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Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia

Abstract Above- and belowground biomass distribution, isotopic composition of soil and xylem water, and carbon isotope ratios were studied along an aridity gradient in Patagonia (44–45°S). Sites, ranging from those with *Nothofagus* forest with high annual rainfall (770 mm) to *Nothofagus* scrub (520 mm), *Festuca* (290 mm) and *Stipa* (160 mm) grasslands and into desert vegetation (125 mm), were chosen to test whether rooting depth compensates for low rainfall. Along this gradient, both mean above- and belowground biomass and leaf area index decreased, but average carbon isotope ratios of sun leaves remained constant (at –27‰), indicating no major differences in the ratio of assimilation to stomatal conductance at the time of leaf growth. The depth of the soil horizon that contained 90% of the root biomass was similar for forests and grasslands (about 0.80–0.50 m), but was shallower in the desert (0.30 m). In all habitats, roots reached water-saturated soils or ground water at 2–3 m depth. The depth profile of oxygen and hydrogen isotope ratios of soil water corresponded inversely to volumetric soil water contents and showed distinct patterns throughout the soil profile due to evaporation, water uptake and rainfall events of the past year. The isotope ratios of soil water indicated that high soil moisture at 2–3 m soil depth had originated from rainy periods earlier in the season or even from past rainy seasons. Hydrogen and oxygen isotope ratios of xylem water revealed that all plants used water from recent rain events in the topsoil and not from water-saturated soils at greater depth. However, this study cannot explain the vegetation zonation along the transect on the basis of water supply to the existing plant cover. Although water was accessible to roots in deeper soil layers in all habitats, as demonstrated by high soil moisture, earlier rain events were not fully utilized by the current plant cover during summer drought. The role of seedling establishment in determining species composition and vegetation type, and the indirect effect of seedling establishment on the use of water by fully developed plant cover, are discussed in relation to climate change and vegetation modelling.

Key words Patagonia-vegetation · Root distribution · ^{13}C-, ^{18}O-, D-Isotope composition · Water · Plant succession

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Introduction

Rooting depth and root distribution are important parameters for global-scale climate models. Together they define the soil volume from which plants can potentially extract water and nutrients. Thus, rooting patterns determine the storage term in the terrestrial water balance. However, it remains unclear to what extent soil water within the accessible soil horizon is utilized for transpiration in different ecosystems, and whether water availability satisfactorily explains the observed vegetation patterns at a regional scale. An answer to this question is important because the hydrological balance has been used for predictions of plant production since Walter (1939) and de Witt (1958). It is also used in global-scale models predicting plant migrations in response to global climate change (e.g. Melillo et al. 1996). An independent assessment of the relations between vegetation and water availability is crucial as a test for these models.

Recent reviews on global patterns of root distribution (Jackson et al. 1996) and rooting depth (Canadell et al. 1996) have demonstrated that vegetation zones can differ distinctly in their rooting patterns. For example, on a global average, desert vegetations reach a maximum rooting depth of 13.4 m with 37% of the total root biomass below 0.30 m soil depth, while temperate forests have on average a maximum rooting depth of only 3.7 m with 35% of the root biomass below 0.30 m soil depth. These vegetation types contrast with relatively shallow-rooted temperate grasslands, which reach on average only 2.4 m soil depth with only 17% of their total root biomass below 0.30 m soil depth.

These broad generalizations conform with conventional ecological knowledge, but they average individual observations that were made under specific conditions, and they have not been tested rigorously along a contiguous sequence of rainfall or vegetation types. Therefore, this study tests these generalizations along a precipitation transect to determine the extent of their applicability in global climate ecosystems modelling. We investigated vegetation patterns, rooting depth and water extraction levels along an aridity gradient in Argentinean Patagonia, South America. Located in the rain shadow of the Andes, where rainfall and vegetation range from >1000 mm per year of precipitation in the west, with evergreen and deciduous forests dominated by the genus *Nothofagus*, to about 300 mm rainfall and associated temperate grasslands of *Festuca* and *Stipa*, and finally to deserts with 100 mm rainfall in the east of Patagonia (Soriano 1983). This distinct change in rainfall and vegetation seems ideal for exploration of the functional significance of rooting depth. We tested the hypothesis that over a rainfall gradient decreasing precipitation will lead to increasing depths of rooting and of the horizons from which roots extract water. This should be most evident at the end of a dry season (March). However, contrary to our expectations, we found no correlation between rooting depth and rainfall, but rather wet soils or ground water at 2–3 m soil depth across all sites. We discuss factors such as seedling establishment, which might determine the composition of plant cover and water use along the Patagonian aridity gradient.

