

Global patterns of root turnover for terrestrial ecosystems

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SUMMARY

Root turnover is a critical component of ecosystem nutrient dynamics and carbon sequestration and is also an important sink for plant primary productivity. We tested global controls on root turnover across climatic gradients and for plant functional groups by using a database of 190 published studies. Root turnover rates increased exponentially with mean annual temperature for fine roots of grasslands ($r^2 = 0.48$) and forests ($r^2 = 0.17$) and for total root biomass in shrublands ($r^2 = 0.55$). On the basis of the best-fit exponential model, the Q_{10} for root turnover was 1.4 for forest small diameter roots (5 mm or less), 1.6 for grassland fine roots, and 1.9 for shrublands. Surprisingly, after accounting for temperature, there was no such global relationship between precipitation and root turnover. The slowest average turnover rates were observed for entire tree root systems (10% annually), followed by 34% for shrubland total roots, 53% for grassland fine roots, 55% for wetland fine roots, and 56% for forest fine roots. Root turnover decreased from tropical to high-latitude systems for all plant functional groups. To test whether global relationships can be used to predict interannual variability in root turnover, we evaluated 14 yr of published root turnover data from a shortgrass steppe site in northeastern Colorado, USA. At this site there was no correlation between interannual variability in mean annual temperature and root turnover. Rather, turnover was positively correlated with the ratio of growing season precipitation and maximum monthly temperature ($r^2 = 0.61$). We conclude that there are global patterns in rates of root turnover between plant groups and across climatic gradients but that these patterns cannot always be used for the successful prediction of the relationship of root turnover to climate change at a particular site.

Key words: root turnover, root production, belowground cycling, terrestrial biomes, global change.

INTRODUCTION

Root turnover is a central component of ecosystem carbon and nutrient cycling, and will probably be sensitive to many of the factors considered in global change analyses (Aber *et al.*, 1985; Bloomfield *et al.*, 1996). In particular, discerning how plant attributes, soil processes, and climatic patterns influence rates of root turnover is important given current and projected future climate and vegetation change (Vitousek, 1994; Parton *et al.*, 1995; Jackson *et al.*, 2000). Although it is important to understand the mechanisms controlling root longevity and turnover for an individual root or plant, it is also desirable to identify broad-scale patterns in root turnover among plant functional types and across large climatic gradients. Understanding differences between plant

groups might be helpful in modeling how changes in plant functional types influence root standing crop, hydrology, and nutrient dynamics. In addition, examining how root turnover is related to temperature and precipitation regionally could help to identify which plant groups are most sensitive to climate change.

A number of studies have demonstrated that soil temperature, moisture status, and nutrient availability control, in part, the timing and duration of root growth (Nadelhoffer *et al.*, 1985; Vogt *et al.*, 1986; Pregitzer *et al.*, 1993, 2000; Hendrick & Pregitzer, 1997; Nadelhoffer, 2000). Individual root longevity is determined primarily by soil microsite conditions (Friend *et al.*, 1990; Pregitzer *et al.*, 1993, 2000; Joslin *et al.*, 2000), root development patterns (Marshall & Waring, 1985), growing season length, and plant mineral nutrient conservation (Eissenstat & Yanai, 1997; Eissenstat *et al.*, 2000). Soil temperature probably has a strong role in determining

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root turnover, given that the onset of production is often keyed by soil warming in the spring and that the costs of root maintenance increase exponentially with temperature (Ryan, 1991; Hendrick & Pregitzer, 1997; Fitter *et al.*, 1998; Atkin *et al.*, 2000). In addition, land cover change is altering the abundance and distribution of plant functional types globally, influencing belowground allocation patterns and regional carbon and nutrient cycles (Connin *et al.*, 1997; Gill & Burke, 1999).

Temperate grasslands allocate between 24% and 87% of net primary production belowground (Sims & Singh, 1978). In forests, belowground net primary productivity (BNPP) typically accounts for 30–50% of total net primary production (Vogt, 1991). Given that little, if any, retranslocation of nutrients occurs before fine-root senescence, root turnover is a strong nutrient sink for most plants (Aerts, 1990; Nambiar & Fife, 1991; Gordon & Jackson, 2000). Studies with minirhizotrons have shown that a subset of roots in both grasslands and forests is highly dynamic, having a lifespan of days to weeks (Hendrick & Pregitzer, 1997; Gill, 1998; Arnone *et al.*, 2000; Tingey *et al.*, 2000). Ryser (1996) hypothesized that plants growing in nutrient-poor environments might increase root lifespan to avoid nutrient loss. Potentially, if soils warm as a result of climate change, maintenance costs of roots and nutrient availability might increase and contribute to higher rates of root turnover. Furthermore, the efficiency of nutrient uptake for a single root over its lifetime might decrease with increasing temperature (Eissenstat & Yanai, 1997).

Our objectives in this paper are as follows: (1) to synthesize root turnover data for major biomes and plant life forms globally, (2) to generate broadscale patterns of root turnover along climatic gradients, and (3) to contrast regional and local environmental controls over root turnover. We illustrate this last objective by using regional patterns to predict site-level responses to global change.

MATERIALS AND METHODS

Building on prior analyses in Jackson *et al.* (1996, 1997), we assembled a database of approx. 190 papers from journals, book chapters, technical reports, and unpublished manuscripts that included information on live root standing crop and BNPP (Appendix 1). The papers described research on every continent except Antarctica, although most were from North America (Fig. 1). In the database, the plant functional type and biome coverage were most abundant for grasslands and temperate zones (Appendix 1). Coverage in South America, Australia and north central and eastern Asia was particularly sparse (Fig. 1). The data were categorized according to latitude, longitude, mean annual temperature, mean annual precipitation, maximum mean monthly

temperature, minimum mean monthly temperature, soil texture, sampling method, plant age, and root diameter class, although not all information was available for every study. In cases where authors did not differentiate between live and dead biomass, we recorded total root biomass. When climate variables were not reported, we used the CLIMATE database version 2.1 (W. Cramer, pers. comm.) to reconstruct mean climate values based on latitude and longitude coordinates. For each study, we recorded the dominant vegetation type and the vegetation sampled (i.e. forest, grassland, shrubland, wetland). When a single paper included information for multiple vegetation types, we averaged species within a type but reported turnover for each unique vegetation. We further categorized sites as tropical, temperate, or high latitude. Sites that included BNPP and standing crop values for more than a single year were averaged across years for the global comparison. If more than one method had been used to estimate BNPP, both turnover estimates were included. The data for a particular site were averaged when more than one equation had been used to calculate BNPP.

Several calculations have been used in previous studies to determine root turnover (Dahlman & Kucera, 1965; Aerts *et al.*, 1992; Hendrick & Pregitzer, 1993). We determined root turnover with a slight modification of the model initially proposed by Dahlman & Kucera (1965). We calculated root turnover by using the equation:

Root turnover =

$$\frac{\text{annual belowground production}}{\text{maximum belowground standing crop}} \quad \text{Eqn 1}$$

with root turnover in units of yr^{-1} . Alternatives to the Dahlman & Kucera (1965) model include Aber *et al.* (1985) and Aerts *et al.* (1992), who defined turnover as BNPP/mean standing crop, or Hendrick & Pregitzer (1993), who defined turnover as BNPP/minimum standing crop. Other definitions of turnover were the equivalent of BNPP and were not considered for this analysis (Van Praag *et al.*, 1988; Schlöpfer & Ryser, 1996). We chose the Dahlman & Kucera (1965) calculation because it is an extensively used model of root turnover and because of its heuristic value. In the Dahlman–Kucera model, an annual plant would have a turnover of 1.0 yr^{-1} if all of the roots that it produced were to die at the end of the growing season.

Approximately one-third of the studies that included estimates of BNPP and root standing crop provided mean rather than maximum biomass. In consequence, we transformed mean root standing crop to maximum root standing crop by using a regression based on mean root biomass and belowground net primary productivity, using the 20 datasets that included both mean and maximum root biomass (Appendix 1). The following linear model

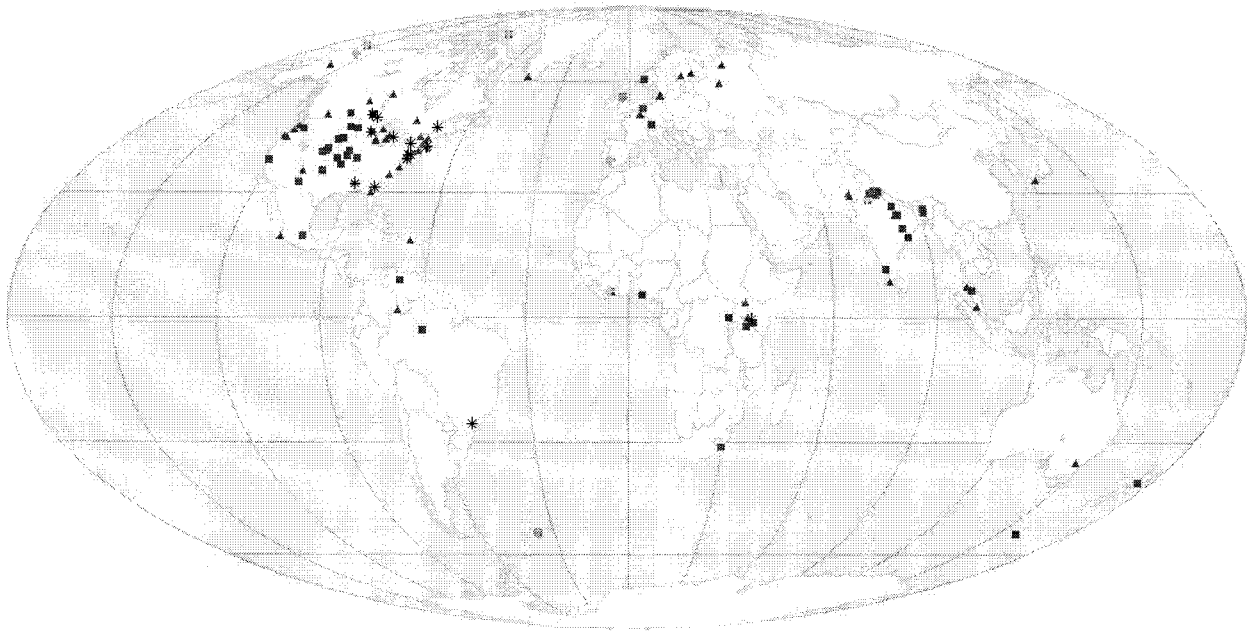


Fig. 1. The distribution of sites included in the root turnover database. Triangles, forest; squares, grassland; crosses, shrubland, stars, wetland.

