

Vertical root distributions of northern tree species in relation to successional status¹

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Received August 21, 1986

Accepted February 11, 1987

GALE, M. R., and GRIGAL, D. F. 1987. Vertical root distributions of northern tree species in relation to successional status. *Can. J. For. Res.* **17**: 829–834.

Measurements of root biomass, number, diameter, and length by soil depth for northern tree species were assembled from 19 published papers, yielding a total of 123 vertical root distributions. Species were classified into three tolerance classes based on successional status. A nonlinear function, $Y = 1 - \beta^d$, where Y is the cumulative root fraction from the soil surface to depth d in centimetres, was fit to the data for each excavation. The regression coefficient, β , was considered to be a measure of vertical root distribution and was used as a response variable to test whether significant differences in vertical root distributions existed among tolerance classes. Early successional or intolerant species had a significantly greater proportion of roots occurring deeper than did late successional or tolerant species. Differences in vertical root distributions are presumed to be related to the inherent genetic potential of early successional species for deep exploitation of a more homogeneous substrate, resulting from either geologic deposition or nutrient and water redistribution following forest disturbance. Early successional species are also able to adapt to sites limiting in water and nutrients because of their ability to exploit larger volumes of soil. Late successional or shallow-rooted species are better adapted to sites where resources are concentrated near the soil surface as the result of biocycling and soil development.

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Les mesures du nombre de racines ainsi que leur diamètre, longueur et biomasse suivant la profondeur du sol pour des essences nordiques furent assemblées à partir de 19 publications donnant un total de 123 distributions verticales de systèmes racinaires. On a classé les essences en trois classes de tolérance à l'ombre d'après leur statut dans la succession. La fonction non linéaire $Y = 1 - \beta^d$, où Y représente la portion cumulative des racines depuis la surface du sol jusqu'à la profondeur d exprimée en centimètres, fut appliquée aux données de chaque excavation. Le coefficient de régression β fut estimé comme une mesure de la distribution verticale des racines et employé comme variable pour déterminer l'existence de différences significatives dans la distribution verticale des racines parmi les classes de tolérance. Les essences intolérantes ou pionnières avaient une plus grande proportion de leurs racines en profondeur que les essences tolérantes ou climaciques. On présume que les différences observées dans la distribution verticale des racines sont liées au potentiel génétique inhérent aux essences pionnières leur permettant d'exploiter en profondeur un substrat plus homogène résultant soit de la déposition géologique, soit d'une redistribution de l'eau ou des éléments nutritifs par suite d'une perturbation forestière. Les essences pionnières possèdent aussi la capacité de s'adapter à des stations où l'eau et les éléments nutritifs sont des facteurs limitatifs à cause de leur facilité à exploiter de plus grands volumes de sol. Les essences climaciques à enracinement superficiel sont mieux adaptées à des stations dont les ressources sont concentrées près de la surfaces du sol par suite des cycles biologiques et du développement du sol.

[Traduit par la revue]

Introduction

Succession is a basic concept of plant ecology. Ecological theories of succession have ranged from a holistic concept based on autogenic plant responses to a reductionist concept based on random neo-Darwinian plant responses (McIntosh 1980). Interpretations of the significance of these theories have generated much discussion (Finegan 1984; Whitmore 1985). Most of the debates have centered on the specific plant mechanisms that control successional changes; these have been difficult to assess or quantify.

Certain morphological and physiological characteristics have been found to differ between early and late successional tree species (Finegan 1984). Rates of photosynthesis, respiration, and light compensation points are higher for early successional species than for late successional species (Bazzaz 1979). Competition for light, as it affects these characteristics, is one of the key factors influencing the successional status of a tree species (Kramer and Kozlowski 1979; Zeide 1980). Loach

(1967) and Went (1957) related differences in physiological rates to the shade tolerance of a tree species. Tolerance, a term that has often been used to describe the ability of a tree to survive and grow in the understory, focuses on the competition for light (Spurr and Barnes 1980; Zeide 1980). Although most of the research emphasis on adaptations relating to succession has been on light availability, some work has suggested that competition by roots for soil moisture is also important (Toumey 1929; Toumey and Kienholz 1931; Korstian and Coile 1938; Spurr and Barnes 1980). Strong and La Roi (1983b) have attributed possible successional change in a forest type to vertical root density (shallow versus deep). More recently, Strong and La Roi (1985) suggested that the vertical position of roots was important in the interception of nutrients and the regulation of nutrient cycling within a forest.

