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Fructan dynamics in the underground organs of *Chresta exsucca* (Asteraceae), a dry season flowering species

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ABSTRACT

Climatic seasonality has an influence on the phenology of native Cerrado plants. Herbs and subshrubs tend to flower in the rainy season, although some species of these habits flower in the dry season. Reserve carbohydrates, stored in the underground organs, are used to support phases of high energy-demand, but also may protect plants from damage during periods of environmental limitation. In this study we evaluated variation in fructan levels in the underground organs of field-grown plants of *Chresta exsucca* among different phenological phases. *Chresta exsucca* flowers in the dry season and possesses a diffuse underground system, which stores inulin-type fructans. Resprouting was continual during the sampling period. Oligosaccharide content was always higher than polysaccharide content, except during senescence, the only phase with an oligosaccharide: polysaccharide ratio < 1. Fructan accumulation occurred during vegetative growth until flowering. Fructan mobilization was prominent during resprouting until the beginning of vegetative growth. Fructans stored in the underground organs of *C. exsucca* serve to fulfill the energetic demands of development and maintenance of this complex structure. In this way, fructans are essential to the persistence of this species in the environment of the Cerrado by ensuring reproduction in harsh conditions, such as drought.

Keywords: Cerrado, drought, inulin, non-structural carbohydrate, phenology

Introduction

Cerrado occupies nearly 23 % of the territory of Brazil, and its vegetation comprises several phytophysiognomies that are spread throughout a wide geographical area (Ratter *et al*. 1997). Cerrado phytophysiognomies constitute a gradient of forms, from grasslands to woodlands, which are determined by abiotic factors, mainly soil fertility, depth of the water table and fire frequency (Franco *et al*. 2014). Rainfall seasonality is another crucial determinant of Cerrado phytophysiognomies. The rainy season occurs from October to April with average monthly rainfall ranging from 150 to 500 mm. In the dry season, from May to September, rainfall is considerably reduced to 0-50 mm per month (Silva *et al*. 2008), resulting in soil water deficit, particularly for herbs and subshrubs (Rossatto *et al*. 2013).

Though herbs and subshrubs are affected by seasonal drought, they predominate in the open physiognomies of the Cerrado, and are much more diverse than trees (Ratter *et al*. 1997). Herbs and subshrubs also have a high proportion of underground phytomass (Haridasan 2000), very often represented by several morphological types of perennial organs with buds and reserve compounds (Appezzato-da-Glória *et al*. 2008). Such underground organs enable regrowth following seasonal drought or fire.

Seasonality may also influence the phenological cycle of herbaceous plants of the Cerrado. Herbs and subshrubs

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typically sprout with the first rains, after a variable period of dormancy, and gradually develop as the rainy season progresses (Mantovani & Martins 1988). Reproduction occurs during higher water availability (Batalha & Martins 2004). Aerial shoots senesce after reproduction, at the beginning of dry season, and only the underground organs of the plants remain, dormant in the environment (Mantovani & Martins 1988). This pattern is exemplified by the Asteraceae species *Chrysolaena obovata* (previously named *Vernonia herbacea*), *Aldama discolor* (previously named *Viguiera discolor*), *Ichthyothere terminalis* and by the Amaranthaceae species *Gomphrena macrocephala* and *Gomphrena marginata* (Carvalho & Dietrich 1993; Isejima & Figueiredo-Ribeiro 1993; Vieira & Figueiredo-Ribeiro 1993; Silva *et al*. 2013; Almeida *et al*. 2017). All of these species accumulate fructans in their underground organs.

Fructans are fructose-based polymers and are present as a reserve compound in 15 % of all Angiosperms, including the derived Asteraceae (Hendry 1993). In this family, fructans are linear molecules with β(2,1) linkages between fructosyl units and a terminal glucose residue, constituting the inulin-type. Edelman & Jefford (1968) proposed a model for inulin synthesis in *Heliantus tuberosus* tubers, which starts with the fructosyl transfer between two sucrose molecules by the enzyme sucrose:sucrose 1 fructosyltranferase (1-SST), producing the trisaccharide 1-kestose and free glucose. Subsequently, the enzyme fructan:fructan 1-fructosyltransferase (1-FFT) transfers fructosyl units between fructan molecules, producing one fructan molecule with a high degree of polymerization (DP), and another with a low DP. Inulin hydrolysis is the function of fructan exohydrolase (1-FEH), which removes terminal fructosyl units.

Inulin stored in underground organs is used to resume growth during resprouting or defoliation (Raccuia & Melili 2010), since these processes require carbon in the absence of aerial organs, which precludes carbon accumulation by photosynthesis. Additionally, fructans are believed to protect plants against environmental constraints, such as cold and drought, since fructan-accumulating plants are common in the flora of temperate and arid zones, with seasonal frost and drought, respectively (Hendry 1993). This protective role can be achieved by membrane stabilization (Hincha *et al*. 2007) and by antioxidant properties (Peshev *et al*. 2013).

