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Root distribution, standing crop biomass and belowground productivity in a semidesert in México

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Abstract

In a semidesert community in México (Zapotitlán de las Salinas, Puebla) the vertical distribution of roots and root biomass was estimated at 0–100 cm depth on two sampling dates, November 1995 (wet season) and January 1998 (dry season). Root productivity at 7 to 14.5 cm depth was estimated with the in-growth core technique every two months from March 1996 to February 1998. The relationship between environmental factors and seasonal root productivity was analyzed. Finally, we tested the effect of an irrigation equivalent to 20 mm of rain on root production. Seventy four percent of the total number of roots were found at 0-40 cm depth. Very fine roots ($<$1 mm diameter) were found throughout the soil profile (0-100 cm). In contrast, fine roots (1-3 mm diameter) were found only from 0–90 cm depth, and coarse roots ($>$3 mm diameter) from 0–60 cm depth. The root biomass was 971.5 g m^{-2} (S.D. = 557.39), the very fine and fine roots representing 62.9% of the total. Total root productivity, as estimated with the ingrowth core technique, was 0.031 Mg ha^{-1} over the dry season and 0.315 Mg ha^{-1} over the wet season. Only very fine roots were obtained at all sampling dates. Rainfall was significantly correlated with very fine root production. The difference between fine root production in non-watered (0.054 g m^{-2}) and watered (0.429 g m^{-2}) treatments was significant. The last value was the same as that predicted for a rain of 20 mm, according to the exponential model describing the relation between the production of very fine roots and rainfall at the site.

Introduction

Root production and decomposition are important processes in the dynamics of carbon and nutrients in terrestrial ecosystems (McClaughterty et al. 1982; Aber & Melillo 1991; Fahey & Hughes 1994). It has been estimated that the assignment of resources to belowground parts can be as high as 80% of net primary productivity (Coleman 1976; Fogel 1983; Caldwell & Richards 1986). Despite the above information, the study of roots in deserts has received little attention and the estimate of standing biomass is scarce (Ehleringer & Mooney 1982). Belowground productivity in deserts has frequently been estimated as a constant percent (40%) of the aboveground productivity or assuming that the biomass ratio root:shoot is equal to the productivity ratio root:shoot (Newbould 1968; Herman 1977; Ehleringer & Mooney 1982; MacMahon & Wagner 1985). Nevertheless such estimates of belowground productivity should be taken cautiously as these estimates have not yet been considered for the fine roots, and the biomass ratio root:shoot changes according to the dominant species of the community (Coleman 1976; Kummerow et al. 1978; Ehleringer & Mooney 1982; Nadelhoffer et al. 1985).

Root productivity of a plant community can be affected by temperature, rain, availability of nutrients and soil physical properties (Bell & Bliss 1978; Nadelhoffer et al. 1985; Gross et al. 1993; Sánchez-Gallén & Alvarez-Sánchez 1996; Mou et al. 1997; Fitter et al. 1998). Even though in arid zones water is the most limiting resource for productivity (Fisher & Turner 1978; Noy-Meir 1973, 1985; Ludwig 1987), the effect of the seasonal variation from the rain over the belowground productivity has not been documented.

This study describes the vertical distribution of roots and standing crop biomass in a semidesert area of México. We quantified the belowground productivity and analyzed how it was affected by certain environmental factors. Finally, we analyzed how a watering (equivalent to 20 mm of rain) affected root production. According to the pulse-reserve theory used in desert communities (Noy-Meir 1973; Fisher & Turner 1978), where a pulse of carbon assimilation is triggered by water supply, we hypothesized that the most important factor in primary belowground plant productivity is the seasonal variation in water availability.

Methods

Study area

This study was conducted in Zapotitlán de las Salinas, Puebla, México. The area is part of the Tehuacán-Cuicatlán province, which has a large floristic and endemic diversity (Rzedowski 1978).

