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Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level

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Abstract

The relationship of global climate change to plant growth and the role of forests as sites of carbon sequestration have encouraged the refinement of the estimates of root biomass and production. However, tremendous controversy exists in the literature as to which is the best method to determine fine root biomass and production. This lack of consensus makes it difficult for researchers to determine which methods are most appropriate for their system. The sequential root coring method was the most commonly used method to collect root biomass data in the past and is still commonly used. But within the last decade the use of minirhizotrons has become a favorite method of many researchers. In addition, due to the high labor-intensive requirements of many of the direct approaches to determine root biomass, there has been a shift to develop indirect methods that would allow fine root biomass and production to be predicted using data on easily monitored variables that are highly correlated to root dynamics. Discussions occur as to which method should be used but without gathering data from the same site using different methods, these discussions can be futile. This paper discusses and compares the results of the most commonly used direct and indirect methods of determining root biomass and production: sequential root coring, ingrowth cores, minirhizotrons, carbon fluxes approach, nitrogen budget approach and correlations with abiotic resources. No consistent relationships were apparent when comparing several sites where at least one of the indirect and direct methods were used on the same site. Until the different root methods can be compared to some independently derived root biomass value obtained from total carbon budgets for systems, one root method cannot be stated to be the best and the method of choice will be determined from researcher's personal preference, experiences, equipment, and/or finances.

Introduction

Global climate change scenarios associated with attempts to increase the sequestration of carbon in ecosystems to reduce atmospheric CO_2 levels have generated much interest in synthesizing forest biomass data, especially since forests have been suggested to play an important role in controlling global carbon pools and fluxes (Dixon et al., 1994; Vogt et al., 1996). Many models are being developed to predict how human activities are changing carbon pools and fluxes over large regions (Aber and Federer, 1992; Landsberg et al., 1995) but the development of these models is hampered by the incomplete data that exist for some ecosystems and/or their components and our inability to balance the global carbon cycle (Taylor, 1993; Vogt et al., 1996). Since root production has been suggested to contribute about half of the carbon being cycled annually in many forests (Vogt et al., 1996) and 33% of the global annual net primary production (Jackson et al., 1997), obtaining accurate estimates of belowground biomass are important. Root biomass should not be treated as a black box or predicted using relationships developed in other ecosystems for scaling up in global modelling efforts or used as part of a model

to predict forest growth responses to environmental stresses (Dixon et al., 1990).

A uniform agreement of how root biomass and production should be sampled and calculated, however, does not exist in the literature. Most of the controversy for estimating fine root dynamics are associated with the estimates of production and turnover, and how different abiotic resources may change these parameters (Aber et al., 1985; Gower et al., 1992; Grier et al., 1981; Milchunas and Lauenroth, 1992; Publicover and Vogt, 1993; Singh et al., 1984; Vogt et al., 1986a). One of the reasons for controversies in estimating fine root production and turnover in forests is that trees have highly variable allocations of photosynthate to fine roots (varying from 4–69% of total plant carbon annually fixed) which can therefore significantly affect the ecosystem-level processes (Vogt et al., 1996). In contrast to the apparently low variability in how much photosynthate is allocated to fine root biomass under different conditions, its production and turnover appear to be highly sensitive to the environment and is a major response mode of plants adjusting to a changing environment (Eissenstat and Van Rees, 1994; Gower et al., 1992, 1994; Persson et al., 1995; Vogt et al., 1990). The high labour-intensive requirements of most techniques to measure root biomass means that any attempt to build consensus on different approaches has been difficult because few studies have been designed to measure and compare different methods at the same time.

Since roots are the 'hidden half' of most terrestrial ecosystems (Waisel et al., 1991), our ability to design sampling protocols have been limited by our inability to visibly monitor the dynamics of an entire root system of a plant. Visible aboveground roots are characteristic of tropical rainforests (Benzing, 1991), but unfortunately, they are not a generality for most forests or other natural ecosystems. It also follows that sampling protocols for roots are easier to design when the physical boundaries are clear as in tropical forests where adventitious roots grow into the organic detrital layers trapped in the canopy of trees (Nadkarni, 1981), or where roots (Sanford, 1987) or nodules of nitrogen-fixing plants are found climbing along the trunks of adjacent trees (Publicover and Vogt, 1992). But, those root habitats are mostly the exception rather than the rule. Researchers are handicapped in root studies by having to design sampling protocols without having prior information on the root distribution patterns, phenology or seasonality of root growth or how root biomass or morphological characteristics respond to the abiotic environments or to a changing environment.

Due to the inherent difficulties of studying plant root dynamics in general in the field, there has been a tendency to focus on collecting data on root biomass and their distribution within the soil profile (Böhm, 1979; Vogt and Persson, 1991). This type of focus is valid when examining the ecosystem role of roots in forest carbon cycles, however, it does not assess the direct or indirect influences roots have on soil biological and chemical activities, or even that roots may have other adaptations for increasing their acquisition of abiotic resources (e.g., mycorrhizas) that a biomass estimate does not reflect (Caldwell, 1979; Eissenstat and Van Rees, 1994; Van Noordwijk, 1983; Vogt et al., 1991). Data documenting the impact of these other activities of roots on ecosystem functions are needed as part of field experiments but this is beyond the scope of this paper. Root systems may also respond to environmental changes by increasing the inputs of soluble (e.g., exudates) or volatile organic carbon compounds into the soil environment (Schwab et al., 1983) or by changing their respiration rates (Lambers and Poorter, 1992; van der Werf et al., 1994). These contributions by roots to ecosystem carbon pools and fluxes are typically ignored in the field because of inadequate tools for measuring these processes. Similarly, the carbon flow to fungal or bacterial symbionts on root systems should be included as part of field estimates of belowground production (Fogel and Hunt, 1983; Rygiewicz and Andersen, 1994; Vogt et al., 1982) but, again, are not because of sampling difficulties.

When the research question is related to carbon budgets and carbon allocation at an ecosystem level, coarse root biomass and production data should also be collected. Methods for measuring coarse root biomass are well developed and not controversial. Large, structural roots can be estimated using allometric equations developed from an above-ground measurements (see Santantonio, 1990) as their growth is similar to above ground branches. However, only a small portion of annual root production occurs in this root size fraction (see Grier et al., 1981). Therefore, methods for determining coarse root biomass and production will not be discussed in this paper.

Many different approaches have been used to study fine root biomass in the field, with some techniques used more frequently than others. However no one technique has been accepted universally as the best. Due to the high labour-intensive requirements of most field techniques, researchers have also attempted to

indirectly estimate fine root biomass. This paper will present some of the advantages and limitations of the most commonly used direct and indirect methods for quantifying fine root biomass in forests. This will not be an intensive review of all the research conducted world-wide on fine root biomass (see Vogt et al., 1996) but will utilize those studies where several methods were used on the same site. The direct root methods examined include sequential soil coring, ingrowth cores, and minirhizotrons while the indirect methods include carbon fluxes or nitrogen budget approaches and correlations of root biomass or production to pools or fluxes of limiting abiotic resources. The purpose of this paper is to give the reader an understanding of existing root biomass methods and what are their advantages and disadvantages. A carbon budget approach that determines the total amount of carbon fixed by a plant and how carbon is allocated to growth and maintenance (i.e., tissues, respiration, secondary chemicals, symbionts etc.) has the best chance for validating any belowground biomass numbers produced, however, few studies have attempted to estimate total carbon pools and fluxes concurrent with direct measures of fine root biomass (for exceptions see Ågren et al., 1980; Ewel et al., 1987; Gholz et al., 1986).

