Vertical Growth and Mycorrhizal Infection of Woody Plant Roots as Potential Limits to the Restoration of Woodlands on Landfills

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Abstract

We assessed the vertical growth and mycorrhizal infection of woody plant roots on a closed landfill, using tree and shrub clusters that had been previously installed in patches of increasing size to establish protocols for woodland restoration. The density of the fine roots of shrubs, which had poor-to-moderate mycorrhizal infection, decreased strongly with increasing depth. Oak (*Quercus*) seedlings planted within and outside patches were assessed for ectomycorrhizal infection. Oak root systems were mycorrhizal, but root-tip proliferation was improved and ectomycorrhizal composition was influenced by woody debris in the mineral soil. Most surviving oaks were found within patches, but all seedlings showed poor growth: most taproots were deflected horizontally above the boundary between surface soil and subsoil layers (≥ -15 cm). Abrupt decreases in pH between surface and subsurface horizons (6.9 versus 5.3), together with poor drainage and aeration of the latter soil, were probably responsible for poor root growth. Root growth of greenhouse-grown pine and maple seedlings was similarly restricted in pots packed with topsoil over subsoil material. Our results suggest that many current specifications for the cover of closed landfills will not permit restoration of native woody plant communities because of physical limitations to root growth and infectivity. The structure of the engineered soil must address basic plant growth requirements as well as traditional concerns of drainage and barrier protection.

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Introduction

Development of a closed forest canopy, typical of old-field succession in eastern North America is frequently arrested in abandoned urban landfills (Robinson et al. 1994). Biotic limitations to the establishment and growth of woodland plant cover are often attributed to aboveground ecological interactions, such as a lack of seed dispersers or pollinators (Robinson et al. 1992; Robinson & Handel 1993), but constraints from belowground processes, such as poor root growth or a paucity of mycorrhizal propagules and rhizosphere organisms, also must be considered. Soils used in final cover designs of urban landfills are heavily disturbed and highly engineered; most of what is known about root and mycorrhizal performance in reconstructed soil profiles, however, has been learned from studies of revegetated mine spoils (Reeves et al. 1979; Miller et al. 1985; Miller 1987; Allen 1988; Harris et al. 1989; Miller & Jastrow 1992).

During landfill closure in the United States and elsewhere, the top and sides of the mounded trash are carpeted with a synthetic waterproof fabric (geomembrane) or are covered with a layer of compacted clay. The liner or cap prevents wetting of the contents and subsequent pulses of leachate that might otherwise contaminate surrounding lands and waters, while trapping decomposition gases that emanate from the garbage (Lutton 1982; Miller 1988; Anonymous 1989; Oweis 1989; Dobson & Moffat 1993, 1995). Both types of liner are then covered with a mantle of soil material, which is expected to function as a barrier-protection layer, drainage channel, and growth medium. In New York City, typical of this region, the closure materials include a 60 cm subsoil layer of sandy material with low organic matter content adjacent to the liner, which is intended to facilitate drainage, and a 15 cm thick surface layer of "topsoil," which is supposed to have a sandy-loam texture, particles no larger than 2.5 cm in diameter, and 10–20% organic matter content.

This soil material, if sufficiently deep, should be able to accommodate a variety of plant communities, including both herbaceous and woody vegetation (Carnell &

Insley 1982; Bradshaw 1984). But recent studies (Dobson & Moffat 1995; Robinson & Handel 1995; Handel et al. 1997) suggest that variability in edaphic properties between surface and subsurface cover layers can render landfill soils inadequate substrates for woody plant growth by restricting vertical root system expansion. Handel et al. (1997) reported frequent problems with highly acid materials at the interface between the sand layer and the clay. In addition to restricted root growth, they found that roots in the lower portion of the landfill soil profile had poor mycorrhizal infection rates (20% of fine roots).

We carried out a study of root growth, mycorrhizal infection, and soil conditions on a landfill in the Fresh Kills landfill complex (Staten Island, New York City) to test these observations and to determine whether the commonly used procedures for establishing soil covers on closed landfills limit belowground processes essential for the restoration of natural plant communities on these sites. In this study, woody plant patches of varying size (increasing numbers of trees and shrubs) were established across the face of the landfill. We tested the hypothesis that soil profiles constructed following currently accepted procedures for landfill closure are unsuitable for vigorous and deep root growth. The discontinuity created by differences in soil properties between surface and subsurface layers, which was previously reported by Handel et al. (1997), was predicted to strongly limit vertical extension of woody plant roots, both in the patches and in soil profiles reconstructed in the greenhouse. We tested a second hypothesis that unfavorable growing conditions belowground will be improved by planting large patches of woody plants. Larger patches are predicted to be more effective than smaller patches in attracting a variety of mutualists, ameliorating microclimate conditions and trapping litter; we posit that larger patches of woody vegetation may be more attractive to potential mammalian dispersers of mycorrhizal spores (Johnson 1996), thus promoting better growth of both roots and mycorrhizae.

Materials and Methods

Study Site

The study was conducted on one of the landfill mounds (Section 3/4) within the Fresh Kills sanitary landfill complex on Staten Island, which is operated by the New York City Department of Sanitation (NYC-DOS). The west-facing lower tier of this mound was closed in 1991 following the department's standard protocol for soil materials and seeding with a mixture of native and nonnative grasses and forbs. The municipal refuse was encased by a barrier of compacted clay (45 cm thick), covered by a subsurface layer of loamy sand (60 cm, the barrier protection layer), and a 15 cm surface layer of "topsoil." The surface soil was sown with grasses and legumes, which formed a dense lawn by the time trees and shrubs were planted.

