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The Dynamics of Living and Dead Fine Roots of Forest Biomes across the Northern Hemisphere

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Abstract: Research Highlights: A detailed picture of the seasonality in fine root biomass (FRB), necromass (FRN), and the biomass/necromass ratio (FRBN) throughout the whole year is crucial to uncover profound effects of long-term environmental changes on fine root dynamics. Materials and Methods: We used meta-analysis to characterize the variability of FRB, FRN and FRBN, and determined their relations with climatic (monthly versus annual), edaphic and geomorphic factors for tropical, temperate and boreal forest biomes across the Northern Hemisphere. Results: Boreal forests exhibited the highest FRB and FRN, while tropical forests yielded the lowest FRN, and thus the greatest FRBN. FRB and FRN significantly decreased with sampling depth, but increased with soil organic carbon content and elevation, while an opposite pattern was found for FRBN. Temperature and precipitation at different time scales (monthly versus annual) and latitude had varying influences on fine roots. High FRB and FRN were observed during dry season for tropical forests, but in the late growing season for temperate forests. The three forest biomes exhibited the high root activity (measured as FRBN) in June or July. Conclusions: It is crucial to realize the universal and specific responses of fine roots to multiple environmental factors when attempting to incorporate these parameters into fine root monthly dynamic models in forest ecosystems. The biome-specific fluctuation of fine roots contributes to identify the influence factors on fine root seasonal patterns throughout the whole year. Our analysis is expected to improve the understanding of the key role of fine roots at monthly level in modeling and predicting carbon budget of various forest biomes under future climate change.

Keywords: fine root biomass; fine root necromass; forest biome; monthly; precipitation; seasonal dynamics; temperature

1. Introduction

"Fine root dynamics" is a category of root traits which circumscribes growth and death of fine roots, including production, mortality and decomposition, and the "fine root system" is the category of root traits which describes the standing crop or mass of fine roots [1]. Both, fine root dynamics and system have also been widely recognized as an important biogeochemical process in forest ecosystems [2,3], because fine roots represent a large carbon cost to trees and are an important carbon source to the soil [4–6]. Growth, death and decomposition of fine roots appear to occur continuously and simultaneously throughout the whole year, and stocks of living (biomass) and dead fine roots (necromass) represent the end products of these processes [2,7,8]. Nevertheless, it is difficult to clarify the ecological impact of long-term environmental changes on forest carbon cycling without a detailed picture of the seasonality of fine root dynamics [9,10]. Additionally, it seems not be accurate that current climate models treat fine roots as a fixed, synchronous fraction of aboveground growth [11]. Thus, modeling responses of forest ecosystems to global changes can benefit greatly from a better characterization of the fine root stock patterns and dynamics [12–14]. Overall, little has been done to characterize and quantify the magnitude of the seasonal fine root biomass and necromass on a monthly basis throughout the whole year at large scale (e.g., biome, hemisphere, globe).

It has been indicated that fine roots, as highly dynamic parts of the root system, are subjects to seasonal fluctuations over various temporal and spatial scales in global forest ecosystems [1]. Seasonal patterns of living fine root mass in forest ecosystems have been reported to range from stands with no distinct seasonal pattern to those with modal or bimodal statistically significant peaks of biomass followed by periods of high necromass [4,15,16]. Temporal variations of air temperature and precipitation as well as associated fluctuations in soil resources may be responsible for the fine root patterns [17,18]. However, earlier studies were conducted with temperature or precipitation at annual level, thus, it is important to determine whether the relationships identified earlier can be maintained as more data are collected on a monthly basis. In addition, seasonal patterns of fine root biomass and necromass are powerfully influenced by biotic factors such as carbon allocation strategies of the trees [19]. Therefore, a better understanding of the varying fine root dynamics is crucial in attempting to incorporate fine root parameters into dynamic carbon models of forest ecosystems [20–22].

