Peatland shrub fine roots increase resource acquisition with warming

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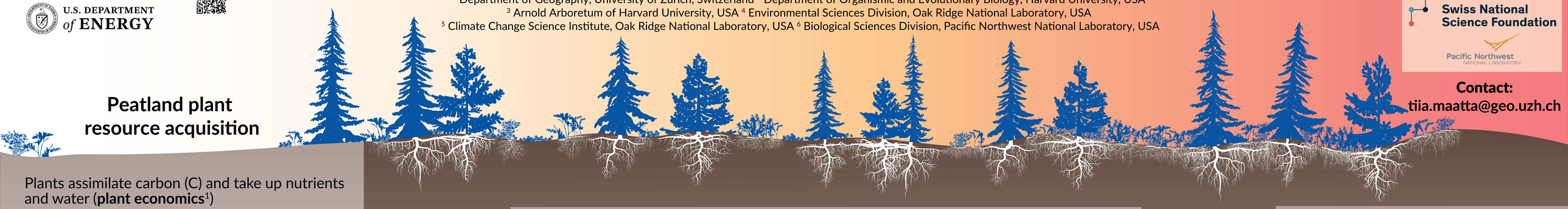
Abstract:



Peatland plant resource acquisition

Plants assimilate carbon (C) and take up nutrients and water (**plant economics**[1])

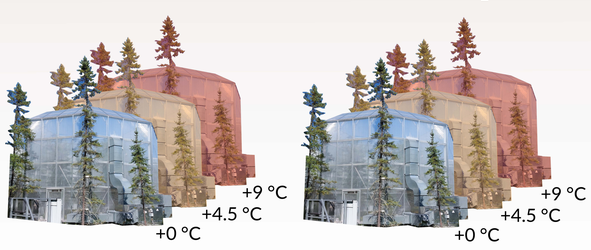
Plant resource acquisition strategies have often been studied aboveground, leaving belowground processes understudied[2]

Peatland plant resource acquisition may differ from upland ecosystems[3,4] and **climate warming** may alter peatland vegetation communities, leading to **changes in plant resource acquisition strategies and C cycling**

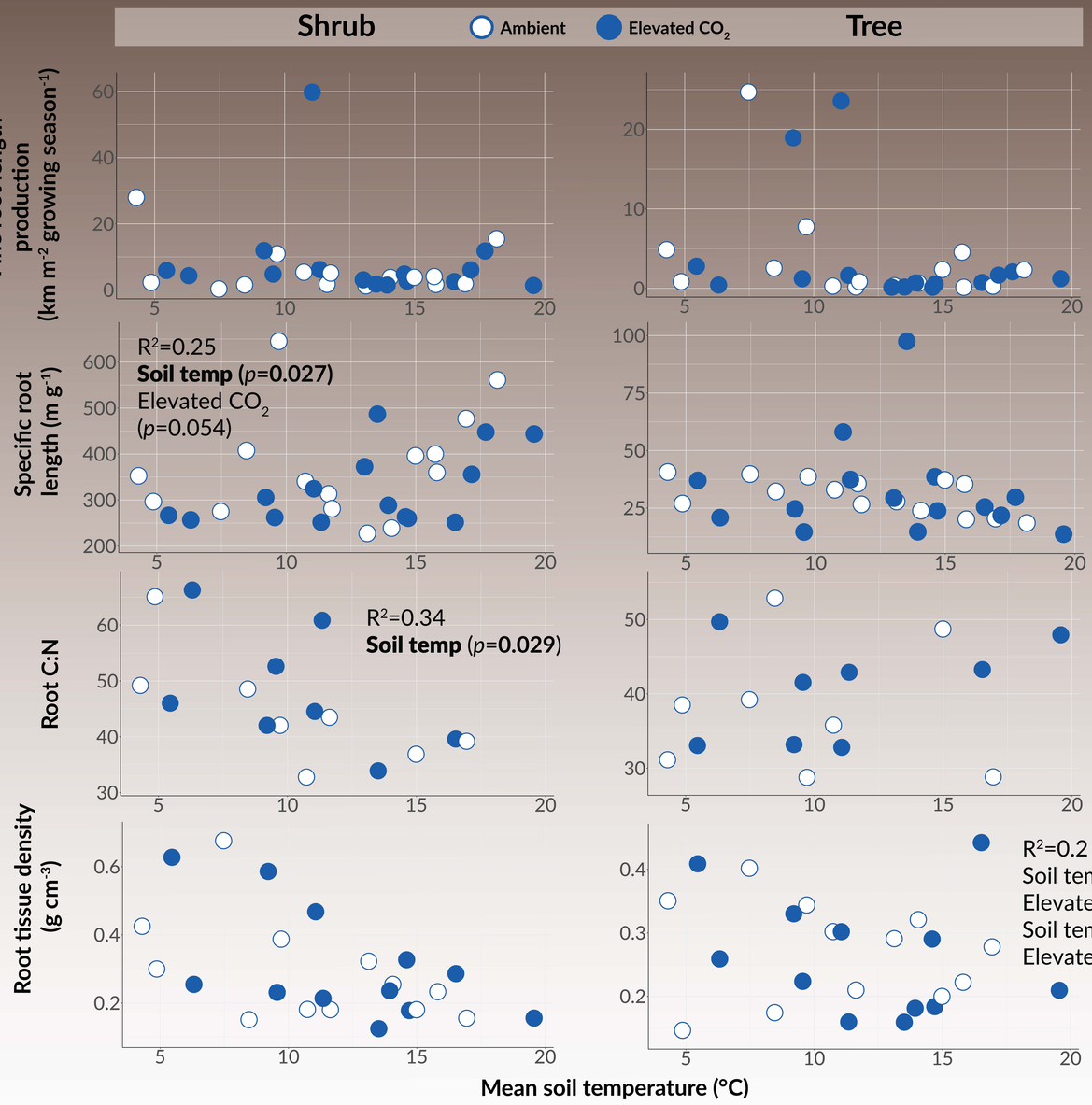
How do shrub and tree root economic traits change with warming and elevated CO_2 in a peatland?

