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RESEARCH ARTICLE

Dynamics of initial carbon allocation after drought release in mature Norway spruce—Increased belowground allocation of current photoassimilates covers only half of the carbon used for fine-root growth

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Abstract

After drought events, tree recovery depends on sufficient carbon (C) allocation to the sink organs. The present study aimed to elucidate dynamics of tree-level C sink activity and allocation of recent photoassimilates (C_{new}) and stored C in c. 70-year-old Norway spruce (*Picea abies*) trees during a 4-week period after drought release. We conducted a continuous, whole-tree ^{13}C labeling in parallel with controlled watering after 5 years of experimental summer drought. The fate of C_{new} to growth and CO_2 efflux was tracked along branches, stems, coarse- and fine roots, ectomycorrhizae and root exudates to soil CO_2 efflux after drought release. Compared with control trees, drought recovering trees showed an overall 6% lower C sink activity and 19% less allocation of C_{new} to aboveground sinks, indicating a low priority for aboveground sinks during recovery. In contrast, fine-root growth in recovering trees was seven times greater than that of controls. However, only half of the C used for new fine-root

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growth was comprised of C_{new} while the other half was supplied by stored C. For drought recovery of mature spruce trees, in addition to C_{new}, stored C appears to be critical for the regeneration of the fine-root system and the associated water uptake capacity.

KEYWORDS
^{13}C labeling, belowground carbon allocation, carbon partitioning, climate change, drought recovery, forest ecosystems, *Picea abies*, watering

1 | INTRODUCTION

Forests store ~45% of terrestrial carbon (C), which is in form of carbon dioxide (CO_2) a rapidly increasing greenhouse gas (IPCC, 2021). Thus, conditions and C sequestration capacity of forests have a large impact on the global C cycle (Bonan, 2008; Lal et al., 2018). As a consequence of climate change, forests are globally facing repeated droughts leading to immense tree dieback (Allen et al., 2010; Hartmann et al., 2018; Schuldt et al., 2020). Under these circumstances, tree survival depends not only on water availability, but also on C supply to each above- and belowground tree organs (Hartmann et al., 2020; Ruehr et al., 2019; Sala et al., 2010). Previous studies revealed that allocation of both, structural (i.e., growth) and non-structural (i.e., maintenance and storage) C, was altered to increase tree survival: for example, enhanced C allocation to root growth (Gaul et al., 2008; Hommel et al., 2016; Meier & Leuschner, 2008; Poorter et al., 2012) and C storage (Blessing et al., 2015; Chuste et al., 2020; Hart et al., 2021).

Because the frequency of drought events is predicted to increase in the future (IPCC, 2021), recovery from these events is an important aspect of tree survival, which has attracted less attention compared with direct drought effects (Ruehr et al., 2019). On the one hand, drought release can increase aboveground C sink activity for repair processes such as growth of new xylem and embolism refilling (Brodersen & McElrone, 2013; Ruehr et al., 2019; Zang et al., 2014) or C storage to prepare for future droughts (Galiano et al., 2017; Rehschuh et al., 2021). On the other hand, drought release can stimulate belowground C sinks such as root production, mycorrhizal and microbial activity, and associated soil respiration (Brunner et al., 2019; Gao et al., 2021; Hagedorn et al., 2016; Joseph et al., 2020; Werner et al., 2021). Fine-root growth dynamics are especially challenging to assess (Ruehr et al., 2019), are typically tree species-specific, and therefore difficult to generalize (Nikolova et al., 2020; Zwetsloot & Bauerle, 2021).

To improve our understanding of the tree recovery processes from drought, it is crucial to analyze the whole-tree C allocation including belowground sinks, which has been often restricted to young trees (Brüggemann et al., 2011; Hartmann et al., 2018). Recovery of tree function can be expected only if the increased C sink activity after drought release can be met by available C that is newly assimilated C (C_{new}, see Table 1 for terms and abbreviations) and stored C. A previous study using young European beech trees directly related allocation of C_{new} belowground to the capacity of trees to recover from drought (Hagedorn et al., 2016). However, for mature trees, recovery from repeated drought events is critically understudied and experimental evidence on the allocation of both C_{new} and stored C for tree recovery processes is still scarce (Gao et al., 2021; Joseph et al., 2020; Werner et al., 2021).

The present study was conducted as part of the Kranzberg forest roof (KROOF) project, which was established to investigate mature Norway spruce (*Picea abies* [L.] Karst.) trees exposed to 5 years of experimental summer droughts (Grams et al., 2021). This long-term repetitive drought treatment significantly reduced leaf and twig growth (Tomasella et al., 2018), stem growth (Pretzsch et al., 2020), fine-root growth (Nickel et al., 2018; Zwetsloot & Bauerle, 2021), total C uptake (Brunn et al., 2022), and C storage pools (Hesse et al., 2021) in Norway spruce. To gain insight into the recovery processes, the drought-stressed trees were watered in early summer of the sixth year (Grams et al., 2021). In parallel with the watering, we performed a continuous ^{13}C labeling and assessed the use of both C_{new} and stored C at the whole-tree level for tree recovery from drought.

In this study, leaves were considered C sources, and we focused on the allocation of newly assimilated C (C_{new}) exported

TABLE 1 Terms and abbreviations used in this study

Terms	Unit	Abbreviations	Explanation
Newly assimilated C	g C	C_{new}	Labeled, newly assimilated C
Stored C	g C	-	C originating from C reserves within a tree
C sink activity	g C tree^{-1} 28 days^{-1}	-	Total C that was used for growth and respiratory sinks (cumulative sum during 28 days after drought release)
Amount of C_{new}	g C tree^{-1} 28 days^{-1}	-	Total amount of C_{new} allocated to each C sink (cumulative sum during 28 days after drought release)
Proportional allocation of C_{new}	%	-	Proportion of C_{new} in each C sink to the total C_{new} detected in the whole tree
Fraction of labeled C	%	f_{Label}	Proportion of C_{new} to the C sink activity at each measurement point
Contribution of C_{new} to each C sink activity	%	contC_{new}	Proportion of C_{new} to the C sink activity at the new isotopic equilibrium (asymptote of Equation 11)

from leaves to the different above- and belowground sinks. We examined the following three aspects: (i) whole-tree C sink activity (in g C used for growth and respiration, see Table 1), (ii) allocation of C_{new}, and (iii) contribution of C_{new} to each C sink activity (contC_{new}). We expected the regeneration of the water-absorbing fine roots to be a high priority for drought-recovering spruce trees and thus we hypothesized a higher C sink activity belowground and correspondingly a lower C sink activity aboveground compared with control trees [H1] and that the high belowground C sink activity of recovering trees would be supported by preferential allocation of C_{new} into belowground sinks at the expense of aboveground sinks [H2]. Due to reduced leaf and twig growth under drought, the total C uptake per tree can be expected to be much lower in recovering trees even after drought release compared with controls. Thus, we further hypothesized that for recovering trees, the relative contribution of C_{new} to the different sinks (i.e., contC_{new}) would be lower compared with control trees, particularly when sink activity is increased [H3].