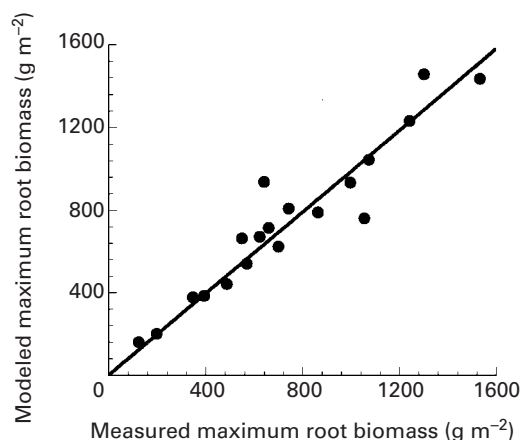


Fig. 2. Modeled versus measured maximum root biomass based on the equation maximum biomass = $0.45 \times \text{belowground production} + \text{mean biomass}$ ($r^2 = 0.90$, $P < 0.01$).

explained 90% of the variation for predicting maximum root biomass ($r^2 = 0.90$, $P < 0.001$; Fig. 2):

$$\text{Maximum root biomass} = 0.45 \times \text{BNPP} + \text{mean root biomass} \quad \text{Eqn 2}$$

The 20 studies used to determine this relationship came from across all biome types, and the biomass estimates spanned the range of potential mean biomass reported.

To evaluate whether global patterns between climate and root turnover are applicable at smaller scales, we used a long-term dataset from the short-grass steppe long-term ecological research site in northeastern Colorado, USA ($40^\circ 49' \text{ N}$, $104^\circ 46' \text{ W}$) (see Lauenroth & Milchunas (1992) for a description

of the site). We calculated turnover for 14 yr by using data from Sims & Singh (1978), Milchunas & Lauenroth (1992), D. G. Milchunas & W. K. Lauenroth (unpublished), and Gill (1998). Annual precipitation ranged between 264 and 557 mm, and mean annual temperature ranged from 7.6 to 10.9°C during the 14 yr reported. This interannual range in temperature is similar to the $2\text{--}3^\circ \text{C}$ change in temperature that is predicted for the central grasslands region of the USA (Parton *et al.*, 1993). The site-level data allowed us to determine whether interannual variability in weather produced the same patterns in root turnover as those observed across regional and global climatic gradients.

We analyzed the relationship between climate variables and root turnover within and across plant life forms by using stepwise multiple regression (SAS, Cary, NC, USA). Climate variables considered in the model were mean annual temperature (MAT), mean maximum monthly temperature (MMXT) and minimum monthly temperature (MMNT), mean annual precipitation (MAP) or the ratios of MAP to MAT and MAP to MMXT. We log-transformed turnover before conducting our statistical analyses to linearize the metric and to normalize the distribution. Our access to reliable long-term weather data at the Central Plain Experimental Range (CPER) allowed us to include growing season precipitation as a possible variable in the site-level analysis. Within forests, we evaluated turnover for both fine and total root systems for live root biomass. We used all studies that reported fine-root production and standing crop where the diameter increment considered was 5 mm or less, although there was some variability in the maximum

root diameter considered ‘fine’. We also compared turnover between plant life forms and across latitudinal zones by using unbalanced ANOVA and Fisher’s LSD (SAS, Cary, NC, USA). In cases where there was an exponential relationship between temperature and root turnover, we calculated a Q_{10} (the increase in reaction rate for a 10°C increase in temperature) based on the Arrhenius equation (Winkler *et al.*, 1996).

We acknowledge that there are several problems associated with analyzing these data with standard parametric statistics. The nature of the dataset makes it difficult to apply standard meta-analytic statistics because very few studies provide a variance estimate for standing crop or BNPP. Therefore, the only variance that is considered in this analysis is variation between studies, potentially violating the assumption of absence of heteroscedasticity. In addition, the data might not be completely independent owing to non-phylogenetic independence between species, methodological bias, or habitat redundancy. The problems of applying inferential statistics to these data therefore make it necessary to be extremely conservative in the conclusions that can be drawn statistically.

RESULTS

There was a strong, positive exponential relationship between root turnover and mean annual temperature for grasslands, shrublands and all fine roots pooled

together, with turnover increasing from boreal zones to the tropics (Fig. 3; $r^2 = 0.48$ for grasslands; $r^2 = 0.55$ for shrublands; $r^2 = 0.40$ for all fine roots). There was also a weak relationship between MAT and fine-root turnover in forests ($r^2 = 0.17$ for forest fine roots). On the basis of the exponential models, the Q_{10} for root turnover was 1.6 for fine roots globally and in grasslands, 1.9 in shrublands, and 1.4 for forest fine roots. Total root turnover in forests ($P < 0.09$) and wetland belowground turnover ($P < 0.16$) showed no significant relationship to any of the climate variables (Fig. 3). In all regression models, once mean annual temperature was included, no other climate variables or ratios were significant, including precipitation. When we factored out all studies that reported root dynamics in periodically flooded or saturated soils, we found a weak correlation between mean annual precipitation and root turnover ($r^2 = 0.32$), although mean annual precipitation was not a significant component of the multiple regression model (Fig. 4). In the high latitudes, average root turnover for graminoids, shrubs, and tree fine roots was 13% of maximum root standing crop annually, with an increase to 40% in temperate zones, and nearly 73% in tropical zones.

Whole-tree root systems had the lowest turnover values of any of the plant functional types analyzed in this study (10%). Shrubland species had the next lowest root turnover (34%) followed by grasses and fine roots of trees (53% and 56%, respectively).

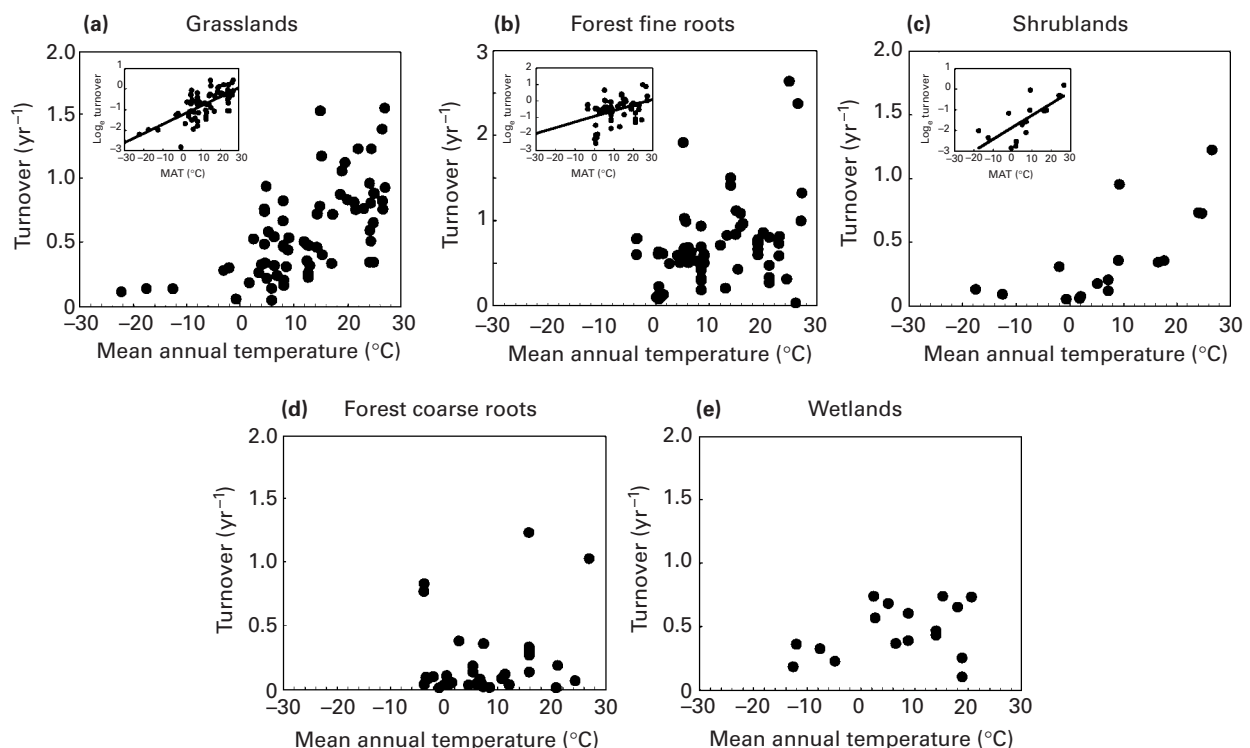


Fig. 3. Relationship between root turnover and mean annual temperature by vegetation type ($r^2 = 0.48$ for grasslands; $r^2 = 0.55$ for shrublands; $r^2 = 0.17$ for forest fine roots of 5 mm or less). Note that panel (b) has a different y-axis scale.

