

## Plant Development, Water Relations, and Carbon Allocation of Heart-Podded Hoary Cress

Richard F. Miller,\* Tony J. Svejcar, Jeffrey A. Rose, and Michael L. McInnis

### ABSTRACT

Attempts to control the noxious weed heart-podded hoary cress [*Cardaria draba* (L.) Desv.] in the Pacific Northwest have been relatively ineffective, and this species has expanded its distribution from irrigated hayland onto adjacent semiarid rangelands. The objective of this study was to define the seasonal pattern of development and biological activity of heart-podded hoary cress growing on semiarid rangeland. The study was conducted in the field over a 2-yr period on a terrace site that has deep Cumulic Haploxeroll soil and an adjacent upland site that has a shallow Lithic Argixeroll soil. Soil water content, phenology, xylem pressure potential and leaf conductance were measured at both sites. Above- and belowground biomass and spring C allocation pattern, determined by labeling plants with  $^{13}\text{C}$ , were measured at the terrace location. Regardless of location, no heart-podded hoary cress seedlings were found; all shoots developed from rhizome buds. The majority (76%) of heart-podded hoary cress biomass was located belowground. Although drought occurred earlier on the upland than the terrace site, phenology was similar on the two sites. Carbon was translocated to belowground tissues within 1 h of labeling and reached peak accumulation within 24 h. The greatest  $^{13}\text{C}$  enrichment of roots and rhizomes occurred during the flowering stage. The peak in belowground C allocation occurred at a stage when leaf conductance was declining rapidly. The short period of maximum C allocation to belowground tissue, the large proportion of belowground tissue, and the wide variation of phenology among plants at a given time may account for the difficulty in chemically controlling this species.

R. F. Miller and J. A. Rose, Dep. of Rangeland Resources, Oregon State Univ., and T. J. Svejcar, USDA-ARS, Eastern Oregon Agric. Res. Ctr., HC 71 4.51 Hwy 205, Burns, OR 97720; and M. L. McInnis, Dep. of Rangeland Resources, Oregon State Univ., Corvallis, OR 97331. The Eastern Oregon Agric. Res. Ctr., including the Burns and Union stations, is jointly operated by the Oregon Agric. Exp. Stn. of Oregon State Univ. and the USDA-ARS. Funding for this project was provided by the USDA Integrated Pest Management Project (CRIS No. 0136449) and the Eastern Oregon Agric. Res. Ctr. Tech. 10,361. Received 5 Apr. 1993. \*Corresponding author.

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**H**EART-PODDED HOARY CRESS [*Cardaria draba* (L.) Desv.], also commonly known as whitetop, is a noxious, introduced weed. It is a deep-rooted perennial, capable of sexual reproduction from seed and vegetative propagation from rhizomes (Mulligan and Findlay, 1974). Since its introduction from Europe in 1862, this species has invaded cropland and rangeland in British Columbia, Alberta, Saskatchewan, Washington, Oregon, Idaho, northern California, and Nevada. Of three primary species of hoary cress, heart-podded hoary cress has the widest distribution in the USA (Mulligan and Findlay, 1974) and is the most abundant in Oregon (T. Whitson, personal communication, 1984). It grows in open areas and is adapted to alkali soils. Heart-podded hoary cress can produce large numbers of viable seed and vegetative shoots which allows it to rapidly invade cultivated and disturbed areas (Selleck, 1965). It can gradually dominate stands of alfalfa and has a major economic impact on crop yields (Scrufield, 1962; Mulligan and Findlay, 1974; PNW Ext., 1974). *Cardaria* spp. are adapted to moist sites, and their growth is reduced in semiarid environments in Saskatchewan (Selleck, 1965). In the USA, however, heart-podded hoary cress commonly migrates from cultivated fields to adjacent semiarid upland sites dominated by big sagebrush (*Artemisia tridentata* Nutt.) communities. In eastern Oregon, heart-podded hoary cress occupies >100 000 ha (T. Whitson, personal communication, 1984) and grows in big sagebrush communities in different seral stages and in communities seeded to crested wheatgrass [*Agropyron desertorum* (Fischer ex Link) Schultes and *A. cristatum* (L.) Gaertner]. Selleck (1965) stated that shrubs were the most effective compet-

