Genet Resour Crop Evol
DOI 10.1007/s10722-013-0022-0

RESEARCH ARTICLE

Ontogeny and total sugar content of yacon tuberous roots and other three *Smallanthus* species (Heliantheae, Asteraceae), insights on the development of a semi-domesticated crop

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Received: 4 March 2013 / Accepted: 4 July 2013

Abstract The ontogeny of the tuberous roots of yacon (*Smallanthus sonchifolius*), an ancient Andean crop, is described for the first time along with three other wild species of *Smallanthus*: *S. connatus, S. macroscyphus* and *S. siegesbeckius*. Tuberous storage roots are present in the four species. Tuberization results from unusual secondary thickening. A meristematic endodermis maintains the primary cortex by generating cortex cells continuously. Secretory schizogenous canals develop adjacent to the endodermis in opposition to the phloem poles. Phellogen originates in the outer layers of the parenchymatic cortex. The four species develop a parenchymatous pith that stores mainly fructooligosacharides (FOS) and plays an important role in storing water, protecting the plant from drought stress and environmental hazards in the Andean climate. In yacon, domestication has produced a wide pith that stores water, reducing sugars and FOS with low degree of polimerization, that could have eventually made it more palatable as compared to the wild counterparts.

Keywords Domestication · Fructooligosacharides · Ontogeny · Root anatomy · *Smallanthus sonchifolius* · Yacon

Introduction

Yacon, *Smallanthus sonchifolius* (Poepp. et Endl.) H. Robinson, is an ancient Andean crop that has awakened worldwide interest due to its numerous nutritional and dietary properties. Probably a hybrid, yacon is a polyploid species (Grau and Rea 1997) and it has been classified by Dempewolf et al. (2008) as a semi-domesticated crop probably based on a long history of cultivation in the Andean region. As many other polyploid species, seeds are unfertile and the propagation of the crop is done by using rhizome sections (Seminario et al. 2003).

Yacon produces large edible tuberous roots traditionally consumed as "fruits", similar to sweet

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potatoes in appearance, juicy with a rather sweet taste but lacking starch. It has been recognized as a food of relatively low nutritive value since early times, being the origin of the common name "yacon" from the quechua term *yakku*, adjective meaning watery or insipid. In spite of the high productivity of this crop and some medicinal properties (Seminario et al. 2003) it seems likely that its reduced nutritive value has contributed to the reduction of the area of cultivation, particularly in the last two centuries, up to the point that it remained cultivated in small plots for family consumption.

In recent times however, much international interest has been generated by its unique carbohydrate composition (Rea 1994; Grau and Rea 1997). In a new scenery, with obesity and diabetes being epidemic diseases, people may benefit from the long-thought disadvantages of this crop. Forty to 70 % of the root dry matter corresponds to fructooligosaccharides (FOS, inulin type, i.e. β (2 → 1) fructofuranosylsaccharose) with low degree of polymerization, a type of carbohydrate with low caloric value. Reducing sugars (fructose, glucose and sucrose) account for 15–40 % of dry matter (Kortsarz González 2009). FOS content declines during post harvest storage as they hydrolyse into reducing sugars (Asami et al. 1991; Fukai et al. 1997; Lachman et al. 2003). Yacon roots also contain considerable amounts of phenolic compounds with a predominance of chlorogenic acid (Lachman et al. 2003) and caffeic acid derivatives (Takenaka et al. 2003). Roots exhibit pharmacological properties such as antioxidant activity (Simonovska et al. 2003) and beneficial effects on obesity and insulin resistance (Genta et al. 2009). The root cortex is a rich source of kaurenoic acid and derivatives (Coll Aráoz et al. 2010).

Smallanthus siegesbeckius (DC.) H. Robinson, *S. macroscyphus* (Baker ex Martius) A. Grau, *S. connatus* (Spreng.) H. Robinson, *S. riparius* (H·B.K.) H. Robinson, *S. meridensis* (Steyerm.) H. Robinson, *S. suffruticosus* (Baker) H. Robinson along with *S. sonchifolius* form the so-called "yacon group" because they share the southern area of distribution of the genus, the habit of growth and similar morphology of the aerial parts (Grau and Rea 1997). *S. sonchifolius* coexists in proximity with the wild species in the region of origin, the eastern slopes of the Andes, from northern Bolivia to central Peru and it is very likely that at least two of these wild species have contributed to the yacon genome (Grau and Rea 1997). This work is intended to increase knowledge on yacon and the wild relatives that may be used in developing advanced cultivars and to evaluate their potential as FOS sources. Also a comparative study with closely related species gives the opportunity to study how traits have responded to anthropic selection in yacon. There is a previous study on the morphology and anatomy of the tuberous roots of yacon (Machado et al. 2004), but no data concerning ontogeny are available and little is known about the wild species of the genus (Coll Aráoz et al. 2008; Mercado et al. 2009). Here we describe the morphology, anatomy, ontogeny and FOS content of the tuberous roots of four *Smallanthus* species (*S. sonchifolius*, *S. connatus*, *S. macroscyphus* and *S. siegesbeckius*).