2 | MATERIALS AND METHODS

2.1 | Experimental site and ^{13}C labeling

The present study was conducted at the Kranzberg Forest experimental site, a mixed forest in southern Germany (11°39′42″ E, 48°25′12″ N; 490 m a.s.l.). A long-term drought experiment was established in 2014, which is described in detail by Grams et al. (2021). In brief, this experimental site consists of 12 plots with c. 70-year-old Norway spruce (*P. abies* [L.] Karst.) trees. The plots were trenched 4 years before the start of the drought treatment and separated by buried plastic tarps from the surrounding soil (Pretzsch et al., 2014). Half of the plots were equipped with under-canopy roofs, thereby excluding precipitation throughfall throughout the entire growing season (from April to November) between 2014 and 2018 and leading to recurrent summer droughts; remaining control plots were exposed to natural rainfall events. Accordingly, 459 ± 21 mm (69 ± 7% of the annual precipitation) was excluded during the growing seasons and predawn leaf water potential of drought-stressed trees significantly decreased to as low as −1.8 MPa (Grams et al., 2021). In early summer of 2019, all drought plots were watered to initiate the recovery processes (Grams et al., 2021) by supplying c. 90 mm water over 40 h to increase the soil water content to the control level (around 20%–30%, Grams et al., 2021). Accordingly, the predawn leaf water potential of previously drought-stressed trees fully recovered from −0.93 ± 0.03 MPa to −0.69 ± 0.05 MPa within 7 days after watering, while that of control trees remained constant at −0.61 ± 0.02 MPa (Grams et al., 2021; Hikino et al., 2022). In parallel with the watering, we conducted a continuous ^{13}C labeling experiment in four control and three recovering spruce trees on two neighboring plots (Figure 1a, for details see Hikino et al., 2022). In brief, each tree (average height of 32.3 ± 0.7 m, Table S1) was equipped with perforated PVC tubes, which continuously released ^{13}C-depleted CO_2 ($\delta^{13}C$ of −44.3 ± 0.2‰) into the entire crowns from 5 a.m. to 7 p.m. (CET). The CO_2 exposure started at the same time as watering on July, 4th 2019 (day 0), lasted until July, 17th 2019 (day 13) and CO_2 concentration and its stable C isotopic signature ($\delta^{13}C$) were monitored by means of a cavity ring-down spectroscopy (CRDS, ESP-1000; PICARRO). The change of the CO_2 concentration and $\delta^{13}C$ of individual crown air during labeling were on average +126 ppm and −7.3‰ for control trees, +80 ppm and −5.1‰ for recovering trees, due to different wind exposure of each tree. The individual shift in crown air (Table S1) was considered in the tree-specific analyses. To assess the whole-tree C allocation, we investigated the following C sinks (Figure 2): Growth and/or CO_2 efflux of branch, upper and lower stem, coarse-root, fine-root, ectomycorrhizae (ECM), fine-root exudates, and soil. Because the ^{13}C label in soil CO_2 efflux showed a peak 14–20 days after the start of labeling/watering and a rapid decrease until day 28 (Hikino et al., 2022), C allocation during the first 4 weeks (28 days) of drought release was considered. In addition to the seven labeled trees, three control and three recovering spruce trees on non-labeled plots were assessed to correct for the effect of watering and weather influences on $\delta^{13}C$ of studied parameters.

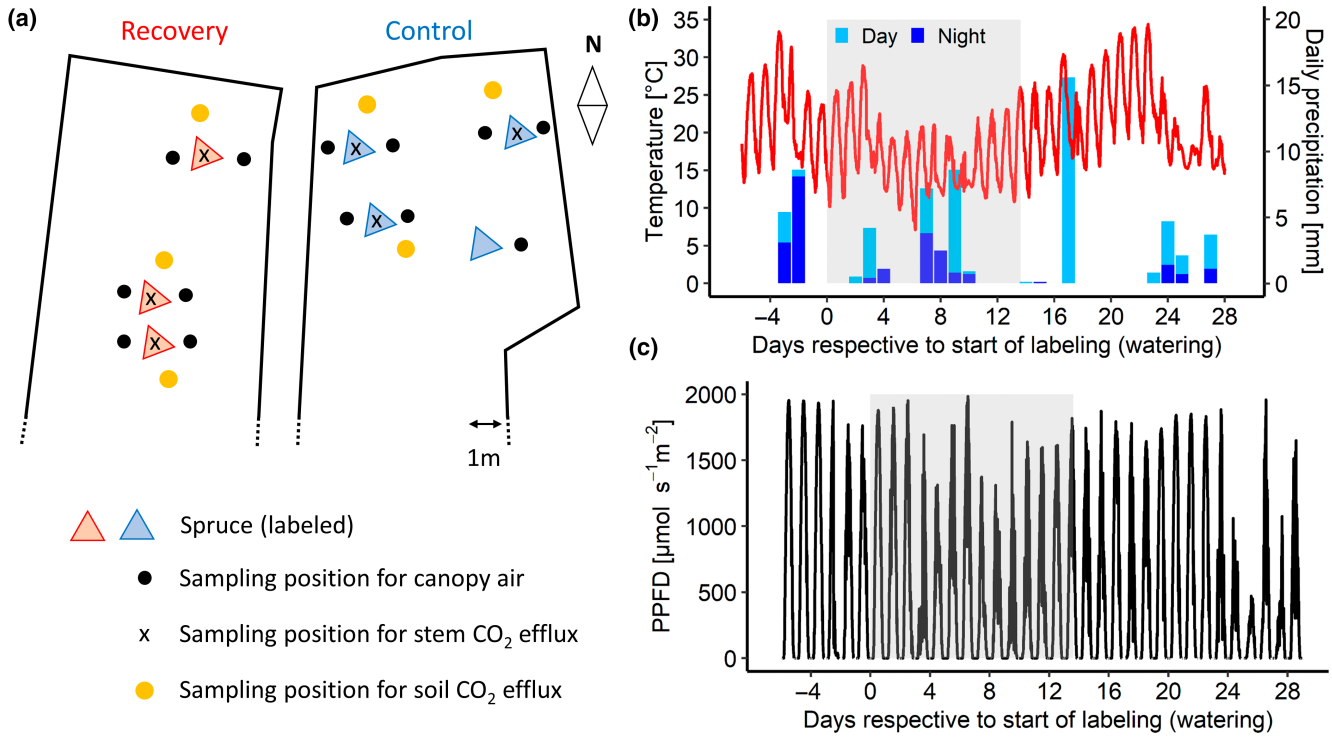


FIGURE 1 (a) Overview of the two ^{13}C-labeled plots: Control and recovery (previously drought-stressed), giving positions of trees (red and blue triangles = labeled spruce trees), sampling points of canopy air (black circles), stem CO_2 efflux (x), and soil CO_2 efflux (yellow circles). Modified from Hikino et al. (2022). (b) Temperature (red lines), daily precipitation (blue bars), and (c) photosynthetic photon flux density (PPFD) before and after the watering until day 28. Precipitation amount is split into day (5 a.m.–7 p.m. CET, fumigation hours, light blue), and night (7 p.m.–5 a.m., dark blue). Day 0 is the day of the watering. The gray areas show the labeling days (day 0–13). ^{13}C labeling started in parallel with the watering on day 0.

2.2 | Weather data

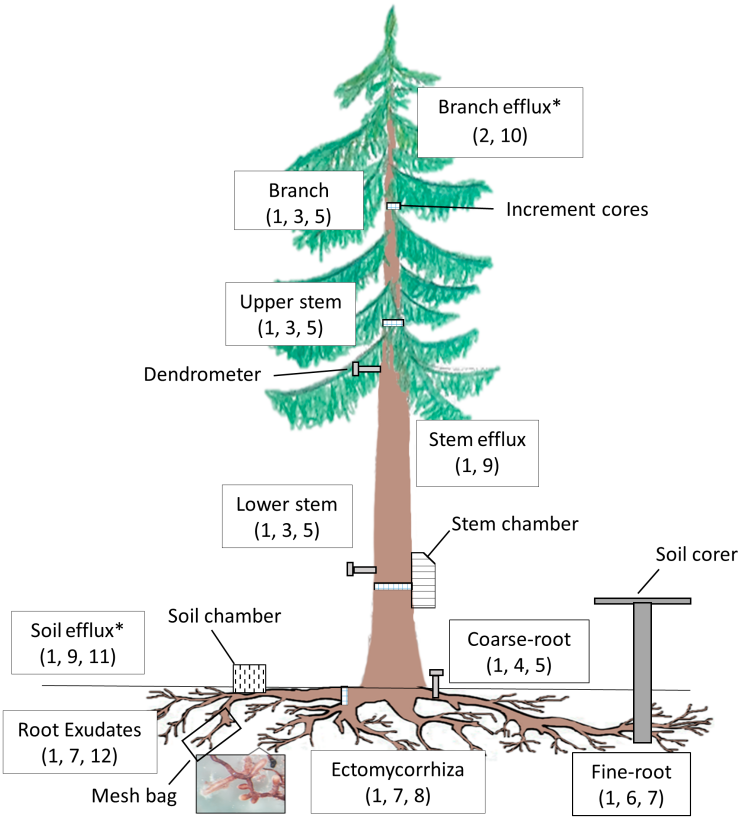
Daytime (from 5 a.m. to 7 p.m., CET), mean temperature during the experiment (i.e., 0–28 days after watering) was 21.4 ± 5.4 (1SD) °C (Figure 1b) with a mean vapor pressure deficit of 0.6 ± 0.4 (1SD) kPa. There were prolonged periods with minor daytime precipitation on days 9 (7.8 mm) and 17 (15.6 mm). The mean daytime photosynthetically active photon flux density was 772 ± 545 (1SD) µmol m^{-2} s^{-1} (38 ± 14 [1SD] mol m^{-2} day^{-1}, Figure 1c).