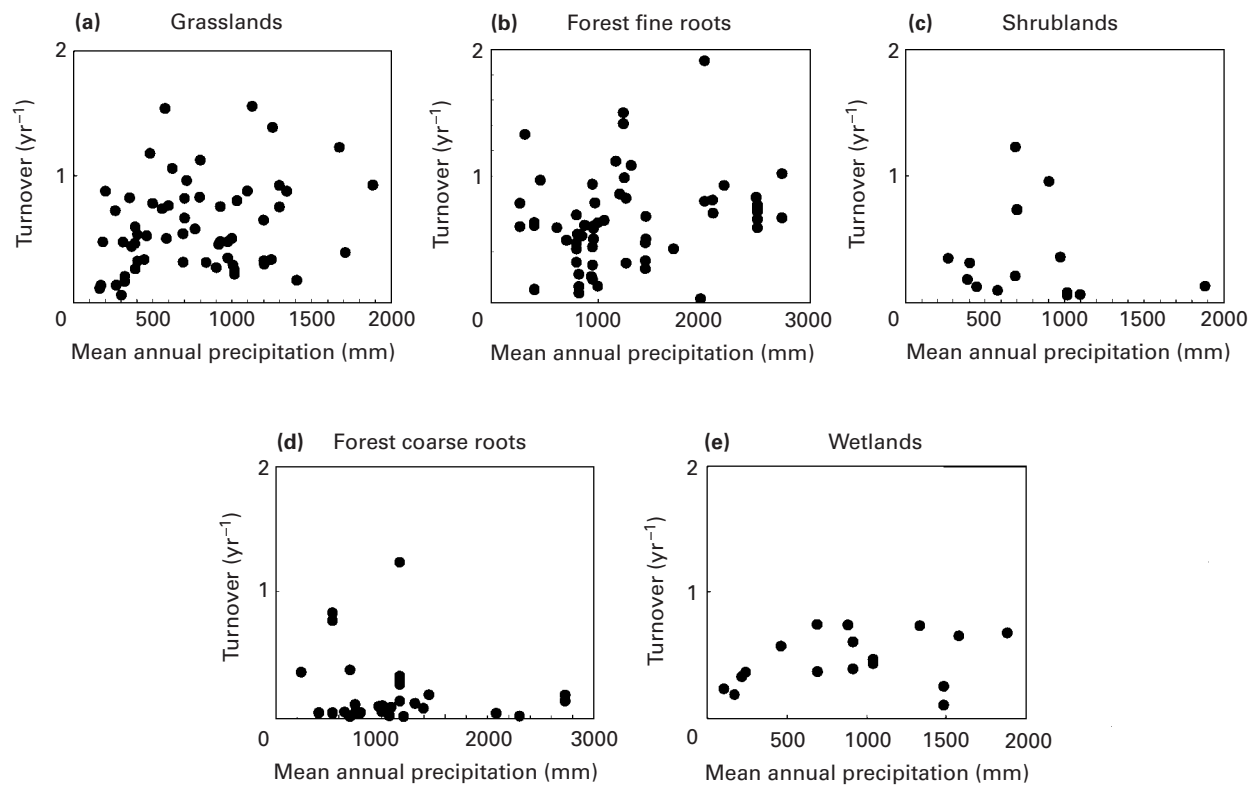


Fig. 4. Relationship between root turnover and mean annual precipitation by vegetation type.

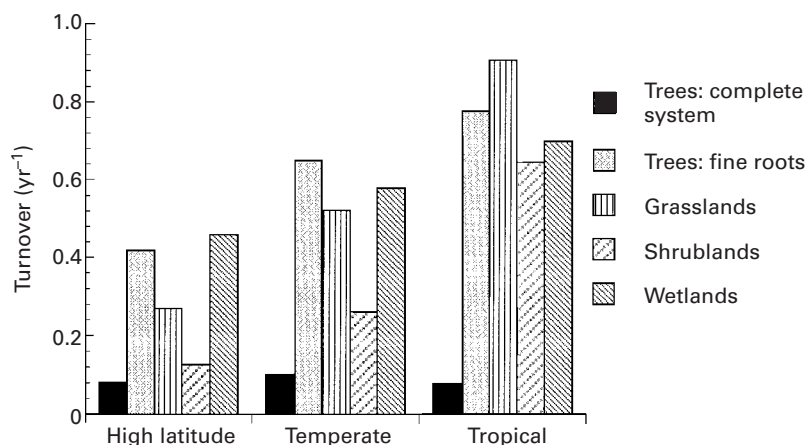


Fig. 5. Root turnover for vegetation types separated by latitudinal zone.

Mean annual turnover rate for roots of wetland species was 55%. The relative order of turnover rate among plant functional types was maintained within latitudinal zones, with grasslands = tree fine roots = wetlands > shrublands > tree whole root system for high latitude, temperate, and tropical zones (Fig. 5). Not surprisingly, the diameter class used to define a fine root in forests had a strong role in determining fine-root turnover. As the diameter class increased, root turnover decreased (Fig. 6). In the 0–1 mm diameter class turnover was 1.2 yr⁻¹, decreasing to 0.10 yr⁻¹ in the 0–10 mm diameter class. Most of the studies in this review used 0–3 mm or 0–5 mm diameter classes to distinguish fine roots; these two classes were not significantly different with an

average turnover of 0.52 yr⁻¹. The average across all diameter classes was 0.56 yr⁻¹. The inconsistency in defining ‘fine’ roots in the forestry literature makes it difficult to compare turnover estimates across studies.

At the long-term ecological research site in northeastern Colorado, USA, mean annual temperature was not a significant factor in explaining root turnover (Fig. 7a). However, there was a strong, positive correlation between root turnover and the ratio of growing season precipitation:maximum mean monthly temperature ($r^2 = 0.61$; Fig. 7b). Thus, although temperature was the most important variable globally for explaining patterns of root turnover, it was not nearly as useful as was an index

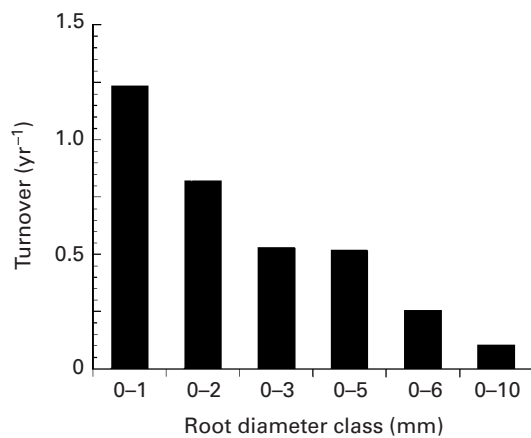


Fig. 6. Root turnover for forest fine roots separated by diameter class.

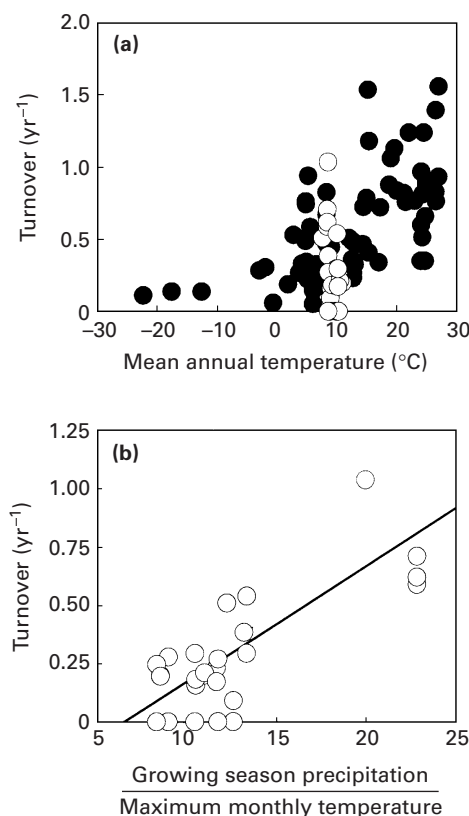


Fig. 7. (a) Relationship between mean annual temperature and root turnover for grasslands globally (closed circles) ($r^2 = 0.45$) and for the shortgrass steppe of northeastern Colorado, USA (open circles). (b) Relationship between root turnover and growing season precipitation/maximum monthly temperature at the Central Plains Experimental Range (CPER) for 16 yr (1970–71 and 1984–97) ($r^2 = 0.61$).

of temperature and precipitation for explaining the year-to-year variation in root turnover at that particular site.

DISCUSSION

We found global and regional relationships between mean annual temperature and rates of root turnover in grasslands, shrublands, and forest fine roots.

Potential explanations for an increase in turnover with higher temperatures include the following; (1) the exponential increase in maintenance respiration with temperature, (2) increased nutrient mineralization rates with higher temperatures, and (3) an increase in pathogen and herbivore load in warmer soils and in soils that do not freeze (Ryan, 1991; Eissenstat & Yanai, 1997). As maintenance respiration increases, the optimal lifespan for a root decreases, thus requiring higher root turnover rates in warmer climates. Microbial activity also shows an exponential increase with soil temperature, and might result in higher nutrient availability (Holland *et al.*, 1995). In addition, the absence of a hard freeze in soils might allow populations of root-feeding herbivores to increase. This effect is particularly interesting within a climate change context, given that the strongest trend in warming trend is seen in daily minimum temperatures (Alward *et al.*, 1999). The disproportionate increase in daily minimum temperature might increase parasite and herbivore loads in systems beyond what would be expected simply as a result of increased mean annual temperature. However, climate variables alone were insufficient predictors of root turnover for total root systems in forests and wetlands.

We found that, within plant functional types, root turnover increased consistently from boreal to tropical zones. This might reflect the influence of seasonality on root turnover, implying that tropical zones require a higher belowground productivity to maintain the same belowground biomass as temperate or boreal systems.

The strength of the relationship between mean annual temperature and turnover in grasslands and shrublands might be the result of a strong correlation between air and soil temperatures in systems with low leaf area. In forests and wetlands, the temperature experienced by an individual root might be moderated by the forest canopy or by site hydrology. In broadleaf forests, the forest canopy can cause a significant decrease in soil temperature compared with non-shaded soils. We were unable to analyze the influence of daily minimum temperatures on root turnover because the data were infrequently reported. Hendrick & Pregitzer (1997) found that soil temperature was a critical factor in determining fine-root lifespan in temperate forests, and therefore our ability to predict root turnover across regional gradients could be improved by including data on soil temperature.

