Weed Science

www.cambridge.org/wsc

Research Article

Cite this article: Becker RL, Mentz RS, Smith AG, Annor GA, Singh N, Sarangi D, Anderson NO, Heuschele DJ, Katovich EJ, Clark MD (2025). Seasonal nonstructural carbohydrates in the crowns and rhizomes of in situ populations of Japanese knotweed (*Polygonum cuspidatum*) and the hybrid Bohemian knotweed (*Polygonum ×bohemicum*). Weed Sci. **73**(e38), 1–9. doi: 10.1017/wsc.2025.11

Received: 27 September 2024
Revised: 19 February 2025
Accepted: 25 February 2025

Associate Editor:
Lovreet Singh Shergill, Colorado State University

Keywords:
Assimilates; buds; herbicide; mowing; phenology; starch; translocation

Corresponding author:
Roger L. Becker; Email: becke003@umn.edu

Seasonal nonstructural carbohydrates in the crowns and rhizomes of in situ populations of Japanese knotweed (*Polygonum cuspidatum*) and the hybrid Bohemian knotweed (*Polygonum ×bohemicum*)

Roger L. Becker[1], Ryan S. Mentz[2], Alan G. Smith[3], George A. Annor[4], Navjot Singh[5], Debalin Sarangi[6], Neil O. Anderson[3], D. Jo Heuschele[7], Elizabeth J. Katovich[8] and Matthew D. Clark[9]

[1]Emeritus Professor, Department of Agronomy and Plant Genetics, University of Minnesota, St Paul, MN, USA; [2]Research Associate, Syngenta Seeds, Clinton, IL, USA; formerly: Department of Agronomy and Plant Genetics, University of Minnesota, St Paul, MN, USA; [3]Professor, Department of Horticultural Science, University of Minnesota, St Paul, MN, USA; [4]Associate Professor, Department of Food Science and Nutrition, University of Minnesota, St Paul, MN, USA; [5]Graduate Research Assistant, Department of Agronomy and Plant Genetics, University of Minnesota, St Paul, MN, USA; [6]Assistant Professor, Department of Agronomy and Plant Genetics, University of Minnesota, St Paul, MN, USA; [7]Research Agronomist, USDA, Plant Science Research Unit, and Adjunct Assistant Professor, Department of Agronomy and Plant Genetics, St Paul, MN, USA; [8]Research Scientist, Department of Agronomy and Plant Genetics, University of Minnesota, St Paul, MN, USA and [9]Associate Professor, Department of Horticultural Science, University of Minnesota, St Paul, MN, USA

Abstract

Herbaceous perennials must annually rebuild the aboveground photosynthetic architecture from carbohydrates stored in crowns, rhizomes, and roots. Knowledge of carbohydrate utilization and storage can inform management decisions and improve control outcomes for invasive perennials. We monitored the nonstructural carbohydrates in a population of the hybrid Bohemian knotweed [*Polygonum ×bohemicum* (J. Chrtek & Chrtková) Zika & Jacobson [*cuspidatum × sachalinense*]; syn.: *Fallopia ×bohemica* (Chrtek and Chrtková) J.P. Bailey] and in Japanese knotweed [*Polygonum cuspidatum* Siebold & Zucc.; syn.: *Fallopia japonica* (Houtt.) Ronse Decr.]. Carbohydrate storage in crowns followed seasonal patterns typical of perennial herbaceous dicots corresponding to key phenological events. Starch was consistently the highest nonstructural carbohydrate present. Sucrose levels did not show a consistent inverse relationship with starch levels. Lateral distribution of starch in rhizomes and, more broadly, total nonstructural carbohydrates sampled before dormancy break showed higher levels in rhizomes compared with crowns. Total nonstructural carbohydrate levels in crowns reached seasonal lows at an estimated 22.6% of crown dry weight after accumulating 1,453.8 growing degree days (GDD) by the end of June, mainly due to depleted levels of stored starch, with the estimated minimum of 12.3% reached by 1,220.3 GDD accumulated by mid-June. Depletion corresponded to rapid development of vegetative canopy before entering the reproductive phase in August. Maximum starch accumulation in crowns followed complete senescence of aboveground tissues by mid- to late October. Removal of aboveground shoot biomass in late June to early July with removal of vegetation regrowth in early September before senescence would optimize the use of time and labor to deplete carbohydrate reserves. Additionally, foliar-applied systemic herbicide translocation to belowground tissue should be maximized with applications in late August through early fall to optimize downward translocation with assimilate movement to rebuild underground storage reserves. Fall applications should be made before loss of healthy leaf tissue, with the window for control typically ending by late September in Minnesota.

Introduction

A recent review of the history of knotweed (*Polygonum* spp.) invasiveness (Drazan et al. 2021) and an assessment of the impacts and costs of management (Hocking et al. 2023) provide a comprehensive background on the need to manage invasive *Polygonum* spp. and the challenges to doing so. Herbaceous perennials such as invasive *Polygonum* spp. must annually rebuild their aboveground photosynthetic architecture and do so by storing nonstructural carbohydrates in crowns, rhizomes, and roots between growing seasons (Child and Wade 2000). Seasonal patterns of nonstructural carbohydrates in crowns have long been used to optimize crop production in herbaceous perennials such as alfalfa (*Medicago sativa* L.) (Bélanger et al. 1999; Chatterton et al. 1974; Jung and Smith 1962; Sheaffer et al. 1988; Sheaffer and Marten 1990; Smith 1962). Conversely, depleting carbohydrates to manage aggressive herbaceous perennial invasive plants is also not a novel concept (Arny 1932; Bakke et al. 1939; Barr 1936). Timmons and Bruns (1951) found that a shallow wheel hoeing at a 4-wk interval was optimal to eliminate hemp dogbane (*Apocynum cannabinum* L.) in 3 yr, with longer intervals reducing effectiveness, and shorter intervals increasing the number of operations necessary to achieve the same outcome. A similar study by Seely (1952) defined a 4-wk shoot-removal interval optimal to control Canada thistle [*Cirsium arvense* (L.) Scop.]. Although not stated, because *C. arvense* flowering is induced with long days, with buds developing into open flowers beginning the last week of June following summer solstice, the 4-wk interval coupled with the trial start time means the first shoot removal occurred in June in their four-cut system, the time of lowest storage energy reserves (Welton et al. 1929). Similarly, the lowest reserves and reversal of seasonal carbohydrate flow occurred at initiation of flowering for *A. cannabinum* (Becker and Fawcett 1998) and purple loosestrife (*Lythrum salicaria* L.) (Katovich et al. 1998).