Over **5 growing seasons** (2014-2017[5], 2022), we collected fine roots from **root ingrowth cores** (min 10 cm depth):

from 6 warming treatments (**+0, + 4.5, +9 °C**) with **ambient** (n=3) **and elevated CO_2** (+500 ppm, n=3) at a peatland at the SPRUCE experiment, Minnesota, USA:



Scan this to learn more about SPRUCE: (https://mnspruce.ornl.gov/)



Only models with marginal $R^2 \geq 0.2$ shown. Supplementary information with linear mixed effects model results:

Trends suggest more and longer shrub roots

Shrubs invest C more on length than mass

Shrubs acquire more N relative to C in their tissue

Trees may decrease root mass per unit volume with elevated CO_2

Shrub fine roots shift to a "fast" resource acquisition strategy with warming
Trees did not show significant changes with warming

(but warming may have decreased and elevated CO_2 increased ectomycorrhizal colonization in trees[6,7])

References

[1] Bloom (1985). *Annu. Rev. Ecol. Syst.*, 363-392.
[2] Laliberté, E. (2017). *New Phytol.*, *213*(4), 1597-1603.
[3] Pan et al. (2020). *Nat. Commun.*, *11*(1), 4519.
[4] Iversen et al. (2018). *Plant Soil*, *424*, 123-143.
[5] Malhotra et al. (2020) [dataset]. ORNL. https://doi.org/10.25581/spruce.077/1607860
[6] Defrenne et al. (2021). *PPP*, *3*(5), 640-652.
[7] Duchesneau et al. (2024). *New Phytol.*, *242*(3), 1333-1347.
Soil temperature data: Hanson et al. (2016) [dataset]. ORNL. https://doi.org/10.3334/CDIAC/spruce.032

Supplementary information for EGU25-11448 Peatland shrub roots increase resource acquisition with warming

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1. Detailed linear mixed effects model (fitted with restricted maximum likelihood) results shown in the poster. Significant (p<0.05) terms are highlighted with an asterisk. All models shown here are the final models after backward variable selection with log likelihood ratio tests. See full models in table 2. Note that in all, except tree root C:N, models, the trait (response variable) was log-transformed to meet normality assumptions. The R^2 values shown in the poster are marginal R^2. In all models, the reference level for CO_2 treatment was "ambient". SE = standard error, SRL = specific root length (m g^{-1}), RTD = root tissue density (g cm^{-3}), soil temp = soil temperature (°C), soil moist = soil moisture (g/g), eCO_2=elevated CO_2 treatment. Unit of fine root length production is km m^{-2} growing $season^{-1}$.

