

Vertical distribution of fine roots of *Tamarix ramosissima* in an arid region of southern Nevada

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ABSTRACT

To increase our understanding of soil water and nitrogen use strategies of invasive *Tamarix ramosissima* during dry seasons, the vertical distributions of fine roots and their associations with soil properties were examined in the Virgin River floodplain, southern Nevada, United States. We measured morphological traits of fine roots, such as fine-root mass density, fine-root length density, specific root length and specific root area at 10 cm increments to a depth of 2 m. Soil properties were analyzed at 20 cm increments. More than 60% of fine root length and biomass was concentrated at depths between 20 and 60 cm. Soil nitrogen (N) concentration had strong and positive relationships with fine-root mass and length densities, suggesting that the fine-root distribution may be influenced by soil N availability. A weak but positive relationship was observed between soil moisture and fine-root mass density. Soil salinity had no relationship with root morphological traits. These findings suggest that *T. ramosissima* fine roots may contribute to N uptake from the upper soil layers during dry seasons. This might be an important advantage over native riparian tree species in arid riparian areas of the southwestern United States.

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1. Introduction

Fine roots are a key link for soil water and nutrient uptake for plants in terrestrial ecosystems, and thus play an important role for plant growth and development. In most ecosystems, fine roots concentrate near the soil surface and exponentially decrease with increasing soil depth (Schenk, 2008). This enables more soil resource uptake since water enters the soil profile predominantly from the soil surface in most ecosystems, and nutrient concentrations are commonly higher in the upper soil layers (Schenk, 2008; Schenk and Jackson, 2002). Therefore, the properties of fine root distributions often depend on soil water and nutrient availability in soils (Bennett et al., 2002; Drew, 1975; Eissenstat and Caldwell, 1988; February and Higgins, 2010; Hodge, 2004; Imada et al., 2008; Iverson, 2010; Zhou and Shangguan, 2007).

In arid regions, soil water is the limiting factor for plant primary production (Fisher et al., 1988; Smith et al., 1997). Many perennial plants in such regions have shallow roots to absorb soil water from rainfall and/or deep roots to access groundwater and deep soil moisture (Batouny, 2001) thereby taking up water from

groundwater, surface processes or both sources (Chimner and Cooper, 2004; Dawson and Pate, 1996). During dry season, woody phreatophytic plants are mainly dependent on deeper water sources for most of their water requirement, yet they can utilize soil water recharged by precipitation (Chimner and Cooper, 2004; Dawson and Pate, 1996; Xu et al., 2007). Examining the vertical distribution of fine roots of phreatophytic plants is important for understanding the water use strategy of plants. However, the number of studies on the fine root distribution of woody species is small (February and Higgins, 2010; Gwenzu et al., 2011; Zhou and Shangguan, 2007).

Soil nitrogen availability is a secondary influential factor on plant production in arid regions (Batjes, 1996; Smith et al., 1997). While water uptake in deeper soil can be important for woody phreatophytes in such regions, the uptake of nutrients may be limited primarily to upper soil layers (Jackson et al., 1996). Thus, understanding relationships between vertical distributions of fine roots and soil water and N concentrations are valuable for evaluating soil resource use of plants. In addition to soil resources, high salinity, alkalinity and other extreme characteristics possibly limit plant growth and production in such regions. To address the strategy of plants for water and nutrient use and environmental tolerance, understanding the response of fine roots to the soil environment is important. Some studies have investigated the vertical distribution of fine roots for woody species, suggesting their association with soil moisture,

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N concentration or pH (February and Higgins, 2010; Gwenzi et al., 2011; Zhou and Shangguan, 2007).

Tamarix is an invasive plant in arid regions of the western United States (Di Tomaso, 1998; Shafroth et al., 2005; Stromberg et al., 2009). This invasive plant has displaced native plants and occupies more than 400 000 ha along many river systems in the region, having negative ecological and economic effects (Shafroth et al., 2005). One of the commonly cited reasons for the success of this species is its relatively higher tolerance against soil salinity and drought stresses than native riparian trees (Cleverly et al., 1997; Glenn et al., 1998; Pataki et al., 2005; Vandersande et al., 2001). For example, during the dry season *Tamarix* rapidly shifts its primary water sources with declining water tables, thus maintaining constant water potential and photosynthesis (Nippert et al., 2010). However, although photosynthesis is strongly affected by soil nitrogen availability (Lambers et al., 1998), nitrogen uptake by these species is not well understood. Knowledge of nitrogen uptake can contribute to understanding of how this invasive plant maintains its population in invaded areas and may be important information to assist in managing *Tamarix* forests.