Materials and methods

Study sites and vegetation

The study was carried out in March 1995 which is late summer or autumn in the Southern Hemisphere (leaf colour change in *Nothofagus*). Five sites were selected along a 140-km transect at the east slope and the pediment of the Andes, reaching from Lago La Plata (west of the settlement Alto Rio Senguer) to the Rio Senguer northeast of Rio Mayo, Argentina. The transect covers a change in rainfall from almost 800 mm to about 100 mm (Table 1). All sites have similar rainfall seasonality, with a rainfall maximum in May to July, and a rainfall minimum in February. During the sampling year of 1995, the dry season was terminated by a major rain event in mid-February. Maximum soil water extraction takes place in September/October when the vegetation is fully developed and rainfall decreases.

Differences in annual rainfall are associated with differences in vegetation, ranging from deciduous forests where precipitation is high, to scrubland, grassland, semi-desert and desert as precipitation decreases (Walter 1966; Soriano 1983). The deciduous forest canopy was dominated by only one tree species, but exhibited a diversity of herbs and shrubs in the understorey. As rainfall decreased, species diversity of the dominant vegetation and the proportion of bare soil increased (Aguiar and Sala 1994). Thus, the vegetation reflected the expected change in stand structure with rainfall, providing a model situation for investigating the role of rooting depth in different vegetation types.

Methods

Aboveground biomass and leaf area were determined by statistical sampling according to vegetation structure. In the deciduous forest and the scrubland, biomass harvests followed the procedure described by Schulze et al. (1995). Breast height circumferences of trees were measured on a 900-m² plot. The 209-year-old forest stand had a uniform size distribution [23% of the trees with <0.15 m diameter at breast height (dbh), 19% with 0.15–0.30 m dbh, 41% with 0.30–0.40 m dbh and 17% with >0.40 m dbh]. Trees were harvested ($n=5$) over the range of dbh, and the biomass of stem, branches and leaves was related to breast height basal area [total tree biomass (kg)= $-18.48+0.72\times$basal area (cm²), r^2 0.98, $P<0.01$]. Subsamples were taken for the determination of fresh to dry mass ratio, wood volume to dry mass ratio, and for leaf area, nutrient and isotope analyses. Stand biomass was calculated using the biomass/basal area relation per tree and the size distribution of trees on a plot basis. In the *Nothofagus* scrubland, all plant material was harvested on 25-m² plots ($n=3$) and separated into species and compartments.

In both types of grassland, aboveground biomass was determined according to the procedure used in the forest stand, but canopy diameter of shrubs rather than basal areas of stems was used to characterize the population on a plot basis (900-m² plot; $n=1$). For instance, *Mulinum spinosum* grows in cushions with diameters of up to 3 m. One cushion was harvested for each size class with a 0.25-m increase in canopy diameter ($n=12$). A relation between cushion area and biomass was established [biomass (kg)= $-0.169+0.273\times10^{-3}$ canopy area (cm²), r^2 0.98, $P<0.01$ in the *Festuca* grassland; biomass (kg)= $-0.0448+0.156\times10^{-3}$ canopy area (cm²), r^2 0.97, $P<0.01$ in the *Stipa* grassland), and these relations were used to estimate *Mulinum* biomass on a plot basis. The same approach was used for the shrubs *Adesmia campestris* and *Senecio filaginoides*. The aboveground biomass of herbaceous and grass vegetation was determined on subplots of 1 m² between *Mulinum* cushions and shrubs ($n=5$). In the desert vegetation, which was dominated by *Nassauvia*, all plant material was harvested on 1-m² plots ($n=5$). Subsamples were used to determine fresh to dry mass ratio, and for leaf area, nutrient and isotope analyses.

Belowground biomass was determined from three replicate trenches (5–10 m long, up to 3 m deep), which were dug by an excavator and by hand near the base of a tree. In forest and scrubland, the biomass of the tree stocks and the associated main roots was determined after excavation. Coarse- and fine-root biomass and root density distribution were determined from 0.20×0.20 m cuts (chimneys), which were dug from the soil surface into deeper soil horizons along the edge of the trench. In the forest, one or two such chimneys were dug per harvested tree, at a distance from the tree base that represented about half of the tree crown radius (1–2 m from the tree base in the forest and 0.5 m from the tree base in the scrubland). All soil and root materials in the chimneys were collected and washed for roots in the laboratory, except for big stones that were cleaned from roots in situ. In the grasslands and desert, the chimneys ($n=3$ to 5) were cut under grass tussocks, shrubs and bare soil. At all sites, trenches and chimneys were dug to the depth of the deepest visible root or to the depth where wet soil or ground water were found.

