Influence of root growth of two pioneering plant species on soil development during the initial stage of ecosystem genesis in the Lusatian post mining landscape

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Boldt, K., Schneider, B. U., Fritsch, S. and Hüttl, R. F. 2012. **Influence of root growth of two pioneering plant species on soil development during the initial stage of ecosystem genesis in the Lusatian post mining landscape**. Can. J. Soil Sci. **92**: 67–76. To characterize the role of root growth of *Lotus corniculatus* L. (bird's-foot trefoil) and *Calamagrostis epigeios* L. Roth (chee reed grass) in soil development during the initial stage of ecosystem genesis, the root systems of these plant species growing in soils from quaternary calcareous sediments were studied. The spatial distribution pattern of root systems varied considerably. Both plant species contributed to the accumulation of organic carbon in the bulk soil, although the highest concentrations were from the legume *L. corniculatus*. Total nitrogen concentration in the bulk soil was not affected, but increased in the rhizosphere soil of both plant species. There were clear indications that both plant species contributed to homogenizing phosphorus distribution, resulting in phosphorus depletion of those soil compartments where root proliferation was highest. Pronounced differences were detected between plant species, which led to the conclusion that the homogenizing effect caused by one species on a plot level may be overridden by the heterogeneity of patches composed of different plant species at the ecosystem level. All considered components suggest that the development of root systems of herbaceous pioneer plant species provides significant contributions to land reclamation in a natural way.

Key words: Monolith, root sampling, soil development, *Lotus corniculatus*, *Calamagrostis epigeios*, soil organic carbon

Boldt, K., Schneider, B. U., Fritsch, S. et Hüttl, R. F. 2012. **Impact de la croissance des racines de deux plantes pionnières sur le développement du sol pendant l'étape initiale de genèse d'un écosystème après exploitation minière, en Lusace**. Can. J. Soil Sci. **92**: 67–76. Les auteurs ont étudié le système racinaire du lotier corniculé (*Lotus corniculatus* L.) et de la calamagrostide commune (*Calamagrostis epigeios* L. Roth) poussant sur un sol contenant des sédiments calcaires du Quaternaire en vue de préciser le rôle des racines dans le développement du sol lors de l'étape initiale de la genèse d'un écosystème. La répartition des racines varie considérablement dans l'espace. Les deux espèces concourent à l'accumulation du carbone organique dans le sol brut, mais c'est au lotier, une légumineuse, qu'on doit la plus forte concentration. La concentration d'azote total dans le sol brut n'est pas affectée, cependant elle augmente dans le sol de la rhizosphère des deux plantes. Tout indique que les deux espèces contribuent à rendre la répartition du phosphore homogène, ce qui entraîne l'épuisement de cet élément dans les parties du sol où leurs racines prolifèrent le plus. Les auteurs ont décelé des variations prononcées entre les deux espèces, ce qui les incite à conclure que l'homogénéisation causée par une espèce dans une parcelle peut être compensée, au niveau de l'écosystème, par l'hétérogénéité observée aux endroits où poussent diverses espèces. Tous les éléments examinés laissent croire que le développement d'un système racinaire par les herbacées pionnières concourt de manière sensible à la restauration naturelle des sols.

Mots clés: Monolithe, échantillonnage des racines, développement des sols, *Lotus corniculatus*, *Calamagrostis epigeios*, carbone organique du sol

Opencast mining of coal, lignite, oilsands and minerals is a dominant economic factor in numerous countries worldwide. In Germany, lignite production from surface mining accounts for almost one-third of the national net energy supply (Deutscher Braunkohlen-Industrie-Verein e.V 2009) and is currently the largest world-wide (Bundesanstalt für Geowissenschaften und Rohstoffe 2009). Twelve mining areas, including the three main mining areas Rhineland, Central Germany and Lusatia, are currently actively managed. Since the beginning of mining activity in Germany until 2006 a total area of 1685 km^2 has been mined, with the greatest mining area (83 km^2) in Lusatia (Stoll et al. 2009).

Surface mining activities degrade a vast surface area comprising natural and managed landscapes, and cause profound disturbances to biological, chemical and physical soil properties (Ussiri 2006; Lorenz and Lal 2007). Due to the large aerial dimension of this disturbance and to the absence or slowness of soil rebuilding processes in the dumped overburden sediments, rapid and reliable reclamation is required to return economic and social functions.

Overburden sediments are generally characterized by deficiency in macronutrients, lack of organic matter, absence of microbial populations, elevated salt concentrations and low water retention capacity (Ussiri 2006). Hence, reclamation efforts are expected to re-establish or stimulate development of respective soil functions so as to foster conditions for successful revegetation of forest, agricultural and natural ecosystems (Barnhisel and Hower 1997; Bradshaw 1997). In the search for ecologically sound and economically effective optimization of reclamation efforts, in-depth studies on soil development and natural plant succession prior to alteration of mine site substrates may improve our understanding of key natural processes that trigger regeneration without anthropogenic influence. A broader understanding of these key processes in the initial phase of natural ecosystem development on sites prior to reclamation could also provide insights for developing successful reclamation technologies and strategies. Once these natural processes are elucidated, development of more advanced concepts to adapt and enhance them can take place.

