Ben F. Roché, Jr., Department of Natural Resource Sciences, Washington State University, Pullman, Washington 99164-6410

Cindy T. Roché, Department of Plant, Soil, and Entomological Sciences, University of Idaho, Moscow, Idaho 83844-2339

and

Roger C. Chapman, Department of Natural Resource Sciences, Washington State University, Pullman, Washington 99164-6410

Impacts of Grassland Habitat on Yellow Starthistle (*Centaurea solstitialis* L.) Invasion

Abstract

Yellow starthistle, a Mediterranean winter annual introduced in southeastern Washington around the turn of the century, expanded rapidly in foothills rangeland of the Blue Mountains in the early 1960s, invading and dominating bluebunch wheatgrass communities on deeper soils of south-facing slopes. Examination of site differences (soil depth and aspect) revealed a high correlation of yellow starthistle with stored soil moisture on south-facing slopes. Yellow starthistle roots grew rapidly and continuously during the winter giving it access to moisture stored deep in the soil profile not depleted by the native plant association. Yellow starthistle seedlings grown under reduced light produced shorter roots, larger leaves, more erect rosettes and fewer flowers than plants grown in full sunlight. Interaction of shade and moisture stress appeared to reduce yellow starthistle invasion of four species of perennial grass treated with four seasonal clipping regimes: May, July, October, and no clipping. The two sod forming cultivars, "Oahe" intermediate wheatgrass and "Luna" pubescent wheatgrass were generally less susceptible to starthistle invasion under all clipping regimes than the two bunchgrasses, "Nordan" crested wheatgrass and "Whitmar" bluebunch wheatgrass. Yellow starthistle invaded Whitmar bluebunch wheatgrass clipped any time of year. All four grass species resisted starthistle invasion if left unclipped. Two critical factors limiting starthistle invasion in eastern Washington appeared to be light intensity at the soil surface during the winter and residual soil moisture during the summer.

Introduction

Yellow starthistle, a facultative winter annual native to the Mediterranean region, is a serious rangeland weed in the western United States (Maddox *et al.* 1985), occupying an estimated 3.7 million ha (Roché and Roché 1991). The first permanent record of yellow starthistle in Washington is an herbarium specimen collected from Seattle in 1898 (Roché and Talbott 1986). Within 10 years, residents of Whiskey Creek drainage of Columbia and Walla Walla counties in southeastern Washington found yellow starthistle in an alfalfa seeding (Roché 1965). After an initial lag period, populations appeared to explode on rangeland in Columbia County, expanding from 60 ha in 1954 to 4,000 ha in 1964 (Roché 1965). Ranchers' fears that yellow starthistle would soon dominate the foothill rangeland of the Blue Mountains of Washington and Oregon prompted studies of yellow starthistle ecology to identify environmental limits to its expansion, and life history characteristics that would provide options for its containment. Unfortunately, yellow starthistle populations continued to expand on Pacific Northwest rangelands (Roché and Roché 1988) and currently receive major emphasis in both county and state level weed control programs.

Vegetation of the natural grasslands in southeastern Washington becomes dormant in summer, avoiding seasonal water stress. In striking contrast, yellow starthistle remains vigorously active, flowering and producing seed in July and August in these communities. In theory, if the native bunchgrass community depletes the soil moisture in the process of completing its growth cycle by early summer as described by Daubenmire (1940), drought would restrict seed production in yellow starthistle, giving the competitive edge to the perennials. Clues to interpreting yellow starthistle's successful invasion of these bunchgrass rangelands appeared to lie in the distinct spatial pattern of yellow starthistle dominance on southeast to southwest-facing slopes, especially areas of moderate to deep silt loam soils and its conspicuous absence on north-facing slopes or sparse stands on shallow soils (Roché 1965).

Beginning with the pattern of yellow starthistle invasion in southeastern Washington, this paper reports a series of observations and studies conducted from 1963 through 1974 on the biology and ecology of yellow starthistle. These included the behavior of yellow starthistle roots during establishment (winter 1966-67), the response of yellow starthistle to reduced light (winter 1969-70), and the differences in yellow starthistle invasion of established perennial grasses under different management systems (1971-74).

Methods and Materials

Natural communities: sites and observations

Natural plant communities in Payne Hollow, Columbia County, Washington, were used to investigate the pattern of invasion of a vegetational mosaic within the *Agropyron-Festuca* zone (Daubenmire 1970) in the foothills of the Blue Mountains. Hot, dry summers characterize the area, and winters are comparatively mild for the latitude (46° 15′ N). Average long-term annual precipitation (1901-1960) was 49.6 cm, with 92% received October through June (Phillips 1970). Within the *Agropyron-Festuca* zone, xeric sites support the *Agropyron-Poa* association and cooler, more mesic sites are dominated by rose (*Rosa* spp.) and snowberry (*Symphoricarpos albus*) (Daubenmire 1970).