Leaf material was collected for nitrogen (Carlo Erba, Model NA1500 Element Analyser, Milano, Italy) and carbon isotope ana-

Table 1 Characterization of study sites along an aridity gradient in Patagonia. Species composition and plant life forms (*T* tree, *S* shrub, *G* monocotyledons including grass, *H* dicotyledonous herbs, *D* Dwarf shrub)

Site	1	2	3	4	5
Latitude S	44°50′03″	44°51′17″	44°52′39″	45°24′18″	45°27′04″
Longitude W	71°43′21″	71°34′55″	71°19′36″	70°17′31″	69°49′32″
Elevation (m a.s.l.)	1080	960	1160	700	540
Rainfall (mm year⁻¹)	770	520	290	160	125
Vegetation type	Deciduous forest	Deciduous scrub	*Festuca* grassland	*Stipa* grassland	Desert
Vegetation height (m)	18	3.5	0.5	0.5	0.1
Dominant species	*Nothofagus pumila* (T: 80% cover)	*Nothofagus antarctica* (T: 100% cover)	*Festuca pallescens* (G: 28% cover) *Mulinum spinosum* (cushion S: 11% cover)	*Stipa speciosa* (G: 13% cover) *Mulinum spinosum* (cushion S: 9% cover) *Stipa humilis* (G: 8% cover) *Adesmia campestris* (S: 5% cover) *Senecio filaginoides* (S: 5% cover)	*Nassauvia glomerulosa* (D: 6% cover) *Poa ligularis* (G: 7% cover)
Associated species cover (%)	20	10	7	5	5
Understorey	*Nothofagus pumila* (T) *Calceolaria corymbosa* (H) *Taraxacum officinale* (H) *Berberis pearcei* (S) *Chilliotrichium rosmarinifolium* (S) *Maytenus chubutensis* (S)	*Fragaria chiloensis* (H) *Taraxacum officinale* (H) *Ribes buxifolia* (S) *Berberis magellanicum* (S) *Chillotrium diffusum* (S) *Senecio acanthifolius* (S)	*Carex argentina* (G) *Bromus pictus* (G) *Poa ligularis* (G) *Hordeum commosum* (G) *Hypochoeris incana* (H) *Lathyrus magellanica* (H) *Ephedra frustillata* (S) *Berberis heterophylla* (S) *Lycium ameghinoi* (S)	*Poa ligularis* (G) *Bromus pictus* (G) *Acaena splendens* (cushion S) *Chuquiraga aurea* (cushion D) *Brachycladus lycioides* (cushion S) *Maiuenia* sp. (succulent) *Senecio filaginoides* (S) *Calceolaria* sp. (H) *Nassauvia abrevista* (D)	*Hordeum comosum* (G) *Polygala darwiniana* (H) *Brachycladus lycioides* (S) *Senecio filaginoides* (S) *Azorella* sp. (cushion S) *Chuquiraga aurea* (cushion S) *Doniophyton* sp. (H) *Hoffmannsegia* sp. (H) *Nardophyllum obtusifolium* (S)
Bare soil cover (%)	0	0	52	56	80
Soil texture	Glacial moraine & volcanic +0.03–0 m humus 0 –0.15 m organic horizon 0.15–1.05 m loam >1.05 m large rocks with little fine soil >2.00 m very wet rocks	Alluvial +0.03–0 m humus 0 –0.05 m organic hor. 0.05–0.8 m alluvial silt 0.8 –1.3 m loamy sand 1.3 –1.5 m sand & gravel 1.5 –2.2 m wet sand 2.2 m water table	Alluvial & Moraine +0.05–0 m tussocks 0 –1.0 m alluvial sandy loam & gravel 1.0 –2.0 m large rocks & clay >2.0 m wet rock & clay	Alluvial +0.5 –0 m shrub & tussock 0 –0.15 m fine sand & gravel 0.15–0.4 m fine sand & gravel 0.4 –0.7 m caliche layer 0.7 –1.0 m coarse sand & gravel 1.0 –1.3 m coarse sand 1.3 –2.5 m coarse sand & gravel >2.5 m wet coarse sand, gravel	Alluvial 0 –0.3 m clay with stones 0.3–0.5 m caliche layer 0.5–0.6 m sand 0.6–0.8 m caliche layer & gravel 0.8–1.2 m sandy loam 1.2–1.3 m red sand 1.3–1.6 m sand with stones 1.6–2.6 m sand & small stones >2.7 m moist soil

Table 2 Distribution of above- and belowground biomass (kg m^{-2}) along an aridity gradient in Patagonia

Site	Forest	Scrub	Grassland		Desert
			Festuca	Stipa	
Rainfall (mm)	770	520	290	160	125
Total aboveground	34.08	10.82	0.52	0.71	0.15
Stem & branches	33.78	10.44	0.49	0.62	0.12
Leaves	0.40	0.37	0.03	0.09	0.03
Total belowground	14.84	13.64	2.14	0.77	0.33
Stembase & main root	7.30	9.14			
Roots	7.54	4.50	2.14	0.77	0.33
Total plant biomass	48.92	24.46	2.66	1.48	0.47
Leaf/total plant ratio (%)	0.82	1.53	1.02	6.34	5.50
Below/aboveground ratio	0.44	1.26	4.16	1.08	2.20
Leaf/root mass (%)	5.31	8.29	1.26	12.19	8.00
Leaf area index (m^2 m^{-2})	4.30	4.70	1.00	0.40	0.10

