Effects of precipitation change on fine root morphology and dynamics at a global scale: A meta-analysis

<table>
<thead>
<tr>
<th>Journal:</th>
<th>Canadian Journal of Soil Science</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manuscript ID</td>
<td>CJSS-2018-0114.R1</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Review</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>16-Nov-2018</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Zhang, Xin; Heilongjiang University Xing, Yajuan; Heilongjiang University Yan, Guoyong; Heilongjiang University Han, Shijie; Henan University Wang, Qinggui; Heilongjiang University, College of Agricultural Resource and Environment</td>
</tr>
<tr>
<td>Keywords:</td>
<td>Fine roots, Decomposition, Morphology, Meta-analysis, Precipitation change</td>
</tr>
<tr>
<td>Is the invited manuscript for consideration in a Special Issue?:</td>
<td>Not applicable (regular submission)</td>
</tr>
</tbody>
</table>
Effects of precipitation change on fine root morphology and dynamics at a global scale: A meta-analysis

Xin Zhang¹  Yajuan Xing¹  Guoyong Yan¹  Shijie Han²  Qinggui Wang*¹

¹ College of Agricultural Resource and Environment, Heilongjiang University, 74 Xuefu Road, Harbin, 150080, China
² College of Life Sciences, Henan University, Kaifeng, Henan, 475004, China

* Corresponding author:

Email: qgwang1970@163.com
Tel.: 86 451 86609313; Fax: 86 451 86609487

Author Contribution Statement

QW designed the study, was awarded funding, supervised data collection and contributed to and edited the manuscript. XZ and QW contributed the whole manuscript preparation and design and wrote the main manuscript text. XZ, YX and QW prepared all figures. XZ, YX, GY and SH prepared the table and collected literature. All authors reviewed the manuscript.

Conflict of Interest

The authors declare no competing financial interests.
Abstract We compiled data from 495 observations from 103 papers and carried out a meta-analysis of the responses of fine root biomass, production, decomposition and morphology to precipitation increases and decreases. In addition, we evaluated the effects of plant life form, soil depth and experiment duration on the responses of fine roots to precipitation changes. Our results confirmed that decreased precipitation limited fine root diameter and accelerated turnover. Increased precipitation stimulated fine root elongation and enhanced fine root accumulation. The responses of fine roots to precipitation changes varied among plants of different life forms. Tree fine root production and decomposition and non-tree fine root diameter varied most strongly under decreased precipitation. Specific root length of non-tree fine roots was much higher than that of tree fine roots under increased precipitation. Decreased precipitation limited the growth of fine roots in 20-40 cm soil, whereas increased precipitation promoted the growth of fine roots in both shallow and deep soil layers. The responses of fine roots to decreased precipitation were affected by experiment duration. Results filled the gap of evaluation data on the effect of precipitation change on fine root morphology and dynamics, which are useful for better predicting C cycle under precipitation change.

Key words Fine roots; Decomposition; Morphology; Precipitation change; Meta-analysis

Introduction

Fine root biomass allocation and morphological characters are important for ecosystem carbon (C) cycling following frequently extreme precipitation or drought events. (Osonubi and Davies 1981; IPCC, 2013; McCormack and Guo, 2014). Fine roots are generally classified as
roots with diameter less than 2 mm (Helmisaari et al., 2002) that are non-woody, are short lived, and exhibit rapid turnover (Vogt et al., 1996; McCormack et al., 2015). Previous studies of the responses of fine roots to precipitation decreases and increases have yielded inconsistent results. Fine root biomass, production and decomposition have been found to increase (Gaul et al., 2008; Hertel et al., 2013), decrease (Bakker et al., 2006; Meier and Leuschner, 2008; Fiala et al., 2009; Yuan and Chen, 2010; Moser et al., 2014) or remain unchanged (Gill and Jackson, 2000; Jerbi et al., 2015) under decreased or increased precipitation across plant life forms and soil depths. Therefore, it remains unclear how fine root turnover and accumulation respond to changed precipitation.