Because tree roots are an important component of a forested ecosystem, an understanding of the mechanisms that control their response to favourable or unfavourable site conditions is useful in determining the response of the aboveground components. Toumey (1929), Russell (1977), and Chaney (1981) suggested that root responses are genetically controlled. Some tree species display consistent vertical root distributions across many sites (Bannan 1940; Crossley 1940; Holch 1931; Yen *et al.* 1978; Yeager 1935); other species adapt morphologically to variations in soil properties (Wagg 1967). There is also

¹Funding was provided by the USDA Forest Service and by the Minnesota Agricultural Experiment Station under project 25-54. Published as scientific journal paper No. 14 890 of the Minnesota Agricultural Experiment Station.

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TABLE 1. Species, literature source, adaptation number, number of vertical root samples (*n*), root measure, and mean root distribution coefficient ($\bar{\beta}$) by tolerance class

Species	Source	Climax adaptation No.	<i>n</i>	Root measure	$\bar{\beta}$
Tolerant class					
<i>Acer saccharum</i> Marsh.	Watson and Himelick 1982	10.0	1	Diameter	0.969
<i>Acer platanoides</i> L.	Watson and Himelick 1982	10.0	1	Diameter	0.974
<i>Acer platanoides</i> L.	Watson and Himelick 1982	10.0	1	Length	0.939
<i>Fagus sylvatica</i> L.	Meyer and Gottsche 1971	9.5	1	Number · 100 mL ⁻¹	0.793
<i>Fagus sylvatica</i> L.	Meyer and Gottsche 1971	9.5	2	mg · 100 mL ⁻¹	0.879
<i>Fagus grandifolia</i> Ehrh. (mixed)	Safford 1974	9.5	2	g · L ⁻¹	0.886
<i>Betula lutea</i> L. (mixed)	Hopkins 1939	9.5	3	Number · ft ⁻²	0.898
<i>Betula lutea</i> L. (mixed)	Hopkins 1939	9.5	11	Length · ft ⁻²	0.939
Total			22		
Midtolerant class					
<i>Juglans nigra</i> L. (pure and mixed)	Yen <i>et al.</i> 1978	6.5	6	Number	0.968
<i>Picea glauca</i> (Moench) Voss	Safford and Bell 1972	6.0	1	mg · cm ⁻³	0.829
<i>Picea glauca</i> (Moench) Voss	Safford and Bell 1972	6.0	1	g · m ⁻²	0.886
<i>Picea glauca</i> (Moench) Voss	Sutton 1978	6.0	5	Length	0.862
<i>Picea glauca</i> (Moench) Voss (mixed)	Kimmins and Hawkes 1978	6.0	2	g · m ⁻²	0.870
<i>Picea glauca</i> (Moench) Voss (mixed)	Kimmins and Hawkes 1978	6.0	1	Number · 100 cm ⁻²	0.940
<i>Picea mariana</i> (Mill.) B.S.P.	Strong and La Roi 1983a	6.0	2	Number · dm ⁻²	0.927
<i>Pinus strobus</i> L.	Lutz <i>et al.</i> 1937	4.0	17	Number	0.957
<i>Fraxinus pennsylvanica</i> Marsh.	Watson and Himelick 1982	4.0	1	Diameter	0.981
<i>Fraxinus pennsylvanica</i> Marsh.	Watson and Himelick 1982	4.0	1	Length	0.942
<i>Acer rubrum</i> L.	Watson and Himelick 1982	4.0	1	Diameter	0.974
<i>Quercus alba</i> L.	Gaiser and Campbell 1951	4.0	1	Number · ft ⁻²	0.974
<i>Quercus alba</i> L. (mixed)	Scully 1942	4.0	16	Number	0.954
<i>Quercus rubra</i> L. (mixed)	McClagherty <i>et al.</i> 1982	4.0	1	mg · ha ⁻¹	0.955
<i>Quercus spp.</i> (mixed)	Kochenderfer 1973	4.0	3	Number · 9.3 dm ⁻²	0.972
<i>Prunus serotina</i> Ehrh. (mixed)	Kochenderfer 1973	4.0	5	Number · 9.3 dm ⁻²	0.967
<i>Prunus serotina</i> Ehrh. (mixed)	Bard 1952	4.0	9	Number · 0.18 m ⁻²	0.931
Total			73		
Intolerant class					
<i>Pinus resinosa</i> Ait.	Adams and Chapman 1941	3.0	3	Number	0.925
<i>Pinus resinosa</i> Ait.	Leaf <i>et al.</i> 1970	3.0	2	g · 62 cm ⁻²	0.972
<i>Pinus resinosa</i> Ait. (mixed)	McClagherty <i>et al.</i> 1982	3.0	1	mg · ha ⁻¹	0.966
<i>Liriodendron tulipifera</i> L.	Harris <i>et al.</i> 1977	2.5	2	kg · ha ⁻¹	0.944
<i>Liriodendron tulipifera</i> L. (mixed)	Kochenderfer 1973	2.5	4	Number · 9.3 dm ⁻²	0.975
<i>Populus tremuloides</i> Michx.	Mital 1981	2.0	3	Number · 225 cm ⁻²	0.975
<i>Populus tremuloides</i> Michx.	Strong and La Roi 1983a	2.0	6	Number · dm ⁻²	0.962
<i>Pinus banksiana</i> Lamb.	Adams and Chapman 1941	1.0	4	Number	0.891
<i>Pinus banksiana</i> Lamb.	Strong and La Roi 1983a	1.0	3	Number · dm ⁻²	0.959
Total			28		