The Payne Hollow site was situated at an elevation of 525 m between two cultivated fields, approximately 5 ha fenced separately and historically grazed only occasionally. The soil series was mapped as an Athena silt loam (fine-silty, mixed, mesic Pachic Haploxerolls) (Harrison *et al.* 1973). The soils in the study area appeared as intergrades within the series, including lithosols on the shallow end. Because the mosaic included shallow soils, the study site had never been cultivated. Soil depth and development varied from 12 cm with an undifferentiated profile to 152 cm with well-developed horizons. A soil probe was used to select 10 stands within this range of soil depths which had relatively uniform within stand soil depth. Size and shape of stands were not uniform, but ranged in size from 50 to 200 m in width and length. Slope and aspect were recorded for each stand, ranging from south 3° west to south 59° east on 32 to 50% slopes (Table 1). To determine seasonal water potential changes, two soil samples were analyzed from three random locations within each stand, at 15 cm depth intervals, on 19 May, 2 July and 29 August 1963. Water potentials were determined using standard pressure membrane procedures (Richards 1941) and water content determined gravimetrically. Water content was also determined at −1.5 MPa for samples taken 19 May and 2 July as a rough estimate of state of soil moisture availability to plants.

On 4 April 1963 cover and frequency of yellow starthistle and bluebunch wheatgrass were estimated on 25 plots that measured 2 by 5 dm equally spaced across the longer dimension of each stand, using the canopy-coverage method of Daubenmire (1959). In addition, yellow starthistle density was estimated on half of each plot (2 by 2.5 dm) on 4 April and again on 7 July.

To determine rooting habit and depth of penetration, roots of 10 randomly selected yellow starthistle plants were carefully excavated from deep soil profiles on each of three dates (4 April, 6 July and 28 August).

TABLE 1. Topographic features, soil depth, cover and frequency of bluebunch wheatgrass and yellow starthistle in 10 stands in Payne Hollow, Columbia County, Washington on 4 April 1963, and starthistle density on 7 July 1963.

	Stand									
	1	2	3	4	5	6	7	8	9	10
Aspect	S22E	S22E	S27E	S6E	S59E	S59E	S28E	S9E	S3W	S7E
Slope (%)	42	50	42	41	46	36	41	41	32	35
Soil depth (cm)	12	20	30	46	84	86	98	117	122	122
Bluebunch wheatgrass										
cover (%)	13	33	18	17	40	24	29	2	4	7
frequency (%)	64	80	72	80	96	60	87	12	24	24
Yellow starthistle										
cover (%)	1	6	6	11	16	31	35	27	33	36
frequency (%)	32	100	68	80	100	100	100	100	100	100
density (April) no./0.05m^2	2	10	3	12	17	23	30	27	51	35
density (July) no./0.05m^2	0.4	4	2	6	9	15	10	11	12	9
Survival (%)	18	43	70	49	53	63	34	40	23	26

To investigate aspect influences, another study area was selected at the Payne Hollow site where a knife-edge ridge extending east to west provided an abrupt transition from north- to south-facing slopes. The northerly aspect was dominated by Idaho fescue (*Festuca idahoensis*), while the southerly aspect, normally dominated by bluebunch wheatgrass, was occupied by yellow starthistle. Observations of yellow starthistle density and soil moisture were recorded in April, June, July and August 1963.

Evaluation of factors with artificially established plants

Three studies to test observations in natural communities, including root elongation, response to shade, and invasion of established perennial grass stands, were conducted at the Steffen Research Center at Pullman, Washington, on a south-facing (186°) 5 to 20% slope. The soil was a Palouse silt loam (fine-silty, mixed, mesic Pachic Ultic Haploxerolls) (Donaldson 1980). Average long term annual precipitation was 52 cm, with 90% received October through June (Phillips 1965).

Root elongation study

To observe the rate of root elongation and rosette development in yellow starthistle, plants were grown in 52 mm x 123 cm Pyrex tubes. These were inserted in metal sleeves buried in the soil at a 22.5° angle from vertical. Tubes were filled with silt loam soil from the site. On 26 October 1966, germinated plumed and plumeless yellow starthistle seeds were planted in the top of separate tubes, each replicated 10 times. The tubes were lifted to record root length and rosette diameter on successive dates throughout winter and early spring (Table 5). On 10 June, plants were removed from the tubes by gently flushing the soil from the tubes with a slow stream of water, then tops and roots were oven dried and weighed.