Along natural climatic zones, terrestrial forests can generally be grouped into tropical, temperate and boreal biomes, where biomass characteristics have attracted lasting attention from ecologists [15,23–25]. Trees from these forest ecosystems have evolved contrasting growth and survival strategies for their fine roots to adapt to the tremendous variations in seasonal climates [24,26]. It was found that standing root biomass varied by over an order of magnitude across plant biomes, and the highest root biomass in terrestrial plant biomes was observed in tropical forests [27], due to the continual growing season and the favorable hydrothermal conditions in tropical zones [28]. It can therefore be expected that the fine roots demonstrate different seasonal patterns of biomass and necromass, indicating the absorption capacity of the fine root systems [29,30]. For example, our previous studies had revealed that various forest biomes had differences in responses of fine root biomass, necromass and the biomass/necromass ratios to climate, topography, soil and stand characteristics [25,30]. While these studies have shed light on global patterns of living and dead fine-root stocks, there is only little known about the seasonal variation on a monthly basis. Consequently, size and nature of fine-root pools of the various forest biomes are likely to lead to uncertain estimates for long-term carbon storage [31,32].

The database of research results from tropical to boreal zones in this context would be very beneficial for best predicting fine root biomass and necromass at different levels. Detailed fine-root patterns were combined with information on climatic, edaphic and geomorphic variables, then a more comprehensive picture of the role of various factors in fine-root dynamics of different forest biomes could be produced. This is crucial in the view of forecasting changes in forest ecosystem functioning and potential effects on the global carbon cycle as a result of future global changes. We, therefore, hypothesized that (1) forest biomes have distinct differences in living and dead stocks, in particular, tropical forests tend to have larger amount of their monthly fine root biomass and necromass than temperate and boreal forests; (2) the factors determining the variation in monthly fine root biomass, necromass, and biomass/necromass ratio depend upon forest biome. Accordingly, the objectives of the current study were to characterize and quantify the seasonal variability of the monthly fine root biomass, necromass and the biomass/necromass ratio throughout the whole year, and to identify their potential relationships with climatic, edaphic and geomorphic factors for tropical, temperate and boreal forests across the Northern Hemisphere.

2. Materials and Methods

2.1. Literature Synthesis

There is not much data available on fine roots of forests in the Southern Hemisphere, and thus, we assembled a database of 63 studies that analyzed seasonal dynamics of forest living and dead fine root mass using sequential soil core methods on a monthly scale across the Northern Hemisphere (the list of the data sources shown in Appendix A). We classified forests into three biomes, i.e., boreal, temperate, and tropical biomes, according to the description in the original studies. In that dataset, we identified a total of 1068 observations, including 52 observations for boreal forests, 886 for temperate forests, and 130 ones for tropical forests. These studies were conducted in 125 different forest ecosystems from 66 geographical locations, spanning boreal, temperate and tropical plantation/natural forests from the years 1974 to 2016. The sites had a broad range of climatic factors, e.g., mean annual precipitation from 360 to 4000 mm, and mean annual temperature from −10.3 °C to 29.3 °C. Dry mass per unit soil volume (mg cm^{-3}) was used to estimate the biomass and necromass of fine roots, due to the variation in sampling depth among the studies. Sampling depth in forest mineral soil was not less than 10 cm. When fine roots were collected across soil layers, the data from different soil layers were summed over all sampling depths. If samplings were performed for multiple years within the same stand or for several stands at the same time, the data were treated separately to describe intra-annual variability in fine roots. Climatic factors (precipitation and temperature on the monthly and annual scales) were obtained from the WorldClim data set (http://www.worldclim.org/). If not stated in the articles, edaphic characterizations were available from the harmonized World Soil Database (FAO/IIASA/ISRIC/ISS-CAS/JRC 2012) based on their geographic coordinates. The main topsoil (0-30 cm depth) properties retrieved included soil pH, organic carbon content and bulk density. Moreover, the sampling depth, elevation and dominated tree species were also recorded.

2.2. Statistical Analysis

As the data were not normally distributed and did not show homogeneous variance, the Scheirer-Ray-Hare (SRH) nonparametric two-way test, an extension of the Kruskal-Wallis test, was used to detect the influences of months (n = 12), the forest biomes (n = 3), and their interactions on fine root variables (*scheirerRayHare* function in *rcompanion* package) [33]. Post hoc test of means using the criterion Fisher's least significant difference (*kruskal* function in *agricolae* package; https://cran.r-project.org/web/packages/agricolae/agricolae.pdf) was applied to determine the comparison of different months and forest biomes when the SRH was statistically significant ($p < 0.05$).