In the present study, we investigated the vertical distribution of *Tamarix ramosissima* fine roots in a stand in the Lower Virgin River, Nevada, United States. We also examined its relationships with soil environmental conditions. We hypothesized that soil resource availability, especially N concentration, would affect the vertical distribution of fine roots since this species is able to access groundwater during the dry season, thus decreasing its dependency on surface water. We also predicted that high salinity and alkalinity may adversely affect fine root distributions.

2. Materials and methods

2.1. Study site and sampling locations

The study was conducted in a floodplain area of the Virgin River, about 20 km southwest of Mesquite, Nevada, USA (36°41' N, 114°16' W, elevation 411 m), which is located in the Mojave Desert. The climate of the area is arid. Average annual temperature and mean annual precipitation for the monitoring station at Mesquite from 2000 to 2009 were 20.2 °C and 145 mm, respectively (Desert Research Institute, Nevada, USA, under Community Environment Monitoring Program; <http://www.cemp.dri.edu/cemp/>). In the study year of 2009, average annual temperature and annual precipitation were 20.5 °C and 92.7 mm, respectively. The year 2009 was relatively dry and total precipitation from May to October was less than 20 mm. Depth to water table measured in the following year in a stand of *T. ramosissima*, located approximately 200 m from the river and 1 km northeast of our study site, showed that it ranged from 1.2 to 2.1 m in 2010, when total precipitation from May to October was about 60 mm.

The vegetation of the area is dominated by *T. ramosissima*, often occurring in monotypic stands near the river channel. The soil texture of a mature monotypic *Tamarix* stand in the floodplain is sandy to sandy loam (Devitt et al., 1997). Flooding occurs at intervals of 5–6 years and the last flooding at the site occurred in 2005. Average height, diameter and density of the living stems in three 5 × 5 m² plots of the stand were 158.0 ± 27.7 cm (mean ± S.E.), 1.56 ± 0.51 cm and 6.57 ± 1.41 stems m⁻², respectively. The stand was relatively young: the oldest tree was eight years old based on counts of annual rings of ten harvested trees.

Three sampling locations were chosen at similar distances (about 90 m) from the river's edge. The distances between the sampling locations were at least 10 m from each other. Little litter accumulation was observed on the locations. A pit at least 1.2 m wide and 0.6 m long was dug to a depth of 2 m in the interspace

between trees in each location (P1, P2 and P3) during mid-October 2009. A vertical wall on one side of each pit was used for sampling.

2.2. Root sampling and analyses

For analyzing fine root properties, block samples (10 × 10 × 10 cm) were collected at 10 cm increments from the surface to the bottom along the walls, giving a total of 60 samples. The samples were kept in plastic bags, transported to the laboratory, and maintained at 4 °C until processed. In the laboratory, each soil sample was submerged in water in a container and stirred, and then the root suspension was sieved with a 0.5 mm sieve. This routine was repeated at least three times. Roots in each soil layer were stored in a plastic bag with 80% ethanol and preserved in a refrigerator at 4 °C.

Roots in each layer were divided into two size classes based on root diameter: fine roots (≤1 mm) and coarse roots (>1 mm). Roots were further sorted into live and dead fractions by their color and elasticity. All or parts of living fine roots in each layer were digitally scanned using a flatbed scanner set at 600 dpi and saved as TIF files. Root images were analyzed using image analysis software (WinRHIZO Pro 2008a, Regent Instruments Inc., Quebec City, Quebec, Canada) for root length and surface area. Fine root samples in each layer were oven-dried at 80 °C for at least 48 h and weighed.

The specific root length (SRL, root length per unit of root biomass, m g⁻¹) and specific root area (SRA, root surface area per unit of root biomass, cm² g⁻¹) of fine roots were determined from root dry mass and the corresponding root length and surface area. Then the SRL was used to estimate length for unscanned root samples. Fine-root mass density (FRMD, mg cm⁻³) and fine-root length density (FRLD, cm cm⁻³) were calculated as follows: FRMD = M/V_s and FRLD = L/V_s , where, M and L are fine root dry mass and fine root length, respectively, in each soil block, and V_s is the volume of soil.