The area presents a mean annual rainfall of 400 mm. The wet season extends from May to October and the dry season from November to April. The mean annual temperature fluctuates between 18 °C and 22 °C (Zavala-Hurtado 1982). Soils are derived from sedimentary and metamorphic rocks and has been considered as Lithosols, Xerosols and Rendzinas according to the FAO/UNESCO clasification (Anonymous 1981). The vegetation type is a microphyllous scrublands, dominated by deciduous leguminous shrubs interspersed with columnar cacti and below the shrubs a stratum of chamaephytes and small succulents (Montaña & Valiente-Banuet 1998).

The study was carried out on a plot of 0.5 ha (50 × 100 m), located at 18°20′ N and 97°28′ W on a hillside facing south, with a slope of 33°. Beside the plot, the soil at around 0–20 cm depth has been characterized as loam (41% sand, 37% loam and 22% clay), with pH 8.1 and 3.1% of organic matter content (Alvarez-Aguirre & Montaña 1997). The dominant species are the shrub *Mimosa luisana* with 97 plants in 900 m^2, and the columnar cactus *Neobuxbaumia tetezo* with 69 individuals in the same area.

Biomass and vertical distribution of roots

In November 1995 (wet season) and January 1998 (dry season) four trenches measuring 1.5 × 0.6 m, and 1.2 m in depth were excavated. Vertical root distribution was quantified using the trench wall method (Böhm 1979). Cut roots intercepting the smooth wall were counted over a 100 cm deep and 60 cm wide soil profile for each trench using a 5 cm × 5 cm grid. In order to quantify root biomass, we extracted soil samples of 10 × 10 × 10 cm up to 100 cm in depth on each wall. The roots were carefully separated from the soil and washed under running tap water, using a 0.96 mm^2 sieve. The roots were dried at 90 °C for 48 h (Böhm 1979). We classified the roots in three diameter classes: very fine ($<$1 mm), fine (1–3 mm) and coarse ($>$3 mm) (Wilczynski & Pickett 1993). The roots were weighed to the nearest 0.001 g and the biomass data were converted to g m^{-2}

Fine root productivity

Root productivity was estimated by the in-growth core technique (Caldwell & Virginia 1989; Nadelhoffer & Raich 1992). From March 1996 to May 1998, 40 PVC tubes were filled with sifted soil and buried horizontally at a depth of 7 to 14.5 cm. Each tube was 20 cm long and 7.5 cm in diameter and had circular perforations of 19.6 mm^2 at 0.5 cm intervals. On the plot the tubes were arranged in ten 40 m parallel rows. The distance between rows was 10 m. Each row had four tubes and the distance among them was 10 m.

Every two months the tubes were carefully uncovered, cutting all the roots that grew around the tubes in order to retain only the portions contained in the tubes. The tubes were then refilled with sifted soil and buried again. This re-sampling on time allowed for the clear separation of the production of each period of root collecting and eliminated the possible saturation of roots in the tubes during the period of intense growth. Great care was taken on burying the filled tubes in a different hole always within a circle of 3 m radius. The roots were separated and classified in three diameter classes, as described before.

Environmental factors

Rainfall, minimum and maximum temperature, evaporation and relative humidity were registered by the meteorological station of Zapotitlán de las Salinas located 500 m from the study area. The evapotranspiration was calculated according to Thornthwaite, the photoperiod and solar radiation according to the latitude and longitude of the studied site.

Soil water potential (SWP) and soil water content at 10 cm depth were measured *ex situ* every two weeks from March 1996 to May of 1998. Three soil samples were taken: one from the centre and two from the plot's edges. SWP was measured using a sample chamber C-52 connected to a dew point microvoltmeter HR-33T (Wescor Inc.,USA). Soil water content was measured using the volumetric method (Rundel & Jarrell 1989).

Watering

At the end of the two years of observation, we carried out a watering experiment. On March 6 of 1998 the 40 PVC tubes used to estimate root productivity were assigned at random to an equal proportion of watering and non-watering treatments.

The watering was done using circular plots with 0.56 cm radius, centered on the selected tubes. The plots were delimited by 30 cm tall metallic sheets, buried 5 cm in the soil. Each plot was drip-watered equivalent to a 20 mm rainfall, once in the afternoon of the same day. One day after the watering, the depth that humidity had reached was estimated by digging out two plots without tubes. There was no rain during the experiment. In three watered plots and in three non-watered plots a soil psychrometer PCT-55 (Wescor, Inc., USA) was buried 10 cm in the soil, measuring every two weeks the SWP *in situ*. During the experimental period the mean maximum and minimum air temperature were 27.6 °C and 12.6 °C.

