

Root system morphology of Fabaceae species from central Argentina

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Summary: Root systems of different Fabaceae genera from central Argentina, are studied in relation to habitat conditions. Species of the following genera were analyzed: *Adesmia*, *Acacia*, *Caesalpinia*, *Coursetia*, *Galactia*, *Geoffroea*, *Hoffmannseggia*, *Prosopis*, *Robinia*, *Senna*, *Stylosanthes* and *Zornia*. Seeds of selected species were collected in each soil geographic unit and placed in glass recipients to analyze root system growth and branching degree during the first months after germination. Soil profiles that were already opened up were used to study subterranean systems of arboreal species. Transverse sections of roots were cut and histological tests were carried out to analyze reserve substances. All species studied show an allorhizous system, whose variants are related to soil profile characteristics. Roots with plagiotropic growth are observed in highland grass steppes (*Senna birostris* var. *hookeriana* and *Senna subulata*), and in soils containing calcium carbonate (*Prosopis caldenia*). Root buds are found in: *Acacia caven*, *Caesalpinia gilliesii*, *Senna aphylla*, *Geoffroea decorticans*, *Robinia pseudo-acacia*, *Adesmia cordobensis* and *Hoffmannseggia glauca*. Two variants are observed in transverse sections of roots: a) woody with predominance of xylematic area with highly lignified cells, and b) fleshy with predominance of parenchymatic tissue. The last one is mainly related to water and starch accumulation. The following strategies are observed to increase the parenchymatic zone: formation of big rays (*Stylosanthes montevidensis* var. *montevidensis* and *Adesmia cordobensis*), high production of parenchyma in secondary phloem and phelloderm (*Zornia gemella*), and differential activity of cambium (*Coursetia hassleri*). Besides acting as reserve, high starch accumulation produces an increase of cellular osmotic potential when it hydrolyzes into soluble carbohydrates and, consequently, enhances parenchymatic water retention.

Zusammenfassung: Wurzelsysteme unterschiedlicher Fabaceen-Gattungen aus Zentral-Argentinien wurden in Bezug auf ihre Standortbedingungen untersucht. Die Analyse umfasste Arten folgender Gattungen: *Adesmia*, *Acacia*, *Caesalpinia*, *Coursetia*, *Galactia*, *Geoffroea*, *Hoffmannseggia*, *Prosopis*, *Robinia*, *Senna*, *Stylosanthes* und *Zornia*. Samen ausgewählter Arten wurden mit dem Mutterboden gesammelt und in Glasgefäße gegeben, um Wachstum und Verzweigungsgrad des Wurzelsystems während der ersten Monate nach der Keimung zu analysieren. Bereits ergrabene Bodenprofile wurden für das Studium der unterirdischen Systeme baumförmiger Arten genutzt. Für die Analyse der Reservestoffe wurden Wurzelquerschnitte hergestellt und histologische Tests durchgeführt. Alle untersuchten Arten besitzen ein allorhizes System, dessen Varianten mit Merkmalen der Bodenprofile in Beziehung stehen. Plagiotrop wachsende Wurzeln können sowohl in Hochland-Grassteppen gefunden werden (*Senna birostris* var. *hookeriana* und *Senna subulata*), als auch auf Böden, die Kalziumcarbonat enthalten (*Prosopis caldenia*). Wurzelknospen bilden: *Acacia caven*, *Caesalpinia gilliesii*, *Senna aphylla*, *Geoffroea decorticans*, *Robinia pseudo-acacia*, *Adesmia cordobensis* und *Hoffmannseggia glauca*. In Wurzelquerschnitten können zwei Varianten unterschieden werden: a) holzig, mit vorherrschendem Xylem und stark lignifizierten Zellen und b) fleischig mit überwiegend parenchymatischem Gewebe. Letzteres ist hauptsächlich mit Wasser- und Stärkespeicherung verbunden. Um die parenchymatische Zone zu vergrößern, können die folgenden Strategien beobachtet werden: Bildung mächtiger Strahlen (*Stylosanthes montevidensis* var. *montevidensis* und *Adesmia cordobensis*), starke Produktion von Parenchym in sekundärem Phloem und Phelloderm (*Zornia gemella*) und eine charakteristische Aktivität des Kambiums (*Coursetia hassleri*). Neben der Funktion als Reserve, führt eine starke Stärke-Speicherung im Falle einer Hydrolyse zu löslichen Kohlenhydraten zu einer Steigerung des osmotischen Potenzials einer Zelle und erhöht folglich die parenchymatische Wasser-Retention.

Keywords: Fabaceae, root system, root-borne shoots

Research on subterranean structures of plant communities is important to interpret ecological relationships (SCHUBERT 1983). LINCH (1995) pointed out the architectural role of roots to

achieve an efficient absorption of soil resources. JÄGER (2000) emphasized the importance of characters of roots and survival organs during unfavourable seasons when he referred to data base formation for species conservation.