**Abbreviations:** PDB, Pee Dee belemnite;  $\delta^{13}\text{C}$ , carbon isotope ratio;  $\psi$ , xylem pressure potential.

itors with heart-podded hoary cress, and Rosenfels and Headley (1944) concluded that grasses were ineffective competitors. Attempts to control heart-podded hoary cress have included both chemical and biological treatments (Sexsmith, 1964; Lipa, 1978; Sobhian, 1978; Geronimo, 1978; Brattain and Fay, 1980). The effectiveness of chemical control has been highly variable and unpredictable. Chemical treatments usually must be repeated several times, or combined with tillage for successful control; thus, the treatments are often prohibitively expensive on rangelands. To date, biological control methods have not been effective.

Variability of effectiveness among control treatments indicates that more information on the basic biology of this species is needed to develop effective control measures. Specific objectives of this study were to (i) evaluate the adaptability of heart-podded hoary cress to semiarid upland sites, (ii) define the role of sexual vs. vegetative reproduction in stand maintenance, (iii) determine the distribution of above- and belowground biomass and (iv) define the seasonal pattern of biological activity.

## MATERIALS AND METHODS

The study site is on the south slope of the Wallowa Mountains,  $\approx 5$  km north of Keating, OR, which is situated 25 km northeast of Baker City in northeastern Oregon. Climate is characterized by cold wet winters and hot dry summers. The growing season for heart-podded hoary cress typically begins in early March and ends in mid to late June. The nearest weather station with a similar geographic position is located 36 km east of the study site in Richland, OR. Although weather varies across short distances in this area, precipitation throughout this region was below average during the 1987–1988 crop year (Sept. to June) and near average during the 1988–1989 crop year. In Richland, crop-year precipitation for 1987–1988 and 1988–1989 was 46 and 82% of the 36-yr mean, respectively. Temperatures in the region generally were warmer in 1988 than 1989. Mean maximum and minimum air temperatures recorded at the Richland station were 16 and  $-1^{\circ}\text{C}$  in 1988 and 14 and  $-2^{\circ}\text{C}$  in 1989, respectively. The experiment was designed as a randomized complete block in a strip-plot or split-block arrangement (Peterson, 1976, 1985) across two sites with five replicates. A strip-plot arrangement was used because the terrace and upland sites could not be randomized within blocks. The terrace site had no slope, and the fine silty-loam Cumulic Haploxeroll soils were  $>120$  cm deep. The plant community at the terrace site was dominated by basin big sagebrush (*Artemisia tridentata* subsp. *tridentata* Nutt.) and crested wheatgrass. A few basin wildrye [*Leymus cinereus* (Scribn. & Merr.) A. Löve] plants were present in the understory. The upland site was located  $\approx 10$  m above the terrace site on a 15% west-facing slope with a loamy-skeletal Lithic Argixeroll soil averaging 50 cm in depth. The plant community on the upland site was dominated by Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle) and crested wheatgrass. A few plants of bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve] and Thurber needlegrass (*Stipa thurberiana* Piper) were present. The experiment was conducted during the 1988 and 1989 growing seasons. Soil water availability was determined gravimetrically from five samples collected at 2.5 to 20 cm, 20 to 40 cm, and 40 to 60 cm within each block on each site for each sampling date. In the fall of 1987 and 1988, soil water was also measured at 60 to 80 cm, 80 to 100 cm, and 100 to 120 cm on the terrace site. Soil water release curves were developed using a pressure-plate membrane to estimate soil water potential for each of the three upper soil depths on both sites. Soil temperatures also were recorded at the 15-, 30-,

and 45-cm depths at both sites during late morning on each sampling date. Air temperature and relative humidity were measured with a battery-powered psychrometer on each sampling date.