The complexity of the soil system is determined by numerous interactions among physical, chemical and biological components and is modulated by prevailing environmental conditions (Buscot 2005). In the initial phase of soil development, formation of organic matter is mainly driven by an input of carbon compounds from root formation and subsequent turnover and by release of root debris (Walker and del Moral 2003). Uptake of cations from the rhizosphere and release of exudates may strongly alter the chemical environment at the soil root interface (El-Shatnawi and Makhadmeh 2001). The physical and chemical conditions of the soil will reciprocally influence the amount and distribution of roots. Therefore, how these two processes interact and which one is the prevailing factor in the initial phase of soil development are questions of importance to reclamation.

Over the years, there have been many studies on the effect of plant cover on soil properties of sandy soils (Su et al. 2005; Zhao et al. 2007). Differences among plants species dominating in the initial phase of succession need to be considered, including their specific morphological and physiological characteristics. Establishment of a plant community or cover and development of root systems significantly contribute to soil development. They may foster nutrient and water cycling and redistribution of nutrient pools. Root systems of primary vegetation thus form a prerequisite for further succession processes and development of soils. The objective of this study was to compare the distribution patterns of root systems of two pioneer plant species prevailing in the initial phase of ecosystem development on mine overburden and their effects on chemical properties of the bulk and rhizosphere soils.

MATERIALS AND METHODS

Study Site Description

The study was conducted on a post-mining experimental area within the opencast mining area of Welzow Süd about 30 km south of Cottbus in the State of Brandenburg, Germany. The area had been mined and the overburden soil, from quaternary calcareous sands, was rough dumped on the landscape and bulldozed about 1 yr prior to the study. The temperate, slightly continental climate of this study site is characterized by high summer temperatures and pronounced drought periods in the growing season. Average annual precipitation is approximately 595 mm and average annual air temperature is 9.3°C (Gerwin et al. 2011).

The soil substrate of the study area was characterized in concurrent studies by other researchers as part of a large-scale interdisciplinary research program. This soil developed from quaternary calcareous sands with a high proportion of medium (55.2%) and fine (32.6%) sands (Table 1). The silt and clay components were approximately 2%, indicating an extremely low water storage capacity. Soil texture of bulk soil was analyzed by wet sieving and fractionation according to the DIN ISO 11277 (2002) method on 20 g of each sample, after humus destruction and dispersion with sodium pyrophosphate. Clay is defined by particle sizes <2.0 µm, silt 2 to <63 µm and sand 63 to <2000 µm.

Weekly measurement of soil volumetric water in the immediate vicinity of the sampling areas for this study yielded values between 5 and 18% with lowest values for the topsoil and highest for the deeper soil layers (Gerwin et al. 2011). Soil bulk density showed little differences between top and deep soil layers indicating that soil physical conditions were quite homogeneous and that the substrate had not been compacted, which might have interfered with root development and proliferation.

Vegetation Establishment and Soil and Vegetation Measurements

Two abundant pioneer plants species, *Lotus corniculatus* L. (bird's-foot trefoil) and *Calamagrostis epigeios* L. Roth (chee reed grass) were studied under field conditions using three-dimensional high-resolution root sampling (monolith sampling). *Lotus corniculatus* is a perennial, dicotyledonous plant native to temperate

Table 1. Characteristics of the post-mining soil at the study site

Soil depth (cm)	Bulk density (g cm^{-3})	Sand (%)	Silt (%)	Clay (%)	Organic carbon (%)	Calcium carbonate (%)	PH
0–30	1.60±0.08	96.3	1.6	2.0	<0.01	0.82	8.5±0.08
30–60	1.57±0.03	94.9	2.4	1.8	<0.01	1.20	8.6±0.05

grasslands of Eurasia and North Africa. It belongs to the family *Fabaceae* (*Leguminosae*), which can form a symbiosis with *Rhizobia* and fix atmospheric nitrogen. *Calamagrostis epigeios* is a rhizomatous member of the family *Poaceae*, and occurs mainly in temperate regions of the northern and southern hemispheres.

Each plant species was seeded randomly by hand (seeds from Rieger Hoffmann GmbH, Stuttgart, Germany) in 2008 on a 10-m^2 area within the experimental site. Plants grew under completely naturally climate conditions. The experimental plots were kept free from invasive herbs by pulling any that grew several times a month.

