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Spatio-temporal Dynamics of Root Mass Density in a Coastal Dune in Subarctic Quebec, Canada†

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ABSTRACT

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On coastal dunes, both plant community composition and abiotic factors change along the foredune-established dune sequence. However, little is known about changes in belowground biomass, particularly in root mass, along such gradients. Yet, belowground plant structures are important for substrate cohesiveness and coastal dune integrity. Using soil cores, we determined the spatio-temporal dynamics of root mass density, from the embryo dunes to the stabilised dunes, on a coastal dune system in subarctic Quebec, Canada. Root mass density varied along the gradient, but it did not show a monotonic increase as observed in other studies. Roots were concentrated in the upper layer of the substrate (0-20 cm), except on the embryo dunes where most of the roots were found at 20-60 cm below the surface. Root mass density did not differ among the first three sampling dates (18 June, 07 July and 25 July), probably as a consequence of early root growth in the spring. However, root mass significantly decreased in August at all depths. Root mass density was not significantly correlated with soil water content, but it was correlated negatively with soil pH, and positively with total salts. Because root mass is concentrated near the substrate surface, subarctic coastal dunes may be particularly susceptible to human disturbance, such as trampling.

ADDITIONAL INDEX WORDS: *Primary succession, fine roots, temporal pattern, spatial pattern.*

INTRODUCTION

On coastal dunes, the gradient from the upper beach to the stabilised dunes can reasonably be thought to represent a chronosequence from the initial colonisation to the older, relatively stable and self-sustained stages. Therefore, for ecologists, coastal dune systems epitomise the concept of succession, and many studies have considered plant community structure and species turnover on coastal dunes at various latitudes (DOING, 1985; HESP, 1991; JOHNSON, 1997; HENRIQUES and HAY, 1998). In contrast, information on the belowground community structure and, in particular, on the distribution of roots is scarce (WATERMAN, 1919).

From a geomorphologic point of view, coastal dunes are very dynamic landscapes mostly because of the strong winds to which they are exposed and of the high mobility of their substrate. There, vascular plants reduce wind velocity and cause sand sedimentation. The roots of vascular plants contribute to sand cohesiveness and thus reduce greatly wind erosion (FORSTER and NICOLSON, 1981). The spatial distribution of the roots, both vertically and horizontally, likely influences the cohesiveness of the sandy substrate along the foredune-stabilised dune sequence (see several chapters in NORDSTORM *et al.,* 1990). Furthermore, belowground biomass represents a large part of the total production in most ecosystems (NEIL, 1992) and provides the primary input of organic carbon in soils (GOSS, 1991). Yet, few studies have dealt with the spatial variations of root mass density along the foredune-stabilised dune gradient.

In plant communities, root mass density varies with species composition (JACKSON *et al.,* 1996). Because the vegetation structure progressively changes along the upper beach-stabilised dune gradient on coastal dunes (*e.g.* HUNDT, 1985; OLFF *et al.,* 1993), root mass may be expected to change similarly (CONN and DAY, 1993; OLFF *et al.,* 1993; CONN and DAY, 1997). Furthermore, root vertical distribution, an important element of belowground processes (WATERMAN, 1919; JACKSON *et al.,* 1996), differs among plant species, and may thus be expected to vary along the sequence (CONN and DAY, 1993). Root mass may also show some pattern through time, as does aboveground biomass. Indeed, aboveground and belowground growth during the season should be correlated to one another. Temporal patterns in root mass density should also be influenced by the dynamics between growth and decay through time.

Various soil characteristics, such as pH and moisture, affect root growth and decay (GREGORY, 1987; VOSKO, 1991; CONN and DAY, 1997). On coastal dunes, along the inferred successional sequence, soil characteristics usually vary. For instance, patterns of primary production lead to an increase in soil organic matter, which contributes to increase soil moisture and decrease soil pH (OLFF *et al.,* 1993; BERENDSE

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et al., 1998). Furthermore, total salt content, another abiotic factor affecting root growth (MISTRIK *et al.,* 1992), decreases with distance from the beach, mostly in relation to decreasing salt spray (HESP, 1991). These abiotic factors may also be expected to vary with depth and through time.