Factors to be considered when designing sampling protocols

There are several factors that need to be considered when designing root sampling protocols for the field: (1) minimize the disturbance to the site caused by sampling (e.g., large monoliths and excavations of roots will disturb a sizable portion of the study site which is unacceptable if the study site will be monitored over a long-time scale); (2) attempt to collect data on intact roots instead of always destructively sampling roots (e.g., after the disturbance associated with initial installation, minirhizotrons is a non-destructive manner for monitoring root activity in the field; remeasurement of the same root section when measuring root respiration in the field) (Smucker et al., 1987; Vogt et al., 1989); (3) coordinate sampling in the field to the plant's phenology so the peaks and lows of root growth can be determined (thereby decrease sampling intensity during these periods) (Vogt et al., 1986a): (4) sample over longer time scales to determine the seasonal and year-to-year variability in root activity (see Santantonio and Hermann, 1985, for the high year to year variability in root dynamics); (5) utilize functional criteria (i.e., not just structural root categories or an arbitrary root diameter classification) to categorize roots during laboratory processing or as part of the visual monitoring of roots on glass window surfaces (Vogt and Persson, 1991) and (6) sample the spatial heterogeneity of a site instead of trying to homogenize sampling. When deciding on what is appropriate sampling technology, the physical constraints of the soil environment (e.g., high percent rock content of soil, presence of hard pans or impermeable layers) or the potential existence of functional roots as deep as 50 m in the soil (Freckman and Virginia, 1989; Jackson et al., 1996; Nepstad et al., 1994; Stone and Kalisz, 1991) can cause problems in directly applying any of the root biomass techniques. Because soil physical factors can modify the quantity, density, branching patterns, diameter classes, depth of rooting and longevity of roots (see Barber, 1984; Rendig and Taylor, 1989), they will indirectly affect the sampling protocols. In forest ecosystems, rocks, hard pans, and dense clays can mechanically impede and/or affect root growth as well as make coring or digging difficult or impossible (Ruark et al., 1982).

With each method of collecting root data, one has to keep in mind that root distribution is highly variable and is constrained by the microsite spatial variability created by the soil environment or by the different plant species existing on each site (Roy and Singh, 1995; Vogt et al., 1995). If the environment is very heterogeneous, the sampling intensity will have to be increased to insure that the site is sufficiently sampled to obtain an accurate mean site value (it may be impossible on some sites to collect enough samples to be confident of the sample mean at the 95% level and researchers will have to accept lower statistical significances but sampling at a level able to show significant differences between sites or treatments) . At times, it will be necessary to specifically sample the different substrates (e.g., large woody residues, mineral soil, etc.) on a site separately (e.g., stratified sampling) and also determine how much of the ground surface area is associated with each substrate type. The sampling intensity should be adjusted so one can be confident of (1) determining an accurate mean value for the site when using the sequential coring technique or ingrowth core technique, or (2) sufficiently monitoring a representative surface area of the soil horizons on the root observation windows of a rhizotron and the minirhizotron observation tubes.

When trying to identify functional/structural relationships of plant roots using experimental manipulations in the field, the potential connectiveness (i.e.,

root grafting) of several plants can cause problems in understanding the nutrient and the carbon dynamics of fine roots at the ecosystem level. For example, root grafting between the same tree species or even between different species is quite common and transfer of materials can occur through these connections (Bormann and Graham, 1958; Graham and Bormann, 1966; Vogt et al., 1993). When roots from one plant extend a considerable distance from the base of a tree trunk, it is almost impossible to identify the specific tree origin of the roots and therefore to identify the spatial scale relevant for that tree (Stone and Kalisz, 1991). For example, Waisel (1972) measured a root of *Tamarix aphylla* extending 37 m from its base. This type of extensive root growth means that any type of fertilizer treatment must insure that the entire rooting zone is in the treatment zone or uptake of nutrients could be occurring outside of that zone. It is more labour intensive to design a sampling scheme that takes into consideration this extensive spread of roots and their irregular distribution (Henderson et al., 1988; Roy and Singh, 1995) and growth into nutrient rich microsites (Eissenstat and Caldwell, 1988; Friend et al., 1990; St. John et al., 1983). Whole plant root excavations can be conducted to determine root extension for different ecosystems (see Persson and Baitulin, 1996) but this can be a major commitment of field research time if fine root biomass is desired for forest ecosystems.

Root research also needs to be able to separate roots into vitality classes since many researchers are interested in changes in the live root component (equivalent to fine root production) but, because of an inability to continuously monitor changes in live fine root biomass in the field, changes in dead root biomass become important to quantify (Santantonio and Grace, 1987). Fine root vitality classes have been developed using a variety of visual, mechanical and chemical techniques (Joslin and Henderson, 1984; McQueen, 1968; Ruark and Bockheim, 1987; Van Praag, 1988; Vogt and Persson, 1991). Roots are usually visually sorted into live and dead categories based on criteria that utilizes the tensile strength of the root itself and color of the root tissues. However, some fine roots are difficult to categorize as either live or dead using visual criteria so some researchers have been forced to develope a third category for roots that are not clearly live or dead but at some stage of senescence (Clemensson-Lindell and Persson, 1995; Gholz et al., 1986). To overcome this limitation of visual separation of roots, a series of chemical analyses have been proposed (Clemensson-Lindell, 1994; Joslin and Henderson, 1984). Joslin and Henderson (1984) used triphenyltetrazolium chloride to evaluate the ratio of live to dead tissues in oak. This technique works quite successfully on roots that are translucent since the extraction process will not contribute color which can confound spectrophotometric analyses. Clemensson-Lindell (1994) and Clemensson-Lindell and Persson (1995) also used triphenyltetrazolium chloride combined with three vitality classes based on morphology (i.e., degree of suberization of fine roots). Clemensson-Lindell (1994) showed that the vitality classes based on morphological groupings did not duplicate those found with the extraction groupings formed with triphynltetrazolium chloride – this enzyme technique was only able to distinguish between clearly live and clearly dead roots but could not distinguish those root conditions in the third group where the root condition was not morphologically distinctive. Furthermore, stressing the forest stand by changing its nitrogen content was also reflected by changes in the enzyme levels. Therefore, environmental stress changed the relationship between root vitality class and enzyme activity (Clemensson-Lindell, 1994).