2.3. Soil sampling and analyses

Soil samples were collected at 20 cm increments from the surface to bottom on the walls using a cylindrical soil core (100 cm³). The soil samples were kept in plastic bags and transported to the laboratory. Soil water content was measured using a subsample of approximately 5 g before and after drying at 80 °C for at least 48 h. Remaining soil samples were sieved with a 2-mm sieve and air-dried at least 48 h for the following analyses. Soil pH was measured using a 1:5 soil water suspension. Soil electrical conductivity (EC) of a saturated water extract was measured at the Environmental Analysis Laboratory, University of Minnesota. The soluble Ca²⁺, K⁺, Mg²⁺ and Na⁺ concentrations in the same extract were also determined simultaneously by Inductively Coupled Plasma Atomic Emission Spectrometry at the University of Minnesota. Total soil C and N concentrations were measured with a CN coder (MT-700 CN analyzer, Yanaco, Kyoto, Japan).

2.4. Data analysis

A Kruskal–Wallis test was used to examine the variation in each root morphological parameter (FRMD, FRLD, SRL or SRA) by depth. Relationships among vertical distributions of root morphological traits of samples taken from the three pits were analyzed with Spearman rank correlation coefficients since the data for fine root mass and length densities were not normally distributed. A Kruskal–Wallis test was also used to determine the effects of depth on each soil environmental parameter (water content, pH, EC, soluble ion concentrations, total N concentration or C/N ratio).

The values of root morphological traits were averaged at 20 cm intervals. Relationships between soil environmental factors and the

averaged values of root morphological traits were examined in each soil layer for all three pits. Spearman rank correlation analysis was conducted between root morphological traits and soil environmental factors. Further, canonical correlation analysis was used to describe the relationships between root morphological traits and soil environmental conditions. To avoid multicollinearity, we removed FRLD and SRL from root morphological factors as well as pH, soluble Na^+ , K^+ and Mg^{2+} concentrations from soil environmental factors used in canonical correlation analysis. Stepwise linear regression analyses were performed using each root morphological trait as the dependent variable and soil environmental factors as the independent variables. We also removed soil environmental factors described above in regression analyses to avoid multicollinearity among independent variables. These analyses were conducted by using SPSS software version 18.0.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Vertical distribution of fine roots

Fine-root mass and length densities differed significantly among soil depth layers (Kruskal–Wallis test, $P = 0.027$ and $P = 0.047$, respectively) (Fig. 1a, b). The FRMD and FRLD were very low at the top 20 cm and accounted for only 3% of their respective totals at this layer. Most fine roots were concentrated at depths between 20 and 60 cm, which accounted for 64% and 61% of total FRMD and FRLD, respectively. Average fine root biomass was $4.0 \pm 0.5 \text{ Mg ha}^{-1}$ (mean \pm S.E.) in soil layers from 0 to 200 cm.

There were significant differences in SRL and SRA among soil depth layers (Kruskal–Wallis test, $P = 0.008$ and $P = 0.021$, respectively) (Fig. 1c, d). The values of SRL and SRA tended to be higher at depths between 100 and 140 cm. Vertical distributions of SRL and SRA were not consistent among the sample pits.

3.2. Profiles of soil environmental factors

Average soil water content was highly variable among the soil depths although the differences were not significant (Kruskal–Wallis test, $P = 0.119$) because of the high variability of the data (Fig. 2a). The water content at the 20 cm depth was very low (less than 0.01 g g^{-1} in each pit). Higher values were found at the 60, 80 and 120 cm depths, and lower values at the 20 and 140 cm depths. In each pit, values were highly variable, and peaks were found at the 60, 80 and 200 cm depths in P1, at the 120 cm depth in P2, and at the 60 and 120 cm depths in P3 (data not shown).

The total N concentration was also not significantly different among depths (Kruskal–Wallis test, $P = 0.091$). The total N concentration was lower at the 20 cm depth than at the 40 and 60 cm depths, and it was consistently low at layers below 100 cm (Fig. 2h). In each pit, peak values were found at the 60 cm depth in P1, the 40 and 120 cm depths in P2, and the 40 cm depth in P3 (data not shown).

The average soil pH differed significantly by depth (Kruskal–Wallis test, $P = 0.026$) and the values ranged between 8.0 and 9.1 (Fig. 2b). The average EC was not significantly different among depths (Kruskal–Wallis test, $P = 0.056$), ranging between 2.3 and 8.0 dS m^{-1} (Fig. 2c). The pH and EC values indicated that the soil