The primary objectives of the present study were to (i) investigate the horizontal and vertical patterns of root mass density along a natural sequence representing a primary sere on a coastal dune system, (ii) to determine the temporal variation of these spatial patterns over one growing season, and (iii) to determine the relation between root mass density and substrate pH, total salt content and moisture.

METHODS

Study Site

The study was conducted on a dune system in Subarctic Quebec, near the village of Kuujjuaraapik (55°17′N, 77°46′ W), on the east coast of Hudson Bay. This coast is subjected to isostatic uplift at a rate of 1 m per century, resulting from the retreat of the Laurentide ice sheet (ALLARD and TREMBLAY, 1983). In the study area, sedimentary processes due to the estuary of the Grande Rivière de la Baleine lead to foredune development. Near the mouth of the river, the dune system advances towards the bay at a rate of 0.5 m/yr., and, on average, one ridge develops per 100 yrs (RUZ and ALLARD, 1994). The dune system we studied is ca. 5 km from the mouth of the river. It is ca. 2 km long, has a global NE-SW orientation and the chronosequence develops along a NW-SE axis. Mean annual temperature is −4.5°C, and the frost free period lasts ca. 77 days. Annual precipitation averages 615 mm, of which 40% falls as snow (ATMOSPHERIC ENVIRONMENT SERVICE, 1993).

The Chronosequence

In June 1997, nine transects perpendicular to the shoreline and 10 m apart were marked. The transects started from the upper part of the beach and continued 105 m towards the stabilised dunes and treeline. Along each transect, eight positions 15-m apart were defined, *i.e.* distance 0 m to distance 105 m from the embryo dunes. The successional sequence has been extensively described by BOURNERIAS and FOREST (1975). Here, we just described the trends. On the upper part of the beach (distance 0 m), embryo dunes are initiated by the perennial *Honckenya peploides* (Caryophyllaceae). The foredune is ca. 15 m from the embryo dunes and is colonised by *Leymus mollis* (Poaceae) and *Lathyrus japonicus* (Fabaceae). Both species are dominant along the foredune-stabilised dune gradient, although their density varies spatially. The crest of the foredune is at a distance of 30 m from the embryo dunes, and *Leymus mollis* and *Lathyrus japonicus* still are dominant species. Farther inland (distance 45 m), species such as *Achillea millefolium* and *Festuca rubra* are abundant. At a distance of 60 m to 105 m from the embryo dunes, the substrate is mostly covered by lichens (*Cladina* spp.) and mosses (*Polytrichum* spp.), but vascular plant species are still present. Along the 105-m sequence, from the embryo dunes to the lichen and moss-covered dunes, 20 plant species have been recorded during summer 1997 (Imbert and Houle 2000). All of them, except *Rhinanthus minor* spp. *borealis,* are herbaceous perennials and have either a tap root or a rhizome as perennating organ.

Data Collection

Because of the presence of an all-terrain vehicle path, four transects had to be shortened: two transects were 75-m long (six positions) and the other two were 90 m in length (seven positions). The five other transects were 105-m long (eight positions). Along the transects, at each position, we marked one 1-m^2 quadrat. Soil samples were taken with a root auger (diameter 6.16 cm, surface 29.8 cm^2) on four occasions : 18 June, 7 July, 25 July, and 13 August in 1997. We sampled five depths: 0–20, 20–40, 40–60, 60–80 and 80–100 cm. Root mass (live roots) was determined from a 100-cm^3 subsample of the thoroughly mixed 596-cm^3 sample from each depth, position and transect. After sorting, live roots were rinsed free of soil and dried at 75°C for 36 hours. Rhizomes were not considered in this study since it would have required substantially larger soil samples.

Another soil subsample was analysed for moisture (mass difference between fresh and dried material), pH and total salts (TDS). For pH and TDS determinations, 70 cm^3 of distilled water were added to 17 cm^3 of soil. The mixture was stirred regularly over a 12-h period before measurements were made with a portable meter (M-90, Corning Inc., New York).