Changes in fructan metabolism have been observed throughout the seasonal growth of Cerrado herbs with the typical phenological cycle. Generally, herbs accumulate carbohydrates during vegetative growth, which are later used for reproduction and resprouting in the rainy season (Carvalho & Dietrich 1993; Isejima & Figueiredo-Ribeiro 1993; Vieira & Figueiredo-Ribeiro 1993; Almeida *et al*. 2017). However, there are variations in this pattern. Phenological notes from a floristic study of the tribe Vernonieae (Asteraceae) reported that some species differ in their period of reproduction by flowering in the dry season, as exemplified by species of the genus *Chresta* (Moreira & Teles 2014). This raises the question of how reserve dynamics occurs in dry season flowering species. We hypothesize that fructan dynamics is mainly governed by phenology, since phenological phases have distinct energy requirements. Thus, the main objective of this study was to evaluate fructan variation among different phenological phases in underground organs of field-grown plants of *Chresta exsucca*, a species with reproduction in the dry season.

Materials and methods

Study site

The study was carried out in Parque Nacional da Chapada dos Veadeiros, Alto Paraíso de Goiás, Goiás, Brazil (13°51'-14°10'S 47°25'-47°42'W; 800- 1,650 m). This site is known for its high levels of biodiversity richness and endemism (Munhoz & Felfili 2006), and contains a variety of Cerrado phytophysiognomies, of which rocky outcrops and open grasslands predominate (Lenza *et al*. 2011). Meteorological data for the period from October 2015 to September 2016 were obtained from the meteorological station closest to the study site, located in Posse, Goiás, Brazil (www.inmet.gov.br) (Fig. 1).

Plant material

Chresta exsucca DC. is an herbaceous species that is 0.6 – 2.0 m high, syncephalous, and with lilac flowers and cypsela-type fruits (MacLeish 1985). A voucher specimen was deposited in the herbarium of the Universidade Federal de Goiás (UFG 50894). Individuals of *C. exsucca* were evaluated for identification of their phenological phase. Four distinct plants, separated by more than 10 m, with the same phenological phase were sampled in October 2015, December 2015, February 2016, May 2016, and July 2016. Thickened underground organs were washed in distilled water, cut and weighed. Aliquots of fresh material (1.5 g) were boiled in aqueous ethanol (80 %) for 15 min for enzyme inactivation, and then kept in ethanol until arriving at the laboratory where the following extraction procedures were performed. Water content (WC) was determined by oven drying (50 °C) aliquots of fresh material (1.0 g) to constant dry mass (DM), and expressed as a percentage of fresh mass. These analyses were performed for four distinct individuals for each phenological phase: resprouting (RE), vegetative growth (VG), flower buds (FB), flower opening (FO), fruiting (FR) and senescence (SE).

Extraction and analysis of soluble carbohydrates

In the laboratory, samples stored in aqueous ethanol were homogenized and filtered through nylon cloth. Residues were re-extracted twice in aqueous ethanol (80 %)