Model	*p*-value	Slope	SE	Marginal R^2	Conditional R^2	Degrees of freedom	Random variation explained (%)
Fine root length production							
Shrub model				0.11	0.54		48.3
- Intercept	0	8.076	0.291			22	
- Soil temp	0.077	0.085	0.046			22	

- eCO_2	0.358	0.185	0.197			22	
- Soil temp: eCO_2	0.065	-0.096	0.049			22	
Tree model				0.1	0.67		62.8
- Intercept	0	7.043	0.552			24	
- Soil moist*	0.024	-0.542	0.224			24	
SRL							
Shrub model				0.25	0.51		35.1
- Intercept	0	5.893	0.09			23	
- Soil temp*	0.027	0.034	0.014			23	
- eCO_2	0.054	-0.162	0.08			23	
Tree model				0.09	0.15		5.7
- Intercept	0	3.36	0.083			24	
- Soil temp	0.123	-0.031	0.019			24	
Root C:N							
Shrub model				0.34	0.48		21.5
- Intercept	0	3.744	0.068			12	
- Soil temp*	0.029	-0.033	0.013			12	
Tree model				0.03	0.4		21.5
- Intercept	0	38.218	3.745			12	
- eCO_2	0.442	2.569	3.231			12	
RTD							
Shrub model				0.07	0.74		72.7
- Intercept	0	-1.352	0.207			19	
- Soil temp	0.183	-0.03	0.022			19	
Tree model				0.2	0.6		50.4
- Intercept	0	-1.277	0.133			17	
- Soil temp	0.82	-0.004	0.015			17	
- eCO_2	0.057	-0.181	0.088			17	
- Soil temp:eCO_2	0.045	-0.04	0.018			17	

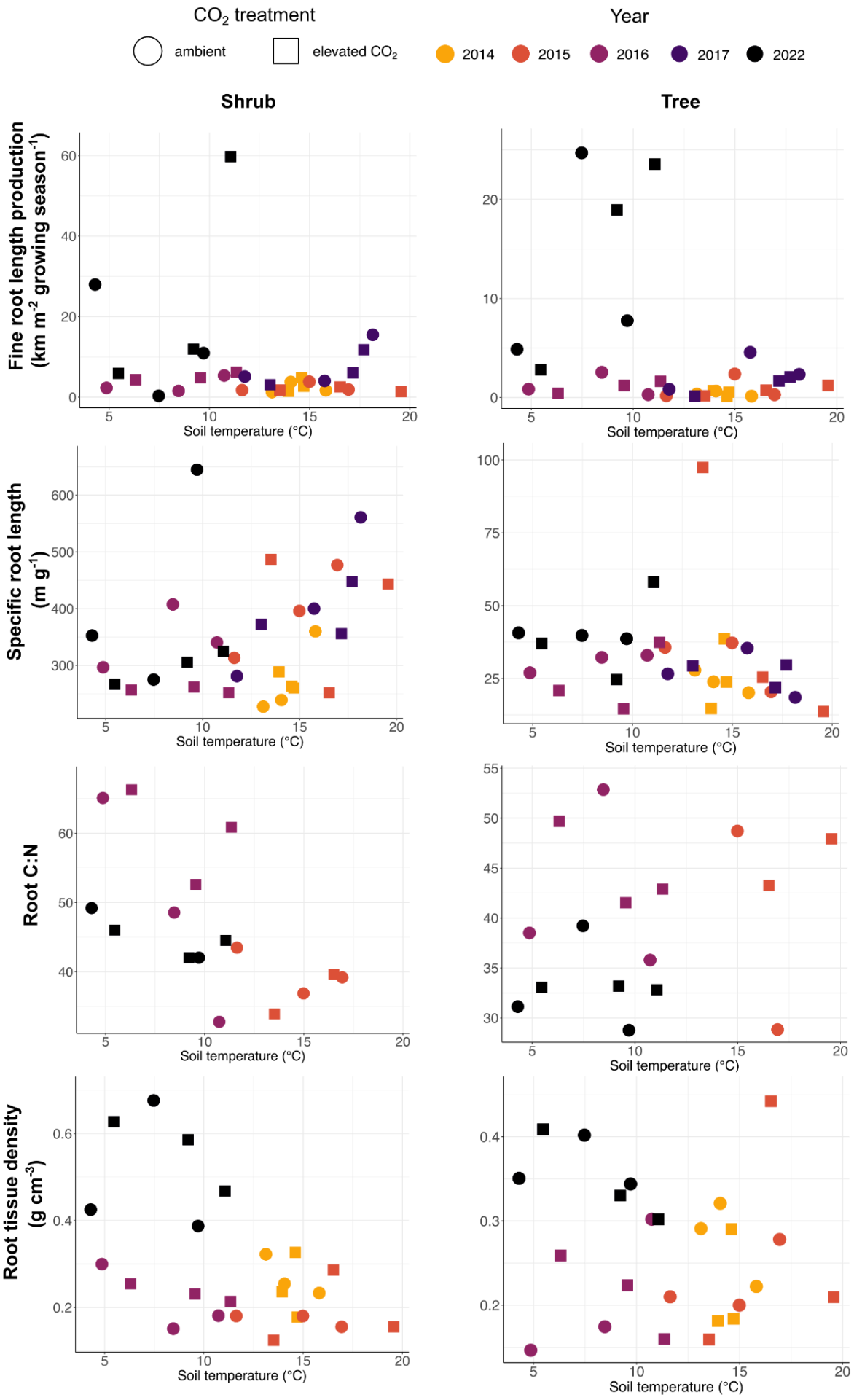
2. Full linear mixed effects model (fitted with restricted maximum likelihood) results. Significant (p<0.05) terms are highlighted with an asterisk. Note that in all, except tree C:N, models, the trait (response variable) was log-transformed to meet normality assumptions. In all models, the reference level for CO_2