2.3 | Sample collection

After the 2019 growing season, increment cores (diameter 0.5 cm) were collected at three different stem heights (breast height, crown base, mid-crown), and from coarse-roots (Figure 2) and immediately dried at 64°C for 72 h. Tree rings from 2019 were separated with a razor blade and subsequently thin-sectioned (c. 5 µm) in radial direction, using a microtome (Sledge Microtome G.S.L.1; Schenkung Dapples).

To record the isotopic signature of fine-root tips and mycorrhizae and trace fine-root growth, vital fine-roots (diameter ≤2 mm) were selected based on their turgescent appearance and active meristems, and placed in mesh bags as follows. In April 2019, eight fine-roots for each sampling day and treatment were excavated within the first 10 cm of the soil, photographed, placed in 1/3 soil filled nylon mesh bags (12.5 × 6.5 cm, mesh width 80 µm, open area of 29%), sprayed with water to enhance root soil contact, and covered with soil. Seven days before and weekly after the watering, roots were harvested from the mesh bags and photographed. Additional fine roots from 0 to 10 cm depth were also randomly sampled within the plots daily to gain a more detailed time resolution of the change in C isotope signature (Table S2). Thus, a total of 1166 root tips were sampled. After sampling, vital ECM and non-mycorrhizal root tips were distinguished by the presence/absence of a hyphal mantle using a stereomicroscope (M125; Leica), and dried for 1 h at 60°C.

Root exudates were collected according to the method described by Phillips et al. (2008) and Brunn et al. (2022). Excavated root branches were rinsed with a nutrient solution (0.5 mM NH_4NO_3, 0.1 mM KH_2PO_4, 0.2 mM K_2SO_4, 0.15 mM $MgSO_4$, 0.3 mM $CaCl_2$) after attached soil was gently removed with tweezers. Roots were then left to recover in a 1:1 mixture of native soil from the site and sand for 48 h, cleaned, and placed into 30 ml glass syringes with sterile glass beads. Syringes were flushed three times with the nutrient solution, equilibrated for 48 h, flushed again, and left shielded with aluminum foil and leaf litter. Between days −5 and 7, and 20 and 24 (Table S2), exudates trapped in the syringes were collected from the same root branches every 48 h by adding 30 ml of nutrient solution, extracted using a membrane pump, filtered through sterile



Parameters	Methods used for measurement
Fraction of labeled C (f_{Label})	1) Stable C isotope measurements (IRMS, IRIS, or isoTOC cube)
	2) Values adopted from stem efflux
Growth	3) Allometry (DBH)
	4) Excavation
	5) Dendrometer
	6) Picture analysis (Mesh bag)
Fine-root and ectomycorrhizal biomass	7) Soil cores
	8) Picture analysis & projection (Mesh bag)
Efflux rates	9) Measuring chambers (IRMS)
	10) Calculation based on literature values
	11) Auto- and heterotrophic ratio taken from literatures
Exudation rates	12) isoTOC cube

* Calculation (partly) based on literatures

FIGURE 2 Overview of C sinks and sampling/calculation methods used for this study. In few cases, data from literature were adopted for calculations (i.e., branch CO_2 efflux and autotrophic soil CO_2 efflux).

syringe filters (0.22 µm, ROTILABO® MCE; Carl Roth GmbH + Co. KG), and stored at −20°C. A blank syringe without roots served as a reference. Root branches were harvested after exudate collection, dried, and total dry biomass recorded to normalize exudation rates to root mass.

2.4 | Analysis of stable C isotopic composition ($\delta^{13}C$), rates of CO_2 efflux, and root exudates

$\delta^{13}C$ of tree ring slices (stem and coarse-roots) and vital root tips (ECM and non-mycorrhizal) were determined with an isotope ratio mass spectrometer (IRMS, delta V Advantage; Thermo Fisher Scientific) coupled to an Elemental Analyzer (Euro EA; Eurovector).

Rates and $\delta^{13}C$ of stem CO_2 efflux were assessed approx. every 80 min at c. 1 m height on stems of six labeled ($n = 3$ per treatment, Figures 1a and 2) and six non-labeled trees as controls with custom-built stem chambers connected to an isotope ratio infrared spectrometer (IRIS, DeltaRay; Thermo Fisher Scientific), as described in detail by Hikino et al. (2022). Soil CO_2 efflux chambers (Li-8100; Li-Cor, Inc.) were installed at a 1 m distance from each measured tree ($n = 3$, Figures 1a and 2), connected to a Li-8150 (Li-Cor, Inc.) multiplexer and a second IRIS. Rates and $\delta^{13}C$ of soil CO_2 efflux were then recorded every 30 min (Table S2). $\delta^{13}C$ of the three soil chambers in the recovering plot was corrected for the physical back-diffusion of soil air during watering (Andersen et al., 2010; Subke et al., 2009; Unger et al., 2010), using an additional chamber installed next to non-labeled trees in the same plot.

$\delta^{13}C$ and total organic C concentration of root exudate samples were analyzed with an isoTOC cube (Elementar).

2.5 | Calculation of total C sink activity

Below, cumulative sum of C sink activity during 28 days (in g C tree^{-1} 28 days^{-1}) after drought release was calculated for each C sink (Figure 2).

2.5.1 | Stem and branch growth

The total growth during the 2019 growing season (Y in kg tree^{-1}) was determined with an allometric function provided for Norway spruce by Forrester et al. (2017), using the diameter at breast height (DBH, d in cm, Table S1) as input parameter:

$$\text{For stem } \ln(Y) = -2.5027 + 2.3404 \cdot \ln(d) \quad (1)$$

$$\text{For branch } \ln(Y) = -3.3163 + 2.1983 \cdot \ln(d) \quad (2)$$

Because crown length was c. 1/3 of the total tree height (Table S1), 1/9 of the total stem growth was assigned to the upper

stem (from top to crown base) and the remaining 8/9 to the lower stem (from crown base to trunk base), assuming a conical shape of the stems.

The total annual growth in 2019 was then multiplied by the proportional growth (in %) during the 28 days after watering (ratio of the radial growth during 28 days to the total annual growth), determined by automatic point dendrometers (DR-type; Ecomatik) installed at 50% tree height (used for branch and upper stem) and breast height (used for lower stem, Figure 2; see Methods S1). The % C of samples was ascertained by IRMS measurement (same for coarse-root growth, fine-root growth, and ECM).