We established patches of woody vegetation using seven species of native, berry-bearing shrubs and trees. The woody species spanned a range of rooting morphologies and canopy architectures, and, except for the large tree species, were installed as bare-root plantings. The species included *Amelanchier canadensis* (L.) Medic. (shadbush), *Celtis occidentalis* L. (American hackberry), *Prunus maritima* Marsh. (beach plum), *Rhus copallina* L. (winged sumac), *Rosa nitida* Willd. (pasture rose), *Rubus allegheniensis* Porter (blackberry), and *Vaccinium corymbosum* L. (highbush blueberry). Except for blueberry, all species are vesicular-arbuscular mycorrhizal (VAM) plants. At planting, the hackberry trees were about 400 cm tall, while shrubs ranged from 60 to 100 cm in height.

The woody plant patches were arrayed along the western slope of the closed lower tier of Section 3/4 (Fig. 1). The study site was bounded by a woodland remnant, a service road, and the main tributary of Fresh Kill on its northern, western, and southern boundaries, respectively. The active upper tier of Section 3/4 formed the eastern perimeter of the site. Patches were constructed as modules of seven plants (i.e., one individual of each species and totals of 1, 3, 6, or 10 modules). Five replicates of each patch type (7, 21, 42, or 70 plants) were distributed across the site, in a blocked design that controlled for slope position (Fig. 1). Within patches, individual plants were spaced 2 m apart; spacing between adjacent patches was about 40 m.

Bulk soil aeration status was indicated qualitatively by the depth to which steel rods rusted. Steel rods (6 mm diameter) were driven into the profile at the center of each patch and then removed after 5–6 months (April

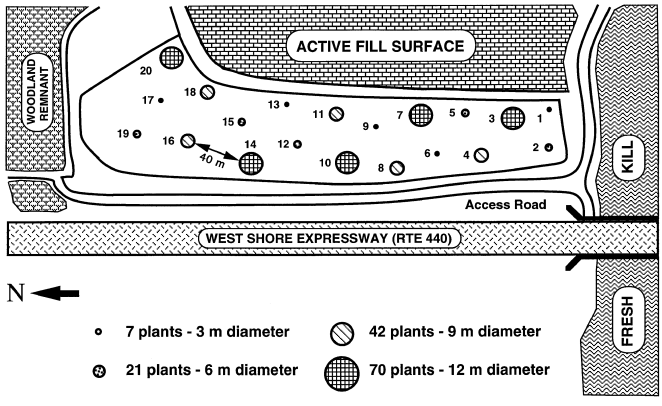

Figure 1. Configuration of woody plant patches on a closed section of Fresh Kills landfill.

1994). Surface corrosion patterns were scored, in 5 cm increments along their lengths, according to criteria devised by Carnell and Anderson (1986). Rods were scoured with steel wool prior to reinstallation for subsequent incubations until December 1994 and June 1995, respectively.

Excavations for Shrub VAM

Rooting depth and incidence of VAM infection were compared in two shrub species (*A. canadensis* and *R. nitida*). One individual of each species was randomly selected in each of three replicates of each patch size, with the restriction that individuals in the two larger patch sizes were located in the interior of the patches. Prior to excavation, aboveground measurements were made for each plant, including shrub height, canopy width (greatest horizontal dimension plus measurement perpendicular to the first, divided by 2), stem diameter, and, for rose, total stem number and proportion of green stems.

Vertical distribution of roots was determined by using a 30 × 30 cm sampling frame, divided into 5 × 5 cm cells, held vertically against the wall of a trench. The trench was excavated 30 cm from the base of the shrub; after root distributions were recorded, the trench was extended 10 cm and then 20 cm towards the shrub, and the measurements were repeated, yielding data at three distances from the base of the stem. Fine woody roots (<3 mm diameter) were tallied in each grid cell; the data were converted from a grid cell basis (counts 25 cm^{-2}) to densities (roots m^{-2}) for each 5 cm depth increment of the sampling frame. Fine roots of the herbaceous species were given a visually estimated cover ranking (none, 0%; sparse, <5%; low, 5–50%; moderate, 50–75%; high, 75–100%). Also, the soil horizon in each grid cell was recorded as 1 for topsoil and 0 for subsoil.

Data were obtained across three sequential trench faces for each field-excavated shrub, and therefore woody root densities at 10 cm, 20 cm, and 30 cm distances were treated as three dependent responses in a multivariate analysis of variance (MANOVA). The three-way MANOVA model was a completely crossed, factorial design that tested for differences in mean root densities across six levels of depth, between two shrub species, and among four levels of patch size. Since depth and patch size were quantitative factors, means were also subjected to trend analysis, by means of orthogonal polynomial contrasts (Woodward et al. 1990). Data were log-transformed ($\log_{10}[Y+1]$) prior to MANOVA to improve normality and homoscedasticity.