All the tubes were collected two months after the watering (May 4, 1998) and the roots were extracted in the way described above.

Statistical analyses

Root number in soil profiles and root biomass for each diameter class were analyzed using nonparametric repeated-measures analysis of variance (ANOVAR) due to the correlation among measurements within soil profiles. A nonparametric ANOVAR involves no assumption about the structure of the covariance matrix and it is applicable under far more general assumptions than the parametric techniques, although there is a loss in sensitivity of the analysis as compared with the parametric tests (Potvin et al. 1990; Winer et al.1991). The Kruskal-Wallis statistic was used to determine the effect of sampling dates as grouping factor with two states (wet season and dry season). The Friedman test was used to determine the effect of depth with ten states (0–10, . . . , 90–100 cm) as a trial factor and the interaction sampling date per depth. In the root biomass analysis, a previous parametric ANOVAR with sampling date as above and depth with two states (0–20 and 20–40 cm) and diameter class with three states (very fine, fine and coarse roots) as trial factors, showed significant difference ($p = 0.039$) among diameter classes, when we used normalized data of the mean root biomass in order to meet assumptions of the test. The biomass data were transformed using the algorithm $y' =$ (biomass $^{0.2} - 1$)/0.00856, obtained through the Box-Cox transformation with the statistical package JMP (SAS 1997).

The very fine root productivity was compared over two seasons, the dry season (November–December, January–February, March–April) and the wet season (May–June, July–August, September–October) using the *t*-statistic. Correlation analyses (Bonferonni adjusted) were used to prove the relation between the environmental factors and very fine root production. This procedure was repeated three times, first using the root production and the environmental data of the same period, and then the environmental data shifted-back one and two months with respect to the production data. As the analyses of correlation showed a significative association between rain and the productivity in the data of the same period, a model of regression was used later to determine the functional relationship between the two variables, with rain as an independent variable. In all analyses of very fine root productivity, the bimonthly mean root production was transformed to $\log_{10}$ (very fine roots $+1$) to normalize the distribution of the data.

A Mann–Whitney *U*-test was used to compare the differences in root production between watered and non-watered plots (Zar 1984). This rank test made possible to consider the plots with nil production. All statistic analyses were done using SYSTAT 5.0 (Systat 1992). The critical α was 0.05 in all cases.

Results

Root density was much higher on the surface, and decreased in accordance to increasing depth. Seventy four percent of the roots were found at 0 to 40 cm in depth (Figure 1). Differences among depths were significant ($p < 0.001$), and there was no interaction between sampling date and depth.

Mean biomass over the two periods was 971.5 g m^{-2} (S.D. $= 557.39$), and the very fine and fine roots represented 62.9% of the total (Figure 2). Eighty-six percent of the root biomass was found between 0 and 40 cm in depth, and only very fine roots were

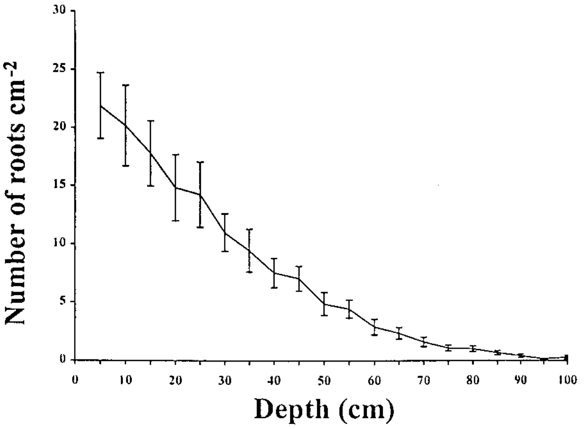

Figure 1. Vertical distribution of roots number in the semidesert of Zapotitlán, Puebla (0–100 cm in depth) during November 1995 (wet season) and January 1998 (dry season). We show the mean ±1 S.E. ($n = 8$). The data of the two sampling period were averaged after that the nonparametric ANOVAR did not show significant differences ($p > 0.05$).