2.5.2 | Branch CO_2 efflux

Total branch and twig surface area was estimated for each tree (Table S3) using field data including length, number, and mean diameter of branches and twigs, separated into each needle class and sun/shade crowns. Based on earlier studies on spruce trees at the same site using a infrared gas analyser (Binos 4b; Emerson Process Management; Kuptz et al., 2011; Reiter, 2004), maintenance respiration rates (R_M), growth respiration rates (R_G), and total CO_2 efflux of branch CO_2 efflux (R_{branch}) were calculated as follows:

$$R_{branch} = R_M + R_G \quad (3)$$

$$R_M = R_{M10} \cdot Q_{10}^{\frac{T-10}{10}} \quad (4)$$

$$R_G = \frac{330 - DOY}{330 - 130} \cdot R_{G\,10max} \cdot Q_{10}^{\frac{T-10}{10}} \quad (5)$$

where R_{M10} represents the maintenance respiration rates at 10°C (0.13 µmol m^{-2} s^{-1} for sun branch, and 0.048 µmol m^{-2} s^{-1} for shade branch), R_{G10max} the maximum growth respiration at 10°C (0.23 µmol m^{-2} s^{-1} for sun branch, and 0.12 µmol m^{-2} s^{-1} for shade branch), Q_{10} the temperature sensitivity (2.45 for both sun and shade branches), and T the temperature. Since rates of stem CO_2 efflux did not significantly differ between control and recovering trees, rates of branch CO_2 efflux were also assumed to be similar.

2.5.3 | Stem CO_2 efflux

Stem efflux rates of each tree (Figure S1a,b) were multiplied by the stem surface area (Table S3), which was calculated using DBH and tree height, assuming a conical shape of the stems. For stems above 6.5 m, efflux rates at the breast height were multiplied by 1.4 as previously assessed on spruce trees from the same site (Kuptz et al., 2011). The mean rates of stem CO_2 efflux of three measured control trees were used for the fourth control tree, which was not assessed in this study (Figure 1a).

2.5.4 | Coarse-root growth

Coarse roots were counted, and the length of one coarse root (root diameter ≥2 mm) per tree was measured on site after excavating. Using root wood density of 0.416 g cm^{-3} (Pretzsch et al., 2018), mean diameter, length, and ring width from 2019 based on coring, the total coarse-root growth in 2019 was determined, and subsequently multiplied by the proportional growth during the 28 days after watering, according to automatic dendrometers installed at one coarse root (diameter of 9.4 ± 1.1 cm) on each tree (Ecomatik, Figure 2) as described above for stem and branch growth.

2.5.5 | Fine-root growth and ECM

To avoid massive soil disturbance in the long-term plots, not more than one coarse-root per tree was excavated. Thus it was not possible to assign the ECM samples, non-mycorrhizal root tips, or root exudates unequivocally to a specific tree. Special care was taken to gain representative samples by avoiding clustered sampling spots and covering the whole area underneath the labeled spruce each sampling day. For this reason, the total C sink activity of fine-root growth, ECM, and root exudates was first extrapolated to the area occupied by spruce trees (Figure 1a). From coring within the plot, we knew that fine-roots of spruce were evenly spread in the spruce area. The total spruce tree C sink activity belowground was then assigned to individual trees according to the area occupied by each tree using a positive exponential relationship between DBH and root biomass (Table S1, spatial contribution belowground and area; Häberle et al., 2012).

The initial fine-root biomass (mg cm^{-3}) was determined with fine roots taken from 10 soil cores (diameter of 1.4 cm) within the first 10 cm of the uppermost soil layers on day −7. Because the biomass values of the two labeled plots differed from all other sampled plots and the previous years, the average initial biomass of all control and recovery plots of the experimental site, which agrees to fine-root area values of Brunn et al. (2022) on the same site and year, was accounted for further calculations. To calculate the fine-root biomass at 10–30 cm depth and thus the total initial fine-root biomass from 0 to 30 cm soil depth (M_{FR30}), a root biomass ratio between upper (0–10 cm) and lower (10–30 cm) soil layer was used, measured in summer 2018 on the same plots (Table 2). The total fine-root gain in the spruce area (Table 2) was calculated:

$$\text{Fine root length growth rate} = \frac{\text{Root length growth}}{\text{Initial root length in mesh bag}} \quad (6)$$

where the initial root length on day −7 and root length growth was determined by image analysis of respective pre- and post-harvest mesh bag root pictures via ImageJ (version 1.53a; National Institute of Health). The biomass gain per soil volume (mg cm^{-3}) was then calculated (Equation 7), assuming a constant fine-root diameter, corrected

TABLE 2 Fine-root (FR) biomass (BM) and its ratio between upper (0–10 cm depth, U) and lower (10–30 cm depth, L) soil layer in summer 2018 to calculate the initial BM and root growth in the lower layer in 2019: In control and recovery (previously drought-stressed) plots

	FR BM summer 2018 (mg cm^{-3})	FR BM ratio U/L	M_{FR} (mg cm^{-3})	M_{ECM} (mg cm^{-3})	FR BM gain (g)	FR length growth rate
Control	1.1 (U)	2.0	1.0 (U)	0.3 (U)	1113	0.1 ± 0.0
	0.6 (L)		0.5 (L)	0.1 (L)		
Recovery	0.6 (U)	1.3	0.9 (U)	0.1 (U)	5905	0.3 ± 0.2
	0.5 (L)		0.7 (L)	0.1 (L)		

Note: Initial FR BM (M_{FR}) and ECM BM (M_{ECM}) display the BM before the watering. FR BM gain reflects the cumulative sum of growth within the plot of each treatment during 28 days after watering (total g biomass per treatment, i.e., sum of four trees for control and three trees for recovery plot). FR length growth rate represents the mean ratio of fine-root growth to initial length during 28 days after watering (calculated by Equation 6, given with SE).

by the average biomass gain on day −7 to exclude root growth between mesh bag placement and first harvest, and extrapolated to the soil volume of the plot at 0–30 cm depth.

$$\text{fine root biomass gain} = \text{fine root length growth rate} \times \text{dry mass per soil volume} \quad (7)$$

Helmisaari et al. (2009) found the most spruce fine roots in the upper soil layer and Zwetsloot and Bauerle (2021) reported no changes in vertical root distribution of the present spruce during drought compared with controls which support a sufficient coverage of our calculated fine-root biomass. For determination of fine-root biomass, we manually selected vital fine-roots based on the same morphologic criteria as for the fine-roots included in mesh bags, which was used to calculate root growth. Within the mesh bag roots, we found that 96% of the sampled fine-roots in control and 57% in recovering trees were colonized by ectomycorrhizal fungi. Assuming no significant change in ECM biomass on root tips during our 28 day study period, since full formation of ECM takes longer (Ineichen & Wiemken, 1992), the biomass of mycorrhized fine-roots (M_{FR-ECM}) at 0–30 cm depth was calculated based on the initial fine-root biomass at 0–30 cm (M_{FR30}, Table 2):

$$M_{FR\_ECM} = \frac{M_{FR30}}{100} \times 96 \text{ (or } 57) \quad (8)$$

ECM biomass (M_{ECM}) was calculated based on the finding by Helmisaari et al. (2007, 2009), that ECM make up 28% of one spruce fine-root's biomass, determined under the same terms as in our study (mature spruce trees, root diameter <2 mm, most fine-roots found within 0–10 cm depth):

$$M_{ECM} = \frac{M_{FR\_ECM}}{100} \times 28 \quad (9)$$

2.5.6 | Root exudates

The total root exudates C contribution was calculated for the soil at 0–30 cm depth using the organic C concentration in root exudates and the total fine-root biomass determined by soil cores.

2.5.7 | Soil CO_2 efflux

Soil efflux rates of each tree (Figure S1c,d) were multiplied by the area belowground occupied by each tree (Table S1). The mean rates of soil CO_2 efflux close to the three measured control trees were used for the fourth control tree, which was not assessed (Figure 1a). For the contribution of autotrophic respiration (root-derived including rhizosphere) to total soil respiration (autotrophic + heterotrophic), we used as value 51% in control and 38% in recovering trees based on previous measurements on spruce trees at the same site in July during 1 year with drought and 1 year without drought (Nikolova et al., 2009). We assumed that the contribution of autotrophic respiration did not significantly change after drought release, as soil CO_2 efflux rates under recovering trees remained unaffected by the drought release (Hikino et al., 2022).