Data Analysis

The sampling design followed the assumption of the split-split plot design, with transects representing the main plots, distances from the embryo dunes representing the sub-plots, and depths as the sub-sub plots. Temporal and spatial variations for abiotic variables and root mass were assessed using analyses of variance for repeated-measures (ANOVAR). In the ANOVARs, we used the GREENHOUSE-GEISSER correction to compute the *P*-value for the time effect and its interactions with the other factors (see LITTELL *et al.,* 1991; VON ENDE, 1993).

For each sampling date, Pearson correlation coefficients between root mass density and soil pH, TDS and water content were computed using the original data set. As previously discussed, soil characteristics are suggested to affect root mass. However, some indirect relations are expected among root mass density and soil characteristics. For instance, because of decreasing salt spray, total salts in the soil should decrease with increasing distance from the upper beach. Therefore, distance from the upper beach may affect both root mass and soil characteristics, and cause indirect relations between them. The same reasoning holds for the vertical distribution of roots and soil characteristics. Thus, for each variable and each sampling date, residual values were computed from a linear model including transect, position and depth as factors, but excluding time. The distance and depth effects were thus removed, and residual values were used to compute the correlations.

To fulfil the assumptions of normality and homogeneity of

Table 1. *Results of the repeated-measures analysis of variance for root mass density in a coastal dune system in Kujjuaraapik, Northern Québec. The data were log-transformed prior to analysis. For the time factor and the interactions involving time, the probability associated with the F-value was computed using the GREENHOUSE-GEISSER correction (G-G epsilon is 0.90). For details see the section on data analyses.*

Source of Variation	DF	MS	F	*P*
Time	3	21.14	52.85	<0.001
Error	627	0.40		
Transect	8	3.51	0.74	0.65
Distance	7	117.22	24.72	<0.001
Error(Transect × Distance)	46	4.74		
Depth	4	114.93	201.63	<0.001
Depth × Distance	28	7.90	13.85	<0.001
Error(Transect × Distance × Depth)	209	0.57		
Time × Transect	24	2.04	3.45	<0.001
Time × Distance	21	1.96	3.32	<0.001
Error(Time × Transect × Distance)	138	0.59		
Time × Depth	12	0.43	1.07	0.38
Time × Depth × Distance	84	0.55	1.37	0.026
Error	627	0.40		

variances, root mass density and salinity data were log-transformed. No transformation was required for the other variables. All statistical analyses were performed using the SAS statistical package (version 6.10, SAS Inc., Cary NC).

RESULTS

We sorted 1,255 soil samples, each of 100 cm^3, and collected 141.4 g of dry root. The average root mass density was 112.70 mg per 100 cm^3 (SE 4.65, range: 0–1,132.7 mg), which represents 225.00 g per m^2 for 20-cm deep cores. Root mass density changed over the growing season (significant time factor, Table 1). The first (18 June, mean 140.68 mg, SE 11.56), second (7 July, mean 115.83 mg, SE 8.62) and third samples (25 July, mean 134.05 mg, SE 10.44) did not differ significantly from one another, but all three differed from the fourth sample (13 August, mean 58.79 mg, SE 3.70, Figure 1). Overall, root mass clearly changed with distance from the embryo dunes (Table 1): it was low on the upper part of the beach (distance 0 m), increased up to about 45 m from the embryo dunes; and then decreased (Figure 1). This spatial pattern along the sequence was not constant over time (significant time×distance interaction, Table 1), and for the last sampling date (13 August) variations along the sequence were less apparent (Figure 1d).

Most of the roots (48.3 ± 3.5%, mean ± SE) were found in the upper layer (0-20 cm, Figure 1) while only 20.2 ± 6.2% of the total root mass was in the 20-40 cm layer (Figure 2). However, vertical distribution changed with distance (significant depth×distance interaction, Table 1). On the stabilised dunes, root mass was concentrated in the upper layer (Figure 2), but on the embryo dunes (distance 0 m) and the foredune (distance 15 m), root mass was higher in the 20-40 and 40-60 cm layers (Figure 2). The vertical distribution of the roots also changed over the season (significant time × depth × distance interaction, Table 1). In particular, on the foredune (distance 15 m), the proportion of roots in the upper layer (0-20 cm) increased over the season from 16.7 ± 6.7 to 36.9 ± 4.1%, while it tended to decrease on the stabilised dunes (Figure 2).