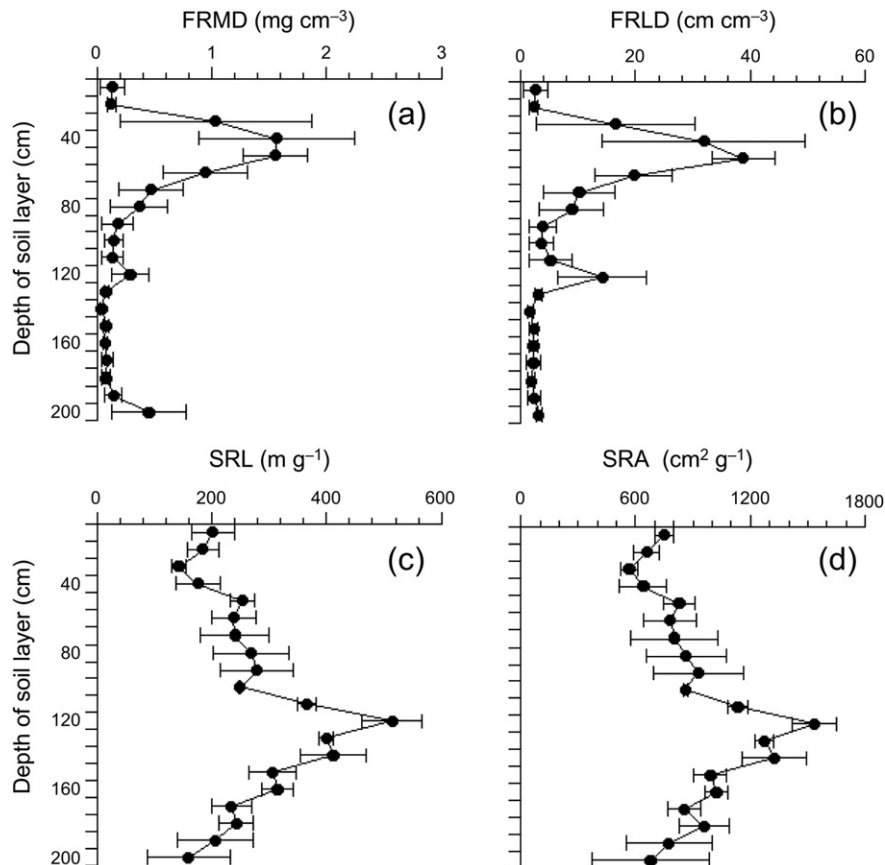


Fig. 1. Vertical distribution of the average fine root mass density (FRMD) (a), fine root length density (FRLD) (b), specific root length (SRL) (c) and specific root area (SRA) (d) in the *T. ramosissima* stand in the Lower Virgin River, Nevada. Data are mean values \pm 1 S.E., $n = 3$.