2.6 | Calculation of fraction of labeled C (f_{Label}) and contribution of C_{new} to each C sink activity ($contC_{new}$)

Fraction of labeled C (f_{Label}) was calculated at each measurement point using the following equation (Kuptz et al., 2011):

$$f_{Label} = \frac{\delta^{13}C_{old} - \delta^{13}C_{sample}}{\delta^{13}C_{old} - \delta^{13}C_{new}} \quad (10)$$

where $\delta^{13}C_{old}$ gives the mean $\delta^{13}C$ before the start of labeling, $\delta^{13}C_{sample}$ is the $\delta^{13}C$ of each measurement, and $\delta^{13}C_{new}$ represents $\delta^{13}C$ at the new isotopic equilibrium (Figure S2, for the calculation of $\delta^{13}C_{new}$ see Methods S2). Rarely occurring negative f_{Label} values were set to zero. f_{Label} of stem CO_2 efflux was used for branch CO_2 efflux, which was not assessed in this study.

$contC_{new}$, representing f_{Label} at the new isotopic equilibrium, was determined by fitting the course of f_{Label} with the following sigmoid curve (Figures S3 and S4).

$$f_{Label} = \frac{cont\ C_{new}}{1 + e^{-\frac{t-t_0}{b}}} \quad (11)$$

where t is the time of measurement, t_0 the inflection point of the curve, and b the slope coefficient of the regression. contC_{new} would be one (100%) if C sink was supplied solely with C_{new} and zero (0%) if supplied exclusively by stored C. Since f_{Label} decreased again after the end of labeling, only f_{Label} before reaching the maximum were used for the fitting.

Similar to C sink activity, we pooled all samples of ECM, non-mycorrhizal root tips, and root exudates for the calculation of contC_{new} for control and recovering trees. Thus, only one value was available for each treatment, so that a statistical test between treatments was not possible for these three C sinks. contC_{new} to soil CO_2 efflux was divided by the contribution of autotrophic part to calculate the contC_{new} to autotrophic soil CO_2 efflux.

2.6.1 | Methods used for branch, stem, and coarse-root growth

For branch, stem, and coarse-root growth, $\delta^{13}C_{old}$ and $\delta^{13}C_{sample}$ (for Equation 10) were determined by fitting the $\delta^{13}C$ of tree ring slices with a piecewise function (R package "segmented", version: 1.3-0) as described by Hikino et al. (2022; for details see Methods S3; Figure S5). The applied labeling with ^{13}C-depleted CO_2 caused a sudden and steep decrease of $\delta^{13}C$, after the ^{13}C-depleted tracer was incorporated into the tree ring. The $\delta^{13}C$ value at this point was determined with a piecewise function (marked by the green horizontal dashed lines in Figure S5a,b) and then defined as $\delta^{13}C_{old}$. After the steep decrease, $\delta^{13}C$ increased again as unlabeled C arrived after the end of labeling. The minimum $\delta^{13}C$ value at this point was determined with the same method (purple horizontal dashed lines) and defined as $\delta^{13}C_{sample}$. In addition to the labeled trees, we also determined the natural shifts of $\delta^{13}C$ of non-labeled control trees for each treatment ($n = 3$) to correct $\delta^{13}C_{sample}$ for the effect of watering, weather fluctuation, and seasonal changes (Helle & Schleser, 2004). Finally, using $\delta^{13}C_{old}$, corrected $\delta^{13}C_{sample}$, and Equation (10), f_{Label} was calculated.

For the course of f_{Label} (Figure S6), C transport rates determined by Hikino et al. (2022) were used to define the day on which the first ^{13}C-depleted tracer arrived at each tree height (i.e., when f_{Label} started to increase). A linear increase of f_{Label} was assumed until the new isotopic equilibrium was reached, that is contC_{new}. contC_{new} calculated with the samples from the middle of the crown was used for branch and upper stem growth. For the lower stem growth, we used the mean contC_{new} calculated for the crown base and breast height.

2.7 | Calculation of allocation of newly assimilated C (C_{new}) to each C sink

Total amount of C_{new} allocated to each C sink during 28 days after drought release was calculated as the cumulative sum of C_{new} after multiplying C sink activity and their respective f_{Label}. As soon as f_{Label} started to decrease due to the end of labeling, sigmoid curves (Equation 11) or in the case of branch, stem, and coarse-root growth (Figure S6) a constant f_{Label} was used. For soil CO_2 efflux, total C sink activity (autotrophic + heterotrophic) was multiplied with respective f_{Label}, since C isotopic signatures and f_{Label} comprise the mixed signal of both autotrophic and heterotrophic efflux. Using the amount of C_{new} (in g C), proportional allocation of C_{new} (in %) to each sink was calculated for each tree.

2.8 | Statistical analysis

All data were analyzed using R (version 4.0.3) in R studio (version 1.3.1093). For the non-linear regression (Equation 11), nls function (package: stats, version: 4.0.3) was applied. The differences in C sink activity, contC_{new}, and allocation of C_{new} between control and recovering trees were tested with a t-test for each C sink. Beforehand, we tested the homogeneity of variances (F-test) and the normality of the data (Shapiro test). If these prerequisites were violated, data were either transformed (logarithms, square root, multiplicative inverse), or wilcox. test (package: stats, version: 4.0.3) was used. Proportional allocation of C_{new} was tested using a linear-mixed model (package: nlme, version: 3.1-151). We defined the treatment and above- and belowground sinks as fixed, and tree as a random effect. Beforehand, we tested the homogeneity of variances (Levene test) and the normality of the residuals (Shapiro test). If the fixed factor was significant, a post-hoc test with Tukey correction (package: lsmeans, version: 2.30-0) was performed. All results are given in mean ± SE, unless otherwise noted.

3 | RESULTS

3.1 | Total C sink activity

We assessed the cumulative sum of C sink activity for each sink (in g C tree^{-1} 28 days^{-1}, Figure 3) during the first 4 weeks after drought release. In aboveground sinks, the recovering trees had a significantly lower sink activity for branch CO_2 efflux with 558 ± 86 g C ($p < .01$, Figure 3) than control trees with 1205 ± 131 g C. The activity of the other aboveground sinks was slightly but insignificantly lower in recovering trees compared with controls.

In belowground sinks of recovering trees, fine-root growth was the major C sink with 965 ± 136 g C, which was seven times higher than that of control trees (136 ± 12 g C, $p < .001$). Sink activity of coarse roots and ECM was 126 ± 48 g C, and 302 ± 43 g C in recovering trees, respectively, which was similar to controls with 98 ± 43 g C and 306 ± 27 g C. Autotrophic soil CO_2 efflux under recovering trees was significantly lower with 649 ± 123 g C than under control trees with 1643 ± 220 g C ($p = .01$). Sink activity of root exudates tended to be higher under recovering trees than