Control of *Polygonum* spp. has been inconsistent (Bailey et al. 2009; Bímová et al. 2001), and the best management approaches are debated (Hocking et al. 2023). Connecting carbohydrate flow to management options via visual growth and development cues or, more concisely, growing degree day (GDD) models should improve herbicidal and mechanical management outcomes. Seiger and Merchant (1997) predicted that at least four cuttings per season would be required to result in a net depletion of *Polygonum* spp. belowground biomass based on same-season rhizome-transplanted container-grown plants. Sink-source interactions with herbicide transport and effectiveness were thoroughly reviewed by Bashtanova et al. (2009) and broadened by Jones et al. (2018). Timing of systemic herbicide application when net assimilate translocation is to belowground sinks should improve efficacy and consistency of control (Becker and Fawcett 1998). Additionally, timing of mechanical or hand removal when carbohydrate reserves in rhizomes and crowns are at seasonal lows reduces the number of removal operations needed to achieve control (Seely 1952; Timmons and Bruns 1951), reducing disturbance events, time, cost, and non-target impacts.

Price et al. (2002) documented assimilate partitioning to roots, shoots, and flowers of Japanese knotweed [*Polygonum cuspidatum* Siebold & Zucc.; syn.: *Fallopia japonica* (Houtt.) Ronse Decr.] at key months of the year in overwintered, container-grown plants using $^{14}CO_2$ labeling as a surrogate for carbohydrate analysis. The work of Callaghan et al. (1981), sparked by the energy crisis of the late 1970s, characterized above- and belowground biomass, biomass recovery following harvest, elemental nutrients, and structural and non-structural carbohydrates as exploratory work to find suitable candidates for plant biomass. Both provide considerable insight as to carbohydrate quantity and quality in *Polygonum* spp. An in situ developmental, seasonal assessment of *Polygonum* spp. carbohydrate partitioning is needed to optimize mechanical/hand-roguing methods of control and herbicide efficacy to bridge the gaps in Callaghan et al. (1981) and validate the container-grown ^{14}C partitioning work of Price et al. (2002). In addition, this would provide phenology-related nonstructural carbohydrate quality and quantity data to support the ideas put forth by Bashtanova et al. (2009) and expanded by Jones et al. (2018) and Kuehne and Heimer (2023) to improve herbicide translocation efficiencies and therefore efficacy. The objective of our study was to characterize the seasonal variation of nonstructural carbohydrate quality and quantity in crowns of the hybrid Bohemian knotweed [*Polygonum* ×*bohemicum* (J. Chrtek & Chrtková) Zika & Jacobson [*cuspidatum* × *sachalinense*]; syn.: *Fallopia* ×*bohemica* (Chrtek and Chrtková) J.P. Bailey] and *P. cuspidatum* in the context of developmental phenology.

Materials and Methods

We monitored representative populations of the two most common *Polygonum* spp. in Minnesota, *P.* ×*bohemicum* and *P. cuspidatum* (Drazan 2022) to characterize nonstructural carbohydrates in the crowns from April through December and included a distribution sampling of lateral rhizomes on April 2, 2021. All populations were known to have been established for at least 7 yr and were undisturbed. The *P.* ×*bohemicum* samples were collected in Brooklyn Center, MN (45.073506°N, 93.331595°W) in 2020 and in Bloomington, MN (44.814635°N, 93.267628°W) in 2021. In 2021, a *P. cuspidatum* population was also sampled near Cottage Grove, MN (44.846527°N, 92.981658°W). The sampled patches were 7 to 10 m in diameter. We moved to the Bloomington site 30 km south-southeast of the Brooklyn Center site for the 2021 samples, because the Brooklyn Center site was inadvertently disturbed by park staff. The *P. cuspidatum* site was approximately 37 km southeast of the Brooklyn Center site and 23 km east-southeast of the Bloomington site. The 2020 *P.* ×*bohemicum* site was in a city park in the open without any nearby trees, the 2021 *P.* ×*bohemicum* site was at the edge of a city park partially overstoried by mature mixed hardwood trees that opened into a city right-of-way that was maintained as bluegrass (*Poa pratensis* L.) turf, and the *P. cuspidatum* 2021 site was partially overstoried by mature mixed hardwood trees in a right-of-way for a regional flood control earthen drainage causeway in Washington County. We targeted April 1 as the first sample date, as the ground was still frozen to the depth of sample removal in March. Due to historically mild fall temperatures for Minnesota, we were able to obtain samples through early December each year, as surficial freezing did not prevent sample removal. Samples were obtained ±4 d of the first day of each month. Phenology notes were taken at each sample date at each collection site. In addition, weekly phenology observations were made in a common garden established on the St Paul campus in 2019 that included both taxa plus a population of giant knotweed (*Polygonum sachalinense* F. Schmidt ex Maxim.; syn.: *Fallopia sachalinensis* (F. Schmidt ex Maxim.) Ronse Decr.]. Additionally, Montgomery et al. (2024) have since released a GDD model linked to phenology based on citizen scientist observations during our study period that accurately predicted the phenology events of our sites (data not shown).

The crown was defined as the woody, enlarged area in the transition region between the root, rhizomes, and stems, often with numerous new shoots emerging among dead shoots from the previous season. For each month, three randomly selected crowns were sampled from each site, with each crown considered a replication. Stems were cut to 25 cm above the soil surface, and the crown and associated rhizomes were removed around each crown in a radius of 25 cm and to a depth of 30 cm. Excess soil was removed, and the samples were placed on ice for transport to the lab. For the April 2, 2021, samples, rhizomes attached to sampled crowns were excavated until either ending when another secondary crown was encountered or when physical obstructions prevented following the rhizome farther. For all other sample periods, rhizomes attached to the central crown were discarded.

Anecdotally, the *P. cuspidatum* population had shorter inter-crown distances than *P.* ×*bohemicum*, and *P. cuspidatum* had a higher number of rhizomes proliferating from individual crowns. Smith et al. (2007) measured rhizome networks in *P. cuspidatum* and found 0.27- to 1.60-m separations among 10 crowns along a rhizome. Anecdotally, in our study, inter-crown distances were 1.40 to 1.63 m for *P.* ×*bohemicum* and 0.76 to 1.27 m for *P. cuspidatum*, within the apical dominance determined distances noted by Smith et al. (2007). *Polygonum* ×*bohemicum* rhizomes tended to be thicker than those of *P. cuspidatum* (1.9 to 3.2 vs. 1.0 to 2.5 cm in diameter, respectively). Rhizomes of both taxa tended to run laterally at similar depths ranging from 10 to 25 cm. The crowns of *P.* ×*bohemicum* were typically 5 to 10 cm in diameter versus 2.0 to 5.0 cm diameters for *P. cuspidatum*. Sampled crowns and rhizomes had three to six and two to five annual rings, respectively, visible in cross section.