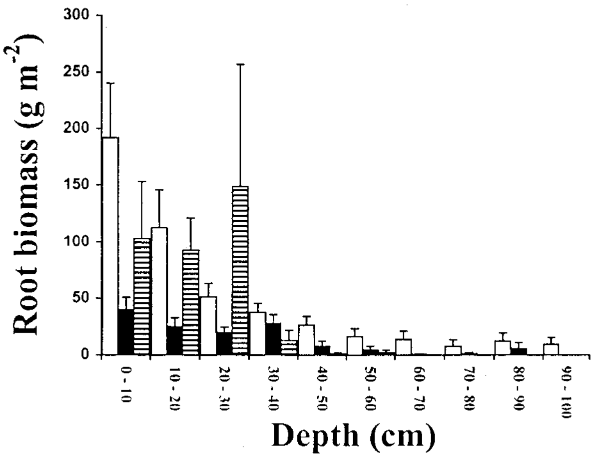

Figure 2. Vertical distribution of root biomass determinated in the semidesert of Zapotitlán, Puebla. We show the mean ±1 S.E. ($n = 8$). The roots were classified in three diameter classes: □ very fine (<1 mm), ■ fine (1–3 m) and ⊟ coarse (>3 mm). The data shown are averages of two sampling dates because ANOVAR's for each diametrical class did not show significant differences ($p > 0.05$).

found from the surface to 100 cm depth. ANOVAR for each diameter class showed a significant difference among depth ($p < 0.001$) but not between sampling dates.

Root productivity was mainly composed of very fine roots (Figure 3). The coarse roots were only obtained during the first year of the study. Bimonthly mean root productivity for the dry season was 0.252 g m^{-2} (S.E. = 0.053, $n = 6$), and 2.553 g m^{-2} (S.E. = 0.871, $n = 6$) for the wet season; differences were significant ($t = 2.768$, $p = 0.02$).Three times the bimonthly mean root productivity is equivalent to the season productivity between 5 and 14.5 cm. Considering that 24.3% of root biomass was found at this depth (Figure 2), the extrapolation of the season production at surface to 100 cm in depth, gives an estimated of 0.031 Mg ha^{-1} for the dry season and 0.315 Mg ha^{-1} for the wet season, or 0.346 Mg ha^{-1} for the year.

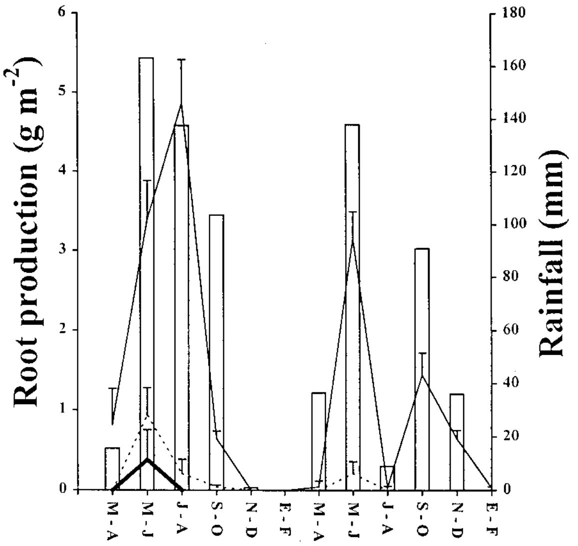

Figure 3. Seasonal variation of root production from March 1996 to February 1998 in the semidesert of Zapotitlán, Puebla. We show the mean ±1 S.E. ($n = 40$) of the root biomass collected every two months and the rainfall (bars), for the same period. The biomass was classified in three root diameter classes: — very fine (<1 mm), – – fine (1–3 mm) and ▬ coarse (>3 mm).