lyses (delta S, Finnigan MAT, Bremen, Germany). The $\delta^{13}C$ values are expressed in parts per thousand (‰) (PDB standard). Rainwater was collected at the forest site during a rain event at the time of biomass sampling. Deuterium and ^{18}O analyses of water were carried out on soil and on aboveground plant stems, which were collected in 10-ml glass flasks, and tightly closed with Parafilm. The water was extracted by distillation under vacuum. Hydrogen isotope ratios (δD) were analyzed (Finnigan MAT delta S) after zinc reduction of water (Coleman et al. 1982) and expressed in parts per thousand (SMOW standard). δ ^{18}O was determined after CO_2 equilibration using 1 ml of H_2O (Socki et al. 1992). Soil water contents were determined gravimetrically, using the same soil samples as for the isotope analyses. The gravimetric water contents were converted into volumetric water contents by multiplication with bulk density of the soil fraction (bulk density without gravel and stones; Rawls 1983).

Results

Total plant biomass decreased by 2 orders of magnitude from about 49 kg m^{-2} in the deciduous forest to 0.47 kg m^{-2} in the desert (Table 2). This reduction in biomass was mainly seen in the compartment of aboveground stem and branches. However, root biomass decreased also with decreasing rainfall (Fig. 1). Root biomass was highly correlated with aboveground biomass [root biomass=0.5+0.148 total plant biomass (kg m^{-2}) r^2 0.98, $P<0.01$]. Thus, the root to shoot ratio changed very little initially, but increased with decreasing rainfall (Fig. 1). Leaf area and leaf mass were lower only after the vegetation had changed from tree to grass cover, below 500 mm rainfall. The low leaf mass of the Festuca grassland site may have resulted from heavier grazing than that of the Stipa site. These trends are similar to what has been described for other aridity or altitudinal gradients (Whittaker and Niering 1975), although we added the root compartment to the aboveground biomass.

Root biomass and root density serve for water uptake as well as nutrient acquisition. Generally, roots in the upper soil layers serve mainly for nutrient uptake, while roots at greater soil depth have a greater role in water uptake (Dawson 1993; Caldwell 1994). In all Patagonian

vegetation types, root biomass and root density decreased with soil depth (Table 3), but the relationship with rainfall was weak. Furthermore, the soil depths containing 50% (Fig. 1, R_{50}) or 90% (Fig. 1, R_{90}) of total root biomass were almost independent of the vegetation cover, except when rainfall dropped below 150 mm (Fig. 1). Generally, 50% of the total root biomass was located in the upper 0.20 m of the soil profile, or even only the upper 0.10 m in the desert habitat. Furthermore, 90% of total root biomass was reached by about 0.60 m depth, and again, this level decreased to about 0.30 m in the desert habitat. In addition, there was a strong rainfall effect on the average root density of the upper 0.50 m of the soil profile, which correlated with the change in total root biomass (Fig. 1, $P<0.01$). Also, the maximum soil depth that was exploited by the remaining 10% of the total root biomass increased from about 1.30 m in forest vegetation to 2.2 m in Stipa grassland, and reached almost 2.7 m in desert vegetation. However, in all habitats, the maximum rooting depth reached a soil depth at which either wet soil (desert, grassland), dripping free water (forest), or ground water (scrub) were observed. Therefore, all vegetation types had access to water at field capacity at a soil depth of 2–3 m at the time of our sampling, which was the end of a dry season.