Shifts in dominant plant life form have occurred globally and have been implicated in altered system hydrology and carbon and nutrient dynamics (Connin *et al.*, 1997; Gill & Burke, 1999). The differences that we found between plant functional types suggest that shifts in plant life form might also influence rates of root turnover in ecosystems. For instance, much of the semiarid and arid USA has

experienced an increase in shrub density in historically grass-dominated ecosystems (Bogusch, 1952; Schlesinger *et al.*, 1990; McClaran & McPherson, 1995). Given the differences in root turnover among shrubs and grasses we might expect that a lower proportion of root biomass would turn over annually in shrub-invaded ecosystems than in grasslands, influencing both carbon and nutrient cycling.

Our conclusion that the broad-scale patterns that we observed were not useful predictors of inter-annual variability at an individual site is not unique (Lauenroth & Sala, 1992). Gower *et al.* (1996) found that the global pattern of belowground carbon allocation used by Nadelhoffer & Raich (1992) was not a useful predictor of belowground allocation across years at individual sites. One potential reason for the divergence between correlative factors at different scales might be the resolution of the data necessary to predict root turnover at a local site. We found a strong relationship between the ratio of growing season precipitation to maximum monthly temperature and root turnover. Unfortunately, we could not test this same prediction with our database, because we lacked the data necessary to generate this ratio for most of the sites. Furthermore, turnover at a single site might be determined by the ability of a few species to respond to interannual variability and might be buffered by species-specific allocation patterns (Lauenroth & Sala, 1992). Previous reviews have used smaller datasets to show that climate and nutrient availability are valuable predictors of fine-root standing crop or belowground production in forests (Nadelhoffer *et al.*, 1985; Vogt *et al.*, 1986; Gower, 1987). However, many of the relationships found in smaller datasets were lost or changed when the numbers of studies included in the analysis were enlarged or when the number of taxa considered increased (Vogt *et al.*, 1996). Vogt *et al.* (1996) found that the variables useful in predicting fine root standing crop were often different from variables useful in estimating belowground production.

The high variability in root turnover estimates might partly be explained by methodological constraints. The methods used to measure and calculate belowground biomass and production might have a strong role in determining estimates of root turnover. For instance, Aber *et al.* (1985) used both a maximum–minimum approach (McClagherty *et al.*, 1982) and a budgetary approach to determine belowground productivity. Their study illustrates that at a single site in a single year different methods can give estimates of turnover that vary by an order of magnitude. For a site to have a turnover rate greater than 1, there must be some factor included in the calculation that allows total annual production to exceed maximum biomass, something that is mathematically impossible with the traditional peak–trough methods. Several calculations have been

proposed to account for concurrent production and death or some estimate of decomposition of roots during the growing season (Arthur & Fahey, 1992; Garcia-Moya & Montanez, 1992; Garkoti & Singh, 1995). Validating models that incorporate estimates of root turnover will be difficult as long as estimates of BNPP vary by more than an order of magnitude depending on the method used.

Understanding patterns and controls over root turnover is crucial, given the desire to predict consequences of climate and land cover change. We found that across broad climatic gradients, root turnover is positively correlated with mean annual temperature in many terrestrial ecosystems. Although it is unlikely that mean annual temperature is the proximate determinate of root turnover, particularly given the inability of the relationship to be predictive at an individual site, our results help to clarify important questions that need to be addressed. What is the role of temperature seasonality in root longevity? Does daily maximum or minimum temperature have a role in determining root maintenance cost or parasite load? What belowground characteristics are correlated with mean annual temperature that might be related to root turnover? The variability in data included in this model also indicates that refining methods of estimating root turnover and understanding site-specific characteristics will be important for fully understanding controls over root turnover.

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Appendix 1. Plant functional type and biome coverage

Vegetation type	Location	Lat. and long.	Mean annual temperature (°C)	Mean annual precipitation (mm)	Root collection method	BNPP calculation method	Root type	Fine-root size	Root turnover†	Species	References
Tropical Mixed forest	Himalaya, India	30° 15' N 78° 25' E	15.3	1710	Monolith	Σ Δ biomass	Fine		0.443 (0.394–0.492)	<i>Quercus leucotrichophora</i> , <i>Pinus roxburghii</i>	Sah <i>et al.</i> (1994)
	Kaimur Range, India	24° 19' N 82° 59' E	24.3	1000	Monolith	Allometry	Total		0.073		Singh <i>et al.</i> (1991)
	Puerto Rico	18° 9' N 65° 49' W	22.9	3810	Ingrowth/coring	Maximum growth into ingrowth cylinder	Fine	≤2	0.736	<i>Pinus caribaea</i>	Cuevas <i>et al.</i> (1991)
	Kodiyar, India	8° 29' N 77° 15' E	27	3146	Coring		Total; Fine	≤3		<i>Terminalia paniculata</i>	Sundarapandian & Swamy (1990a,b)
Broadleaf	Meghalaya, India	25° 34' N 91° 56' E	19	2500	Coring	Σ Δ biomass and necromass		<1; 1–2; 2–5; 5–10; 10–15	(<1) 0.60; (1–2) 0.69; (2–5) 0.73; (5–10) 0.75; (10–15) 0.78	<i>Eupatorium adenophorum</i> , <i>Pinus kesiya</i> , <i>Quercus dealbata</i>	Arunachalam <i>et al.</i> (1996)
	Puerto Rico	18° 19' N 65° 49' W	22.9	3810	Ingrowth/coring	Maximum growth into ingrowth cylinder	Fine	≤2	0.591	Tierra Firme Forest	Cuevas & Medina (1988); Cuevas <i>et al.</i> (1991)
	San Carlos de Rio Negro, Venezuela	1° 54' N 67° 03' W	26	1961	Ingrowth	Σ in biomass in six media	Fine		0.036	Jordan & Escalante (1980)	
	Puerto Vallarta, Mexico	19° 30' N 105° 05' W	24.9	748	Coring	Balancing transfer	Fine	≤1	2.644	<i>Caesalpinia eriostachys</i> , <i>Jatropha chamadensis</i>	Kummerow <i>et al.</i> (1990)
Savanna (herbaceous layer)	Kakuma, Northern Kenya	3° 43' N 34° 51' E	27.2	318	Coring	Peak-trough; balancing transfer; compartment flow	Fine	≤2	1.33 (0.87–1.97)	<i>Acacia saligna</i>	Lehman & Zech (1998)
	Ivory Coast	6° 17' N 5° 13' W	26.5	1285	Coring	Balance transfer	Fine	≤2	2.379	<i>Terminalia superba</i>	Schroth & Zech (1995)
	Varanasi, India	24° 54' N 83° 07' E	24.3	1057	Monolith		Fine	≤6	0.316	<i>Anogeissus-diospyros</i> , <i>Buchanania</i>	Singh & Singh (1981)
	Southern India	11° 47' N 36° 50' E	25	1098	Monolith	Σ Δ biomass			0.890 (0.563–1.564)	<i>Themeda triandra</i>	Devidas & Puyravaud (1995)
Grassland	Burla, India	21° 25' N 83° 52' E	24.9	1345	Monolith	Σ Δ biomass			0.891 (0.86–0.94)	<i>Morinda tomentosa</i> , <i>Butea monosperma</i> , <i>Boswellia serrata</i>	Joshi <i>et al.</i> (1990)
	Ivory Coast	6° 13' N 5° 02' W	26.6	1300	Monolith	Σ Δ biomass			0.766 (0.458–1.086)	<i>Loudeia simplex</i> , <i>Andropogoneae</i>	Menaut & Csar (1979)
	Vindhyan Plateau, India	24° 19' N 82° 59' E	26.2	926–1145	Monolith	Σ Δ biomass				<i>Heteropogon contortus</i> , <i>Chrysopogon fulvus</i>	Pandey & Singh (1992)
	Central Himalaya, India	29° 24' N 79° 30' E	18.7	201	Monolith	Σ significant Δ biomass				<i>Bohrtrichia pertusa</i> , Understorey of <i>Shorea robusta</i> , <i>Pinus roxburghii</i> , <i>Quercus leucotrichophora</i>	Rana & Rikhari (1994)
	Calabozo, Venezuela	8° 56' N 67° 25' W	27	1300	Monolith	Σ significant Δ biomass using Mann Whitney U test			0.935 (0.932–0.937)	<i>Trachypogon montufari</i> , <i>T. plumosus</i>	San Jose <i>et al.</i> (1982)
	Kumarganj, India	26° 47' N 82° 12' E	24.8	1248	Monolith	Σ Δ biomass			0.350	<i>Brachiaria mutica</i>	Saxena <i>et al.</i> (1996)
	Nylsley, South Africa	24° 39' S 28° 42' E	19	623		Σ Δ biomass and necromass			0.970	<i>Eragrostis pallens</i> , <i>Digitaria eriantha</i> , <i>Panicum maximum</i>	Scholes & Walker (1993); Scholes & Hall (1996)
	Uttar Pradesh, India	24° 36' N 83° 03' E	24.3	1035	Monolith	Σ Δ biomass			0.814	<i>Chrysopogon fulvus</i>	Singh (1993)
	Kaimur Range, India	24° 50' N 83° 00' E	24.3	1000	Monolith	Maximum root biomass			0.515		Singh <i>et al.</i> (1991)
	Texcoco, Mexico	19° 27' N 98° 51' W	15.1	579	Coring				1.535 (1.49–1.58)	<i>Distichlis spicata</i>	Long <i>et al.</i> (1989); Garcia-Moya & Castro (1992)
	Kurukshetra, India	29° 58' N 76° 51' E	20	795	Monolith	Σ Δ biomass			0.839 (0.755–1.109)	<i>Sebania hispidosa</i> , <i>Dichanthium annulatum</i> , <i>Aristida adscensionis</i>	Gupta & Singh (1982)

Appendix 1 (cont.)