Density ratings of herbaceous roots were represented on an ordered, semi-quantitative scale. Therefore, these data were subjected to categorical analysis by multinomial ANOVA (Program GANOVA; Woodward et al. 1990). Wald Chi-square statistics (as maximum likelihood estimates) rather than *F* values were computed in the multinomial ANOVA, based on the five-category response variable. In addition to conventional tests of independence among factors or homogeneity of proportions that are usually applied to row-by-column and higher-order contingency tables, the ANOVA tested for differences among treatments on the main effects of species, depth, and patch size, and the associated two-way and three-way interaction terms.

In each excavated woody root system, a grab sample of fine roots was collected above the surface-subsurface soil interface (i.e., about 15 cm depth). Roots were rinsed free of soil particles in the field, wrapped in moist paper towels, and frozen (−20°C) in resealable plastic bags for later study. When thawed, roots were cut into 2 cm pieces, cleared in 2.5% KOH (at 90°C), and stained with 0.05% trypan blue in glycerol-lactic acid solution (Koske & Gemma 1989). Wet mounts of the prepared roots were assessed for arbuscule and vesicle infection, following the magnified intercept method of McGonigle et al. (1990).

Percentages of shrub fine roots that were colonized by arbuscules and vesicles were subjected to two-way MANOVA, which included species and patch size as factors. Hyphae were excluded as a dependent variable in the MANOVA because the numbers of positive intercepts for this category likely were inflated by inclusion of saprophytic or parasitic fungi in the tallies.

Ectomycorrhizal Bioassays

In the autumn of 1994, *Quercus prinus* L. (chestnut oak) acorns were sown into the patches at densities of one, two, three, and four seeds per patch of each size, respectively, to assess the ectomycorrhizal inoculum potential of the site. A single acorn also was installed in the herbaceous cover 5 m from the edge of each patch at the same elevation (this is referred to below as the "0-plant treatment"). In addition, *Q. rubra* L. (red oak) seedlings, which had been germinated in Ray Leach tubes (Stuewe & Sons, Corvallis, Oregon) containing a sterile sand-perlite-peat moss mixture, were planted in a similar fashion during the following spring. The 150 bioassay acorns and seedlings were surface-sterilized with bleach solution in the field prior to planting. Also, the relative position of each oak on the closed tier was flagged and recorded as the upslope distance (m) from the base of the slope.

Surviving oak seedlings were harvested in mid- to late summer of 1995. During excavation, as much of the root system as possible was recovered. We noted the type of substrate (mineral soil versus decaying wood) in which the seedlings were rooted and the degree to which fine roots proliferated along the tap roots (sparse,

moderate, profuse); inadequate screening of cover soils for construction scraps and decaying stumps resulted in randomly distributed inclusions of wood fragments in the landfill profile. Tap root deformities also were recorded, together with the depth at which horizontal deflection, "*J* rooting," or coiling occurred and whether or not vertical root growth resumed. These observations were assigned a qualitative rating, from 0 for slight to no deviation from a vertical growth path to 5 for severe horizontal deflection and tap root stunting, with no resumption of vertically oriented growth.

Intact seedlings were wrapped in moist paper towels, sealed in polyethylene bags, and returned to the laboratory. Roots were frozen (−20°C) until they could be examined for mycorrhizal infection at low magnification (30×). Root tips were classified as mycorrhizal or nonmycorrhizal, and subsequently as active or nonactive ectomycorrhizae, according to the morphological criteria of Harvey et al. (1976). Active mycorrhizae were classified into morphological types, which were based on the structure and color of the fungal mantle sheathing the root tips. Proportions of root systems occupied by active tips were estimated with a gridded petri plate, as were different morphotypes. After scoring for mycorrhizal infection, masses of fine roots and tap roots were determined separately, and length measurements were made of the latter. Seedling heights and stem diameters were measured, after the tissues were dried to constant mass (at 70°C for 48 hours).

An index of plant performance was constructed by transforming the seedling measurements to principal component scores. Each variable (mass, stem diameter, and height of shoots; length and mass of tap roots; mass of fine roots) was normalized to unit variance prior to principal components analysis (PCA in Statview 4.02, Abacus Concepts, Berkeley, California). Proportions of surviving seedlings as well as active mycorrhizae were subjected to one-way multinomial ANOVA and contingency-table analysis (Program GANOVA; Woodward et al. 1990).

Greenhouse Study

The field excavations were complemented by a greenhouse study in which a VAM species, *Acer rubrum* L. (red maple), and an ectomycorrhizal species, *Pinus strobus* L. (white pine), were grown from seed in 2 L pots containing topsoil (6 cm depth) over sandy subsoil (6 cm; "bilayer" treatment) or topsoil only (12 cm; "monolayer" treatment). Soils were collected from open trenches on Section 3/4, sieved to pass a 5 mm screen and air-dried prior to use. Two seeds were planted per pot, and 20 (maple) or 25 (pine) pots were prepared for each profile type. During the growing season, treatment replicates were randomly assigned to locations on an outdoor greenhouse bench, and positions were changed with twice-weekly watering.

Seedlings that survived overwintering in cold frames were harvested the following summer (18 months after planting). Monolayer pots were carefully slit and peeled away from the bulk soil plug. After we trimmed roots that grew along the walls of the pot, we washed the soil away from the remaining root ball. Bilayer pots were treated similarly, but surface soil was carefully dislodged from the root ball down to the subsurface layer. Roots that penetrated into the lower horizon were counted, then severed. Roots in the two layers were rinsed and oven-dried to constant mass, as were the shoots (at 70°C for 48 hours). Gravimetric moisture content also was determined from a subsample of each soil layer in order to determine the bulk densities of the two horizons; pH was determined from a second subsample (20 g soil: 10 mL deionized water).