Using stable hydrogen and oxygen isotopes of soil and xylem water, we attempted to identify the soil layers from which the plants obtained their water. At the Stipa grassland site, near the experimental station Rio Mayo, long-term average rainfall generally reached a minimum of 4 mm in February, and 9 mm per month for the period from November to March (see also Walter 1966). Thus, we expected to see a distinct profile in water content and isotopic composition of soil water at the time of our study, reflecting winter precipitation input and summer drought. However, in February 1995, 1 month before this study took place, an unusual February rainstorm of 36 mm terminated the dry season earlier than usual, although rainfall was below average (4 mm per month) for a 7-month period between August 1994 and February 1995.
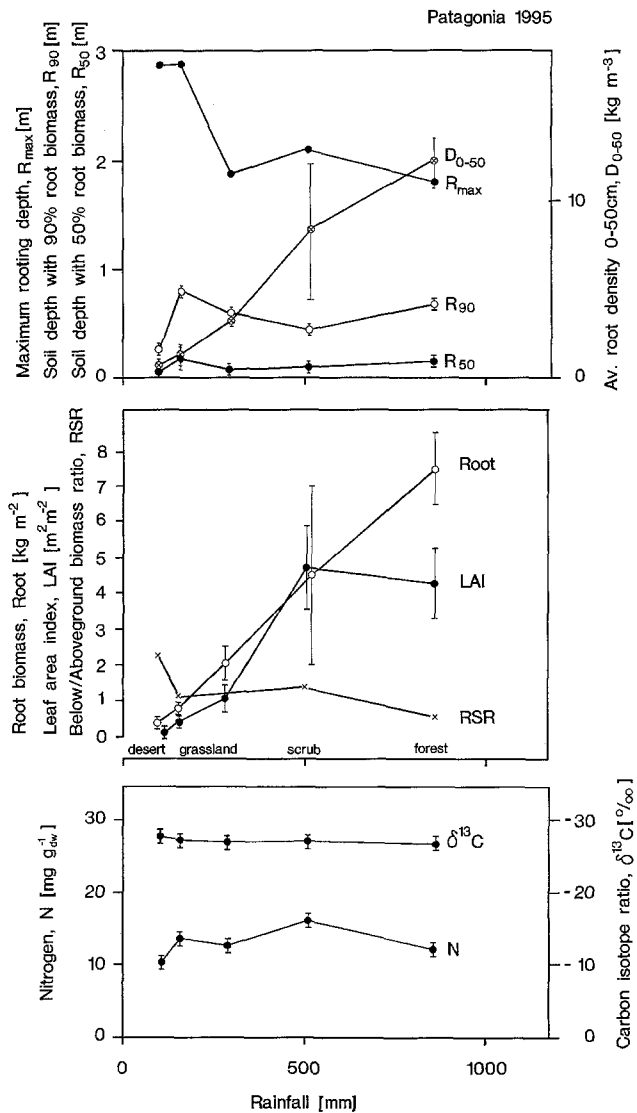
Fig. 1 Plant parameters characterizing drought response and carbon allocation are related to rainfall along an environmental gradient in Patagonia. *Above*: R_{max} maximum rooting depth, D_{0-50} averaged root density between 0 and 0.50 m soil depth, R_{50} soil depth containing 50% and R_{90} 90% of root biomass. *Centre*: *Root* root biomass, *LAI* leaf area index, *RSR* root/shoot ratio. *Below*: Carbon isotope ratios (δ^{13}C values in ‰ based on PDB) of sun leaves and *N* nitrogen concentrations. Data represent averages and standard errors ($n=3$ to 5), except for root:shoot ratio

The depth profiles of δD and δ^{18}O in soil water (Fig. 2) showed a maximum at the soil surface and a distinct minimum in the upper 0.10–0.30 m (0.60 m in forest site). Apparently, this first minimum resulted from the February rainstorm prior to our study, while the maximum at the soil surface was due to evaporation (and thus enrichment of heavy isotopes). Following the first minimum of δD and δ^{18}O, both isotope ratios increased for a short distance in soil depth and decreased again to a second minimum at about 1 m depth. This minimum probably indicates December rain events (11 mm). A third minimum at greater depth may contain the signal of November (9 mm). The peaks of early summer are not as

distinct because these rainstorms occurred at higher temperatures and thus had higher δD and δ^{18}O values (Dawson 1993). Most important in the further analysis is the fact that the water at 2–3 m soil depth contained an isotopic signal that was different from that of the upper profile, apparently originating from rain events that occurred several months or even a year prior to this study.

The soil profiles in Fig. 2 represent data from one chimney per site only, because different trenches reached different depths at each site, and because differences in infiltration rates and soil structure caused small-scale variations. The most extreme variation was observed for the δD depth profile in the desert habitat (Fig. 2). While the first δD minimum was at 0.20 m depth in two trenches, it had already reached 0.60 m in a third trench. At all other sites, the observed profiles were more similar.

Figure 2 also shows the volumetric water contents as calculated from the bulk density of the soil fraction and the gravimetric water content of the soil samples taken for isotopic analyses. The volumetric water contents are not shown for the forest sites because wet stones led to an underestimate of the actual water contents. Generally, the volumetric water content shows a trend that is inverse to the isotope signals. This is most pronounced in the dry habitats (desert, *Stipa* and *Festuca* grasslands) where the topsoil is dry and isotope ratios are most positive. At depths between 0.10 and 0.50 m, the volumetric water contents increased and the isotope ratios decreased, indicating the February rain event. This is followed by horizons where the soil is very dry (<10% volumetric water content) and the isotope signals increased again, indicating water extraction and evaporative enrichment of the remaining soil water during the course of the past dry season. All habitats show increasing soil water contents below 2 m, associated with decreasing isotope ratios. This horizon is reached by roots at all sites. Although the *Nothofagus* scrubland showed highest volumetric water contents in the humus horizon despite of increasing isotope ratios, the overall trend is similar to the grassland and desert sites. Thus, the data on volumetric water contents confirm the observation that water was available to roots at greater depths.