Shade study

To study the effect of light reduction on yellow starthistle, plants were grown under tents of Saran cloth[1] which reduced ambient light levels to 70, 53, 45, 37, 27, 20 and 6% of full sunlight. A-frame tents 183 cm long were constructed with a continuous vent along the top, one end open and the opposite end equipped with a small electric fan for air ventilation. Tents were situated with the lengthwise dimension from east to west on a south-facing, 9% slope. Each treatment was replicated twice. Under each shade condition, yellow starthistle was grown in tubes to measure root growth and directly in the soil to measure plant size and flower production. Tubes were buried in rows 45 cm apart and 68 cm away from the edge of the frame, at 22.5° from vertical as in the root elongation study with 10 tubes per light level. Both direct seeding and seeding in the tubes were done on 3 October 1969. Due to the dry fall, irrigation was necessary for seed germination. Canvas soaker hoses were used to wet the soil to 1.5 cm until the seedlings emerged. The tubes were watered to replace moisture lost to evaporation in the top 5 cm. On 14 November, yellow starthistle plants were thinned to one per tube and to 15 cm apart within rows in the direct seeding, and the shade tents were set over the plants. On 18 November 1969 and 24 March 1970, root length, size of largest leaf, and distance from that leaf to the ground were measured on tube-grown plants. On 7 July 1970, the height, rosette area and number of flowers per plant were recorded for direct seeded plants, which were then harvested. Weight of above ground biomass was recorded for oven dried plants.

Invasion of seeded grass

Four species of rangeland forage grasses were established in plots 2.7 x 2.7 m by seeding 4.7 cm spaced rows during the fall of 1970. These included two sod forming species, Oahe intermediate wheatgrass and Luna pubescent wheatgrass (*Elytrigia intermedia* (Host) Nevski), and two bunchgrasses, Nordan crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schultes) and Whitmar bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love ssp. *inermis* (Scribner & Sm.) A. Love). Nomenclature for grass cultivars follows U.S.D.A. Soil Conservation Service (1992). The four management treatments included clipping at one of three times (May, July, October) and no clipping, simulating light conditions under a canopy of grazed at boot stage, grazed after flowering, grazed at ripe-seed stage, and not grazed. Each treatment was replicated 4 times in a randomized complete block design. Clipped plots were cut to 10 cm height with a Gravely™ mower, except the center m^2 of each plot in which the grass was hand clipped, leaving the yellow starthistle plants

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[1] Chicopee Manufacturing Company, Cornelia, Georgia

unclipped. The clipping regime began fall of 1971 and continued through summer 1974. Each fall beginning in 1971, yellow starthistle seeds were planted 2 cm apart between the center three rows of each plot of the established grasses. The number of seeds available for potential establishment did not remain uniform through the study period because some additional seed was produced by successful yellow starthistle plants in 1972 and 1973. This pattern approximates natural conditions of yellow starthistle invasion.

The number of yellow starthistle plants in each plot was recorded on 1 October 1973, and 21 April and 13 September 1974. General observations of starthistle height, phenology and seed production were also recorded. No data were recorded for 1972 because of severe rodent damage to the plots.

Statistical analyses

The strength of the associations between starthistle cover and soil depth and moisture, and plant response to light reduction were quantified using Pearson's correlation coefficient. Student's t-test was used to compare mean root lengths, rosette diameter and biomass between seedlings from plumed and plumeless seeds in the winter root elongation study. In grass variety experiments, statistical comparison of means with unequal variances and unequal sample sizes was done using Tukey's Honestly Significant Difference Test (Toothaker 1993, Klockars and Sax 1986).

Results and Discussion

Observations in natural communities

In the absence of major environmental disturbances, yellow starthistle had invaded and dominated bluebunch wheatgrass communities on the deeper soils of southeast- to southwest-facing slopes in Payne Hollow. Yellow starthistle cover was positively correlated ($r=0.94$, $P \leq 0.001$) with increasing soil depth (Table 1).

Differences in phenology between bluebunch wheatgrass and yellow starthistle in the study area were striking. On 19 May, bluebunch wheatgrass was flowering and yellow starthistle plants were still small rosettes, 7 to 13 cm in diameter. On 2 July, the bluebunch wheatgrass bore mature seed heads, retaining some yellow-green color only in the lower portions of the bunch whereas yellow starthistle was just entering its reproductive stage, with fewer than 1% of the heads showing yellow flowers. On 29 August, except for shrubs and yellow starthistle, the vegetation had matured and was dormant. Yellow starthistle was still producing a few flowers, although most heads were maturing and dispersal of plumed seeds had begun.

Excavation of yellow starthistle roots from deep soil sites revealed a consistent rooting pattern. Each seedling root developed one primary taproot with short secondary branches. By 4 April, taproots of fall-germinated yellow starthistle plants exceeded 30 cm, although rosettes remained less than 6 cm in diameter. On 6 July, plants growing on deep soil, averaging 25 cm tall, had taproots with a mean depth of 66 cm. The unbranched primary root habit continued through the growing season until 28 August, when the primary taproot was observed to have branched where it reached broken rock 91 cm below the soil surface. On shallow soil sites, root depth was restricted by rock.