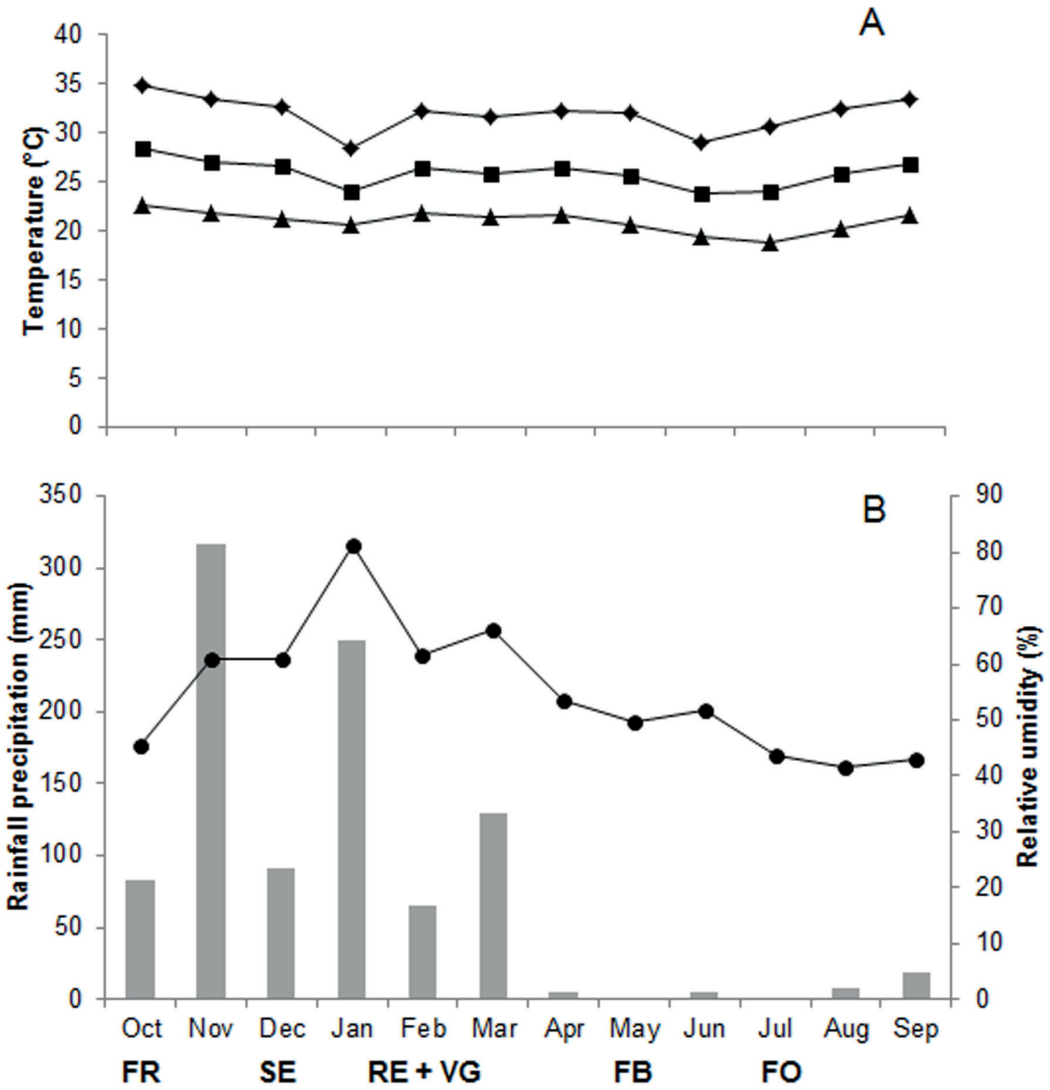

Figure 1. Monthly means of maximum (diamonds), average (squares) and minimum (triangles) temperatures (**A**), and rainfall (bars) and relative air humidity (circles) (**B**) from October 2015 to September 2016 in Posse, Goiás, Brasil, (www.inmet.gov.br). Resprouting (RE), vegetative growth (VG), flower buds (FB), flower opening (FO), fruiting (FR) and senescence of the aerial organs (SE).

at 80 °C for 15 min. All the ethanolic filtrates were pooled and consisted mainly of mono-, di- and oligosaccharides, hereafter referred to as the oligosaccharide fraction. Residues were extracted twice in distilled water (60 °C) for 30 min. The aqueous filtrates, consisting of predominantly polysaccharides, were collected and hereafter referred to as polysaccharide fractions (Carvalho *et al*. 1998). Both fractions were vacuum-concentrated in a rotary evaporator (39 °C) and analyzed independently.

Soluble carbohydrate of the oligosaccharide and polysaccharide fractions was quantified by the phenol-sulfuric method using glucose as standard at 490 nm (Dubois *et al*. 1956). Total soluble carbohydrate was obtained by the sum of the soluble carbohydrate of both fractions. All quantifications were done in triplicate for each of the four biological replicates.

The oligosaccharide and polysaccharide fractions were deionized using ion exchange resins (Amberlite IRA 120, cationic and Amberlite IRA 410, anionic), eluted with 10 volumes of ultrapure water (18 MΩ). The purified fractions had their pH checked, and neutralized if necessary, prior to being concentrated in a rotary evaporator and solubilized in ultrapure water. Free and combined fructose content was determined in each purified fraction using anthrone reagent with fructose as a standard at 620 nm (Jermyn 1956). Fractions were adjusted to the final concentration of 400 μg. mL^{-1} of fructose equivalents.

The purified fractions were filtered through membranes (0.45 μm) and analyzed by high-performance anion exchange chromatography with integrated pulsed amperometric detection (HPAEC/IPAD) in a CarboPac PA100 column (4 x 250 mm), with the corresponding guard column, coupled to a

ICS 5000 chromatograph (Dionex). Mobile phase was a gradient of sodium acetate (500 mM) in sodium hydroxide (100 mM) with the following schedule: 0-10 min: 5 mM; 10.1 - 35min, 5 - 50 mM; 35.1 - 40 min, 50 - 375 mM; 40.1 - 45min, 500 mM, eluted at 1 mL.min^{-1} (Silva *et al*. 2015). Chromatograms were prepared in the same scale of time and detector response. Extracts obtained from *Helianthus tuberosus* L. (Asteraceae) tubers were used as standard for comparison and identification of soluble carbohydrate. Qualitative analysis was performed by comparison of the relative area of a certain sugar peak among the different phenological phases, since the detector signal decreased with elution time. Quantification of glucose, fructose and sucrose was performed by the external standard method using authentic standards in Chromeleon 6.8 software (Dionex). Means obtained for each sugar in both fractions were expressed as a percentage in 400 μg. mL^{-1} of fructose equivalents.