In order to identify the water source used by the plants, we compared the isotopic composition of xylem water of different dominant species with the isotopic composition of soil water of the adjacent profile, assuming that δD and δ^{18}O of soil water represents water accessed by roots. At the forest site, *Nothofagus pumila* tree xylem contained water of similar δD and δ^{18}O values as that found in soil water at about 0.40 m depth, while tree saplings and other understorey species contained water that was much more enriched, thus resembling water at 0.10 m soil depth. We cannot exclude the possibility that forest canopy trees took water from a range of soil depths and thereby averaged isotopic signals, but obviously tall trees used deeper soil layers for water uptake than the understorey layer. In the *Nothofagus antarctica* scrubland, the isotope values in aboveground xylem water did not allow a clear distinction of

Table 3 Change of root biomass (g m⁻²) and root density (g m⁻³) with soil depth (m) along an aridity gradient in Patagonia. The data represent averages (*Ave*) and standard errors (*SE*, n=3 to 4). The letter W indicates visible free water at that soil depth (dripping water at the forest site, water table at the scrub site, water droplets at the grassland and desert sites)

Site	Forest		Scrub		Grassland				Desert	
					Festuca		Stipa			
Rainfall (mm)	770		520		290		160		125	
Soil depth	Root biomass (g m⁻²)									
	Ave	SE	Ave	SE	Ave	SE	Ave	SE	Ave	SE
0.00–0.10	1414	497	1369	699	925	199	297	58	216	49
0.11–0.30	2949	296	2424	1429	645	94	174	18	84	29
0.31–0.50	1846	391	316	87	301	77	73	10	17	5
0.51–0.75	1013	127	115	33	114	30	79	15	3	1
0.76–1.00	168	48	86	30	91	59	98	48	0	
1.01–1.25	167	2	67	24	38	15	16	1	0	
1.26–1.50	87	<1	55	12	16	3	12	3	2	1
1.51–1.75	6		48	0	13	0	5	2	1	<1
1.76–2.00	W 2		14	0	W<1	0	9	2	0	
2.01–2.25			W 8	0			7	0	0	
2.26–2.50							1		0	
2.51–2.75							<1		0	
2.76–3.00							W<1		2	<1
Soil depth	Root density (g m⁻³)									
	Ave	SE	Ave	SE	Ave	SE	Ave	SE	Ave	SE
0.00–0.10	14143	4968	13688	6995	9252	1986	2968	583	2155	488
0.11–0.30	14746	1480	12121	7144	3224	470	870	91	433	133
0.31–0.50	9228	1954	1578	435	1503	384	363	50	74	19
0.51–0.75	4051	507	458	130	457	119	316	58	13	4
0.76–1.00	672	191	344	199	363	236	390	192	1	0
1.01–1.25	275	156	267	97	86	59	64	5	2	1
1.26–1.50	24		206	44	66	14	48	13	7	3
1.51–1.75	7		192		53	14	21	6	4	1
1.76–2.00	W 2		55		W 2		40	13	1	0
2.01–2.25			W 31				28	7	0	
2.26–2.50							1	0	0	
2.51–2.75							1	0	0	
2.76–3.00							W<1		W 8	

the dominant soil layer for water uptake. Water could have been taken up from 0.50–1.00 m depth, or from 2 m depth.

In both the *Festuca* and *Stipa* grasslands, the dominant grasses used surface water (as clearly indicated by the $\delta^{18}O$ values of *Festuca* and *Stipa*). These patterns contrast with those of the cushion shrub, *Mulinum*, which took water from 0.50–0.75 m depth, while most other associated species were using surface water except for the deep-rooted *Berberis* shrub. In the desert, *Nassauvia* used surface water, while *Senecio* may have taken water from greater soil depths.

In general, plants at all sites used water from the upper soil profile and did not use water from greater soil depths, maybe because of the specific weather situation during the late summer season of 1995. However, in order to see whether the vegetation would show signs of long-term water stress along this aridity gradient, we analysed the $\delta^{13}C$ values of sun leaves as an integral measure of plant water status over the entire growing season (Farquhar et al. 1982). The $\delta^{13}C$ values of sun leaves were constant at a low value across all habitats (Fig. 1, average of 5 sites±SD, –27±0.3), indicating that no water stress occurred in any of the habitats investigated during the time of foliage growth (September/October prior to this study in March). However, this does not exclude the possibility that water stress could occur in the dry season after termination of leaf growth (Sala et al. 1989). The $\delta^{13}C$ values of sun leaves in forest vegetation were 2–3‰ less negative than the $\delta^{13}C$ values of plants in the understorey. Understorey data were not included in Fig. 1, since factors other than water stress influence the $\delta^{13}C$ values in the understorey. The nitrogen concentrations in sun leaves were similar for all habitats (Fig. 1).