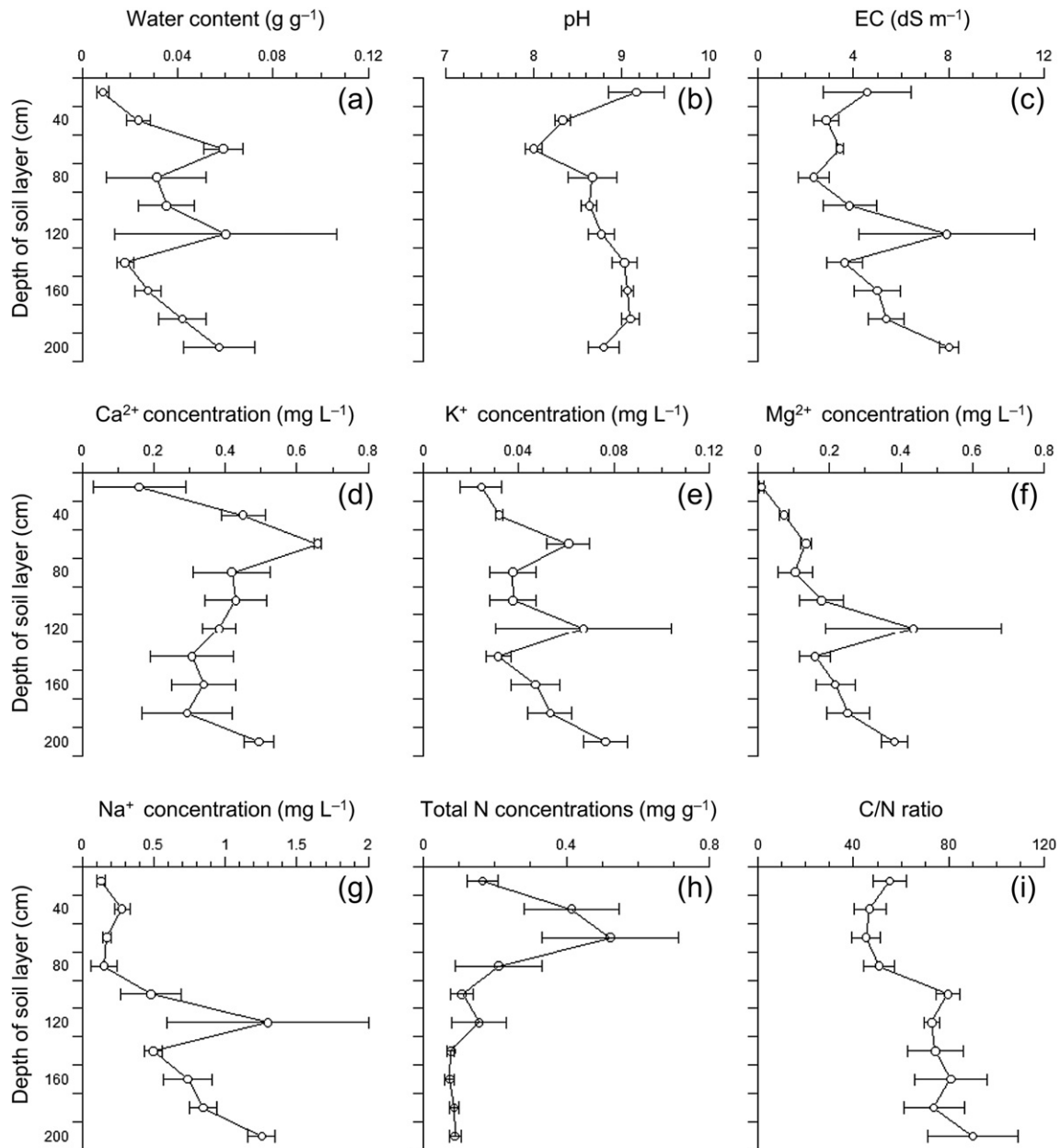


Fig. 2. Profiles of average soil water content (a), pH (b), electrical conductivity (EC) (c), soluble Ca^{2+} (d), K^{+} (e) Mg^{2+} (f) and Na^{+} (g) concentrations, total N concentration (h), and C/N ratio (i) in the *T. ramosissima* stand in the Lower Virgin River, Nevada. Data are mean values \pm 1 S.E., $n = 3$.

was saline–alkaline at the 20, 120, and deeper than 160 cm depths, nonsaline at the 40 and 60 cm depths and nonsaline alkaline at the 80, 100 and 140 cm depths (USSS Staff, 1954). Soluble Mg^{2+} and Na^{+} concentrations were significantly different among depths (Kruskal–Wallis test, $P = 0.018$ and $P = 0.007$, respectively) (Fig. 1f, g) but Ca^{2+} and K^{+} concentrations (Kruskal–Wallis test, $P = 0.110$ and $P = 0.100$, respectively) (Fig. 1d, e) and C/N ratios were not significantly different (Kruskal–Wallis test, $P = 0.076$) (Fig. 2i).

3.3. Relationships between soil environmental factors and root morphological traits

Vertical distributions of both FRMD and FRLD were positively correlated with total N (Fig. 3c, d) and Ca^{2+} concentrations, and negatively correlated with pH and C/N ratio (Table 1). The FRMD had a positive correlation with soil water content but no correlation

was found between FRLD and soil water content (Fig. 3a, b, Table 1). Vertical distributions of SRL and SRA were positively correlated with C/N ratio and negatively correlated with total N, but no relationship was found with other soil environmental factors (Table 1).

Canonical correlation analysis (Fig. 4) showed that the correlation for the first factor was significant ($F1: R = 0.87, P < 0.001$; $F2: R = 0.32, P = 0.597$). The redundancy analysis indicated that the first and second factors explained 45% of the relationship from soil environmental factors to root morphological traits where the first factor alone explained 44%. Total N for the soil environmental factors as well as FRMD for the root morphological traits mainly explained the variance of the first factor; the second factor was mainly explained by C/N ratio as well as SRA (Table 2). The canonical correlation analysis also indicated a strong positive association of FRMD with soil total N concentration as well as a positive association of SRA with soil C/N ratio (Fig. 4). Stepwise multiple