The morphological traits of fine roots predict root water and nutrient acquisition and biomass allocation. However, our understanding of the linkages between root morphology and function remains in its infancy (Iversen, 2014; Smith et al., 2014). Fine root length and diameter play important roles in water absorption and transport. Decreased precipitation was known to limit root length due to nutrient deficiency (Collet et al., 1997; Arend et al., 2011). However, Hertel et al. (2013) suggested that deep-reaching roots with high water-absorption efficiency at dry sites should not be neglected. A previous study reported lower specific root area (SRA) and higher root tissue density (RTD) in water-deficient soil (Hertel et al., 2013), whereas Zhong et al. (2016) found no clear effects of decreased precipitation on SRA and RTD. Where precipitation is abundant, fine roots may exhibit a strategy that promoted resource acquisition by increasing total root length, SRL and SRA, in accordance with resource economics theory (Verburg et al., 2013; Weemstra et al., 2016). However, Bakker et al. (2006) found that total fine root length was significantly lower at a humid site than at a dry site. It remains unclear how fine root morphology
responds to precipitation changes.

The heterogeneity of the responses of fine roots to decreased and increased precipitation is multifactorial. First, the responses of fine roots differ among plant life forms. Göransson et al. (2016) found that different plants exhibited different rooting strategies in response to water stress. In the study of Olmo et al. (2014), shrubs (*Pistacia lentiscus* L.) with higher plasticity were more drought resistant than trees (*Fraxinus angustifolia* Vahl.). There is little information on how the dynamics of the fine roots of grasses respond to precipitation change. Beidler et al. (2015) indicated that the exploratory root growth of grasses differed from that of trees. Second, the sensitivity of soil moisture to precipitation has been found to differ between shallow and deep soil layers (Salve et al., 2011; Chen et al., 2015; Liu et al., 2017); soil moisture directly or indirectly affects fine root morphology and biomass allocation (Osonubi and Davies 1981; Norby and Jackson, 2000; McCormack and Guo, 2014). Jerbi et al. (2015) found significant differences in SRL among different soil depth groups under increased precipitation, and they considered vertical growth of fine roots to be primarily a function of the moisture gradient in the soil profile. Thus, it is important to determine the responses of fine roots in the soil profile to precipitation changes to predict belowground C cycling. In addition, the responses of fine roots to precipitation changes have been show to differ between the earlier and later periods of response (Joslin et al., 2000). Previous studies indicated that under a single drying event, plants probably stopped growth before fully adjusting their biomass allocation and increased production to restore fine-root biomass (Joslin et al., 2000; Poorter and Nagel, 2000). A long-term experiment identified multiple mechanisms for biotic acclimation under precipitation change (Zhou et al., 2016). Furthermore, changes of fine root traits in water-adequate or -limited environments have been found to be
complex across submillimeter scales (Larson and Funk, 2016). Thus, more efforts to understand the relationships between fine root variations and precipitation change on a global scale are urgently needed.

Here, we collected data on fine root biomass, production, decomposition and morphology under the conditions of decreased and increased precipitation across the world from the literature. We studied the responses of fine roots to decreased and increased precipitation considering plant life form (trees, shrubs and grasses), soil depth (0-20 cm, 20-40 cm, >40 cm) and experiment duration (short, <1 years; intermediate, 2-3 years; long, >3 years). By performing a meta-analysis, the following research questions were addressed: (i) How do fine roots balance turnover and accumulation under precipitation changes? (ii) How do fine roots adjust their morphology to optimize resource absorption under decreased and increased precipitation? (iii) What factors affect the responses of fine roots to precipitation changes?