In the ten stands on the south-facing slope, yellow starthistle cover and density were related to soil moisture. Cover of yellow starthistle was highly correlated with total soil moisture on 19 May ($r=0.93$, $P \leq 0.001$), on 2 July ($r=0.92$, $P \leq 0.001$) and on 29 August ($r=0.95$, $P \leq 0.001$) (Tables 1 to 4). Correlations between yellow starthistle cover and soil moisture in excess of -1.5 MPa on 19 May ($r=0.88$, $P \leq 0.01$) and 2 July ($r=0.75$, $P \leq 0.05$) were also significant. Percent survival of yellow starthistle between 4 April and 7 July did not increase with soil depth (Table 1). Density reduction was apparently due to severe depletion of soil water in the top 30 cm in all soils (Tables 2 and 3): by 19 May, only 1.6 cm water remained in the shallowest soil (12 cm) and by 2 July water in the top 30 cm of soil in all stands was held at tensions greater than -1.5 MPa. Although yellow starthistle roots undoubtedly extract soil moisture at greater tensions, these values indicate a pattern of soil moisture depletion. Because the soil water potentials from which mature yellow starthistle can extract water are not known, -1.5 MPa was used as a recognizable reference point.

Root elongation study

The rooting pattern of yellow starthistle seedlings in observation tubes was the same as roots excavated in the natural community: one main taproot with short side branches. Mean root length of

TABLE 2. Soil moisture (cm) by 15 cm depth intervals in 10 stands in Payne Hollow, Columbia County, Washington, on 19 May 1963.

Soil Depth (cm)	Stand									
	1	2	3	4	5	6	7	8	9	10
0-15	1.6	2.7	1.2	2.6	2.9	2.9	2.7	2.7	2.9	2.8
15-30		1.0	1.9	3.5	3.9	3.7	3.6	3.7	3.6	3.7
30-45				3.7	4.0	3.8	3.7	3.7	3.5	3.7
45-60					4.1	3.9	3.8	3.8	3.6	3.7
60-75					4.0	3.7	3.7	3.7	3.3	3.5
75-90					1.8	2.5	4.1	3.9	3.4	3.5
90-105							1.8	4.1	3.4	3.6
105-122								2.7	2.7	3.7
Total	1.6	3.7	3.1	9.8	20.8	20.5	23.2	28.3	26.4	28.2
−1.5 MPa	0.0	3.2	0.05	5.4	8.6	9.3	9.6	16.6	11.3	13.7

TABLE 3. Soil moisture (cm) by 15 cm depth intervals in 10 stands in Payne Hollow, Columbia County, Washington, on 2 July 1963.

Soil Depth (cm)	Stand									
	1	2	3	4	5	6	7	8	9	10
0-15	1.1	1.4	0.7	1.1	1.7	1.7	1.7	1.9	1.8	1.9
15-30		0.6	1.1	1.8	2.1	1.9	2.1	2.2	1.9	2.0
30-45				3.0	2.1	2.0	2.1	2.2	2.0	2.0
45-60					2.2	2.2	2.3	2.4	2.2	2.1
60-75					2.3	1.9	2.2	2.3	1.9	2.0
75-90					0.8	1.2	2.4	2.6	1.8	2.0
90-105							1.0	2.6	2.0	2.4
105-122								1.8	1.7	2.4
Total	1.1	2.0	1.8	5.8	11.3	11.0	13.8	18.0	15.3	16.7
−1.5 MPa	0.0	0.02	0.0	0.7	1.3	2.2	2.8	8.6	4.7	6.7

TABLE 4. Soil moisture (cm) by 15 cm depth intervals in 10 stands in Payne Hollow, Columbia County, Washington, on 29 August 1963.

Soil Depth (cm)	Stand									
	1	2	3	4	5	6	7	8	9	10
0-15	0.5	1.0	0.2	1.0	1.1	1.1	0.9	1.0	1.3	1.1
15-30		0.4	1.1	1.3	1.5	1.5	1.6	1.4	1.5	1.5
30-45				1.2	1.6	1.7	1.9	1.5	1.5	1.5
45-60					1.5	1.8	1.9	1.5	1.7	1.6
60-75					0.7	1.5	1.5	1.4	1.5	1.5
75-90						0.9	0.6	1.4	1.4	1.4
90-105								1.4	1.5	1.5
105-122								0.9	1.2	1.4
Total	0.5	1.4	1.3	3.5	7.9	8.4	9.8	10.5	11.6	11.5