We employed the multimodel inference approach to estimate the effect of each predictor. This approach makes inferences based on a set of best models, rather than one single best model, and therefore can provide more stable and reliable inference results than traditional statistical inference [34]. For each fine root variable, we constructed a linear mixed model that included climatic (mean monthly precipitation, mean monthly temperature, mean annual precipitation, mean annual temperature), edaphic (soil pH, soil organic carbon content, soil bulk density and sampling depth), and geomorphic factors (elevation, latitude). Data source, sampling year, sampling month, dominant soil group, and tree family of sites were treated as random factors to account for the non-independence of fine roots from the same author, year, month, soil group, and tree family. The model was compared to all possible combinations of models with various subsets of predictors using the *dredge* function in *MuMIn* package [35]. The best model was defined as the combination of predictors that produced the lowest corrected Akaike Information Criterion (AICc). Further analyses were conducted on a subset of models considered most informative and best supported by the data with ΔAIC values <2. Using this subset of informative models, a summed Akaike weight was determined for each predictor variable using the *importance* function, which indicates relative variable importance in predicting the response. Predictors with Akaike weight >0.50 were considered important variables [34].

3. Results

3.1. Monthly Fine Root Biomass, Necromass and the Biomass/Necromass Ratio

Across the Northern Hemisphere, monthly fine root biomass (FRB, living fine root mass on the monthly basis) was significantly affected by forest biome and its interaction with month (Table 1). Month, forest biome and their interactions markedly influenced monthly fine root necromass (FRN, dead fine root mass on the monthly basis) and the biomass/necromass ratio (FRBN; Table 1). Boreal forests had the highest average FRB (± 1SE) (1.13 ± 0.12 mg cm^{-3}) and FRN (1.05 ± 0.32 mg cm^{-3}) among the three forest biomes (Figure 1a,b). Lower values of FRB were recorded for temperate (0.89 ± 0.03 mg cm^{-3}) and tropical forests (0.80 ± 0.07 mg cm^{-3}; Figure 1a). However, compared to boreal forests (1.05±0.32 mg cm^{-3} for FRN and 6.77 ± 1.48 for FRBN) and temperate (0.71 ± 0.06 mg cm^{-3} for FRN and 6.17 ± 0.30 for FRBN), tropical forests yielded the lowest FRN (0.54 ± 0.11 mg cm^{-3}) and the highest FRBN (7.84 ± 0.70) (Figure 1b,c).

Table 1. Effects of biome, month and their interactions on monthly fine root biomass (FRB; n = 1068), necromass (FRN; n = 1068) and their biomass/necromass ratio (FRBN; n = 1068) using a two-way nonparametric Scheirer-Ray-Hare (SRH) test. H-values of SRH test are given.

		FRB			FRN			FRBN		
Factors	**DF**	**SS**	**H**	***p***	**SS**	**H**	***p***	**SS**	**H**	***p***
Biome	2	690358	7.26	**<0.05**	2540387	26.71	**<0.001**	1666605	17.52	**<0.001**
Month	11	1604304	16.86	0.11	4062906	42.72	**<0.001**	3856547	40.54	**<0.001**
Biome × Month	17	2891658	30.40	**<0.05**	3774040	39.69	**<0.01**	3636098	38.22	**<0.01**
Residuals	1037	96323028			91091014			92355612		

DF, degree of freedom; SS, sum square. Significant p-values (<0.05) were in bold.

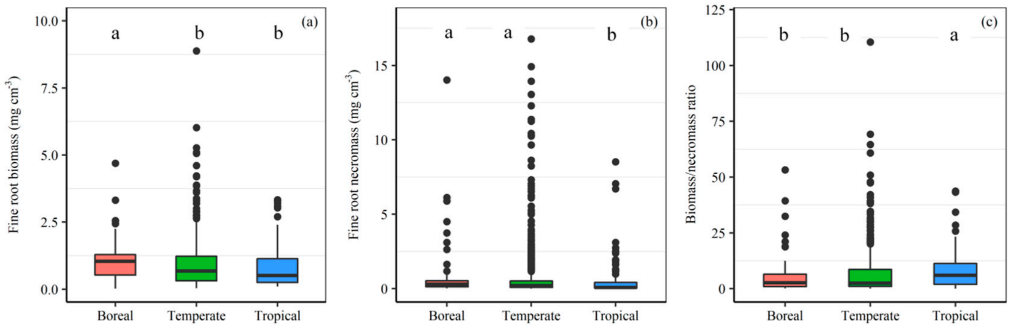

Figure 1. Monthly fine root biomass (**a**), necromass (**b**) and their biomass/necromass ratio (**c**) among boreal, temperate and tropical forests.