Statistical analysis

Water content, oligosaccharide and polysaccharide levels, and the oligosaccharide:polysaccharide ratio, plus glucose, fructose, sucrose and fructans with DP ≥ 3, of samples collected during different phenological phases were submitted to Kruskal-Wallis analysis of variance, followed by Dunn´s test for multiple comparisons ($p < 0.05$). This test was chosen since these data did not meet the requirements for parametric analysis. All statistical analyses were conducted in BioEstat v. 5.3.

Results

Chresta exsucca has a diffuse underground system with thickened organs with orthogravitropic and diagravitropic growth. Resprouting plants were found throughout the study period, but were more intense in the rainy season, followed by vegetative growth. The development of reproductive organs occurred in the dry season, with the development of flower buds, flower opening and fruiting. Senescence of the shoots occurred in the rainy season (Fig. 2). Plants resprouted before the full senescence of the old aerial shoots.

Water and carbohydrate content

The water content of the underground organs of *C. exsucca* was lower in resprouting plants (rainy season) and during flower opening (dry season), compared to plants in vegetative growth (rainy season). Medians ranged from 52.9 % in flower opening to 67.37 % in vegetative growth (Fig. 3A). Total soluble carbohydrate (oligo- + polysaccharides) in the underground organs ranged 6 – 23 % (Fig. 3B). The oligosaccharide levels detected in plants with flower buds and fruiting were higher than those found in resprouting and senescence (Fig. 3C). Polysaccharide contents during senescence and in plants with flower buds were significantly higher than in plants undergoing flower opening (Fig. 3D). Oligosaccharide content was always higher than polysaccharide content, except during senescence, as demonstrated by the oligosaccharide:polysaccharide ratio, which was always greater than 1. The oligosaccharide:polysaccharide ratio during flower opening differed from that found during senescence (Fig. 3E), the only phase with values less than 1.

The percentage of glucose and sucrose during vegetative growth was higher than that found in fruiting and senescence. The opposite trend was observed for DP ≥ 3 sugars. Fructose percentage was also higher during vegetative growth compared to plants with flower buds and in senescence (Tab. 1).

Qualitative analysis of carbohydrates

Thickened underground organs of *C. exsucca* store inulin-type fructans. In all analyzed phases, glucose, fructose, sucrose, 1-kestose (DP3) and nystose (DP4) peaks were detected (Fig. 4). During resprouting, chromatograms showed oligosaccharides with higher glucose and fructose peaks than during the other phases. In the oligosaccharide profile, peaks with DP > 3 were low, while in the polysaccharide fraction DP > 3 peaks were pronounced. During vegetative growth, low DP sugar peaks remained high in both fractions, and high DP fructans in the polysaccharide fraction were substantially lower than in the resprouting chromatograms. The oligosaccharide chromatograms for plants developing floral buds showed lower glucose, fructose and sucrose peaks compared to the previous phases. In this phase the oligosaccharides of the inulin series peaks were well-defined, compared to the other phases. Some non-identified peaks, probably of the inulo-n-ose series were also present. In the polysaccharide fractions, low-DP sugar peaks were low, while high-DP fructans were well-defined and reached DP > 50. In the subsequent phase, flower opening, glucose and fructose peaks were as high as in resprouting and vegetative growth with well-defined DP > 3 sugar peaks in both fractions, including some non-identified peaks. At fruiting, low DP sugars and fructan peaks were present in both fractions, but were lower than in the previous phase, and there were no non-identified peaks. In senescence, glucose and fructose peaks were lower than in the other phases, oligosaccharide peaks were well defined and high-DP fructan peaks were higher than in the other phases, reaching DP > 50.

Discussion

Chresta exsucca has a diffuse underground system with numerous superficial parts with diagravitropic growth such that one individual can occupy a large area. Appezzato-da-Glória *et al*. (2008) described a bud-forming diffuse underground system of radicular structure for the congener