2 month old plants exceeded 30 cm and during the next month of growth (by 19 January); they doubled their length to 67 cm. Growth of roots of plants from plumeless seed was not significantly different than those from plumed seeds ($P \leq 0.05$). On 19 January, roots of 2 plants from plumeless seeds had grow out the bottom of the 123 cm long tubes; this number increased to 5 "plumeless" roots and 2 "plumed" roots by 24 February (Table 5). By 10 April, roots of all the plants from plumeless seeds and 80% of plants from plumed seeds had exceeded the length of the tubes. Mean root growth generally exceeded 0.5 cm per day after the plants were a month old (Table 5). During March, yellow starthistle roots grew 1.0 to 2.1 cm per day (Table 5). Roots of cheatgrass (*Bromus tectorum*) seedlings grown in the same tubes at the same site in a different year (4 October 1963 to 2 June 1964) also grew rapidly during the winter but showed a different growth form: cheatgrass developed numerous adventitious roots in contrast to yellow starthistle's taproot (Harris 1965, 1967). Because cheatgrass formed normal branching in the tubes, and yellow starthistle roots in the natural community had the same form as those in the tubes, we concluded that the tubes did not appreciably alter the rooting pattern under winter growth conditions.

Yellow starthistle's growth strategy appeared to allocate resources first to root extension, then later to leaf expansion. Rosettes grew slowly during the first 86 days, with the starting diameters of 1.1 cm (plumeless) and 1.2 cm (plumed) on 4 November increasing only to 2.6 cm (plumeless) and 2.3 cm (plumed) by 19 January (Table 5). During this time the roots extended their length more than 10 fold, from 6.1 cm to 67.3 cm. Between 19 January and 10 April, rosettes grew more rapidly, increasing to 8.4 cm. The size difference between rosettes from plumed and plumeless seeds was not significant (Table 5). Harris (1977) reported a similar pattern in cheatgrass and medusahead (*Taeniatherum asperum*), both of which grew primary roots during winter when leaves showed little growth. However, by 10 June, when starthistle began to elongate a flowering stem, aboveground biomass was significantly greater than below ground biomass ($P \leq 0.01$). Differences between plumeless (rosette 2.9 g, root 2.2 g) and plumed (rosette 2.9 g, root 2.3 g) were not significant.

TABLE 5. Mean rosette diameter and mean daily root growth of fall germinated yellow starthistle grown in tubes at Pullman, Washington, from 26 October 1966 to 10 April 1967.

		Plumed seed			Plumeless seed		
Date	Age (days)	Rosette diameter (cm)	Root growth† (cm/day)	Roots >123 cm (%)	Rosette diameter (cm)	Root growth† (cm/day)	Roots >123 cm (%)
4 Nov 66	10	1.1 (0.03)*			1.2 (0.04)		
8 Nov 66	14	1.2 (0.04)	0.2 (0.1)		1.2 (0.05)	0.3 (0.1)	
15 Nov 66	21	1.3 (0.04)	0.2 (0.1)		1.4 (0.04)	0.4 (0.1)	
22 Nov 66	28	1.5 (0.05)	0.3 (0.1)		1.5 (0.1)	0.5 (0.04)	
29 Nov 66	35	1.7 (0.1)	0.5 (0.1)		1.7 (0.1)	0.8 (0.1)	
8 Dec 66	44	1.7 (0.1)	0.6 (0.1)		1.8 (0.1)	0.8 (0.1)	
22 Dec 66	58	1.8 (0.1)	0.7 (0.1)		1.9 (0.1)	0.8 (0.1)	
4 Jan 67	71	1.8 (0.1)	0.6 (0.1)		1.9 (0.1)	0.7 (0.1)	
19 Jan 67	86	2.3 (0.1)	1.4 (0.2)		2.6 (0.1)	1.9 (0.3)	20
24 Feb 67	122	2.7 (0.1)	0.7 (0.1)	20	3.1 (0.1)	0.9 (0.2)	50
6 Mar 67	132	3.2 (0.02)	1.3 (0.1)	20	3.6 (0.2)	1.5 (0.1)	60
15 Mar 67	141	3.7 (0.2)	1.4 (0.2)	20	4.0 (0.2)	1.8 (0.5)	80
24 Mar 67	150	5.0 (0.2)	1.0 (0.1)	40	5.2 (0.2)	2.1 (0.1)	90
3 Apr 67	160	6.6 (0.3)	1.6 (0.5)	80	6.2 (0.3)		90
10 Apr 67	167	8.6 (0.3)	1.1 (0.4)	80	8.2 (0.4)		100

† Calculation of mean root growth per day includes only those roots which had not reached the end of the tube by the beginning of the growth period. No mean was calculated when fewer than two roots remained inside the tubes.

* Numbers in parentheses represent the Standard Error.