Materials and methods

Three different accessions of *Smallanthus sonchifolius* (Poepp. et Endl.) H. Robinson (UNT-LIEY 97-1, UNT-LIEY 97-2 and UNT-LIEY 97-3) and one accession of *S. connatus* (Spreng.) H. Robinson, *S. macroscyphus* (Baker ex Martius) A. Grau and *S. siegesbeckius* (DC.) H. Robinson cultivated in experimental plots at Centro Universitario Horco Molle (CUHM), Tucumán, Argentina 26°47′S, 65°19′W, 547 m a.s.l. were studied (Table 1). All the plant material is part of the collection of Universidad Nacional de Tucumán (UNT) and is maintained under cultivation since 1997, propagated vegetatively from fleshy rhizomes in August and harvest every year in May.

Harvest Index (HI) were calculated as mean from 3 replicates of 10 plants each. *S. sonchifolius* and *S. siegesbeckius* were harvested on May 2008 and *S. macroscyphus* in February 2008, prior to the other two species due to a shorter lyfe cycle. In all cases material was in flowering state. Flowering state indicates the physiological maturity of the crop (Vilhena et al. 2003).

Voucher specimens were deposited in the Herbarium of the Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina:

Smallanthus sonchifolius UNT-LIEY 97-1: Tucumán. Dep. Yerba Buena: Horco Molle, Centro Universitario Horco Molle (CUHM), M. I. Mercado y G. I. Ponessa. s/n° (LIL 607173, 607174). *Smallanthus sonchifolius* UNT-LIEY 97-2: Tucumán. Dep. Yerba Buena: Horco Molle, CUHM, M. I. Mercado y G. I. Ponessa.

Table 1 Material cultivated in CUHM

Species	Code	Origin
S. sonchifolius	UNT-LIEY 97-1	Erquis, Tarija, Bolivia
S. sonchifolius	UNT-LIEY 97-2	Probably Ecuador, cultivated in New Zealand
S. sonchifolius	UNT-LIEY 97-3	Condado, Salta, Argentina
S. macroscyphus		Rearte, Tucumán, Argentina
S. connatus		Punta Lara, Buenos Aires, Argentina
S. siegesbeckius		Ahuabamba, Cuzco, Peru

s/n° (LIL 607176). *Smallanthus sonchifolius* UNT-LIEY 97-3: Tucumán. Dep. Yerba Buena: Horco Molle, CUHM, M. I. Mercado y G. I. Ponessa. s/n° (LIL 607175). *S. connatus*: Tucumán. Dep. Yerba Buena: Horco Molle, CUHM, A. Grau s/n° (LIL 607374), *S. macroscyphus*: Tucumán. Dep. Yerba Buena: Horco Molle, CUHM, A. Grau s/n° (LIL 607375) and *S. siegesbeckius*: Tucumán. Dep. Yerba Buena: Horco Molle, CUHM, A. Grau s/n° (LIL 607376).

Anatomical studies

Samples of the three accessions of *S. sonchifolius*, *S. siegesbeckius*, *S. connatus* and *S. macroscyphus* used for morphological and anatomical studies were obtained from CUHM in May 2006, 2007 and 2008. *S. macroscyphus* collected in August 2006 from wild populations in Rearte, Trancas 26°20′S, 65°32′W, 1,450 m a.s.l. and in February 2006 Los Yacones, Salta, Argentina, 1,572 m a.s.l. were also used for morphological and anatomical studies.

Roots were fixed in FAA (formalin, acetic acid, 50 % ethanol, 5:5:90 v/v/v). Fragments of adventitious roots of varying diameter were sampled. The material was dehydrated and embedded in paraffin. 20 μm Thick cuts of the embedded material were made with a rotation microtome, stained with safranin-fast green and mounted in Canada balsam (Johansen 1940). Although the sections illustrated in the figures are transverse, longitudinal cuts were also made. Hand made cuts of fresh material were stained with cresyl violet and Sudan IV Or. Cuts were visualized with a Zeiss Axiolab microscope and an Olympus SZ61 stereoscopic microscope. Photographs were taken with a Canon PowerShot A 310 digital camera. Schemes were made using Metcalfe and Chalck (1950) symbols.