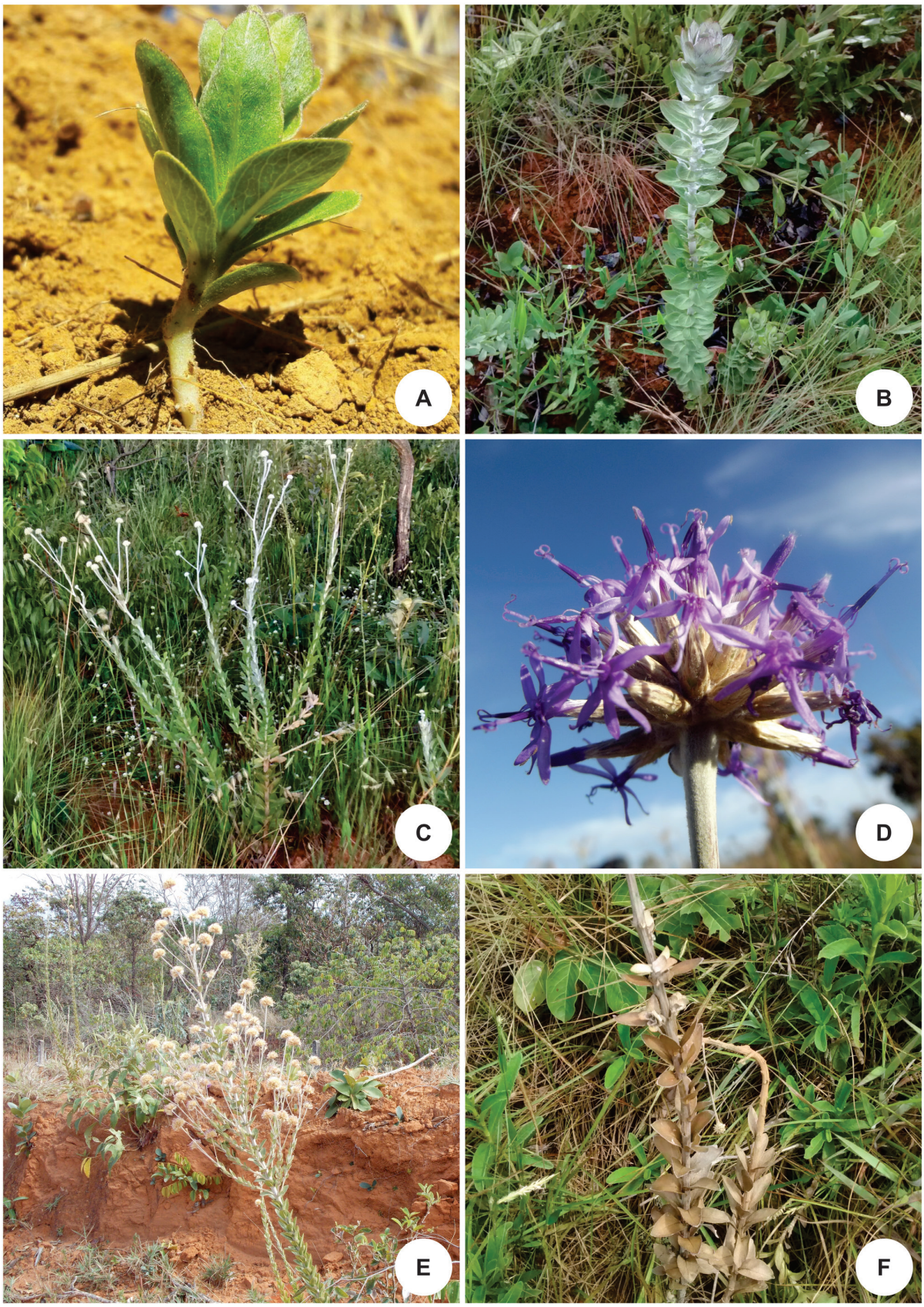

Figure 2. Individuals of *Chresta exsucca* growing in Parque Nacional da Chapada dos Veadeiros, GO, Brazil at different phenological phases: resprouting (A), vegetative growth (B), flower buds (C), flower opening (D), fruiting (E) and senescence of the aerial organs (F).

C. sphaerocephala. The aerial stems of a single individual of this species can be found up to 10 m distant from each other. This feature seems to be similar in *C. exsucca*, however, anatomical studies are necessary to confirm if they have cauline or root origin. The development of diffuse systems spread over a large area could enable the exploitation of areas of different soils, which could increase the possibility of obtaining water and minerals and the subsequent distribution of these resources among ramets. Evidence of physiological integration among ramets was observed in experimentally drought-stressed *Populus balsamifera*, where irrigated ramets supplied water for the connected water-deprived ramets (Adonsou *et al*. 2016).

Diffuse underground systems may bear buds (Appezzato-da-Glória *et al*. 2008) and contribute to clonal reproduction, which is an important feature in ecosystems with limited resources and/or that experience climatic limitations (Couteron *et al*. 2014). As diffuse systems grow to occupy a large space, they can come to represent a strong sink for photoassimilates, not only due to the demands of growth but also for storage, which, in the case of *C. exsucca*, occurs mainly as fructans (Fig. 4).

Water content

Water content detected in the underground organs of field grown *C. exsucca* during flower opening and resprouting was lower than that during vegetative growth. In the underground organs of *I. terminalis*, water content was found influenced mainly by soil water availability (Almeida *et al*. 2017). In general, water content of the sampled underground organs was lower than that reported for other species. For example, rhizophores of irrigated *C. obovata* plants had 85 % water content (Garcia *et al*. 2011), while the tuberous roots of irrigated *A. discolor* had 80 % (Oliveira *et al*. 2013). Dimorphic thickened roots of field-grown *I. terminalis* plants had 61-85 %, with the highest values being during the rainy season (Almeida *et al*. 2017). Our results suggest that water content in underground organs may also be affected by phenological shifts and developmental stage, since plants in resprouting and in vegetative growth were collected at the same time.