General overview of direct root methods

It must be remembered that all of the techniques discussed in this section can be used to obtain data on root biomass and net primary production (NPP). However, each method has significant advantages or disadvantages that frequently will determine whether it should be used in preference over another. Understanding the advantages and limitations of each method may then determine the choice of method used for a given ecosystem.

Sequential soil coring

The most common approach to determining fine root biomass and NPP (Net Primary Production) in the field has been the sequential coring method (Vogt and Persson, 1991). This method was also used in the field to estimate mycorrhizal biomass and production (see Fogel and Hunt, 1983; Vogt et al., 1982). Since a mean fine root biomass value is usually obtained by summing all sampling dates during a year, mean fine root biomass values do not fluctuate as much during a year and there are less errors in obtaining this value than measurements of net primary production. Since fine root biomass contributes such a small (typically

<5%) portion of the total tree biomass biomass, errors in estimating this parameter will contribute little to analysis error at the ecosystem level (Vogt et al., 1996).

Several different approaches have been used (sometimes even concurrently; see Table 1) to analyze data obtained with the sequential soil coring approach. Of the three methods used for estimating fine root NPP, the most commonly used approach in the past was to use differences in biomass between the maximum and minimum fine root biomass measured during a year. This first approach should be used only when significant changes are recorded between the maximum and minimum (Vogt et al., 1986a), even though it has been used to estimate NPP when no significant differences were found to exist between sampling dates (Table 1). A second approach introduced by Santantonio and Grace (1987), called a Compartmental Flow model or Decision Matrix method, incorporates changes in live and dead root biomass and losses from dead root biomass due to decomposition. This approach was introduced because root growth, mortality and replacement do not occur disjunct from one another so that root production would be underestimated. This approach has not been utilized as readily by researchers since it requires the simultaneous determination of fine root decomposition during the study year and this is a measurement that has been difficult to obtain as well as potentially introducing more errors to the calculations if not done correctly. The third approach was introduced by Persson (1978) where all positive differences in root biomass between each sequence of sampling dates were summed. Since significant differences were not used with this approach, all data were corrected for overestimation by subtraction of a correction factor that was determined as the difference between the estimated values and the expected values produced from purely stochastic variable generation (see Persson, 1978 for greater detail).

When estimating fine root NPP using sequential soil cores, a good approach to calculate NPP is to use the decision matrix method. However, the amount and type of data required for such an analysis usually result in the minimum–maximum approach being commonly used and researchers stating that this underestimates production. If the second approach (compartmental flow method) is used, the following equation has been recommended to estimate net primary production of fine roots (e.g., NPP_r) (see Santantonio and Grace, 1987; Vogt et al., 1989):

$$NPP_r = B_{t2-t1} + M_{t2-t1} + D_{t2-t1},$$

where B_{t2-t1} (B = biomass) is the statistically significant change in live fine root biomass between time 1 and time 2; M_{t2-t1} (M = mortality) is the statistically significant change in dead root biomass between time 1 and time 2; and D_{t2-t1} (D = decomposition) is an estimate of root decay between time 1 and time 2 (Vogt et al., 1989). If non-significant positive increments in live root biomass due to random fluctuations are summed, this can lead to the overestimation of productivity (Kurz and Kimmins, 1987) and then one would have to correct for this overestimation as presented by Persson (1978). Statistically significant increments should be used when calculating production (Vogt et al., 1986a); even though this may not be possible if distinctive peaks of fine root growth do not exist. If a site does not have statistically significant changes in root biomass between sampling dates, as was recorded by Nadelhoffer et al. (1985) in forests in Wisconsin, the sequential coring technique by itself is not the best approach to use. In such cases, it is important to separate roots into the different vitality classes from sequential cores (e.g., Clemensson-Lindell and Persson, 1995) and to combine sequential coring with the minirhizotron method to detect peaks of root growth. Non-significant changes in root biomass should be expected in ecosystems where plant growth is asynchronous from one another; such as some of the grasslands where species dominance changes during the growing season (Vogt et al., 1986a). Since this equation also does not include exudation and respiratory losses of carbon, it should be considered an underestimate of total carbon transfers to roots (Lambers and Poorter 1992; Schwab et al., 1983). The magnitude of carbon transfers to roots will also vary based on the species of mycorrhizal fungi found colonizing the roots and the nutrient status of the site which changes the amount of respiratory losses of carbon as part of nutrient uptake by plant roots (Rygiewicz et al. 1994; Van der Werf et al., 1994). Ideally the equation given above should be modified to include these components as given below:

$$NPP_r = B_{t2-t1} + M_{t2-t1} + D_{t2-t1} + E + R + Myc$$

where E = carbon losses as exudation, R = carbon losses with respiration and Myc = carbon allocation to mycorrhizal tissues.

To estimate production using the equation for the second approach presented above requires data on live

Table 1. Comparison of different methods used to calculate fine root production on the same forest site

Ecosystem	Sequential Soil Coring/ Max-Min method using significant differences	Sequential Soil Coring - Decision Matrix method where $NPPr = \Delta B_{t2-t1} + \Delta M_{t2-t1} + D^{**}_{t2-t1}$	Sequential Soil Coring - Σ positive biomass changes and over-estimation corrected (Δ biomass + Δ necromass)****	Soil CO_2 efflux+ litterfall method $R_s - P_a = P_b + R^*_r$	N budget approach $N_{fr} = N_a - N_w - N_{al}$ & $NPP_{fr} = N_{fr}/N^{*****}_{conc}$	References
	g m^{-2} yr^{-1} [study year]	g m^{-2} yr^{-1} [study year]	g m^{-2} yr^{-1}	g m^{-2} yr^{-1} [study year]***	g m^{-2} yr^{-1}	
Pinus resinosa (Wisconsin, USA)						Haynes and Gower (1995)
Control	251 [1991]	284 [1991]	–	1516 [1991]	–	
Control	180 [1992]	150 [1992]	–	1236 [1992]	–	
Fertilized	94 [1991]	150 [1991]	–	1070 [1991]	–	
Fertilized	194 [1992]	208 [1992]	–	506 [1992]	–	
Northern Hardwood (New York, USA)	150 (231[#])	200	–	270	–	Burke and Raynal (1995)
Pinus resinosa (Wisconsin, USA)						Gower et al. (1996)
Control	407	–	–	560 (280)	–	
Fertilized	184	–	–	420 (210)	–	
Pinus ponderosa (Montana, USA)						Gower et al. (1996)
Control	115	–	–	520 (260)	–	
Fertilized	149	–	–	520 (260)	–	
Pinus elliottii (Florida, USA)						Gower et al. (1996)
Control	115	–	–	1480 (740)	–	
Fertilized	139	–	–	1160 (580)	–	
Pinus sylvestris (Sweden)						Persson (1978)
Calluna dominated	–	–	152 (284)	–	–	
Non-Calluna dominated	–	–	165 (407)	–	–	
Pinus resinosa (Massachusetts)	410[#]	1090[#]	–	–	420	Aber et al. (1985); McClaugherty et al. (1982)