evidence of genotypic and environmental interactions in the process of nutrient uptake by roots (Goddard and Hollis 1984). Shade intolerant species such as *Pinus banksiana* Lamb. and *Pinus resinosa* Ait. are better able to grow in soils deficient in moisture, nitrogen, and phosphorus than are midtolerant species such as *Picea glauca* (Moench) Voss and *Pinus strobus* L. (Shirley 1943).

Although soil properties affect root form, our hypothesis was that vertical root distributions are genetically determined and are related to successional status or shade tolerance. We hypothesized that intolerant trees are more-deeply rooted than are tolerant species. This rooting morphology would enable intolerant species to more effectively exploit an unoccupied and more homogeneous substrate. Conversely, tolerant species would better compete for nutrients concentrated near the surface

owing to biocycling. The objectives of this study were to (i) quantify the vertical root distributions of northern tree species and (ii) test our hypothesis of differences in vertical root distributions as related to successional status or shade tolerance.

Methods

Published vertical root distributions for northern tree species were used in this analysis. Root distributions chosen for this study were from trees growing in either planted or natural stands. Stands were either of pure or mixed species composition and even- or uneven-aged, with the median age being 40 years. Soils ranged in texture from clay to sand with most studies being on silt loams; some soils had restricting layers and one soil was organic. Vertical root distributions were measured using a wide variety of techniques ranging from the core method to pit estimation to actual excavations. Root measurements included biomass, number, diameter, and length by soil depth (Table 1).

Species were classified into three tolerance classes based on Curtis's (1959) climax adaptation numbers: tolerant (adaptation numbers 10.0-9.5), midtolerant (adaptation numbers 6.5-4.0), and intolerant (adaptation numbers 3.0-1.0) (Table 1). Separation into classes was also based on Baker's (1950) and Graham's (1954) classification. Species not occurring in Curtis's system were classified using Baker's and Graham's system. Classification of stands of mixed species was based on the major species on the site.

The cumulative root distribution from the surface, or the cumulative fraction of roots (Y) from the surface to any depth (d), was calculated for all vertical root distributions. An asymptotic nonlinear model of the following form was used to describe each vertical root distribution:

$$[1] Y = 1 - \beta^d$$

where Y is the cumulative root fraction from the surface to soil depth d in centimetres and β the estimated parameter. Because we were interested in data from a variety of species, it was necessary to use a wide variety of measures of vertical root distribution. This function standardized the variety of root measures and simply described the decreasing proportion of roots with increasing soil depth. Since β was the only estimated parameter in the model, it was used as a measure or index of the vertical root distribution. High values of β (ca. 0.97) are associated with a larger proportion of roots at deeper soil depths relative to low values of β (ca. 0.92), which are associated with a larger proportion of roots near the soil surface (Fig. 1). Because of both the possible lack of normality of observations within each tolerance class and the variety of data and collection techniques used in each study, a simple nonparametric test, Kruskal-Wallis, was used to test the differences in rooting distributions as measured by the estimated coefficient β among tolerance classes (Conover 1971).