Root masses (per pot or layer) were converted to a volumetric basis (mg root cm^{-3}), correcting for differences in bulk density among soil layers and pot types. We expected roots and shoots to be strongly correlated, so we included shoot mass as a covariate when comparing total root mass between bilayer and monolayer pots (analysis of covariance, SuperANOVA, Abacus Concepts, Berkeley, California).

Results

Shrub Excavations

For both shrub species, root densities were high or remained fairly constant with depth to 20 cm, then decreased strongly with increasing distance down the soil profile (Table 1, *F* tests; Fig. 2). A significant quadratic trend characterized root densities, but only at a 10 cm distance from the shrub bases ($p < 0.001$). Fine roots of shadbush were evenly distributed between 0 and 20 cm depth, but rose roots tended to be found mainly above 15 cm (orthogonal contrasts of 0–15 cm versus 15–30 cm depth increments: 10 cm distance, $F = 14.28$, $p < 0.001$; 20 cm distance, $F = 6.64$, $p = 0.012$; 30 cm distance, $F = 8.49$, $p < 0.005$, $df = 1,90$).

Fine roots of shadbush and rose both were sparsely distributed throughout the upper 30 cm of the cover profile, but fine root densities were frequently one to two orders of magnitude greater for rose than shadbush at all distances from the shrub bases (Table 1). Mean root densities decreased progressively with increasing distance from the shrubs (Fig. 2). Patch size did not affect woody fine root densities (Table 1).

Densities of woody fine roots also were affected by the position of the topsoil-subsoil boundary, typically located 15–20 cm down into the soil profile. Higher woody fine root densities were associated with the

Table 1. Multivariate and univariate analyses of variance on log-transformed fine woody root densities in trenches excavated beside 12 pasture roses and 11 shadbushes.*

		Univariate F *Statistics* (p *value*) *(distance from plant base)*			*MANOVA Statistics*	
Source	df	*10 cm*	*20 cm*	*30 cm*	*Wilks' Λ*	F (p *value*)
Patch (P)	3	0.28 (0.837)	1.64 (0.187)	2.64 (0.055)	0.894	1.12 (0.347)
Species (S)	1	13.27 (< 0.001)	19.32 (< 0.001)	13.09 (< 0.001)	0.785	8.02 (< 0.001)
Depth (D)	5	8.04 (< 0.001)	6.91 (< 0.001)	2.59 (0.031)	0.580	3.53 (0.397)
S × P	3	1.05 (0.375)	2.70 (0.050)	0.86 (0.466)	0.900	1.06 (0.397)
S × D	5	0.25 (0.940)	0.83 (0.531)	1.52 (0.234)	0.853	0.97 (0.493)
P × D	15	1.07 (0.396)	0.77 (0.708)	0.52 (0.922)	0.652	0.90 (0.649)
S × P × D	15	0.48 (0.945)	0.21 (0.999)	0.57 (0.894)	0.776	0.52 (0.995)

*One shadbush selected for root assessments was dead. Trenches were dug 10, 20, and 30 cm from each shrub base.
Mean square error terms associated with the univariate *F* tests for root densities at 10, 20, and 30 cm from the shrubs are 1.098, 0.932, and 1.065, respectively, with 90 error degrees of freedom. Acceptance levels for *F* values have been Bonferroni-corrected ($p = 0.016$).

presence of the topsoil layer than with subsoil materials (point-biserial correlation: $r_{ptbis} = 0.456$, $p = 0.004$). As for woody roots, the presence or absence of herbaceous fine roots was strongly dictated by the presence or absence of topsoil, with more roots appearing above the junction than below it ($r_{ptbis} = 0.714$, $p < 0.001$).

Herbaceous root density varied with species of shrub (Wald $\chi^2 = 39.18$, $p < 0.001$, $df = 4$; Fig. 3) but did not vary with patch size. Higher abundances of herbaceous roots at shallow depth were associated with shadbush, but these roots decreased more rapidly with depth than under rose (interaction of species by depth, Wald $\chi^2 = 53.31$, $p < 0.001$, $df = 20$; Fig. 3). Furthermore, densities of herbaceous and woody fine roots only were strongly correlated throughout the cover profile under rose (Spearman's rank correlation: $r_s = 0.461$, $p < 0.001$), compared to shadbush ($p > 0.50$).