Materials and Methods

Data compilation

We established a meta-database that included 495 sets of data on fine root biomass, production, decomposition, diameter, length, specific root area (SRA), specific root length (SRL) and root tissue density (RTD) in 103 published studies between 1985 and 2017 related to precipitation change (i.e., decreases and/or increases) at a global scale (Fig. 1, Supplementary Data - Table S1). These plant root traits regulate plant nutrient and water uptake, belowground C
inputs, and play critical roles in plants growth adaptively and ecosystem C storage. (Vogt et al., 1996; Leuschner et al., 2003; Iversen, 2010; Nie et al., 2013; Herzog et al., 2014; McCormack et al., 2015). Fine root biomass was quantified by weighing fine root dry weight or estimated from the mini-rhizotron system. Fine root production and decomposition were quantified by production and loss. Fine root length and diameter were quantified by the mini-rhizotron system or length measurement with a ruler (Nie et al., 2013). SRL according to fine root length and biomass. RTD according to biomass and the volume of the fine root. SRA according to fine root surface area and biomass. In our research, we defined a precipitation decrease as a lack of water and a precipitation increase as an excess of water. The literature was searched (Supplementary Data) via Web of Science and Google Scholar using a combination of key words that included "fine roots morphology", “fine roots biomass”, “fine roots production”, “fine roots turnover”, “fine roots decomposition” and either “rainfall”, “precipitation”, “moist”, “precipitation”, “humid” or “drought”, “dry”. To avoid bias in the selection of publications, the following criteria were applied to select appropriate studies: (i) only growing season precipitation manipulation (precipitation decrease and/or increase) was performed (i.e., no winter studies were included); (ii) only control and treatment (decreased or increased precipitation) data were reported, and the interacting effects were excluded in the multifactorial studies (e.g., fertilization); (iii) at least one of the variables of interest was measured in both the control and experimental treatments; (iv) the same plant species was used in the control and treatment plots, and environmental conditions, including climatic and soil conditions, were the same across plots; (v) all data compiled into a database were taken from original papers and the cited data were not examined to ensure the independence of the studies; and (vi) the means, standard deviations/errors, and sample sizes of the chosen variables were
reported. Fine root decomposition was defined as fine root biomass loss in our meta-analysis.

For each study, we compiled the means, standard deviations, and samples sizes of the variables in both the control and experimental treatments. Where standard deviations were not reported, they were calculated from standard errors and sample sizes. Sample size referred to the number of treatment plots that is the replicate of experimental facilities in the experiment (Bai et al., 2013; Li et al., 2016). We compiled data on environmental variables including latitude, mean annual temperature, and mean annual precipitation directly from the included papers or papers cited by the included papers or extracted data from the database at http://www.worldclim.org/ using the location information provided in the study (e.g., latitude and longitude, Supplementary Data) (Zhou et al., 2016). We also recorded the precipitation treatment (increase or decrease), experiment location, plant life form (Fig. 1), sampled soil depth and experiment duration (Supplementary Data). Data were compiled directly from tables or extracted by GetData software (v2.22) from figures in the original publication or supplementary Data.

To test for differences in the responses of fine roots to altered precipitation among different plant life forms, three categories of plants were established in our study: trees, shrubs and grasses. Soil moisture affects the vertical distribution of fine root growth in the growing season (Hartle et al., 2006). Therefore, we compared fine root dynamics among the shallow (0-20 cm), deep (20-40 cm) and very deep (>40 cm) soil layers under the conditions of precipitation change. Furthermore, we grouped the experimental durations into short (<1 years), intermediate (2-3 years) and long (>3 years) categories and explored whether the responses of fine roots to precipitation changes vary with experimental duration.
Meta-analysis

The response ratio (RR) was used to quantify the effects of decreased and increased precipitation on fine roots, that is, the natural log of the ratio of the mean value of the fine root variables in precipitation treatment (Xₜ) to that in control group (Xₑ, Eq. (1)) (Hedges et al., 1999; Luo et al., 2006).

\[
RR = \ln \left( \frac{X_t}{X_c} \right) = \ln (X_t) - \ln (X_c) \quad \text{.................................................................(1)}
\]

The variance (v) of each RR was calculated by Eq. (2).

\[
\begin{align*}
v &= \frac{s_t^2}{n_tX_t^2} + \frac{s_c^2}{n_cX_c^2} \quad \text{.................................................................(2)}
\end{align*}
\]

where \(s_t\), \(s_c\), \(n_t\) and \(n_c\) represent standard deviation of treatment groups and control groups, and replicate numbers of treatment and control groups, respectively.