treatment was "ambient". SE = standard error, SRL = specific root length (m g^{-1}), RTD = root tissue density (g cm^{-3}), soil temp = soil temperature (°C), soil moist = soil moisture (g/g), eCO_2 = elevated CO_2 treatment. Unit of fine root length production is km m^{-2} growing $season^{-1}$.

Model	*p*-value	Slope	SE	Marginal R^2	Conditional R^2	Degrees of freedom	Random variation explained (%)
Fine root length production							
Shrub model				0.13	0.41		32.1
- Intercept	0	8.094	0.251			21	
- Soil temp	0.171	0.067	0.047			21	
- Soil moist	0.295	-0.163	0.152			21	
- eCO_2	0.509	0.141	0.21			21	
- Soil temp: eCO_2	0.056	-0.106	0.052			21	
Tree model				0.1	0.76		73.2
- Intercept	0	7.242	0.697			21	
- Soil temp	0.455	0.065	0.086			21	
- Soil moist	0.069	-0.492	0.257			21	
- eCO_2	0.232	-0.421	0.342			21	
- Soil temp: eCO_2	0.597	0.043	0.08			21	
SRL							
Shrub model				0.25	0.52		36.7
- Intercept	0	5.89	0.096			21	
- Soil temp	0.101	0.031	0.018			21	
- Soil moist	0.913	0.007	0.059			21	
- eCO_2	0.077	-0.16	0.086			21	
- Soil temp: eCO_2	0.666	0.009	0.02			21	
Tree model				0.16	0.26		11.6
- Intercept	0	3.334	0.12			21	
- Soil temp	0.211	-0.035	0.027			21	
- Soil moist	0.111	0.149	0.089			21	
- eCO_2	0.772	0.043	0.147			21	
- Soil temp: eCO_2	0.649	0.016	0.035			21	

Root C:N							
Shrub model				0.4	0.51		19.5
- Intercept	0	3.703	0.086			9	
- Soil temp	0.065	-0.035	0.016			9	
- Soil moist	0.453	-0.044	0.055			9	
- eCO_2	0.559	0.062	0.102			9	
- Soil temp: eCO_2	0.956	-0.001	0.023			9	
Tree model				0.04	0.47		44.8
- Intercept	0	37.057	4.771			9	
- Soil temp	0.653	-0.365	0.784			9	
- Soil moist	0.711	0.991	2.592			9	
- eCO_2	0.322	4.651	4.44			9	
- Soil temp: eCO_2	0.452	0.639	0.813			9	
RTD							
Shrub model				0.12	0.74		70.2
- Intercept	0	-1.384	0.217			16	
- Soil temp	0.225	-0.035	0.028			16	
- Soil moist	0.633	-0.041	0.084			16	
- eCO_2	0.572	0.068	0.117			16	
- Soil temp: eCO_2	0.738	-0.009	0.027			16	
Tree model				0.17	0.64		57
- Intercept	0	-1.31	0.136			16	
- Soil temp	0.857	0.003	0.018			16	
- Soil moist	0.198	0.068	0.051			16	
- eCO_2	0.202	-0.127	0.095			16	
- Soil temp: eCO_2	0.062	-0.04	0.02			16	