Vegetation type	Location	Lat. and long.	Mean annual temperature (°C)	Mean annual precipitation (mm)	Root collection method	BNPP calculation method	Root type	Fine-root size	Root turnover†	Species	References
Grassland (cont.)	Hat Yai District, Thailand	6° 20' N 100° 56' E	27	1130	Coring	Σ Δ biomass, necromass, and estimate decomposition loss			1.558 (Mean turnover of 7.7 months)	<i>Eulalia trispicata</i> , <i>Lophopogon intermedius</i>	Kammalrut & Evenson (1992)
	Nairobi National Park, Nairobi, Kenya	1° 20' S 36° 50' E	19.6	800	Coring	Σ Δ biomass, necromass, and estimate decomposition loss			1.130 (0.95–1.31)	<i>Themeda triandra</i>	Long <i>et al.</i> (1989); Kinyamario & Imbamba (1992)
	Serengeti National Park	2° 20' S 34° 50' E	21.2	775 (350–1200)	Coring				0.821 (0.333–0.961)	<i>Aristida setacea</i> ; <i>Bothriochloa odorata</i>	McNaughton <i>et al.</i> (1998)
	Berhampur, India	19° 16' N 84° 53' E	24.8	1200	Monolith	Σ Δ biomass			0.661	<i>Stenotaphrum secundatum</i>	Misra & Misra (1984)
	Gujarat, India	22° 00' N 72° 00' E	26.5	353	Monolith	Σ Δ biomass			0.83	<i>Stenotaphrum secundatum</i> ; <i>Aeluropus lagopoides</i>	Pandya & Sidha (1987)
	Adiopodoum, Ivory Coast	5° 30' N 4° 30' E	26.5	1257	Coring	Σ Δ biomass, necromass, and estimate decomposition			1.180	<i>Panicum maximum</i>	Picard (1979)
	Garhwal, Himalaya, India	30° 00' N 78° 00' E	24.5	1674	Monolith	Σ Δ biomass			1.238 (1.038–1.566)	<i>Crysogonon aciculatus</i> , <i>Digitaria ciliaris</i>	Rajwar & Ramola (1990)
	Kumaun, Himalaya, India	29° 80' N 70° 20' E	17.3	2488	Monolith	Trough-peak + 1/5 leaf fall			1.07	<i>Arundinaria falcata</i>	Ravat <i>et al.</i> (1994)
	Garhwal, Himalaya, India	30° 15' N 78° 25' E	15.3	1710	Monolith	Σ Δ biomass			0.408 (0.358–0.494)	<i>Agrostis pilosa</i> , <i>Themeda anathera</i>	Sah <i>et al.</i> (1994)
	Kumarganj, India	26° 47' N 82° 12' E	24.0	1248	Monolith	Σ Δ biomass			0.350	<i>Brachiaria mutica</i>	Saxena <i>et al.</i> (1996)
Shrubland	Transkei, South Africa	31° 17' S 30° 00' E	17	1200	Coring	Σ Δ biomass			0.340 (0.24–0.50)	<i>Tristachya leucothrix</i> , <i>Cymbopogon validus</i>	Shackleton <i>et al.</i> (1988)
	Meghalaya, India	25° 04' N 91° 42' E	21.5 (16.5–22)	7462 (2871–16247)	Monolith	Trough-peak			0.762 (0.649–0.853)	<i>Setaria glauca</i> , <i>Arundinella nepalensis</i> , <i>A. khasiana</i>	Shankar <i>et al.</i> (1993)
	Karnal, Haryana, India	29° 58' N 76° 51' E	24.1	713	Monolith	Σ significant Δ biomass			0.969	<i>Dichanthium amulatum</i> , <i>Panicum miliare</i>	Singh & Yadava (1974)
	Rvenzori National Park, Uganda	0° 11' S 29° 53' E	23	600	Coring	Peak-trough			0.770 (0.747–0.794)	<i>Themeda triandra</i> , <i>Hyperthemia filipendula</i>	Strugnell & Pigott (1978)
	Pauri City, India	30° 10' N 78° 47' E	22	1294 (1226–1363)	Monolith	Σ Δ biomass			1.238 (1.201–1.272)	<i>Eriarthus rufipilus</i>	Tiwari (1986)
	Rajasthan, India	28° 23' N 75° 37' E	24.1	388	Monolith	Peak-trough	Total		0.737	<i>Capparis decidua</i> , <i>Balanites aegyptiaca</i>	Kumar & Joshi (1972)
	Kuman Himalaya, India	29° 45' N 72° 20' E	24.7	1711	Allometry		Total		0.732	<i>Lantana camara</i>	Rawat <i>et al.</i> (1994)
	Ivory Coast	6° 17' N 5° 13' W	26.6	1285	Coring	Balance transfer	Total		1.228	Hedgerow	Schroth & Zech (1995)
	Lake Naivasha, Kenya	0° 45' S 36° 20' E	15.3	688	Monolith		Total			<i>Cyperus papyrus</i>	Jones & Muthuri (1997)
	Amazonas, Brazil	3° 15' S 60° 00' W	23.3	2100	Ingrowth	Change in biomass + material + amount decomposed	Total			<i>Echinocloa polystachya</i>	Long <i>et al.</i> (1989); Piedade <i>et al.</i> (1992)
Tidal marsh	Paranagua Bay, Brazil	25° 16' S 48° 25' W	18	1577	Monolith		Total			<i>Spartina alterniflora</i>	Lana <i>et al.</i> (1991)
Temperate Broadleaf forest	Wisconsin, USA	43° 38' N 89° 47' W	8.5	950	Coring	Peak-trough	Fine	≤ 3	0.299 (0.177–0.344)	<i>Acer saccharum</i> , <i>Quercus alba</i> , <i>Q. boris</i> , <i>Q. velutina</i>	Aber <i>et al.</i> (1985)
	Wisconsin, USA	43° 38' N 89° 47' W	8.5	950	Coring/N mineralization	N budget	Fine	≤ 3	0.937 (0.670–1.12)	<i>Acer saccharum</i> , <i>Quercus alba</i> , <i>Q. boris</i> , <i>Q. velutina</i>	Aber <i>et al.</i> (1985); Hendricks <i>et al.</i> (1993); Nadelhoffer <i>et al.</i> (1985)
	Massachusetts, USA	42° 29' N 72° 11' W	9.1	960	Coring	Peak-trough	Fine	≤ 3	0.608	<i>Quercus-Acer</i>	McClougherty <i>et al.</i> (1982); Aber <i>et al.</i> (1985)
	Massachusetts, USA	42° 29' N 72° 11' W	9.1	960	Coring/N mineralization	N budget	Fine	≤ 3	0.506	<i>Quercus-Acer</i>	McClougherty <i>et al.</i> (1982); Aber <i>et al.</i> (1985)

Wisconsin, USA	43° 05' N 89° 22' W	8.5	800	Coring	Peak-trough	Fine	≤3	0.425 (0.188–0.574)	<i>Quercus alba</i> , <i>Q. boris</i> , <i>Acer saccharum</i>	Aber <i>et al.</i> (1985)
Wisconsin, USA	43° 05' N 89° 22' W	8.5	800	Coring/N mineralization	N budget	Fine	≤3	0.694 (0.398–1.05)	<i>Quercus alba</i> , <i>Q. boris</i> , <i>Acer saccharum</i>	Aber <i>et al.</i> (1985)
New York, USA	4° 00' N 74° 13' W	5.3	1060	Coring	Peak-trough; Σ significant Δ biomass and necromass; aboveground litterfall	Fine	≤3	0.653	<i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Betula alleghaniensis</i> , <i>Acer rubrum</i>	Burke & Raynal (1994)
Tennessee, USA	36° 01' N 84° 16' W	13.3	1265	Core	Trough-peak	Fine	≤5	0.829	<i>Liriodendron tulipifera</i>	Edwards & Harris (1977)
Portugal	39° 21' N 9° 24' E	16.3	463	Ingrowth		Fine	≤2	0.968	<i>Eucalyptus globulus</i>	Fabião <i>et al.</i> (1985)
New Hampshire, USA	43° 56' N 71° 45' W	5.7	1250	Ingrowth	2 × biomass in ingrowth cores	Fine	≤1	0.990 (0.827–1.256)	<i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Betula alleghaniensis</i>	Fahay & Hughes (1994)
Virginia, USA	37° 00' N 80° 00' W	14	1240	Core		Fine	≤2	1.416	<i>Acer rubrum</i> , <i>Robinia pseudoacacia</i>	Fredericksen & Zedaker (1995)
Central Himalaya, India	30° 29' N 80° 00' E	0.5	749	Coring	Σ Δ biomass + estimated mortality	Coarse		0.110 (0.089–0.269)	<i>Acer cappadocicum</i> , <i>Betula utilis</i> , <i>Rhododendron campanulatum</i>	Garkoti & Singh (1995)
Michigan, USA	43° 40' N 86° 09' W	7.6	850	Minirhizotron	Σ Δ length	Fine	≤2	0.560*	<i>Acer saccharum</i>	Hendrick & Pregitzer (1993)
Michigan, USA	44° 23' N 85° 50' W	5.8	810	Minirhizotron	Σ Δ length	Fine	≤2	0.523*	<i>Acer saccharum</i>	Hendrick & Pregitzer (1993)
Missouri, USA	38° 40' N 92° 12' W	13	939	Coring	Σ Δ biomass + decomposition	Fine	≤5	0.208	<i>Quercus alba</i>	Joslin & Henderson (1987)
Canberra, Australia	35° 23' S 148° 45' E	20.8	1205	Allometry		Coarse		0.019	<i>Eucalyptus pauciflora</i>	Keith <i>et al.</i> (1997)
Canberra, Australia	35° 23' S 148° 45' E	20.8	1205	Budget	Soil CO ₂ efflux–litterfall	Fine	≤5	0.862	<i>Eucalyptus pauciflora</i>	Keith <i>et al.</i> (1997)
Mirwart, Belgium	50° 02' N 5° 14' E	7.3	1071			Coarse		0.022	<i>Fagus sylvatica</i>	Kestemont (1982)
Virginia/North Carolina, USA	36° 30' N 76° 30' W	15.8	1170	Ingrowth	Σ Δ biomass	Coarse		0.214	<i>Taxodium distichum</i>	Powell & Day (1991)
Virginia/North Carolina, USA	36° 30' N 76° 30' W	15.8	1170	Coring		Coarse		0.189	<i>Quercus laurifolia</i> , <i>Taxodium distichum</i> , <i>Nyssa aquatica</i> , <i>Quercus laurifolia</i>	Megonigal & Day (1988)
Central Himalaya, India	29° 24' N 79° 30' E	23	2076	Monolith	Σ significant Δ biomass	Fine	≤2	0.819	<i>Shorea robusta</i>	Rana & Rikhari (1994)
Central Himalaya, India	29° 24' N 79° 30' E	14.9	2488	Monolith	Σ significant Δ biomass	Fine	≤2	0.841	<i>Quercus floribunda</i>	Rana & Rikhari (1994)
Virginia/North Carolina, USA	36° 30' N 76° 30' W	15	1170	Coring	Σ significant Δ biomass	Fine	≤5	1.119	<i>Nyssa aquatica</i> – <i>Acer rubrum</i>	Symbula & Day (1988)
Virginia/North Carolina, USA	36° 30' N 76° 30' W	15.8	1170	Coring	Σ significant Δ biomass	Total		1.555	<i>Nyssa aquatica</i> – <i>Acer rubrum</i>	Symbula & Day (1988)
New York, USA	40° 54' N 72° 52' E	10.7	1088	Allometry		Coarse		0.064	<i>Quercus alba</i>	Whittaker & Woodwell (1969)
New Hampshire, USA	43° 56' N 71° 45' W	–3	1393	Allometry		Coarse		0.085 (0.080–0.092)	<i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Betula lutea</i>	Whittaker <i>et al.</i> (1974)
Wisconsin, USA	43° 38' N 89° 47' W	8.5	950	Coring	Peak-trough	Fine	≤3	0.187 (0.171–0.206)	<i>Pinus resinosa</i> , <i>P. strobus</i>	Aber <i>et al.</i> (1985)
Wisconsin, USA	43° 38' N 89° 47' W	8.5	950	Coring/N mineralization	N budget	Fine	≤3	0.443 (0.43–0.463)	<i>Pinus resinosa</i> , <i>P. strobus</i>	Aber <i>et al.</i> (1985); Hendricks <i>et al.</i> (1993); Nadelhoffer <i>et al.</i> (1985)
Massachusetts, USA	42° 29' N 72° 11' W	9.1	960	Coring	Peak-trough	Fine	≤3	0.590	<i>Pinus resinosa</i>	McClougherty <i>et al.</i> (1982); Aber <i>et al.</i> (1985)
Massachusetts, USA	42° 29' N 72° 11' W	9.1	960	Coring/N mineralization	N budget	Fine	≤3	0.601	<i>Pinus resinosa</i>	McClougherty <i>et al.</i> (1982); Aber <i>et al.</i> (1985)
Wisconsin, USA	43° 05' N 89° 22' W	8.5	800	Coring	Peak-trough	Fine	≤3	0.473 (0.447–0.490)	<i>Pinus strobus</i> , <i>P. resinosa</i>	Aber <i>et al.</i> (1985)
Wisconsin, USA	43° 05' N 89° 22' W	8.5	800	Coring/N mineralization	N budget	Fine	≤3	0.322 (0.301–0.350)	<i>Pinus strobus</i> , <i>P. resinosa</i>	Aber <i>et al.</i> (1985)
Christchurch, New Zealand	42° 52' S 172° 45' E	10.8	658	Allometry		Fine	≤5	1.1†	<i>Pinus radiata</i>	Arnell <i>et al.</i> (1998)