Discussion

This study shows that soil water was available at 2–3 m soil depth, and that roots reached this depth at all sites, along a distinct rainfall gradient across Patagonia, ranging from forest to desert vegetation. The rooting patterns as well as hydrogen and oxygen isotopes of soil and xylem waters indicate that the major supply of water for

Patagonia 1995
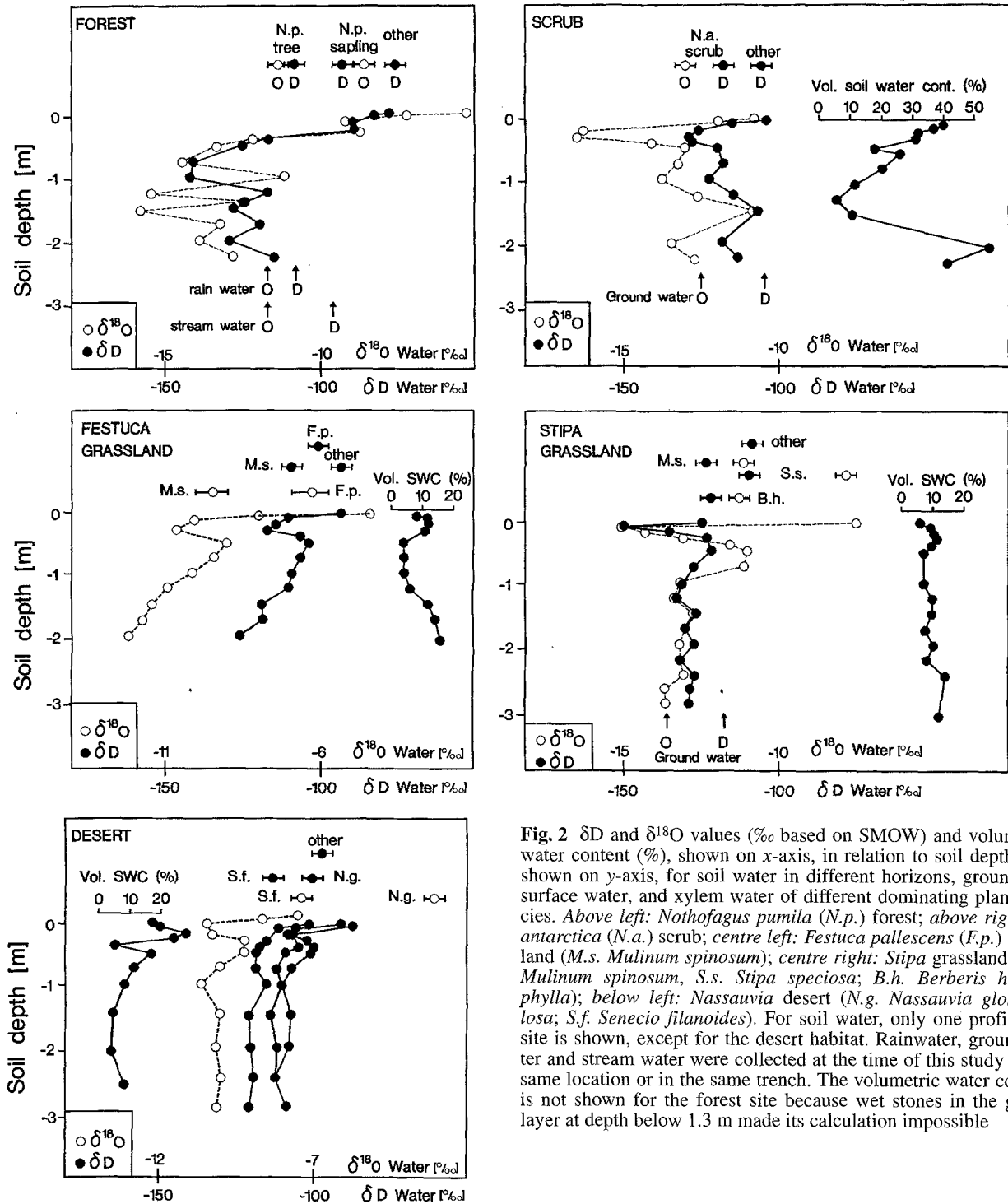
Fig. 2 δD and δ¹⁸O values (‰ based on SMOW) and volumetric water content (%), shown on x-axis, in relation to soil depth (m), shown on y-axis, for soil water in different horizons, ground and surface water, and xylem water of different dominating plant species. *Above left: Nothofagus pumila (N.p.)* forest; *above right: N. antarctica (N.a.)* scrub; *centre left: Festuca pallescens (F.p.)* grassland *(M.s. Mulinum spinosum); centre right: Stipa* grassland *(M.s. Mulinum spinosum, S.s. Stipa speciosa; B.h. Berberis heterophylla); below left: Nassauvia* desert *(N.g. Nassauvia glomerulosa; S.f. Senecio filanoides).* For soil water, only one profile per site is shown, except for the desert habitat. Rainwater, groundwater and stream water were collected at the time of this study at the same location or in the same trench. The volumetric water content is not shown for the forest site because wet stones in the gravel layer at depth below 1.3 m made its calculation impossible

these vegetation types generally came from upper soil horizons. The main rooting zone (90% of root biomass) was almost the same for forest and grassland, and was shallower rather than deeper in the desert. Thus, only a minor fraction of roots reached deep water. Also, the observed maximum rooting depth was shallower than expected from the global survey (Canadell et al. 1996), probably due to the presence of high soil moisture at greater depth.