Table 1. Continued

Ecosystem	Sequential Soil Coring/ Max-Min method using significant differences	Sequential Soil Coring - Decision Matrix method where $NPPr = \Delta B_{t2-t1} + \Delta M_{t2-t1} + D^{**}_{t2-t1}$	Sequential Soil Coring - Σ positive biomass changes and over-estimation corrected (Δ biomass + Δ necromass)****	Soil CO_2 efflux+ litterfall method $R_s - P_a = P_b + R^*_r$	N budget approach $N_{fr} = N_a - N_w - N_{al}$ & $NPP_{fr} = N_{fr}/N^{*****}_{conc}$	References
	g m^{-2} yr^{-1} [study year]	g m^{-2} yr^{-1} [study year]	g m^{-2} yr^{-1}	g m^{-2} yr^{-1} [study year]***	g m^{-2} yr^{-1}	
Quercus rubra/ Acer rubrum (Massachusetts)	510#	1140#	–	–	400	Aber et al. (1985); McClaugherty et al. (1982)
Quercus rubra (Wisconsin)	52#	–	–	–	524–550	Aber et al. (1985); Nadelhoffer et al. (1985)
Quercus belutina (Wisconsin)	174#	–	–	–	591–610	Aber et al. (1985); Nadelhoffer et al. (1985)
Quercus alba (Wisconsin)	115#	–	–	–	410–413	Aber et al. (1985); Nadelhoffer et al. (1985)
Pinus strobus (Wisconsin)	97#	–	–	–	250–257	Aber et al. (1985); Nadelhoffer et al. (1985)
Pinus resinosa (Wisconsin)	69#	–	–	–	198–200	Aber et al. (1985); Nadelhoffer et al. (1985)

Table 1. Continued

Ecosystem	Sequential Soil Coring/ Max-Min method using significant differences	Sequential Soil Coring - Decision Matrix method where $NPPr = \Delta B_{t2-t1} + \Delta M_{t2-t1} + D^{**}_{t2-t1}$	Sequential Soil Coring - Σ positive biomass changes and over-estimation corrected (Δ biomass + Δ necromass)****	Soil CO_2 efflux+ litterfall method $R_s - P_a = P_b + R^*_r$	N budget approach $N_{fr} = N_a - N_w - N_{al}$ & $NPP_{fr} = N_{fr}/N^{*****}_{conc}$	References
	g m^{-2} yr^{-1} [study year]	g m^{-2} yr^{-1} [study year]	g m^{-2} yr^{-1}	g m^{-2} yr^{-1} [study year]*****	g m^{-2} yr^{-1}	
Acer rubrum (Wisconsin)	110#	–	–	–	402-550	Aber et al. (1985); Nadelhoffer et al. (1985)
Quercus rubra (Wisconsin)	253#	–	–	–	120	Aber et al. (1985)
Pinus strobus (Wisconsin)	162#	–	–	–	140	Aber et al. (1985)
Quercus alba (Wisconsin)	305#	–	–	–	340	Aber et al. (1985)
Quercus rubra (Wisconsin)	235#	–	–	–	250	Aber et al. (1985)
Acer rubrum (Wisconsin)	106#	–	–	–	650	Aber et al. (1985)

*R_s = annual soil respiration; P_a = litterfall (aboveground detritus production); P_b = belowground detritus production; R_r = root respiration.
**NPPr = $\Delta B_{t2-t1} + \Delta M_{t2-t1} + D_{t2-t1}$, where NPPr = net primary production of fine roots, ΔB_{t2-t1} = statistically significant increments of biomass between two sampling dates, ΔM_{t2-t1} = statistically significant increments of necromass between two sampling dates, and D = decomposition of roots between the two sampling dates.
***Calculated by multiplying authors data by 2.
****Summation of positive changes in root mass between each sampling date, corrected for overestimation by subtraction of a correction factor (difference between the estimated values of belowground net primary production and belowground necromass and the 'expected values for the correspondingly purely stochastic variables') (Persson, 1978).
*****$N_{fr} = N_a - N_w - N_{al}$, where N_{fr} = N allocation to fine roots, N_a = nitrogen availability, N_w = nitrogen allocated to woody biomass, N_{al} = nitrogen allocated to aboveground litter. NPPfr = Nfr/N concentration, where NPPfr = fine root net primary production, Nfr = total allocation of nitrogen to fine roots, N concentration = measured N concentration in fine roots.
Data did not use significant differences in calculations.

and dead fine root biomass at each sampling time plus an estimate of root decay during these time intervals. Since root growth, mortality and decay can occur simultaneously (Santantonio and Grace, 1987), it is important to know all the transfers that can occur between these components. For example, even if a similar live root biomass is measured at two time intervals, there is no way of knowing whether the same live root pool is being measured or whether there was a cycle of death and replacement which makes it appear unchanged. Furthermore, it is essential to know the disappearance rate of dead roots (as measured by the decomposition rate) since fine roots are being lost from the dead root pool due to decomposition but new dead roots are also being added to the dead root pool during the same time interval. Using a simulation model approach, the accuracy of fine root net primary production was most affected by the decay rates (Publicover and Vogt, 1993). If the rate of transfer into and out of the dead root pool is the same, it will appear as if no change in dead roots has occurred. Exactly for the same reasons, total (live + dead not separated into vitality classes) fine root data should not be collected as the final goal of data acquisition. The proportion of live and dead root biomass may be fluctuating significantly during the sampling intervals but is not apparent as any significant change in the total value because both components balance one another in association with root decomposition to produce a non-fluctuating total biomass (see Singh et al., 1984; Vogt et al., 1986a). The actual starch concentrations and seasonal variations in starch content will also influence the dry weight estimates especially when starch can be up to 30% of the dry weight of root tissues (Ericsson and Persson, 1980) and can decrease to less than 1% depending on the time of year (Vogt et al., 1985).

One of the problems that has to be addressed with all root methods, but is especially relevant for the sequential root coring method, is whether the approach underestimates or overestimates root production (Kurz and Kimmins, 1987; Persson, 1978; Publicover and Vogt, 1993; Santantonio and Grace, 1987; Singh et al., 1984; Vogt et al., 1986a). Earlier it was assumed that all root production estimates were underestimates because other carbon losses are not accounted for from roots (e.g., exudation, respiration or root sloughing) and also root growth that does occur between the sampling periods is not measured. In addition, periods of growth, mortality and decomposition of root tissues may occur simultaneously and are probably occurring between two sampling periods which contributes to underestimating root production (Santantonio and Grace, 1887). In contrast, Sala et al. (1988) suggested that belowground NPP is always overestimated because of sampling errors that accumulate as the frequency of sampling increases during a year (they suggest this error occurs even when significant differences are examined). For forest ecosystems, many of the positive changes in fine root biomass between sampling dates are typically not significant (Gower et al., 1992; Grier et al., 1981; Vogt et al., 1982) so the type of error accumulation suggested by Sala et al. (1988) are not common. Because of the difficulty of designing an experiment that would allow a researcher to examine sources of error in root production estimates, most reported analyses of calculation errors have been based on models or computer simulations (Kurz and Kimmins, 1987; Publicover and Vogt, 1993; Singh et al., 1984). It is clear that if non-significant differences between sampling dates are summed to determine root growth, fine root production will be over-estimated since random errors and biases will accumulate when summing differences between sampling dates. It is also apparent that using significant differences between sampling dates only using changes in live roots will underestimate production since changes in the live and dead pools and losses to decomposition are occurring between sampling dates and are not accounted for, and none of the other losses of carbon (e.g., respiration, exudation) from root tissues are added to the estimates.