Carbohydrate extraction and analysis

Samples of the three accessions of *S. sonchifolius* and of *S. siegesbeckius*, *S. macroscyphus* and *S. connatus* used for carbohydrates analysis were obtained from CUHM in May 2005, 2006 and 2008. Every year six plants of each species were used in these analyses.

Fresh tuberous roots were peeled and chopped with a knife. The resulting pieces were weighed and juice was obtained with a centrifugal juicer. Three root juice aliquots of 1 mL were separated for each species and 3 mL of methanol 80 % was added leaving the samples in incubation in a hot bath (80 °C) for 20 min following centrifugation. Supernatants were recovered and solvent was evaporated under vacuum. The residues obtained were dissolved in 1.5 mL of bi-distilled water and desalted using a mixed bed resin (Amberlite MB3, Sigma). Samples were stored at −18 °C until use.

Extracts were diluted 1:40 mL in distilled water and aliquots of these solutions were used for analysis. The total water-soluble carbohydrate content was determined by the phenol–sulphuric assay (Dubois et al. 1956). Quantification was calculated from calibration curve of Glucose (Sigma).

Samples were chromathographed by HPLC on a RSO Oligosaccharide Phenomenex column 200 x 10 mm (4 % crosslinked resin, silver ionic form) with a Rezex RSO Oligosaccharide guard column, 60 x 10 mm using deionized water as mobile phase at 70 °C. Flow rate: 0.3 mL min^{-1}. A Gilson 322 HPLC pump with a refractive index detector and Rheodyne injector with a 20 μL loop were employed.

Results

The four species analyzed have subterranean systems formed by a sympodial rhizome or rizophore carrying the aerial shoots and adventitious tuberous and fibrous roots. Tuberous storage roots are present in the four species (Fig. 1). In the three different *S. sonchifolius* accessions and *S. siegesbeckius*, the tuberous roots can reach 25 cm in length, and can have a diameter of almost 10 cm (Fig. 1a, b). In contrast to these species, *S. macroscyphus* and *S. connatus* have tuberous roots that usually exceed 60 cm in length but are less than 3 cm in diameter (Fig. 1c, d).

Normally the aboveground structures and the fibrous roots senesce and die in the winter. The rhizome and tuberous roots survive (overwinter) to give rise to the new stems and roots in the spring.

Table 2 shows total fresh weight of roots produced by plants of *S. macroscyphus*, *S. siegesbeckius* and *S. sonchifolius*. *S macroscyphus* was harvested prior to the other species due to a shorter life cycle. No data concerning *S. connatus* are available due to the difficulties in the maintenance of this species in the field because it is potentially invasive. Harvest index represents the weight of the harvested product as a percentage of total plant weight.

Tuberous root anatomy

All the studied *Smallanthus* species presented notably few fine absorbent roots compared to the large biomass they produce.

Tuberous roots of the four species responded to a single unusual secondary growth pattern. They emerge from the rhizome as thick primary roots with many protoxylematic poles.

Table 2 Total roots fresh weight (RFW) of the different wild *Smallanthus* species and *S. sonchifolius* accessions. *S. macroschyphus* was harvested on February 28th, 2008

Species/clones	RFW g per plant	HI
S. sonchifolius UNT-LIEY 97-1	10,284a	0.47
S. sonchifolius UNT-LIEY 97-2	9,409a	0.54
S. sonchifolius UNT-LIEY 97-3	8,064ab	0.39
S. siegesbeckius	5,609b	0.31
S. macroscyphus	5,801b	0.17

The three *S. sonchifolius* accessions and *S. siebesbeckius* were harvested on May 28th, 2008. Each treatment consisted of 3 replicates of 10 plants each