3.2. Climatic, Edaphic and Geomorphic Influences on Monthly Fine Root Variation

The diverse variables retained in the average best-fitting models demonstrated that the main factors influencing fine roots differed with forest biome (Tables 2 and 3). All models included sampling depth, soil organic carbon content and elevation, indicating the most important explanatory factors for monthly fine root variation (Tables 2 and 3). FRB and FRN significantly decreased with increasing sampling depth, but they increased with increasing soil organic carbon content and elevation in the three forest biomes, while FRBN in the three forest biomes showed an opposite pattern (Table 2). The effects of climatic and other edaphic factors on fine root variables seemed to be dependent upon forest biomes (Table 3). In boreal forests, FRBN significantly increased with mean monthly precipitation, whereas FRN significantly increased with mean monthly temperature, but significantly decreased with mean annual precipitation, mean annual temperature, soil bulk density, soil pH and latitude (Table 2). Both FRB and FRBN of temperate forests were positively correlated with mean monthly precipitation and soil pH, but negatively correlated with mean monthly temperature and soil bulk density. Temperate forests' FRN significantly decreased with mean monthly precipitation, but it increased with soil bulk density (Table 2). In tropical forests, FRB significantly decreased with mean monthly precipitation, soil bulk density, but it was positively correlated with mean annual precipitation, mean annual temperature and latitude. Tropical forests' FRN significantly increased with mean annual temperature and soil bulk density (Table 2).

Table 2. Linear mixed effects model coefficient estimated from the average best-fitting models (conditional average), predicting the monthly fine root biomass, necromass and their biomass/necromass ratio for boreal forests (n = 52), temperate (n = 886) and tropical (n = 130). Non-significant results were shown if they were retained in the model. Significant results were shown in bold and marked with asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The values of monthly fine root biomass, necromass and the biomass/necromass ratio were log(x + 1) transformed. The temperature transformation log(x + 273) was used.

		Boreal Forests			Temperate Forests			Tropical Forests		
		FRB	**FRN**	**FRBN**	**FRB**	**FRN**	**FRBN**	**FRB**	**FRN**	**FRBN**
Climatic	MMP	0.13		**1.19 ***	**0.04 ***	**−0.05 *****	**0.35 *****	**−0.34 *****		−0.41
	MMT	2.44	**7.25 *****	−12.38	**−1.74 *****		**−4.74 ****	−1.32	−1.32	−4.40
	MAP	−0.91	**−2.99 *****		−0.02	0.04	−0.06	**0.16 ****		0.35
	MAT		**−78.53 *****	−94.72	−0.49	−0.54	0.86	**10.51 *****	**2.00 ***	17.61
Edaphic	D	**−0.25 *****	**−0.54 *****	0.51	**−0.34 *****	**−0.42 *****	**0.22 ****	**−0.35 *****	**−0.55 ****	**1.16 *****
	SOC	0.16	0.31	−0.56	**0.14 *****	**0.10 *****	−0.10	**0.21 *****	**0.22 *****	**−0.63 ***
	SBD		**−2.07 ***		**−0.48 ****	**0.58 *****	**−2.91 *****	**−1.52 ****	**2.36 *****	**7.88 *****
	pH		**−2.17 *****	3.02	**0.16 ***	−0.04	0.37	0.28		1.02
Geomorphic	E	**0.15 *****	**0.55 *****	**−0.61 ****	**0.08 *****	**0.14 *****	**−0.28 *****	0.06	0.02	−0.11
	L		**−4.69 *****	−5.06	0.05	0.19	−0.22	**0.49 ****	0.07	1.24
	Intercept	−2.02	122.81	92.40	**11.37 *****	1.48	**27.21 ****	**−56.50 ****	11.98	−85.92

FRB, monthly fine root biomass (mg cm^{-3}); FRN, monthly fine root necromass (mg cm^{-3}); FRBN, monthly fine root biomass/necromass ratio; MMP, mean monthly precipitation (mm); MMT, mean monthly temperature (°C); MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C); D, sampling depth (cm); SOC, soil organic carbon content (%); SBD, soil bulk density (g mm^{-3}); pH, soil pH; E, elevation (m); L, latitude (°).