If distinct maximum and minimum periods of root biomass occur on a site, it is important that core sampling frequency and intensity is sufficient during those periods to insure collecting data that reflects these peaks and not the periods of transition between them. Production estimates obtained from cores collected during the transition period between the minimum and maximum root biomass periods will underestimate production. Measurement must be scheduled for appropriate time points during an annual growth cycle, so that all significant changes in fine root growth and/or mortality can be sampled. Since year to year variation may occur in the timing of significant increases in root biomass (see Keyes and Grier, 1981; Santantonio and Hermann, 1985), the temporal sampling design should consider that root growth cycles may be offset from year to year by a month or two.

Some information exists in the literature concerning seasonal cycles of root and shoot growth by plant species and whether they are evergreen or deciduous (Keyes and Grier, 1981; Lyr and Hoffman, 1967; Vogt

et al., 1986b). This type of information can be very useful to help decide when root growth is minimal or maximal, especially if researchers are unable to monitor root phenology for the site prior to collecting sequential cores. General patterns of root biomass change have been identified for many ecosystems. For example, temperate deciduous trees generally have a peak in root biomass prior to shoot growth in the spring, with maximum root growth often occurring in June or July and decreasing by August or September (Lyr and Hoffman, 1967). Midsummer cessation of root growth is often tied to environmental influences such as drought and/or high temperatures, and/or the fact that the shoots are a greater sink for carbohydrates during this time of year (Mooney 1972; Waring and Schlesinger, 1985).

The most serious disadvantage to the use of the sequential coring technique is (1) the amount of time and labour, and the resultant financial costs, associated with the cleaning and sorting roots from the cores and (2) the problem of deciding what is the best way of predicting fine root production after the root cores have been processed (Kurz and Kimmins, 1987; Publicover and Vogt, 1993; Singh et al., 1984; Vogt et al., 1986a). Errors can arise even in the process of making the decisions of whether to separate roots into live and dead categories (Clemensson-Lindell, 1994; Clemensson-Lindell and Persson, 1995; Joslin and Henderson, 1984). It is nearly impossible to visually identify roots that are senescing therefore adding ambiquity into the classification of roots into viability classes (Vogt and Bloomfield, 1991). Even data on root decay are difficult to obtain because of methodological problems (Vogt et al., 1991). Roots can be examined microscopically and with the use of stains but this is feasible only on a subsample of roots or the sorting process slows down until it becomes impractical to do this type of work.

Ingrowth cores

Ingrowth cores is a method that replaces an intact soil core removed from the ground with an equivalent area of root free soil from the site or with sand (see Vogt and Persson, 1991 for more details). The root free soil added back into the hole is contained within a sleeve with mesh openings that can be used to remove the cores after leaving them in the field for different time intervals. The subsequent growth of roots into this core is used to estimate fine root production in the field.

This method was introduced by Flower-Ellis and Persson in 1980 and has been applied to both agricultural crops and forest ecosystems. Ingrowth cores are very effective in studying ecosystems where root growth is rapid (e.g., wet tropics). As a tool, ingrowth cores can be used to obtain data on (1) relative growth rates of roots in different environments (root production), (2) the effect of different nutrients (for example using either P, Ca or N additions), trace elements, or symbiotic microorganisms on root growth by spiking individual cores with one of the above, and (3) to identify the role of pathogens or toxic trace elements (i.e., Al) in sites by reciprocally transplanting healthy versus diseased soil into ingrowth cores (Adams and Hutchinson, 1992; Cuevas and Medina, 1983; Fabiao et al., 1985). In some ecosystems, ingrowth cores are an extremely useful tool to compare root growth between sites or between experimental manipulations. For example, Cuevas and Medina (1983) used ingrowth cores to study the interactions among nutrient availability, organic matter decomposition and root production in tropical forests in Venezuela.

An understanding of root phenology is just as important for ingrowth cores as for the sequential coring method because cores must be left out long enough for active periods of root elongation to occur and for roots to grow into the cores. Even here, the use of minirhizotrons or rhizotrons to identify fine root phenological patterns could be very useful. Phenological data could be used to determine when to establish (avoid placement during active periods of root elongation) and to retrieve ingrowth cores. It is during periods of root elongation that fine roots will grow into the root-free space existing in the ingrowth core sleeve (in conifers this may occur during the spring and in the autumn).

Root production estimates at an ecosystem level are based on a given spatial area and over a given time period (usually one year). When using ingrowth cores, it is important to define what time period to begin measuring root regrowth into the root-free space interval; zero time is typically set when the ingrowth cores are installed in the field. All root growth that occurs into this core per given time period is then standardized to an annual increment (i.e., root production). However, if it takes almost a year in some ecosystems for roots to even begin to grow into this core, the time of installing ingrowth cores cannot be used as the start of an annual cycle to estimate fine root production. For example, in boreal and temperate coniferous forests root growth rates can be very slow – root recolonization of ingrowth cores did not start until 6–9 months after cores were installed in a low elevation *Pseudotsuga menziesii* stand in Washington and a year was

needed before roots were recorded on the window of a rhizotron in a subalpine *Abies amabilis* stand in Washington (Keyes, 1982; Vogt and Persson, 1991). This time lag is not a problem in tropical or agricultural systems in which root recolonization of the re-established cores can occur in a matter of months (Cuevas and Medina, 1983). In cases where it takes a long time for roots to even grow to the edge of an ingrowth core, it may become necessary to increase the temporal sampling frequency (which then requires a larger spatial area for the increased number of cores that need to be installed) to identify when root growth occurs into cores to establish the zero time frame. Ingrowth cores have been used to estimate fine root production but if these values are to be realistic (1) the timing of root growth must be determined and (2) the magnitude of root growth that would occur into a previously root occupied space should be known from that occurring into a root free area. Even though problems may exist in using ingrowth cores to obtain production numbers for fine-roots, Persson (1984) did find a similar production number when using ingrowth cores and sequential coring in Sweden.