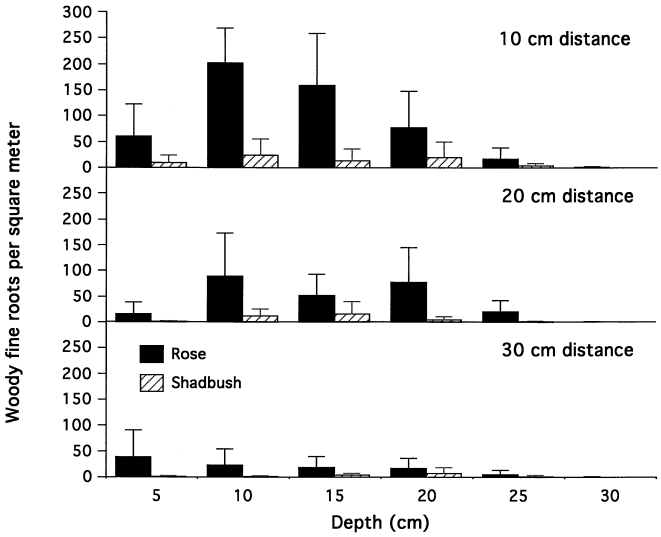

Figure 2. Vertical distribution of shadbush and rose fine roots. Back-transformed logarithmic mean densities are plotted in 5 cm depth increments, at 10, 20, and 30 cm from shrubs. Upper standard errors associated with mean $\log_{10}$ (numbers $m^{-2} + 1$) are presented.

VAM colonization of the shrub roots was low, ranging from 0 to 11.4% for arbuscules and 0 to 20% for vesicles in the roots examined. Arbuscular infection was four times higher in shadbush than in rose: 6.48% versus 1.46% (Wilks' $\Lambda = 0.449$, $F = 7.98$, $p = 0.005$, $df = 2,3$). No species effect was found for levels of vesicle infection ($p > 0.50$), which was 5.17 ± 1.12% for shadbush and 6.67 ± 2.10% for rose, respectively (mean ± standard error). There was evidence of an effect of patch size, but only for shadbush (significant quadratic regression, $p < 0.001$) supporting a maximum of arbuscules at a patch size of 42 plants.

The depth to which the soils were well aerated, as indicated by rust deposits on the upper ends of the steel rods, ranged from 7 to 60 cm. Subsoils frequently had orange and gray mottles, which suggested periodically saturated conditions. Unlike rooting depth, the depth of aerated soil varied with patch size (7 plants, 30.8 ± 3.6 cm; 21 plants, 39.6 ± 3.8 cm; 42 plants, 42.7 ± 4.0 cm; 70 plants, 29.8 ± 4.6 cm), although the association was weak ($r^2 = 0.159$, $p = 0.03$). On the other hand, vesicle colonization was significantly correlated ($p = 0.02$) with depth of aerated soil, although the correlations were equal but opposite in sign for the two shrub species (percentage vesicles versus rusting depth for December rod incubations: shadbush, $r = 0.735$; rose, $r = -0.733$).

Oak Bioassays

Seedling survival was low inside and outside the patches, ranging from 0 to 4% in chestnut oak and 0 to 21% in red oak. Fewer seedlings of chestnut oaks were alive at harvest than red oaks (i.e., 9 versus 29 individuals); all but one of the seedlings that did survive were situated within medium to large patches. Within the herbaceous vegetation, rodent damage to oak stems was common and likely was the cause of seedling death.

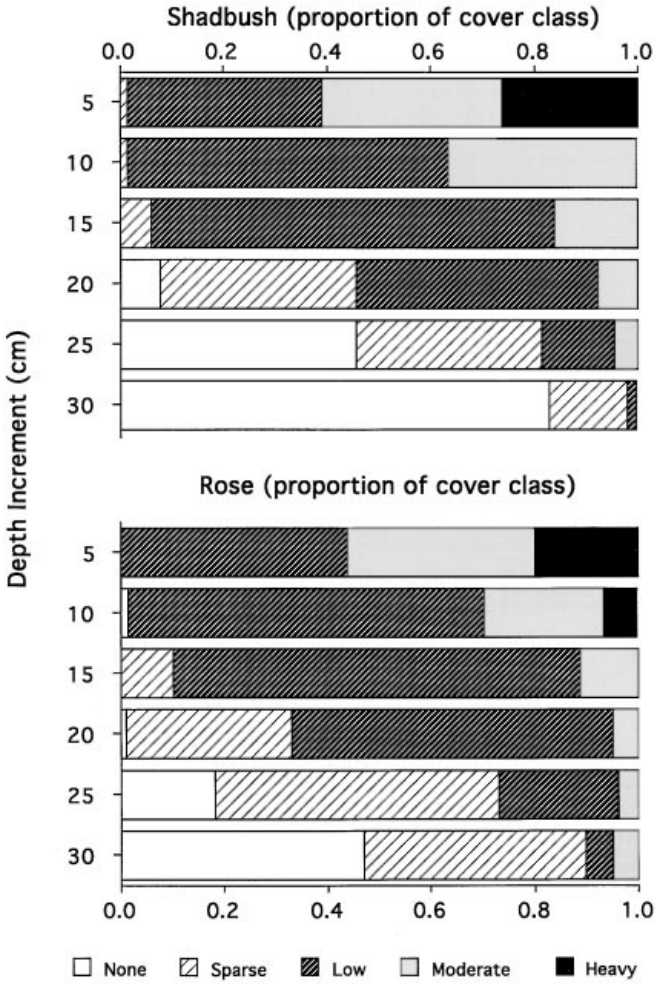

Figure 3. Herbaceous root density with depth, plotted as categorical responses by species, which departed significantly from random expectation ($G = 36.09$, $p < 0.001$, $df = 4$).