Results and discussion

Quantification of vertical root distributions

Rooting data from 19 published studies, for a total of 123 vertical distributions, were used in the analysis (Table 1). Equation 1 explained between 90 and 96% of the variation in cumulative root fraction by depth for each of the 123 distributions. Hesketh and Moss (1963) used the same functional form to describe the relationship between photosynthetic rates of understory plants and decreasing light intensity. Just as root numbers or biomass decrease exponentially from the soil surface to maximum rooting depth, rates of photosynthesis also decrease from the top of the crown to the soil surface.

The frequency distributions of the parameter β for each tolerance class ranged from a Poisson-like distribution for the intolerant class to a more normal distribution for the tolerant class (Fig. 2). The range of observed β 's increased with increasing tolerance, while the mean, median, and mode decreased (Fig. 2). The mean β for the intolerant, midtolerant, and tolerant classes were 0.95, 0.94, and 0.92, respectively. The hypothesis that the three distributions were the same was rejected at the $p < 0.05$ level, suggesting that intolerant species are proportionally more deeply rooted than tolerant species.

Although absolute differences in the mean β 's between tolerance classes appear to be small, these differences lead to large differences in vertical root distributions. For example, using mean β 's from the tolerant ($\beta = 0.92$) and intolerant ($\beta = 0.95$) classes, approximately 57% of the roots of a tolerant species lie above 10 cm but only 40% of the roots of an intolerant species lie above that depth. Although the β 's were calculated from a variety of root measures, no relation between root measure and the size of the parameter β could be determined (Table 1). Wood *et al.* (1984) also noted that vertical distributions for surface area, biomass, and density of fine (<0.6 mm) roots in a hardwood forest were similar. The use

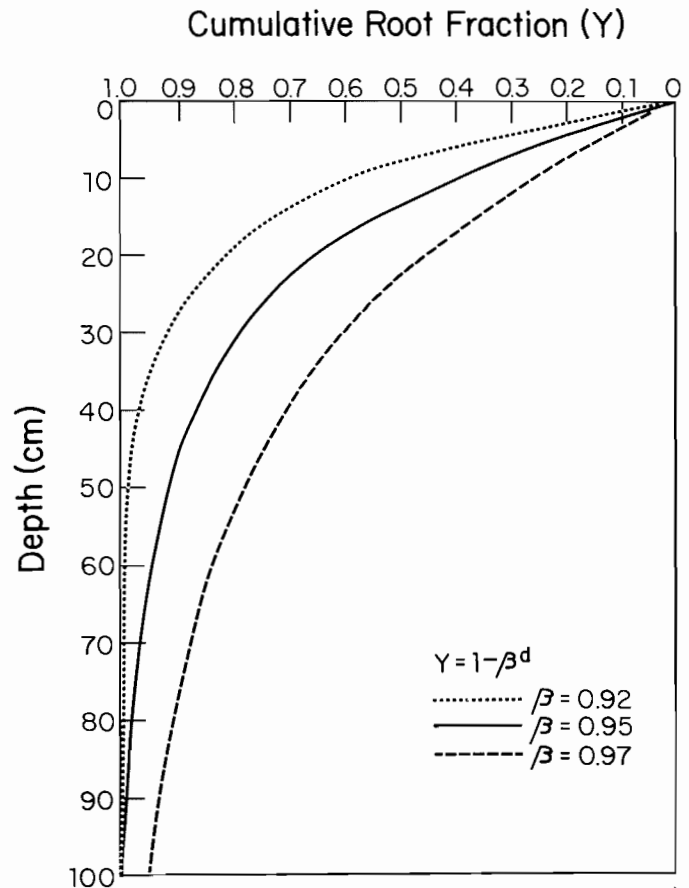


FIG. 1. Vertical root distributions for different β 's for the function $Y = 1 - \beta^d$, describing cumulative root fraction (Y) by depth (d).