Mean values of pH and TDS, over the four sampling dates, decreased with increasing distance (between-distance factor: $F_{7,46}$ = 51.86, and $F_{7,46}$ = 14.77, respectively, with $P < 0.001$ for both values, Figures 3a and b), while water content increased ($F_{7,45}$ = 3.65, P = 0.02, Figure 3c). Soil characteristics also varied with depth (Figure 3). Samples from the surface (0-20 cm) had a lower pH (between-depth factor: $F_{4,28}$ = 265.99, $P < 0.0001$, Figure 3a) and a higher salt content ($F_{4,28}$ = 285.72, $P < 0.0001$, Figure 3b) than samples at greater depths. However, this vertical pattern changed according to distance from the embryo dunes (significant interaction between the factors depth and distance, $P < 0.001$, Figures 3a and b). There was a clear vertical pattern in soil water content on the upper beach (distance 0 m), but not on the stabilised dunes (Figure 3c); while the depth factor was marginally significant ($F_{4,159}$ = 2.31, P = 0.059), the interaction distance × depth was highly significant ($F_{28,159}$ = 2.61 $P <$ 0.001). The time factor was significant for all three soil variables ($P < 0.001$): pH decreased (mean 6.13 in 18 June and 6.06 in 13 August), and TDS increased (from 8.51 mg/L to 9.52 mg/L) over the season. There were also some variations in soil water content, but no general trend was evident (mean values of 34.06, 28.06, 36.03 and 31.08 mg per gram of fresh soil, respectively, for each of the four sampling dates). The time × distance interaction was not significant for either one of the three variables ($P > 0.66$), but the time × depth interaction was significant ($P < 0.01$). The time × depth × distance interaction was significant only for TDS ($P < 0.001$).

Dry root mass density was negatively correlated with pH for the second (07 July) and third (25 July) sampling periods, and positively correlated with TDS at all four sampling dates (Table 2). The linear model used to describe variation in root mass density accounted for more than 80% of the total variance, as it did for pH and TDS (Table 2). Using the residual values, some correlations remained significant. For instance, root mass density and pH showed a significant negative correlation at the second and third sampling dates (Table 2). There was no significant correlation between root mass density and soil water content.