Soil was removed with pressurized water at the lab. If samples could not be processed the day they were harvested, they were stored at in a deep freeze at −18 C until processing. Depending on the diameter of the crown, four to six 0.5-cm-thick subsample cross sections were cut from the 15-cm midsection of crowns with a band saw. Rhizomes from the April 2, 2021, sampling were subdivided into three to five representative sections depending on the length of rhizome obtained. Three to five representative subsamples for carbohydrate analysis were cut from the midsections of each rhizome subsection with hand-pruning shears. Rhizome and crown samples were then cut into small 2- to 7-mm chips with end-cutting nippers or pruning shears to expedite drying, weighed, and dried at 32 C until stable weights were obtained (usually 3 d). Dried samples were pre-ground to 6 mm using a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) and halved in volume twice using a sample splitter; the resulting subsample (which averaged 27.2 g) was ground to 1 mm in a Cyclone mill (Foss, Hillerød, Denmark) for carbohydrate analysis.

Ground samples were analyzed for their total starch content using the Megazyme total starch assay kit according to the AACC method 76-13.01 (Cereals & Grains Association n.d.). Sugars were extracted and analyzed according to the method described by Boakye et al. (2022) using a high-performance anion-exchange chromatography (HPAEC) system (Dionex ICS-5000$^+$ HPAEC System, Dionex, Sunnyvale, CA, USA) equipped with a pulsed amperometric detector. The separation of saccharides was performed on a Thermo Scientific Dionex CarboPac PA200 analytical column (3 by 250 mm) protected by its corresponding guard column (3 by 50 mm). The eluents used were 225 mM sodium hydroxide (A), 500 mM sodium acetate (B), and ultrapure water (C). A composite of five crowns sampled from the Brooklyn Center site on October 1, 2019, was used as the lab standard for carbohydrate analysis.

For GDD calculations, daily temperature data were obtained for the study period from the nearest weather station with the most complete, quality weather data. Data for 2020 were obtained from NOAA Station MN087 (elevation 282.5 m, 45.0961°N, 93.4500°W). Data for 2021 were from NOAA Station ID AU649 (elevation 276.1 m, 44.8261°N, 92.9122°W). Daily GDD were estimated from daily temperature data using the equation from McMaster and Wilhelm (1997):

$$\mathrm{GDD} = \left[\left(\frac{T_{\max} + T_{\min}}{2}\right) - 0\right] \qquad [1]$$

where $T_{\max}$ and $T_{\min}$ refer to daily maximum and minimum temperatures, respectively.

Cumulative GDD were calculated using the following equation:

$$\text{Cumulative GDD} = \sum\nolimits_{i=1}^{n} \mathrm{GDD} \qquad [2]$$

Unable to find research-based values for these taxa, we use the minimum and maximum of 0.0 and 30.0 C, respectively, to match the data used in Montgomery et al. (2024) to develop their citizen science-based phenology research model for *P. cuspidatum*.

To investigate the variation in temporal and lateral distribution of nonstructural carbohydrates, we utilized generalized additive mixed-effects models (GAMM) using the MGCV package in R v. 4.4.0 (R Core Team 2024; Wood 2017). The 3 site-years of data (2 for *P.* ×*bohemicum* and 1 for *P. cuspidatum*) were considered random variables and combined for analysis. Note that *P.* ×*bohemicum* is a hybrid of *P. cuspidatum* and *P. sachalinense*, and much of the germplasm in Minnesota is heavily backcrossed to *P. cuspidatum* and *P.* ×*bohemicum* rather than *P. sachalinense*, as *P. sachalinense* is rare in Minnesota (Drazan 2022), so we did not foresee a biological basis for the taxa to differ in carbohydrate quantity nor quality. Percent dry weight data for each of the carbohydrates were regressed over cumulative GDD using thin-plate regression spline, where the site-year was considered as a random effect (Wood 2003). Similarly, percent dry weight data for carbohydrates were regressed over the lateral distance of crown and rhizomes from the central crown, with taxa considered as a random effect. Based on lower Akaike information criterion (AIC) values and suitability of beta distribution to model data values between 0 and 1, GAMM models were constructed using beta distribution and the logit link function in R. Furthermore, carbohydrates were classified into two groups. Group 1 included the major contributors to the carbohydrate pool starch and sucrose, and the sum of all nonstructural carbohydrates monitored termed total carbohydrates. Group 2 included the minor carbohydrates comprising glucose, fructose, raffinose, and stachyose. Separate models were fit for each group to account for the substantial difference in mean values between them and the visual clustering of residuals, which indicated the necessity of distinct variance structures for the two groups. To restrict the potential overfitting, the number of effective degrees of freedom was restricted to four ($k = 5$). Predicted mean carbohydrate percent values and 95% simultaneous confidence intervals were plotted. Additionally, cumulative GDD values corresponding to the lowest percent dry weight for each carbohydrate were estimated using the *predict* function in the MGCV package (see the GAMM parameters in Supplementary Material 1 for details).

Results and Discussion

Phenology and GDD

Montgomery et al. (2024) developed phenology models based on cumulative GDD. Relating carbohydrate quantity and quality to cumulative GDD or to key phenology events allows managers to improve outcomes of management practices. In April through May in the St Paul campus common garden, shoot emergence and elongation was nonuniform and occurred over an extended period within each population. The attainment of full bloom in September and complete senescence in October was more uniform, occurring within a relatively short period of time. In the St Paul metropolitan area, soil frost-free dates historically occur in late March to early April. Crown buds had swollen and deepened to a reddish-pink color the first week of April, with initial shoot emergence occurring the second and third weeks of April, and widespread shoot emergence and elongation began the last 2 wk of April. Uneven shoot elongation continued through May, reaching maximum shoot height by the end of June. Continued canopy development via leaf expansion peaked mid- to late July. Freestanding shoot heights in July for the sampled *P. ×bohemicum* populations averaged 3.4 m in height, with a maximum shoot height of 3.7 m. The sampled *P. cuspidatum* population averaged 2.4 m in shoot height, reaching a maximum of 3 m.

In the common garden, early onset of first floral buds began August 9 in 2020 and August 18 in 2021, when a few developing flower buds were clearly visible in leaf axils as the racemes began to elongate (erect racemes to 10 mm in length composed of a compact cluster of developing panicles). Early development and elongation of individual male panicles were broadly visible by the end of the second and third weeks of August. Female panicles began to elongate the last week of August through the first week of September, approximately 10 to 14 d after male flower development. Plants reached full bloom the second week in September each season and by the end of September, male flowers were in sharp decline, mostly senesced, leaving bare racemes of erect panicle “skeletons.” Females had mature seed by the end of September to the first week in October, within the time frame observed by Bram and McNair (2004), with leaf senescence beginning at the same time. Change in tepal color began the end of September, transitioning from greenish-white to brownish-white coloration during October 15 through October 26 and was not uniform.