Sampling of roots and soil started 1 yr after sowing in late April to early July 2009. Three areas per plant species, 50 × 50 cm in size, with different vegetation densities were randomly selected from the larger 10-m^2 areas. Vegetation densities (number of plants) selected were classified as low = 4–5 plants, intermediate = 6–7 plants and high = 8–11 plants. To obtain data on three dimensional distributions of roots and soil chemistry, the sampling was carried out in soil monoliths, 50 × 50 × 50 cm in size. The sampling design is depicted in Fig. 1. A pit was dug in front of each sampling area. Starting from the front of the monolith, there were 25 samples taken from each of the 0- to 10-cm, 10- to 20-cm and 20- to 30-cm depth increments and nine samples taken from each of the 30- to 40-cm and 40- to 50-cm depth increments. Sampling was done sequentially by hand with metal cuboids of 1 L volume, which were cut into the soil. The controls were unvegetated soil monoliths, sampled as described above, to compare soil conditions without the influence of plants. Samples (containing soil and roots) were transferred into plastic bags and immediately stored for 2–4 h in thermo boxes and subsequently in the laboratory refrigerator at 4°C for 1–4 wk until analyses.

Samples were air dried in open parchment paper bags for 3 wk in a separate room in the greenhouse and then passed through a 2-mm sieve and thoroughly mixed. This soil was designated as bulk soil. Roots were collected from the sieve and stored in plastic bags for 2 wk at 4°C. Soil adhering to the roots, the rhizosphere soil, was air dried for 5 min on the roots and then was gently removed from the roots with a brush and stored separately from bulk soil samples in small parchment paper bags for subsequent chemical analyses. After harvesting of rhizosphere soil, roots were cautiously washed. The roots were taken with forceps and rotated in a dish with deionised water. Water was exchanged several times in the cleaning process, and was checked by microscope to determine if the roots were soil free.

Root surface area, number of root branches and root length density were calculated for moist root samples using an Epson perfection V700 scanner at 400 dpi resolution and WinRHIZO software (Regent Instruments, Inc., QC, Canada, version 2009a) for digitalization and further processing of the images.

Soil pH of bulk and rhizosphere soil was measured in a 1 to 2.5 water extract (Meiwes et al. 1984). Total carbon and nitrogen of bulk and rhizosphere soil were determined using a CNS Analyser (Elementar Vario EL, Hanau, Germany) according to the DIN ISO 10694 (1996) method. Carbonate was determined by the gas volumetric carbonate method (DIN ISO 10693). Calculation of organic carbon was performed by subtraction of carbonate bound carbon in the soil samples from the total carbon.

Total water extractable phosphorus was determined from a 1 to 2.5 soil-water extract. Samples were shaken for 1 h then stored for 16 h at room temperature. After centrifugation for 5 min at $g = 3000$ rpm the supernatant was filtered (512 ½ folding filter, Whatman; Dassel, Germany) (Schlichting et al. 1995). Concentrations of nutrients in the water extract were detected by inductive coupled plasma spectrometry (iCAP 6000 series, Thermo scientific, Germany).

The total biomass (roots and shoots) of plants from each sampled monolith was determined. The shoot (above-ground) biomass of each monolith was cut off with a scissors just above ground level, then stored in closed plastic bags 2–4 h in thermo boxes and

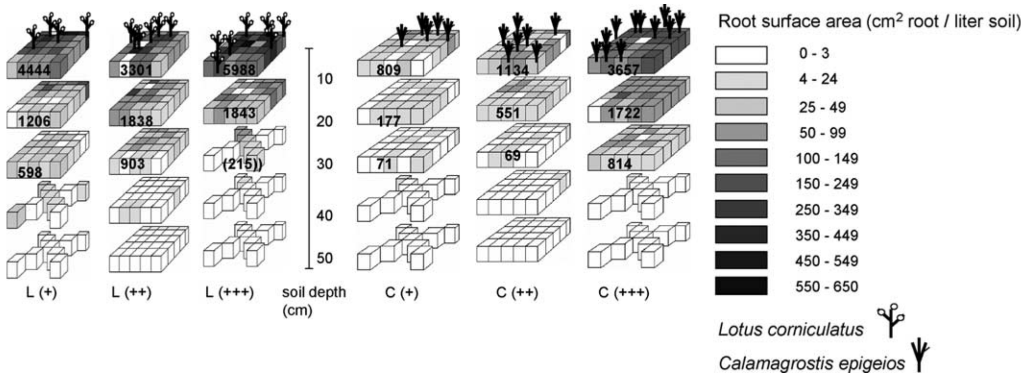

Fig. 1. Spatial distribution of root surface area of *Lotus corniculatus* (L) and *Calamagrostis epigeios* (C) (cm^2 L^{-1} soil) for high (+ + +), intermediate (+ +) and low (+) vegetation density. Total root surface area per full sampled soil layers are given by number.

subsequently in the laboratory refrigerator at 4°C for 1 d until analyses. Shoot biomass was oven dried at 65°C for 72 h. The corresponding root (below ground) biomass (see harvesting method above) were dried the same way. Biomass of roots and shoots were weighed separately to obtain total root and shoot biomass (g) per monolith.