Availability of soil moisture at crucial times often determines whether plants succeed (Daubenmire 1972). Cheatgrass, a prior invader of the same grasslands, succeeded because its rapid root growth throughout the winter enabled it to avoid drought by entering summer dormancy as seeds 5 to 7 weeks earlier than bluebunch wheatgrass (Harris 1977). However, yellow starthistle's later flowering produced mature seed 6 to 8 weeks later than bluebunch wheatgrass, requiring a different strategy to overcome the summer drought. In the bluebunch wheatgrass community, the growing season which ends in early summer appears to be related to species phenology and rooting zone soil moisture depletion. In southwestern Oregon rangeland communities, yellow starthistle invaded annual grasslands by utilizing residual soil moisture left by earlier maturing annuals (Borman *et al.* 1992). In the same manner, moisture in deeper soils not used by the native plant community before entering summer dormancy may allow yellow starthistle invasion in southeastern Washington.

The *Agropyron-Festuca* and *Agropyron-Poa* associations lack shrubs, except for scattered rabbitbrush (*Chrysothamnus* spp.). In grassland communities of the Great Basin and Columbia Plateau, native shrubs and forbs are deeper rooted than the large perennial bunchgrasses such as bluebunch wheatgrass (Dobrowolski *et al.* 1990). Daubenmire (1970) reported that in the drier area immediately west of the *Agropyron-Poa* zone, moisture percolated below the reach of grass roots often enough to maintain a stand of big sagebrush (*Artemisia tridentata*) through the rainless summer. From this he suspected that scattered rabbitbrush in the *Agropyron-Poa* zone indicated the existence of unused resources in the form of deeper soil moisture.

If soil moisture were the only factor in successful yellow starthistle invasion, starthistle should have invaded north-facing slopes. In spite of differences in vegetation, observations of soil moisture (total and depth distribution) on 9 June, 2 July and 29 August did not differ between the fescue-dominated north-facing slope and the starthistle-dominated south-facing slope. This observation is consistent with research by Borman and others (1992) who reported similar moisture extraction by yellow starthistle and perennial grasses to depths of 60 cm. Because yellow starthistle seed fell in the perennial grass area, aspect-related factors of light and temperature might have influenced starthistle establishment.

Shade study

Under reduced light, seedling yellow starthistle developed large leaves in upright rosettes (measured as the distance from the tip of the largest leaf to the ground) in contrast to compact, decumbent rosettes in full light (Figure 1). Leaf size and distance to the ground were negatively correlated with light level ($r=-0.95$, size; -0.93, distance; $P \leq 0.001$). A change in growth habit from prostrate to erect leaves in response to shade (Palmer 1956, Harper 1977) and increased leaf area has been reported for other species (Boyd and Murray 1982, Dall'Armellina and Zimdahl 1988). By 24 March, two plants under 6% light and one plant under 20% light had died. Root length correlated positively ($r=0.94$, $P \leq 0.001$) with light level (Figure 1). Measurements made on 8 July showed that height, rosette area and above ground biomass declined with decreasing light ($r=0.80$, height; $r=0.91$, area; $r=0.93$, biomass; $P \leq 0.01$) (Figure 1). Shade reduced reproductive capacity as shown by failure of plants grown under 6% full sunlight to flower. Mean number of flowers increased with light: 0.3 flowers per plant under 20-27% light; 0.6, 37-45%; 1.6, 55%; 1.1, 70%; and 6, 100%.

Prodan (1930) characterized yellow starthistle as an obligate heliophyte, probably referring to starthistle's prevalence in warm sunny habitats. In Washington, yellow starthistle rosettes appeared to exploit favorable microclimatic conditions at the soil surface on south-facing slopes, allowing it to develop rooting depth during winter while moisture is not limiting. In a study of winter annuals, Regehr and Bazzaz (1976) found that not only was rosette leaf temperature significantly higher than air temperature, but net photosynthesis was maintained even at low irradiance and temperatures down to the point of freezing of leaf tissue. In contrast, studies of bluebunch wheatgrass maintenance of photosynthetically active tissue through the winter in the Great Basin concluded that its primary function is to facilitate faster growth in the early spring (Nowak and Caldwell 1984). Yellow starthistle accumulated enough energy during the winter to grow actively, especially in root development. Photosynthesis by starthistle rosettes on north-facing slopes would be reduced directly by lower irradiation and indirectly by lower leaf temperatures,

