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Seasonal Changes in Soluble Carbohydrates of Russian Knapweed's Rhizomes

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ABSTRACT

The soluble carbohydrates play a major role in germination, growth, reproduction, defense and survival of perennial plant species reproducing with rhizomes under normal and adverse environmental conditions. The information regarding the amount of carbohydrates present in the rhizomes of such species could provide valuable insights for making decisions regarding the best time to control these species. Therefore, seasonal changes in the concentrations of soluble carbohydrates (fructose, glucose, sucrose) and their sum termed as total amount of soluble carbohydrates (TSCs) in the rhizomes of Russian knapweed were investigated during 2013-2014. The TSCs were low at sprouting and then slightly increased until mid-June (beginning of flowering). Thereafter, TSCs were slightly decreased from mid-June to minimal values in August (flowering period) (6.2 mg/g), and then gradually increased until the highest values in January (170.6 mg/g). Fructose (131.5 mg/g) was detected as the main soluble carbohydrate, followed by sucrose (98.8 mg/g) and glucose (73.1 mg/g). Keeping in view the results of current study, the best time to control Russian knapweed is flowering, where the amount of TSCs in the rhizomes is minimal. It is therefore recommended that the species should be controlled either at flowering stage or during the production of first rhizomes for its sustainable management in the country.

Introduction

Rhaponticum repens (L.) Hidalgo (formerly *Acroptilon repens* L.) is known as Russian knapweed in North America, whereas the other names of the species include mountain bluet, Russian cornflower, hardhead, Turkestan thistle, and creeping knapweed (Zimmerman 1996). Russian knapweed, a member of the Asteraceae, is an important perennial creeping plant that propagates by rhizomes (Watson 1980, Özer et al. 1999,). It is endemic to Mongolia, West Turkistan, Iran, and

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Turkey (Maddox et al. 1985), also found in Russia, Ukraine, Argentina, Australia, and most of the Asian countries. In its non-native range, Russian knapweed is considered a weed with natural superior competitive and adaptive ability to ecological changes, causing serious damage to agricultural systems. In North America, Russian knapweed is designated as an invasive weed and has created serious problems in agricultural crops and disturbed natural flora (Watson 1980, Mullin et al. 2000, Rice 2006). Russian knapweed contains some allelopathic compounds that may contribute to its competitive behavior (Fletcher and Renney 1963, Stevans 1986, Musiyaka et al. 1993). Amines, sterols, phytotoxic and neurotoxic sesquiterpene lactones are the compounds found in the aboveground organs of the species (Mallabaev et al. 1982, Stevens and Merrill 1985, Stevens 1986, Robles et al. 1998, Choi et al. 2000). Additionally, the roots and root exudates have phytotoxic thiophene polyacetylene. These compounds are believed to have a relationship with allelopathic activity (Quintana et al. 2008).

Russian knapweed spreads by rhizomes as well as seeds, but reproduction is mainly through rhizomes, which emerge once the soil temperatures are above freezing. The plant can cover an area of 12 m^2 within 2 years, expanding radially in all directions (Watson 1980). In the first year of plant development, the rhizomes grow 2-2.5 meters and can range from 5-7 meters in the second year, growing up to 7 meters belowground. Russian knapweed can produce 100-300 rhizomes per m^2 and can persist in all types of soil. These properties mean that Russian knapweed can spreads very quickly in a short time and compete very well with other plant species (Watson 1980, Maddox et al. 1985, Sözeri 1993, Zimmerman 1996, Mangold et al. 2006). The most important role of the rhizomes is the storage of carbohydrates required for energy and carbon to initiate spring growth (Brandle and Crawford 1987, Kubin and Melzer 1996, Koppitz, 2004). The other tasks of rhizome are long-distance spread (Čižková-Končalová et al. 1992), support to the roots, help to survive under adverse environmental conditions (Granéli et al. 1992), and regeneration after heavy disturbance (Archibald, 1995). The carbohydrates are stored as non-structural forms (sucrose, glucose, fructose, starch, and fructans) (Ho 1988) in the rhizome. Sucrose, glucose, and fructose are water-soluble carbohydrates that are transferred from aboveground to belowground organs, but not at a consistent rate (Asaeda et al. 2008). The translocation rate of carbohydrates is affected by several factors, including temperature, growth stage, and mechanical damage to the aboveground organs (McNaughton 1974, Tworkoski 1992, Pohl et al. 1999, Asaeda et al. 2006).