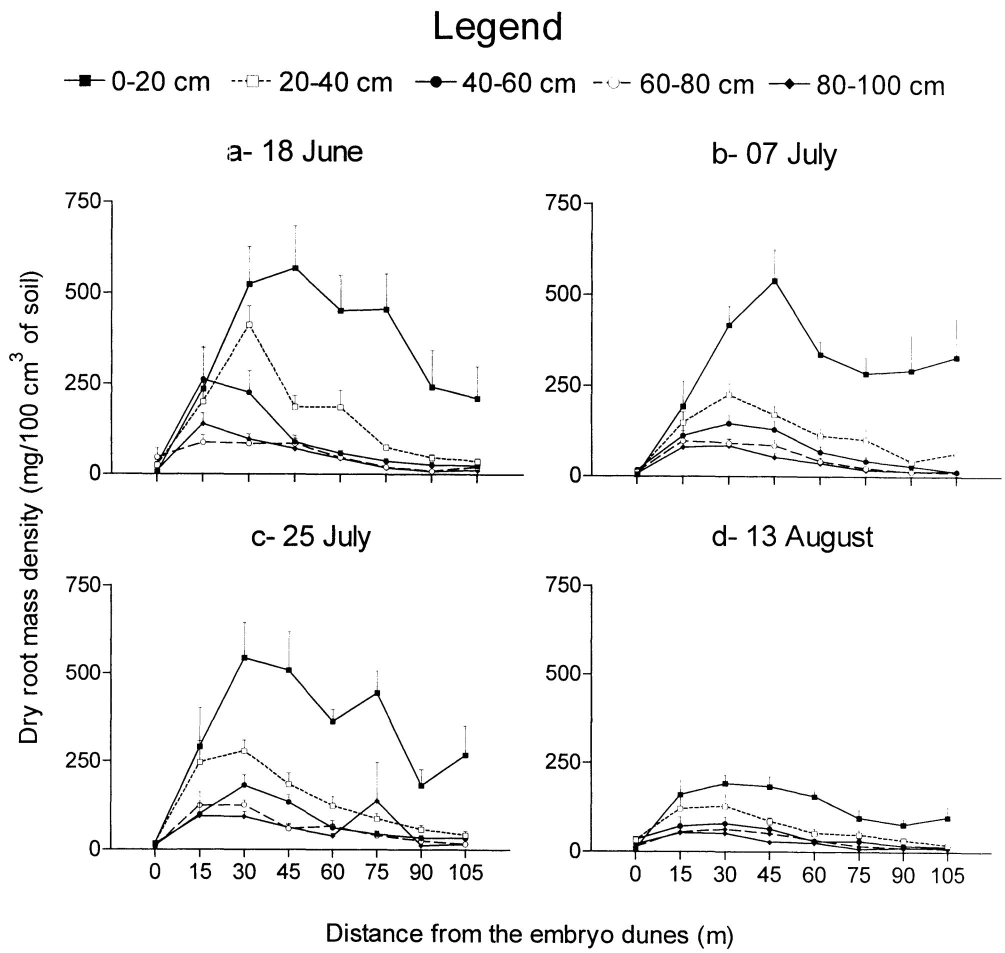

Figure 1. Mean root mass per 100 cm^3 (+ 1 SE) at different depths (cm) and distances from the embryo dunes (m) at four sampling dates, in a coastal dune system in Kujjuaraapik, Northern Quebec.

DISCUSSION

Root mass density varies significantly among terrestrial biomes and is usually low in ecosystems with low primary production, such as deserts and tundra (JACKSON *et al.,* 1996). Our study was performed on a coastal dune in the Subarctic of northeastern North America where climatic conditions reduce the length of the growing season and, consequently, limit primary production. In comparison to data collected in coastal dune systems at lower latitudes (CONN and DAY, 1993; OLFF *et al.,* 1993), the root mass values we obtained were low. Yet, consistent with changes recorded in the plant community along the sequence (IMBERT and HOULE, 2000), root mass density varied with distance from the embryo dunes; however, the pattern was not simple.

On sandy coasts where there is a sequential change in the dominant life-form during succession, root mass typically increases from the foredune to the established dunes. This is most likely because annual species typical of the high beach and foredune have low belowground biomass while perennials which are dominant on the stabilised dunes have an extensive root system and well-developed belowground perennating organs (CONN and DAY, 1993; OLFF *et al.,* 1993). In the coastal dune system we studied, no monotonic increase in root mass was observed along the sequence and all but one of the species were perennials. The increase in root mass density between the upper beach and the foredune was associated with an increase in aboveground biomass and plant density, following initial colonisation. Belowground biomass reached a maximum on the crest and the landward flank of the foredune (distance 30 m and 45 m from the embryo dunes), where the plant community was dominated by *Leymus mollis* and *Lathyrus japonicus.* Farther inland, plant composition changed (BOURNERIAS and FOREST, 1975) and root mass density decreased. On the stabilised dunes, the substrate was mostly covered -up to 80%- by non-vascular species (mosses and lichens) and therefore root mass decreased as the proportion of vascular plant species declined.

Sandy soils are known to be nutrient-poor (WILLIS, 1963; KACHI and HIROSE, 1983; SYKES and WILSON, 1991); on such substrates, organic matter mineralisation greatly contributes to the nutrient budget of the plants (OLFF *et al.,* 1993; BERENDSE *et al.,* 1998). This role of nutrient supply from the or-