GROFF & KAPLAN (1998) proposed a structural analysis of possible topographical relationships between root and sprouting system, accentuating the importance of their morphology rather than the anatomy and physiology, i.e. taking the plant as a unit. Moreover, these authors recognized four structural types for vascular plants. AESCHIMANN & BOCQUET (1980), BARLOW (1986) and HARPER (1985), complemented these studies. BELL (1994) discussed descriptions of behaviour of root systems, based on CANNON (1949) and JENIK (1978) models for arboreal plants. RAUH (1937) studied sprout formation in roots and its importance for plant growth forms. TROLL (1967), WEBER (1953) and WAISEL et al., (1996) analyzed root system behaviour, especially in vascular plants.

Subterranean systems in relation to growth form of Fabaceae species were studied in several research works carried out in the Córdoba province, Argentina (KRAUS et al., 1995; BASCONSUELO et al., 1997; BIANCO et al., 1998; BIANCO & WEBERLING, 1999; BASCONSUELO, 2001; WEBERLING et al., 2002; BIANCO, 2002), but an exhaustive analysis of the external morphology and root structure of different growth forms is lacking. Therefore, the objectives of this work are to study root systems of species of several Fabaceae genera from central Argentina, and to relate them to their habitat.

Materials & Methods

Root systems in certain soil geographical areas of the Córdoba province, were analyzed in respect to branching degree and root orientation (KUTSCHERA & LICHTENEGGER, 1992). Seeds were collected and placed in glass containers to analyze root growth and branching degree during the first months after germination. The size of the glass containers were 0,40 m x 0,44 m x 1 m. Soil profiles that were already opened up were used to study subterranean systems of arboreal species. Transverse sections of roots were cut and histological tests were carried out to analyze reserve substances according to D'AMBROGIO DE ARGÜESO (1986) method. Species of the following genera were studied: *Acacia* (*A. caven* (Molina) Molina), *Adesmia*, (*A. cordobensis* Burkart), *Caesalpinia* (*C. gilliesii* (Wal. ex Hook.) D. Dietr.), *Coursetia*, (*C. hassleri* Chodat), *Desmodium* (*D. uncinatum* (Jacq.) DC.), *Galactia* (*G. latisiliqua* Desv. var. *latisiliqua*, *G. texana* (Scheele) A. Gray var. *texana*), *Geoffroea* (*G. decorticans* (Gillies ex Hook. & Arn) Burkart var. *decorticans*, *Hoffmannseggia* (*H. glauca* (Ortega) Eifert), *Prosopis* (*P. caldenia* Burkart, *P. campestris* Griseb.), *Robinia*, (*R. pseudo-acacia* L.), *Senna* (*S. aphylla* (Cav.) H. S. Irwin & Barneby, *S. birostris* (Domb. ex Vog.) H. S. Irwin & Barneby var. *hookeriana* (Hook.) H. S. Irwin & Barneby), *S. subulata* (Griseb.) H. S. Irwin & Barneby), *Stylosanthes* (*S. hippocampoides* Mohlenbr., *S. montevidensis* Vogel. var. *montevidensis* and *Zornia* (*Z. gemella* (Willd.) Vogel, *Z. trachycarpa* Vogel).

Characterization of the area of study.

The South American environment is enormously varied. This applies to climate, vegetation, physiography and lithology and, as a consequence, also to soils.

In order to give a survey of the soil geography, the continent has been divided into three major structural elements: lowlands, uplands, and Andes. These elements have been subdivided into ecological regions with a characteristic climate-vegetation-soil pattern.

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The area of this study covers the central part of Argentina and includes Lowlands (A9, Argentinian pampa; A 10, Chaco and Peripampa) and Uplands (B11, Central Argentina), map of FAO-Unesco, 1971, p 91 fig. 7.

Argentinian Pampa (Provincia Pampeana, CABRERA, 1971): the western pampa has a drier climate, and the sediments are coarser. Locally, sand dunes can be observed which are still actively moving. Soils in the southwestern pampa are underlain at varying depths by a cemented calcareous layer, *tosca*. The *tosca* is probably a result of soil evolution and subsequent erosion during an earlier geological period. *Tosca* is generally related to the undulations in the land and occurs under Phaeozems, Planosols and Solonetz.

Chaco y Peripampa (Provincia Chaqueña and Provincia del Espinal, CABRERA, 1971): the Chaco is a huge plain built up of sediments derived mainly from the eastern Andes. Because of the arid climate, primary minerals and soluble salts are abundant. In this region reddish Kastanozems with argilic horizons are dominant and are associated with Planosols and Solonetz. The Peripampa region is a wide flat sedimentary plain dissected by wide valleys, Kastanozems without argilic B horizons are dominant in association with Regosols.