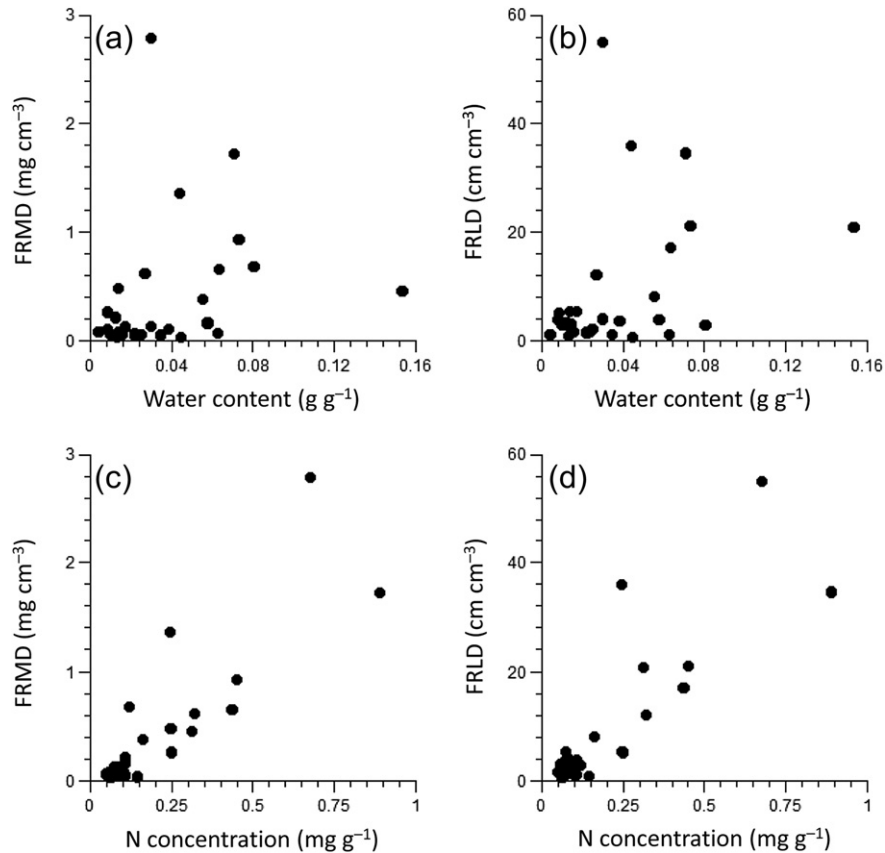


Fig. 3. Relationships of each of fine root mass density (FRMD) and fine root length density (FRLD) with soil water content (a, b) or total N concentration (c, d) in the *T. ramosissima* stand in the Lower Virgin River, Nevada.

linear regression confirmed that changes in total N concentration significantly affected the variations in both FRMD ($R^2 = 0.736$, $P < 0.001$) and FRLD ($R^2 = 0.715$, $P < 0.001$) and C/N ratio significantly influenced SRA ($R^2 = 0.197$, $P = 0.014$).

4. Discussion

Fine roots are concentrated near the soil surface in most ecosystems (Schenk, 2008) including some arid zones (February and Higgins, 2010; Gwenzi et al., 2011; Zhou and Shangguan, 2007). In our study area, located near the Virgin River in the Mojave Desert, however, *T. ramosissima* fine roots were concentrated below the soil surface; only 3% of fine root length and biomass between 0 and 200 cm depths were observed in the upper 20 cm and more than 60% were located at depths between 20 and 60 cm. Uncharacteristically low root biomass in the top 20 cm has been found in deserts, savanna, grassland and dry forests during growing seasons (Schenk and Jackson, 2002). The low root length and biomass at the top 20 cm soil layer in this study is likely because soil moisture and

N concentrations were relatively low at the soil surface. The soil moisture was comparable to an air-dry soil water content of 0.005 g g^{-1} . A linear reduction of fine root growth with decreasing soil moisture at less than field capacity has been reported for *Populus alba* cuttings (Imada et al., 2008). It was also found that 10% of the total fine root biomass was concentrated deeper than 150 cm and 6% of the total fine root biomass was at the bottom 10 cm (190–200 cm depth layer) of the pits. The species appears to produce fine roots to acquire soil resources from upper and deeper horizons at this site.

Fine root distribution is largely influenced by soil resource availability (Bennett et al., 2002; Drew, 1975; Eissenstat and Caldwell, 1988; Hodge, 2004; Imada et al., 2008; Iverson, 2010; Zhou and Shangguan, 2007). In this study, both fine root length and biomass were strongly and positively correlated with total N concentration in the soil, although other soil factors may have influenced the fine root distribution. This observation was also supported by the canonical correlation analysis of fine root properties and soil environmental conditions. Fine roots tend to

Table 1

Spearman rank correlation coefficients between each of fine root mass density (FRMD), fine root length density (FRLD), specific root length (SRL) and specific root area (SRA) and soil water content (WC), pH, electrical conductivity (EC), soluble ion (Ca^{2+} , K^+ , Mg^{2+} and Na^+) concentrations, total N concentration (total N), and C/N ratio in each soil layer for all three sampling pits in the *T. ramosissima* stand in the Lower Virgin River, Nevada.