During the two periods of data collection (October to June), phenology was recorded for heart-podded hoary cress plants in five permanently marked 0.25-m<sup>2</sup> plots located in each block on both sites on six dates. Winter survival of leaves initiated in the fall was evaluated by marking five leaves with indelible ink in each plot in October of 1987 and 1988. Leaves were marked only on the terrace site because few leaves developed during fall on the upland site in either year.

Above- and belowground biomass was measured during flowering in three of the five blocks on the terrace site in 1989. Five 1.0-m<sup>2</sup> plots were located within each block in the middle of pure stands of heart-podded hoary cress. Aboveground biomass was harvested from the 1.0-m<sup>2</sup> plots by clipping to ground level. Plant material was dried at 60°C for 48 h and weighed. A root and rhizome sample was collected to a depth of 60 cm in each of the 1-m<sup>2</sup> plots using a 6.4-cm-diam. sampling probe. Samples were separated for three depths (0 to 20, 20 to 40, and 40 to 60 cm), soaked in buckets, washed in a root washer and dried at 60°C for 48 h. Roots and rhizomes were then separated and weighed.

Plant water relations were recorded on five dates during each of the two growing seasons within each block on both sites. Xylem pressure potential ( $\psi$ ) was measured on a mature green leaf within each block  $\times$  site combination with a pressure chamber (Scholander et al., 1965) at predawn (0430 h) and midday (1400 h). Leaf samples were removed from the plants and immediately measured in the pressure chamber. Leaf conductance was measured with a steady state porometer (Model LI-1600, Li-Cor, Lincoln, NE) on a single leaf for each block  $\times$  site combination following completion of the midday measurements of  $\psi$ .

The seasonal pattern of C allocation from leaves to belowground components was determined by labeling plants with <sup>13</sup>C (Svejcar et al., 1990) on the terrace site. Five plots were labeled at five phenological stages in both years. The phenological stages measured were rosette (vegetative), bolt (reproductive shoots elongating and flower buds visible), early bloom (stem elongated and petals emerging from buds), flowering and seed formation. Chambers (30 by 45 by 30 cm) were placed over the plots early in the day for  $\approx 0.5$  h. Relative change in CO<sub>2</sub> concentration inside the chambers was monitored with an LI-6000 portable infrared photosynthesis system (note that the LI-6000 underestimates <sup>13</sup>CO<sub>2</sub> concentrations). A gas-tight syringe was used to inject 40 mL of 99 atom % <sup>13</sup>CO<sub>2</sub> into the chambers. Total CO<sub>2</sub> inside the chambers increased to 460  $\mu\text{L L}^{-1}$  immediately following injection, then decreased to  $<200$   $\mu\text{L L}^{-1}$  by the end of each labeling period. Roots, rhizomes, and the current year's shoot material were collected at 1, 24, 72, and 120 h after labeling in 1988 and 1, 24, and 72 h after labeling in 1989 (levels of <sup>13</sup>CO<sub>2</sub> did not significantly change between 72 and 120 h). Roots and rhizomes of labeled and five additional unlabeled plants (for measurement of baseline <sup>13</sup>C levels) were collected to a depth of 30 cm and placed on dry ice. Following collection, plants were brought in from the field and separated into below- and aboveground parts. Roots and rhizomes were thoroughly washed to remove adhering soil particles and soaked in 0.8 M HCl for  $\approx 1$  h to remove any exogenous carbonates from the root surface (Svejcar et al., 1990). Both root and shoot samples were dried for 72 h at 60°C and ground in a Cyclone sample mill (Udy Corp., Fort Collins, CO) to 0.5 mm. Samples were analyzed for <sup>12</sup>C/<sup>13</sup>C ratio with an isotope ratioing mass spectrometer at the Stable Isotope Laboratory at the University of Utah, and results were calculated as C isotope ratio ( $\delta^{13}\text{C}$ ), which is expressed as per mil (‰) relative to the Pee Dee belemnite (PDB) international standard (derived from a lime-



stone fossil of *Belemnitella americana* from the Cretaceous Pee Dee formation in South Carolina). Precision of the analysis was  $\pm 0.01\%$  and sample replication averaged  $\pm 0.1\%$ .