Central Argentina (Pcia del Monte, CABRERA, 1971): the climate is desertic, rainfall varying between 100 and 200 mm/year. The soils are weakly developed due to the dry climate. Regosols occur together with calcareous greyish Yermosols without argilic B horizons.

Mountains, which are mainly located in the area of study include the following systems: Sierra de San Luis, Sierra del Morro, Sierra de los Comechingones, Sierra de los Cóncores and Sierra de las Peñas.

Readers are directed to BUOL et al. (1997) for details of soil morphology and soil characterization.

Results

The presence of buds in root systems is rather common in woody and herbaceous species of the Fabaceae family (Fig. 1). These buds are generally placed in the proximal part of first order roots in trees and shrubs. They are horizontally oriented, i.e. parallel to the soil level, a situation that is clearly observed in cliff profiles (Fig. 1 A,B,D). Root buds regularly appear every 50 cm, as can be found in shrubs, such as *Senna aphylla* and *Caesalpinia gilliesii*, where the equidistance between individuals in the field is easily observed. Furthermore, the acropetal differentiation of buds is evidenced by the centrifugal decrease of individual size compared to the mother plant size (Fig. 1 E).

Acacia caven shows a typical allorhizous system, where the taproot shows the strongest development. In samples observed taproot length is generally twice or more the plant height (Fig. 1A). Branches are scarce and only those that have root buds acquire a considerable diameter and length. They are situated at 0,50 to 1 m deep, corresponding to soil type. These roots are shallower in shrubs, as can be observed in *Caesalpinia gilliesii* and *Senna aphylla* (Fig. 1 E). Some species, such as *Robinia pseudo-acacia* and *Geoffroea decorticans*, form populations regionally called "islets" (Fig. 1C). Older individuals are situated in the centre of these islets and, in some places, they constitute a problem because they behave as weeds hardly to eradicate.

