CrossMark

Fine roots of *Prosopis flexuosa* trees in the field. Plant and soil variables that control their growth and depth distribution

Aranzazú Guevara [ID] · Verónica Pancotto · Leandro Mastrantonio ·
Carla Valeria Giordano

Abstract Fine root growth in natural vegetation is difficult to predict due to its regulation by soil and plant factors. Field studies in arid ecosystems show a variety of root responses to soil resources and to plant aboveground phenology that sometimes differ from root responses predicted by controlled experiments. There is a pressing need to cover a greater diversity of plant species and ecological scenarios in field studies. In this paper, we have studied fine roots of *Prosopis flexuosa* trees living with or without access to phreatic water in an inter-dune valley and a dune flank, respectively, in the Central Monte Desert, Argentina. We have described fine root growth over time and at different depths by rhizotron observations and soil core auger samples in relation to soil water and nutrients, tree crown phenology, plant water and nutrient status. We have found that surface soil moisture from rainfall is the variable that best predicts seasonal topsoil fine root growth. Access to groundwater advanced leaf sprouting with respect to rainfall, but did not advance root growth that stayed linked to rainfall in valley and dune flank trees. Trees without access to phreatic water produced deeper and thicker or denser roots, which is consistent with the poor soil resource content of dunes. Variations in rainfall dynamics due to global climate change may have a

A. Guevara
Instituto de Bio y Geociencias del NOA (IBIGEO),
CONICET, UNSA, Avenida 9 de julio 14 (4405), Rosario
de Lerma, Salta, Argentina

A. Guevara
Facultad de Ciencias Naturales, UNSA, Sede Regional
Orán, Rudecindo Alvarado, 751 (4530), San Ramón de la
Nueva Orán, Salta, Argentina

V. Pancotto
Centro Austral de Investigaciones Científicas (CADIC)
CONICET, UNTDF, Bernardo Houssay 200, Ushuaia,
Tierra del Fuego, Argentina

L. Mastrantonio
Facultad de Ciencias Agrarias, UNCUYO, Almirante,
Chacras de Coria, Brown 500, 5519 Mendoza, Argentina

C. V. Giordano (✉)
Instituto Argentino de Investigaciones en Zonas Áridas
(IADIZA), CONICET, UNCUYO, Av. Ruiz Leal s/n,
Parque General San Martín, 5500 Mendoza, Argentina
e-mail: cgiordano@mendoza-conicet.gob.ar

🙂 Springer

particular impact on fine roots and ecosystem processes such as biogeochemistry and carbon budget in dune flank trees as well as in valley trees.

Keywords Root proliferation · Phenology · Soil fertility · Soil water content · Rhizotron · Soil core auger

Introduction

Arid ecosystems are characterized by low water and nutrient levels varying in time and space. Desert plants exhibit a host of adaptations enabling them to cope with such scarcity and variability. These adaptations afford plants the ability to tolerate and avoid drought along with high efficiency in acquiring water and nutrients. Size, architecture and plasticity of root systems contribute to these adaptive features affecting seedling establishment, plant growth, species distribution and competitiveness (Caldwell et al. 1996; Casper and Jackson 1997; Schenk and Mahall 2002; Hodge 2003; Padilla and Pugnaire 2007). Desert vegetation is usually dominated by woody plants (trees and shrubs) with extensive root systems that give access to deep nutrient and water reservoirs more stable than shallow deposits (Schenk and Jackson 2002; Vonlanthen et al. 2010). In spite of the central role of root systems in desert vegetation, we have little information about their dynamics and regulation in natural habitats. The present work aims at filling up this gap of knowledge.

Root systems of woody plants exhibit a wide range of root diameters and branching orders varying from coarse lignified roots at the base to fine lignified or non-lignified roots in the distal section. Fine roots (≤ 2 mm in diameter) are functionally heterogeneous and constitute the most dynamic fraction of woody root systems (Pregitzer 2002, Guo et al. 2008). The most distal and finest roots do not develop secondary growth, are involved in water and nutrient absorption and have a short lifespan, whereas the others develop secondary growth, are involved in water and nutrient transport and have a longer lifespan than absorptive roots (McCormack et al. 2015; Liu et al. 2016).

Root systems are plastic organs that respond to their environment by means of variations in growth and fine root location. Where water or nutrients are heterogeneously distributed in soil, fine root growth is induced locally inside resource-rich patches, resulting in precise foraging for soil resources (Pregitzer et al. 1993; Wang et al. 2005; Péret et al. 2012). At the same time, fine root response to soil resources is modulated by the shoot through long-distance signaling with the root. This shoot–root communication can repress fine root growth in nutrient-rich patches when plants are well-nourished, adjusting root growth to whole plant nutrient demand (Zhang et al. 1999; Alvarez et al. 2012). Root system plasticity tied to soil resource availability has positive effects on plant growth and survival, mainly when plants are growing with few resources or under resource competition (Drew 1975; Malamy 2005; Hodge 2010).

Seasonal fine root growth is coordinated with seasonal shoot growth as well. In woody plants, this coordination may be more or less dephased by processes that promote root growth before leaf growth or that arrest root growth temporarily. Examples of these processes are early mobilization of carbohydrate reserves for root growth, development of flowers or fruits that may compete with roots as sinks for photosynthates (Reynolds et al. 1999; Steinaker et al. 2010; Abramoff and Finzi 2015).

How to predict fine root dynamics of natural vegetation in different ecological scenarios remains unclear due to the complex regulation of fine root growth driven by exogenous and endogenous signals (Osmont et al. 2007). Field studies of arid ecosystems show that in herbaceous and woody plants from natural flora, water or nutrient enrichment is not always followed by fine root growth, despite extreme shortage of both resources in deserts. The published literature indicates that fine root response to soil resource availability in arid ecosystems depends on plant species, seasonality of root growth, seasonality of soil resource availability, type of nutrient and light level (Jackson and Caldwell 1989; Reynolds et al. 1999; Wilcox et al. 2004; Salguero-Gómez and Casper 2011; Verburg et al. 2013).

We must broaden the scope of our field studies to cover a greater diversity of plant species, ecosystems and ecological situations, so as to deepen our understanding of fine root growth regulation in desert vegetation. This project is aimed at studying topsoil fine root growth of *Prosopis flexuosa* trees living with or without access to the water table in an arid ecosystem known as the Central Monte Desert in

Argentina, in relation to plant and soil factors. *P. flexuosa* trees grow in woodlands at inter-dune valleys with access to phreatic water and also grow sparsely on dune flanks without access to phreatic water (Guevara et al. 2010; Jobbágy et al. 2011).We hypothesize that topsoil fine root growth follows leaf growth in valley trees, which develops independently of rainfall dynamics due to groundwater access and that root and leaf growth are tightly coupled to rainfall in dune flank trees. We also hypothesize that dune flank trees assign more biomass to fine root growth, producing thicker or denser roots than valley trees, associated with the lower level of soil resources in dunes, and the higher water stress of dune flank trees. We have followed root growth at rhizotron windows and by soil core auger sampling, together with description of tree crown phenology, plant water and nutrient status, soil moisture and nutrient dynamics.