Statistically significant differences among means were identified using analysis of variance (ANOVA) at  $P \leq 0.05$  for a randomized complete block design in a strip-plot arrangement, split by years. When measurements were recorded over time, time was set as a variable in addition to site. Means were separated using least significance difference (LSD) at  $P \leq 0.05$  as described by Petersen (1985) for a strip-plot design.

## RESULTS AND DISCUSSION

Although precipitation was less the first year, soil water content at the 2.5- to 40-cm depth did not differ between years. Soil water content averaged across dates was not significantly different between sites, except for the 2.5- to 20-cm layer during the first growing season. Soil water content declined significantly during the growing season for all profiles in both years; however, there was a significant date  $\times$  site interaction. Soil water concentration in the 2.5- to 20-cm depth generally was greater on the terrace site during the first half of the growing season (Fig. 1). Late in the growing season, soil water percentage was similar between sites. Soil water percentage was greater several weeks later during the 1989 than the 1988 growing season (June), reflecting greater precipitation and cooler temperatures in the region in 1989 compared with 1988.

Although soil water content was low during the fall in the upper 120 cm on the terrace site, new leaves developed in October 1987 and 1988. Only a few plants developed leaf tissue on the upland site. Leaf tissue did not survive over winter in either year. Terminal buds just below the soil surface initiated new leaf growth in late March. Early de-

velopment of leaves in the spring from rhizomes directly beneath the soil surface probably contributes to the competitiveness of heart-podded hoary cress. Reproductive stems began to develop by late April, became fully elongated by early May and flowered by mid May. Seeds were in the milk to dough stage by early June. Although predawn  $\psi$  was near  $-1.5$  MPa on the upland site by mid May of 1988 (Fig. 2), heart-podded hoary cress completed flowering and seed development. Phenology on the terrace and upland sites was similar during the 2 yr, despite differences in  $\psi$ . Leaf development on the upland site was more advanced than on the terrace site only during the early part of the growing season. Considerable phenological variability occurred within sites. When the majority of the stand was flowering, some plants were still in the rosette stage.

Shoot growth of heart-podded hoary cress on both sites was initiated from rhizomes. Although heart-podded hoary cress can produce large amounts of viable seed (Selleck, 1965; Mulligan and Findlay, 1974), no plants in the permanent phenology plots developed from seed; however, heart-podded hoary cress seedlings did grow on disturbed soils adjacent to badger holes and gopher mounds on both sites in 1988 and 1989. Another study indicated that seedling establishment of heart-podded hoary cress was greatest in annual communities and on disturbed soil surfaces (Larson et al., 1989).

Seventy-six percent of heart-podded hoary cress biomass was located belowground. Zobel and Antos (1987) reported similar values for other rhizomatous forbs. Heart-podded hoary cress belowground biomass ( $1237 \text{ g m}^{-2}$ ) consisted of 56% rhizomes and 44% roots. The majority of the root biomass was located in the upper 20 cm, whereas rhizomes were more evenly distributed throughout the upper 60 cm of the soil profile (Table 1). The large proportion of biomass allocation to roots and rhizomes provides