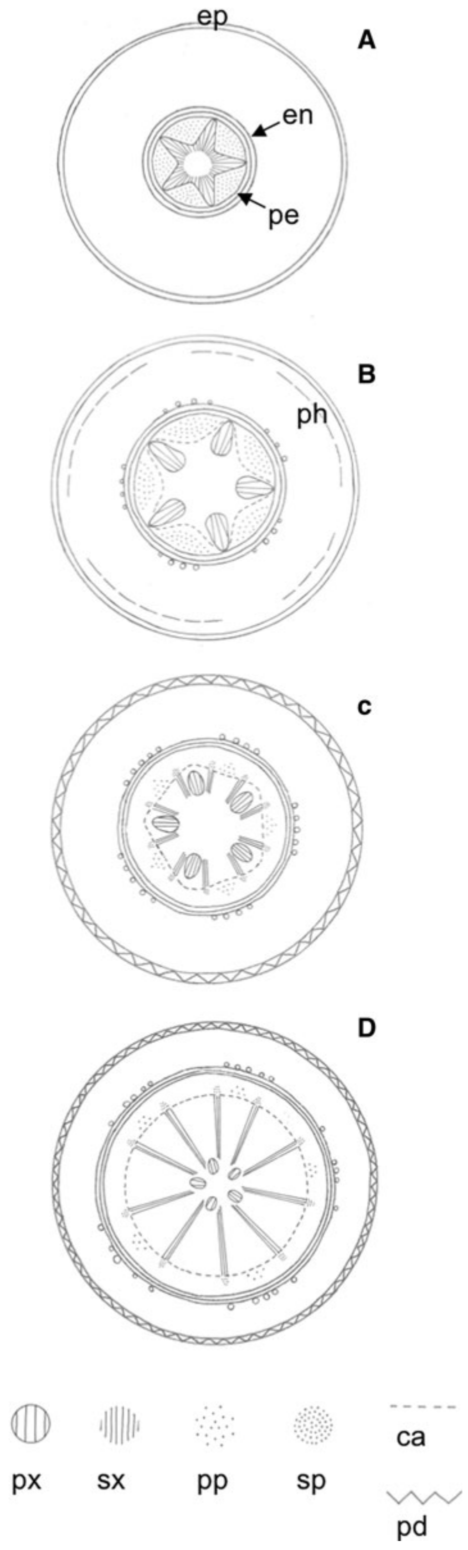
HI harvest index (roots)

Different letters indicate significant differences (Tuckey, $p < 0.05$)

The transverse sections of the primary roots of the four species show a polyarch stele with phloem occupying the indentations between the xylem arms (Figs. 2a, 3a). Unistratified rhizodermis with root hairs can be observed.

The primary growth stage is very brief and secondary growth is initiated almost immediately after the emergence of the root. Vascular cambium arises from procambial cells between the phloem and the primary xylem. These regions of the cambium

Fig. 1 Tuberous roots of *S. sonchifolius* (**a**) *S. siegesbeckius* (**b**). *S. macroscyphus* (**c**) and *S. connatus* (**d**)



◀ **Fig. 2** Schemes showing different developmental stages of the root. **a** Young root showing polyarch vascular cylinder. **b** Early stage in secondary growth, with the cambium derived from procambial cells and phellogen arising from the parenchymatous cortex. **c** Stage with cambium as a continuous meristem. Cambium derived from pericycle adjacent to protoxylem poles produces parenchymatous radii. **d** Cut of an adult root showing the position of the primary xylem and secondary xylem. Primary xylem (px), secondary xylem (sx), primary phloem (pp), secondary phloem (sp), cambium (ca), periderm (pd), phellogen (ph), epidermis (ep), endodermis (en), pericycle (pe)

become active before it becomes continuous around the outer edges of the protoxylem (Figs. 2b, 3b). Pericycle cells adjacent to the protoxylem poles also give rise to cambium and join the existing strand to form a continuous multiseriate meristem (Figs. 2c, d, 3e). Cambium derived from procambial cells divides periclinally to give rise to a secondary phloem and parenchyma toward the outer section of the root, and little secondary xylem and abundant parenchyma toward the inner section. The result is widely spaced phloem clusters separated by phloem parenchyma and secondary xylem elements radially distributed surrounded by a fiber sheath separated by parenchymatic radii. Cambium derived from the pericycle adjacent to the protoxylem produces parenchyma both centrifugally and centripetally, generating multiserial homocellular parenchymatous radii (Fig. 3d, e).

Secondary xylem fibers are more abundant in the specimens of *S. macroscyphus* growing in rocky areas compared to plants cultivated in experimental plots (Fig. 3f, g).

The parenchymatous pith is formed by divisions and volume increase of parenchymatous cells of the primary xylem.

Photographs of five sections of 1 cm wide of five tuberous roots from each species were used to calculate the xylem conductive area. Transverse cuts were stained with cresil violet and photographed. Xylem area was calculated by standard image analysis software. Xylem conductive area was reduced to less than a half in all the studied accessions of *S. sonchifolius* in comparison with *S. siegesbeckius*, *S. macroscyphus* and *S. connatus* (8.6, 18.2, 19.6 and 17 % of the total area of the transverse cut respectively) (Fig. 4a–d).