Carbohydrates are the main energy source for organisms. The structural constituents of the cells largely consist of carbohydrates. Carbohydrates produced by the plant leaves are translocated toward different sinks for use or storage during plant growth and development (Geiger 1987). Carbohydrate accumulation in storage organs of perennial plants is essential for perennation

(Hendry 1987), and the amounts of stored carbohydrates in these organs can vary according to several factors, such as winter temperatures (Dickerman and Wetzel 1985), nutritional condition (Grace and Wetzel 1981), plant size (Asaeda et al. 2006, King et al. 2014), mechanical damage to aboveground tissue (Mordovets et al. 1972, Becker and Faecett 1998, Pohl et al. 1999), plant genotype, and altitude (Leoš et al. 1999, Clevering et al. 2000, Asaeda et al. 2005, Koppitz 2004). The concentrations of nonstructural carbohydrates typically exhibit a persistent imbalance that is reflected in the production and consumption of photosynthetic carbon (Tissue and Wright 1995, Mirjam et al. 2005). The continuous accumulation of photosynthetic products reflects the considerable ecological role of storage carbohydrates (Xu et al. 2008).

Many studies have examined the seasonal carbohydrate dynamics of various plant species in different geographic regions of the world. However, little research has been done to determine the seasonal carbohydrate dynamics of Russian knapweed growing anywhere in the world. No studies have satisfactorily documented the seasonal fluctuations in the carbohydrates present in the rhizome of Russian knapweed; however, determination of this seasonality is important for the understanding of population ecology. The aim of the present study was to determine the carbohydrate fluctuations in the rhizomes of Russian knapweed. The result of the current study will improve our understanding to the control Russian knapweed in agricultural ecosystems.

Materials and Methods

Study area

This study was carried out at Department of Plant Protection, Faculty of Agriculture, Ankara University, Ankara, Turkey during 2013-2014. Ankara lies in Central Anatolia Region of Turkey, situated 860 m above sea level and located at latitude 39° 57' north and longitude 32° 52' east. The total precipitation, average temperature, and relative humidity of the experimental site were 297.7 mm, 13.1 ºC, and 55.1%, respectively during 2013. The total precipitation was 295.6 mm from January to July in 2014, while average temperature and relative humidity were 14.3 ºC, and 59.1%, respectively. Average precipitation, temperature, and relative humidity for the years (1970-2014) were 416.6 mm, 12.8 ºC, and 59.6%, respectively (Table 1). The soil of the experimental area was clay-loam, slightly alkaline, with medium organic matter, good nitrogen, phosphorus, and potassium (Table 2).

Table 1. Historical and current weather data of the experimental site during the study period.

Months	Precipitation (mm)			Temperature (^oC)			Relative Humidity (%)		
	1970 -2012	2013	2014	1970-2012	2013	2014	1970 -2012	2013	2014
January	39.3	45.3	32.7	1.1	3.2	3.1	80.5	79.4	82.7
February	33.5	35	14	2.8	6.4	5.8	72.1	71.5	58.6
March	36.9	60.7	58	7.1	8.6	8.3	64.2	59.5	59.2
April	49.9	44.5	43.2	11.9	13.2	13.3	58.1	59.7	53.7
May	50.6	21.7	88	16.9	19.5	16.2	55.7	45.1	61.3
June	50.2	22.3	65	21.2	21.7	19.7	50.4	43.6	57.2
July	15.5	17	8.7	24.8	23.5	25.5	43.5	41.4	41
August	12.0	1.6	-	25	24.1	-	39.6	38.7	-
September	17.5	2	-	19.7	18.2	-	43.7	43.1	-
October	33.3	23.8	-	13.7	11.6	-	59.5	50.3	-
November	35.4	19.9	-	7.4	8.5	-	70.3	62.1	-
December	42.5	3.9	-	2.6	-0.9	-	77.9	67.8	-
TP (mm)	416.6	297.7	309.6						
MT (^oC)				12.8	13.1	13.2			
RH (%)							59.6	55.1	59.1

TP: Total precipitation, MT: Main temperature, RH: Relative humidity

Table 2. Physico-chemical properties of the experimental site.