Water content of underground organs varies among species of Asteraceae, as well as fructan content (Tertuliano & Figueiredo-Ribeiro 1993), because storage of resources depends on the relative distribution of tissues in a specific organ (Moraes *et al*. 2013). During dry periods, water maintenance in vegetative organs depends on the interaction of different factors including the presence of osmoprotectants that regulate osmotic adjustment (Singh *et al*. 2015). Soluble carbohydrates are significant osmotic-active compounds and fructans stand out because they are reserve carbohydrates, protect membranes and proteins and removing reactive forms of oxygen (Peshev *et al*. 2013), which are features that contribute for plant preservation during environmental constraints.

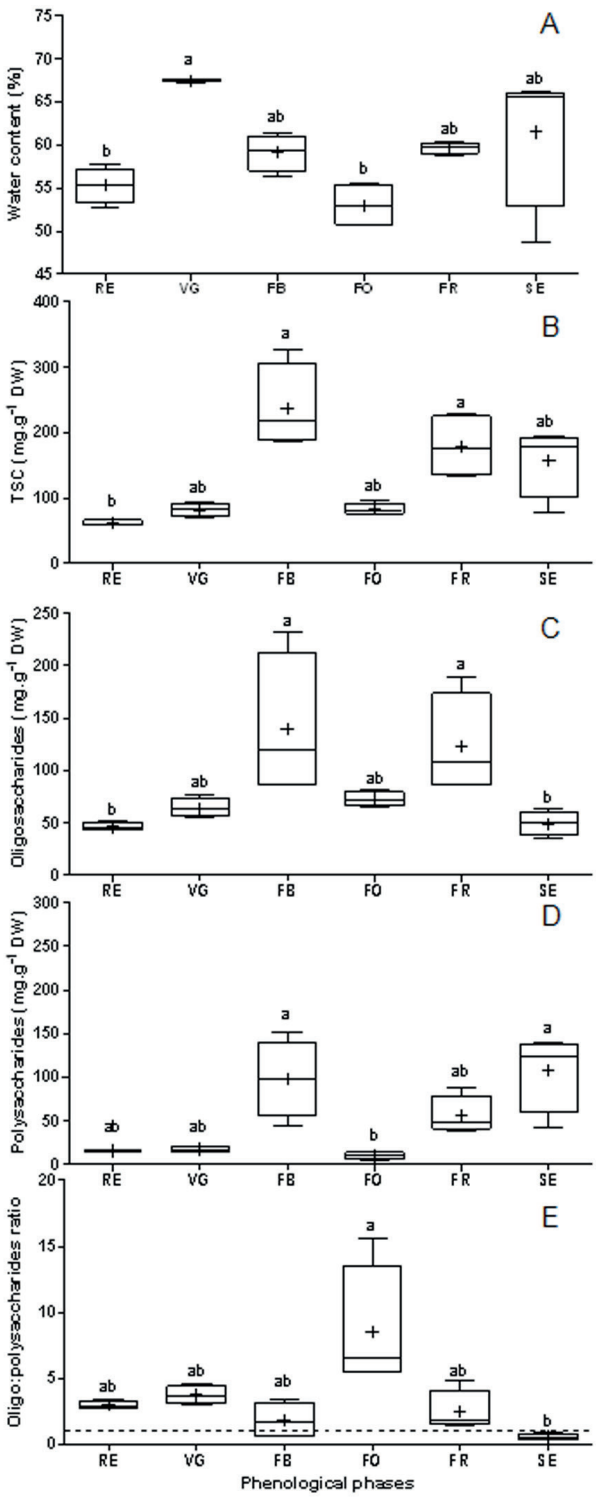

Figure 3. Box-plot showing water (**A**), total soluble carbohydrate (**B**), oligosaccharide (**C**), polysaccharide (**D**) content, and oligosaccharide:polysaccharide ratio (**E**) of underground organs of field-grown Chresta exsucca plants in different phenological phases. Resprouting (RE), vegetative growth (VG), flower buds (FB), flower opening (FO), fruiting (FR) and senescence of the aerial organs (SE), total soluble carbohydrate (TSC). Dashed line in E indicates oligosaccharide:polysaccharide ratio = 1. Different letters indicate different medians (n = 4, $p < 0.05$).

Table 1. Percentages of glucose, fructose, sucrose and fructans with degree of polimerization ≥ 3 in total free and combined fructose in underground organs of field-grown *Chresta exsucca* plants. Different letters indicate different medians (n = 4, $p < 0.05$) comparing phenological phases for each sugar (columns).