When secondary growth is initiated, part of the primary structure is maintained. The cortex never rips out due to a meristematic uniseriate endodermis that divides periclinally and anticlinally generating cortex cells continuously (Fig. 3c–g). Secretory schizogenous

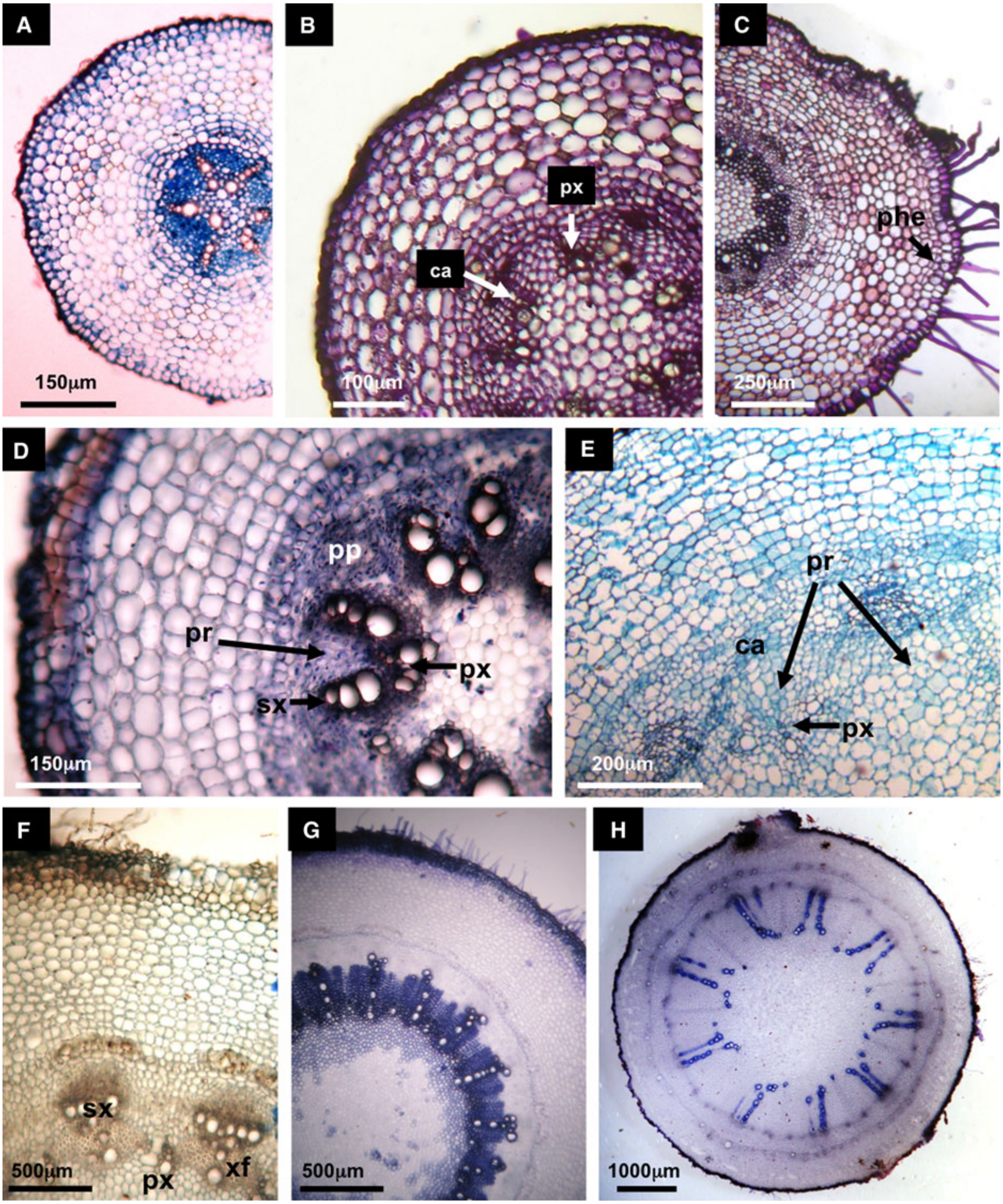


Fig. 3 Transversal sections of adventitious roots. **a** *Smallanthus macroscyphus* primary root. **b** *S. connatus* with cambium derived from procambial cells between the phloem and the primary xylem. **c** *S. siegesbeckius* with phellogen (phe) arising in the cortex. **d, e** *S. sonchifolius* showing continuous cambium (ca), primary xylem (px), secondary xylem (sx), primary phloem (pp), parenchymatous radii (pr). F, *S. macroscyphus* showing primary xylem (px), secondary xylem (sx) and xylem fibers (xf). G, *S. macroscyphus* root growing in rocky environment with many protoxylematic poles and many secondary xylem rays with xylem fibers. Root hairs are also observed in the periderm. **f** *S. macroscyphus* growing in cultivated plot with scarce xylem fibers