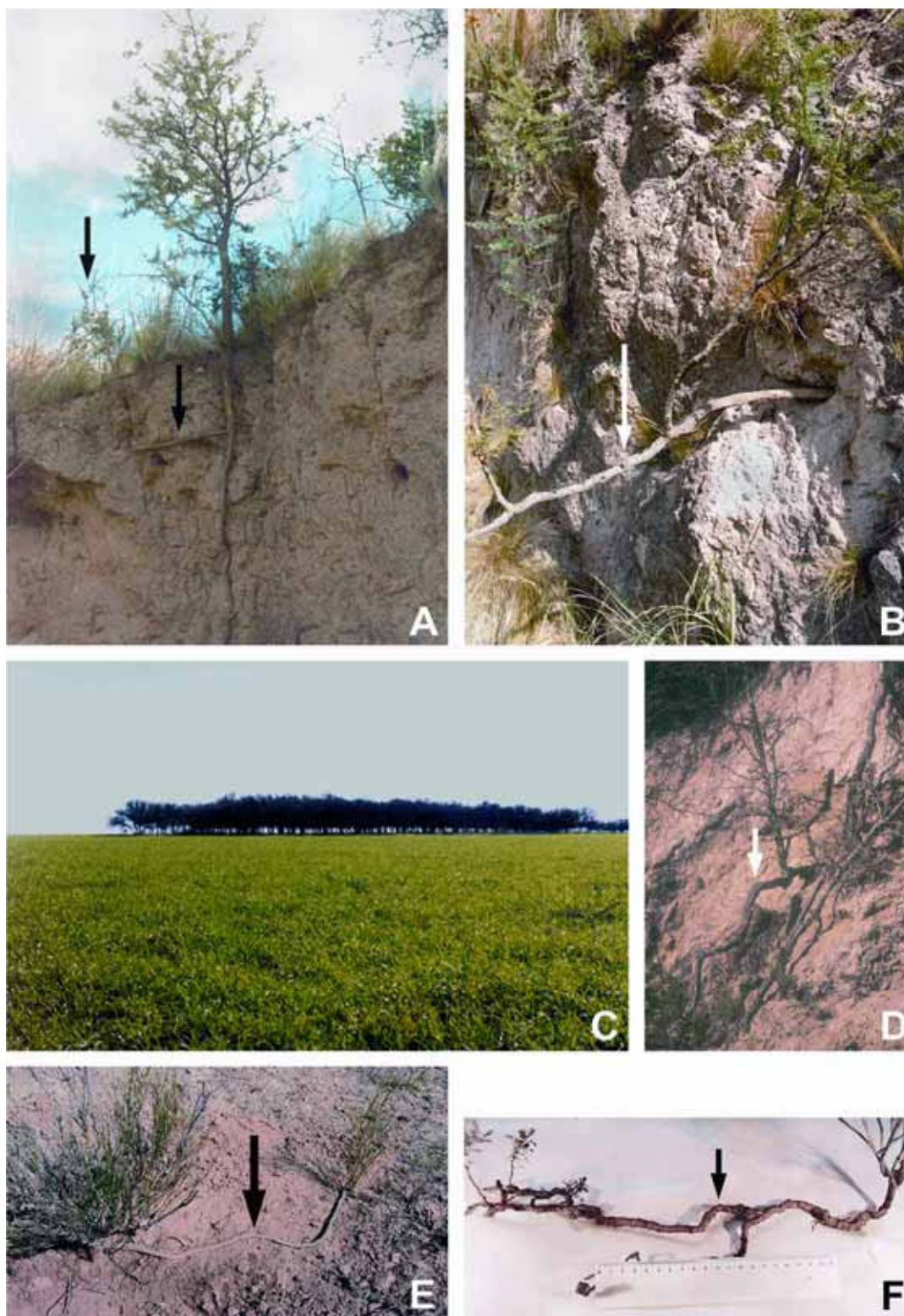


Figure 1: Plant, forming root-borne shoots. A) *Acacia cavern*, B) *Caesalpinia gilliesii*; C–D) *Geoffroea decorticans*; E) *Senna aphylla*; F) *Adesmia cordobensis*. Arrows indicate root-borne shoots.

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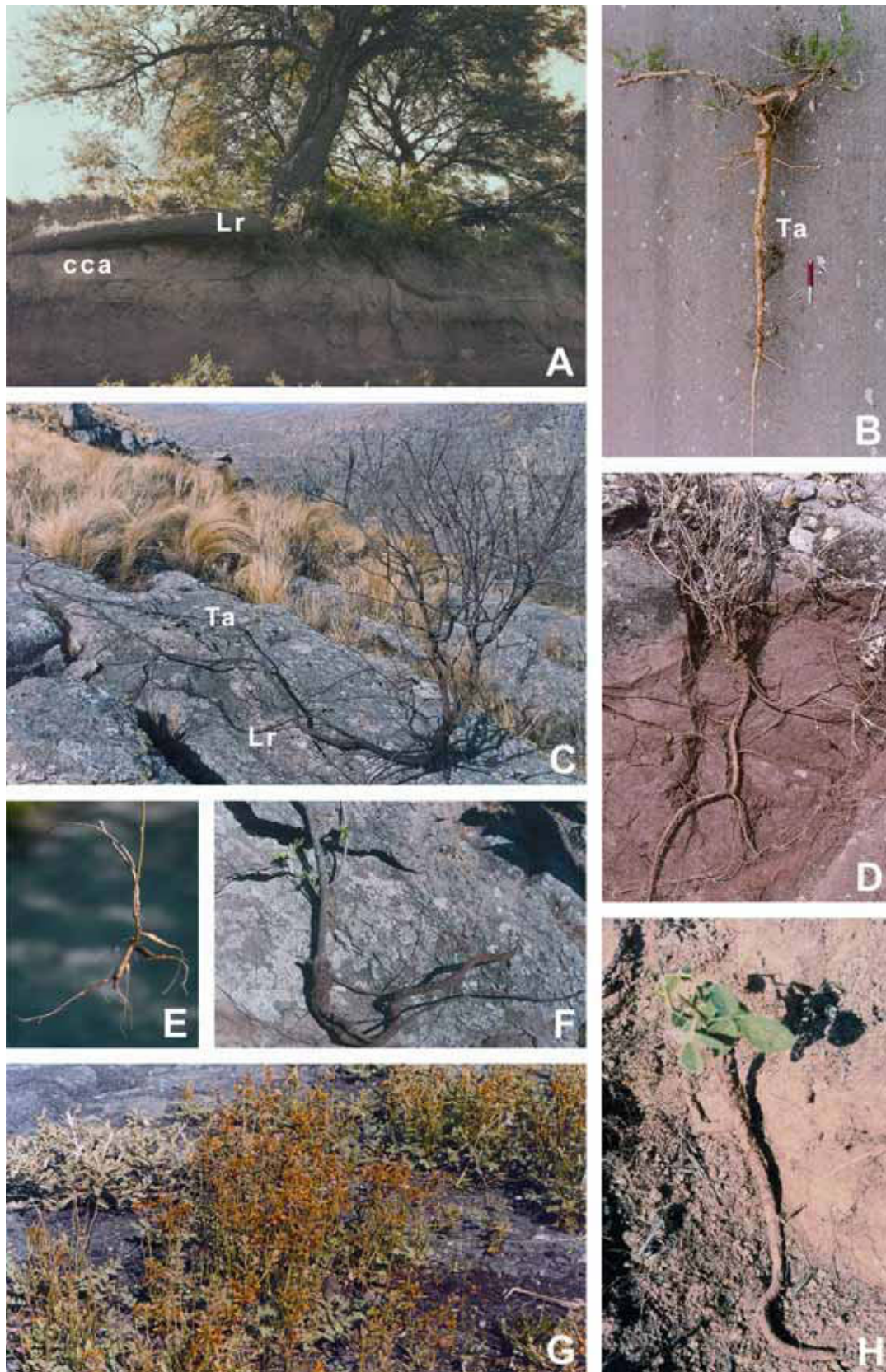
Hoffmannseggia glauca, a 20 cm high-perennial herb, generally shows thin roots of approximately 3 mm in diameter. Root buds are observed in main and lateral roots. They are abundant and regularly situated surrounding the root, at a distance of 3 to 10 cm between each other (Fig. 3 E). The bud that grows vertically before emerging from the soil has cataphylls in its first nodes. Root tubers are developed by lateral roots (Fig. 3E). Commonly one can observe big populations in natural ambients (Fig. 2G), modified places, and cropped environments. The aerial part dies in winter, but sprouts develop from the innovation zone of the previous aerial stems and from root buds during the following season. This species is found in loam-sandy soils, or under naturally saline conditions.