To enhance the precision of the effect estimate, we used the weighted response ratio (RR⁺⁺) of each fine root variable as a metric of effect size (Eq. (3)) (Hedges et al., 1999; Lu et al., 2013).

\[
RR_{++} = \frac{\sum_{i=1}^{m} m \sum_{j=1}^{k} w_{ij} RR_{ij}}{\sum_{i=1}^{m} m \sum_{j=1}^{k} w_{ij}} \quad \text{.................................................................(3)}
\]

The standard error of RRₜₜ was calculated by Eq. (4):

\[
s(\overline{RR}_{++}) = \frac{1}{\sqrt{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij}}} \quad \text{.................................................................(4)}
\]

A 95% confidence interval (95% CI) for the RRₜₜ was derived by the following Eq. (5):

\[
95\% \text{CI} = \overline{RR}_{++} \pm 1.96 \times s(\overline{RR}_{++}) \quad \text{.................................................................(5)}
\]

Data analysis
We calculated the log-transformed response ratio (RR) and variance of RR for all observations in MetaWin 2.1 (Hedges et al., 1999). As expected, there was significant residual heterogeneity in our study; following Koricheva et al. (2013), we assumed that there was random variation among studies in addition to sampling variation among studies in ecology. Hence, we applied a random-effects model using MetaWin 2.1 to evaluate the effects of precipitation changes on fine roots and then employed a categorical random-effects model to test the effects of categorical variables (plant life form, soil depth and experiment duration) on the responses of fine roots to precipitation decreases and increases. \( Q_b \) was defined as the difference among group cumulative effect sizes. Ninety-five percent confidence intervals (95% CIs) on the weighted effect sizes were generated using bootstrapping (9999 iterations). If the 95% CI of an effect size for a variable did not overlap zero, the effect of precipitation change on the variable was considered significant (Luo et al., 2006); the results are shown in Supplementary Data. The effects of climate type (i.e., arid, semiarid, semimoiest, moist, and Mediterranean), plant life form (i.e., trees, shrubs and grasses), precipitation treatment (i.e., decreased and increased), duration (i.e., <1 year, 1-2 years and >3 years), soil depth (i.e., 0-20 cm, 20-40 cm and >40 cm) and their interactions on the RR of the variables of interest were tested by ANOVA (Table 1, SPSS 16.0, SPSS Inc., Chicago, IL, USA). A plot of the effect sizes against sample size (not shown) revealed a funnel-shaped distribution of the data points \( Z = -0.372, P = 0.832 \), as would be expected in the absence of publication bias (Palmer, 1999; Koricheva et al., 2013)

**Results**
Effects of decreased and increased precipitation on fine root biomass, production, decomposition and morphology

Precipitation treatment significantly influenced fine root biomass distribution (Table 1). Decreased precipitation significantly limited fine root biomass and significantly stimulated decomposition (Supplementary Data - Table S2, Fig. 2a), whereas increased precipitation significantly increased fine root biomass and production (Table S2, Fig. 2b). Climate type and other variables (i.e., precipitation treatment, experiment duration and soil depth) exhibited significant interaction effects on the response ratio of fine root biomass to altered precipitation (Table 1). Decreased and increased precipitation had different effects on fine root morphology and fine root growth.

Decreased precipitation had significantly negative effects on fine root diameter and SRA (Table S2, Fig. 2a), whereas increased precipitation had significant positive effects on RTD, length, SRA and SRL (Table S2, Fig. 2b).

Effects of altered precipitation on the fine roots of trees, shrubs and grasses

Decreased precipitation had a significant negative effect on fine root biomass only in trees, i.e., not in shrubs and grasses (Supplementary Data - Table S3, Fig. 3a). In addition, decreased precipitation had positive effects on fine root production and decomposition in trees (Table S3, Fig. 3c and 3e). Increased precipitation had significant positive effects on tree fine root biomass and non-tree fine root production (Supplementary Data - Table S4, Fig. 3b and 3d). The mean effect size of decreased precipitation on fine root diameter in trees, shrubs and grasses was -0.14,
-0.28 and -0.42, respectively (Table S3, Fig. 4a), indicating changes in fine root diameter under decreased precipitation in the following order: grasses > shrubs > trees. Increased precipitation had a significant effect on tree fine root length and SRL (Table S4, Fig. 4d and 4f). The effect size of increased precipitation on shrub SRL was larger than that on tree SRL (Table S4, Fig. 4f).