Statistical Analyses

All variables were tested for normality (Kolmogorov-Smirnov) and for homogeneity of variance (*F*-test) for statistical validity of the results. Significances for organic carbon concentration of different vegetation densities (Fig. 3 A, B), pH differences between bulk and rhizosphere soil (Table 3) and the organic carbon ratio of bulk and rhizosphere soil between *Lotus corniculatus* and *Calamagrostis epigeios* (Table 4) were analyzed by student's *t*-test. Statistical analyses were carried out using SPSS Inc. (2008) Statistics 17.0.

RESULTS AND DISCUSSION

Root Distribution

Competition between shoots and roots for photosynthesis products plays an important role in the survival strategy of species that dominate in the initial phase of succession, and appears to be ruled by specific genotypes. However, the relationship between shoot and root growth (shoot-root ratio) may be strongly modified by external factors such as nutrient and water availability, light conditions, and heterogeneity of soil physical conditions and may even change during plant ontogenesis.

Total leaf area and root surface area were much higher for *Lotus corniculatus* than for *Calamagrostis epigeios* (Table 2). Correspondingly, a significantly higher ratio of total leaf area to total roots surface area was found for *Lotus corniculatus*. Root and shoot biomass of *Lotus corniculatus* differed little between the different vegetation densities. In comparision, root and shoot biomass of *Calamagrostis epigeios* were strongly affected by increases in intraspecific vegetation density. This might indicate plant species related adaptation strategies to plant densities and rooting of soils.

Figure 1 shows the three dimensional distribution of the root surface area for both plant species. Root surface area per volume of soil in the 0- to 10-cm depth increment was significantly higher for *Lotus corniculatus* than for *Calamagrostis epigeios* for all vegetation densities. Root proliferation to greater soil depths of 30–50 cm was similar for both species. Pronounced differences in root surface area between plant species were detected at high and low vegetation densities. Areas with higher vegetation density of *Lotus corniculatus* had 30% more root surface area than areas with low vegetation density. The same result was detected for *Calamgrostis epigeios*, although compared with *Lotus corniculatus*, root surface area of plants from the high-density vegetation area was nearly 80% greater than that of plants from low-density vegetation area. Further investigations on an adjoining area with similar soil conditions confirmed these results (data not shown).

Soil pH

Physical and chemical conditions may influence the vitality and proliferation of roots. In return, roots can affect their physical and chemical environment (Walker and del Moral 2003). Due to the calcium carbonate ($CaCO_3$) content (0.4 ± 0.28%) after mining of the quaternary overburden material, the initial pH (pH of unvegetated bulk soil in 2009) of the experimental area was weakly alkaline (Table 1). Average pH from the rhizosphere and associated bulk soil samples is shown for monoliths covered by *Lotus corniculatus* and *Calamagrostis epigeios* of different vegetation densities and for unvegetated soil in Table 3. Average soil pH was highest for substrates without plant cover. These results support those obtained from numerous studies showing that vegetation development in general, and root system development and activity in particular, induce a drop in soil pH and especially in rhizosphere pH (Hinsinger 1998; Dakora and Philipps 2002; Xu et al. 2006). These results clearly show that the decrease in pH of the bulk soil depends both on the plant species and the density of the vegetation cover and respective root density. This applies for both plant species, and is most pronounced in the densely rooted top soil horizon of samples taken from soil monoliths.

Table 2. Growth parameters for 2-yr old *Lotus corniculatus* (L) and *Calamagrostis epigeios* (C) plants

	Vegetation density[z]					
	L (+)	L (+ +)	L (+ + +)	C (+)	C (+ +)	C (+ + +)
Total shoot biomass (g)	11.96	8.93	12.35	0.53	2.12	9.34
Total root biomass (g)	13.35	14.80	17.32	1.69	13.44	13.53
Specific leaf area (cm^2 g^{-1})	179	179	179	136	136	136
Total leaf area (cm^2)	2140	1598	2214	72	288	1273
Total root surface area (cm^2)	6452	6427	8046	1057	1754	6272
Leaf projected area/root surface area ratio (relative units)	0.33	0.25	0.28	0.07	0.16	0.20

[z] Vegetation density: high (+ + +), intermediate (+ +), low (+).