Phenological phase	Sugar (%)			
	Glucose	Fructose	Sucrose	DP≥3
Resprouting	4.64 ab	6.03 ab	5.51 ab	83.82 ab
Vegetative growth	6.43 a	7.78 a	6.97 a	78.82 b
Flower buds	1.37 ab	1.29 b	3.73 ab	93.61 a
Flower opening	4.81 ab	6.49 ab	4.22 ab	84.48 ab
Fruiting	0.94 b	1.88 ab	2.53 b	94.65 a
Senescence	0.12 b	0.80 b	2.64 b	96.44 a

Phenology

The timing of phenological shifts in *C. exsucca* differs from that of other species of Asteraceae from the Cerrado, as exemplified by *C. obovata* (Carvalho & Dietrich 1993; Rigui *et al*. 2015), *A. discolor* (Isejima & Figueiredo-Ribeiro 1993; Itaya *et al*. 1999) and *I. terminalis* (Almeida *et al*. 2017). These species have a well-defined phenological cycle with seasonal development, characterized by resprouting in the beginning of the rainy season, senescence and abscission of the aerial organs at the end of the rainy season, and dormancy of the underground organs in the dry season. In the Cerrado, a great proportion of the herbaceous species flower with increased rainfall (Batalha & Martins 2004). However, in *C. exsucca* flowering occurred during a 3-4 month period in the dry season and senescence of the aerial organs in the rainy season. Furthermore, resprouting was continual throughout the year. These differences suggest the occurrence of distinct strategies to regulate water content and metabolism of reserve compounds, since the use of these resources may be high due to intense resprouting and flowering in the dry season.

Since *C. exsucca* has a short period without aerial organs, relative to other herbaceous species, the extended presence of leaves indicates the potential for the synthesis of photoassimilates, even in the dry season. Studies on photosynthesis of herbaceous species of the Cerrado are scarce, but native trees are known to have several photosynthetic strategies for the rainy and dry seasons. Some species reduce the rate of carbon assimilation in the dry season, while others maintain rates unchanged. There are also tree species with reduced carbon assimilation rates even in the rainy season (Palhares *et al*. 2010). This suggests that herbs and shrubs may have several photosynthetic strategies for responding to climatic seasonality.

Soluble carbohydrates

Soluble carbohydrates, predominantly as inulin-type fructans (Fig. 4), are present in 5 to 33 % of the dry mass of the underground organs of *C. exsucca* (Fig. 3B). These carbohydrates are the main reserve compounds for species of Asteraceae (Hendry 1993). Carbohydrate storage occurs when photoassimilate production exceeds the demand for growth and maintenance of metabolism (Pollock 1986), which varies according to phenological phase and shifts in environmental factors. Phenological shifts modify source-sink relationships in fructan accumulators. In phases of high energy demand, such as regrowth and flowering, higher oligosaccharide levels are expected, while in phases with intense sugar translocation for storage organs, such as the senescence of aerial organs, polysaccharide content is higher. Such a phenological shift was also found for *C. obovata* (Carvalho & Dietrich 1993; Portes & Carvalho 2006), *Cichorium intybus* (Ende & Laere 1996a), *A. discolor* (Itaya *et al*. 1999), *Taraxacum officinale* (Wilson *et al*. 2001) and *I. terminalis* (Almeida *et al*. 2017).

Variation in fructan level among phenological phases of *C. exsucca* was similar to that reported for other species of Asteraceae. Higher oligosaccharide levels occurred in vegetative growth until fruiting (Fig. 3C). The chromatograms in these phases confirm this observation (Fig. 4). However, in resprouting, vegetative growth and flower opening, the peaks of glucose, fructose and low DP sugar were higher, as occurred in *A. discolor*, in which oligosaccharides of up to DP4 were predominant during sprouting and flowering (Itaya *et al*. 1999). The distribution of fructan molecules with varied DP is the result of the activity of fructan metabolizing enzymes. Higher free fructose peaks suggest intense 1-FEH activity or side 1-FFT activity transferring free fructose to water (Ende *et al*. 1996; Roover *et al*. 1999). Generally, 1-FEH has low activity, but it can be stimulated by defoliation, sprouting, flowering and environmental factors such as cold (Roover *et al*. 1999; Vergauwen *et al*. 2000; Asega & Carvalho 2004; Asega *et al*. 2011). The field-grown plants in uncontrolled environmental conditions studied here were thus subjected to a set of factors and phenological demands that resulted in the obtained fructan profiles. Since the monosaccharide peaks of plants with flower buds and fruiting were not as high as in resprouting, vegetative growth and flower opening (Fig. 4), photoassimilate production may have a greater contribution to supporting the energetic requirements of these phases, without the need of intensify fructan hydrolysis in the underground organs, even at the beginning of the dry season.