Adesmia cordobensis is a herbaceous species higher than the previous one (40 cm). Its roots are fleshy and thick, with a diameter of 1 cm or more. They show prominent contractions on their surface and explore most of the substrate plagiotropically (Fig. 3 A). Root buds are observed in lateral roots, although they are not frequent. Therefore, it can be inferred that their origin is due to some external factor and is not an ordinary behaviour of the plant (Fig. 1 F). This species is found in poorly developed soils.

The taproot is always distinguishable in the shrubs studied that do not have root buds. The variants observed are mainly related to soil profile characteristics, like the taproot of *Senna birostris* var. *hookeriana* that is mainly plagiotropic. In this species, the taproot length exceeds the plant height many times. First order roots are abundant in the zone close to the shoot, but they are scarce at some distance from the apical meristem and regularly situated approximately every 0.50 m (Fig. 2 C). *Senna birostris* var. *hookeriana* grows in highland grass steppes, where the soil has a dark brown A horizon that is few centimeters thick and a rocky C horizon that cannot be penetrated by roots, so its roots have to look for nutrients in the surface horizon, exploring a big area by getting far away from the mother plant. Roots from the basal zone assure plant fixation, an important advantage taking into account that there are constant winds in this environment. *Senna subulata* grows in the same habitat, so it shows similar characteristics (Fig. 2 F). On the contrary, other species of the same genus that grow at lower altitudes and in more developed soil type, i.e. with A, B, and C horizon, show a taproot with higher branching degree that vertically penetrates the substrate.

Prosopis caldenia is an arborescent species that grows in well-drained plains with tuff (tosca) exposures. Main and lateral roots are plagiotropic and show a similar development (Fig. 2A). They grow rather shallow in the first meters of the profile due to calcium carbonate accumulation, and get far away from the crown. Evidently, this root system derives from an allorhizous model influenced by the previously mentioned soil characteristics. Another species of this genus, *Prosopis campestris*, a shrub of low height (20–40 cm), grows in bottom hills, where the soil has a loam-sandy texture with gravel, with a 20 cm-A horizon and a transition between the previous one and the C horizon. The taproot is well-developed, 4 cm or more in diameter, scarcely branched, and highly lignified. It grows vertically due to soil characteristic (Fig. 2 B).

Root systems of perennial herbaceous species are observed in Fig. 3. The taproot of *Stylosanthes hippocampoides* does not prevail, so first order roots acquire great diameters. On the other hand, in *Coursetia hassleri* (Fig. 3 B) the proximal part of the main root and the lateral roots are thick, because of the accumulation of reserve substances, while the distal parts remain thin.