Table 3. Bulk soil and rhizosphere soil pH from monoliths

		Vegetation density[z]						
Soil type	Soil depth (cm)	Control	L[y] (+ + +)	L (+ +)	L (+)	C[y] (+ + +)	C (+ +)	C (+)
Bulk soil	0–10	8.50 ± 0.11	8.11 ± 0.14	8.38 ± 0.12	8.45 ± 0.07	8.31 ± 0.06	8.46 ± 0.05	8.62 ± 0.06
	10–20	8.50 ± 0.10	8.51 ± 0.10	8.53 ± 0.07	8.65 ± 0.03	8.42 ± 0.07	8.50 ± 0.06	8.67 ± 0.04
Rhizosphere soil	0–10		7.62 ± 0.26	8.00 ± 0.20	8.06 ± 0.14	8.12 ± 0.18	8.19 ± 0.06	8.2 ± 0.11
	10–20		8.18 ± 0.18	8.23 ± 0.17	8.18 ± 0.24	8.23 ± 0.07	–	–
Difference in pH for bulk soil/rhizosphere soil	0–10		0.54 ± 0.26*a*	0.40 ± 0.17*a*	0.40 ± 0.18*a*	0.20 ± 0.15*b*	0.29 ± 0.08*b*	0.43 ± 0.07*a*
Difference in pH for bulk soil/rhizosphere soil	10–20		0.35 ± 0.20*b*	0.33 ± 0.14*b*	0.47 ± 0.24*a*	0.22 ± .10*b*	–	–

[y] L = *Lotus corniculatus*, C = *Calamagrostis epigeios*.

[z] Vegetation density: high (+ + +), intermediate (+ +), low (+).

a, *b* Means and standard deviation (±) are given in data. Within variables, measures with different letters are significantly different at $P \leq 0.01$; $n = 11$.

Soil pH was significantly higher in *Calamagrostis epigeios* samples than *Lotus corniculatus* samples, particularly in the upper 0–10 cm. Lowest soil pH was detected in the rhizosphere soil with a most pronounced gradient for *Lotus corniculatus* (Table 3). These results indicate that release of hydrogen ions (H^+) during cation uptake and excretion of exudates (Marschner 1990; Dakora and Philipps 2002) may contribute significantly to the acidification of the rhizosphere and the bulk soil. Nitrogen plays a prominent role in cation and anion uptake and, thus, in rhizosphere pH. The cation uptake of plants living in symbiosis with nitrogen-fixing bacteria is ruled by ammonium (Kurvits et al. 1980; Marschner 1990). The uptake of ammonium induces a high release of hydrogen ions in the rhizosphere and, therefore, strongly contributes to acidification of the rhizosphere soil (Römheld 1986; Gahoonia et al. 1992). Between 30 and 60% of the energy produced by nitrogen fixation is released via rhizobial bacteria in the form of hydrogen (H_2). This explains why bulk soil pH was much lower for *Lotus corniculatus* than for *Calamagrostis epigeios* and why differences between rhizosphere and bulk soil pH were highest for *Lotus corniculatus*.

Soil Organic Carbon and Total Nitrogen Content

Considering all the pools and fluxes within ecosystems, carbon cycling below ground is one of the most significant components (Jackson et al. 1997; Zak and Pregitzer 1998). Formation and turnover of plant roots are expected to play an important role in accumulation of organic matter in the initial phase of ecosystem development (Rasse et al. 2005; Ussiri and Lal 2005). During primary plant succession various species of pioneer plants may influence soil conditions in a very different way. Yoshitake et al. (2011) found evidence of a close relationship between distribution of organic carbon and primary vegetation development and that different vegetation types led to varying accumulations of organic material on an initial soil of glacier foreland.

One of the objectives of our study was to assess the potential of pioneer plant species for accumulation and allocation of nitrogen and organic carbon under different vegetation covers. The results clearly show that particularly the organic carbon content of the bulk soil is closely correlated to root biomass for both plant species (Fig. 2A). For the legume *Lotus corniculatus* an increase in root biomass clearly coincided with an increase in total nitrogen content in both bulk and rhizosphere soils. These results support those of Fornara and Tilmann (2008) showing that an increase in plant below-ground biomass influences soil organic carbon and nitrogen accumulation.

In biological crusts, roots of the first herbaceous plants in primary succession of an ecosystem play an important role in initial nitrogen accumulation (Evans and Johanson 1999; Belnap 2002). In addition to atmospheric deposition (Fenn et al. 2003; Vourlitis et al. 2007) nitrogen-fixing legumes are key components of natural succession, especially in the early stage of ecosystem development (Fornara and Tilman 2008). For the legume *Lotus corniculatus* the concentration gradient between the bulk and rhizosphere soils was much more pronounced for organic carbon and total nitrogen content, whereas no such gradients were observed for *Calamagrostis epigeios* (Fig. 2 A, B, Table 4). These results indicate that growth and turnover of roots, especially of *Lotus corniculatus*, strongly contribute to accumulation of total nitrogen and organic carbon in soils and that this process is clearly correlated with density of vegetation cover.