Texture Class	pH	EC*	Lime(%)	Organic Matter (%)	N (%)	P (ppm)	K (ppm)
Clay loam	7.67	0.43	8.32	2.21	0.16	17.40	458.00

*EC= Electrical conductivity

Rhizome Collection

Russian knapweed rhizomes were collected from an area of ~100 m^2 at the study site. Rhizome samples were collected for a period of one year starting from 20th of August 2013. Four replicates of rhizome samples were collected monthly at randomly selected points from 1-25 cm soil depths. The collected rhizomes were dried in an oven until constant weight (Karunaratne et al. 2014). The dried rhizome samples were then stored at -20 °C until use (Kohl et al. 1998).

Total Soluble Carbohydrate Analysis

The soluble carbohydrate contents in each dried rhizome samples were determined by adding 7.5 ml of acetonitrile and 2.5 ml of pure water to 1 g of the sample, homogenizing the tissue in a homogenizer, and storing the homogenized mixture at 4 °C for 1 day. The samples were then thoroughly ground in a mortar and the liquid was filtered through a sample decantation filter (pore size 0.45 µm). An 8 ml volume of the filtrate was diluted with 2 ml of a 75:25 (v/v) acetonitrile-water mixture to obtain a final volume of 10 ml. This preparation was analyzed by high performance liquid chromatography (HPLC) (on an Agilent Technologies system equipped with an Agilent analysis column (4.6 × 250 mm, 5 micron) and refractive index detector (RID). The column temperature was maintained at 30 °C and the flow rate of the mobile phase [acetonitrile:water; 75:25 (v/v)] was 1 ml/min. The data were analyzed using Kruskal-Wallis test.

Results and Discussion

The Kruskal-Wallis test indicated significant differences ($X^2_{(11.48)} = 45.67$, $p<0.5$) among collection months for the total amount of soluble carbohydrates (TSCs) present in the rhizomes. The concentrations of TSCs varied with the months, with the highest total amount (170.6 mg/g) obtained in January (Fig. 1) when air temperature was quite low (3.1 °C) (Table 1), followed by December (30.5 mg/g) and November (18.3 mg/g). The lowest amount of carbohydrates was obtained in August (6.2 mg/g) (Fig. 1) when air temperature was 24.1 °C (Table 1), followed by July (7.9 mg/g) and September (8.3 mg/g). The TSCs in the rhizomes of Russian knapweed was low at sprouting and then slightly increased until mid-June (beginning of flowering). Thereafter TSCs were slightly decreased from mid-June to minimal values in August (flowering period), and then increased gradually until maximal values in January when plant development slows down at the end of growing season. Fructose (131.5 mg/g) was detected as the main soluble carbohydrate, followed by sucrose (98.8 mg/g) and glucose (73.1 mg/g) (Figure 1).