Table 3. Relative importance (expressed as Akaike weights) of explanatory variables of best models for monthly fine root biomass (FRB), necromass (FRN) and their biomass/necromass ratio (FRBN) of the different forest biomes. Bold values are greater than 0.50, representing important explanatory variables. The abbreviations of variables were provided in Table 2.

		Boreal Forests			Temperate Forests			Tropical Forests		
		FRB	**FRN**	**FRBN**	**FRB**	**FRN**	**FRBN**	**FRB**	**FRN**	**FRBN**
Climatic	MMP	0.24		**1.00**	**1.00**	**1.00**	**1.00**	**1.00**		0.35
	MMT	0.24	**1.00**	0.28	**1.00**		**1.00**	0.29	0.20	0.07
	MAP	0.12	**0.88**		0.19	0.36	0.10	**1.00**		0.09
	MAT		0.29	0.14	0.19	0.23	0.09	**1.00**	**0.65**	**0.82**
Edaphic	D	**1.00**	**1.00**	0.28	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**
	SOC	**0.57**	**1.00**	0.15	**1.00**	**1.00**	0.28	**1.00**	**1.00**	**1.00**
	SBD		0.12		**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**
	pH		**1.00**	**0.79**	**1.00**	0.12	**0.69**	**0.54**		0.43
Geomorphic	E	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**0.65**	0.14	0.07
	L				0.22	0.26	0.09	**1.00**	0.15	0.09

3.3. The Dynamics of Monthly Fine Root Biomass, Necromass and the Biomass/Necromass Ratio

Large seasonal variations in FRB, FRN, and FRBN were observed in all the three forest biomes (Figure 2). Boreal forests' FRB peaked in August (1.60 ± 0.27 mg cm^{-3}), while FRN peaked in both July (1.91 ± 1.54 mg cm^{-3}) and October (1.54 ± 0.63 mg cm^{-3}), with the lowest values appearing in April (0.34 ± 0.01 mg cm^{-3}) and September (0.17 ± 0.04 mg cm^{-3}; Figure 2a). In temperate forests, FRB did not exhibit strong seasonality (Figure 2b). Following the lowest value found in February (0.52 ± 0.08 mg cm^{-3}), FRB of temperate forests continued to rise and reached the highest value in November (1.20 ± 0.18 mg cm^{-3}; Figure 2b). Temperate forests' FRN fluctuated significantly throughout the whole year, for example, it declined from 1.03 ± 0.25 mg cm^{-3} in April to 0.41 ± 0.14 mg cm^{-3} in July, then it rose and reached the second peak in November (0.98 ± 0.32 mg cm^{-3}; Figure 2b). FRB of tropical forests peaked in February (1.38 ± 0.35 mg cm^{-3}), September (0.96 ± 0.24 mg cm^{-3}) and October (0.93 ± 0.22 mg cm^{-3}), respectively, while the depressions occurred in April (0.44 ± 0.11 mg cm^{-3}), June (0.41 ± 0.11 mg cm^{-3}) and December (0.47 ± 0.13 mg cm^{-3}; Figure 2c). FRN of tropical forests varied up-and-down, the minimum value appearing in April (0.04 ± 0.01 mg cm^{-3}) and the maximum value appearing in March (1.51 ± 0.84 mg cm^{-3}; Figure 2c).