Materials and methods

The study site

This research work was carried out in the Central Monte Desert, in the northeastern region of Mendoza, Argentina. This is an arid ecosystem, with yearly rainfalls averaging 159 mm (1972–2007), mostly occurring in late spring and summer. The average annual temperature is 18.5 °C, with a record high of 48 °C in summer and an all-time low of -10 °C in winter (Alvarez et al. 2012). An extensive system of sand-dunes (~ 20 m in height) that alternate with inter-dune valleys characterizes landscape physiognomy. Inter-dune valleys are covered by open woodlands dominated by the winter deciduous tree *P. flexuosa,* while dunes are covered in shrubs and grasses with *P. flexuosa* trees only sparsely dotting their flanks (Contreras et al. 2011). *P. flexuosa* trees access phreatic water at depths of 7–14 m in valleys, whereas trees on the flanks lack access to groundwater and grow entirely depending on rainfall (Guevara et al. 2010; Jobbágy et al. 2011).

The experimental site was set up near "Puesto La Penca" (32°25′S 68°00′W) inside Telteca Natural Reserve. It comprised a valley and an adjacent dune flank, encompassing a study area of approximately 6 km^2. Seven adult *P. flexuosa* trees were selected at each landscape unit with similar basal diameter (DAB,

16.05 $\pm$ 1.12 cm), crown diameter (4.25 $\pm$ 0.20 m) and height (3.74 $\pm$ 0.25 m). These trees had been studied in the past, and isotopic, physiological and tree-ring evidence emerged that valley trees access phreatic water, whereas dune flank trees do not (Jobbágy et al. 2011; Giordano et al. 2011; Giantomasi et al. 2013). Some observations and measurements were performed on the whole set of selected individuals, while others were done on a subset of individuals. As a whole, measurements were taken in two consecutive spring–summer seasons, from 2009 through 2011.

Seasonal root growth and tree crown phenology

With the aim of studying seasonal root growth, and its relationship with tree crown phenology, we recorded root growth by relying on rhizotron window observations and described tree crown phenology through direct observation.

Root growth observation at rhizotron windows

Of the 14 trees preselected, 6 individuals (3 in the valley and 3 on the dune flank) were chosen for root growth monitoring. To this effect, one rhizotron was installed under each tree crown. Rhizotrons consisted of 1 m $\times$ 1 m $\times$ 0.75 m wooden boxes with one 1 m $\times$ 0.75 m side replaced by a transparent acrylic panel (Fig. 1a). Rhizotrons were buried into the ground in such way as to leave the viewing window ~ 1 m away from the tree trunk and ~ 40 cm parallel to a coarse root of ~ 2.5 cm in diameter, extending from the south side of the tree trunk (Fig. 2). We localized the pathways of these coarse roots by inserting stakes that were left on the ground in 2008, after coarse root temporary excavation had been performed for research purposes (Guevara et al. 2010). In addition, we removed grasses and shrubs in the proximity of the rhizotrons, to prevent intrusion of roots belonging to other plant species. In this manner, unhindered observation of *P. flexuosa* fine roots was guaranteed. The topside of the box was a removable cover allowing access for root observation (Fig. 1b). The acrylic viewing window and the top removable lid were covered with low density expanded polystyrene panels and black polyethylene sheets for thermal insulation and protection against sunlight (Fig. 1b, c). Metallic structures were fastened
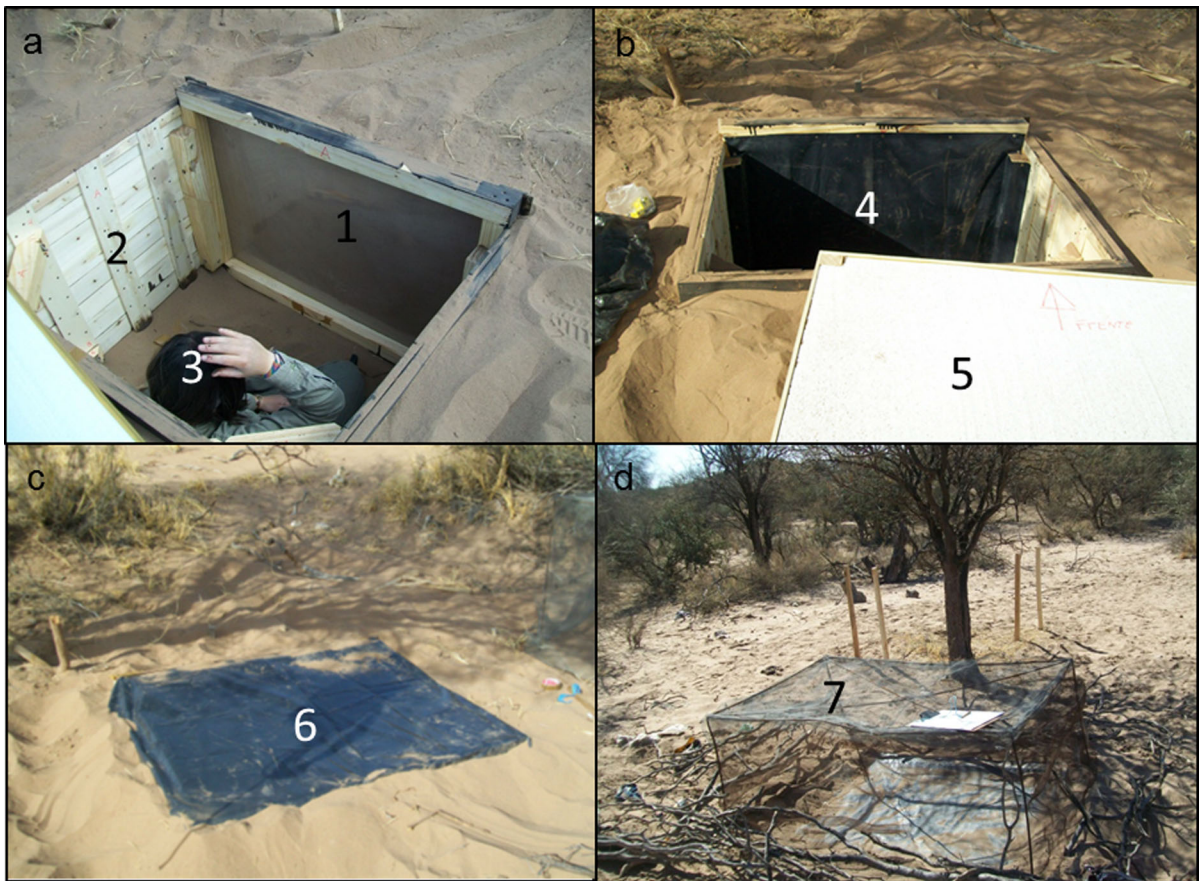
Fig. 1 a Rhizotron settled up in the field, completely uncovered, showing the acrylic window (1), wooden structure (2) and the observation position (3). **b** Acrylic window covered with expanded polystyrene and black polyethylene (4) for thermal insulation and sunlight block. Top removable lid made of 10 cm wide expanded polystyrene (5). **c** Rhizotron top at ground level covered with black polyethylene sheet (6). **d** Metallic structure over the rhizotron to prevent animals from falling inside (7)

on top of each rhizotron in order to prevent animals from falling inside (Fig. 1d). The rhizotrons were placed in the field in winter (August 2009), as trees were dormant. Observations at rhizotron windows were done every 20 days during the first growing season and every 30 days during the second growing season. We started observations in October 2009. New root segments were traced with water proof markers at each observation date. We recorded cumulative root length at the rhizotron window and expressed it as root segment length per rhizotron window area (cm cm^{-2}).