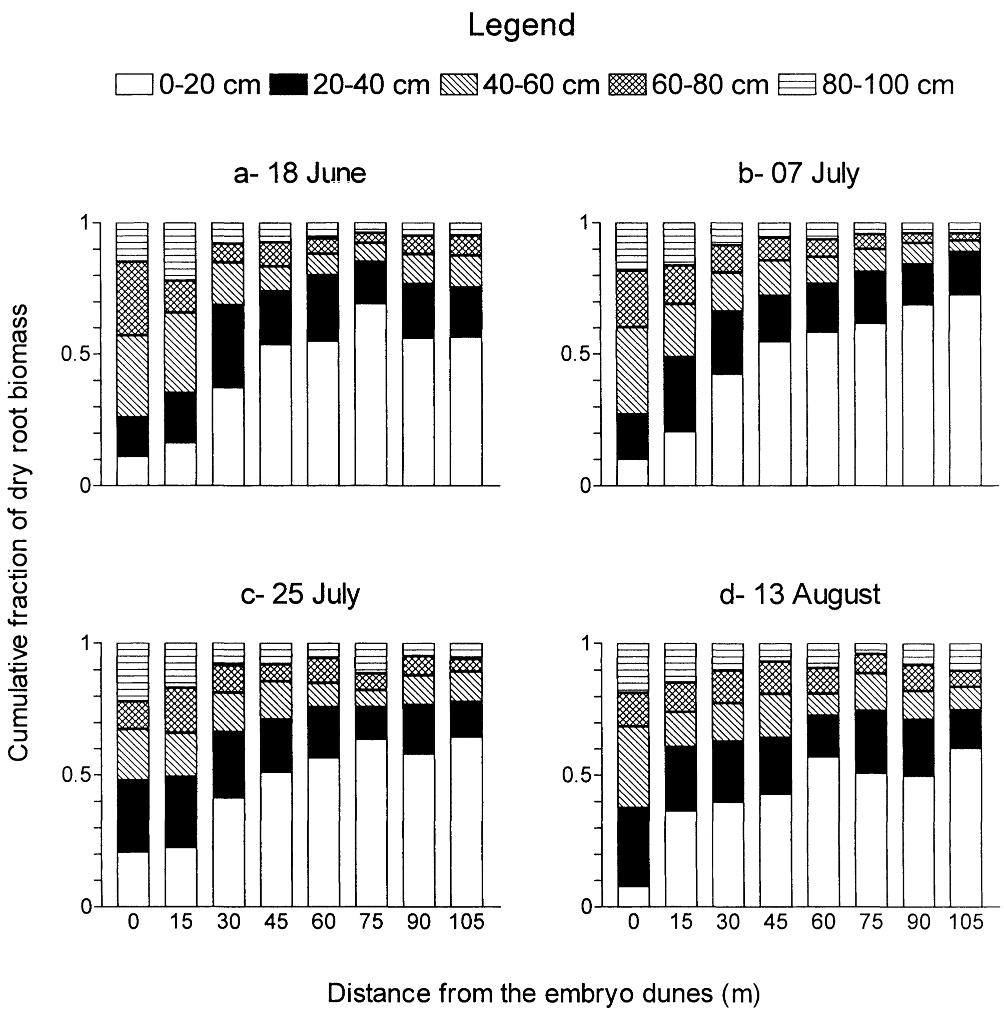

Figure 2. Cumulative fraction of root mass density at four sampling dates at different distances from the embryo dunes (m) and depths (cm), in a coastal dune system in Kujjuaraapik, Northern Quebec.

ganic matter was reflected, on our study site, by the concentration of the roots in the upper substrate layers where organic matter was concentrated (IMBERT and HOULE, 2000; see also: JACKSON *et al.,* 1996; STEVENSON and DAY, 1996). Root concentration in the upper layers was also related to the strictly herbaceous nature of the plant community. However, the vertical distribution of the roots changed through the season and along the sequence. For instance, on the embryo dunes, the proportion of root mass in the surface layer was small early in the season, but increased through the summer. In the Subarctic, most sand accumulation occurs during the fall and winter (RUZ and ALLARD, 1994), at a time when plant growth is not active. Thus, on the upper beach where sand accumulation is the greatest, it may take some time for the roots to occupy the newly deposited substrate.

Root growth has been proposed to increase as aboveground biomass accumulates through the growing season, making more demands for water and nutrients (STEVENSON and DAY, 1996). In the system studied, increased aboveground biomass and ramet density during the growing season were evident for the two dominant species, *Leymus mollis* and *Lathyrus japonicus* (IMBERT and HOULE, 2000). However, our results showed that root mass density did not increase between the first—18 June—and the third sample—25 July; this suggests that root growth occurred very early in the season as temperatures increased and that thereafter growth only compensated for decay (see also BELL and BLISS, 1978). By the end of August, root mass decreased, perhaps because of nutrient translocation to the rhizomes as the growing season ended.