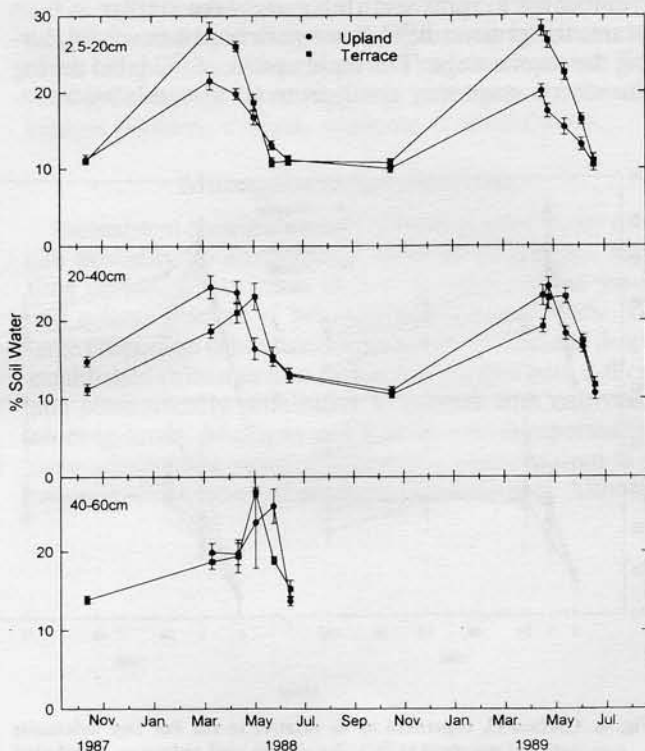


Fig. 1. Percent soil water (w/v). Values are means ( $n = 5$ ); vertical bars indicate  $\pm 1$  SE.

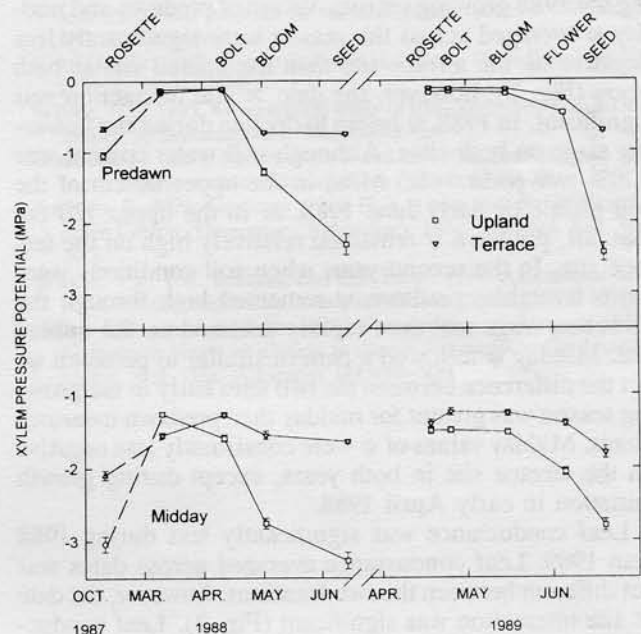


Fig. 2. Xylem pressure potential for heart-podded hoary cress. Values are means ( $n = 5$ ); vertical bars indicate  $\pm 1$  SE.

**Table 1. Above- and belowground biomass during flowering of heart-podded hoary cress on the terrace site, 1989.**

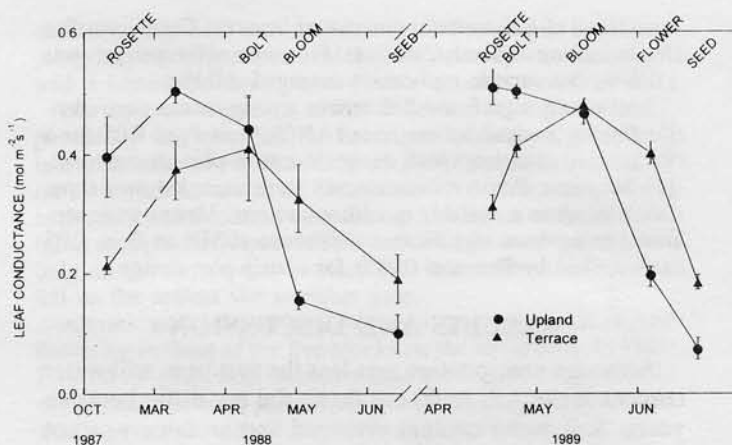
	Soil depth, cm		
	0-20	20-40	40-60
Root-to-rhizome ratio	1.41	0.33	0.40
% biomass†			
Roots	73	16	11
Rhizomes	40	38	22

† Percentage of total root or rhizome biomass.