Tree crown phenology

We monitored tree crown phenology of the six trees whose roots were being observed at rhizotron windows, to correlate root growth with tree crown phenology. At the same time, we monitored crown phenology on the rest of the selected trees in the study area (14 individuals), to determine whether the subset of six root-observed individuals followed the phenological trend of the tree populations in each landscape unit. *P. flexuosa* branches have nodes with multiple buds that give origin either to a crown of leaves separated by short internodes ("short branches"; the most numerous); or to a branch with fewer leaves and longer internodes than short branches ("long branches"); or to multiple inflorescences. We selected ten branches of similar length per tree around the tree crown at a height of ∼ 1.7 m, which were marked and observed on every measurement date. On each selected branch, we marked the apical third and recorded the phenological state of every node within this branch portion. This was done because *P. flexuosa*
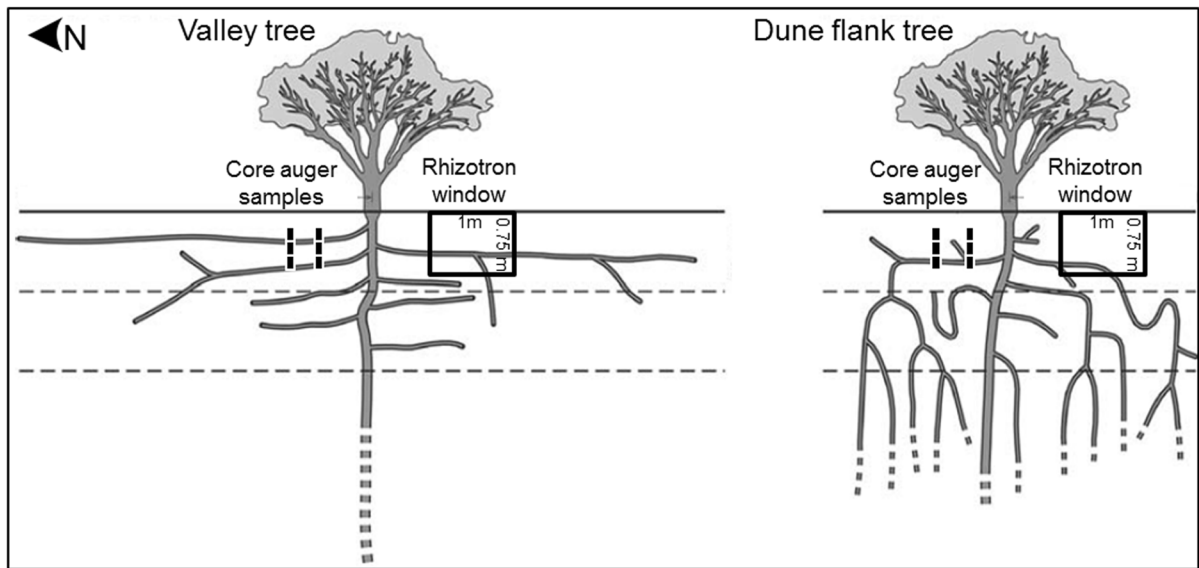
Fig. 2 Schematic representation of the coarse root system of a valley tree and a dune flank tree. There are indicated position and dimensions of rhizotron windows, together with sites of core auger samples for root growth measurement

trees expand leaves in nodes that are proximal to the branch apex, leaving numerous nodes with dormant buds, which results in leaf flushing at the periphery of the tree crown.

Leaf expansion

We followed the presence of expanded leaves by counting the number of nodes that showed short branches with more than 50% expanded green leaves and calculating the proportion of nodes with green leaves per tree as follows: # of nodes with > 50% green leaves/# of nodes observed.

Leaf senescence

We followed the presence of senescent leaves by counting the number of nodes that showed short branches with more than 50% of their leaves exhibiting > 50% abscised or yellow leaflets and calculating the proportion of nodes with senescing leaves per tree as follows: # of nodes with > 50% senescing leaves/# of nodes observed.

Flowering and fructification

We marked the start of the flowering or fructification period when the presence of at least one flower or fruit was noted in the observed nodes.

Root growth: soil exploration and depth distribution

In order to quantify root growth per soil volume and depth distribution, we measured length of root segments per soil volume known as root length density (RLD; cm cm^{-3}) and root dry biomass per soil volume (g cm^{-3}). Then, we divided the total length of root segments in a given soil volume by their biomass and obtained the specific root length (SRL, m g^{-1}), an indicator of root thickness or density. We measured root parameters in 10 trees (5 valley trees and 5 dune flank trees), including those whose roots were being studied in rhizotrons. To this effect, we took soil samples with an 800-ml core auger under each tree crown. In all cases, the sampled soil surrounded a coarse root that extended from the northern side of each trunk (Fig. 2), localized as explained before. Samples were taken in mid-summer during the 2009–2010 growing season (in January). Samples were taken at three depths: 0.15–0.30 m, 0.30–0.45 m and 0.45–0.60 m in two parallel columns at a distance

of 1/2 and 3/4 tree crown radius from the tree trunk, respectively (Fig. 2). Same depth samples were mixed together. Samples were kept cold in the field, and once at the laboratory, they were sieved using a N° 18 mesh to separate roots from soil. We kept the fraction of the roots $\leq$ 2 mm as these matched the average thickness of roots observed on rhizotron windows and fitted the definition of fine roots based on size used in several research publications. We separated living from dead roots after a tetrazolium vitality test (Sturitre et al. 2005). Living roots were put in a water-filled transparent container to be separated by floating and scanned with a standard scanner (Epson Scan TX115©). Root segment length was measured with the DatInf® Measure 2.1 program (DatInf GmbH, Tübingen, Germany), to calculate RLD. After scanning, roots were oven-dried at 60 °C for 48 h and weighed on a precision scale (OhausPioneer[TM]PA214) to determine their dry biomass. Armed with these two parameters, we calculated the specific root length.