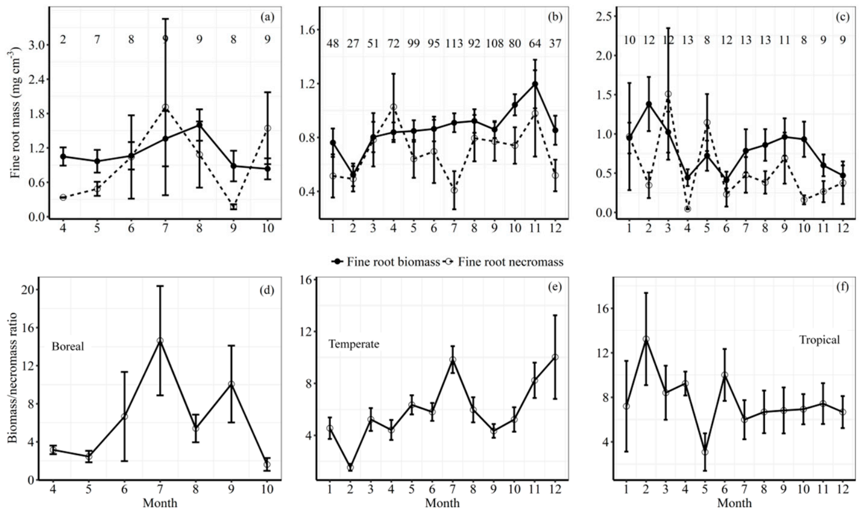

Figure 2. Monthly variation of fine root biomass, necromass and their biomass/necromass ratio for boreal (**a**,**d**), temperate (**b**,**e**) and tropical forests (**c**,**f**). Values were expressed as mean ± 1 standard error. The numbers indicate the sample size.

Although there were various seasonal changes, all the three forest biomes showed the highest FRBN in summer (14.63 ± 5.74 for boreal forests and 9.83 ± 1.03 for temperate forests in July, and 10.01 ± 2.33 for tropical forests in June; Figure 2d,f). An additional peak of FRBN appeared in September for boreal forests (10.07 ± 4.03), December for temperate forests (10.02 ± 3.22) and February for tropical forests (13.24 ± 4.14; Figure 2d–f). Low FRBN was observed in May (2.45 ± 0.61) and October (1.62 ± 0.67) for boreal forests, February (1.54 ± 0.27) and September (4.35 ± 0.53) for temperate forests, and May (3.09 ± 1.69) for tropical forests (5.00 ± 1.23; Figure 2d,f).

4. Discussion

We found that monthly fine root biomass, necromass and their ratio were biome-specific across the Northern Hemisphere. It was unexpected that boreal forests contained the highest average monthly fine root biomass and necromass of the three forest biomes. In comparison, the lowest average monthly fine root necromass, subsequent largest fine root biomass/necromass ratio were observed in tropical forests. The findings partly supported the first hypothesis on the important role of forest biomes in summarizing fine root pattern, however, the results were not consistent with the statement that tropical forests are characterized by the largest fine root biomass and necromass on average [25,31,36]. The higher monthly fine root biomass recorded in boreal forests could be explained by tree species having low-temperature-induced lower respiration rates and lower turnover rate of tissues [22,37]. The large fine root biomass and necromass indicated that forests store and move large quantities of carbon (33%) to belowground parts [2,5]. With rising temperatures and changing precipitation, some boreal forests might shift from an evergreen-dominated region to a region which increasingly is populated by temperature tree species [38]. Therefore, the biome-specific fine root pattern in this study signified that the "biome shift" would lead to major changes in carbon budgets that feedback to affect climate.