Regarding the window for absorption of foliar-applied herbicides, leaves began to senesce, developing a uniform, yellowish cast in early to mid-September. Some early leaf senescence began the third week of September and progressed to full leaf loss by early to mid-October, while stems remained green and moist. Stems of all *Polygonum* taxa appeared completely dry by the third week of October, enough so that movement of assimilates could no longer occur even within the stem. Note that total nonstructural carbohydrates continued to accumulate in crowns through the beginning of November and occasionally December (Figure 1) after complete leaf loss. Assimilate flow and canopy health indicate that early August through the third week of September would have been the ideal application window for systemic herbicides corresponding to approximately 2,400 to 3,400 GDD (Figure 1). Very high utilization by pollinators may push some managers to a narrow application window before bud to first bloom in the second to third week of August (approximately 2,300 to 2,700 GDD), or waiting until flowing ends in the third to fourth week of September (approximately 3,200 to 3,300 GDD) (see GDD phenology, Supplementary Material 2). The end of this application window depends on the canopy health to support herbicide absorption. Healthy leaf tissue to support herbicide absorption and translocation was no longer present by the end of September for *P. cuspidatum* and *P. sachalinense* and was no longer present approximately 1 wk later for *P. ×bohemicum* in our common garden. Key phenology stages estimated via GDD calculations with the research model of Montgomery et al. (2024) and the GAMM estimates for seasonal lows for key storage carbohydrates are available in the GDD phenology supplement (Supplementary Material 2). The actual lab sample carbohydrate data are also available in the carbohydrate data supplement (Supplementary Material 3).

Seasonal Carbohydrate Storage and Utilization

Estimated values for nonstructural carbohydrates on a dry weight basis are shown in Figures 1 to 4. Starch was the most common nonstructural carbohydrate present, followed by sucrose (Figure 1). At much lower concentrations, glucose and fructose were the next most common, and finally, of the carbohydrates monitored, raffinose and stachyose grouped as the lowest seasonal concentrations (Figure 2). The estimated GDD and nonstructural carbohydrate minimums are shown in Table 1. Inulins, the primary storage polysaccharides in Jerusalem artichoke (*Helianthus tuberosus* L.) (Rubel et al. 2021) and chicory (*Cichorium intybus* L.) (Van Laere and Van Den Ende 2002) were not a key nonstructural carbohydrate in either *Polygonum* taxon.

We found monthly average minimum to maximum starch levels on a dry matter basis ranged from 5.2% to 23.3%, a broader range than the 9.1% to 19.3% noted by Callaghan et al. (1981) (Table 2), and total nonstructural carbohydrate levels ranged from 13.9% to 41.3% versus their 19.2% to 38.5% range. The level of starch in *Polygonum* spp. was somewhat lower overall compared with the 7% to 38% starch range in *A. cannabinum* (Becker and Fawcett 1998) and the 4% to 32% range in *L. salicaria* (Katovich et al. 1998). In general, the highest total carbohydrate and starch levels occurred in the fall following the reproductive phase or in early spring before dormancy break and shoot elongation (Figure 1; Table 2).

Glucose and fructose tended to fluctuate month to month in unison, as did raffinose with stachyose (Figure 2). Midseason fluctuations in levels of glucose and fructose approximated the trends for starch as intermediary building blocks of sucrose, the translocated carbohydrate. Even though average monthly sucrose levels (4.8% to 16.5%; Table 2) were higher compared with *A. cannabinum* (3.9% to 7.8%; Becker and Fawcett 1998) and *L. salicaria* (6.6% to 12.8%; Katovich et al. 1998), starch was still consistently the highest nonstructural carbohydrate present. Sucrose levels did not show a consistent inverse correlation with starch metabolism as the growing season progressed (Pearson’s r = −0.05 to 0.35; data not shown) (Figure 1). A negative correlation with starch levels would be expected to reflect metabolism of starch reserves to sucrose for transport to metabolic sinks during the season. The month-to-month fluctuations of glucose and fructose were positively correlated with each other (Pearson’s r = +0.92 to 0.99; data not shown), as were raffinose and stachyose (Pearson’s r = +0.88 to 0.96; data not shown). Of note, significant aboveground tissue loss due to frost damage occurred when shoots were to 0.3 to 1.5 m in height midway between the May and June sample collection both years. Additionally, Japanese beetle (*Popillia japonica*) feeding damage occurred mid-July through August 5 in both years with up to 50% leaf tissue loss in the upper one-half of the canopies. These defoliation events may account for some of the fluctuations in total nonstructural carbohydrates in the samples collected following those events.

Respiration losses during the winter have been shown for alfalfa and red clover (*Trifolium pratense* L.) (Jung and Smith 1962), with as much as a 50% loss of nonstructural carbohydrates observed in alfalfa (Sheaffer et al. 1988). There were only minor losses of nonstructural carbohydrates over winter for *A. cannabinum* (Becker and Fawcett 1998) and *L. salicaria* (Katovich et al.

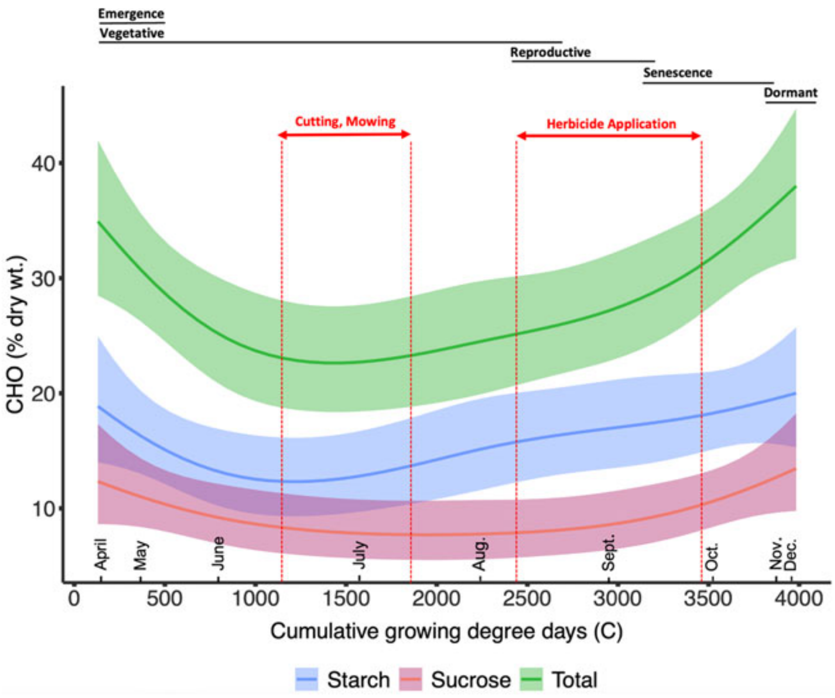

Figure 1. Estimated major nonstructural carbohydrates (CHO) by cumulative growing degree days (GDD) of *Polygonum ×bohemicum* in 2020 and *P. ×bohemicum and Polygonum cuspidatum* in 2021 sampled at the beginning of each month April through December. Annotations added to show observed phenology, recommended management windows, and approximate first of each month. Shaded areas denote 95% simultaneous confidence intervals.

