ore.

Watson, A.K. 1985. Integrated management of leafy spurge. 93-104. In: A.K. Watson, (ed.) Leafy spurge. Weed Sci. Soc. Am., Champaign, Ill.

Young, J.A., R.A. Evans, and Weaver. 1976. Estimating potential downy brome competition after wildfires. J. Range Manage. 29:322-325.