The increase in nitrogen content in the rhizosphere soil had no significant effect on the nitrogen content in the bulk soil 2 yr after planting. The reason for the low nitrogen content in the bulk soil may be the strong interplay between vegetation and nitrogen dynamics during primary succession, where no appreciable reservoir of soil nitrogen exists (Hobbie et al. 1998). Nitrogen, as a key macronutrient, particularly in this early stage of

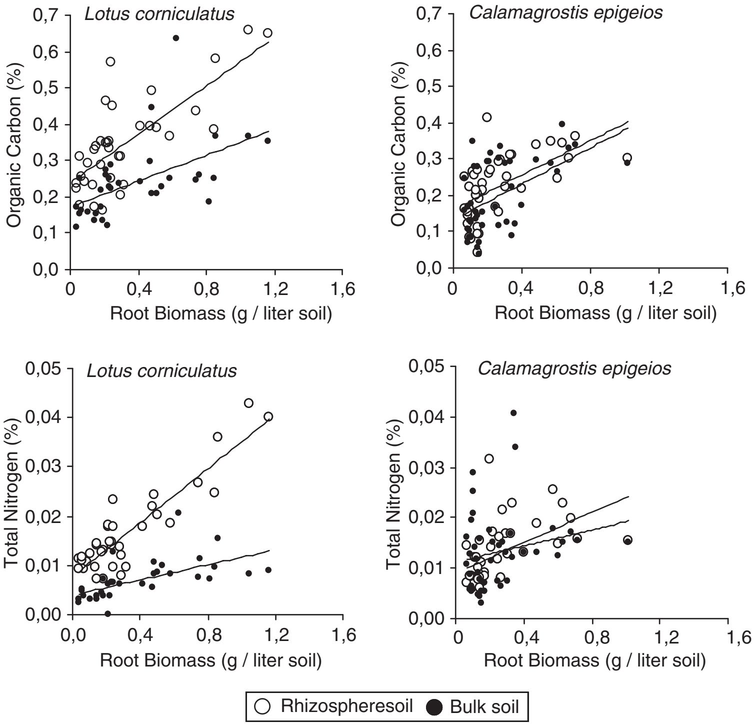

Fig. 2. Root biomass (g L^{-1} soil) of *Lotus corniculatus* and *Calamagrostis epigeios* in relation to (A) organic carbon and (B) total nitrogen content of rhizosphere and bulk soil in the 0- to 20-cm soil depth. Correlation coefficient (*r*) is given by number (*n* = 30–40).

soil development, is taken up immediately after its release or fixed by soil microorganisms (Rosswall 1976; Hawkes 2003). In contrast to total nitrogen, a significant increase in organic carbon in the rhizosphere and in the bulk soil for both plant species was detected.

Comparing the amount of carbon stored in soil monoliths with and without plant cover emphasizes the effect vegetation had 2 yr after establishment (Fig. 3). Irrespective of airborne transport and deposition of carbon from active mining areas nearby, almost no organic carbon ($\leq$0.1%) was found when plants were absent, whereas organic carbon content peaked at 0.58% with plant cover. These results support those of West and Wali (2002) who emphasized the high potential of overburden sediments to store organic carbon after dumping. Yet, the rate of carbon accumulation differed significantly between the plant species under study (Fig. 3A, B). It was surprising to see that an increase in organic carbon content also occurred at greater soil depths despite the decreasing or even absent influence of roots (Fig. 3A, B). For *Lotus corniculatus* this increase was observed in the 0- to 10-cm soil depth irrespective of low, medium and high vegetation densities (Fig. 3 A). For middle and high vegetation cover, comparable organic carbon contents were also detectable in deeper soil layers. For *Calamagrostis epigeios* a similar increase in organic carbon content was found only under high vegetation cover (Fig. 3B), whereas for low and medium vegetation cover values were not significantly different from those in soil monoliths without plants. This indicates that either the stability of organic compounds derived from root turnover may have been lower for *Calamagrostis epigeios* than for *Lotus corniculatus* or that turnover was much more

Table 4. Relationship between rhizosphere and bulk soil carbon and nitrogen content

Plant Species	Soil depth (cm)	Organic carbon Rhizosphere soil/bulk soil	Total nitrogen Rhizosphere soil/bulk soil
Lotus corniculatus	0–10	1.6 ± 0.3*a*	2.9 ± 1.0*a*
	10–20	1.5 ± 0.5*a*	2.9 ± 0.9*a*
Calamagrostis epigeios	0–10	1.2 ± 0.9*b*	1.3 ± 0.6*b*
	10–20	1.2 ± 0.4*b*	1.1 ± 0.5*b*

a, *b* Means and standard deviation (±) are given in data. Within variables, measures with different leetters are significantly different at $P \leq 0.01$; $n = 11$.