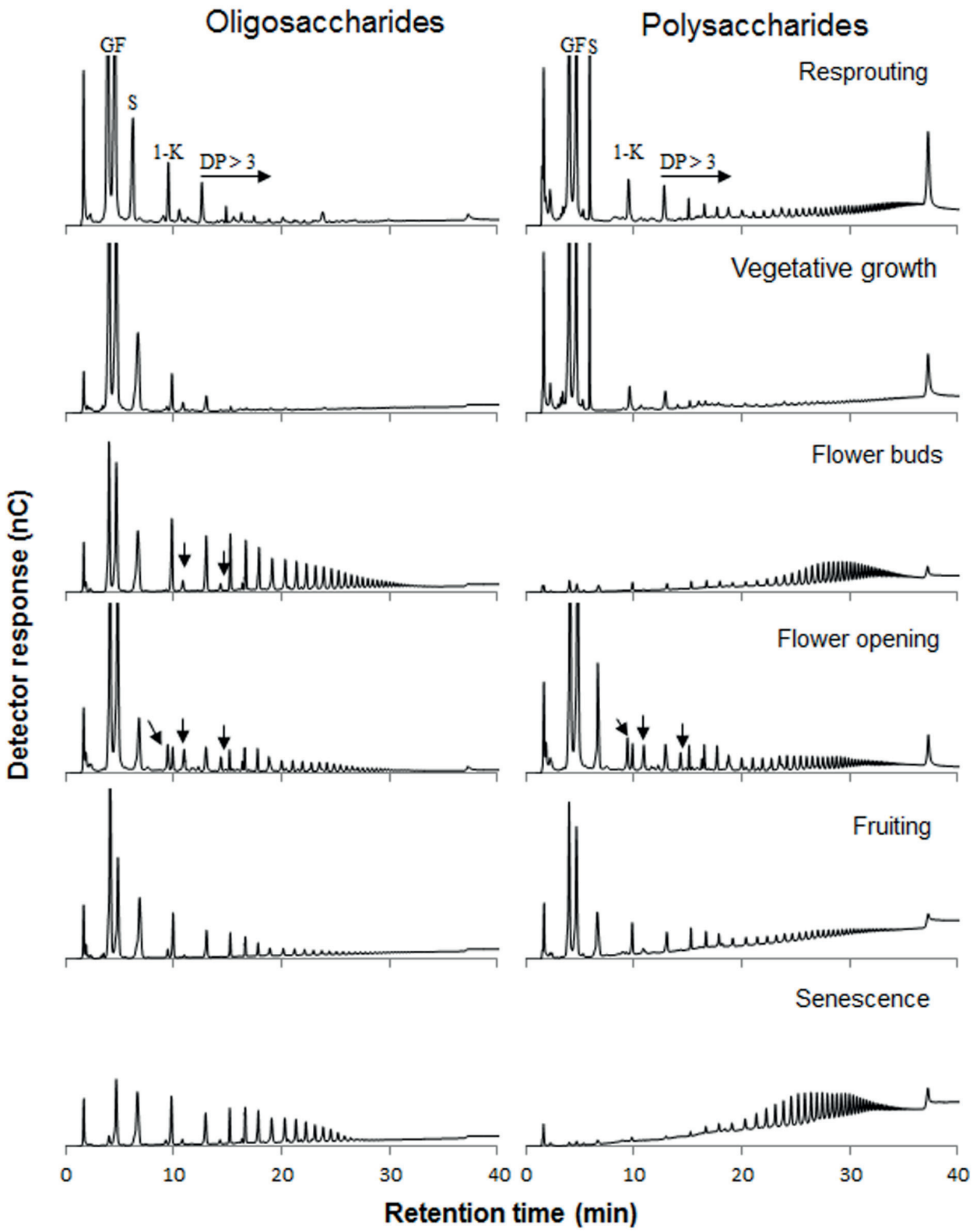

Figure 4. HPAEC/IPAD profiles of oligosaccharides and polysaccharides of underground organs of *Chresta exsucca* in different phenological phases. Glucose (G), fructose (F), sucrose (S), 1-kestose (1-K), degree of polymerization (DP). Arrows indicate unidentified peaks.

During senescence of aerial organs, the oligosaccharide: polysaccharide ratio was < 1, which is the result of the prevalence of polysaccharides relative to oligosaccharides during this phase (Fig. 3C-E), as supported by the chromatogram profile (Fig. 4). This indicates intense fructan synthesis and polymerization, which are catalyzed by 1-SST and 1-FFT, respectively. Increased 1-SST activity is induced by high sucrose levels (Ende & Laere 1996b), which could be a result of photoassimilate translocation from the senescing shoots towards underground organs, as is known to occur in *Chrysolaena obovata* (Rigui *et al*. 2015). In all other phases, oligosaccharide levels were higher than polysaccharide levels, as expressed by a oligosaccharide:polysaccharide ratio > 1 (Fig. 3C- E), indicating the constant use of photoassimilates to sustain plant development, especially flowering in the dry season. When the oligosaccharide:polysaccharide ratio is < 1, the sink activity of the underground organs may be intense for carbon storage. In addition to phenology, environmental factors may also influence this ratio, as noticed in water-stressed plants of *C. obovata*, which exhibited an increase in the oligosaccharide:polysaccharide ratio (Garcia *et al*. 2011; 2015).

In this work we verified that phenology has a strong influence on fructan dynamics in the underground organs of field-grown *C. exsucca* plants. Fructan storage supplies the energetic demands for the development and maintenance of the complex structure of the underground organs of *C. exsucca*, which is essential for the persistence of this species in the environment of the Cerrado, and to ensure reproduction in harsh conditions, such as drought.

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