3. Shrub and tree root traits with year of sampling shown in different colors. Note: year was a random effect in the linear mixed effects models. Note also the different y axis scales between shrub and tree plots.


CO2 treatment
ambient
elevated CO2
Year
2014
2015
2016
2017
2022
Shrub
Tree
Fine root length production (km m-2 growing season-1)
Specific root length (m g-1)
Root C:N
Root tissue density (g cm-3)
Soil temperature (°C)

4. Linear regression (with year as a fixed effect and without random effects or variance structures) results. All the results are based on "full" models without backward variable selection. Significant (*p*<0.05) terms are highlighted with an asterisk. Note that in all, except root C:N and shrub RTD, models, the trait (response variable) was log-transformed to meet normality assumptions, and that interactions with year and the treatments were not included due to the small sample size. In all models, the reference level for CO_2 treatment was "ambient" and for year "2014" (the beginning of the SPRUCE experiment). SE = standard error, SRL = specific root length (m g^{-1}), RTD = root tissue density (g cm^{-3}), soil temp = soil temperature (°C), soil moist = soil moisture (g/g), eCO_2=elevated CO_2 treatment. Unit of fine root length production is km m^{-2} growing $season^{-1}$.

Model	*p*-value	Slope	SE	Adjusted R^2	Model *p*-value
Fine root length production					
Shrub model				0.15	0.174
- Intercept	<0.001	7.343	0.636		
- Soil temp	0.214	0.129	0.1		
- Soil moist	0.83	0.067	0.309		
- eCO_2	0.439	0.297	0.377		
- Year					
- 2015	0.816	-0.139	0.59		
- 2016	0.291	1.133	1.046		
- 2017	0.166	1.028	0.716		
- 2022	0.055	2.021	0.995		
- Soil temp: eCO_2	0.437	-0.069	0.087		
Tree model				0.66	<0.001
- Intercept	<0.001	6.063	0.545		
- Soil temp	0.189	0.126	0.093		
- Soil moist	0.179	-0.375	0.27		
- eCO_2	0.214	-0.435	0.34		
- Year					
- 2015	0.988	-0.008	0.529		
- 2016	0.17	1.311	0.922		
- 2017	0.348	0.596	0.62		
- 2022*	0.0002	4.029	0.884		
- Soil temp: eCO_2	0.566	0.047	0.08		
SRL					
Shrub model				0.36	0.021
- Intercept	<0.001	5.475	0.143		
- Soil temp*	0.027	0.054	0.023		
- Soil moist	0.262	0.08	0.069		

- eCO_2	0.097	-0.147	0.085		
- Year					
- 2015*	0.018	0.34	0.133		
- 2016*	0.026	0.563	0.235		
- 2017*	0.014	0.434	0.161		
- 2022*	0.005	0.707	0.224		
- Soil temp: eCO_2	0.605	0.01	0.02		
Tree model				0.1	0.251
- Intercept	<0.001	2.962	0.241		
- Soil temp	0.701	-0.016	0.041		
- Soil moist	0.076	0.223	0.119		
- eCO_2	0.708	0.057	0.15		
- Year					
- 2015	0.1	0.406	0.234		
- 2016	0.39	0.358	0.408		
- 2017	0.127	0.436	0.275		
- 2022	0.122	0.631	0.391		
- Soil temp: eCO_2	0.684	0.015	0.035		
Root C:N					
Shrub model				0.38	0.101
- Intercept	<0.001	42.208	5.219		
- Soil temp	0.101	-1.897	1.039		
- Soil moist	0.646	-1.442	3.032		
- eCO_2	0.444	3.94	4.917		
- Year					
- 2015	-	-	-		
- 2016	0.837	1.92	9.079		
- 2017	-	-	-		
- 2022	0.363	-8.711	9.098		
- Soil temp: eCO_2	0.924	-0.108	-0.098		
Tree model				0.17	0.281
- Intercept	<0.001	41.277	6.029		
- Soil temp	0.47	-0.771	1.022		
- Soil moist	0.793	0.765	2.829		
- eCO_2	0.291	5.086	4.533		
- Year					
- 2015	-	-	-		
- 2016	0.864	-1.737	9.833		
- 2017	-	-	-		
- 2022	0.218	-12.983	9.798		
- Soil temp: eCO_2	0.449	0.655	0.828		
RTD					
Shrub model				0.74	<0.001
- Intercept	<0.001	0.285	0.056		
- Soil temp	0.355	-0.009	0.01		
- Soil moist	0.601	-0.015	0.028		
- eCO_2	0.562	0.021	0.036		
- Year					