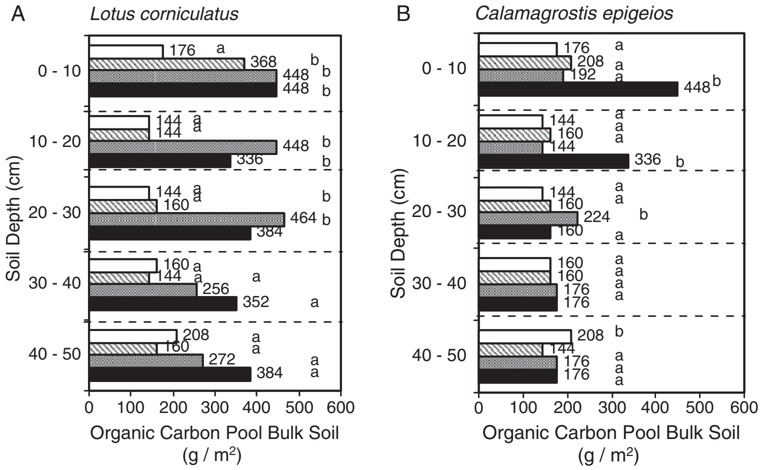

Fig. 3. Organic carbon pool (g m^{-2}) of soil monoliths in control (C), unvegetated and with high (+ + +), intermediate (+ +) and low (+) vegetation density. Means are given in numbers and bars. Within variables, measures with different superscripts are significantly different at P $\leq$0.01; $n = 25$ (layer 1–3); $n = 9$ (layer 4–5).

accelerated for roots of *Lotus corniculatus* than for those of *Calamagrostis epigeios*. The high nitrogen content in roots of the legume may foster an accelerated turnover (Swift et al. 1979; Chapin 1995), which also explains why the distribution pattern of organic carbon in the soil monoliths up to depths of 50 cm appeared to be more homogenous for *Lotus corniculatus* than for *Calamagrostis epigeios*.

Water Soluble Soil Phosphorus

Geochemical sorption and biological demand control phosphorus retention and availability in soils (Olander and Vituosek 2005). Only a small part of total soil nutrients (2–20%) is available to plants (Scheffer and Schachtschabel 2010). Compared with other nutrients, phosphorus is the least mobile and available nutrient to plants under most soil conditions because of the strong reactivity of phosphate (PO_4^{3-}) with different soil minerals (Zhao et al. 2010). In our study, only a very small portion of the total phosphorus (1–2%) in the bulk soil was extractable with water (Table 1).

A comparison of the water extractable phosphorus from the bulk soil of the monoliths with and without plant cover clearly reflected the significance of vegetation cover for soil nutrient content and distribution (Fig. 4 A). Without vegetation, spatial distribution of extractable phosphorus was extremely heterogeneous with elevated concentrations in the upper 10 cm and particularly in the 40- to 50-cm depth increment, indicating that part of the phosphorus fraction had been mobilized and allocated to deeper soil layers after having started from a homogenous distribution pattern.

These results support the hypothesis that vegetation has a significant influence on concentration and distribution patterns of phosphorus and other nutrients in the soil. In soil layers with high root density (Fig. 1) such as the 0- to 30-cm soil depth, the amount of water extractable phosphorus was generally lowest (Fig. 4 C, D, F). At the same time, for both plant species under study, the spatial distribution of this phosphorus fraction was much more homogeneous than in the same substrate without vegetation cover (Fig. 4 B–G). At low *Lotus corniculatus* cover the homogenizing effect was less pronounced and limited to the upper 10 cm, but could be clearly seen at medium and high vegetation density down to 50-cm soil depth. The content of water extractable phosphorus on the bulk soil remained higher in deeper than upper soil layers. Hooper and Vitousek (1998) showed that plants exhibit interspecific and intraspecific variation in their demand, utilization and mobilization strategy and the same applies to the whole ecosystem.

Overall, both plant species seem to have a similar demand on phosphorus. The results indicate that in the initial phase of vegetation development plants contribute to fixation of nutrients via the root system and to redistribution of nutrients via root turnover (Bradshaw 1997; Titus et al. 2002), thus altering initial soil conditions in a very profound way.