Rainfall, soil moisture, and soil nutrients

Rainfall was recorded with a rain gauge connected to a data logger (HOBO event, Onset) placed at the Park Rangers Headquarters, 8 km west of the experimental site. Soil moisture and soil nutrients were measured around rhizotrons in most of the dates of root length recording. We took soil samples with a 200-ml core auger at a distance of 2 m from the rhizotrons and at a depth of 0.6 m. Samples were subdivided in 2 batches intended for moisture and nutrient determination, respectively. Soil moisture was calculated gravimetrically. Ammonium (NH_4^+) and nitrate (NO_3^-) were extracted by a KCl 2 M solution. NH_4^+ content was determined by the phenol-hypochlorite method (Weatherburn 1967), and NO_3^- content was determined by the Spongy Cadmium method (Jones 1984). Phosphate (PO_4^{-3}) content was measured by carbonic extraction following the Arizona technique (Mc George 1939).

Plant water and nutrient status

We measured water and nutrient status in the set of 14 trees. During both growing seasons, we measured predawn leaf water potential ($\psi_{L\ PD}$) in the dry period before the rains (December) and during the wet period

after the rains (February). To this effect, we selected 3 branches per tree at a height of $\sim$ 1.7 m, covered them with bags during the night to prevent transpiration and measured leaf water potential before dawn with a pressure chamber (Bio-Control, Buenos Aires, Argentina) following Scholander et al. (1965). Plant nutrient status was determined at the end of summer (February) for both growing seasons, when leaves were fully expanded. For every tree, 30 leaves were collected around the tree crown, oven-dried at 70 °C and ground to powder. Samples were separated in two batches, one for phosphorous (P) quantification and the other for total nitrogen (N) determination. P concentration was determined by inductively coupled plasma atomic emission spectrometer (Shimadzu, ICPE-9000) after digestion in hot concentrated $HNO_3/HClO_4$ (2:1), at LANAQUI, CERZOS-CONICET Bahia Blanca." Total N was determined by semi-micro Kjeldahl (Nelson and Sommers 1973).

Statistical analysis

Differences in root biomass, RLD and SRL between valley and dune flank trees and between depths were tested by two-way ANOVA. Differences over time in soil moisture, PO_4^-, NO_3^- and NH_4^- concentration between valley and dune flank were analyzed by repeated measures ANOVA. The measurements in all sampling sessions from both landscape units were compared using a Bonferroni posttest. Differences in ψ_{LPD}, leaf N and P concentration between trees with or without access to phreatic water were tested by a two-tailed t test. We analyzed differences in ψ_{LPD} before and after the rains using a paired t test. When the homoscedasticity assumption was not met, we used a Welch correction. Relationship between root length from rhizotron observation and soil variables was tested with time series cross-correlation analysis for each experimental unit. For this, we calculated the net amount of root length, soil moisture, soil PO_4^{-3} and soil N (NO_3^- plus NH_4^+) for each time period between two consecutive sampling dates, as the difference between the variable value at the end of the time period and the variable at the beginning of it. This resulted in series of 8 (2009–2010) or 7 (2010–2011) time periods that were matched and analyzed in phase (lag 0) or dephased (lag 1, lag 2). In the latter case, we matched root length of a given time period with the soil variable of the previous ones. We
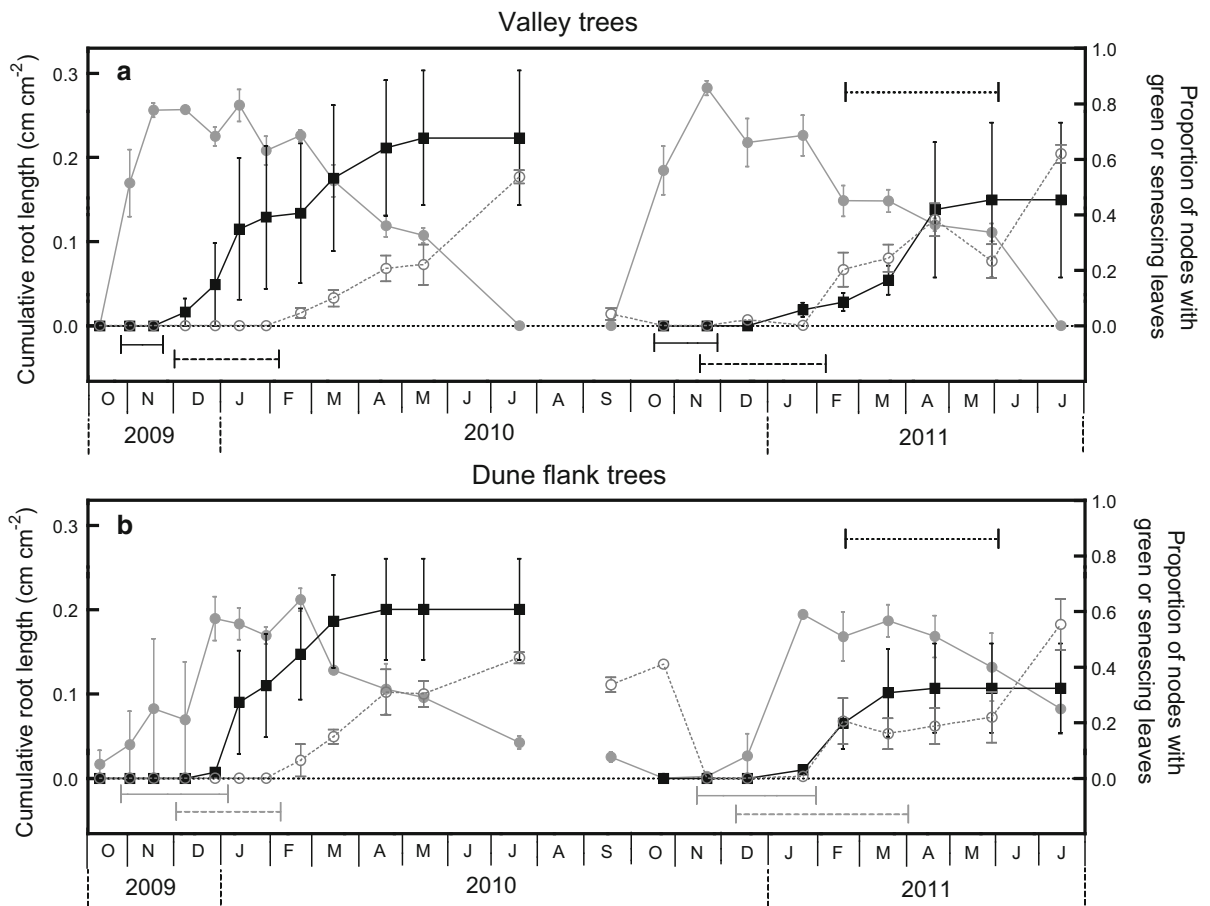
Fig. 3 Seasonal fine root growth and crown phenology of valley trees (**a**) and dune flank trees (**b**). The graphics show root growth from rhizotron measurements (black squares, solid line), tree crown development (gray closed circles, solid line), leaf senescence (open circles, dashed line), flowering (full bar below) and fruiting (dashed bar below). The period when *Colias lesbia* attack caused tree defoliation is indicated with the dotted line above each graphics. Symbols are means $\pm$ 1 s. e. m

obtained the magnitude and significance of the correlation between root length and a soil variable at different time lags and showed the most significant for each experimental unit. The whole range of analyses was done using the InfoStat statistical package (2008 version, InfoStat group, FCA, UNC, Argentina).