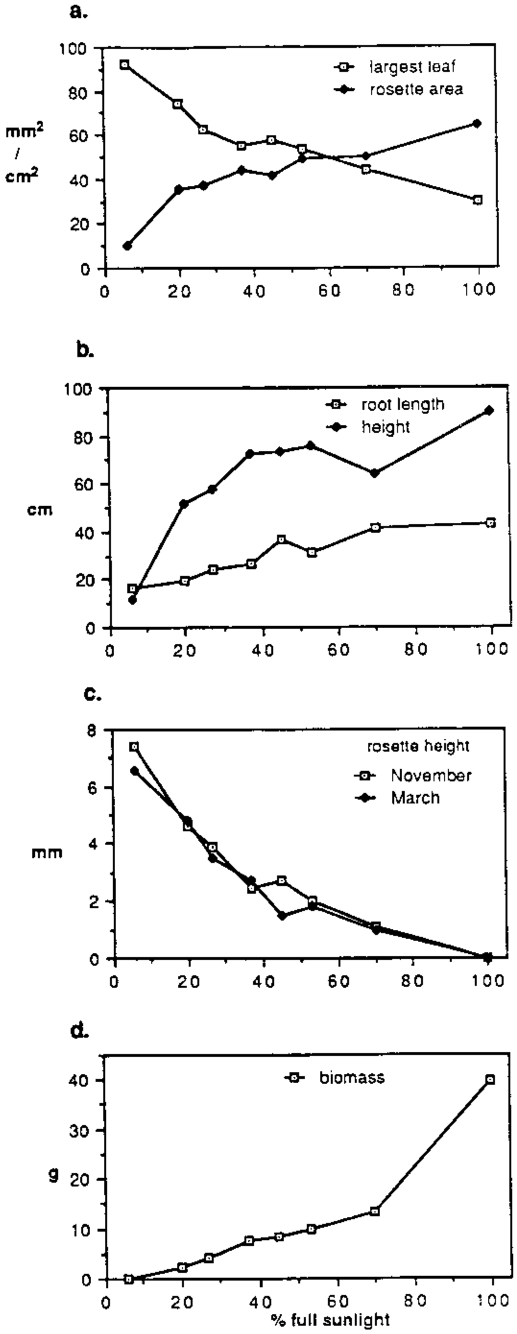

Figure 1. Trends of plant characteristics of yellow starthistle grown under shade tents in Pullman, Washington: a) size of largest leaf in mm^2 and rosette area in cm^2 on 18 November; b) root length in cm on 18 November and plant height in cm on 7 July; c) distance from rosette leaf to ground in mm on 18 November and 24 March; and d) total above ground biomass in g on 7 July.

which likely accounts for failure to invade native vegetation on the north aspect in Payne Hollow.

Dillon (1967) reported dramatic differences in natural revegetation of north- and south-facing steep (65%) slopes in Walla Walla County. In 1901, a railroad fill was constructed of silt loam soil and livestock were fenced out. Sixty-four years later, the north-facing slope was 80% bluebunch wheatgrass and 20% Sandberg bluegrass (*Poa sandbergii*), while the south-facing slope was dominated by annuals: 60% cheatgrass, 30% *Centaurea* (yellow starthistle) and 5% tumble mustard (*Sisymbrium altissimum*).

Invasion of seeded grass

In 1973 no yellow starthistle plants invaded any of the established perennial grass varieties that were not clipped (Table 6). Levels of yellow starthistle invasion were not significantly different in fall and summer clipping of the sod-forming grasses and spring clipping of Luna pubescent wheatgrass (Table 6). Clipped bunchgrasses were much more susceptible to invasion than the sod-forming grasses. Yellow starthistle was particularly successful in spring or fall clipped Whitmar bluebunch wheatgrass. Observations of plant size, relative vigor and seed production revealed that yellow starthistle in the sod-forming grasses were smaller, weaker and produced less seed. However, plants that survived to October produced some seed.

In 1974 counts of yellow starthistle plants in April and September showed high mortality during the summer (Tables 7 and 8). Although starthistle seedlings were present in all treatments in April, the number remaining in September 1974 in the unclipped plots was similar to the number in fall 1973. Summer and fall clipping of the sod-forming species allowed less starthistle survival than spring clipping (Table 8). Whitmar bluebunch wheatgrass clipped during any season was susceptible to invasion, as was Nordan crested wheatgrass clipped during spring or summer and Luna pubescent and Oahe intermediate wheatgrasses clipped in the spring (Table 8). In April yellow starthistle seedlings in plots shaded by grass litter and standing crop appeared weak and spindly with erect yellowish-green leaves compared to vigorous blue-green leaves of prostrate rosettes grown in grass-free control plots. The rosette growth form is particularly vulnerable to shading by overtopping vegetation (Regehr and Bazzaz 1976). The similarity

TABLE 6. Mean number of yellow starthistle plants in the center m² of seeded grass variety plots ± Standard Deviation (S.D.) by clipping regime on 1 October 1973.