**Effects of altered precipitation on fine roots in each soil depth**

Decreased precipitation had significant negative effects on fine root biomass in both the 0-20 cm and 20-40 cm layers (Table S3, Fig. 3a). Decreased precipitation also significantly increased fine root decomposition at the 20-40 cm soil depth (Table S3, Fig. 3c). Increased precipitation had a significant positive effect on fine root production only in the 20-40 cm soil layer (Table S4, Fig. 3d). Decreased precipitation significantly decreased fine root diameter and length at 20-40 cm soil depth (Table S3, Fig. 4a and 4c). In contrast, increased precipitation induced increases in fine root length at the 0-20 cm and 20-40 cm soil depths (Table S4, Fig. 4d). A significant effect of increased precipitation on SRL was found only at the 0-20 cm soil depth (Table S4, Fig. 4f).

**The responses of fine roots to precipitation changes over different experimental durations**

The mean effect size of decreased precipitation on fine root biomass in short-, intermediate- and long-term experiments was -0.19, -0.41, and -0.13, respectively (Table S3, Fig. 3a), whereas increased precipitation significantly increased fine root biomass only in short-term experiments (Table S4, Fig. 3b). Decreased precipitation significantly increased fine root production and
decomposition only in the intermediate-duration experiments (Table S3, Fig. 3c and 3e). Decreased precipitation significantly decreased fine root diameter in the short-duration experiments and decreased SRL in the intermediate-duration experiments (Table S3, Fig. 4a and 4e). Increased precipitation significantly increased fine root length in the long-term experiments and increased SRL in the intermediate- and long-durations experiments involving increased precipitation (Table S4, Fig. 4d and 4f). Significant interaction effects of experiment duration and soil depth were found on the responses of fine root biomass to altered precipitation (Table 1).

Discussion

Opposite effects of decreased and increased precipitation on fine root biomass, production and decomposition

Understanding how the balance of belowground C budgets is affected by precipitation is crucial for identifying terrestrial ecosystem processes under climate change. In this paper, decreased and increased precipitation exerted opposite impacts on fine root biomass (negative and positive impacts, respectively; Fig. 2a and 2b). Similarly, the meta-analysis of Zhou et al. (2016) indicated that decreased and increased precipitation had opposite effects on the plant C pool, which included fine root biomass. In our meta-analysis, fine root decomposition was significantly stimulated by decreased precipitation, which had little effect on root production. In contrast, under increased precipitation, fine root production increased and decomposition remained largely unchanged. Thus, throughout the growing season, decreased precipitation probably results in decreased in fine
root biomass, whereas increased precipitation probably results in increases. Decreased precipitation inhibited photosynthesis by the reduction of leaf area and stomatal conductance (Monclus et al., 2010; Hertel et al., 2013), which led to a shortage of carbohydrates. Consistent with Hertel et al. (2013), we consider a sufficient C source to be a prerequisite for plant C allocation, but insufficient photosynthetic C irritated fine root turnover and lowered fine root accumulation to reduce maintenance consumption, which reflected the trade-off between C revenue and consumption under precipitation decrease.