Results

Seasonal root growth and tree crown phenology

Roots observed at rhizotron windows revealed that root growth initiation was coordinated in valley and dune flank trees and delayed with respect to leaf burst. This delay was more marked in valley trees, as a result

of crowns developing earlier and faster than dune flank tree crowns. Root growth followed flowering without overlapping and went on during fructification and the beginning of leaf senescence in both tree types. Two pulses of root growth were evident in valley trees and less evident but distinguishable in dune flank trees during the first growing season. A single and slow pulse of root growth was registered during the second season that overlapped with defoliation by larvae of *Colias lesbia* F. (Lepidoptera). The whole root growth period extended from late spring to autumn, with maximum rates in summer. Mean growth profile of the whole season shows higher root growth during 2009–2010 than during 2010–2011 in both tree types (Fig. 3). These results indicate that access to phreatic water may affect timing and magnitude of tree crown
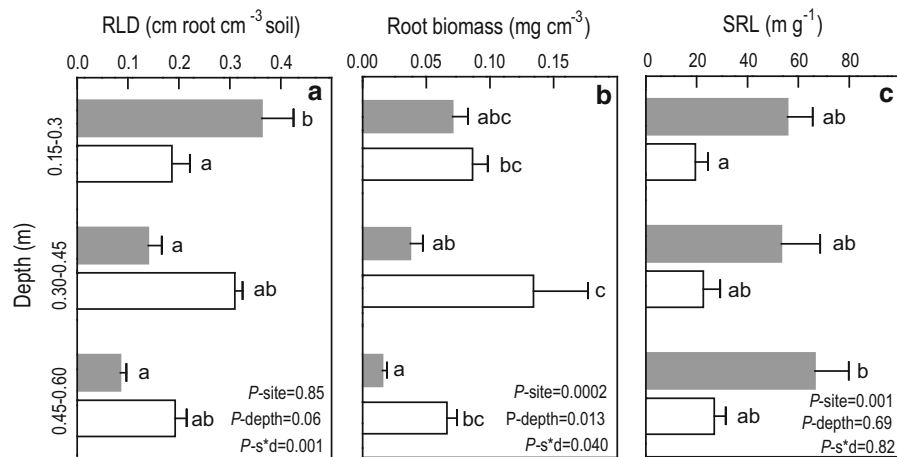
Artwork with GraphPad Prism 6

Fig. 4 Fine root growth parameters of valley (gray bars) and dune flank trees (white bars), calculated from soil core auger samples taken at three different depths (0.15–0.3 m, 0.3–0.45 m and 0.45–0.6 m). **a** Root length density (RLD), **b** root biomass and **c** specific root length (SRL). Bars are means ± 1 s. e. m. *P* values from two-way ANOVA are reported. Different letters represent significant differences after Bonferroni posttest

leaf development, but may not affect timing of root growth. Fructification did not stop root growth.

Roots observed in rhizotron windows were white, between 0.2 and 2 mm thick, with the first-, second- and third-order branches organized in a herringbone-like topology (Online Resource 1), consistent with previous observations (Guevara et al. 2010). Trees undergoing root observation followed the same phenological pattern as the rest of similar-sized adult trees at each landscape unit (Online Resource 2), indicating that they were representative of their corresponding populations.

Root growth: soil exploration and depth distribution

To quantify depth distribution of roots per soil volume, we measured root growth parameters at three depths, during active root growth in mid-summer (January 2010) with a soil core auger. We found that valley and dune flank trees showed similar RLD within the upper 60 cm of soil (0.19 ± 0.03 and 0.20 ± 0.03 cm cm^{-3}, respectively, $P = 0.89$), but distributed differently in the soil profile. Valley trees showed the highest RLD within the top 30 cm of soil, while dune flank trees showed the highest RLD at depths of 30–45 cm (Fig. 4a). Dune flank trees allocated more biomass to roots than valley trees (0.09 ± 0.01 and

0.04 ± 0.01 mg cm^{-3}, respectively, $P = 0.002$). Depth distribution of root biomass followed the same profile as RLD in both tree types (Fig. 4b). Roots of dune flank trees were coarser or denser than roots of valley trees (Fig. 4c).

Rainfall, soil moisture and nutrient dynamics, water and nutrient status of trees

Soil moisture profiles within the top 60 cm of soil mirrored rainfall events since December (first season) or January (second season) (Fig. 5a, b) Soil moisture was higher in the valley than in the dune flank. This difference was more pronounced during the driest season (2010–2011) than during the wettest one (2009–2010) (Fig. 5b). The valley and the dune flank showed similar NO_3^- and NH_4^+ concentrations, but different PO_4^{-3} concentrations, with the valley showing higher PO_4^{-3} values in both growing seasons. Seasonal profiles of NO_3^-, NH_4^+ or PO_4^{-3} concentration did not follow soil moisture profiles (Fig. 5c, d, e). In December, at the beginning of the rainy season, trees without access to phreatic water on the dune flank were more water-stressed than trees with access to the water table in the valley. Dune flank trees were released from water stress in February of the wettest season (2009–2010) and alleviated from water stress in February of the driest season (2010–2011), when

Table 1 Water and nutrient status of *P. flexuosa* trees

Tree type	$\Psi_{L\ PD}$[a] (Mpa)			Leaf P (ppm)	Leaf N (% N/g)
	December	February	P value		
2009–2010 season					
Valley trees	− 1.8 (± 0.11)	− 1.5 (± 0.15)	0.0158	1181.6 (± 174.16)	3.1 (± 0.43)
Dune flank trees	− 2.3 (± 0.08)	− 1.6 (± 0.11)	0.0007	1132.6 (± 143.91)	3.2 (± 0.18)
P value	0.002	ns		ns	ns
2010-2011 season					
Valley trees	− 1.8 (± 0.08)	− 1.2 (± 0.09)	0.0014	1048.7 (± 182.67)	3.3 (± 0.23)
Dune flank trees	− 4.4 (± 0.26)	− 1.4 (± 0.06)	< 0.001	1177.2 (± 177.88)	3.5 (± 0.39)
P value	< 0.0001	0.004		ns	ns

ns, not significant

[a] $\psi_{L\ PD}$ was measured in December and February, before and after major rain events, respectively, in both seasons. Values represent means (± 1 s.e.m). *P* values from two-tailed *t* test are reported

they remained slightly more stressed than valley trees (Table 1). Valley and dune flank trees did not differ in N and P leaf content by the end of summer (Table 1).

Our results indicate that the soil around roots in the valley was richer in resources (water and PO_4^{-3}) than the soil around roots on the dune flank. Access to phreatic water decoupled water status of valley trees from rainfall and surface soil moisture availability, while rainfall and soil moisture dynamics were determinant of dune flank tree water status. Differences in soil PO_4^{-3} between landscape units were not reflected in leaf P levels, which were similar in both tree types.