Along the sequence we studied, substrate pH and total salts decreased, whereas water content increased. Such spatial changes in soil characteristics are similar to those reported for other dune systems at various latitudes (*e.g.* VAN DER VALK, 1974; SYKES and WILSON, 1991; HENRIQUES and HAY, 1992; CORDAZZO and SEELIGER, 1993). The originality of our results lies in the demonstration that soil characteristics also presented a vertical structure, with pH being lower

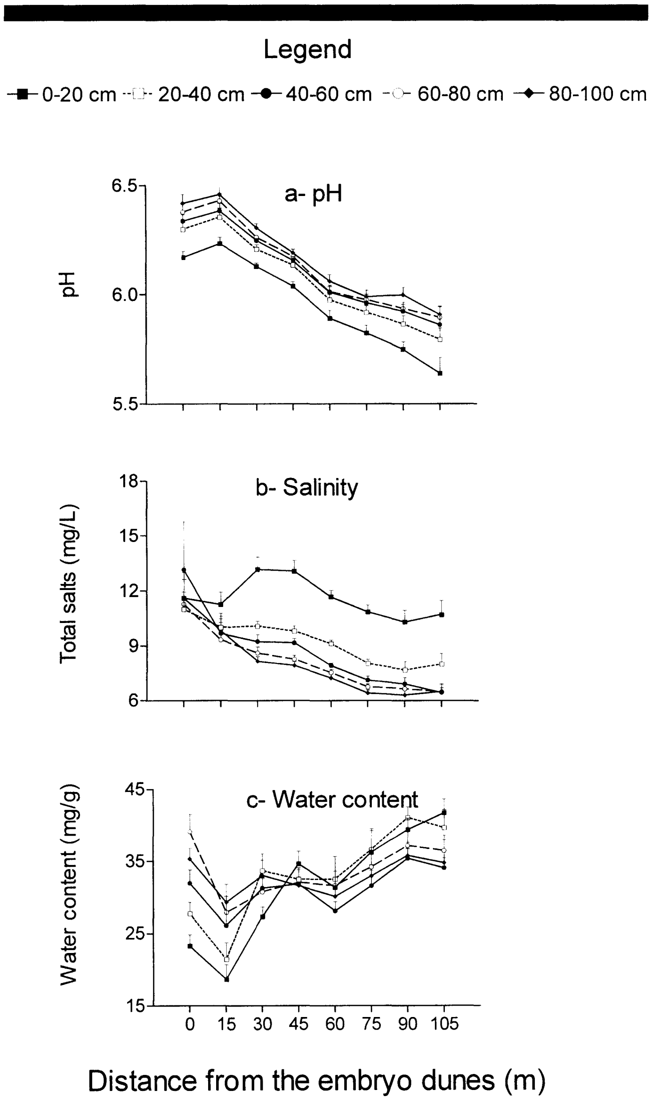

Figure 3. Mean values (+ 1 SE) for soil pH, total salts and water content at different distances from the embryo dunes (m) and depths (cm), in a coastal dune system in Kujjuaraapik, Northern Quebec.

and salt content being higher at the surface, and a temporal pattern, with pH decreasing and salt content increasing as the growing season progressed. These patterns in space and time were consistent with our initial hypotheses. For instance, soil pH decreased as organic matter increased both from the embryo dunes to the stabilised dunes and from deeper substrate layers to the surface. Micro-organism activity and organic matter accumulation contributed to lower pH values as the season progressed. Spatio-temporal patterns of total salts (mainly influenced by salt spray) and water content (equilibrium between rainfall, evapotranspiration and soil water capacity as affected by organic matter) also followed the expected patterns. Such spatio-temporal variations in soil characteristics affect both root growth and root decay (GREGORY, 1987; VOSKO, 1991). For instance, STEVENSON and DAY (1996) suggested that the position of the water table influenced root mass production in a barrier island. This was interpreted either as a positive effect—increasing water availability decreased root allocation—or a negative effect—saturated conditions decreased oxygen availability to the roots (see also GREGORY, 1987; DUMORTIER, 1990). In the present study, soil water content increased with distance from the embryo dunes and with depth, whereas root mass density generally decreased. However, no significant correlation was obtained between root mass and soil water content, either using the original data set or the residuals. Actually, mean values of water content ranged between 2% and 5%, which are typical values for coastal dunes (VAN DER VALK, 1974); such low variability could thus not explain the great variation we observed for root mass. Using residual values, root mass density was shown to be negatively correlated to pH on 7 July and 25 July, and positively correlated to TDS on 7 July. Because a correlation only reflects a statistical relation, we cannot suggest direct causal links between pH, TDS and root mass. However, our results suggest that further experiments should be performed under controlled conditions to investigate the effects of substrate characteristics on the root dynamics of the dominant species in this dune system.