Patch size had a pronounced effect on seedling survival ($p < 0.025$) and on the size of surviving seedlings (correlation of patch size with leaf number, $r = 0.645$, $p < 0.001$; with seedling height, $r = 0.483$, $p = 0.002$; with shoot mass, $r = 0.444$, $p = 0.004$). For red oak seedlings, survival increased progressively with increasing patch size (linear trend contrast, Wald $\chi^2 = 13.64$, $p < 0.001$, $df = 1$), and could be ordered as: 0.0%, 0 plants; 2.7%, 7 plants; 4.0%, 21 plants; 10.7%, 42 plants; and 21.3%, 70 plants.

Principal components ordination identified two significant factors. The first component reflected shoot growth, while the second component reflected root growth (Table 2). Shoot growth was higher on the northern end of the site and increased with increasing patch size (Table 3), while root growth was greater in upslope positions, where soil aeration was higher (Table 3). The positive relationship between root growth and depth of soil aeration was particularly pronounced for chestnut oak (PC Axis 2 scores versus December rod rusting: $r = 0.758$, $p = 0.027$). Root growth for both oak species was also correlated with the index of root deformity (PC Axis 2 scores versus deformity: $r = -0.493$, $p = 0.006$); better growth in the upper slope positions was associated with straighter taproots. About 85% of the seedlings, however, had *J*-form roots, with the taproot deflected at a depth of 7.6 ± 0.5 cm, which was above the topsoil-subsoil junction.

Fine roots were colonized by ectomycorrhizal fungi, but active infections were low, rarely involving more than 50% of the root tips. Active mycorrhizal infection was not related to the degree to which fine roots branched along the tap roots ($p = 0.066$), although root biomass was strongly correlated with the latter (root tip proliferation versus fine root biomass: $r_s = 0.726$, $p < 0.001$). Localized increases in fine roots, which were associated with incorporation of woody debris into the mineral soil, led to higher numbers of active ectomycorrhizal root tips (*G* test, wood versus mineral soil: $G = 22.11$, $p < 0.001$, $df = 1$). Ectomycorrhizal infection was also affected by substrate pH (partial correlation, controlling for patch size and slope, $r = -0.822$, $p < 0.005$). There was no association between patch size and ectomycorrhizal development.

The low levels of mycorrhizal infection were paralleled by low ectomycorrhizal diversity. Only three distinct mycorrhizal morphotypes were recognized from examination of the root systems. The three types were arbitrarily denoted A, B, and C. Types A and B were characterized by a monopodial or short-root, single-tip structure. Type A root tips were straight and had a smooth, beige to cream-colored mantle, which contrasted with the tortuous, dark-brown and scurfy appearance of type B. Type C had a dark and rough-surfaced mantle like type B, but the type C had a tortuous and profusely branched coralloid habit. Even though the red oaks had been germinated in the greenhouse, field-grown seedlings had mycorrhizae that differed markedly in appearance from those morphotypes found on the same plants grown in the laboratory. Fine roots of greenhouse-grown red oaks had rough-textured, white-to-cream mantles that ended characteristically in *Y*-shaped tips. Low ectomycorrhizal diversity encountered in the field bioassay plants could not be ascribed simply to initial contamination of the seedlings.

The morphotypes A, B, and C were found on both oak species in the field but in differing proportions depending upon the substrate. The second morphotype (B) occurred less frequently in mineral soil than in decayed wood (12.0 ± 5.5% versus 34.1 ± 11.2%, respectively; Mann-Whitney *U* test, $p = 0.01$). When red oak was considered alone, there were strong differences between mineral soil and decayed wood in the occurrence of types B (13.0 ± 6.9% versus 38.4 ± 11.8%, respec-

Table 2. Shoot and root measurements following harvest of surviving *Q. rubra* (red oak) and *Q. prinus* (chestnut oak) seedlings.*

Species	*Fine Root Mass (g)*	*Tap Root Mass (g)*	*Tap Root Length (mm)*	*Shoot Mass (g)*	*Shoot Diameter (mm)*	*Shoot Height (mm)*
Q. rubra	0.742 (0.094)	2.870 (0.223)	216.17 (11.30)	1.72 (0.14)	4.00 (0.02)	132.03 (7.29)
Q. prinus	0.087 (0.020)	1.848 (0.251)	163.33 (21.49)	0.79 (0.31)	2.70 (0.27)	105.11 (14.13)
U tests (*p*)	***	†	†	**	***	
PCA 1	0.315	0.304	−0.094	0.750§	0.847†	0.898†
PCA 2	0.741	0.849†	0.800†	0.404	0.189	−0.033

*Means (± SE) for the species are based on sample sizes of 29 and 9, respectively. Differences in seedling properties were tested between species by means of Mann-Whitney *U* tests. The data were combined in principal components analysis. PCA 1 and PCA 2 explained 50.9% and 22.4% of variation in the data, respectively. Where superscripted, the loadings of the six variables on the components differ from random expectation. $n = 39$.
§$p < 0.10$, †$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

tively; *U* test, $p = 0.011$) and type C (40.1 ± 9.8% versus 0.0%, respectively; *U* test, $p = 0.016$).

Greenhouse Study

Fewer red maples survived (70–80%) than white pines (84–96%), yet seedling root mass was 6–10 times greater for the maples than the pines, especially in pots containing only topsoil (Table 4). The growth of the maples was significantly inhibited by the presence of a layer of subsoil material; this result emerged from analyses based on per-pot biomass and on root mass per unit volume, corrected for covariation in shoot mass (Table 4). Pine showed poor growth of roots and shoots in the mono- and bilayer treatments, although the roots in both cases appeared to be infected by ectomycorrhizae. Notably, pine roots did not enter the subsoil material, unlike the maple roots (Table 4).