The most serious drawback to the use of the ingrowth cores are (1) the ability to physically and chemically reconstruct the root free soil environment so that similar root production is measured inside and outside the core (is the initial root-free, homogenized soil a good approximation of root growth that would normally occur in the competitive, non-homogenized soil environment?), and (2) to determine how root production differs in a root-free zone from that already occupied by roots and whether root free soil produces microsites of higher root growth as recorded previously (Friend et al., 1990; St. John et al., 1983). If a soil matrix different from the site (e.g., sand) is used to fill the ingrowth cores to facilitate root processing and to insure that no root remnants confound the analyses, the root production estimates will be different from the bulk soil if that soil does not have a sand texture. If a soil of a different textural class is used to refill the holes, the physical properties of the soils will result in discontinuities in water flow through the soil (Buol et al., 1980) and can disrupt root growth into the cores. The soil in the core may end up being either more wet or dry compared to the surrounding soil matrix depending on the site; in other words, the core environment will not be representative of the bulk soil.

Minirhizotrons

The minirhizotron technique is a visual method of studying roots in which clear tubes are inserted into the ground into which miniature cameras can be inserted to capture photographic images of fine-root growth at different depths outside of the tube surface (Hendrick and Pregitzer, 1992; Smucker et al., 1987). In contrast to the single permanent installation of the rhizotron technique, the minirhizotron technique avoids the problem of insufficient spatial sampling by the placement of multiple observation tubes in the ground. Good discussions of the minirhizotron observation tubes are presented by Taylor (1987) and Ferguson and Smucker (1989). There used to be a problem where researchers collected hundreds of images from the tubes but the appropriate algorithms had not been developed to analyze the data collected by the camera but presently several software programs exist that can be used to analyze the video image root data collected with the minirhizotron. RHIZOGEN, a program for analyzing minirhizotron data, has been extensively used with agricultural plants and descriptions of its use are available in the literature (Smucker et al., 1987). Another software package called ROOT has been developed specifically to be used in forest ecosystems (Hendrick and Pregitzer, 1992).

The minirhizotron technique can be used to obtain (1) quantitative information on root length, rooting density, root dynamics, lateral root spread and the depth of rooting, and separation of roots into structural/functional diameters (McMichael and Taylor, 1987), and (2) qualitative information on root color, percent suberization, branching characteristics, patterns of senescence and observations of parasitism and symbiosis (Hendrick and Pregitzer, 1993; Lussenhof and Pregitzer, 1991; Majdi et al., 1992; Smucker et al., 1987; Upchurch and Richie, 1983). This technique is also very useful in monitoring the effects of various experimental manipulations (e.g., fertilization, application of herbicides or pesticides, clipping or pruning parts of aboveground vegetation, including drought or moisture stress, and soil compaction) on root and aboveground growth simultaneously (Hendrick and Pregitzer, 1993; McMichael and Taylor, 1987; Pregitzer et al., 1995). To convert minirhizotron data to root biomass numbers requires the simultaneous collection of root cores that can be sorted and processed to develop correlations to convert the length and diameter data to biomass values.

When using minirhizotrons, careful consideration has to be given to the installation phase in order to

minimize changing root growth patterns. For example, a higher accumulation of roots can occur near the minirhizotron observation tube interface with the soil, although the proper orientation of the observation tube in the ground alleviates much of this problem (Brown and Upchurch, 1987). In addition, (1) soil compaction and (2) temperature and moisture may also be greater at the tube/soil interface compared to the bulk soil which would modify the rooting density and growth pattern of the roots. Sampling protocols should incorporate into the design the spatial variability existing on the site, adjust for the difficulty of installing observation tubes in soils that are not agricultural nor sandy, and deal with the mathematical and statistical manipulation and analysis of images from video type recordings to convert them to quantitative numbers. To effectively analyze data obtained from minirhizotron observation tubes will require an initial high capital investment for all the equipment (e.g., proper camera set-up, etc.) necessary to handle data collection in the field to produce quality video images and requires the computer capability of handling the large data sets generated as video images using the proper algorithms (Smucker et al., 1987). There is considerable literature discussing the interpretation and statistical considerations necessary to understand information derived from minirhizotrons (Taylor, 1987).

Since minirhizotrons can be monitored on a relatively continuous basis, this method does not have the weakness associated with the sequential coring method of guessing when cycles of root growth and mortality are occurring. Unlike the sequential coring technique, data on root decay are not needed for the minirhizotron because the rates of root death are more realistic since the same root can be monitored until it disappears from the surface of the tube (assumed to be due to root mortality).

Applications and limitations of indirect methods

Because of the time-consuming nature of direct methods for estimating fine-root biomass and production and because of the difficulty of identifying root vitality classes, a number of researchers have attempted to generate indirect methods to estimate fine-root biomass and production. At least six general approaches have been used by researchers to indirectly estimate root biomass and/or production (Table 1): (1) N Budget Approach (Aber et al., 1985; Nadelhoffer et al., 1985); (2) Ecosystem Carbon Balance Approach (Ågren et al., 1980); (3) Starch Approach (Marshall and Waring, 1985; Vogt et al., 1985); (4) Carbon Fluxes Approach (Raich and Nadelhoffer, 1989); and (5) Correlations with abiotic variables (Vogt et al., 1986b, 1996). A brief discussion of these approaches will be presented to give the reader an understanding of some of the problems that need to be considered with indirect approaches.

N Budget Approach

For the N Budget Approach to work, information is needed on all of the following: (1) N inputs into an ecosystem, (2) N storage in all plant tissues, and (3) N mineralization rates in the soil (Aber et al., 1985; Nadelhoffer et al., 1985). This approach assumes that root production is driven by mineral soil N and that root production can be predicted from this single index. This approach also has several assumptions that need to be satisfied for it to work: (1) no N retranslocation from roots, (2) steady-state conditions, (3) mineralizable N is totally taken up by plants, and (4) N limits plant growth. Several of these assumptions are not valid for all ecosystems since N does appear to be retranslocated from fine roots of some cold temperate conifers (Meier et al., 1985; Vogt et al., 1995) but not pines (Nambiar, 1987), steady-state conditions do not generally exist, microbes are effective competitors with plants for nutrients so that all mineralizable N in the soil is not taken up by plants (Ballard, 1979) especially if a natural disturbance has occurred and microbial populations change, and nutrients other than N limit plant growth and water can be just as important in controlling plant growth (Gower et al., 1992; Ingestad and Ågren, 1992). A central assumption of the N Budget approach is a particular response by plant roots to low and high N availability – a major point of frequent discussion in the literature. Studies have not supported a uniform response by plant roots to soil N with some studies reporting a positive linear correlation between fine root production and forest site quality (Aber et al., 1985; Nadelhoffer et al., 1985) while others did not (Gower et al., 1992; Haynes and Gower, 1995; Vogt et al., 1990).

An assumption made with the N Budget approach is that the plant available N is measured using a N incubation technique (a fact not always supported by the literature, Binkley and Hart, 1989). In many cases plants may not be effective competitors with microbes for soil nutrients (E A Paul, personal communication) and our ability to quantify this competition are quite poor. For example, in fertilizer studies with pines only 3–49% of the N, P and K fertilizer applied to stands

was recovered in the plants (Ballard, 1979). Furthermore, root growth patterns in response to nutrients are scale dependent (e.g., increases in fine-root growth occurring in response to higher nutrient microsites while the total root biomass decreased at the ecosystem level; Friend et al., 1990). Even the dominant form of available N has to be also considered since plants respond differently to ammonium versus nitrate (Aber et al., 1985; Vogt et al., 1990).