CONCLUSION

By studying spatial changes in ecosystem characteristics along coastal dune sequences, we may be able to better understand coastal dune development over time. The present study provided original results on the temporal patterns of root mass density, along the inferred successional sequence. For instance, we showed that root mass was concentrated in the upper soil layers on the stabilised dunes. This particular feature emphasizes the fragility of coastal dunes, even at high latitudes, with regards to human perturbations. Indeed, when agents, such as all-terrain vehicles, disturb the substrate and destroy the root network, they destroy the most cohesive part of the dunes. Although most of the vascular plant species on the dune studied are perennials, rhizomes of these species usually occur below 20 cm. Rhizomes also have a role in dune stability, but fine roots are primordial for sand cohesiveness near the surface. Our study also demonstrated that root mass density did not increase monotonically along the sequence. Actually, root mass was at a maximum on the foredune, where the grass *Leymus mollis* has its greater density and biomass (IMBERT and HOULE, 2000).

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□ RÉSUMÉ □

Nous avons étudié la dynamique spatiale et temporelle de la masse racinaire dans une communauté végétale située sur une dune côtière du Québec subarctique. Contrairement à ce qu'ont montré les rares études sur ce sujet, nous n'avons pas

Table 2. *Pearson coefficient of correlation (and probability for H_0: $\rho = 0$) between root mass density and soil pH, total salts content (TDS), and water content for the four sampling dates. Coefficients have been computed first using the original data (ρ with root), and second using residual values (ρ between residuals) computed with the linear model: transect + distance + depth + transect×distance + distance×depth. The proportion of variance explained by the linear model, i.e. r^2 model, is given for each variable (all values are significant at P < 0.01). Root mass density and TDS data have been log-transformed prior to the analyses.*

	Sampling Date			
	18 June	7 July	25 July	13 August
Root mass density				
r^2 model	0.81	0.89	0.86	0.80
pH				
ρ with root	0.10 (0.06)	−0.18 (<0.01)	−0.11 (0.05)	0.10 (0.06)
ρ between residuals	0.005 (0.92)	−0.14 (0.01)	−0.12 (0.03)	0.08 (0.12)
r^2 model	0.94	0.93	0.94	0.95
TDS				
ρ with root	0.31 (<0.01)	0.42 (<0.01)	0.36 (<0.01)	0.39 (<0.01)
ρ between residuals	0.02 (0.70)	0.17 (<0.01)	−0.02 (0.77)	0.06 (0.27)
r^2 model	0.82	0.89	0.88	0.90
Water content				
ρ with root	−0.04 (0.42)	−0.05 (0.38)	−0.01 (0.79)	−0.08 (0.12)
ρ between residuals	0.07 (0.19)	0.08 (0.15)	−0.01 (0.77)	0.01 (0.83)
r^2 model	0.68	0.74	0.52	0.55

observé d'augmentation de la masse racinaire le long du gradient dunes embryonnaires-dunes stabilisées. De plus, nous avons montré que la plus grande partie de la masse racinaire se situe dans les couches supérieures du substrat, une caractéristique qui rend ce système très susceptible aux perturbations anthropiques. La masse racinaire n'augmente pas au cours de l'été, ce qui suggère que la croissance racinaire doit se faire très tôt au printemps. La densité de racines est faiblement corrélée au pH du sol et à la teneur totale en sels, mais pas à la teneur en eau.

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