Conifer forest

Appendix 1 (cont.)

Vegetation type	Location	Lat. and long.	Mean annual temperature (°C)	Mean annual precipitation (mm)	Root collection method	BNPP calculation method	Root type	Fine-root size	Root turnover†	Species	References
Conifer forest (cont.)	Colorado, USA	40° 19' N 105° 42' W	1.5	1000	Allometry; coring	N budget	Coarse; Fine	≤5	Coarse: 0.056; Fine: 0.137	<i>Picea engelmannii</i> ; <i>Abies lasiocarpa</i>	Arthur & Fahey (1992)
	Pukuri, New Zealand	36° 45' S 172° 45' E	12.5 (14, 11)	1400 (1300–1500)	Whole-plant harvest	Allometry	Fine	≤5		<i>Pinus radiata</i>	Beets & Whitehead (1996)
	Quebec, Canada	48° 30' N 79° 20' W	0.6	823	Ingrowth	Σ Δ biomass	Fine	≤2	0.613	<i>Abies amabilis</i> , <i>Picea glauca</i> , <i>Betula papyrifera</i>	Campbell <i>et al.</i> (1998)
	British Columbia, Canada	50° 09' N 115° 48' W	–3.4	973	Monolith; coring	Allometry; Σ Δ biomass	Coarse; Fine	≤5	Coarse: 0.097, Fine: 0.791	<i>Pinus contorta</i>	Comeau & Kimmins (1989)
	Oregon, USA	44° 32' N 123° 22' W	11.3	1312 (848–1775)	Coring	Σ Δ biomass + detritus	Coarse		0.123 (0.081–0.159)	<i>Pseudotsuga menziesii</i>	Fogel (1983); Fogel & Hunt (1983)
	Virginia, USA	37° 00' N 80° 00' W	14	1240	Coring	Balance transfer	Fine	≤2	1.503	<i>Pinus taeda</i>	Fredericksen & Zedaker (1995)
	Florida, USA	30° 00' N 82° 00' W	21.1	1445	Coring	Σ significant Δ biomass using ANOVA	Range		(<1) 0.477, (<1–5) 0.199, (<5–10) 0.066; (<10) 0.063	<i>Pinus elliotii</i>	Gholz <i>et al.</i> (1986)
	New Mexico, USA	35° 15' N 107° 34' W	12.1	2080	Coring	Decision matrix	Coarse; fine	≤5	Coarse: 0.042; Fine: 0.714	<i>Pseudotsuga menziesii</i>	Gower <i>et al.</i> (1992)
	Oregon, USA	44° 00' N 122° 30' W	8.5	2300	Allometry		Coarse	> 5	0.019 (0.016–0.019)	<i>Pseudotsuga menziesii</i>	Grier & Logan (1977)
	Washington, USA	47° 20' N 122° 00' W	5.4	2300	Allometry		Coarse; fine	≤5	Coarse: 0.283 (0.085–0.393); Fine: 0.680 (0.641–0.730)	<i>Abies amabilis</i>	Grier <i>et al.</i> (1981)
Savanna (herbaceous layer) Grassland	Wisconsin, USA	46° 10' N 89° 40' W	4.55	3246	Excavation; core	Max-min; decision matrix	Coarse; fine	≤1	Coarse: 0.037; Fine: 0.507–0.548	<i>Pinus resinosa</i>	Haynes & Gower (1995)
	Washington, USA	46° 00' N 122° 00' W	6.7	1000	Rhizotron & core	Root biomass × (no. of new roots/existing roots)	Coarse; fine	≤5	Coarse: 0.094 (0.047–0.141); Fine: 0.633 (0.556–0.667)	<i>Pseudotsuga menziesii</i>	Keyes & Grier (1981)
	Virginia/North Carolina, USA	36° 30' N 76° 30' W	15.8	1170	Ingrowth; coring	Σ biomass	Total		0.337	<i>Chamaecyparis thyoides</i>	Megonigal & Day (1988); Powell & Day (1991)
	Oregon, USA	44° 14' N 122° 13' W	5.2	2000	Core	Σ interval estimates	Fine	≤1	1.918 (1.524–2.569)	<i>Tsuga heterophylla</i>	Santantonio <i>et al.</i> (1977); Santantonio & Hermann (1985); Santantonio & Grace (1987)
	Washington, USA	46° 00' N 122° 00' W	5.4	2730	Coring		Coarse; fine	≤2	Coarse: 0.356 (0.118–0.594); Fine: 1.029	<i>Abies amabilis</i>	Vogt <i>et al.</i> (1982, 1986, 1987, 1996); Vogt (1991)
	Pilani, Rajasthan, India	28° 23' N 75° 37' E	24.1	388	Monolith	Trough-peak				<i>Capparis decidua</i>	Kumar & Joshi (1972)
	Central Netherlands	50° 02' N 5° 50' E	8.2	700	Coring	Σ significant Δ biomass and necromass Tukey's Studentized Range test			0.601 (0.560–0.737)	<i>Balanites aegyptiaca</i>	Aerts <i>et al.</i> (1992)
	Central Netherlands	50° 02' N 5° 50' E	8.2	700	Minirhizotron	Σ significant Δ biomass and necromass Tukey's Studentized Range test			0.828	<i>Deschampsia flexuosa</i> , <i>Molinia caerulea</i>	
	Minnesota, USA	45° 34' N 93° 35' W	6.5	690	Coring				0.673	<i>Deschampsia flexuosa</i> , <i>Molinia caerulea</i>	Aerts <i>et al.</i> (1992)
	North Dakota, USA	46° 39' N 99° 21' W	4.8	446	Coring	Difference method			0.324	<i>Poa pratensis</i>	Bernard (1974)
Missouri, USA	Missouri, USA	38° 57' N 99° 20' W	12.5	973	Coring				0.343 (0.212–0.479)	<i>Poa pratensis</i> , <i>Agropyron smithii</i>	Biondini <i>et al.</i> (1998)
	Missouri, USA	38° 57' N 99° 20' W	12.5	973	Coring				0.360	<i>Andropogon gerardi</i> , <i>Schizachyrium scoparium</i>	Buyanovsky <i>et al.</i> (1987)
	Missouri, USA	38° 57' N 99° 20' W	12.5	973	Coring				0.489	<i>Andropogon gerardi</i> , <i>Schizachyrium scoparium</i>	Buyanovsky <i>et al.</i> (1987)
	Saskatchewan, Canada	50° 48' N 107° 57' W	3.6	388	C pool dilution	Regression			0.267 (0.150–0.387)	<i>Agropyron dasystachyum</i> , <i>A. smithii</i> , <i>Stipa comata</i> , <i>S. spartea</i>	Coupland (1992)