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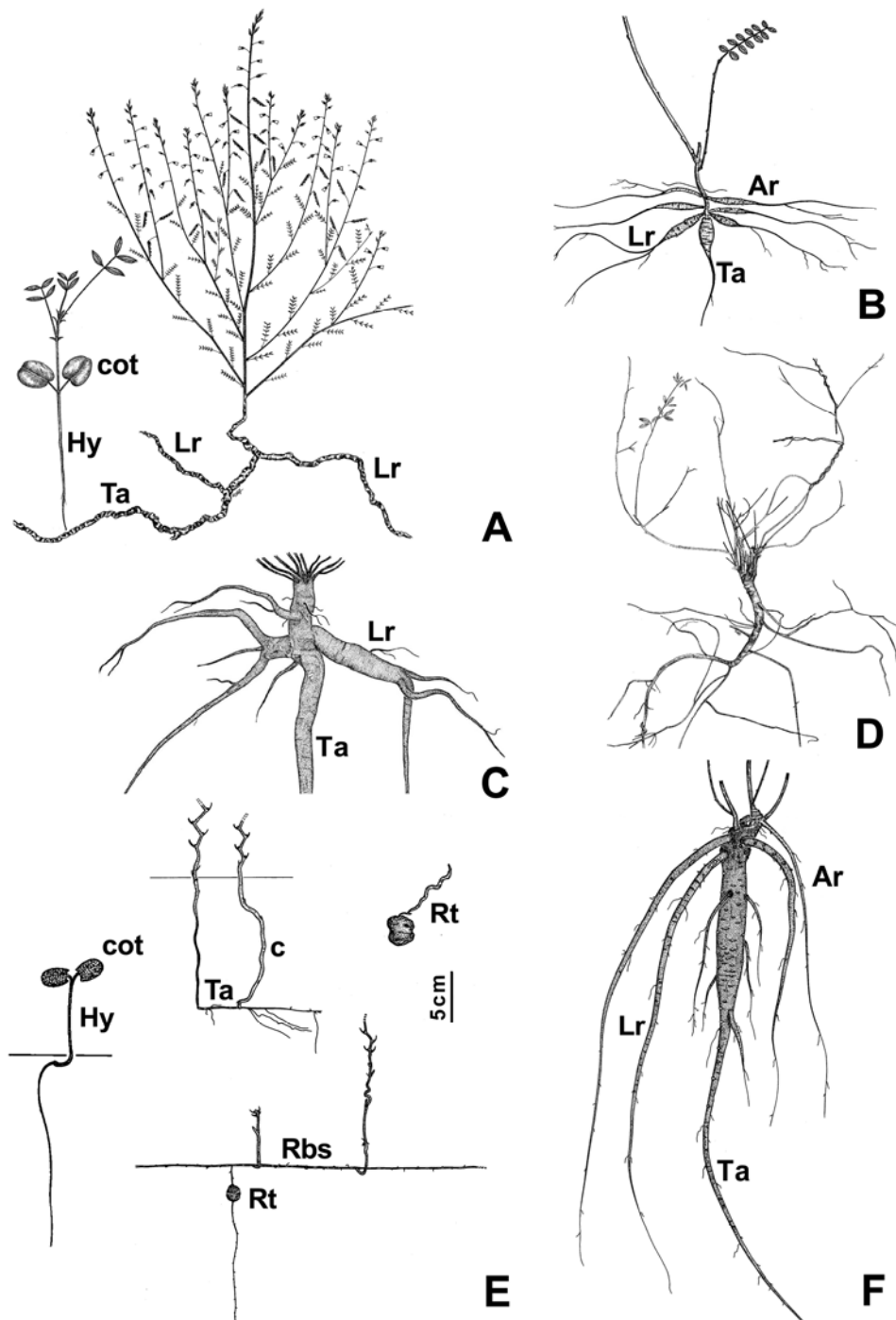
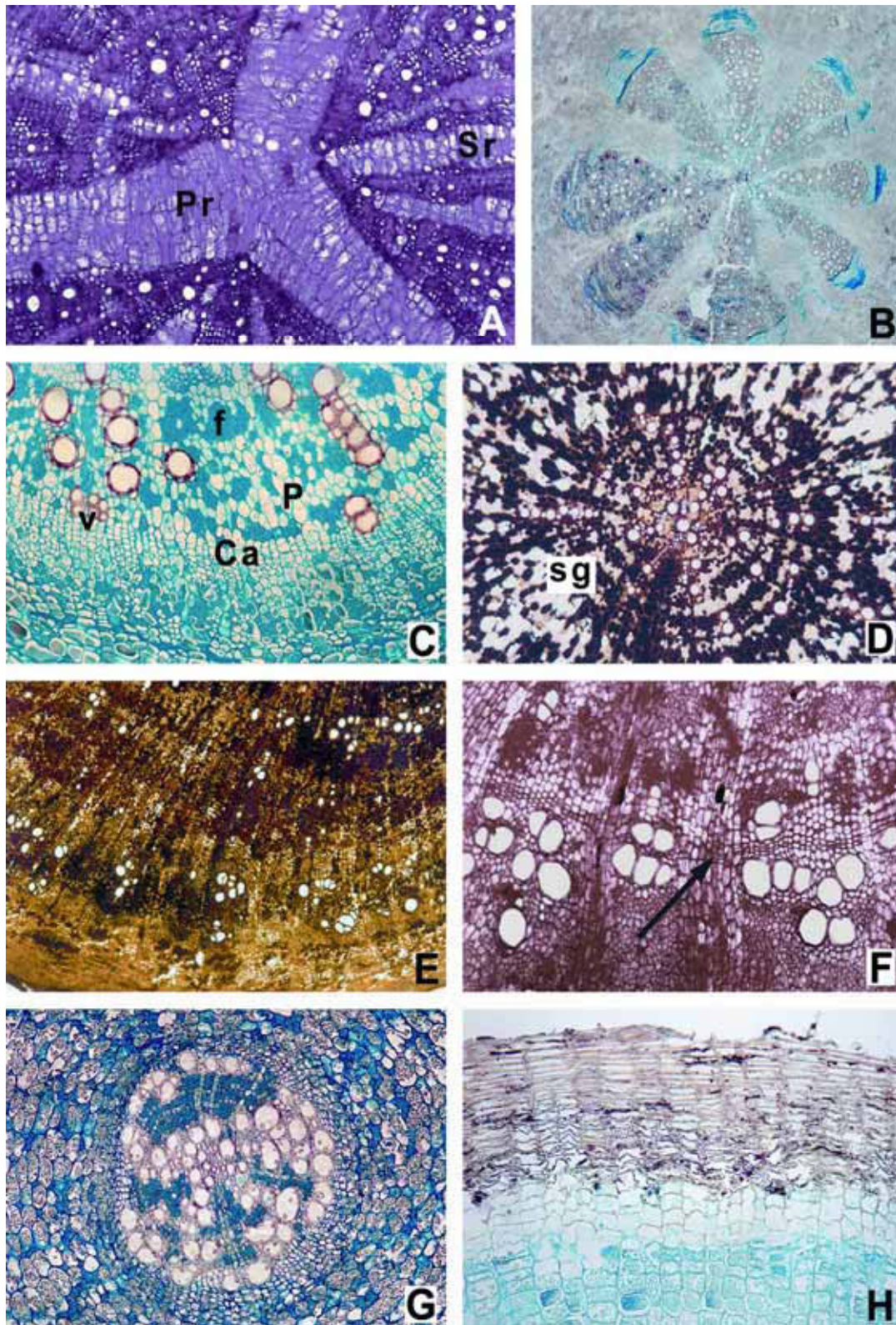