The influence of N on root production is not uniform across all ecosystems. Therefore, the N Budget approach should only be used in those systems where the relationship was developed and not generalized for all systems. Since root growth does appear to be strongly tied to nutrient availability (Vogt et al., 1996), knowledge of nutrient cycling characteristics are valuable predictors to pursue for estimating root biomass, production and turnover. If soil N available to plants could be accurately determined (at present most methods have some inherent errors) in ecosystems where N availability limits plant growth, then using this method to predict fine-root biomass and production could be powerful.

Ecosystem Carbon Balance Approach

The Carbon Balance Approach makes the assumption that data are available for all other biomass components of a tree and that the carbon allocation patterns within the tree are well understood. The utility of this approach is predicated on the researcher having relatively good information on, or the ability to model, plant photosynthesis and respiration rates that can be scaled up to the whole plant and ecosystem levels (Ågren et al., 1980). This endeavor is not easy since a tree has respiration rates that can vary by a factor of seven within the canopy of a forest, resulting in a poor ability to predict respiration rates for individual plants (Sprugel et al., 1995). When we are better able to model plant carbon storage and fluxes, this approach to estimate root production will be ideal to set the boundaries of what are realistic belowground production values. The research synthesized in Ågren et al. (1980) was a very nice study because it not only modelled all carbon pools and fluxes but used independent estimates of these pools and fluxes that also included fine-root production.

Starch Approach

The Starch Approach is based on a relationship that carbon needed for root production is correlated to the amount of starch stored in the plant (e.g., in the stem wood or coarse roots) and also temperature (Marshall and Waring, 1985; Vogt et al., 1985). This method is very site and species specific. Thus the major limitation to this approach is that the predictive regression equation would have to be determined for each site and species before it could be utilized. Therefore, one would have to use one of the direct approaches just to develop the relationship. For long-term studies (e.g., Long-Term Ecological Research [LTER] sites) this method could prove fruitful to pursue.

Carbon Fluxes Approach

The Carbon Fluxes Approach was developed to estimate carbon used belowground by utilizing the extensive databases that exists around the world for soil respiration or CO_2 efflux from the soil (Raich and Nadelhoffer, 1989). By measuring CO_2 efflux and aboveground litterfall inputs, total carbon allocation to roots (which includes belowground detritus respiration and root respiration) is estimated by the difference between input and output (Raich and Nadelhoffer, 1989). The advantage of the Carbon Fluxes approach is that the component most difficult to measure, the belowground carbon compartment, is estimated by measuring aboveground parameters that are relatively easy to monitor (litterfall and soil respiration). As with the N Budget approach, this method also assumes steady state conditions.

Problems exist in the estimation of soil respiration rates since different techniques do not always give the same results. Similar to the temporal sampling problems presented for the sequential coring technique, soil respiration is typically measured during a 24 hour period and then averaged across a month using temperature to predict CO_2 evolution for the remainder of the month. The soil respiration measurements are further confounded by the fact that the proportion contributed by individual components (e.g., roots, decomposers, etc.) to the total respiration amount will vary between different ecosystems and by latitude. In other words, there will not be a consistent linear relationship between litterfall input and the amount of CO_2 evolution that can be attributed to the microbes. Ideally the soil respiration measurements should be obtained during the same time interval in which the litterfall data are collected (litterfall inputs can vary dramatically between years; Bray and Gorham, 1964). The amount of litterfall input is probably not as critical in driving decomposition rates as is the chemical quality of the litter (Bloomfield et al., 1993; Vogt et al., 1987) which determines how much CO_2 evolution will occur during

the decay process and how much is retained in microbial tissues (Vogt and Staffeldt, 1977). Only a rough estimation of the upper limit of actual root production can be obtained using this approach. If a study does not require the accuracy for root production measurements, then this method could be ideal for ease of use.

Correlations with abiotic variables

Correlations have been developed between fine root biomass and/or production and ecosystem level parameters indicative of the cycling of nutrients (litterfall nutrients, forest floor nutrient mean residence times) at the ecosystem level and with climatic variables (precipitation, temperature, temperature/precipitation ratios) (Gower et al., 1994; Vogt et al., 1986b, 1996). These relationships are not generalizable across all ecosystems since these relationships are specific to certain forest climatic types, certain soil orders and vary by species. The relationships that effectively predict root dynamics are those that limit plant growth in a system and in which the plant is not adapted to mitigate this limitation. In certain cases adaptations of plants to their environment reduces the ability to predict root growth using specific abiotic variables since these plants are not sensitive to these environmental limitations (Vogt et al., 1996). These correlations have a strong ability to contribute to predicting how root growth varies depending on experimental manipulations or land-use changes since variables are being monitored that reflect the changes that are occurring in the ecosystem. The relationships developed in some sites have also demonstrated how water and nutrients may each limit plant growth (Gower et al., 1992), which then caution us to identify the major limitations to plant growth.

The major limitation to the use of the correlations is the need to develop and understand these relationships for less studied ecosystems. These correlations should be driven by a mechanistic and functional understanding of the relationships. This approach has the potential to be quite effective at predicting root dynamics when the relationships are mechanistically based and needs to be further pursued. However, as mentioned in the preceding Carbon Fluxes approach, this method is most accurate when derived site-specifically. The derived data should be considered as a rough estimate that are useful for general comparisons but may not be accurate at a site specific level.

Comparison of different approaches

Because of the controversies that exist with how root dynamics are analyzed, it is interesting to compare the few studies that utilized more than one approach to study roots (Table 1). Comparison of these techniques cannot necessarily be used to say one method is better than another since this would require an independent determination (for example, the Carbon Balance Approach using models). These comparisons do allow you to identify which methods may give you lower or higher values.

Comparison of different direct approaches and analysis procedures

When data were collected using the sequential soil coring approach but calculated using two difference approaches (Maximum–Minimum; Decision–Matrix), there was no consistent relationship between them that would give the ability to state that one approach would consistently result in higher or lower values (Table 1). For example, similar mean production estimates (differing by $<20\%$) were obtained by Burke and Raynal (1995) for a hardwood forest. However when the maximum–minimum method was used with significant differences only, this approach had root production decreasing from 230 g m^{-2} yr^{-1} to 150 g m^{-2} yr^{-1}, the lowest level obtained with all three calculation approaches. The maximum–minimum technique has been suggested to overestimate root production by the incorporation of random errors into the estimates but only when non-significant differences are used, as seen by the decrease in root production when significant differences were used in the Burke and Raynal (1995) study. Similar results were obtained in pine and hardwood sites in Massachusetts where the Decision–Matrix approach (not using significant differences) resulted in fine-root NPP values that were more than 2–3 times higher than when using the Maximum–Minimum approach (Aber et al., 1985; Nadelhoffer et al., 1985).