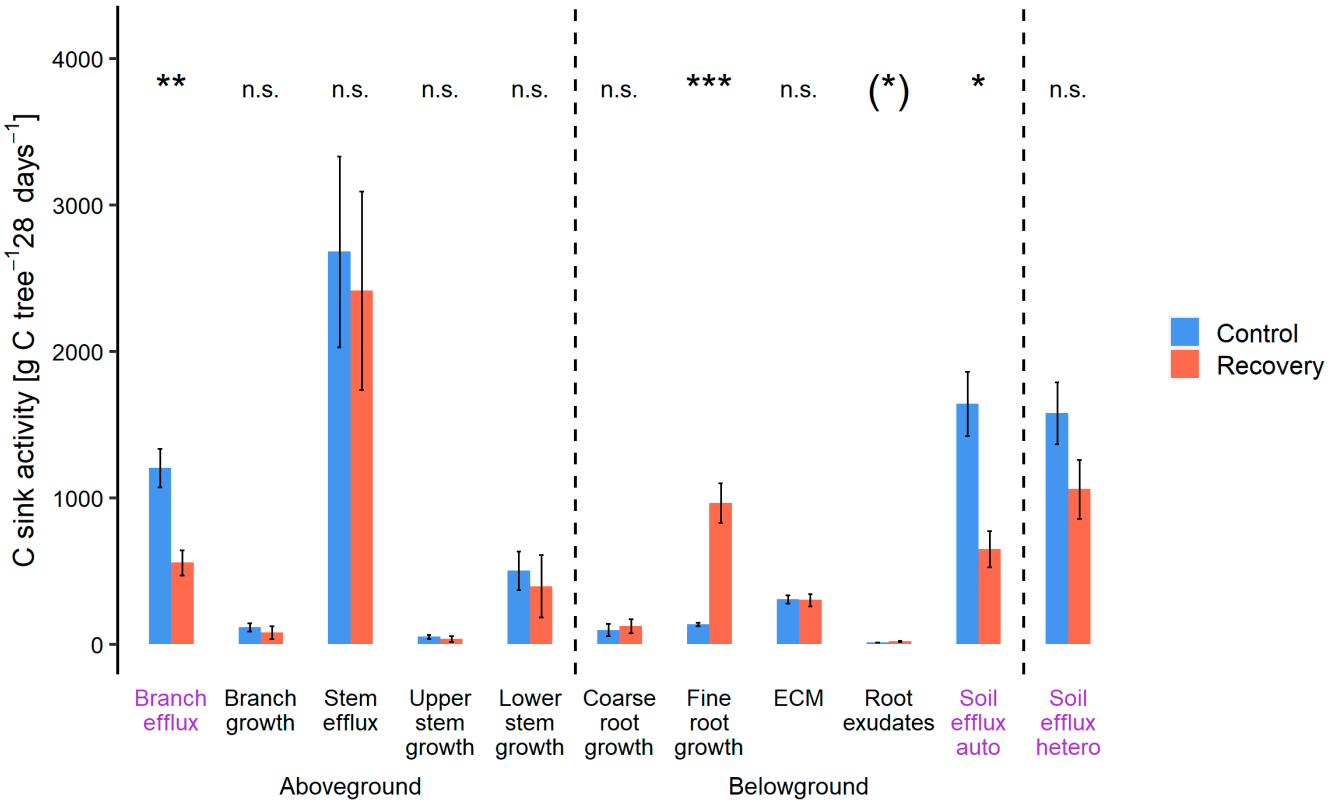


FIGURE 3 Total C sink activity (cumulative sum during 28 days after watering in g C tree^{-1} 28 days^{-1}) in each above- and belowground sink in four control and three recovering (previously drought-stressed) trees (mean ± SE): In branch CO_2 efflux, branch growth, stem CO_2 efflux, upper and lower stem growth, coarse-root growth, fine-root growth, ectomycorrhizae (ECM), root exudates, and soil CO_2 efflux (autotrophic and heterotrophic). C sinks which were (partly) not directly measured are marked with purple color. Asterisks indicate significant results based on *t*-tests comparing control and recovering trees, ***$p < .001$; **$p < .01$; *$p < .05$; (*), $p < .1$; n.s., not significant.

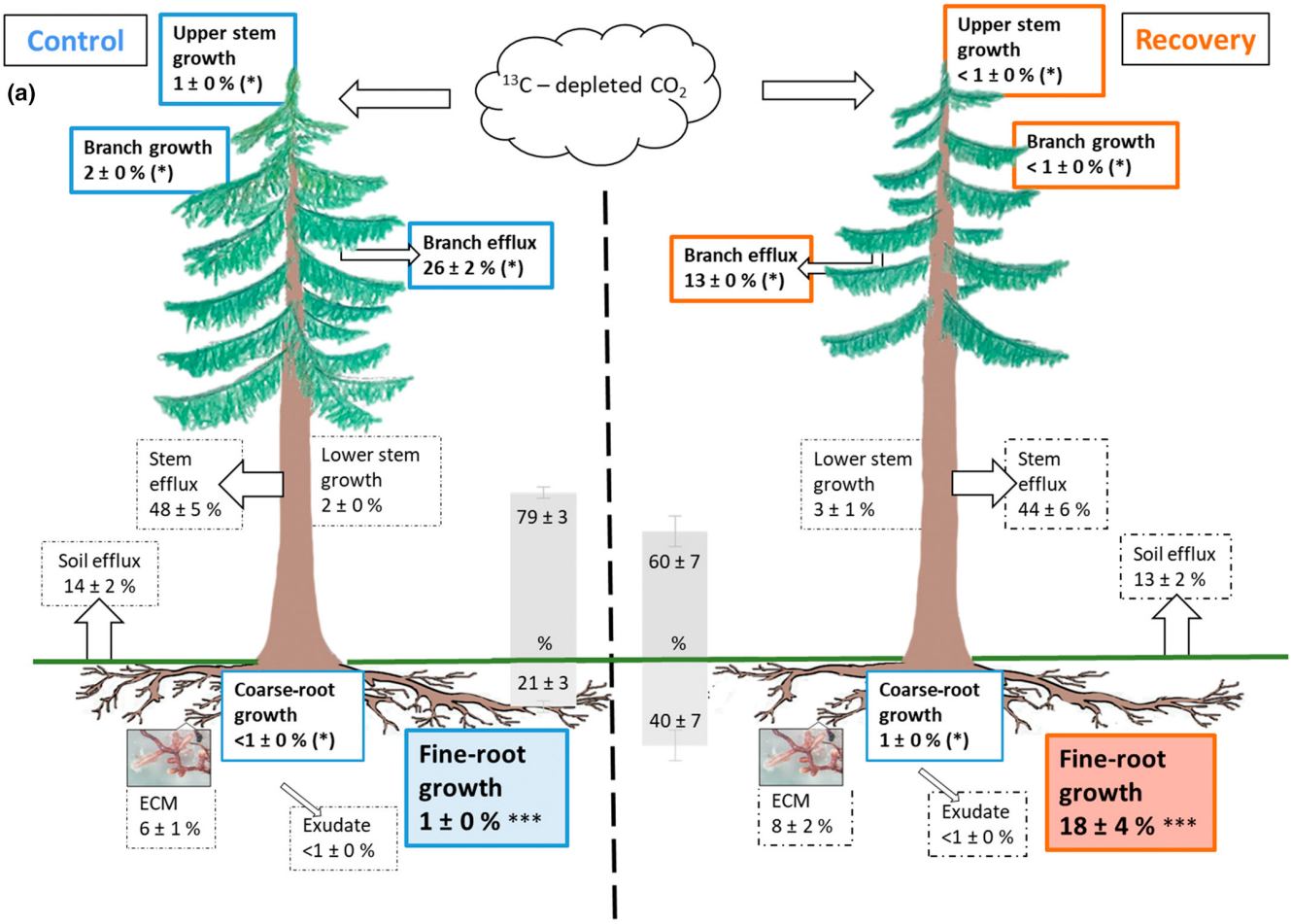
controls ($p < .1$) although it was very small with <20 g C in both treatments.

3.2 | Allocation of newly assimilated C (C_{new})

We calculated the cumulative sum of C_{new} allocated to each sink (in g C tree^{-1} 28 days^{-1}, Figure 4b) during the first 4 weeks after drought release, and the proportional allocation of C_{new} to the total C_{new} detected in the whole tree (in %, Figure 4a). At the whole-tree level, recovering trees tended to shift allocation towards belowground sinks (although not significant, $p = .14$, Figure 4a), that is, 60 ± 7% to aboveground and 40 ± 7% to belowground sinks, compared with control trees (79 ± 3% aboveground and 21 ± 3% belowground).