Relationship between seasonal root growth, root depth distribution and soil and plant water and nutrient status
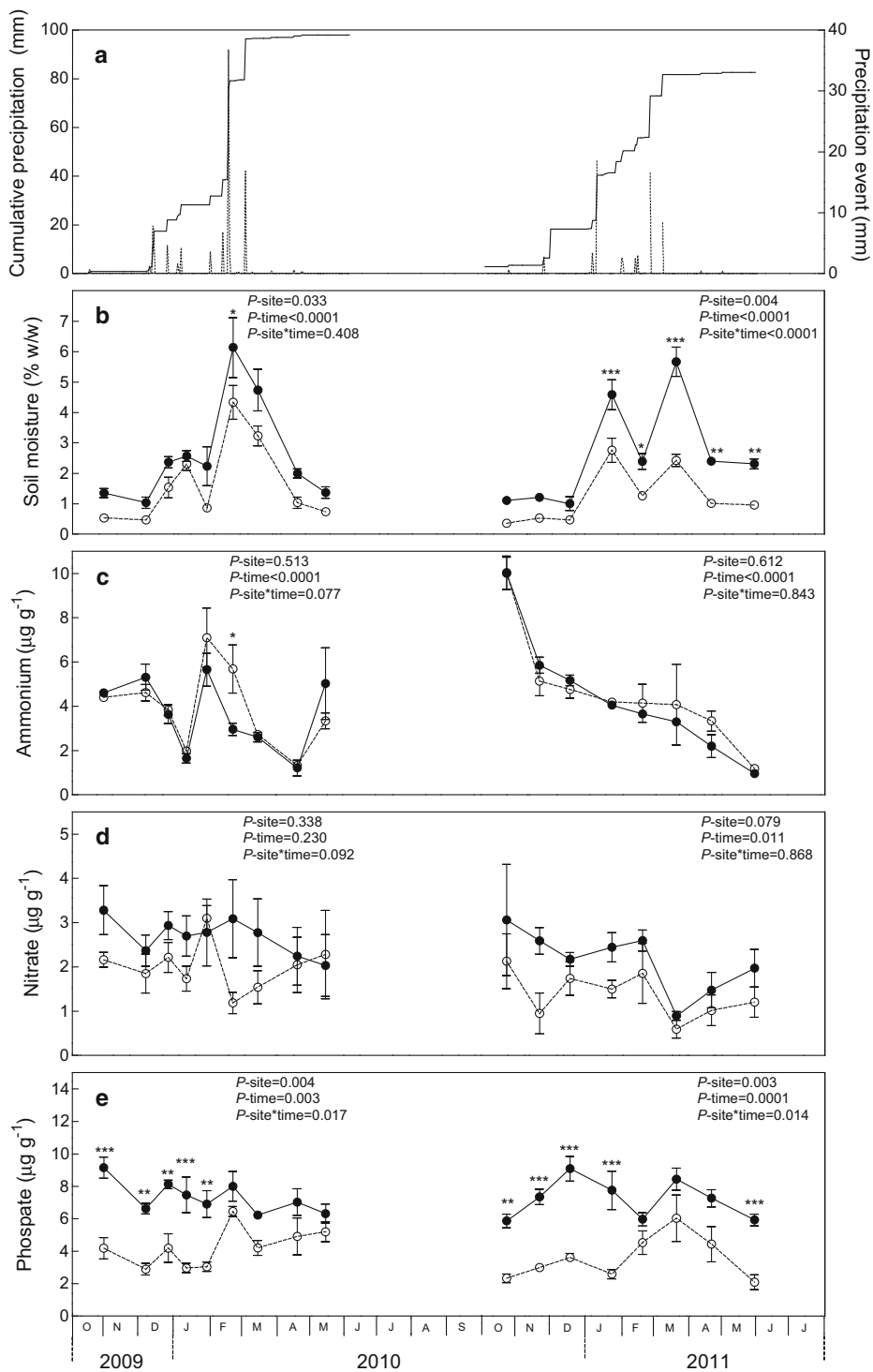
To determine which soil variable correlated positively with seasonal root growth, we carried out a cross-correlation analysis between pairs of time series from rhizotron determinations: root length versus a soil variable, calculated as their net variation between two consecutive sampling dates (see "Materials and methods" for detail). We found that the soil variable that correlated positively and significantly with root length the most of the cases was soil moisture, in both valley and dune flank trees. In the majority of the cases, significant correlations between root growth and soil moisture were obtained when root length records were compared with soil moisture records from the preceding sampling date (lag 1). In contrast,

soil nutrient dynamics did not correlate positively and significantly with root growth dynamics as frequently as soil moisture did (Table 2). Access to phreatic water and a good water status in valley trees were not enough to speed up root growth before the rains, which stayed linked to rainfall dynamics in the same way as in dune flank trees.

Biomass allocation to roots is usually favored when soil resources are scarce. We found that soil moisture and PO_4^{-3} concentration around roots were lower on the dune flank than in the valley (Fig. 5b, e). Low resource levels at the topsoil layer on the dune flank, together with inaccessibility to phreatic water, were reflected in leaf water status but not in leaf nutrient content in dune flank trees (Table 1). Dune flank trees allocated more biomass to roots at the topsoil layer and produced thicker or denser roots than valley trees, consistently with predictions for poor resource environments and water-stressed plants.

Discussion

Our study shows that surface soil moisture from rainfall pulses is the best predictor of seasonal topsoil fine root growth of *P. flexuosa* trees in the Monte Desert. Access to phreatic water had an impact on tree crown phenology, but did not affect root growth. Valley trees that access phreatic water were exposed to less water stress before the rains, which resulted in earlier and more profuse development of tree crowns during the season than in dune flank trees without

a

b

P-site=0.033
P-time<0.0001
P-site*time=0.408

P-site=0.004
P-time<0.0001
P-site*time<0.0001

c

P-site=0.513
P-time<0.0001
P-site*time=0.077

P-site=0.612
P-time<0.0001
P-site*time=0.843

d

P-site=0.338
P-time=0.230
P-site*time=0.092

P-site=0.079
P-time=0.011
P-site*time=0.868

e

P-site=0.004
P-time=0.003
P-site*time=0.017

P-site=0.003
P-time=0.0001
P-site*time=0.014

Artwork with GraphPad Prism 6

◀ **Fig. 5** Rainfall and soil resources dynamics along 2009–2010 and 2010–2011 growing seasons. **a** Rain events (dashed line) and cumulative precipitation (solid line) in the study area. **b** Soil moisture; **c** soil NO_3^- concentration; **d** soil NH_4^+ concentration, and **e** soil PO_4^{-3} concentration. Data from the valley (closed circles, solid line) and the dune flank (open circles, dashed line) are shown. *P* values from repeated measures ANOVA are reported. Asterisks represent significant differences after Bonferroni posttest

access to the water table. However, root growth did not follow tree crown phenology, but stayed linked to surface soil moisture dynamics in both tree types. Variations in soil nutrients such as N and PO_4^{-3} did not explain seasonal root growth rate. Dune flank trees allocated more biomass to fine roots and produced thicker or denser roots than valley trees, consistently with low soil resources on the dune. They also grew roots deeper into the soil profile than valley trees, in coincidence with deeper surface coarse roots in dunes (Guevara et al. 2010).