Grass	Clipping Regime			
	None	Fall	Summer	Spring
Luna	0a	5.0 ± 9.3a	5.0 ± 7.1a	1.8 ± 2.9a
Oahe	0a	6.8 ± 6.2a	4.8 ± 3.2a	7.5 ± 5.3a
Nordan	0a	17.0 ± 7.6bc	10.3 ± 8.4abc	21.8 ± 14.2cd
Whitmar	0a	26.3 ± 19.7bcde	17.5 ± 17.1bcd	31.8 ± 23.4e

Means are compared across rows and columns so that those followed by the same letters anywhere in the table are not significantly different, as determined by the HSD test at the 5% level of significance.

TABLE 7. Mean number of yellow starthistle plants in the center m² of seeded grass variety plots ± Standard Deviation (S.D.) by clipping regime on 21 April 1974.

Grass	Clipping Regime			
	None	Fall	Summer	Spring
Luna	20.5 ± 14.2b	73.8 ± 92.9e	53.0 ± 73.6e	84.8 ± 33.1f
Oahe	51.8± 82.9e	76.5 ± 51.2e	61.5 ± 38.5d	52.5 ± 62.9e
Nordan	11.5± 12.2a	85.5 ± 105.7f	85.0 ± 42.1f	51.5 ± 30.8e
Whitmar	5.3± 1.7a	64.3 ± 51.7d	55.8 ± 62.3cd	70.0 ± 71.5de

Means are compared across rows and columns so that those followed by the same letters anywhere in the table are not significantly different, as determined by the HSD test at the 5% level of significance.

TABLE 8. Mean number of yellow starthistle plants in the center m² of seeded grass variety plots ± Standard Deviation (S.D.) by clipping regime on 13 September 1974.

Grass	Clipping Regime			
	None	Fall	Summer	Spring
Luna	1.0 ± 1.5a	7.0 ± 12.1ab	0 ± 0a	30.8 ± 25.3e
Oahe	0.5± 0.6a	1.0 ± 2.0ab	0.8 ± 1.5a	14.8 ± 11.2bc
Nordan	0.3± 0.5a	5.8 ± 10.8a	30.0 ± 1.5e	44.0 ± 32.9ef
Whitmar	0.8± 1.5a	43.3 ± 36.7ef	19.3 ± 33.5d	59.7 ± 50.8g

Means are compared across rows and columns so that those followed by the same letters anywhere in the table are not significantly different. as determined by the HSD test at the 5% level of significance.

of yellow starthistle seedlings in unclipped perennial grass stands to plants grown under tents implicated shade as the stress factor. The failure of starthistle seedlings to develop normal rooting depth under shade tents implicated drought stress as the reason starthistle seedlings died between April and September in perennial grass stands on deep silt loam soil. Unfortunately, direct comparison of shade conditions could not be made because equipment to appropriately measure photosynthetically active radiation (Patterson 1979) was not available for the study.

Conclusions

A survey of the distribution of the 54,000 ha of yellow starthistle in eastern Washington (Roché and Roché 1988) suggested that the factors identified in the Payne Hollow study may be important determinants for starthistle invasion over a broader area of eastern Washington. The North American yellow starthistle invasion that reaches its supremacy in California (Maddox *et al.* 1985) appears to approach the northern limits of its ecologic amplitude at 48° 45′ N Lat. in northeastern Washington (Talbott 1987). Approximately 80 years after its introduction, 93% of the yellow starthistle in Washington remained south of the Snake River (Roché and Roché 1988) within the *Agropyron/Festuca* zone (Daubenmire 1970). With increasing distance north from this zone, yellow starthistle invasion has been restricted to warmer sites. In northeastern Washington, yellow starthistle has been limited primarily to steep south-facing slopes of natural grasslands, in contrast to its wider distribution in southeastern Washington on gentle slopes and bottomlands (Talbott 1987). The critical factors at the northern limits of its ecologic amplitude appear to be short and longwave radiation during the winter, both of which are less limiting on steep south-facing slopes at north latitudes. These observations concur with reports that yellow starthistle did not persist in northern Europe, even following repeated introductions (Prodan 1930).

In the hotter, drier climate of southcentral Washington, yellow starthistle has invaded shrub steppe rangelands only where disturbance eliminated or severely reduced perennial vegetation or in topographic positions with deep soils that receive and store additional water (Talbott 1987).

Optimal conditions in southeastern Washington natural grasslands, i.e., south-facing slopes and deep silt loam soils, indicated that dual requirements of light for winter growth and soil moisture for reproduction during the summer drought period may be the critical limiting factors for yellow starthistle.

The implications of these studies are that, on deeper soils and climatic conditions of eastern Washington, a stand of adapted perennial grass can limit yellow starthistle if it is managed to provide two conditions: 1) shade over the soil surface from fall through spring and 2) soil water depletion from late spring through summer. Shallow soils do not have the potential to support enough vegetation to shade yellow starthistle, but in the absence of summer precipitation, perennials deplete soil moisture before normal starthistle maturation, limiting its competitiveness.

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