heart-podded hoary cress with a competitive root system, a large C pool and extensive belowground meristems. The concentration of roots in the upper 20 cm of the soil profile is similar to the root distribution of many cool-season perennial grasses (Ganskopp, 1988; Dobrowolski et al., 1990). The overlap in root distribution potentially increases the intensity of interspecific competition between heart-podded hoary cress and other herbaceous species. Fall growth and predawn  $\psi$  on the terrace site suggest that roots were able to acquire deep soil water. The ability of heart-podded hoary cress to maintain plant water potential in the fall may result from an extensive root system that explores a large soil volume. Both roots and rhizomes of heart-podded hoary cress were observed at the bottom of our soil pits (120 cm). Selleck (1965) traced the roots of *Cardaria pubescens* (Mey.) Jarm. to the water table, 6.5 m below the surface. Based on root distribution, heart-podded hoary cress probably has more capacity than perennial grasses to extract soil water and nutrients at greater soil depths.

Predawn and midday xylem potentials were significantly more negative during 1988 than 1989. Although the year  $\times$  location interaction was significant, the *F*-values for main effects were 10 times greater, indicating that the response of the main effect may overshadow the interactions. However, the year  $\times$  date interaction was strongly significant for both predawn and midday measurements, reflecting an earlier decline in total xylem potentials during the 1988 growing season. Values of predawn and midday  $\psi$  averaged across the season were significantly less negative on the terrace site than the upland site in both years (Fig. 2); however, the date  $\times$  site interaction was significant. In 1988,  $\psi$  began to decline during the flowering stage on both sites. Although soil water content was <10% w/v (near -1.5 MPa) in the upper 60 cm of the soil profile by early June 1988, or in the upper 120 cm that fall, predawn  $\psi$  remained relatively high on the terrace site. In the second year, when soil conditions were more favorable, predawn  $\psi$  remained high through the flowering stage and then rapidly declined on the upland site. Midday  $\psi$  followed a pattern similar to predawn  $\psi$ , but the difference between the two sites early in the growing season was greater for midday than predawn measurements. Midday values of  $\psi$  were consistently less negative on the terrace site in both years, except during growth initiation in early April 1988.

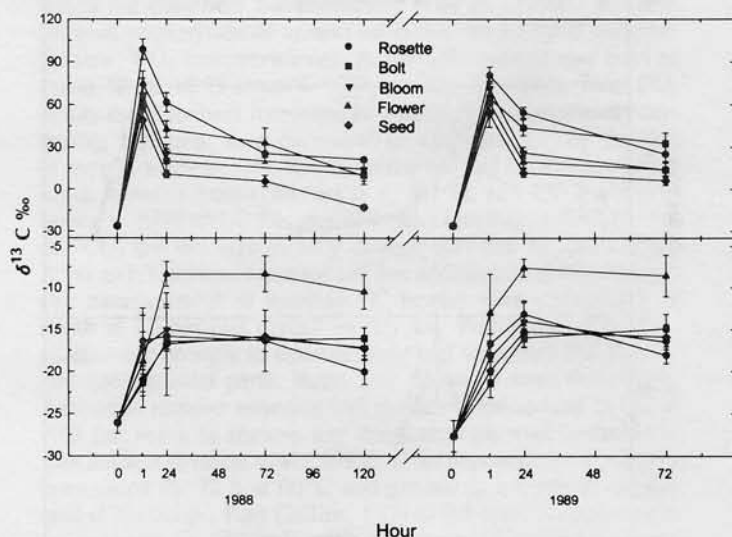
Leaf conductance was significantly less during 1988 than 1989. Leaf conductance averaged across dates was not different between the two locations; however, the date  $\times$  site interaction was significant (Fig. 3). Leaf conductance was greater on the upland site during the rosette and early bolting stage in 1988 and 1989. Leaf conduc-



**Fig. 3. Midday leaf conductance for heart-podded hoary cress. Values are means ( $n = 5$ ); vertical bars indicate  $\pm 1$  SE.**

tance was similar on the two sites during bolting in 1988 and bloom in 1989 and rapidly declined on the upland site during flowering and seed formation in both years.