In arid ecosystems, access to underground water reservoirs, a more stable hydric source than rainfall, can decouple plant vegetative or reproductive phenology from rain pulses. This was evident in the tree crown phenology of valley trees, which started to develop two months before the first seasonal rains. Consistent with our observations, phreatophyte shrubs from North-America deserts, flowered, fruited, and grew uncoupled from the influences of precipitation (Nilsen et al. 1987; Pavón and Briones 2001). Nevertheless, although tree crown phenology uncoupled from rainfall dynamics in valley trees, root growth did not. Root growth can precede seasonal shoot growth fueled by stored non-structural carbohydrates, as reported in perennial woody plants from arid ecosystems. Instances of such process can be observed in the deep-rooted shrub *Lithraea caustic*, the shallow-rooted shrubs *Cryptocarya alba*, *Artemisia tridentata*, *Atriplex confertifolia* and *Ceratoides lanata* (Fernandez and Caldwell 1975; Montenegro et al. 1982). However, this is not the case with *P. flexuosa* trees, not even in those that access groundwater, whose relatively high hydric status in spring before the rains might enable root growth. Consistent with our observations, root growth was also linked to rainfall in two shrubs from a semiarid habitat, the deciduous *Trevoatri nervis* and the semideciduous *Colliguaya odorifera* (Montenegro et al. 1982).

However, in those species root growth was also synchronic with shoot growth, in contrast with our results.

Although root growth may be stimulated by soil moisture and nutrients, it ultimately depends on the interaction with other factors, such as shoot phenology, plant water and nutrient status. We found that soil moisture dynamics from rainfall is the best predictor of *P. flexuosa* root growth dynamics in both tree types. In particular, we found that the best positive correlations were obtained when root growth records were compared with soil moisture records from the preceding measurement date. This, together with the fact that roots started growth after leaf burst, indicates that *P. flexuosa* roots are responsive to the local action of soil water once leaves are present in the tree crown providing photosynthates for root growth. Roots appeared to be more responsive to soil moisture than to plant water status, because roots of valley trees did not grow before the rains, despite the good water status of these plants. Studies about fine root responses to soil moisture in plants from desert habitats report contrasting results that vary among species. In accordance with our observations, the herbaceous subshrub *Cryptantha flava* and the woody shrubs *Ambrosia dumosa* and *Ephedra nevadensis* show a positive correlation between root growth and soil moisture content in their natural habitats (Wilcox et al. 2004; Salguero-Gómez and Casper 2011). On the other hand, root growth of the shrubs *Larrea tridentata*, *Lycium pallidum* and *Prosopis glandulosa* did not correlate with soil moisture content, indicating that in their natural habitat, root growth is sensible to other factors (Reynolds et al. 1999; Wilcox et al. 2004; Verburg et al. 2013). While *P. flexuosa* root growth dynamics correlated positively with soil moisture dynamics, it did not correlate with variations in soil nutrients. Here, it is important to highlight that trees from the valley and the dune flank had similar nutrient status, so that control of the plant over root responses to the local action of soil nutrients can be considered equal in both tree types. Field studies in arid environments indicate that roots proliferate in response to soil nutrient supply and that vary with species and nutrient identity (Eissenstat and Caldwell 1988; Jackson and Caldwell 1989). In contrast, our observations indicate that roots of *P. flexuosa* trees do not respond to fluctuations in natural levels of soil N or PO_4^{-3}.

Table 2 Time series cross-correlation coefficients between fine root length (cm) and soil resources for each experimental unit and season

Tree type	EU[a]	Soil moisture			Soil N[b]			Soil PO$_4^{3-}$		
		Lag[c]	Coef[d]	P value	Lag	Coef	P value	Lag	Coef	P value
2009–2010 season										
Valley trees	1	ns	ns	ns	ns	ns	ns	2	− 0.98	0.0045
	2	1	0.87	0.076	0	− 0.68	0.0357	ns	ns	ns
	3	1	0.61	0.0049	ns	ns	ns	0	− 0.63	0.0408
Dune flank trees	1	0	− 0.77	0.0173	0	0.70	0.0309	− 1	0.83	0.0199
	2	1	0.81	0.0230	2	0.72	0.0307	ns	ns	ns
	3	1	0.94	0.0051	2	1.14	0.0006	ns	ns	ns
2010–2011 season										
Valley trees	1	0	0.96	0.0055	ns	ns	ns	ns	ns	ns
	2	1	0.73	0.0328	ns	ns	ns	ns	ns	ns
	3	1	0.73	0.0337	0	0.66	0.0525	2	− 0.93	0.0071
Dune flank trees	1	ns	ns	ns	ns	ns	ns	− 1	1.101	0.0219
	2	0	1.07	0.0022	2	− 1	0.0324	− 2	0.72	0.0371
	3	1	0.67	0.0697	-2	0.69	0.0429	0	0.93	0.0071

ns, not significant

[a] EU, experimental unit

[b] Soil N, the addition of soil NO_3^- and NH_4^+

[c] Lag, minimum period of time needed to get a significant correlation between variables

[d] Coef, correlation coefficient

Soil water or nutrient scarcity may increase biomass allocation to roots as a way to compensate for resource deficiency and to increase resource foraging and uptake. The dune flank has lower soil moisture and PO_4^{-3} concentration than the valley. Consistent with this, trees from the dune flank allocated more biomass to topsoil layer roots than trees from the valley. However, this root biomass was not used to enhance soil exploration, because RLD was the same for both tree types. Instead, it was used to generate thick or dense roots that have a long lifespan, are resistant to pathogen attack and increase biomass use efficiency (Leuschner et al. 2004). These traits are advantageous in resource-poor environments. In addition, trees from the dune flank grew roots deeper in the soil profile than trees from the valley, in coincidence with their coarse root position (Guevara et al. 2010).

In summary, leaf growth and tree crown development of *P. flexuosa* trees is markedly affected by groundwater subsidy, while topsoil fine root growth remains coupled to rainfall dynamics in trees with or without access to phreatic water. Fine roots are active in water and nutrient absorption, and their production and turnover contribute significantly to ecosystem biomass cycling, primary productivity and carbon budget (Jackson et al. 1997; Gill and Jackson 2000; Mokany et al. 2006). The study of fine root growth and the factors governing it is the first step toward building a general picture at the level of whole plant or ecosystem processes. In a context of global change, the increase in precipitations predicted for the studied area may increase fine root growth of *P. flexuosa* trees in dunes as well as in valleys, with effects on water dynamics, nutrients and carbon (Labraga and Villalba 2009). It may also advance aboveground phenology of dune trees, with minor effects over aboveground phenology of valley trees.