Differences in fine root morphology between decreased and increased precipitation

Our study suggests that decreases in fine root diameter play a key role in optimizing C allocation under decreased precipitation and that increases in fine root length are important contributors to root biomass accumulation under increased precipitation. There are several possible mechanisms underlying the significant decrease in fine root diameter under decreased precipitation: (i) A lack of available water causes a reduction in carbohydrates, resulting in lower amounts of C allocated to fine roots (Hertel et al. 2013). (ii) Smaller-diameter roots with a thin cortex reduce hydraulic resistance and enhance survival in drier environments (Kong et al., 2017). (iii) The benefit-to-cost ratio in terms of resource acquisition and investment in fine root construction is higher under conditions of insufficient water resources (Santantonio and Hermann, 1985; Eissenstat and Yanai, 1997; Mainiero and Kazda, 2006). In addition, the findings of thinner-diameter fine roots with higher decomposition under decreased precipitation indicate higher resource-acquisition capacity and lower consumption to maintain the survival of fine roots. The thinner, lower SRA and higher...
RTD roots observed under decreased precipitation in this study is consistent with the findings of Hertel et al. (2013) and may be due to the higher resistance to embolism of roots with smaller, narrower xylem vessels and higher lignification and suberization (Steudle, 2000; Alameda and Villar, 2012). Fine roots with high SRL and SRA exhibit an efficient foraging system (Curt and Prévosto, 2003). Our results are consistent with the findings of Ryser (2006) that increased SRL and SRA under increased precipitation provide rapid and efficient resource acquisition to attain rapid growth, and they probably enhance productivity under increased precipitation.

Factors influencing the responses of fine roots to decreased and increased precipitation

The response of fine root biomass to precipitation changes was less affected by the main effects of individual climatic factors than by the interaction effects of climate type and other variables. Therefore, the heterogeneity of fine root responses to precipitation changes at a global scale may be the result of the interactions of different experimental factors and climatic conditions.

We found that in trees, fine roots responded to decreased precipitation by redistributing biomass and accelerating turnover to reduce maintenance consumption, whereas in shrubs and grasses, the responses to decreased precipitation tended to involve morphological adjustment. Plant adaptation strategies to promote water uptake rely on morphological adjustment to enhance C input utilization (Metcalfe et al., 2008). In this paper, the inhibitory effects of decreased precipitation on the diameter of fine roots decreased in the order grasses > shrubs > trees (Fig. 3a), indicating the non-trees are more responsive to decreased precipitation. This difference between
tree and non-tree forms is probably because non-trees often exhibit greater belowground biomass and greater C allocation than trees (Bai et al., 2010) and because the proportion of fine roots to total plant roots is higher in non-trees than in trees (Wang et al., 2015). Although the sample sizes in this study were limited for shrubs and grasses, Arnqvist and Wooster (1995) stated that meta-analysis can potentially allow the detection of an effect even where the included studies show non-significant results because of low statistical power. However, increased precipitation led to increases in fine root length, which significantly promoted the growth of tree roots. Furthermore, increased precipitation enhanced the fine root SRL of trees and shrubs, with a stronger enhancement in shrubs than in trees. This result indicates that the fine roots of shrubs had higher water absorption efficiency than did those of trees.

We found that fine root biomass was severely decreased in the deep layer (20-40 cm) under decreased precipitation. There may be two reasons for this: (i) increased water stress and (ii) increased fine root mortality in the deep layer. Decreased precipitation likely resulted in stronger water deficiency in the deep soil layer than in the shallow layer, which hindered the water uptake of fine roots in the deep layer. This interpretation is supported by the findings of decreased fine root diameter and length in the deep layer. In addition, the higher fine root decomposition in the 20-40 cm soil than in the shallow layer under decreased precipitation was likely due to water shortage, which resulted in increased mortality. Some previous studies found that single events of decreased precipitation increased fine root mortality (Jump, Hunt and Penuelas, 2006; Meier and Leuschner, 2008; Hertel et al., 2013). Increased precipitation provides sufficient soil moisture to deep soil layers, resulting in fine root elongation and expansion into deep soil layers. The significant increases in absorption efficiency in fine roots both in the shallow and deep soil layers
Experimental duration was demonstrated to be important in explaining the response lag and biotic acclimation under disturbance (Beier et al., 2012). Our results showed that the negative effects of decreased precipitation on fine root biomass were highest in the short-duration experiments and then decreased over the intermediate- and long-term experiments. Fine root production and decomposition were significantly increased only in the intermediate-term experiments, represented by limited sample size. In addition, based on the effects of the interaction between duration and soil depth on the responses of fine roots to altered precipitation, shown in Table 1, we deduced that fine root production potentially exhibits a “lag-response” that can supplement the loss of fine root biomass in earlier stages. Furthermore, the findings showed a transition of fine roots from adjustment to stability under decreased precipitation. Zhou et al. (2016) considered that the long-term resistance of plants to decreased precipitation cannot be separated from the multiple responses induced during plant acclimation. And changes in root dynamics in response to climate change are not only influenced by precipitation, but also by other abiotic factors. For example, Warming temperatures probably exacerbate drought where they are not accompanied by increases in precipitation (Jump et al., 2006). In the future, long-term multi-factor changed experiments are needed to study the dynamics of fine roots.