CONCLUSIONS

The root system plays a key role in the initial phase of plant succession and pedogenesis in fixation and allocation of nutrients and accumulation of organic matter. The satisfactory growth of both *Lotus corniculatus* and *Calamagrostis epigeios* on a soil with low phosphorus concentrations reflected the low phosphorus requirement of the plants and high adaptability of plants to phosphorus deficiency. Different plant species of primary succession are able to influence soil organic carbon and total nitrogen content and phosphorus nutrient cycling within a very short period of time. The influence of higher intraspecific vegetation density and the accompanying increased root biomass on soil pH, organic

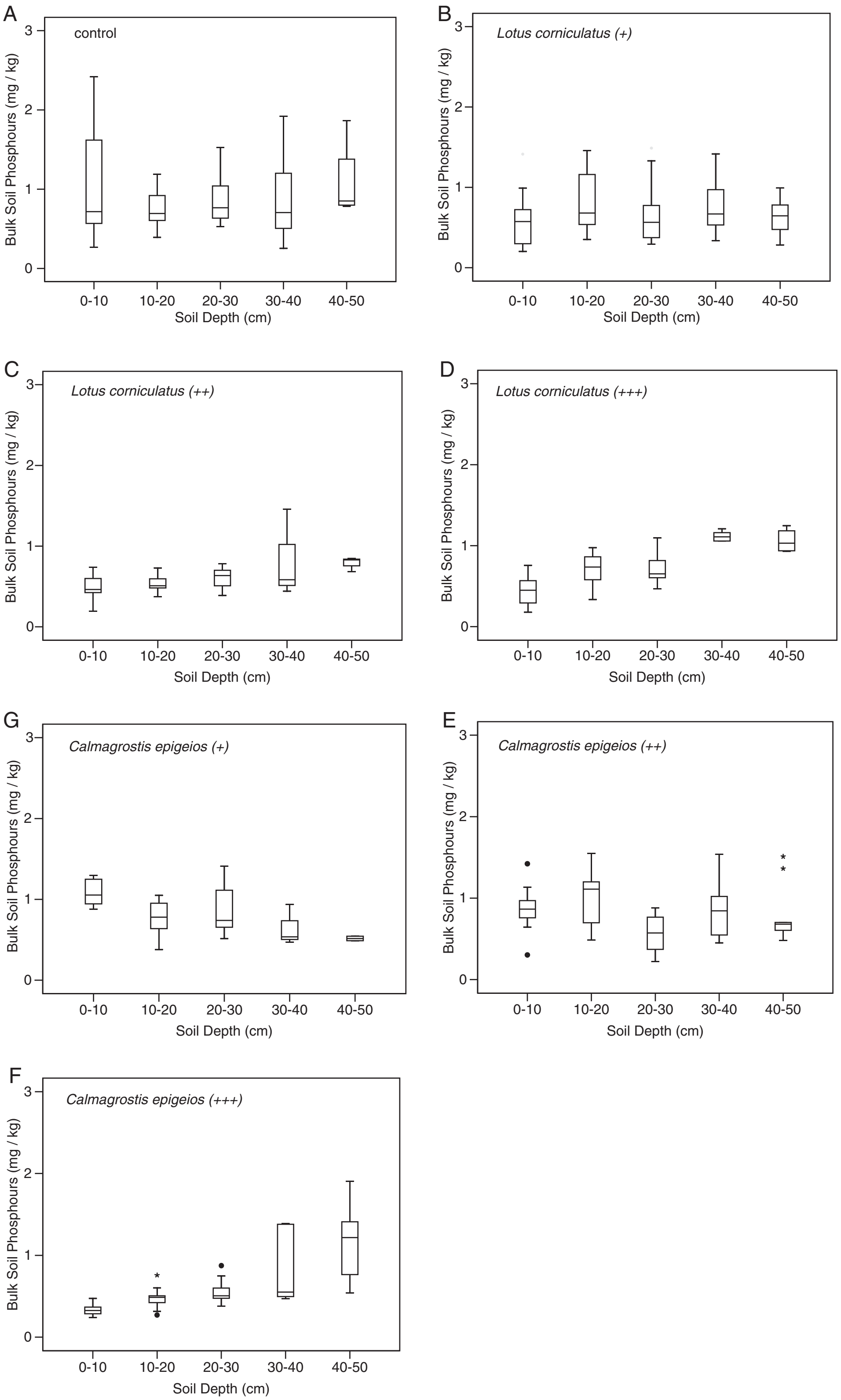

Fig. 4. Fraction of water soluble phosphorus (mg kg^{-1}) in the bulk soil of monoliths with high (+ + +), intermediate (+ +) and low (+) vegetation densities of *Lotus corniculatus* (L) and *Calamagrostis epigeios* (C) and unvegetated control. Means (line within the column) ± standard deviation (bars) is given ($n = 25$ layer 1–3; $n = 9$ layer 4–5).

carbon and nitrogen accumulation differ between plant species. Further studies are needed to see whether these differences account for variability of the secondary vegetation at a later stage of ecosystem genesis.

Our results strongly emphasize the need to study root systems of plants prevailing in the initial phase of plant succession to understand the similarities and differences of how the various species influence soil development particularly in the initial phase of ecosystem genesis. The outcome of this study shows that depth studies on root systems of primary vegetation may help to further develop the current concept of reclamation, and facilitate development of alternative methods of reclamation, such as use of the capacity of respective species to ameliorate the soil and to enhance secondary succession.

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