| | WC (g g^{-1}) | pH | EC (dS m^{-1}) | Ca^{2+} (mg L^{-1}) | K^+ (mg L^{-1}) | Mg^{2+} (mg L^{-1}) | Na^+ (mg L^{-1}) | Total N (mg g^{-1}) | C/N ratio |
|-------------------------------------|--------------------------|-----------|---------------------------|---|-------------------------------------|---|--------------------------------------|--------------------------------|-----------|
| FRMD (mg cm^{-3}) | 0.424* | -0.654*** | 0.004 | 0.634*** | 0.287 | 0.005 | -0.154 | 0.698*** | -0.618*** |
| FRLD (cm cm^{-3}) | 0.352 | -0.677*** | -0.076 | 0.596** | 0.203 | -0.001 | -0.131 | 0.658*** | -0.529** |
| SRL (m g^{-1}) | -0.163 | 0.165 | -0.024 | -0.152 | -0.116 | 0.158 | 0.147 | -0.414* | 0.375* |
| SRA ($\text{cm}^2 \text{g}^{-1}$) | -0.162 | 0.303 | 0.062 | -0.255 | -0.117 | 0.212 | 0.228 | -0.566** | 0.501** |

N = 30. Marked correlations are significant at $P < 0.05^*$, $P < 0.01^{**}$ and $P < 0.001^{***}$.

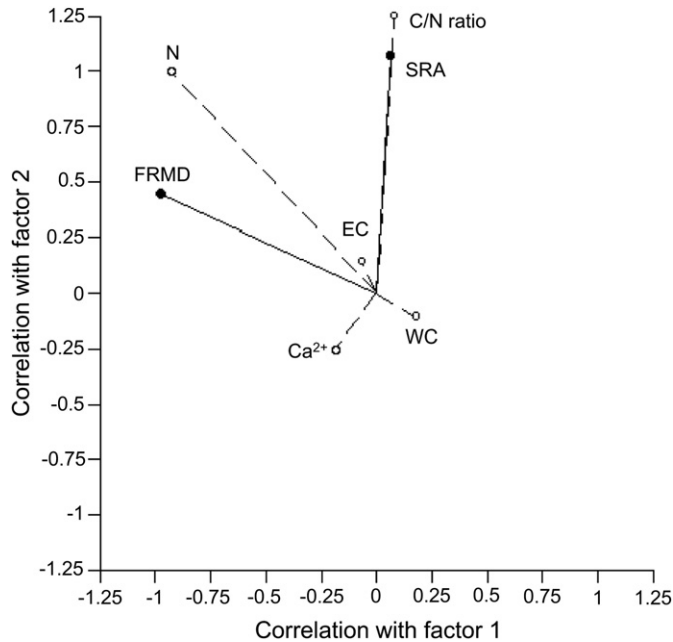


Fig. 4. Canonical correlation between root morphological traits (fine root mass density, FRMD; specific root area, SRA) and soil properties (water content, WC; electrical conductivity, EC; soluble ion Ca^{2+} concentration; total N concentration, total N; C/N ratio) in the *T. ramosissima* stand in the Lower Virgin River, Nevada.

proliferate at a zone with high N concentration (Drew, 1975; Eissenstat and Caldwell, 1988; Hodge, 2004) in order to capture more N from the zone (Hodge, 2004). *T. ramosissima* is likely to distribute its fine roots at the layers where N concentrations were higher, since soil N concentration is associated with organic matter pool (Jobbágy and Jackson, 2001). Our result is consistent with previous findings indicating that soil N concentration was closely related to fine-root distribution patterns of tree and grass species in a broad-leafed woody savanna (February and Higgins, 2010) and roots of native shrubs in the Mojave Desert (Garcia-Moya and McKell, 1970).