Conclusions

Altered precipitation (decreased or increases) will strongly affect ecosystem structure and function. Our meta-analysis revealed the complex responses of fine roots to decreased and
increased precipitation. The findings indicated that decreased precipitation accelerated fine root turnover and that increased precipitation enhanced fine root accumulation. Under decreased precipitation, thinner-diameter fine roots to facilitate water absorption were observed. Under increased precipitation, increases in fine root length contributed to root biomass accumulation. Trees and shrubs resisted decreased precipitation by undergoing biomass redistribution and morphological adjustment, respectively. In addition, under increased precipitation, the fine roots of non-trees possessed higher absorption efficiency than did those of trees. Fine root growth was severely restricted in the deep layer (20-40 cm) under decreased precipitation, whereas fine root elongated and expanded into the deep soil layer under increased precipitation. Under decreased precipitation, fine roots transitioned from adjustment to stability following the increase of experiment duration, and a “lag-response” of fine root production was observed in the short-term. The results of this meta-analysis have provided a thorough understanding of fine roots optimize their adaptive strategy under changing precipitation conditions, and improved understanding of the underlying mechanisms of precipitation effects on plants and ecosystem functions.

Acknowledgements

This research was supported by grants from the National Natural Science Foundation of China (41330530, 41773075, 41575137, 31370494, 31170421).
References


aboveground biomass, production, and nitrogen use in Scots pine stands in eastern Finland.


Phytol. **213**: 1569-1572.


For Review Only


https://mc.manuscriptcentral.com/cjss-pubs


Table 1 Results of an ANOVA evaluated the effects of climate type (Clim., i.e., arid, semiarid, semimoiost, moist, and Mediterranean), plant life form (Plant, i.e., trees, shrubs and grasses), precipitation treatment (Treat., i.e., decreased and increased), experiment duration (Dura., i.e., <1 year, 1-2 years and >3 years) and soil depth (Depth, i.e., 0-20 cm, 20-40 cm and >40 cm) on fine root biomass, production, decomposition, length and diameter.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass</td>
<td>1.592 (0.183)</td>
<td>0.279 (0.757)</td>
<td><strong>6.315</strong> (0.014)</td>
<td><strong>5.925</strong> (0.004)</td>
<td>2.006 (0.14)</td>
<td><strong>3.688</strong> (0.048)</td>
<td><strong>5.391</strong> (0.006)</td>
<td><strong>3.437</strong> (0.036)</td>
<td><strong>5.085</strong> (0.003)</td>
</tr>
<tr>
<td>Production</td>
<td>0.146 (0.699)</td>
<td>-</td>
<td>0.104 (0.751)</td>
<td>0.794 (0.385)</td>
<td>0.442 (0.649)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Decomposition</td>
<td>1.046 (0.418)</td>
<td><strong>13.327</strong> (0.005)</td>
<td>0.735 (0.414)</td>
<td><strong>8.446</strong> (0.009)</td>
<td><strong>8.545</strong> (0.008)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td><strong>31.174</strong> (0.0000)</td>
<td><strong>16.62</strong> (0.0000)</td>
<td>0.011 (0.919)</td>
<td>-</td>
<td>0.52 (0.477)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Diameter</td>
<td>2.22 (0.147)</td>
<td>0.037 (0.946)</td>
<td>-</td>
<td>0.002 (0.968)</td>
<td>0.41 (0.527)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

**Note:** The values in brackets are significance.

*F values and P-values (in parentheses) are shown in the column.

a F > 0.05; *P < 0.05; **P < 0.01; ***P < 0.001
Figures 1-4

Fig. 1 Distribution map of the included studies on the responses of fine roots to precipitation changes at a global scale. Triangle denotes research on trees, black square denotes research on shrubs, and black circle denotes research on grasses. This map was cited from https://www.ipcc.ch/.