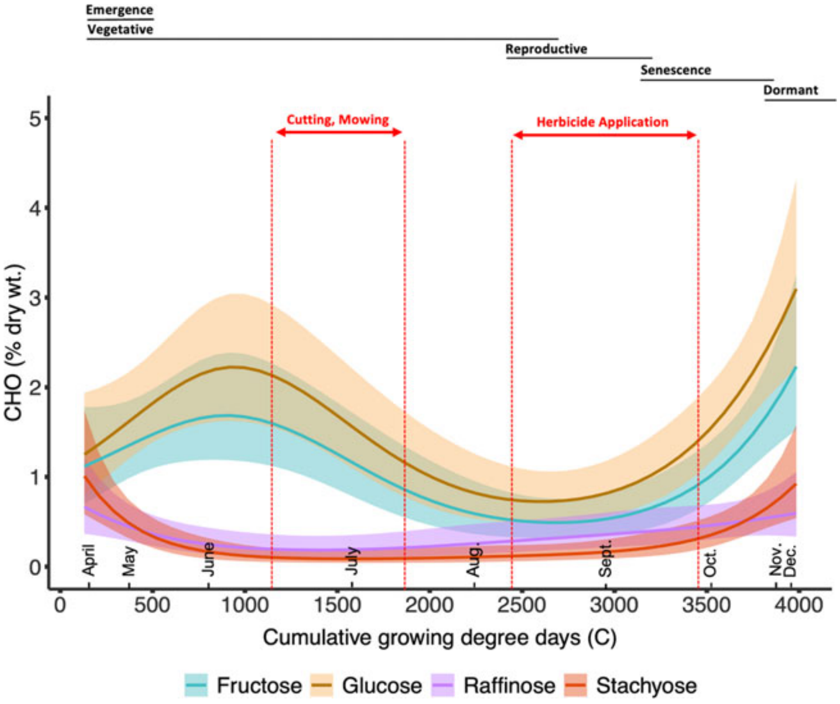

Figure 2. Estimated minor nonstructural carbohydrates (CHO) by cumulative growing degree days (GDD) of *Polygonum ×bohemicum* in 2020 and *P. ×bohemicum and Polygonum cuspidatum* in 2021 sampled at the beginning of each month April through December. Annotations added to show observed phenology, recommended management windows, and approximate first of each month. Shaded areas denote 95% simultaneous confidence intervals.

1998). Despite the inability to sample the same site one year to the next, our season-beginning carbohydrate levels were similar or slightly lower than season-end carbohydrate levels, supporting the findings of Price at al. (2002) that *Polygonum* spp. use little to no carbohydrate for respiration during winter, indicating full dormancy. Additionally, in *A. cannabinum*, starch levels dropped in November each year from the seasonal high that occurred early September with a corresponding rise in ethanol-soluble reducing

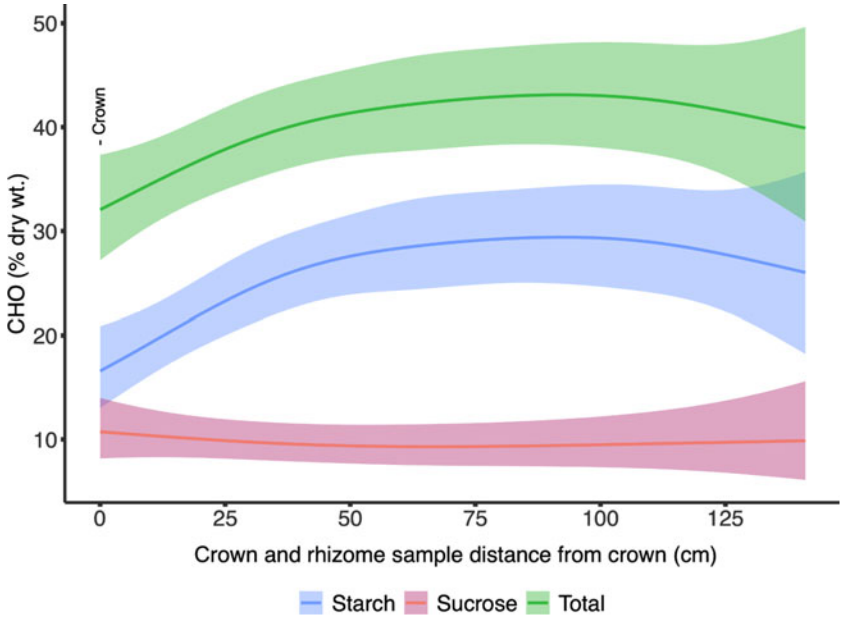

Figure 3. Estimated lateral distribution of major nonstructural carbohydrates (CHO) for each of three crowns and associated rhizomes of *Polygonum* ×*bohemicum* and *Polygonum cuspidatum* sampled April 2, 2021. Shaded areas denote 95% simultaneous confidence intervals.

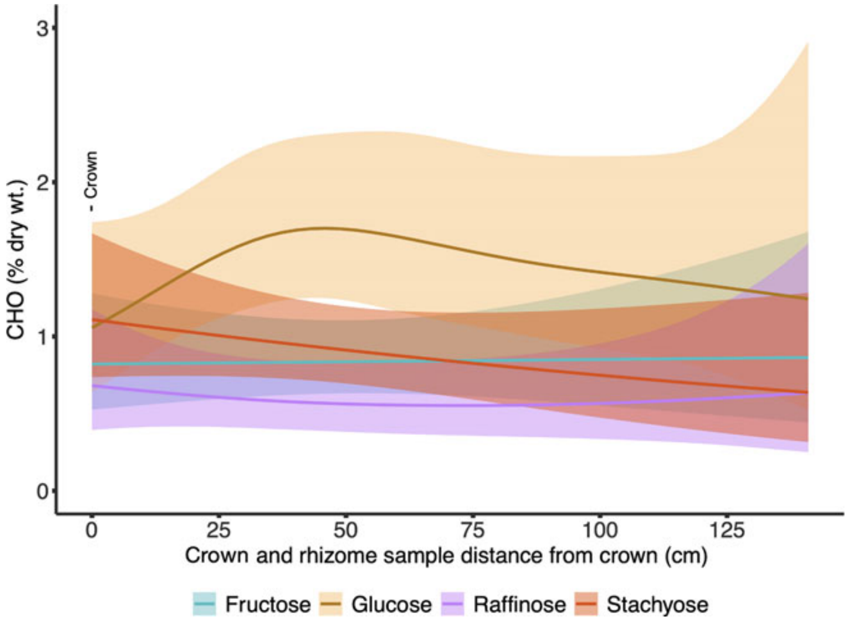

Figure 4. Estimated lateral distribution of minor nonstructural carbohydrates (CHO) for each of three crowns and associated rhizomes of *Polygonum* ×*bohemicum* and *Polygonum cuspidatum* sampled April 2, 2021. Shaded areas denote 95% simultaneous confidence intervals.

and nonreducing sugars (Becker and Fawcett 1998). Barr (1936) observed a similar rise in soluble sugars in field bindweed (*Convolvulus arvensis* L.) as fall temperatures lowered, termed “hardening off.” We observed a similar rise in sucrose (Figure 1) and in glucose and fructose (Figure 2), possibly indicating physiological hardening-off for winter.