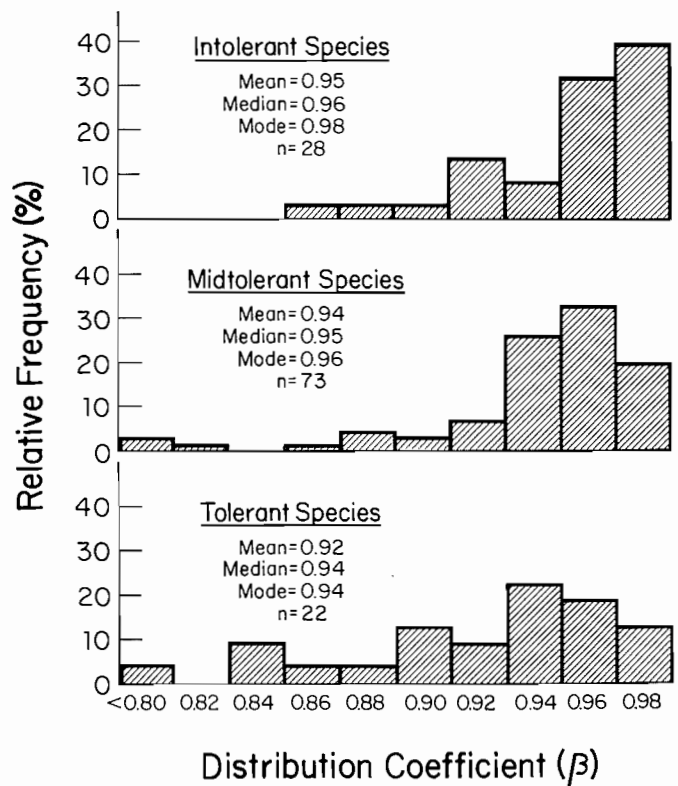


FIG. 2. Relative frequency distributions of parameter β by tolerance class. Class midpoints are indicated.

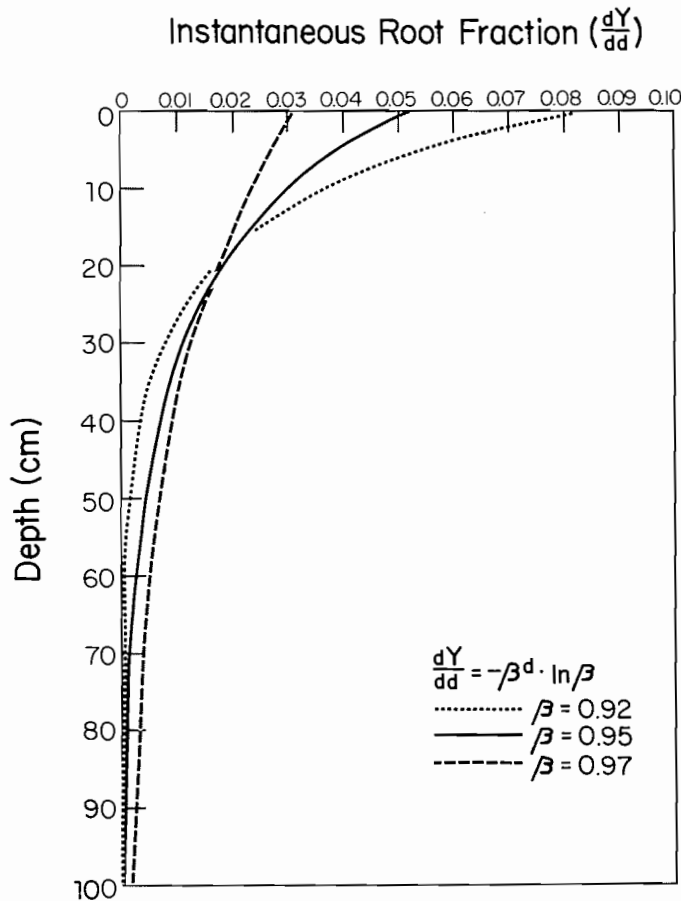


FIG. 3. "Instantaneous" vertical root (dY/dd) distributions for different β 's for the function $dY/dd = -\beta^d \cdot \ln\beta$, describing root fractions at depth d .

of eq. 1, based on proportional distributions instead of actual measures, tends to standardize the data. Differences in data quality and suitability, however, may have led to some of the spread in frequency distributions of parameter β (Fig. 1).