According to the data of the same period only the rainfall was significantly correlated with the $\log_{10}$ (very fine roots production +1) ($p = 0.01$; $n = 12$). The exponential model for very fine roots production (g m^{-2}) $= -1 + 10^{(0.015+0.004\ (\text{rainfall, mm}))}$ explained 83% of the total variation. During 1996 major root productivity (4.866 g m^{-2}) was obtained during July and August. In this period rainfall was 138.6 mm, which represented 33% of the rainfall for that year. However, during the same months of 1997, root productivity decreased to 0.036 g m^{-2}, when 9.3 mm of rain were recorded, which represented 3% of the rainfall of that year. The environmental factors shifted-back one and two months with respect to the root production were not significantly correlated.

A day after the watering experiment, in each plot watered SWP was −0.4 MPa and the moisture reached 40 cm in depth. On the 20th day SWP decreased to

-3.5 MPa. Subsequently, SWP was too low in order to measure it with the psychrometric equipment. We considered that from day 21th to the 60th after the watering, SWP was less than -3.5 MPa. In non-watered plots SWP was < -3.5 MPa from the beginning until the end of the experiment.

The Mann–Whitney *U*-test showed a significant difference in very fine root production between watered and unwatered treatments ($U = 90$, $p = 0.002$). The watering produced an average of 0.429 g m^{-2} (S.E. $= 0.122$, $n = 20$), and unwatered plots produced an average of 0.054 g m^{-2} (S.E. $= 0.029$, $n = 20$). The difference in fine root production obtained during the watering experiment and the estimated value (0.244 g m^{-2}; S.E. $= 0.126$) for the exponential model was not significant ($t = 1.46$, $p > 0.05$).

Discussion

Root distribution in the study area was superficial, as in other desert ecosystems (Canadell et al. 1996; Schulze et al. 1996; Jackson et al. 1996). According to the global model of vertical distribution of roots $Y = 1 - \beta^d$, where Y is a cumulative roots-fraction from the surface to depth (d), and β is the root numeric distribution index, the value obtained from our data (0.967) was similar to that estimated (0.975) in desert ecosystems (Jackson et al. 1996).

Although the roots were not classified by species, we observed that a big part of the roots were from succulent and shrub plants. The columnar cacti *N. tetezo* and the shrub *M. luisana* are the dominant species in the community. Studies done in the same area have shown that these species have mainly shallow roots, ca. 0–30 cm in depth (Valiente-Banuet et al. 1991; Flores-Martínez et al. 1998).

The standing crop root biomass of the site (0.971 kg m^{-2}) was higher than has been found in other deserts, whose values range from 0.077 and 0.73 kg m^{-2} (Evenari et al. 1975; Ehleringer & Mooney 1982; West 1983; MacMahon & Wagner 1985). However, it was lower than that of cold deserts of *Atriplex* (1.88 kg m^{-2}) and *Ceratoides* (1.9 kg m^{-2}) in North America (Caldwell & Camp 1974).

The belowground productivity estimated in the study area was lower than the one estimated for the desert area of Pamir (0.53 Mg ha^{-1} $year^{-1}$) with a mean annual rainfall of 500 mm (Walter & Box 1983) and the cold desert communities in Utah with *Ceratoides lanata* (1.86 Mg ha^{-1} $year^{-1}$) and *Atriplex confertifolia* (4.43 Mg ha^{-1} $year^{-1}$) (Caldwell & Camp 1974). This comparison must be taken coutiously due to the difference of methods used. In Pamir and in Utah indirect methods were used, therefore it is not possible to standarize the results and all the methods used to date to measure root productivity are subject to methodological errors (Vogt et al. 1986; Nadelhofer & Raich 1992). In our site, root cutting during the burial of the tubes and the occasional crumbling of the soil with these inside them could have altered root growth resulting in underestimates of root productivity. Nevertheless the magnitude in difference in the belowground productivity among plant communities are so great that they are probably due to biological characteristics inherent to the sites and not to methodological errors.

The pattern of root production along the year followed basically the rain course and experimental watering stimulated root production during the dry season. Our results show that water is a limiting factor of belowground primary productivity and support the theory that the deserts are water-controlled ecosystems (Noy-Meir 1973; Fisher & Turner 1978).

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