Even Haynes and Gower (1995) had the mean production estimate varying by less than 17% when calculating root production using the Maximum–Minimum and Decision–Matrix approaches for their control pine sites in Wisconsin. However, this pattern was only maintained the first year after fertilization while the second year after fertilization found the Decision–Matrix approach production estimates to be 37% higher (Haynes and Gower, 1995). It is important to monitor root growth for more than one year as seen

by the very different results obtained by Haynes and Gower (1995) between two different years. An excellent example of the high year to year variability in root growth can also be seen in the Santantonio and Hermann (1986) study conducted in Oregon, USA.

When comparing several studies using different direct approaches, there is no consistency in the amount of root production estimated using ingrowth cores and sequential soil coring within the same study site. For example, in Sweden Persson (1983) obtained the same results for pine root production when using the ingrowth cores as when using the sequential coring technique. In contrast, when Neill (1992) compared the sequential coring method to the ingrowth core approach in a prairie marsh in Canada, he recorded much higher fine root production estimates with the ingrowth cores. In this system, soil cores resulted in belowground NPP estimates of 263–324 g m^{-2} compared to the mesh bags of 315–543 g m^{-2}. In the root core technique, adding necromass to the calculation of NPP resulted in higher estimates of 1115 g m^{-2} when non-significant differences were summed but a substantially lower value of 186 g m^{-2} when significant differences only were summed. The values obtained depended on how belowground productivity was calculated, that is whether the maximum and minimum approach or biomass and necromass increments approach was used. The differences between using significant increments versus positive biomass increments showed that lower values in general were obtained with the utilization of significant differences (Neill, 1992). Neill (1992) concluded that using the maximum and minimum approach to calculate NPP would give the most reasonable and consistent results. As would be expected, when seasonal changes in necromass were added to changes in live root biomass, production can almost double in magnitude (Persson, 1978).

When comparing ingrowth cores with monoliths, Majdi et al. (1992) found maize roots in agricultural fields in Michigan were underestimated by the minirhizotron system compared to core samples. In fact, the minirhizotron underestimated root density at the upper horizons. This pattern has also been observed by other researchers and may be due to poor contact between the minirhizotron tube and the soil (McMichael and Taylor, 1987).

Comparison of direct and indirect approaches

Aber et al. (1985) used the sequential coring technique (maximum–minimum calculation) and compared these results to the N budget approach for determining root productivity. They stated that they obtained good agreement between both methods when nitrification rates were low but they measured lower root production levels with the sequential soil coring approach when nitrification rates were high. An examination of their data show that this pattern was not distinctive with respect to nitrification rates, only the extremes (all or none of the soil mineralizable N present as nitrate-N) showed consistent relationships with root production (Table 1). For example, the two stands in Massachusetts, with no detectable soil nitrate, had relatively similar production values when comparing both approaches. When the sites had nitrate comprising 100% of the soil N pool, the N budget approach always estimated fine-root production to be 3–10 times higher than what was calculated using the Maximum–Minimum approach. When the contribution of nitrate to the total N pool varied from 100%, the pattern was less clear and would reverse in some cases so that the Maximum–Minimum approach had higher root production values than the N budget approach.

How root production varies with the form of plant available N is important to determine. Lower root production levels with high nitrification rates may be partially explained by our lack of documenting all the carbon fluxes and costs for producing and maintaining tissues (e.g., respiration, ion uptake). When only examining root biomass changes, one may miss the significant changes in carbon allocated belowground especially when these changes are occurring as respiration and as part of plant uptake of ions (Van der Werf et al., 1994). The ATP requirement for root growth is higher at high nitrate levels but whether this results in lower biomass values is not known. It also appears that the proportion of photosynthate used for maintenance of root function also increases as the relative growth rate of a plant decreases (usually seen in ammonium dominated systems) (Van der Werf et al., 1994). Higher nitrate levels also have an effect on the root growth form which would not be detected from measurements of biomass changes alone – nitrate causing less branching of roots. N also has a strong influence on changing the magnitude and type of secondary chemicals produced in root tissues (Muller et al., 1989; Vogt et al., 1991) which may not be detected as changes in root biomass.

When comparing the sequential soil coring approach with the Carbon Balance Budget approach (litterfall, respiration), the five different studies synthesized in Table 1 generally had significantly higher estimated mean root production using the Carbon Balance Budget approach. When only comparing control sites, pines growing in Wisconsin had 1.4–7 times higher estimated root productivity with the Carbon Balance Budget approach, 4.5 times higher in Montana and 13 times higher in Florida (Table 1). Fertilization of these sites had variable effects on changing the magnitude of difference between the Carbon Balance Budget approach and the sequential soil coring approach which was probably related to how litterfall was affected by the fertilizer treatment.

According to Haynes and Gower (1995), the Carbon Balance Budget approach does not work when the site has been fertilized. This is partially due to fertilization having very different impacts on litterfall and on soil respiration which varied depending on the year of analysis and the pine species. For example, aboveground litterfall was significantly higher in the unfertilized plots compared to the fertilized plots during the first year but foliage litterfall was significantly greater in the fertilized plots during the 2nd to the 4th years (Haynes and Gower, 1995). This contrasted with soil respiration rates which were significantly lower in the fertilized plots during all years. Soil respiration also varied with the species being examined, for example, *Pinus ponderosa* and *P. elliotti* did not have significant changes in soil respiration rates while *P. resinosa* and *Tsuga heterophylla*/*Pseudotsuga menziesii* had significant changes in respiration rates in response to fertilization (Gower et al., 1996). The contribution of roots and mycorrhizas to soil respiration also varied depending on whether a site was fertilized or not. Roots and mycorrhizas contributed 21–30% to the total soil respiration for unfertilized red pine and 4–12% for the fertilized red pine (Haynes and Gower, 1995). Their study did not support the assumption that belowground carbon allocation is positively related to aboveground litterfall as required by the Carbon Balance Budget approach. The litterfall-respiration approach also assumes that detrital pools in the surface litter and soil, and fine-root biomass are constant which was not upheld by the Gower et al. (1996) study.

Summary

Controversy exists in the literature on what are the best methods to use (direct or indirect approaches) for estimating the biomass and production of fine roots at an ecosystem level in forest ecosystems. However, until we develop a totally independent method to determine actual root biomass, these indirect methods need to be used with caution. This suggests that the direct methods should still be utilized when studies are being initiated on a new site. The indirect methods are useful for those ecosystems where data are already available on root biomass and production and they are accompanied with sufficient data on the pools and fluxes of abiotic resources. Is not clear at this stage how readily transferable are the correlations that have been developed with the indirect methods to similar ecosystem types, to different adjacent ecosystems, or to ecosystems where abiotic resource availabilities have been manipulated. Some results suggest that some of these correlations do vary in predictable patterns by ecosystem type and by species (Vogt et al., 1996). Once we have a better understanding of the role of nutrient(s), water and/or light on modifying or controlling root biomass and production, the utility of these correlations can be further verified and their predictive ability determined for use in physiological and ecosystem models.

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