Differences in the parameter β do not reflect differences in root volume or density between trees but only in vertical root distributions relative to depth. Assuming identical root volumes or densities for each successional class, a better comparison of differences in vertical rooting with changes in depth d is the derivative of model 1, an "instantaneous" model of the form

$$[2] \quad dY/dd = -\beta^d \cdot \ln\beta$$

This model describes the actual proportion of roots (dY/dd) at any depth d relative to the total effective rooting depth and standardizes the area under all curves to equal 1.0 (Fig. 3). Use of model 1 or 2 depends on whether the cumulative proportion of roots to a certain depth or the actual proportion of roots at a certain depth is required. Data are not available to fit eq. 2 because of the impossibility of sampling infinitely small depth increments. Since root sampling is always done over increments of depth, mathematical fits of cumulative distributions using eq. 1 are more applicable.

Variation of vertical root distributions

The variability of vertical root distributions within any tolerance class (Fig. 2) may be influenced by both the variety of methods and the type of measurements used in the studies that we consulted, as well as the within and between species

variability. Some authors made no mention of whether roots of woody understory plants were excluded from the analysis or whether roots were sampled from only the mineral soil layers or from both the organic and the mineral soil layers. In most cases, the inclusion of understory roots in the analysis would make the parameter β smaller, as would the inclusion of root estimates from the organic layer. The variability in sampling techniques used in each study as well as possible root deformation owing to outplanting had unknown effects on the parameter β .

The effects of tree age and soil properties on root distribution and form may also be reflected in the variability of vertical root distributions within any tolerance class. Inherent differences in root distributions are more noticeable in tree seedlings than in mature trees (Bannan 1940; Chaney 1981; Holch 1931; Toumey 1929). Maximum rooting depth, however, is usually established during the seedling stage (Lyr and Hoffmann 1967). Coile (1937) found that although root density increases with age, the horizontal and vertical extent of roots is reached at a certain tree age. This indicates that the vertical root distribution is also established.

As a tree develops, root growth patterns are modified by soil properties (Chaney 1981). The extent to which these modifications occur is based on the phenotypic plasticity of a species (Kramer 1980). The increase in variability of the parameter β with increasing tolerance (Fig. 2) may indicate that midtolerant and tolerant species are phenotypically more plastic than intolerant species and are able to adapt or compete within a wider range of forested conditions. *Picea glauca* is a good example of a midtolerant species having a highly plastic root form. Wagg (1967) found the root form of *Picea glauca* to vary considerably by site, producing an elongated taproot on well-drained sites while producing a vestigial or no taproot on soils with excess moisture. While Wagg (1967) found the root form of *Picea glauca* to vary by site, Sutton (1978) found the maximum rooting depth for this species varied little by site. Bannan (1940) found *Pinus banksiana*, an intolerant species, to be nonplastic, consistently producing a taproot with a much deeper rooting system than either *Picea glauca*, *Picea mariana* (Mill.) B.S.P., or *Abies balsamea* (L.) Mill. growing on the same soil.

The possibility existed in our study that intolerant trees occurred primarily on very permeable soils that enhanced deeper rooting, and conversely that midtolerant and tolerant trees were sampled only on heavier soils. Most of our data sets were restricted to one species per site. McClaugherty *et al.* (1982), however, examined root distributions of midtolerant hardwoods (*Quercus-Acer*) and an adjacent stand of intolerant *Pinus resinosa* on the same soil (Entic Haplorthod). Using model 1, β was estimated to be 0.95 for the midtolerant stand and 0.97 for the intolerant stand. These values were similar to the medians for those classes (Fig. 2).

Another significant source of variation may exist within tolerance classes owing to the assignment of climax adaptation numbers (Curtis 1959). Brown and Curtis (1952) stressed that these numbers were not absolute measures of tree physiological characteristics but only relative indices of the behaviour of one species in relation to another. Daubenmire (1947) and Zeide (1980) emphasized that tolerance to light can vary with air temperature, amount of precipitation, and site quality. Thus geographical variation within species can change its tolerance rating. For example, *Pinus strobus* has been considered to be a midtolerant or tolerant species in some regions of Michigan, while in New York it is sometimes considered to be an intolerant species (Curtis 1959).