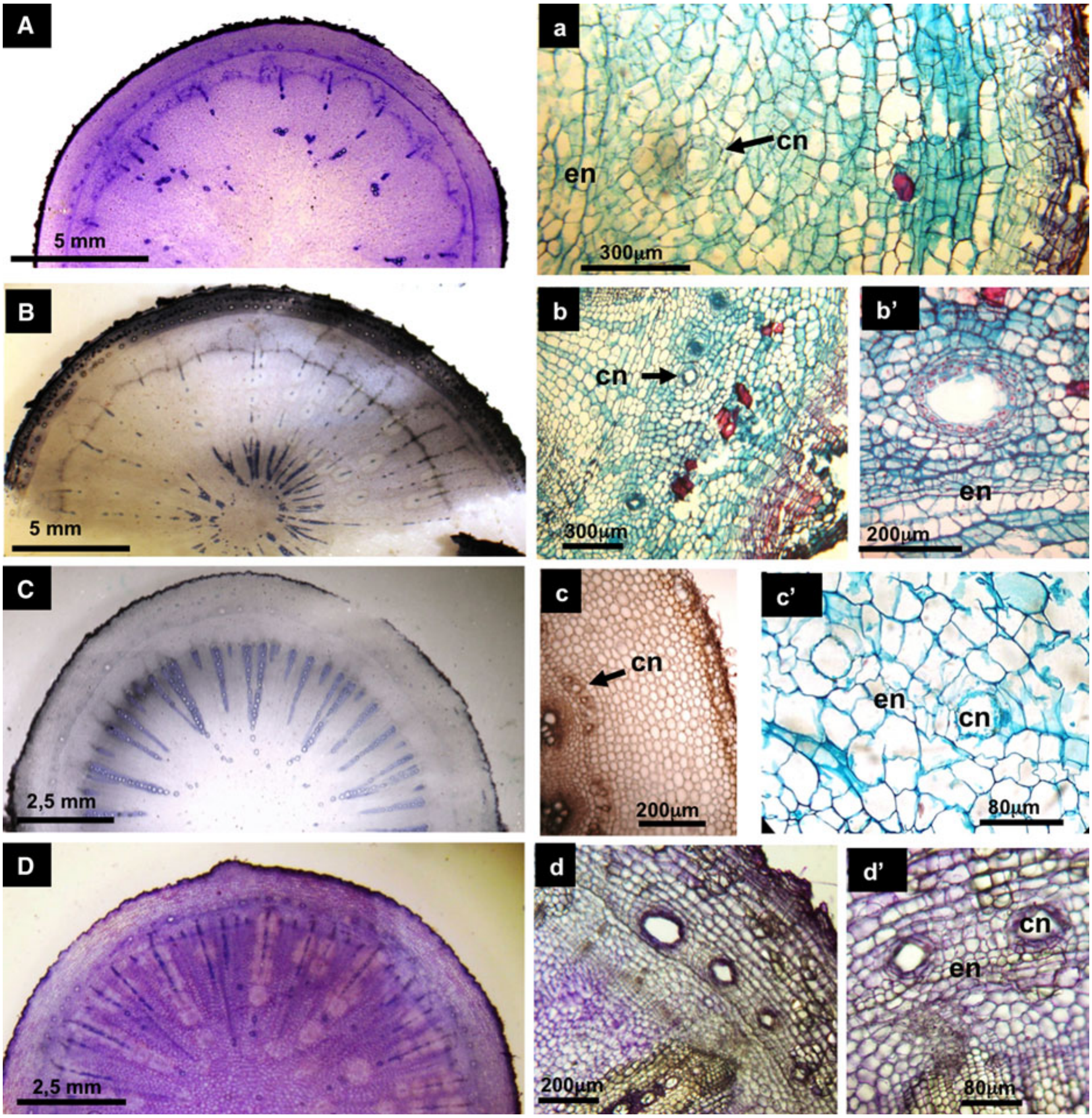


Fig. 4 Transversal sections of tuberous roots. **A** *Smallanthus sonchifolius* adult root; **a** root cortex, arrow pointing at secretory canal (cn). **B** *S. siegesbeckius* adult root; **b**, root cortex; **b′** canal and endodermis (en). **C** *S. macroscyphus* adult root; **c**, root cortex; **c′** root cortex detail showing cannals and endodermis. **D** *S. connatus* adult; **d**, cortex with canals; **d′** cannals and endodermis

canals develop in the cortex adjacent to the endodermis with Caspary stripes (Fig. 4 a, b, b′, c, c′, d, d′) in opposition to the phloem poles. They are originally diamond shaped formed by four epithelial cells (two endodermal cells and two cortical cells). In *S. sonchifolius* and *S. siegesbeckius*, the canals are located in the cortex, separated from the endodermis by several cell layers, although they were originally formed by the endodermis (Fig. 4 a, b, b′). In *S. macroscyphus* fully developed roots, most of the canals remain four celled and generally attached to the endodermis that forms part of the canal epithelium (Fig. 4c, c’). In contrast, the other three species have canals formed by more than four cells in fully developed roots. In *S. connatus* the endodermis does not form the epithelium of the canals but it is adjacent to them (Fig. 4d, d'). In every case the relative increase in the lumen of the secretory canals is achieved by the collapse of two epithelial cells that limit adjacent canals. *S. siegesbeckius* has the largest canals (70–250 µm lumen diameter, occasionally 500 µm). Canals usually present an amber secretion. In the four studied species the epithelial cells of the canal, whether endodermic or not, had dense content that stained with Sudan IV, indicating a lipidic content.