Lateral Distribution of Nonstructural Carbohydrates

The lateral distribution of carbohydrates was a onetime observation intended to inform the implications of sampling only crowns to characterize the broader underground carbohydrate storage potential. Most rhizomes at all sites ended with an ascending, more juvenile crown. There was a trend for increased starch and a corresponding total nonstructural carbohydrate in rhizomes compared with crowns (Figure 3). Lower levels of starch were also noted in crowns than in the roots of *L. salicaria* (14.9% vs. 19.5%, respectively; Katovich et al. 1998), and in *A. cannabinum* crowns versus lateral roots (30.1% vs. a range of 38.5% to 52.3%, respectively) or crowns compared with ascending vertical roots (15.6% vs. a range of 18.6% to 39.4%, respectively) (Becker and Fawcett 1998). Additionally, starch and total sugars were

Table 1. Minimum and maximum nonstructual carbohydrate and corresponding estimated cumulative growing degree days (GDD) for *Polygonum ×bohemicum* in 2020 and for *P. ×bohemicum and Polygonum cuspidatum* in 2021 sampled at the beginning of each month April through December.

	Cumulative GDD[a]		% Dry weight	
Nonstructural carbohydrate	Minimum	Maximum	Minimum	Maximum
Total	1,453.8	3,983.9	22.6	38.0
Starch	1,220.3	3,983.9	12.3	20.0
Sucrose	1,959.8	3,983.9	7.7	13.5
Glucose	2,621.5	3,983.9	0.7	3.1
Fructose	2,699.4	3,983.9	0.5	2.2
Stachyose	1,570.6	130.4	0.1	1.0
Raffinose	1,414.9	130.4	0.2	0.7

[a] GDD were calculated using the base and maximum temperatures of 0.0 and 30.0 C, respectively.

Table 2. Three-crown average and individual crown high and low percent nonstructural carbohydrates among *Polygonum ×bohemicum* in 2020 and *P. ×bohemicum and Polygonum cuspidatum* in 2021 sampled at the beginning of each month April through December.

	Three-crown average		Individual crown	
Nonstructural carbohydrate	High	Low	High	Low
	% Dry weight			
Major contributors				
Total	41.3	13.9	44.4	6.5
Starch	23.3	5.2	25.0	1.1
Total nonstarch	21.0	6.0	23.1	5.4
Sucrose	16.5	4.8	18.3	3.6
Minor contributors				
Glucose	4.96	0.27	5.68	0.19
Fructose	3.62	0.20	4.46	0.18
Raffinose	0.93	0.02	1.10	0.01
Stachyose	1.21	0.01	1.44	>0.00

considerably lower in crowns than in roots of both alfalfa and red clover (Jung and Smith 1962). The uneven distribution we observed may be typical for perennial herbaceous dicots in general.

In Minnesota, the interval from frozen ground to crown bud dormancy break was relatively narrow, with the soil frost-free date centered around the first of April. Crown buds, though not elongating, were swollen and reddish-pink in color, indicating dormancy break was underway. First signs of shoot elongation began approximately 1 wk after the April 2 sampling date, with shoot elongation, although still very uneven, well underway by 2 to 3 wk after this sample date. Adachi et al. (1996) noted apical dominance of crown buds maintaining dormancy of lateral rhizome buds unless the crowns were disturbed. The lateral system was undisturbed at our two sites, so we suspect the first metabolically active site coming out of dormancy was the crown bud area. Thus, lower starch concentrations in the crowns may have been indicative of differential lateral carbohydrate metabolism in preparation for crown bud dormancy break. Adachi et al. (1996) also noted that lateral distribution of colonizing *P. cuspidatum* varied along metabolic gradients, with the main activity in their case in the outer periphery of an expanding population. Perhaps a similar reallocation of carbohydrates away from the established crowns was occurring in our study.

Implications of Seasonality

Our findings clarify the seasonal gaps in Callaghan et al. (1981). Although lacking a full growing season continuum without data for April or July through September, Callaghan et al. (1981) did note that seasonal lows occurred in June. Our work further defined that the seasonal low occurs at the end of June and extends through July, but transport reverses dramatically in August. The lowest levels of total carbohydrate reserves were estimated to occur between 1,200 to 1,800 GDD (Figure 1), with the estimated low in total carbohydrate reserves bottoming out at 1,454 GDD (Table 1). Callaghan et al. (1981) found that shoot nonstructural carbohydrate levels, although not tied to underground carbohydrate allocation, plummeted after their October sampling. Considering the longer growing season in the Callaghan et al. (1981) study, this supports our findings of accelerated accumulation of carbohydrates in the crowns in September through October in Minnesota. Additionally, our research confirms the assumption made by Price et al. (2002), that their ^{14}C-labeled assimilate utilization patterns in container-grown plants do indeed reflect nonstructural carbohydrate utilization patterns of established plants in the field.

Our findings indicate that removal of aboveground biomass from mid-June through mid-July after *Polygonum* spp. had reached maximum vegetative growth but before the initiation of flowering in August could maximize depletion of underground carbohydrate reserves and further deplete remaining underground carbohydrates to rebuild aboveground photosynthetic architecture (Figure 1). Subsequent removal of vegetation two more times that season targeting 30- to 40-d intervals until the growing season ends may provide the optimal depletion strategy, defined as the least amount of labor needed to maximally deplete carbohydrates and weaken a population. This approach would require diligent removal of all shoots in a stand two to three times a season for at least 3 yr, with return visits in years 4 and 5 to remove the few missed plants that may persist.