Figure 3: Root systems of herbaceous species of Fabaceae. A) *Adesmia cordobensis*; B) *Coursetia hassleri*; C) *Stylosanthes hippocampoides*; D) *Galactia texana*; E) *Hoffmannseggia glauca*; F) *Desmodium uncinatum*. Abbreviations: Ar = adventitious roots, c = cataphyll, cot = cotyledon, Hy = hypocotyl, Lr = lateral root, Rbs = root-borne shoots, Rt = root tuber, Ta = tap root.

Figure 2: A) *Prosopis caldenia*; B) *Prosopis campestris*; C) *Senna birostris* var. *hookeriana*; D) *Galactia texana*; E) *Coursetia hassleri*; F) *Senna subulata*; G) *Hoffmannseggia glauca*; H) *Galactia latisiliqua*. Abbreviations: cca = calcium carbonate accumulation, Lr = lateral root, Ta = tap root.

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These distal parts take up water and nutrients. Adventitious roots with similar characteristics develop in the base of the primary axis.

In the species studied here spatial and temporal sequences in the development of the roots show that within 30 days after germination most of them have a primary root approximately 0.30 m length. The aerial part is 6 cm high and first order roots are already present. On the contrary, *Stylosanthes hippocampoides* and *Coursetia hassleri* show less root growth in length (6 cm) due to reserve accumulation during early ontogenetic stages. *Hoffmannseggia glauca*, a species with root-borne shoots, shows an unbranched main root during the first months, that grows deep in the profile (Fig. 3 E).

Two variants are observed in transverse sections of roots: a) woody ones where the xylematic area with lignified cells predominates, and b) fleshy ones where the parenchymatic tissue predominates. The latter one is mainly related to reserve accumulation. Figure 4 shows transverse sections of roots, where different strategies to increase the parenchymatic zone are observed. The first one is ray formation, for example three big primary parenchymatic rays are developed in *Stylosanthes montevidensis* var. *montevidensis*, besides of many secondary rays that are also formed (Fig. 4 A). Another example is *Adesmia cordobensis* that shows cambium activity determining the formation of eight or more cuneiform areas of secondary xylem, separated by wide parenchymatic rays. These rays extend centrifugally adopting a cuneate form at the secondary phloem level (Fig. 4 B). In these two examples xylematic parenchyma, besides the phloematic one, plays an important role in reserve accumulation. Another strategy is shown by *Zornia gemella* which has a taproot of few milimeters in diameter and a small xylematic area. Reserves accumulate in the phloem and phellodermic parenchyma (Fig. 4 G). The third strategy occurs in *Coursetia hassleri*, where the cambium originates secondary vascular elements, abundant fibres and scarce parenchymatic cells, but at a certain developmental point, the relationship among different cell types reverts and the cambium starts producing abundant xylematic and phloematic parenchyma (Fig. 4 C, D). This situation causes a gradual increase of the thickness of the proximal part of the taproot, and after that of first order roots. Starch accumulation is abundant in all tissues of this root.(Fig. 4 D). Periderm of fleshy roots is formed by a complete cylinder. Up to 25 rows of cork cells may be produced. The cells walls are slightly suberized (Fig. 4 H).