We cannot exclude the possibility that the presence of groundwater inhibited roots of *Nothofagus* trees or desert shrubs from growing deeper. The hydrogen and oxygen isotopic composition and the profiles of volumetric water contents indicated that soil water at greater depths originated from rainfalls in the last or even prior to the last rainy seasons ("old" water) rather than water from recent rain events. The reason for the presence of water at 2–3 m

soil depth is probably related to the specific geological situation. In all habitats, soil horizons at greater depth consisted of gravel, probably forming a continuous layer reaching from the Andes into the eastern foothills along the river Senguer watershed. Thus, sub-surface flow of water is highly possible. For example, surface water was present even in the *Stipa* grassland in depressions that were about 3 m below the soil surface. Thus, the maximum rooting depth in the Patagonian arid region was apparently not determined by rainfall, but by the existence of free water at greater depth. The February rain event in 1995 had not yet penetrated to that depth, and thus had not affected this observation.

Although our study did not show water use from greater soil depths, there is an apparent advantage of having roots at these depths to reach more reliable water resources in cases of extreme drought events. The question remains, when and why do roots grow deep. We can only speculate about this process. Most likely, roots follow a front of water by growth. Various fronts of water from distinct rain events were detected in the present investigation, and it is surprising to see that these fronts of water were not used to a greater extent. This observation has already puzzled Soriano et al. (1987) and Soriano (1990). If all water was depleted by plant uptake, roots would probably enter a dormant stage until another infiltration front of water arrives, and then they might continue to grow to greater depth. Probably there is no lack of carbohydrates for root growth, because carbohydrate levels are expected to increase rather than decrease when growth is limited (Stitt and Schulze 1994). Thus, one can see mechanisms that would allow roots to grow deep, although this may be species-specific.

Our results on above- and belowground biomass distribution agree with conventional generalizations on the relationship between vegetation zonation and rainfall: along our aridity gradient, total biomass sharply decreased with decreasing precipitation, but belowground biomass decreased at a lower rate than aboveground biomass, resulting in increasing root:shoot ratios. Plant composition changed with rainfall in spite of water being available at 2–3 m depth all along the transect. Although a minor proportion of roots reached the moist layer at each site, most roots were located in shallower layers. The existence of deep water posed the question of why roots are not exploring these layers to a greater extent. An answer to such a question will need a much better knowledge of the amount of water available in those layers, its annual variability, and the different strategies of the present and potential life forms that make use of deep water. Currently, we can only speculate about the causes for the observed vegetation zonation along the aridity gradient. Apparently, the existing established vegetation has access to a soil volume that is sufficient for growth and survival, even in dry years. However, the different vegetation types contain different structural life forms, which use the deep water according to their specific needs and genetic limitations. Thus, there must be other reasons that limit the migration of native trees into the

grassland, and that separate the two grass genera, *Festuca* and *Stipa*, into different zones.

Earlier investigations in the Patagonian grasslands show that seedling survival explains the observed vegetation pattern and migration of the grasslands (e.g. Soriano and Sala 1986; Aguiar et al. 1992; Aguiar and Sala 1994). It has also been demonstrated that grasses of established tussocks cannot fully exploit water, even in patches of bare soil between plants (Soriano 1990). The steppe vegetation exhibits an incomplete utilization of rain water (Soriano et al. 1987), in spite of the well-known competition for water between shrubs and grasses (Walter 1966; Sala et al. 1989). In contrast to previous studies on establishment of plants and water use within the steppe community, the non-invasion of steppe vegetation by trees has not yet been explored.

Thus, the water balance alone, including soil water accessibility by rooting depth, cannot explain the observed vegetation zonation in Patagonia. We speculate that seedling establishment in the dry period limits migration of species into drier habitats, while light competition during the period of active growth may limit migration of arid species into wetter habitats. Therefore, the plant life forms that coexist at a given site are those that are able to establish (e.g. Soriano and Sala 1986; Aguiar et al. 1992; Aguiar and Sala 1994). However, for those species, there seems to be a tradeoff for the success of establishment between a increased capacity to use water at decreasing rainfall, and a reduced capability to grow tall and develop a large leaf area. We observed free water at greater soil depths in a desert, suggesting that the surviving life form of dwarf shrubs does not use all the water (see also Soriano et al. 1987; Soriano 1990). Our study implies that modelling of vegetation and its migration in response to global change (e.g. Prentice 1992) will have to include the important role of seedling establishment.

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