A single annual renewable energy biomass harvest of shoots of *P. cuspidatum* at various times of the year had little to no effect on rhizome biomass (Callaghan et al. 1981). However, cutting intervals of 4 wk for container-grown *Polygonum* spp. did (Seiger and Merchant 1997), which coincides with the optimal cutting intervals found for *C. arvense* (Seely 1952) and *A. cannabinum* (Timmons and Bruns 1951). Seiger and Merchant (1997) also noted that for *Polygonum* spp., shoot removal once in a season was equally effective in reducing belowground biomass when removed at least 7 wk before senescence. At our locations, this 7-wk time frame would have occurred in early August, when crown carbohydrate reserves consistently began to rebuild. Our observed time of carbohydrate reversal from acropetal to basipetal flow also corresponds with the noted shift from aboveground to belowground biomass accumulation by July 30 (Seiger 1993) and the observed maximum aboveground biomass accumulation (Fabiszewski and Brej 2008; Horn 1997). Baker (1988) controlled *P. cuspidatum* with mowing at 2-wk intervals for 2 yr or hand pulling once at maximum height in

July for 3 yr. In light of our findings, their single hand-pulling operation was done when crown carbohydrate reserves were maximally depleted, and mowing at 2-wk intervals could have been less frequent and likely would have accomplished the same outcome. However, Baker (1988) did also find that attempting to pull shoots in a less-accessible streambank terrain for 10 yr did not control that population, highlighting the potential for inconsistent outcomes when using nonherbicidal control and the need to find and remove all shoots within a colony. A note of caution, repeated use of the same management timing may select for biotypes adapted to that practice, as was done to select alfalfa germplasm tolerant to increased cutting schedules (Chatterton et al. 1974).

We acknowledge the challenges of removing top growth to control *Polygonum* spp. (Jones and Eastwood 2019; Jones et al. 2018; Jones et al. 2020), and particularly the need to prevent vegetative spread through shoot or rhizome fragments. Yet this strategy may be useful for the many small, easily accessible patches where cut or dug material can be managed in place and herbicidal control may not be an option. Larger, more-inaccessible infestations would be best controlled by incorporating the use of herbicide.

Integrating carbohydrate allocation and herbicide movement to improve *Polygonum* spp. management outcomes has been discussed (Kuehne et al. 2023; Jones et al. 2018), although carbohydrate levels have yet to be monitored concomitant with an efficacy study or in a more comprehensive time of application study throughout the growing season. Our work indicates that herbicides that rely on passive translocation with assimilates to belowground reproductive structures would be most effective if applied in a relatively narrow window in late August through mid-September (Figure 1) if not previously disrupted earlier in the season with physical shoot removal or early-season herbicide applications (Boyd et al. 2017). If disrupted earlier in the season, we speculate the window for downward assimilate movement may be pushed later in the season and the herbicide application window possibly narrowed to early to mid-September. However, with climate change, timing for fall application is becoming erratic in Minnesota and uncharacteristically extended through the last week of October for *P.* ×*bohemicum* in 2023 based on foliage conditions conducive for assimilate absorption and translocation. Preference for fall applications also assumes plants are actively growing. We have observed *P.* ×*bohemicum*, *P. cuspidatum*, and especially *P. sachalinense* in the common garden on the St Paul campus were very susceptible to moisture stress and to even short-duration mild frosts (−1.1 to 0 C) at spring emergence or in the fall.

Our findings clarify the quality, quantity, and seasonality of nonstructural carbohydrate utilization in *P. cuspidatum* and the hybrid *P.* ×*bohemicum*. Future work is needed to verify optimal depletion of carbohydrates to control *Polygonum* spp. and the nuances of using management to break apical dominance in rhizomes and lateral buds whether via physical disruptions such as tillage or mowing or improved use of herbicides informed by knowledge of herbicide modes of action, seasonality of transport, and behavior in the environment.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2025.11

Acknowledgments. We are indebted to Ted Jeo for his expertise and assistance in carbohydrate analysis design and sample preparation. We thank Doug Miller for his technical and statistical analysis support. For access to sample sites, we thank the City of Brooklyn Center, David Hanson with the Bloomington Maintenance Division, and Washington County with access provided by Ron Cozad and family, Cottage Grove, MN.

Funding statement. This work was supported by the Minnesota Invasive Terrestrial Plants and Pests Center and the Minnesota Environment and Natural Resources Trust Fund as recommended by the Legislative-Citizen Commission on Minnesota Resources; University of Minnesota Extension; and the College of Food, Agricultural and Natural Resource Sciences; and facilitated by the Minnesota Department of Agriculture.

Competing interests. The authors declare no conflicts of interest.

References

Adachi N, Terashima I, Takahashi M (1996) Nitrogen translocation via rhizome systems in monoclonal stands of *Reynoutria japonica* in an oligotrophic desert on Mt Fuji: field experiments. Ecol Res 11:175–186

Arny AC (1932) Variations in the Organic Reserves in Underground Parts of Five Perennial Weeds from Late April to November. University of Minnesota Agricultural Experiment Station Technical Bulletin 84. July 1932. St Paul, MN: University Farm. 28 p

Bailey JP, Bímová K, Mandák B (2009) Asexual spread versus sexual reproduction and evolution in Japanese knotweed s.l. sets the stage for the "Battle of the Clones." Biol Invasions 11:1189–1203

Baker RM (1988) Mechanical control of Japanese knotweed in an S.S.S.I. Aspects Appl Biol 16:189–192

Bakke AL, Gaessler WG, Loomis WE (1939) Relation of root reserves to control of European bindweed (*Convolvulus arvensis* L.). Iowa State College of Agriculture and Mechanic Arts. Agricultural Research Bulletin. Volume 23, Bulletin 254, p.113–144. May. 1939. 440 p

Barr CG (1936) Preliminary studies on the carbohydrates in the roots of bindweed. Agron J 28:787–798

Bashtanova UB, Beckett KP, Flowers TJ (2009) Review: physiological approaches to the improvement of chemical control of Japanese knotweed (*Fallopia japonica*). Weed Sci 57:584–592

Becker RL, Fawcett RS (1998) Seasonal carbohydrate fluctuations in hemp dogbane (*Apocynum cannabinum*) crown roots. Weed Sci 46:358–365

Bélanger G, Kunelius t, McKenzie D, Papadopoulos Y, Thomas B, McRae K, Fillmore S, Christie B (1999) Fall cutting management affects yield and persistence of alfalfa in Atlantic Canada. Can J Plant Sci 79:57–63

Bímová K, Mandák B, Pyšek P (2001) Experimental control of *Reynoutria* congeners: a comparative study of a hybrid and its parents. Pages 283–290 *in* Brundu G, Brock J, Camarda I, Child L, Wade M, eds. Plant Invasion: Species Ecology and Ecosystem Management. Leiden: Backuys

Boakye PG, Kougblenou I, Murai T, Okyere AY, Anderson J, Bajgain P, Phillipp B, LaPlante B, Schlecht S, Vogel C, Carlson M, Occhino L, Stanislawski H, Swan Ray S, Annor, GA (2022) Impact of sourdough fermentation on FODMAPs and amylase-trypsin inhibitor levels in wheat dough. J Cereal Sci 108:103574