- 2015	0.155	-0.074	0.05		
- 2016	0.194	-0.124	0.092		
- 2017	-	-	-		
- 2022	0.054	0.182	0.01		
- Soil temp: eCO_2	0.601	-0.004	0.008		
Tree model				0.33	0.054
- Intercept	<0.001	-1.605	0.173		
- Soil temp	0.144	0.05	0.033		
- Soil moist	0.112	0.148	0.088		
- eCO_2	0.76	-0.037	0.118		
- Year					
- 2015	0.848	0.032	0.162		
- 2016	0.392	0.261	0.296		
- 2017	-	-	-		
- 2022*	0.016	0.771	0.285		
- Soil temp: eCO_2		-0.026	0.027		

5. Details about statistical methods

As microtopography (hummock and hollow) did not contribute to random variation significantly in linear mixed effects models and none of the traits differed significantly between hummocks and hollows, we aggregated the root trait dataset to the plot-level by taking the mean of hummock and hollow values. We then estimated the effects of soil warming and elevated CO_2 treatments on the individual traits (SRL, RTD and root C:N, as well as fine root length production) using linear mixed effects models with function *lme* from package *nlme* (Pinheiro et al., 2023; Pinheiro & Bates, 2000) in R (v4.3.3 R Core Team 2024). Each model was built for trees and shrubs separately (e.g. separate tree and shrub models for SRL). In the models, soil temperature (mean of half-hourly measurements over the period of ingrowth core deployment per plot), elevated CO_2 treatment (ambient or elevated), soil moisture (gravimetric water content, g/g), and the interaction between soil temperature and elevated CO_2 treatment were fixed effects, while year was a random effect, due to sample sizes and treatment levels varying between years.

The response variables (SRL, RTD, root C:N and fine root length production) were log-transformed (except tree root C:N for which model residuals were normally distributed without transformation), after which the residuals were normally distributed in all models. To avoid multicollinearity arising from the interaction term, soil temperature and soil moisture were also centered. Multicollinearity was checked with variance inflation factor with function *vif* from package *car* (Fox & Weisberg,

2018). In tree RTD and shrub fine root length production models, year caused residual heterogeneity which was allowed for in the models by including it in *varIdent* variance structure (different variances per stratum).

We assessed the most significant trait predictors with backward variable selection using the log likelihood ratio method with AIC and *p*-values (models were fitted with maximum likelihood for model comparisons and restricted maximum likelihood for final model assessments).

To explore the effect of year on the root traits in the experiment, we used linear regressions with function *lm* from package *stats* (R Core Team, 2024), due to the lack of random effects and residual variance heterogeneity. For these models, we did not do backward variable selection but explored only the full models (table 4).

References

Fox, J., & Weisberg, S. (2018). *An R companion to applied regression* (3rd ed.). SAGE Publications.

Pinheiro, J., & Bates, D. M. (2000). *Mixed-effects models in S and S-PLUS* (1st ed.) [PDF]. Springer.

Pinheiro, J., Bates, D. M., & R Core Team. (2023). *nlme: Linear and Nonlinear Mixed Effects Models* (Versions 3.1-164). https://CRAN.R-project.org/package=nlme

R Core Team. (2024). *R: A Language and Environment for Statistical Computing* (Version 4.3.3). R Foundation for Statistical Computing. https://www.R-project.org