The influences of climatic indices on fine roots and their relative importance in best-fitting models greatly varied across the forest biomes, partly supporting our second hypothesis. Fine roots in tropical forests had different responses to mean monthly and annual temperature/precipitation from those in temperate and boreal forests. Focusing on temperatures, they were, on the annual scale, positively related with monthly fine root biomass in tropical forests, but negatively in temperate forests. The previous studies indicated that warm years or months were associated with reduced biomass inputs to belowground parts at middle latitudes, while in tropical areas the opposite pattern was observed [24]. Meanwhile, our findings of the significant and negative relationships of monthly fine root biomass with mean monthly precipitation in tropical forest biome were supported by the experimental study [39]. In temperate and boreal forests, we observed that precipitation on a monthly scale had a strongly positive effect, whereas precipitations on an annual scale negatively influenced monthly fine root biomass. The scale effects of precipitation indicated the contrasting roles of month-scale and year-scale variability in precipitation on the fine root dynamics. Furthermore, the relative importance of precipitation at different scales (monthly versus annual) on monthly fine root biomass suggested that the precipitation at the monthly scale were probably more critical in controlling fine root biomass and necromass. The dispersion of monthly rainfall and heat and the related fluctuations of soil nutrients strongly influenced forest fine root dynamics [4,16]. Larger fine root mass could be yielded in the season, when the rainfall is sufficient and the temperature is high, accompanying with higher soil mineralization rate [16]. However, the variation in annual rainfall or/and temperature were not strong enough to alter the fine root patterns in most forest ecosystems [4]. These results gave paramount implications to the understanding of fine root variation patterns at different temporal scales (the monthly versus annual scales) and to the identification of the factors that drove these patterns.

Fine roots, irrespective of forest biomes, showed a consistent pattern in relation to the soil layer and soil organic carbon content, which does not support our second hypothesis (see Introduction). Specifically, both monthly fine root biomass and necromass decreased with increasing sampling depth, but increased with increasing soil organic carbon content. Additionally, the relative importance of sampling depth in the best-fitting models was consistent across the three forest biomes. These results suggested that the standing stock of fine roots at the month level greatly depended on root distribution in the soil profile. More living and dead fine roots accumulated in the soils with higher soil organic matter representing better nutrient and water conditions [15,27,40]. However, the superficial root system increased the vulnerability of forests especially in boreal zones to abiotic risks, such as high air temperature-induced drought, which might increase in occurrence in the future climate [41]. Furthermore, enhanced fine root biomass/necromass ratios (a powerful measure of root vitality) along with soil layer gradients in this analysis indicated that deep roots were important for water and nutrient absorption.

The responses of fine roots to other edaphic variables, such as soil bulk density and soil pH, were biome-specific. Soil bulk density was more important at explaining variations in monthly fine root patterns in temperate and tropical zones than in boreal zones. By contrast, soil pH seemed to be a key factor for dead fine roots in boreal forests and for living fine roots in temperate forests. Trees demonstrate the multidimensionality of roots at acquiring water and different nutrients with contrasting mobility in the soil and the variable reliance of different plant species on symbiotic associations for resource acquisition [42,43], leading to the lack of consistent relationships between soil properties and monthly fine root mass. For instance, trees can employ morphological adjustments of fine roots to adapt to changing soil environmental conditions. Recent analyses illuminated that changes in root biomass induced by the seasonal fluctuations of soil moisture and soil solution chemistry were largely attributed to altered root morphological traits [44,45]. Overall, although some soil conditions influencing fine roots had been satisfactorily represented in the current models, our results suggested that other soil conditions, such as soil organic carbon content and soil bulk density, should be considered in the models predicting the fine root dynamics at large scales.

We observed that fine roots were in the three forest biomes strongly elevation dependent, with increasing trends of monthly fine root biomass and necromass along elevation gradients. Several previous studies had indicated a marked increase in belowground carbon allocation (increasing root/shoot ratio) towards higher elevations [46–49]. Furthermore, reduced decomposition of dead fine roots and/or increased mortality of living fine roots could explain large amounts of monthly fine root necromass and subsequent lower monthly fine root biomass/necromass ratio at higher elevation [30].

The two-way nonparametric Scheirer-Ray-Hare test indicated significant effects of month on fine root necromass and biomass/necromass ratio across the Northern Hemisphere. Together with the results of significant month and forest biome interactions on fine root biomass, this suggested a biome-specific temporal and spatial variation on fine root dynamics. We observed a distinct intra-annual pattern with modal or bimodal fine root mass peaks for the three forest biomes throughout the whole year. As mentioned above, there were the various effects of exogenous factors including climatic, edaphic and geomorphic variables on fine roots in the three forest biomes (boreal versus temperate versus tropical). Thus, the contrasting selection pressures at fine roots in different climatic zones led to their notable differences in key morphological, architectural and chemical traits [26,50], as well as living and dead fine root accumulation characteristics throughout the whole year.