Woody roots exhibit a predominance of the xylematic area over the phloematic one, as it can be observed in *Galactia texana* and *Desmodium uncinatum* (Fig. 4 E, F). In this last species, besides the allorhizous system, some adventitious roots are originated at the base of the primary axis and the plagiotropic zone of some paraclades (Fig. 3 F).

Figure 4: Transverse sections of roots. A) *Stylosanthes montevidensis*. Pr = primary rays, Sr = secondary rays; B) *Adesmia cordobensis*. Vascular cylinder with wide parenchymatic rays; C–D) *Coursetia hassleri*. Ca = vascular cambium, p = xylem parenchyma, f = fibre, v = vessel, sg = parenchymatous cells containing starch grains. E–F) *Desmodium uncinatum*. A considerable amount of secondary xylem has differentiated. The arrow delimit a season's growth. G) *Zornia gemella*. Vascular cylinder surrounded by parenchymatous cells containing starch grains. H) *Adesmia cordobensis*. Detail from periderm. A,C,F,G = 200x, B,D,E = 80x, H = 400x

Discussion

WEBER (1953) said that differences in root systems are based in main and lateral root length, thickness, branching degree, and on the other side in external factors, such as soil type and humidity. He also cites examples of leguminous species where the taproot predominates, like *Astragalus exscapus*, *Medicago sativa*, *Melilotus albus*, *Trifolium pratense* and *Ononis spinosa*. In this study, most of the species show an allorhizous system. In cases where a tap root is not developed, this corresponds with soil characteristics or modification related to reserve accumulation.

Three out of four structural classes cited by GROFF & KAPLAN (1988) are found among the species studied: bipolar plants, shoot-borne roots, and root-borne shoots. Root-borne shoots or root buds were cited in this family, in the genera *Coronilla* and *Robinia* by WEBER (1953); *Trifolium* by RAUH (1937); *Chamaecytisus*, *Cytisus*, *Laburnum* and *Chamaespartium* by BEIJERINK (1887) and KUTSCHERA & LICHTENEGGER (1992). In this study, the genera *Acacia*, *Caesalpinia*, *Geoffroea*, *Adesmia* and *Hoffmannseggia* were also cited. RAUH (1937) said that those plants that have buds on the root usually do not originate branches with adventitious roots and vice versa. Within the Fabaceae family, there are species that have root buds, as those studied in this research, and there are others that develop aerial or subterranean plagiotropic branches with adventitious roots (WEBERLING et al., 2002).

BASCONSUELO et al. (1997) and BIANCO et al. (1998) cited similar root structures in *Galactia marginalis* and *Rhynchosia edulis*, where the taproot and hypocotyl accumulate reserve substances, and then the adventitious roots of plagiotropic branches acquire similar form and role. The taproot of *Coursetia hassleri* accumulates reserve substances in its proximal portion, but the hypocotyl is not involved as it is in the species previously mentioned. First order roots behave in a similar way. Older plants also develop adventitious roots with similar morphological characteristics from the basal nodes of the orthotropic primary axis. In all these examples, two zones are differentiated that were already cited by TROLL (1967): a distal one with thin branches that specializes in absorption, and a proximal one that accumulates reserve substances. However, the modification in other fleshy roots only consists of increasing considerably their diameter and length. This situation was observed in *A. cordobensis*, where the root system is similar to that of *A. comechingona* (BIANCO & WEBERLING, 1999; BIANCO, 2002).

Transverse sections of roots of the analyzed herbaceous species show that most of them are fleshy, i.e. they have a structure that tends to increase the parenchymatic area, especially in vascular tissues, through ray number and thickness. Similar adaptations were observed by KUTSCHERA & LICHTENEGGER, (1992) in species of the genus *Ononis* that were growing under hydric deficit. BASCONSUELO (2001) described roots of the genera *Rhynchosia* and *Galactia* where parenchyma predominates, but originates from an unusual activity of cambium. The increase of this tissue allows water and starch accumulation for the survival of unfavourable periods and ensures good sprouting in spring.

LINCH (1995) defined root architecture as the spatial configuration of a complex of subunits associated with some functional significance. Evidently, the root system structures studied respond to two different strategies to absorb water. There is scarce branching degree in main

and first order roots of trees, shrubs, and herbs with woody roots, although they allow these plants to explore in depth or large soil surfaces. In these cases, their histological characteristics are also important. KRAUS et al. (1995) showed transverse sections of roots of shrub species of the genus *Senna*, where a big xylematic area with vascular elements of great diameter could be observed. The other ordinary strategy in herbaceous species was the presence of fleshy roots with abundant starch accumulation. Besides acting as reserve, high starch accumulation produces an increase of cellular osmotic potential when it hydrolyzes into soluble carbohydrates and, consequently, enhances parenchymatic water retention. These strategies allow plant survival, especially in steep physiographic areas.

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