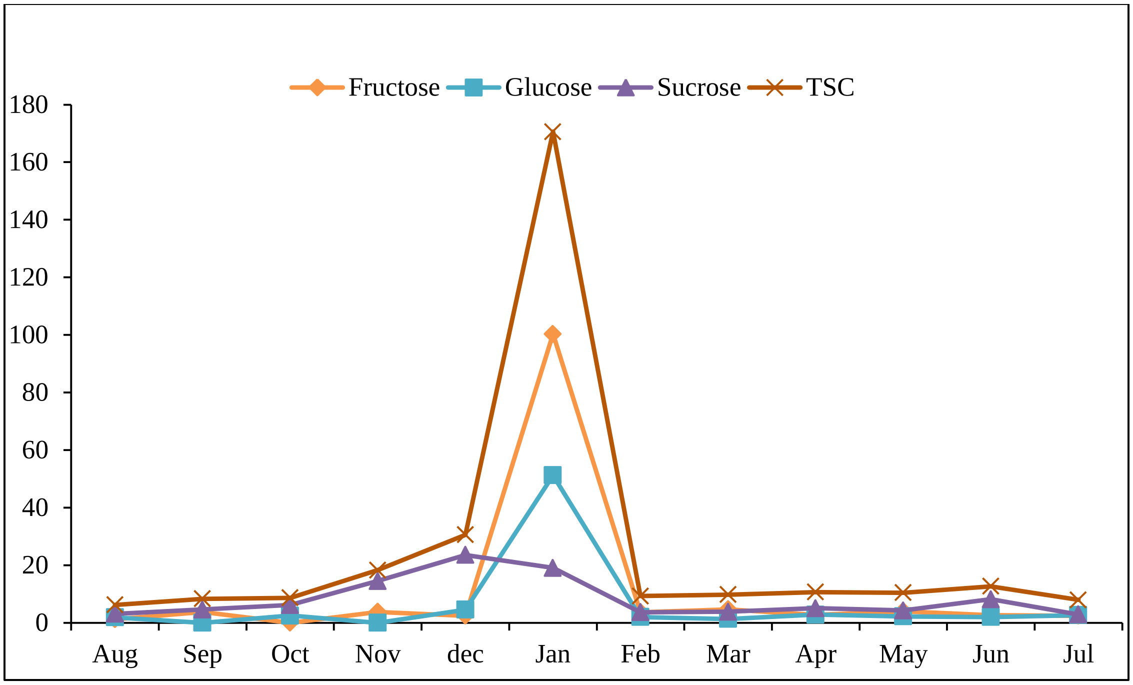

Figure 1. Seasonal changes in the soluble carbohydrates and TSCs present in the rhizomes of Russian knapweed.

The carbohydrates in the rhizomes of Russian knapweed fallen sharply in February (Figure 1) at which time the plant height ranged between 0-10 cm and the first true leaves were not fully developed. Earlier studies with other plant species have indicated that the amounts of soluble carbohydrates in the rhizomes significantly decrease at the end of winter and the beginning of spring, during the eruption of new buds (Walton et al. 2007, Willeke et al. 2012; Song et al. 2016). New shoots can emerge from the soil surface by making use of available carbohydrates sources in the rhizomes. Therefore, the reduction in the amounts of carbohydrate in Russian knapweed quite likely reflected the formation of new growth from the shoot buds. A similar result was observed for the rhizomes of common reed (*Phragmites australis*) and cattail (*Typha latifolia*) by Tursun et al. (2011), who reported the lowest total carbohydrate concentrations in February for common reed and in March for cattail when the plants were initiating new growth. The carbohydrate reserves of rhizomes of creeping thistle (*Circium arvense*) were also the lowest in mid-April during the formation of new growth (Özer 1969). Another study reported reductions in carbohydrate amounts in the rhizomes of creeping thistle reduced in the months of May, June, and July (Amy 1932, Hodgson 1968). Sözeri and Erdiller (1993) similarly recorded that the total soluble carbohydrate reserves in Russian knapweed declined during spring growth. In general, the finding of the lowest amounts of TSCs during new spring growth seems to be a general characteristic of all temperate region perennial plants (Madsen 1997).

After sprouting, the TSCs slightly increased until mid-June and the beginning of flowering, which might reflect the energy needs of the plant as it produces shoots. McAllister and Hederlie (1985) reported an inconsistency in replenishment of the carbohydrate reserves in the rhizomes of creeping thistle during the summer months of active shoot growth and carbohydrate production. The results from the present study are similar to the studies carried out in liquorice (*Glycyrrhiza glabra*) (Özer *et al.* 1977), common reed (*P. australis*), and cattail (*T. latifolia*) (Tursun et al. 2011). The TSCs were slightly decreased from mid-June to August, during the flowering period. Özer and Koch (1977) reported that TSCs in rhizomes of liquorice (*G. glabra*) declined at the time of flowering in June-July. Similarly, Robocker (1972) showed a rapid decrease in carbohydrate amounts in rhizomes of Dalmatian toadflax (*Linaria dalmatica*) that coincided with fast growth of flower stems and blooming. Daer and Willard (1981) also attribute an observed depletion in TSC reserves in roots of bluebunch wheatgrass (*Agropyron spicatum*) to rapid vegetative growth. Backer and Fawcett (1998) showed that TSCs in the roots of hemp dogbane (*Apocynum cannabinum*) were at their lowest levels as the plant began to flower. In our study, we assumed that the observed decrease in TSCs could also be attributed to the rapid vegetative growth and flowering of Russian knapweed. These results were attributed to the high energy requirements incurred by flower production.