Successional implications

The differences in vertical root distributions between deep-rooted intolerant species and shallow-rooted tolerant species are potentially important in nutrient cycling (Strong and La Roi 1985). Changes in nutrient cycling are important in successional development (Odum 1969). Compared with mature successional stages, earlier stages have more rapid nutrient exchange rates between organisms and the environment (Odum 1969), increasing the amounts of nitrogen, organic carbon, and organic material in an initially homogeneous substrate (Crocker and Major 1955). In secondary succession, following a disturbance, the ability of a species to recover nutrients that may have moved into the subsoil is important for forest regeneration and regrowth (Wood *et al.* 1984). The establishment of deep-rooted intolerant species on a disturbed site provides increased nutrients to the forest floor from deeper soil depths via litter fall and foliar leaching (Kimmins and Hawkes 1978).

Lutz (1928) stated that early successional species become the "nurse crop" for later successional species. As intolerant and midtolerant trees mature, increased amounts of root detritus and other organic material enrich the soil, making it more favourable for further root growth (Grier *et al.* 1981). Root channels created by detritus provide new pathways with very little resistance for roots (Rowe and Acton 1985). Since most root detritus occurs in the surface soil, conditions are made more favourable for shallower-rooted trees to invade the site. Strong and La Roi (1983b) concluded that the soil profile has a definite vertical partitioning that favours growth of shallow *Picea glauca* roots over deeper *Pinus banksiana* roots. This is due to the ability of *Picea glauca* to effectively absorb more water and nutrients from a richer soil surface. From experiments in a northern hardwood forest, Wood *et al.* (1984) found phosphorus to be tightly regulated within the surface soil owing to the interaction between processes of biological decomposition and tree nutrient uptake. Midtolerant or tolerant species, once established, maintain the fertility of the surface soil by cycling nutrients from the soil to the tree and back again, effectively "closing" the cycle of nutrients within a forested ecosystem (Odum 1969).

Conclusions

Tree vertical rooting patterns affect the path of plant succession. The inherent genetic potential of a tree has a strong influence on its vertical root distribution and root form. Just as a tree species is identifiable by its aboveground form, so too is the belowground form distinct. This does not mean that shallow-rooted trees will not grow deeply or conversely that deep-rooted trees will never have shallow root systems. However, if under optimum soil conditions a species has a certain vertical root distribution, deviations from that distribution can be considered potentially stressful, decreasing the competitive ability of a tree and thus its aboveground productivity (Grime 1979). Dement and Stone (1968) found that height growth of intolerant *Pinus resinosa* was limited on poorly drained sites, indicating that the site was limiting to the inherent deep-rooting tendency of *P. resinosa*. Fayle (1978) also concluded that *Pinus resinosa* seedlings need to develop a deep vertical root system within the first 10 years for good top growth.

Although we have shown a significant relationship between tolerance or successional status and vertical root distributions of trees, we are not attempting to explain succession based solely on a species' genetic predisposition to a certain vertical root distribution and light response. We do believe, however, that succession, whether primary or secondary, is controlled by both

the above- and below-ground tree responses to their environments. Grime (1979) emphasized that intraspecific differences in competitive ability occur owing to genetic variation and species adaptations to stress-related phenomena such as suboptimal temperatures or low amounts of light, water, or nutrients. A tree's ability to compete for soil resources as well as light is a function of the vertical and horizontal distribution of the absorbing plant surfaces in space and time (Grime 1979).

Analysis of vertical root distributions, and of rates of root growth and elongation, can provide a better physiological understanding of successional paths and a better means of selecting species well adapted to certain site conditions. Empirical techniques as used in this study can also simplify the complexity of deciphering relationships between above- and below-ground components. Our hypothesis would have been subjected to a better test if the data had been collected similarly and a parameter such as surface area or fine root biomass had been the observed root measure. Standardizing techniques in estimating vertical root distributions will help to further refine the determination of significant differences in vertical root distributions and of their relation to successional status.

Acknowledgements

The authors wish to thank all the researchers who took painstaking measures to collect the data used in our analysis. We would also like to thank W. W. McFee, J. S. Rowe, G. D. Mroz, and D. D. Reed for their constructive reviews of this manuscript.

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