Recovering trees tended to allocate less C_{new} to branch CO_2 efflux with 317 ± 83 g ($p = .07$), to branch growth with 19 ± 13 g ($p = .15$), and to upper stem growth with 8 ± 6 g ($p = .17$), compared with control trees with 766 ± 145 g C, 52 ± 15 g C, and 23 ± 7 g C, respectively. Lower stem growth of recovering trees received 76 ± 44 g of C_{new}, which was similar to that of control trees with 66 ± 6 g C. Allocation to stem CO_2 efflux in recovering trees (1209 ± 439 g C) was slightly but insignificantly lower than that of control trees with 1557 ± 474 g C. Looking at the proportional allocation (Figure 4a), branch efflux, branch growth, and upper stem growth of recovering trees received 13 ± 0%, <1 ± 0%, and <1 ± 0% of total C_{new} detected, which all tended to be lower than that of control trees with 26 ± 2%, 2 ± 0%, and 1 ± 0%, respectively ($p < .1$). Proportional allocation to stem CO_2 efflux was also slightly but insignificantly lower in recovering (44 ± 6%) than in control trees (48 ± 5%).

Belowground, the most prominent difference between control and recovering trees was the allocation of C_{new} to growing fine-roots with 406 ± 57 g C in recovering and only 38 ± 3 g C in control trees ($p < .001$). This makes fine-root growth the major belowground sink for the allocation of C_{new} after drought release, representing 18 ± 4% of the total C_{new} detected in recovering trees (1 ± 0% in control trees, $p < .001$). In coarse-root growth, a strong tendency of a higher allocation ($p < .1$) was detected in recovering trees (20 ± 8 g C and proportional allocation of 1 ± 0%) compared with controls (4 ± 3 g C representing <1 ± 0%). Allocation to root exudates was also significantly higher ($p < .05$) in recovering trees with 17 ± 2 g C than in control controls with 7 ± 1 g C (but both <1%). In contrast, there was no significant difference in ECM (171 ± 24 g C and 8 ± 2% in recovering, 174 ± 16 g C and 6 ± 1% in control trees).


(a)
Control
Upper stem growth 1 ± 0 % (*)
Branch growth 2 ± 0 % (*)
Branch efflux 26 ± 2 % (*)
^{13}C – depleted CO_2
Recovery
Upper stem growth < 1 ± 0 % (*)
Branch growth < 1 ± 0 % (*)
Branch efflux 13 ± 0 % (*)
Stem efflux 48 ± 5 %
Lower stem growth 2 ± 0 %
Soil efflux 14 ± 2 %
79 ± 3 %
21 ± 3
60 ± 7 %
40 ± 7
Lower stem growth 3 ± 1 %
Stem efflux 44 ± 6 %
Soil efflux 13 ± 2 %
Coarse-root growth <1 ± 0 % (*)
Fine-root growth 1 ± 0 % ***
ECM 6 ± 1 %
Exudate <1 ± 0 %
Coarse-root growth 1 ± 0 % (*)
Fine-root growth 18 ± 4 % ***
ECM 8 ± 2 %
Exudate <1 ± 0 %

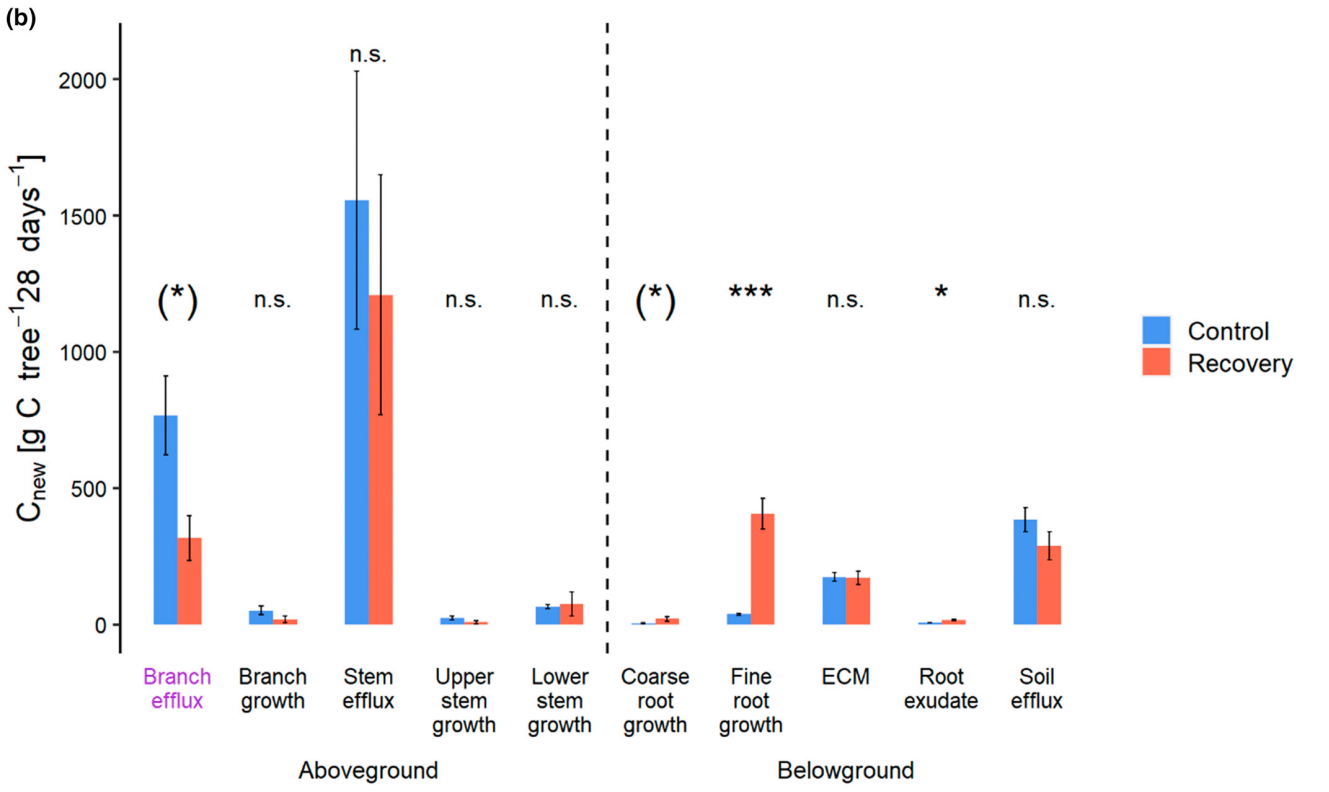

(b)
C_{new} [g C tree^{-1}28 days^{-1}]
2000
1500
1000
500
0
(*)
n.s.
n.s.
n.s.
n.s.
(*)
***
n.s.
*
n.s.
Control
Recovery
Branch efflux
Branch growth
Stem efflux
Upper stem growth
Lower stem growth
Coarse root growth
Fine root growth
ECM
Root exudate
Soil efflux
Aboveground
Belowground

FIGURE 4 (a) Proportional allocation of newly assimilated C (C_{new}) to total C_{new} detected and (b) amount of C_{new} (cumulative sum during 28 days after watering in g C tree^{-1} 28 days^{-1}) allocated to each above- and belowground sink in four control and three recovering (previously drought-stressed) trees, that is, branch CO_2 efflux, branch growth, stem CO_2 efflux, upper and lower stem growth, coarse-root growth, fine-root growth, ectomycorrhizae (ECM), root exudates, and autotrophic soil CO_2 efflux (mean ± SE). C sinks which were not directly measured in this study are marked with purple color. Asterisks give the results of *t*-tests or linear-mixed model comparing control and recovering trees, ***$p < .001$; *$p < .05$; (*), $p < .1$; n.s., not significant.