In our study, the TSCs in rhizomes began to increase from August to October when the plant growth was slowed down. This was followed by a considerable increase in TSCs content from October to January, at the end of the vegetative period. Increased amounts of TSCs at the end of the season have been associated with enhanced cold tolerance or cold hardening in alfalfa (*Medicago sativa*) (Green 1983, Jung and Smith 1961) and leafy spurge (*Euphorbia esula*) (Lym and Messersmith 1987, Frear 1995). In general, autumnal rises in TSCs amounts are thought to reflect an enhancement of chilling tolerance and plant hardiness. After October, the carbohydrates, especially sucrose, started to increase gradually, reaching a maximum level in January. Other studies have shown that a high concentration of soluble sugars at low temperatures is associated with chilling tolerance (Jung and Smith 1961, Risser and Cottam 1968, Rutherford 1977, Green 1983, Lym and Messersmith 1987, Pollock and Cairns 1991, Frear 1995, Wismer et al. 1995, Sowokinos 2001, Follet et al. 2004, Kleijn et al. 2005). Sucrose accumulation at low temperature aids in plant survival, and soluble carbohydrates, including sucrose, are associated with cold tolerance (Xin and Browse 2000, Stitt and Hurry 2002, Walton 2007). During the sample period in this study, the coldest months were December 2013 and January 2014 (Table 1). In our study, fructose was detected as the main soluble carbohydrate (131.5 mg/g), followed by sucrose (98.8 mg/g) and glucose (73.1 mg/g). Tursun et al. (2011) also found that fructose was the prevailing carbohydrate throughout the season in common reed, followed by sucrose and glucose, while cattail contained glucose as the major sugar, followed by sucrose and fructose. The soluble carbohydrate composition of plants clearly varies depending on the species, the developmental stage of plants, the environmental conditions, and ecology. Fructans, primarily the inulin type, are main water-soluble storage carbohydrates in underground storage organs in many of the species of the Asteraceae family, including Russian knapweed (Ernst et al. 1996). They are linear or branched fructose polymers that occur in plant cell vacuoles in all parts of the plant (Vijn and Smeekens 1999) and are involved in drought resistance and frost tolerance (Hendry 1993, Livingston and Henson 1998). Fructans are hydrolyzed to fructose and short-chain fructans by the enzyme fructan 1-exohydrolase (1-FEH) to enable new spring growth (Van den Ende and Van Laere 1996a). The occurrence of the first frost is the critical factor triggering the initiation of fructan breakdown to fructose (Van den Ende and Van Laere 1996b). In the present study, we detected the highest fructose level in January 2014, which may have arisen by hydrolysis of fructans to fructose by 1-FEH.

Conclusion

In summary, seasonal changes in soluble carbohydrates may be one mechanism that allows Russian knapweed to tolerate negative environmental conditions, thereby both providing survival, growth, and reproduction and giving this perennial plant a competitive advantage over other plant species. Furthermore, the effective implementation of the best control strategies at the right time requires an advanced knowledge about the biology and physiology of rhizomatous weeds. Minimizing the energy provided by belowground reproductive organs is the best practice to control perennial species. An understanding of seasonal changes in soluble carbohydrates may allow best timing of biological, mechanical, and chemical control strategies for advanced weed management. The most critical time to control Russian knapweed according to the current study is flowering period where the amount of soluble carbohydrates present in the rhizomes is minimal. The most suitable time to manage Russian knapweed February when carbohydrates in the rhizomes are low and the plant just starts its developmental phase. The plants are weak at this stage; therefore, a systematic herbicide could easily manage the plant at this stage. It is therefore recommended that Russian knapweed must be controlled in February under the climatic conditions of Ankara.

Conflict of Interest

Authors declare no conflict of interest.

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