Phellogen originates from the second subepidermal layer of the parenchymatous cortex (Fig. 3c, d) and produces phellem toward the outside and phelloderm toward the inside, forming a periderm with conspicuous lenticels. Non-glandular trichomes can be observed over the periderm in some tuberous roots (Fig. 3c, f, g) a characteristic found in some other Asteraceae (Melo-de-Pinna and Menezes 2002).

A second type of root with secondary thickening was observed only in *S. sonchifolius*: long thin roots up to 50 cm in length by 1.5 cm in thick. This type of root does not produce a parenchymatous pith and the vascular cylinder is mainly formed by phloem and xylem elements and very little parenchyma. Consequently, the main function of these roots would be anchorage and transport.

Carbohydrate analysis

The sugar content of tuberous roots was analyzed to evaluate if the volume increase of the parenchymatous pith resulted in a greater accumulation of FOS in *S. sonchifolius* compared to the wild species. The total sugar content (TSC), FOS and reducing sugar content in tuberous roots are shown in Table 3. TSC is expressed as mg/g of root fresh weight. The three yacon accessions (UNT-LIEY 97-1, UNT-LIEY 97-2 and UNT-LIEY 97-3) accumulate less sugar per gram of fresh root compared to the wild species.

In the three accessions of *S. sonchifolius* the FOS content consists mostly of trisaccharides (Polimerization degree PD2), tetrasaccharides (PD3) and pentasaccharides (PD4), almost 70 % in UNT-LIEY 97-1 and UNT-LIEY 97-2 and more than 60 % in UNT-LIEY 97-2, while heptasaccharides (PD6) content accounts for more than 72 % in *S. siegesbeckius*, 78 % in *S. connatus* and 81 % in *S. macroscyphus* (Fig. 5).

Table 3 Root total sugar content (TSC), fructooligosaccharides (FOS) and reducing sugars (RS) expressed as mg/g RFW, pooled means of years 2005, 2006 and 2008, $n = 6$

Species/clones	TSC	FOS	RS
S. sonchifolius UNT-LIEY 97-1	121a	94a	27ab
S. sonchifolius UNT-LIEY 97-2	146ab	118ab	27ab
S. sonchifolius UNT-LIEY 97-3	117a	89a	29ab
S. siegesbeckius	172bc	132b	39a
S. connatus	179bc	165c	14b
S. macroscyphus	202c	181c	20b

Different letters indicate significant differences (Tuckey, $p < 0.05$)

Discussion

Many *Smallanthus* species show a clear preference for disturbed habitats, such as riverbanks, landslides, and roadsides (Grau and Rea 1997). Although mountainous forests in Peru, Bolivia and Northern Argentina are supplied with abundant rain water during most of the year, they are subjected to a relative dry winter season of between 2 and 4 months of duration. This dryer and slightly cooler interval could have played a crucial role on the evolution of *Smallanthus* underground system by generating conditions by which a plant species with tuberous roots could have an adaptive advantage since tuberous roots are less susceptible to environmental hazards and constitute a rather energetically stable system. The nutrients and water stored in subterraneous organs enables the plants to generate aerial shoots and leaves when the weather becomes favorable, right before the beginning of the rainy season.

Two characteristics in the anatomy of adventitious roots of *Smallanthus* deserve attention: the presence of meristematic endodermis and secretory canals in the root cortex associated with the endodermis opposite to the phloem poles, traits that may be considered as characteristic of adventitious roots in the Asteraceae (Lotocka and Geszprych 2004; Melo-de-Pinna and Menezes 2002; Luque et al. 1997).

The exudates of the canals might be secreted by the endodermis. The oxidation- reduction of phenols may be one of the main functions of the endodermis that determines the metabolism of lipid substances in this tissue (Van Fleet 1961). In the studied *Smallanthus* species all the epithelial cells of the canal, whether endodermic or not, had a dense content that stained