Soil moisture had a weak but positive relationship with fine-root biomass. It has been reported that *Tamarix* acquired water from both groundwater and vadose zone moisture when depth to water table was around 3 m or shallower (Busch et al., 1992; Nagler et al., 2008; Nippert et al., 2010). Since water table depth observed near the site was 2.1 m in summer 2010, although the 2009 summer was drier than 2010, the peak soil water content at the 200 cm depth was probably derived from capillary fringe of groundwater (Mahoney and Rood, 1998; Nagler et al., 2008). In contrast, high soil water contents between 60 and 120 cm depths in the site suggest that the soil moisture values at these depths were likely the result of hydraulic redistribution, which is the passive movement of water

Table 2

Correlations between the variables (soil environmental factors and root morphological traits) and their respective canonical variables.

| Variables | F1 | F2 |
|---|--------|--------|
| <i>Soil environmental factors</i> | | |
| WC (g g^{-1}) | -0.318 | 0.068 |
| EC (dS m^{-1}) | 0.082 | 0.209 |
| Ca^{2+} (mg L^{-1}) | -0.527 | -0.047 |
| Total N (mg g^{-1}) | -0.987 | 0.066 |
| C/N ratio | 0.643 | 0.716 |
| <i>Root morphological traits</i> | | |
| FRMD (mg cm^{-3}) | -0.998 | 0.058 |
| SRA ($\text{cm}^2 \text{g}^{-1}$) | 0.416 | 0.909 |

from moist to dry soil layers via root systems (Caldwell and Richards, 1989; Caldwell et al., 1998; McCulley et al., 2004). Aanderud and Richards (2009) showed high drying–rewetting cycle in soil stimulated decomposition rates of root litter in summer. Armas et al. (2012) reported that hydraulic redistribution played a positive role in organic matter decomposition, N cycling and N uptake by plants. This hydraulic process also possibly enhances fine root activity (Caldwell et al., 1998) and mobilizes nutrients at the depth where water is provided (McCulley et al., 2004). Thus, the water in the upper soil layers driven probably by root systems may enable the plant to capture N from the soil where N concentration was higher. Dawson and Pate (1996) reported that woody phreatophytic plants derive the majority of their water from deep sources of water during dry seasons. We surmise that while *T. ramosissima* acquired large amounts of water from groundwater, hydraulic redistribution was responsible for the acquisition of N from the upper soil layers.

In arid regions, high salinity and pH associated with soil drying possibly limit fine-root growth and its vertical distribution (Gwenzi et al., 2011; Rewald et al., 2011). In our study, soil pH was negatively correlated with the fine root length and biomass of *T. ramosissima*, which is consistent with the finding that root biomass was very low at soil layers with high pH, probably due to alkalinity-induced root growth limitation (Gwenzi et al., 2011). In contrast, soil salinity did not appear to have any effect on fine root distribution, although EC of soil was up to 8 dS m^{-1} , suggesting that the plant could maintain its fine roots under moderately saline conditions. This maintenance of fine roots may be an important mechanism of this species to tolerate saline environments, which is inconsistent with the strategy of many deep rooted perennials to avoid accessing highly saline water near the surface by using deeper soil water during dry periods (Bennett et al., 2009).

Our canonical correlation analysis also suggested that soil C/N ratio was related to specific root length and specific root area, and this is supported by the multiple regression analysis showing that soil C/N ratio was the only significant predictor of specific root area. One possible explanation of the relationship between C/N ratio and specific root area is that soil C/N ratio indirectly influenced the fine root morphology. A high soil C/N ratio induces an increase in N demand for soil microbes (Lovett et al., 2002). In order to compete for limited N with soil microbes, the plant might increase the surface area of fine roots (Jackson et al., 2008; Schimel and Bennett, 2004). However, the relationship between inorganic N concentration and the fineness of fine roots remains unclear and requires further study.

In conclusion, we found that *T. ramosissima* distributed fine roots at shallower and deeper layers in the stand during a dry season. Soil N concentration was strongly and positively correlated with fine root length and biomass, suggesting that the fine root distribution may be influenced by soil N availability. Soil moisture had a weak but positive correlation with fine-root biomass, suggesting the existence of hydraulic redistribution of water from aquifer to upper dry soil layers through root systems (Caldwell and Richards, 1989; Caldwell et al., 1998), which may enable the uptake of N from the soil during dry seasons (Armas et al., 2012). *Tamarix* have higher N content in leaves compared to native riparian phreatophytic tree species during dry seasons (Hultine and Bush, 2011; Pataki et al., 2005) and can maintain constant photosynthesis rates unlike those species during periods of soil drought (Nippert et al., 2010). The ability to maintain N levels in leaf tissue and constant physiological functioning of *T. ramosissima* in dry seasons may be explained by the pattern of fine root distributions concentrated in layers with higher soil N content, which may contribute to an increase in uptake of N from soil. This might be an important advantage of *T. ramosissima* over native species in the

riparian areas of the southwestern United States. However, our observations were only made during a dry year. Investigating temporal variations in fine root distributions and relationships to soil resource availability are necessary for better understanding of soil water and nutrient use characteristics for this species.

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