References

Abramoff RZ, Finzi AC (2015) Are above and below ground phenology in sync? New Phytol 205(3):1054–1061

Alvarez JM, Vidal EA, Gutiérrez RA (2012) Integration of local and systemic signaling pathways for plant N responses. Curr Op Plant Biol 15(2):185–191

Caldwell MM, Manwaring JH, Durham SL (1996) Species interactions at the level of fine roots in the field: influence of soil nutrient heterogeneity and plant size. Oecologia 106(4):440–447

Casper BB, Jackson RB (1997) Plant competition underground. Annu Rev Syst 28:545–570

Contreras LC, Jobbágy E, Villagra PE, Nosetto MD, Puig de fábregas J J (2011) Remote sensing estimates of supplementary water consumption by arid ecosystems of Central Argentina. J Hidrol 397:10–22

Drew MC (1975) Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytol 75:479–490

Eissenstat DM, Caldwell MM (1988) Seasonal timing of root growth in favorable microsites. Ecology 69(3):870–873

Fernandez OA, Caldwell MM (1975) Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. J Ecol 63:703–714

Giantomasi MA, Roig Juñet FA, Villagra PE (2013) Use of differential water sources by *Prosopis flexuosa* DC: a dendroecological study. Plant Ecol 214:11–27

Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147(1):13–31

Giordano CV, Guevara A, Boccalandro HE, Sartor C, Villagra PE (2011) Water status, drought responses and growth of *Prosopis flexuosa* trees with different access to the water table in a warm South American desert. Plant Ecol 212:1123–1134

Guevara A, Giordano CV, Aranibar JN, Quiroga M, Villagra PE (2010) Phenotypic plasticity of the coarse root system of *P. flexuosa*, a phreatophyte tree, in the Monte desert (Argentina). Plant Soil 330:447–464

Guo D, Mitchell RJ, Withington JM, Fan P-P, Hendricks JJ (2008) Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. J Ecol 96:737–745

Hodge A (2003) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162:9–24

Hodge A (2010) Roots: the acquisition of water and nutrients from the heterogeneous soil environment. In Progress in botany 71. Springer, Berlin Heidelberg, pp 307–337

Jackson RB, Caldwell MM (1989) The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. Oecologia 81(2):149–153

Jackson RB, Mooney HA, Schulze E-D (1997) A global budget for fine root biomass, surface area, and nutrient contents. PNAS 94:7362–7366

Jobbágy EG, Nosetto MD, Villagra PE, Jackson RB (2011) Water subsidies from mountains to deserts: their role in sustaining groundwater-fed oases in a sandy landscape. Ecol Appl 21(3):678–694

Jones MN (1984) Nitrate reduction by shaking with cadmium: alternative to cadmium columns. Water Res 18:643–646

Labraga JC, Villalba R (2009) Climate in the Monte Desert: past trends, present conditions, and future projections. J Arid Environ 73:154–163

Leuschner C, Hertel C, Schmid I, Koch O, Muhs A, Hölscher D (2004) Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. Plant Soil 258:43–56

Liu B, He J, Zeng F, Lei J, Arndt SK (2016) Life span and structure of ephemeral root modules of different functional groups from a desert system. New Phytol 211(1):103–112

Malamy JE (2005) Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ 28:67–77

Mc George WT (1939) Factors influencing the availability of native soil phosphate fertilizers in Arizona soils. College of Agriculture, University of Arizona, Tucson

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Leppälammi-Kujansuu J (2015) Redefining fine roots improves understanding of below ground contributions to terrestrial biosphere processes. New Phytol 207(3):505–518

Mokany K, Raison R, Prokushkin AS (2006) Critical analysis of root: shoot ratios in terrestrial biomes. Glob Change Biol 12(1):84–96

Montenegro G, Araya S, Aljaro ME, Avila G (1982) Seasonal fluctuations of vegetative growth in roots and shoots of Central Chilean shrubs. Oecologia 53(2):235–237

Nelson DW, Sommers LE (1973) Determination of total nitrogen in plant material. Agron J 65(1):109–112

Nilsen ET, Sharifi MR, Virginia RA, Rundel PW (1987) Phenology of warm desert phreatophytes: seasonal growth and herbivory in *Prosopis glandulosa* var. torreyana (honey mesquite). J Arid Environ 13(3):217–229

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: developments in root system architecture. Annu Rev Plant Biol 58:93–113

Padilla FM, Pugnaire FI (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Funct Ecol 21(3):489–495

Pavón NP, Briones O (2001) Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. J Arid Environ 49(2):265–277

Péret B, Li G, Zhao J, Band LR, Voß U, Postaire O, Luu D-T, Da Ines O, Casimiro I, Lucas M, Wells DM, Lazzerini L, Nacry P, King JR, Jensen OR, Schäffner AR, Maurel Ch Bennet MJ (2012) Auxin regulates aquaporin function to facilitate lateral root emergence. Nat Cell Biol 14(10):991–998

Pregitzer KS (2002) Fine roots of trees–a new perspective. New Phytol 154(2):267–270

Pregitzer KS, Hendrick RL, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. New Phytol 125(3):575–580

Reynolds JF, Virginia RA, Kemp PR, De Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. EcolMonogr 69(1):69–106

Salguero-Gómez R, Casper BB (2011) Introducing short roots in a desert perennial: anatomy and spatiotemporal foraging responses to increased precipitation. New Phytol 191(1):173–183

Schenk HJ, Jackson RB (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. J Ecol 90:480–494

Schenk HJ, Mahall BE (2002) Positive and negative plant interactions contribute to a north-south-patterned association between two desert shrub species. Oecologia 132(3):402–410

Scholander PF, Hammel HT, Hemingsen EA, Bradstreet ED (1965) Sap pressure in vascular plants. Science 148:339–346

Steinaker DF, Wilson SD, Peltzer DA (2010) Asynchronicity in root and shoot phenology in grasses and woody plants. Glob Change Biol 16:2241–2251

Sturitre I, Henriksen MT, Breland TA (2005) Distinguishing between metabolically active and inactive roots by combined staining with 2, 3, 5-triphenyltetrazolium chloride and image colour analysis. Plant Soil 271:72–84

Verburg PS, Young AC, Stevenson BA, Glanzmann I, Arnone JA, Marion GM, Holmes C, Nowak RS (2013) Do increased summer precipitation and N deposition alter fine root dynamics in a Mojave Desert ecosystem? Glob Change Biol 19(3):948–995

Vonlanthen B, Zhang X, Bruelheide H (2010) On the run for water–root growth of two phreatophytes in the Taklamakan Desert. J Arid Environ 74(12):1604–1615

Wang L, De Kroon H, Bögemann GM, Smits AJM (2005) Partial root drying effects on biomass production in Brassica napus and the significance of root responses. Plant Soil 276(1–2):313–326

Weatherburn MW (1967) Phenol hypochlorite reaction for determination of ammonia. Anal Chem 39:971–974

Wilcox CS, Ferguson JW, Fernandez GC, Nowak RS (2004) Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite. J Arid Environ 56(1):129–148

Zhang H, Jennings AJ, Barlow PW, Forde BG (1999) Dual pathways for regulation of root branching by nitrate. PNAS 96:6529–6534