Boyd NS, White SN, Larsen T (2017) Sequential aminopyralid and imazapyr applications for Japanese knotweed (*Fallopia japonica*) management. Invasive Plant Sci Manag 10:277–283

Bram MR, McNair JN (2004) Seed germinability and its seasonal onset of Japanese knotweed (*Polygonum cuspidatum*). Weed Sci 52:759–767

Callaghan TV, Scott R, Whittaker HA (1981) The Yield, Development and Chemical Composition of Some Fast-growing Indigenous and Naturalised British Plant Species in Relation to Management as Energy Crops. ITE Project 640. Cumbria, UK: Institute of Terrestrial Ecology, Merlewood Research Station. 190 p

Cereals & Grains Association (n.d.) Method 76-13.01. Total Starch Assay Procedure (Megazyme Amyloglucosidase/alpha-Amylase Method). First approval November 8, 1995; Reapproval November 3, 1999. In AACC Approved Methods of Analysis. 11th ed. St Paul, MN: Cereals & Grains Association. http://doi.org/10.1094/AACCIntMethod-76-13.01. Accessed: November 27, 2023

Chatterton NJ, Carlson GE, Hart RH, Hungerford WE (1974) Tillering, nonstructural carbohydrates, and survival relationships in alfalfa. Crop Sci 14:783–787

Child L, Wade M (2000) The Japanese Knotweed Manual: The Management and Control of an Invasive Alien Weed. Chichester, UK: Packard Publishing. 123 p

Drazan D, Smith AG, Anderson NO, Becker R, Clark M (2021) History of knotweed (*Fallopia* spp.) invasiveness. Weed Sci 69:617–623

Drazan DA (2022) Genetic Diversity, Structure, and Cold Hardiness of Invasive Knotweed (*Fallopia* spp.) in Minnesota. MS thesis. University of Minnesota. 166 p. Retrieved from the University Digital Conservancy, https://hdl.handle.net/11299/241271. Accessed April 1, 2025.

Fabiszewski J, Brej T (2008) Ecological significance of some kenophytes in Lower Silesian National Parks. Acta Soc Bot Pol 77:167–174

Hocking S, Toop T, Jones D, Graham I, Eastwood D (2023) Assessing the relative impacts and economic costs of Japanese knotweed management methods. Sci Rep 13:3872

Horn P (1997) Seasonal dynamics of aerial biomass of *Fallopia japonica*. Pages 203–206 *in* Brock JH, Wade M, Pyšek P, Green D, eds. Plant Invasions: Studies from North America and Europe. Leiden: Backhuys

Jones D, Bruce G, Fowler MS, Law-Cooper Graham RI, Abel A, Street-Perrott FA, Eastwood D (2018) Optimising physiochemical control of invasive Japanese knotweed. Biol Invasions 20:2091–2105

Jones D, Eastwood D (2019) Sustainable control of invasive Japanese knotweed. Outlooks Pest Manag 30:195–206

Jones E, Fowler MS, Hocking S, Eastwood D (2020) Please don't mow the Japanese knotweed! NeoBiota 60:19–23

Jung GA, Smith D (1962) Trends of cold resistance and chemical changes over winter in the roots and crowns of alfalfa and medium red clover. I. Changes in certain nitrogen and carbohydrate fractions. Agron J 53:359–364

Katovich EJS, Becker RL, Sheaffer CC, Halgerson JL (1998) Seasonal fluctuations of carbohydrate levels in roots and crowns of purple loosestrife (*Lythrum salicaria*). Weed Sci 46:540–544

Kuehne L, Heimer D (2023) Efficacy and rates of diquat for reducing invasive knotweeds and potential for sequential use with imazapyr. Weed Biol Manag 23:71–80

McMaster GS, Wilhelm WW (1997) Growing degree-days: one equation, two interpretations. Agric For Meteorol 87:291–300

Montgomery R, Carlson S, Anderson A, Govindan B, Morey A (2024) Online Phenology and Degree-day Models. Integrated Plant Protection Center, Oregon State University. https://uspest.org/dd/model_app. Accessed: February 3, 2025

Price EAC, Gamble R, Williams GG, Marshall C (2002) Seasonal patterns of partitioning and remobilization of ^{14}C in the invasive rhizomatous perennial Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decraene). Evol Ecol 15:347–362

R Core Team (2024) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org

Rubel IA, Iraporda C, Manrique GD, Genovese DB, Abraham AG (2021) Inulin from Jerusalem artichoke (*Helianthus tuberosus* L.): from its biosynthesis to its application as bioactive ingredient. Bioact Carbohydr Diet Fibre 26:100281

Seely CI (1952) Controlling Perennial Weeds with Tillage. Idaho AES Bulletin No. 288. Moscow: Idaho Agricultural Experiment Station. 43 p

Seiger LA (1993) The Ecology and Control of *Reynoutria japonica* (*Polygonum cuspidatum*). Ph.D dissertation. Washington, DC: George Washington University. 117 p

Seiger LA, Merchant HC (1997) Mechanical control of Japanese knotweed (*Fallopia japonica* [Houtt.] Ronse Decraene): effects of cutting regime on rhizomatous reserves. Nat Area J 17:341–345

Sheaffer CC, Lacefield GD, Marble VL (1988) Cutting Schedules and Stands. Pages 411–437 *in* Hanson AA, Barnes DK, Hill RR, eds. Alfalfa and Alfalfa Improvement. Agronomy Monographs 29. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America

Sheaffer CC, Marten GC (1990) Alfalfa cutting frequency and date of fall cutting. J Prod Agric 3:486–491

Smith D (1962) Carbohydrate root reserves in alfalfa, red clover, and birdsfoot trefoil under several management schedules. Crop Sci 2:75–78

Smith JMD, Ward JP, Child LE, Owen MR (2007) A simulation model of rhizome networks for *Fallopia japonica* (Japanese knotweed) in the United Kingdom. Ecol Model 200:421–432

Timmons FL, Bruns VF (1951) Frequency and depth of shoot-cutting in eradication of certain creeping perennial weeds. Agron J 43:371–375

Van Laere A, Van Den Ende W (2002) Inulin metabolism in dicots: chicory as a model system. Plant Cell Environ 25:803–813

Welton FA, Morris VH, Hartzler AJ (1929) Organic Food Reserves in Relation to the Eradication of Canada Thistle. Ohio AES Bulletin 441. Wooster: Ohio Agricultural Experiment Station. 25 p

Wood SN (2003) Thin-plate regression splines. J R Stat Soc B 65:95–114

Wood SN (2017) Generalized Additive Models: An Introduction with R. 2nd ed. Boca Raton, FL: Chapman and Hall/CRC. 496 p