In our data set, the relative abundant monthly fine root biomass was observed in tropical forests during the dry season (such as January-March), representing a considerable investment of stored reserves. We also found significantly negative relationships of monthly fine root biomass with mean monthly precipitation. Deficits in water generally promoted increased belowground investment, which could increase the surface area of fine roots for water and nutrient absorption achieved by a greater fine root biomass [51]. Furthermore, plants in water-limited environments invested in young root tissues (because of their high efficiency in nutrient uptake) and discarded older tissues, which might shorten root lifetime and increase mortality during the dry season [52]. Thus, the changes in belowground/aboveground carbon allocation could partly explain the underlying mechanisms of fluctuating fine root biomass and necromass patterns of tropical forests [11,53].

It was noted that forests in temperate and boreal zones exhibited relatively high monthly fine root biomass and necromass in late growing season, such as November for temperate forests. In cool-temperate zones, the presence of newly-born white root tips of *Pinus sylvestris* was observed in February [54], suggesting that root growth continued throughout winter [55]. As a strategy for nutrient acquisition, *Corydalis conorhiza* produced snow roots growing into snow packs in an alpine environment [56]. Thus, plants in high-latitude zones seem capable of root growth at least at near-freezing temperatures [57], although root growth might be limited below certain temperatures, and large numbers of fine roots might be killed periodically by frost. The results here might indicate that tree roots are not normally dormant during winter, and abundant regeneration occurs continuously year-round if soil moisture and temperature conditions become favorable [58,59]. It is quite apparent that there was a lack of data about seasonal dynamics of living and dead fine roots throughout the whole year for the boreal forests. Overall, with respect to fine roots, to fully understand the consequences of changes in forest composition under climate change, more studies would be needed in more forest types (e.g., boreal forests) to achieve a better success in unraveling the secret of the timing and the magnitude of fine root dynamics throughout the whole year.

Moreover, the fluctuation patterns of fine root mass might be a consequence of the fact on species endogenous mechanisms of root growth [60]. Actually, there was the common autonomous rhythm and seasonal periodicity of root growth in woody plants [61]. Fine root death and renewal in trees was a natural cyclic process and resembles the leaf shedding in evergreen plants [62]. The "phenological programming" theory also indicated that trees yielded an extensive fine root system when the supply of carbohydrates produced by the newly expanded canopy was adequate, as well as soil moisture and temperature conditions were favorable [40,63,64]. Here, we observed that the consistent peak of monthly fine root biomass/necromass ratio (a measure of root activity) in the three forest biomes appeared in June or July to satisfy tremendous water and nutrient requirements for tree growth in growing season. Moving further, it remains to be discovered whether the pattern of forest fine root dynamics ultimately resulted from the different effects of changes in exogenous factors or, alternatively, from endogenous cues such as the availability of photosynthates related to inherent phenological programming. Therefore, it was greatly necessary to carry out complex studies on respective regulatory mechanisms of fine root dynamics throughout the whole year in different forest ecosystems in changing climate [24,65].

5. Conclusions

Our study provides the first comprehensive picture of forest fine root variability at a monthly scale and its association with climate at monthly and annual scale, as well as soil variables across the Northern Hemisphere. We found that forest biomes have, indeed, distinct differences in living and dead stocks, but boreal forests contained the highest average monthly fine root biomass and necromass, which does not support our first hypothesis that tropical forests exhibit the largest fine root biomass and necromass on average. The contrasting influences of climatic indices on fine roots in the best-fitting linear mixed models partly support our second hypothesis. Moreover, we observed that soil characteristics such as soil layer and soil organic carbon content, and also elevation had consistent relationships with fine root variables across the three forest biomes. However, there is still much to do, given that most of the variance has not been explained yet, and the correlation coefficients of most relationships between fine roots and environmental factors were relatively lower. Nevertheless, it is also vital to present relationships formed from existing dataset as a means of guiding future investigation on fine root dynamics and distribution with conspicuous changes in patterns of global climatic variability.

Author Contributions: C.W. and M.H.L. conceived the ideas; C.W. and S.Z. collected the data and performed the analysis; C.W. wrote the first draft of the manuscript; I.B. and M.-H.L. led the writing.

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Appendix A

The list of the data sources

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