Shrubland	North Dakota, USA	46° 53' N 102° 49' W	4.1	403							<i>Agropyron smithii</i> , <i>Stipa spartea</i>	Coupland (1992)
	Missouri, USA	38° 57' N 92° 20' W	12.7	1016	Coring						<i>Andropogon gerardi</i> , <i>A. scoparius</i>	Dahlman & Kucera (1965)
	Missouri, USA	38° 57' N 92° 20' W	12.7	1016	C pool dilution	Regression					<i>Andropogon gerardi</i> , <i>A. scoparius</i>	Dahlman & Kucera (1967)
	Moor House, UK	54° 03' N 2° 48' W	5.1	1883	Minirhizotron	Calibration of root number to biomass					<i>Festuca ovina</i> , <i>Nardus stricta</i> , <i>Juncus squarrosus</i>	Fitter <i>et al.</i> (1997)
	Kansas, USA	39° 10' N 96° 30' W	13	835	Coring	Σ significant Δ biomass					<i>Andropogon gerardi</i>	Hayes & Seastedt (1987)
	South Dakota, USA	43° 26' N 103° 28' W	9.2	402	Coring	Trough-peak					<i>Agropyron smithii</i> , <i>Andropogon scoparius</i>	Ingham & Detling (1984)
	South Dakota, USA	43° 57' N 101° 52' W	8.2	387	Coring	Σ significant Δ biomass						Marshall (1977); Sims & Singh (1978)
	Colorado, USA	40° 49' N 104° 46' W	8.2	311	Coring	Σ significant Δ biomass					<i>Bouteloua gracilis</i>	Marshall (1977); Sims & Singh (1978); Redmann (1992)
	Kansas, USA	38° 52' N 99° 23' W	12	586	Coring	Σ significant Δ biomass						Marshall (1977); Sims & Singh (1978)
	Washington, USA	46° 24' N 119° 33' W	12.8	183	Coring	Σ significant Δ biomass						Redmann (1992); Marshall (1977)
Wetland	Oklahoma, USA	36° 56' N 96° 30' W	14.3	916	Coring	Σ significant Δ biomass					<i>Scizachyrium scoparius</i>	Marshall (1977); Sims & Singh (1978)
	New Mexico, USA	32° 36' N 106° 85' W	14.4	262	Coring	Σ significant Δ biomass						Marshall (1977)
	Texas, USA	35° 18' N 101° 32' W	14.9	499	Coring	Σ significant Δ biomass					<i>Bouteloua gracilis</i>	Marshall (1977); Sims & Singh (1978); Redmann (1992)
	California, USA	38° 03' N 121° 50' W	15.3	484	Coring	Σ significant Δ biomass						Marshall (1977)
	Colorado, USA	40° 46' N 104° 46' W	8.2	322	Coring	Σ significant Δ biomass					<i>Bouteloua gracilis</i>	Ares (1976); Milchunas & Lauenroth (1992)
	Colorado, USA	40° 46' N 104° 46' W	8.2	322	C pool dilution	ANOVA, <i>t</i> -test, SD					<i>Bouteloua gracilis</i>	Milchunas <i>et al.</i> (1985); Milchunas & Lauenroth (1992)
	Wyoming, USA	41° 08' N 104° 49' W	9	365	Coring	Trough-peak					<i>Agropyron cristatum</i> , <i>Bouteloua gracilis</i> , <i>Agropyron smithii</i> , <i>Stipa comata</i>	Redente <i>et al.</i> (1989)
	Palmerston North, New Zealand	40° 18' S 175° 50' E	8.7	1202	C pulse	Regression						Saggar <i>et al.</i> (1997)
	Virginia, USA	37° 25' N 75° 41' W	14.3	1102	Coring, ingrowth core	Σ Δ biomass					<i>Agrostis capillaris</i> , <i>Lolium perenne</i> , <i>Hokas tanatus</i>	Stevenson & Day (1996)
	Nebraska, USA	40° 48' N 96° 42' W	4.8	560	Monolith						<i>Amnophila breviligulata</i>	Weaver & Zink (1946)
Shrubland	Utah, USA	41° 52' N 113° 50' W	7.1	244	Pool dilution						<i>Andropogon furcatus</i> , <i>A. scoparius</i> , <i>Bouteloua gracilis</i>	Caldwell <i>et al.</i> (1977)
	Utah, USA	41° 52' N 113° 50' W	7.1	244	Pool dilution						<i>Atriplex confertifolia</i>	Caldwell <i>et al.</i> (1977)
	Southwest Spain	37° 07' N 6° 12' W	16.5	620	Coring						<i>Ceratoides lanata</i>	Martinez <i>et al.</i> (1998)
	North Carolina, USA	34° 38' N 78° 34' W	17.6	1170	Coring						<i>Cistus libanotis</i> , <i>Halimium halimifolium</i> , <i>Lavandula stoechas</i>	Saterson & Vitousek (1984)
	Michigan, USA	44° 00' N 84° 00' W	9	890							<i>Aristida stricta</i> , <i>Vaccinium crassifolium</i>	Wentz & Chamie (1980)
	Minnesota, USA	45° 34' N 93° 35' W	6.5	690	Coring						<i>Chamaedaphne calyculata</i>	Bernard (1974)
	New York, USA	42° 27' N 76° 30' W	8.8	912	Monolith						<i>Carex rostrata</i>	Bernard <i>et al.</i> (1985)
	Minnesota, USA	45° 43' N 93° 35' W	6.5	690	Monolith						<i>Claudian mariscoides</i>	Bernard & Bernard (1973)
	New York, USA	42° 27' N 76° 30' W	8.8	912	Monolith						<i>Sparganium eurycarpum</i> , <i>Typha glauca</i>	Bernard & Hankinson (1979)
	Czechoslovakia	48° 50' N 14° 48' E	9.0	570	Monolith						<i>Carex rostrata</i>	Fiala (1976); Květ & Westlake (1998)

Appendix 1 (cont.)

Vegetation type	Location	Lat. and long.	Mean annual temperature (°C)	Mean annual precipitation (mm)	Root collection method	BNPP calculation method	Root type	Fine-root size	Root turnover†	Species	References
Tidal marsh	Mississippi, USA	32° 22' N 88° 42' W	18.8	1483	Coring	Fit general periodic regression curve	Total		0.110	<i>Juncus roemerianus</i>	de la Cruz (1973); de la Cruz & Hackney (1977)
	Mississippi, USA	32° 22' N 88° 42' W	18.8	1483	Coring		Total		0.259	<i>Spartina cynosuroides</i>	Hackney & de la Cruz (1986)
	Delaware, USA	39° 34' N 75° 36' W	14	1039	Coring	Maximum–minimum	Total		0.471	<i>Spartina patens</i> , <i>S. alterniflora</i>	Roman & Daiber (1984)
	Delaware, USA	38° 47' N 75° 08' W	14	1039	Coring	Maximum–minimum	Total		0.436	<i>Phragmites australis</i> ;	Roman & Daiber (1984)
	Georgia, USA	31° 19' N 81° 18' W	20.6	1330	Coring		Total		0.737	<i>Spartina alterniflora</i> <i>S. cynosuroides</i>	Schubauer & Hopkinson (1984)
	New Jersey, USA	39° 32' N 74° 39' W	4.8	1030	Coring		Total		0.230	<i>Spartina alterniflora</i>	Smith <i>et al.</i> (1979)
	Massachusetts, USA	41° 31' N 70° 40' W	6.4	1232	Coring		Fine		1.807	<i>Spartina patens</i> , <i>S. alterniflora</i>	Valiela <i>et al.</i> (1976)
	Massachusetts, USA	41° 56' N 70° 06' W	6.4	1232	N budget		Fine		0.954	<i>Spartina alterniflora</i>	White & Howes (1994)
Boreal/alpine Mixed forest	Quebec, Canada	48° 30' N 79° 20' W	0.6	823	Ingrowth	Σ live and dead biomass	Fine	≤ 10	0.077	<i>Populus tremuloides</i> , <i>Abies balsamea</i>	Finer <i>et al.</i> (1997)
	Hardangervidda Norway	60° 36' N 7° 30' E	−2	1006	*		Coarse		0.102	*	Østbye <i>et al.</i> (1975)
	Orivesi, Finland	61° 48' N 24° 19' E	2.6	706	Coring	Σ significant Δ biomass using ANOVA	Fine	≤ 2	0.465	<i>Pinus sylvestris</i>	Finer & Laine (1998)
	Raakkylä, Finland	62° 14' N 29° 50' E	2.8	702	Coring	Σ significant Δ biomass using ANOVA	Coarse		0.382	<i>Pinus sylvestris</i>	Finer & Laine (1998)
	Quebec, Canada	48° 30' N 79° 20' W	0.6	823	Ingrowth	Σ live and dead biomass	Fine	≤ 10	0.077	<i>Thuja occidentalis</i> , <i>Abies balsamea</i>	Finer <i>et al.</i> (1997)
	Sweden	60° 46' N 16° 39' E	4.1	617	Core	Σ interval estimates	Fine	≤ 2	0.593 (0.07–1.217)	<i>Pinus sylvestris</i> , <i>Calluna vulgaris</i> , <i>Vaccinium vitis-idaea</i>	Persson (1978, 1980, 1983)
	Manitoba, Canada	49° 53' N 95° 54' W	2.3	515	Monolith	(Aerial production/aerial biomass) × belowground biomass	Total		0.079	<i>Picea mariana</i>	Reader & Stewart (1972)
	Alaska, USA	64° 45' N 148° 15' W	−3.5	269	Coring		Fine	≤ 2	0.810 (0.52–1.05)	<i>Picea glauca</i> , <i>P. mariana</i>	Ruess <i>et al.</i> (1996, 1998)
	Saskatchewan, Canada	53° 50' N 104° 41' W	−1.1	405	Coring/ingrowth	Δ biomass in ingrowth	Fine	≤ 5	0.087	<i>Pinus banksiana</i> , <i>Picea mariana</i>	Steele <i>et al.</i> (1997)
	Saskatchewan, Canada	53° 50' N 104° 41' W	−1.1	405	Minirhizotron	Σ Δ length × length to biomass conversion factor	Fine	≤ 5	0.294	<i>Pinus banksiana</i> , <i>Picea mariana</i>	Steele <i>et al.</i> (1997)
Broadleaf forest	Manitoba, Canada	55° 56' N 98° 36' W	−4.7	536	Coring/ingrowth	Σ biomass in ingrowth	Fine	≤ 5	0.128	<i>Pinus banksiana</i> , <i>Picea mariana</i>	Steele <i>et al.</i> (1997)
	Manitoba, Canada	55° 56' N 98° 36' W	−4.7	536	Minirhizotron	Σ Δ length × length to biomass conversion factor	Fine	≤ 5	0.372	<i>Pinus banksiana</i> , <i>Picea mariana</i>	Steele <i>et al.</i> (1997)
	Belgium	50° 33' N 6° 05' E	6.1	1450	Core	Budget	Fine	≤ 1	0.507	<i>Picea abies</i>	Van Praag <i>et al.</i> (1988)
	Greenland	61° 06' N 45° 58' W	−0.9	700	Allometry		Coarse		0.014	<i>Betula pubescens</i>	Elkington & Jones (1974)
	Quebec, Canada	48° 30' N 79° 20' W	0.6	823	Ingrowth	Σ biomass	Fine	≤ 10	0.200	<i>Populus tremuloides</i> , <i>Betula papyrifera</i>	Finer <i>et al.</i> (1997)
	Kongalund, Sweden	55° 42' N 13° 38' W	7	750	Allometry		Coarse		0.042	<i>Fagus sylvatica</i>	Nihlgård & Lindgren (1977)
	Langarod, Sweden	55° 59' N 13° 10' W	6	800	Allometry		Coarse		0.046	<i>Fagus sylvatica</i>	Nihlgård & Lindgren (1977)
	Oved, Sweden	55° 45' N 13° 55' W	7	650	Allometry		Coarse		0.049	<i>Fagus sylvatica</i>	Nihlgård & Lindgren (1977)
	Manitoba, Canada	49° 53' N 95° 54' W	2.3	515	Monolith	(Aerial production/aerial biomass) × belowground biomass	Total		0.334	<i>Salix bebbiana</i> , <i>S. serissima</i>	Reader & Stewart (1972)
	Alaska, USA	64° 45' N 148° 15' W	−3.5	269	Coring		Fine	≤ 2	0.673 (0.330–0.94)	<i>Populus balsamifera</i> , <i>Betula papyrifera</i> , <i>Populus tremuloides</i>	Ruess <i>et al.</i> (1996)
	Saskatchewan, Canada	53° 50' N 104° 41' W	−1.1	405	Coring/ingrowth	Σ biomass in ingrowth	Fine	≤ 5	0.072	<i>Populus tremuloides</i>	Stee