Leaves of heart-podded hoary cress readily absorbed  $^{13}\text{C}$  during all five phenological stages in both years (Fig. 4). Levels of  $^{13}\text{C}$  in the leaves were greatest during the first hour following labeling and rapidly declined during the next 24 h. Labeled C was detected in the roots and rhizomes within 1 h of labeling. Maximum levels of  $^{13}\text{C}$  in the roots and rhizomes were reached within 24 h of labeling. Previous studies also demonstrated rapid translocation to belowground structures (Gordon et al., 1977; Lang and Thorpe, 1986; Miller and Rose, 1992). Gordon et al. (1977) suggested that most leaf C is exported within 24 h of assimilation. Seasonal allocation patterns of C, from leaves to roots and rhizomes, were similar in both years; the greatest  $\delta^{13}\text{C}$  shoot enrichment occurred during the rosette stage. The rapid uptake of  $^{13}\text{C}$  label during the rosette stage may result from (i) favorable microcli-



**Fig. 4. Carbon-13, expressed as ‰ relative to the Pee Dee belemnite international standard ( $\delta^{13}\text{C}$ ), for shoots and rhizomes of labeled heart-podded hoary cress. Values are means ( $n = 5$ ); vertical bars indicate  $\pm 1$  SE.**



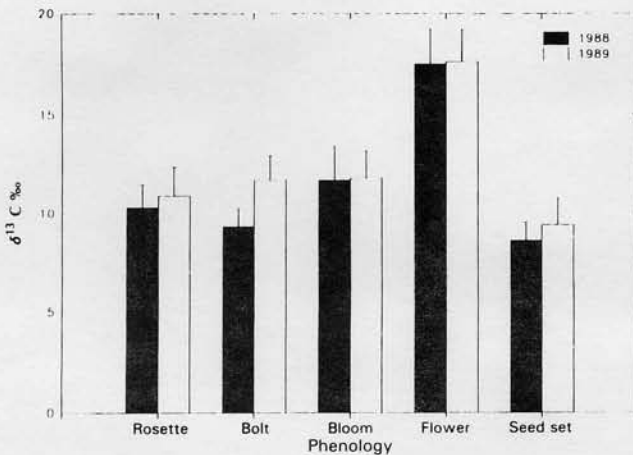


Fig. 5. The relative enrichment of  $^{13}\text{C}$  ( $\delta^{13}\text{C}$  labeled –  $\delta^{13}\text{C}$  prelabel) in belowground tissue of heart-podded hoary cress 24 h following labeling. Vertical bars represent  $\pm 1$  SE (standard error of the mean;  $n = 5$ ).

mate during that labeling period, (ii) high C demand during this rapid growth phase and/or (iii) relatively low leaf area per unit of  $^{13}\text{C}$  label. The comparatively low enrichment during the seed stage probably is a result of reduced physiological activity as plants approach dormancy, as indicated by relatively low values of  $\psi$  and leaf conductance (Fig. 2 and 3).

The greatest  $^{13}\text{C}$  enrichment of roots and rhizomes (Fig. 4) and the greatest proportional flow of C to roots and rhizomes (Fig. 5) occurred during the flower stage. This pattern is supported by the results of Sexsmith (1964), who reported that chemical control of heart-podded hoary cress was most successful during the flower stage. Prior to flowering, C demand by aboveground organs may be greater because of rapid shoot elongation and leaf development. Following flowering, leaves begin to senesce and soil water content becomes limited, reducing C assimilation.

### Management Implications

Inconsistent chemical control of heart-podded hoary cress can probably be attributed to variable phenology, short time period of maximum C flow to belowground tissue, and a large reserve of belowground dormant buds. The large proportion of biomass located belowground and deeply established rhizomes also makes this species both difficult and economically prohibitive to control with cultivation on rangelands. Mulligan and Findlay (1974) reported that three consecutive years of cultivation were required to attain effective control of all three *Cardaria* spp. Although

heart-podded hoary cress is most abundant on potentially arable sites, this species also was apparently well adapted to the Wyoming big sagebrush site with relatively dry shallow soil.

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