Numbers of maple and pine roots penetrating the topsoil-subsoil boundary of the treatment pots were compared by *t* tests. Although the maple roots penetrated the subsoil, their growth there was poor (0.18 ± 0.06 g/pot in subsoil versus 6.26 ± 3.38 g/pot in topsoil); almost all of the root growth of the maples was confined to the topsoil. In the monolayer pots, roots had twice the favorable rooting volume than in the bilayer treatment, and growth was much higher.

Discussion

The results of this study clearly show that woody plants cannot use all of the soil volume created during landfill closure. Roots of both tree seedlings and shrubs only grow within the surface "topsoil"; they either fail to penetrate the subsurface barrier layer, or grow poorly and do not proliferate in this material. These results were found for both vesicular-arbuscular mycorrhizal and ectomycorrhizal species. Other studies of root growth on landfills have similarly found that the soil volume is not completely penetrated by roots, as would be expected in natural soils (Carnell & Insley 1982; Bradshaw 1984; Robinson & Handel 1995; Handel et al. 1997).

There are several possible reasons why the subsurface material is not conducive to vigorous growth of woody plant roots. First, this material has a substantial amount of clay mixed with the sand of which it is constructed (data for a similar site elsewhere in the Fresh Kills complex reported by Handel et al. 1997; clay is evident on inspection of the subsurface soil). The clay

Table 3. Correlations between indices of oak seedling performance (PCA 1 and PCA 2 factor scores) and site characteristics on Section 3/4 of the Fresh Kills sanitary landfill.*

Seedling Descriptor	*Site Characteristic*	*Correlation*	p *value*
PC Axis 1	North-south orientation	0.494	< 0.001
PC Axis 1	Patch size	0.620	< 0.001
PC Axis 2	Upslope-downslope	−0.590	< 0.001
PC Axis 2	Soil aeration	0.582	< 0.001
PC Axis 2	Presence of decayed wood fragments	0.401¶	0.01

*The first two principal component axes describe shoot growth and root growth, respectively. The values are Spearman's rank or point-biserial (¶) correlations, based on $n = 39$.

Table 4. Root and shoot biomass (per pot) of maple and pine seedlings in greenhouse pots containing topsoil-only (monolayer) or topsoil layered over subsoil (bilayer).*

Species	*Soil Treatment*	*Root Mass (g/pot)*	*Root Mass (mg cm^{-3} soil)*	*Subsoil Penetrations*	*Shoot Mass (g/pot)*
Maple	Monolayer	14.99 ± 1.52^a	5.22 ± 0.34^a	N/A	3.36 ± 0.53^a
Maple	Bilayer	6.26 ± 3.38^b	3.46 ± 0.45^b	1.19 ± 0.31	1.85 ± 0.23^b
Pine	Monolayer	1.33 ± 0.21^c	1.28 ± 0.29^c	N/A	0.58 ± 0.08^c
Pine	Bilayer	0.85 ± 0.07^c	1.85 ± 0.28^c	0 (−)	0.41 ± 0.03^c

*Root mass in the surface soil of both treatments is corrected to a volumetric basis to account for density differences between soil layers and is adjusted by ANCOVA for variation in shoot biomass. Means (± SE) superscripted by the same letter do not differ at $p = 0.05$; there were 21–25 maples and 10–14 pines, respectively, per treatment. Numbers of root penetrations into the subsoil layer, where applicable, are on a per-pot basis.
ANCOVA on root mass: species, $F_{1,68} = 40.22$, $p < 0.001$; treatment, $F_{1,68} = 11.84$, $p < 0.001$; species × treatment, $F_{1,68} = 4.19$, $p = 0.045$; covariate, $F_{1,68} = 64.01$, $p < 0.001$.

used to cap these landfills is a pyritic material that generates high acidity when exposed to oxidizing conditions (Robinson & Handel 1995). The large range in subsoil pH, from 3.52 to 7.27, may thus reflect the variability of mixing of clay from the capping layer into the subsoil. Second, the reversed pH gradient through the profile, with the subsoils averaging 1.6 pH units lower than the topsoil, is the reverse of the natural situation, in which the pH of the subsoil horizons is usually higher than that of surface soils in temperate forest ecosystems (Armson 1977). The difference between horizons ranged up to 3.8 pH units, with the subsoil more acid than the surface soil. Third, the lower part of the subsoil horizon tends to be waterlogged and anoxic, as shown by the steel rod studies reported here and by Handel et al. (1997) on an adjacent site. Fourth, the break in the pore-size distribution between the large pores of the sandy subsoil and the small pores of the loamy surface soil may cause hydraulic discontinuities, such that moisture in surface soil cannot be recharged from stored moisture in the subsoil during periods of drought. Our finding that both shrubs and tree seedlings grew better on the north-facing portion of the study site suggests that moisture stress on southern and western exposures may be significant, consistent with the observations of Carnell and Insley (1982). Limited data on the moisture content of the upper portion of the subsoil suggested that it contained less water than did the topsoil (e.g., May of 1993, 18.5 ± 1.0 g H_2O/100 g topsoil versus 13.7 ± 1.0 g H_2O/100 g subsoil; $p < 0.001$). Also, corrosion patterns on the steel rods suggest that water ponds above the clay cap but is not able to move upward into the upper portion of the subsoil and recharge surface soils. The result may be that subsoils are too dry above and too wet below for good growth of roots.