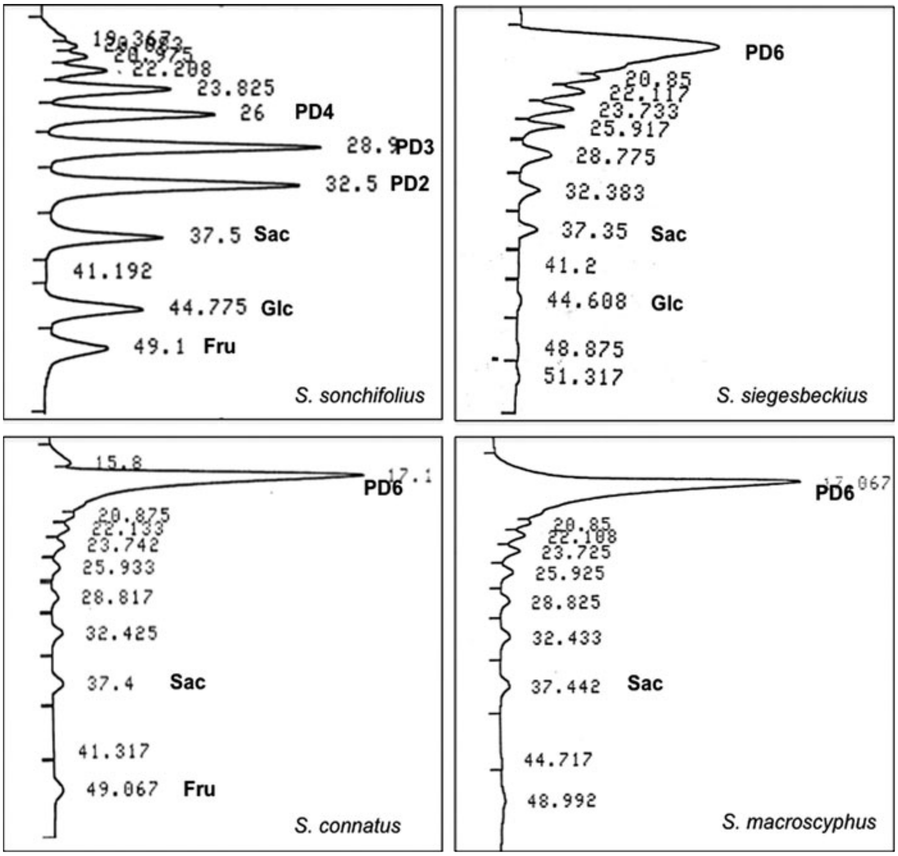


Fig. 5 Typical HPLC chromatograms of root extracts of *S. sonchifolius*, *S. siegesbeckius*, *S. connatus* and *S. macroscyphus*. RSO Oligosaccharide Ag^{++} column. Mobile phase deionized water at 70 °C. Flow rate: 0.3 mL min^{-1}. Glucose (Glu), Fructose (Fru), Saccharose (Sac), FOS polimerization degree (PD)

with Sudan IV, indicating their lipidic content. In every case, the exudates of the canals consisted of *ent*-kaurane type diterpenes (Coll Aráoz et al. 2010) an important class of diterpenes containing a rigid tetracyclic skeleton and exhibiting a wide variety of biological activities such as antitumor, anti-HIV, trypanocidal and antimicrobial (Ghisalberti 1997). *S. siegesbeckius* is a promising species as a kaurane source (Coll Aráoz et al. 2010).

Dempewolf et al. (2008) classified yacon as a semidomesticated crop. Yacon produces a greater number of roots, which are of larger size as compared to those from the wild counterparts. In yacon, domestication has produced roots with a wider parenchymatous pith and significantly less xylem conductive area compared to the wild species (Fig. 4a–d). Interestigly, pith volume increase and a higher proportion of parenchyma with respect to other non-storage tissues, did not correspond with a greater abitity to accumulate reserve substances, as it would be expected. Instead domestication has produced a wider pith that stores water. Yacon has been traditionally consumed raw by Andean habitants as a "fruit", recognized for its capacity to withstand several days of transport and be pleasantly refreshing due to the high water content (National Research Council 1989; Grau and Rea 1997). Another trait that might have been affected by domestication is sweetness, due to a combination of a higher concentration of reducing sugars, consequently higher caloric value for humans, and FOS with a lower degree of polymerization (Fig. 5) that could have eventually made it more palatable. Even though *S. siegesbeckius* has the highest proportion of reducing sugars in the four analyzed species (Table 3), the also high proportion of heptasaccharides FOS (PD6) (Fig. 5) and a biger xylem conductive area make this species unpalatable.

Under modern nutritional and agronomic requirements some traits like high polymerization degree FOS (Fig. 5) and short growth cycle present in the wild relatives *S. macroscyphus* and *S. connatus* (Grau and Rea 1997) may be very useful in breeding programs.

Acknowledgments Dr. Teresa Kraus made valuable contributions to the first draft. This research was supported by ANPCyT (Grant PICTO 2004-503 and PICT 2011-1871), CIUNT A26/403 and CONICET from Argentina.

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