Fig. 2 Weighted response ratio (RR++) of fine root biomass, production, decomposition, diameter, length, specific root area (SRA), specific root length (SRL) and root tissue density (RTD) to decreased (a) and increased (b) precipitation. Error bars represent 95% confidence intervals (CIs). The dashed line represents RR++=0. The effects of decreased and increased precipitation were considered significant if the 95% CI of the weighted response ratio did not overlap zero. The sample size for each variable is shown in parentheses.

Fig. 3 Weighted response ratio (RR++) of fine root biomass (a and b), fine root production (c and d) and fine root decomposition index (decomposition, e and f) to decreased (a, c and e) and increased (b, d and f) precipitation. The variables are categorized into different groups depending on plant life form (trees, shrubs and grasses), soil depth (0-20 cm, 20-40 cm, >40 cm) and experiment duration (short, <1 year; intermediate, 2-3 years; long, >3 years). Error bars represent 95% confidence intervals (CIs). The dashed line represents RR++=0. The effects of decreased and increased precipitation were considered significant if the 95% CI of the weighted response ratio did not overlap zero. The sample size for each variable is shown in parentheses.
Fig. 4 Weighted response ratio (RR++) of fine root diameter (a and b), fine root length (c and d), and specific root length (SRL, e and f) to decreased (a, c and e) and increased (b, d and f) precipitation. The variables are categorized into different groups depending on plant life form (trees, shrubs and grasses), soil depth (0-20 cm, 20-40 cm, >40 cm) and experiment duration (short, <1 year; intermediate, 2-3 years; long, >3 years). Error bars represent 95% confidence intervals (CIs). The dashed line represents RR++=0. The effects of decreased and increased precipitation were considered significant if the 95% CI of the weighted response ratio did not overlap zero. The sample size for each variable is shown in parentheses.
169x80mm (300 x 300 DPI)
<table>
<thead>
<tr>
<th></th>
<th>Decrease</th>
<th>Increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>Biomass</td>
<td>type</td>
</tr>
<tr>
<td>b</td>
<td>depth</td>
<td></td>
</tr>
<tr>
<td></td>
<td>duration</td>
<td></td>
</tr>
<tr>
<td>c</td>
<td>Production</td>
<td>type</td>
</tr>
<tr>
<td>d</td>
<td>depth</td>
<td></td>
</tr>
<tr>
<td></td>
<td>duration</td>
<td></td>
</tr>
<tr>
<td>e</td>
<td>Decomposition</td>
<td>type</td>
</tr>
<tr>
<td>f</td>
<td>depth</td>
<td></td>
</tr>
<tr>
<td></td>
<td>duration</td>
<td></td>
</tr>
</tbody>
</table>

Trees (74)
Grasses (19)

0-20cm (24)
20-40cm (35)
>40cm (14)

Short (57)
Medium (24)
Long (15)

Trees (42)
Grasses (24)

0-20cm (21)
20-40cm (20)
>40cm (13)

Short (27)
Medium (32)
Long (23)

Trees (20)
Grasses (16)

0-20cm (12)
20-40cm (7)

Short (5)
Medium (13)
Long (18)

Trees (12)
Grasses (17)

0-20cm (3)
20-40cm (7)

Short (5)
Medium (13)
Long (11)

Trees (14)
Shrubs (3)

0-20cm (6)
20-40cm (10)
>40cm (2)

Short (7)
Medium (9)
Long (3)

Trees (9)
Shrubs (2)
Grasses (2)

0-20cm (5)
20-40cm (4)

Short (6)
Medium (5)
Long (3)

175x137mm (300 x 300 DPI)