The poor growth and proliferation of fine roots was paralleled by poor development of both VAM and ectomycorrhizae. The percentage of shrub roots with mycorrihizal infection was usually less than 50%; in many roots, although hyphae were present, arbuscules were poorly developed. Similarly, the percentage of oak seedling root tips with active ectomycorrhizae was low. The presence of fragments of decayed wood in the surface soil was associated with both higher rates of mycorrhizal infection in the oak seedlings and with the occurrence of two of the three recognized morphotypes. Pockets of decaying organic matter within mineral soil are known to be favorable sites for mycorrhizal hyphal growth (St. John et al. 1983) and have been shown to serve as refuges for ectomycorrhizal fungi in disturbed or logged forests (Parke et al. 1984; Amaranthus & Perry 1987; Perry et al. 1987, 1989; Borchers & Perry 1990). Thus, these bits of coarse woody debris may promote the survival of both seedlings and their mycorrhizae.

The low rate of ectomycorrhizal infection also might reflect the high pH of the surface soils. Ectomycorrhizal fungi are associated with acid soils, usually those with a pH lower than 5 (Allen 1991); the surface soils on the landfill were as high as 7.62, and all were above 5.3. While VA mycorrhizae are found in plants inhabiting soils with a larger range of pH (Allen 1991), the high pH of the surface material may be inhibitory to mycorrhizae commonly found in old fields of the region, which normally have moderately acid pH values. The variable pH of the landfill soils was probably due to inclusions of calcium-containing building debris (plasterboard, bricks with adhering mortar); soils in the vicinity of these materials could be expected to have unusually low acidity. These results would be consistent with those of related studies in the Meadowlands of New Jersey, where we have measured pH values greater than 7.5—and occasionally in excess of 8.0—on landfill sites containing construction wastes (J. G. Ehrenfeld & W. F. J. Parsons, unpublished data).

A second possible reason for the low degree of mycorrhizal infection is a low level of mycorrihizal inocu-

lum. Routine stockpiling of cover material can impoverish mycorrhizal inocula and the rhizosphere microflora (Miller et al. 1985; Harris et al. 1987, 1989; Jasper et al. 1992). While the history of the materials used to create the surface layer on these landfills is unknown, the conspicuous presence of construction and other debris, and the fact that each landfill is covered by materials obtained from many independent sources, suggests that these soils have been subject to extensive disturbance. Mycorrhizal infection rates of the herbaceous plants are also low (A. Zuller, personal communication), again suggesting that, while inoculum is present, it may be limited in quantity. Mycorrhizal formation can be inhibited by high phosphorus levels (Allen 1991), which we found in analyses of the landfill surface soils in May of 1993 (Bray-extractable PO_4^{-3}; 7.5 ± 3.5 mg P/kg soil), but infection may also be limited by the sparse growth of roots. Insofar as contact between an uninfected and an infected root is an important means of spreading infection (Allen 1991), sparse growth of fine roots will maintain low infection rates.

In conclusion, landfill soil profiles are not currently constructed to promote the establishment and survival of woodland vegetation. Our data show that trees, tall shrubs, and even small shrubs have poor mycorrhizal infection and poor root growth at depth, which is consistent with previous on-site studies (Handel et al. 1997) and which suggests that their long-term survival and growth are likely to be limited. Our data do not suggest that poor root development is due to leakage of methane through the cap, which typically results in "scorched" ground devoid of live vegetation; the inhibition and deformation of the root systems were similar between the greenhouse pot experiments and the field observations. These data, like those obtained in earlier studies (Robinson & Handel 1995), also do not suggest that the depth of soil cover is a limiting factor: tree and shrub roots used only about half the volume of soil available. Rather, these problems probably reflect the following three conditions that could easily be modified in the protocols adopted by government agencies for closing landfills.

(1) Incorporation of clay from the capping layer into the subsoil material promotes the development of highly acid conditions and also promotes waterlogging in the lower portion of this subsoil layer. Both conditions strongly inhibit root growth. This problem could be reduced or prevented by installing a separate layer of sand over the clay cap, thus isolating the subsoil from the clay cap and permitting the subsoil to be installed after any disturbance to the surface of the clay cap has occurred. This would necessitate increasing the total depth of material used to construct the subsoil horizon. On sites where geomembranes are used as a cap instead of clay, the problem disappears.

(2) The presence of building debris in the surface material leads to areas of excessively high pH. Clearly, close quality control over the soils accepted for use in closing landfills is essential. Eliminating the large quantities of foreign materials incorporated into the soil would create pH levels conducive to plant growth.

(3) The high available nutrient content of the surface soils may also be a factor inhibiting the development of abundant mycorrhizal infection. Again, better control over the materials accepted by the landowner, and appropriate specifications, could reduce this problem. Maintenance of lower concentrations of available nutrients and lower pH will be particularly important if the goal is restoration of forest trees and shrubs, which are usually adapted to acid soils. By controlling the quality of the soil cover, restoration of native woody plant communities over large areas of landfill surface would be practical.

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