Grassland	Saskatchewan, Canada	53° 50' N 104° 41' W	−1.1	405	Minirhizotron	Σ Δ length × length to biomass conversion factor	Fine	≤ 5	0.085	<i>Populus tremuloides</i>	Steele <i>et al.</i> (1997)
	Manitoba, Canada	55° 56' N 98° 36' W	−4.7	536	Coring/ingrowth	Σ biomass in ingrowth core	Fine	≤ 5	0.131	<i>Populus tremuloides</i>	Steele <i>et al.</i> (1997)
	Manitoba, Canada	55° 56' N 98° 36' W	−4.7	536	Minirhizotron	Σ Δ length × length to biomass conversion factor	Fine	≤ 5	0.115	<i>Populus tremuloides</i>	Steele <i>et al.</i> (1997)
	Belgium	50° 33' N 6° 05' E	6.1	1450	Core	Budget	Fine	≤ 1	0.507	<i>Fagus sylvatica</i>	Van Praag <i>et al.</i> (1988)
	Devon Island, Canada	75° 33' N 84° 40' W	−17.6	267.1					0.137 (0.095– 0.188)	<i>Carex stans</i> , <i>Eriophorum triste</i>	Bliss (1975)
	Colorado, USA	40° 03' N 105° 35' W	−3	900	Ingrowth cores	Σ new roots			0.283 (0.200– 0.360)	<i>Kobresia myosuroides</i> , <i>Acomastylis rossii</i> , <i>Carex scopulorum</i>	Fisk <i>et al.</i> (1998)
	Moor House, UK	54° 39' N 2° 27' W	5.1	1883			Total		0.181	<i>Calluna vulgaris</i>	Heal <i>et al.</i> (1975)
	Moor House, UK	54° 39' N 2° 27' W	5.1	1883					0.246	<i>Calluna vulgaris</i>	Heal <i>et al.</i> (1975)
	Macquarie Island, Subantarctic	54° 00' S 36° 50' W	4.7	926					0.765	<i>Poa foliosa</i>	Hnatiuk (1993)
	Macquarie Island, Subantarctic	54° 00' S 36° 50' W	4.7	926	Coring				0.490 (0.254– 0.569)	<i>Poa foliosa</i> , <i>Stilbocarpa polaris</i>	Jenkin (1975)
	Alaska, USA	71° 17' N 156° 47' W	−12.6	170	Rhizotron	Cohort life span			0.135 (0.119– 0.155)	<i>Carex-Eriophorum</i> , <i>Dupontia fisheri</i> , <i>Carex-Oncophorus</i> , <i>Carex-Poa</i>	Miller <i>et al.</i> (1980)
	Manitoba, Canada	50° 11' N 98° 19' W	2.7	461	Ingrowth cores	Σ new roots			0.531 (0.119– 0.628)	<i>Scolochloa festuacea</i>	Neill (1992, 1994)
	Manitoba, Canada	50° 11' N 98° 19' W	2.7	461	Coring	Significant difference in max–min			0.531 (0.119– 0.628)	<i>Scolochloa festuacea</i>	Neill (1992, 1994)
	Hardangervidda Norway	60° 36' N 7° 30' E	−2	1006					0.304 (0.273– 0.374)	<i>Descampsia flexuosa</i> , <i>Poa alpina</i> , <i>Anthoxanthum alpinum</i>	Ostbye <i>et al.</i> (1975)
	Himalaya, India	30° 28' N 79° 20' E	7	1586	Monolith	Peak–trough, Σ significant			0.245 (0.241– 0.249)	<i>Danthonia cachemyriana</i>	Ram <i>et al.</i> (1991)
	Himalayan Alpine, India	30° 11' N 49° 40' E	6	1557	Coring	Trough–peak			0.143 (0.100– 0.166)	<i>Trachydium roylei</i> , <i>Danthonia cachemyriana</i> , <i>Kobresia duthei</i>	Rikhari <i>et al.</i> (1992)
	Stordalen, Sweden	68° 22' N 19° 03' E	−0.7	300					0.06	<i>Andromeda polifolia</i> , <i>Vaccinium uliginosum</i>	Roswall <i>et al.</i> (1975)
	Alaska, USA	71° 17' N 156° 47' W	−22.3	162	Rhizotron	Cohort life span			0.116 (0.051– 0.167)	<i>Carex aquatilis</i> , <i>Dupontia fisherii</i>	Shaver & Billings (1975); Shaver & Chapin (1991)
	South Georgia, Subantarctic	54° 36' S 158° 57' E	1.8	1405					0.186 (0.183– 0.194)	<i>Festuca contracta</i> , <i>Poa flabellata</i>	Smith & Walton (1975)
	Garhwal, India	30° 30' N 79° 15' E	5.5	2170	Monolith	Trough–peak			0.587 (0.314– 0.911)	<i>Anaphalis royleana</i> , <i>Geum elatum</i> , <i>Tanacetum longifolium</i>	Singh & Joshi (1979); Sundriyal & Joshi (1990)
Tundra	Suwalki, Poland	54° 07' N 22° 56' E	6.6	583	Root ingrowth	Σ root growth into sand			0.051 (0.043– 0.061)	<i>Dactylis glomerata</i> , <i>Arrhenatherion</i> , <i>Anthyllitritifolietum montani</i>	Szanser (1997)
	Hardangervidda Norway	60° 36' N 7° 30' E	−2	1006			Total		0.313 (0.202– 0.424)		Ostbye <i>et al.</i> (1975)
	Himalayan Alpine, India	30° 12' N 79° 40' E	2.2	1557	Coring		Total		0.079	<i>Rhododendron anthopogon</i>	Rikhari <i>et al.</i> (1992)
	Stordalen, Sweden	68° 22' N 19° 03' E	−0.7	300			Total		0.058	Dwarf shrub; forbs; minor graminoid	Roswall <i>et al.</i> (1975)
	South Georgia, Subantarctic	54° 36' S 158° 57' E	1.8	1405			Total		0.064	<i>Acaena magellanica</i>	Smith & Walton (1975)
	Netherlands	52° 13' N 5° 32' E	9.2	788	Coring		Total		0.958 (0.796–1.071)	<i>Molinia caerulea</i> , <i>Erica tetralix</i>	Berendse <i>et al.</i> (1987)
	Devon Island, Canada	75° 33' N 84° 40' W	−17.6	267.1			Total		0.133	<i>Cassiope tetragona</i>	Bliss (1975)
	Barrow, Alaska	68° 38' N 149° 34' W	−12.6	170			Total		0.095	<i>Salix</i> spp., <i>Luzula</i>	Miller <i>et al.</i> (1980); Webber <i>et al.</i> (1980)
	Quebec, Canada	46° 59' N 70° 33' W	2.4	880	Coring	Maximum–minimum biomass or standing crop; Smalley method	Total		0.740	<i>Eleocharis</i> spp., <i>Sagittaria spp.</i> , <i>Scirpus americanus</i>	Giroux & Bedard (1988)

‡Values in italics were determined by using the equation: turnover = BNPP/(0.45 × BNPP + mean root biomass). *Turnover = BNPP/initial root biomass. †Turnover = BNPP/mean root biomass.

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