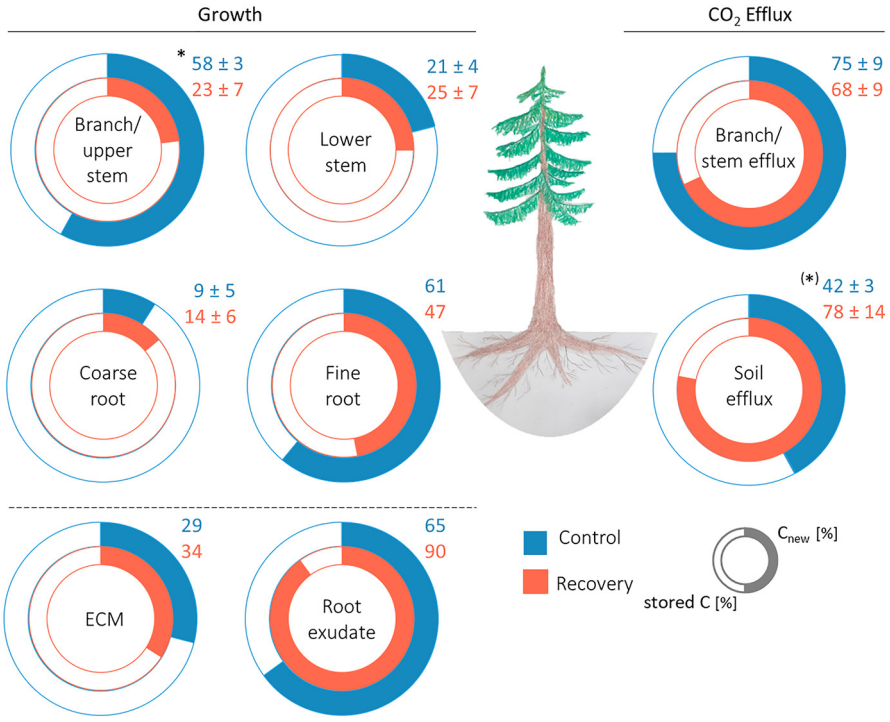


FIGURE 5 Contribution of newly assimilated C (C_{new}) to each C sink activity at the new isotopic equilibrium (contC_{new} in %) in each above- and belowground C sink, that is, stem and branch CO_2 efflux, branch and upper stem growth, lower stem growth, coarse-root growth, fine-root growth, ectomycorrhizae (ECM), root exudates, and autotrophic soil CO_2 efflux, in control and recovering (previously drought-stressed) trees. Numbers next to the charts give means ± SE of each treatment. Asterisk indicates a significant difference between control and recovering trees, *$p < .05$; (*), $p < .1$. For fine-root, ECM, and root exudate, there are no SE, since we pooled all samples for the calculation of contC_{new}. Statistical tests for these three sinks were thus not possible.

Allocation to soil CO_2 efflux was slightly but insignificantly lower in recovering trees (289 ± 51 g C, 13 ± 2%) compared with controls (384 ± 44 g, 14 ± 2%).

3.3 | Contribution of C_{new} to each C sink activity (contC_{new})

contC_{new} represents the contribution (in %) of C_{new} to meet the C sink activity (Figure 5). Belowground sinks with high C sink activity tended to show low contribution of C_{new}.

In aboveground sinks, C_{new} contributed to 23 ± 7% of the C sink activity of upper stem and branch growth in recovering trees, which was significantly lower ($p = .02$) compared with controls with 58 ± 3%. In other aboveground sinks of recovering trees, contC_{new} was similar between control and recovering trees.

In belowground sinks of recovering trees, C_{new} contributed to 47% of the fine-root growth, which was lower compared with control trees with 61%. In root exudates and autotrophic soil CO_2 efflux, contC_{new} tended to be higher in recovering trees with 90% and 78 ± 14% ($p = .08$), compared with controls with 65% and 42 ± 3%. Remaining belowground sinks showed similar contC_{new} between control and recovering trees.

4 | DISCUSSION

The present study elucidates the C sink activity and the allocation of C_{new} and stored C in mature Norway spruce upon drought release after 5 years of experimental summer drought. The recovering trees increased C sink activity of fine-root growth upon drought release, while that of aboveground growth and CO_2 efflux tended to be less (Figure 3), confirming H1 that belowground sink activity would increase with a parallel decrease aboveground. The high belowground C sink activity was supported by a preferential C_{new} allocation to the root system (Figure 4a,b), with a parallel decrease of C_{new} allocation aboveground, which is in line with H2: preferential allocation C_{new} belowground at the expense of aboveground sinks. contC_{new} to fine-root growth was lower in recovering trees compared with controls (Figure 5), which was driven by the high belowground C sink activity in recovering trees, confirming H3 that contribution of C_{new} would be lower under high sink activity. As a result, the preferential allocation of C_{new} to fine-roots was not sufficient to meet the increased C sink activity of these growing roots.

The broad measurement data set used here allowed for scaling from the organ to whole-tree level. Although a broad overview is gained, some uncertainties remain, in particular estimates of branch CO_2 efflux and partitioning of soil CO_2 efflux into autotrophic and

heterotrophic processes due to the lack of direct measurements. However, these uncertainties do not change the main conclusions of this study that enhanced fine-root growth was supported by both, C_{new} and stored C. For example for soil CO_2 efflux, the contribution of autotrophic respiration in control trees may be significantly lower than assumed (e.g. as low as 5%, Muhr & Borken, 2009), which would even reinforce our conclusions that recovering trees increased belowground sink activity compared with controls. Moreover, the contribution of autotrophic respiration might have decreased after drought release (Schindlbacher et al., 2012), but overall it cannot be lower than contC_{new} to total soil CO_2 efflux, that is, around 20%–36%. Within these boundaries, significance of the results do not change.

4.1 | Preferential allocation of C_{new} to enhanced fine-root growth after drought release

In control trees, majority of the aboveground C demand was found in the respiratory sinks. Small C demand and allocation of C_{new} to the aboveground growth in the control trees might be explained by seasonal variations (Arneth et al., 1998; DeLucia et al., 2007), as only 15%–20% of the annual radial growth occurred during the study period (data not shown). Compared with control trees, Norway spruce recovering from drought tended to show lower aboveground C sink activity (Figure 3). Similarly, these recovering trees tended to allocate less C_{new} to aboveground growth and CO_2 efflux (Figure 4b), and had a lower proportional allocation of C_{new} to aboveground (Figure 4a). A comparable decreased allocation of C_{new} to aboveground organs during drought recovery has also been observed in saplings of other tree species (Galiano et al., 2017; Hagedorn et al., 2016). The lower allocation of C_{new} to aboveground sinks likely resulted from reduced C sink activity aboveground as branch and stem growth had significantly decreased during drought (Pretzsch et al., 2020; Tomasella et al., 2018) and remained lower compared with controls 4 weeks after drought release (Figure 3). Before watering in early July, predawn leaf water potential of the recovering trees was c. −0.9 MPa (Grams et al., 2021), which is much higher than the water potential of −4 MPa that could cause a 50% loss of branch xylem conductivity determined for the same trees (Tomasella et al., 2018). Therefore, aboveground repair processes, which would increase the amount of C used for CO_2 efflux (Bucci et al., 2003; Secchi & Zwieniecki, 2011; Trugman et al., 2018; Zang et al., 2014), were unlikely to have played a significant role in the recovery of these trees. This is further supported by rates of stem CO_2 efflux of recovering trees after drought release (Hikino et al., 2022) which were unaffected. Accordingly, smaller growth and the lack of repair processes, both explain the lower C sink activity of aboveground respiratory sinks in recovering trees compared with controls (Figure 3).

Belowground, we observed a seven times greater C sink activity of fine-root growth in recovering trees after drought release compared with controls (Figure 3), which was supported by the preferential allocation of C_{new} to roots (Figure 4a,b). A strong reduction of fine-root growth was observed throughout the drought period (Nickel et al., 2018; Zwetsloot & Bauerle, 2021), corroborating the need to restore the essential functions of fine-roots for resource uptake (Bardgett et al., 2014; Germon et al., 2020; Solly et al., 2018). Thus, the faster transport of C_{new} to fine-root tips (Hikino et al., 2022) and the increased allocation of C_{new} both facilitated the fine-root growth upon drought release. C sink activity and the allocation of C_{new} to coarse-root growth also increased in recovering trees compared with controls (Figure 4a,b), likely supporting the increased fine-root growth and water transport (Zhang & Wang, 2015). Our findings are in agreement with Joseph et al. (2020) who reported that naturally drought-stressed mature pine trees invested more C_{new} into root biomass after rainfall compared with long-term irrigated trees, while the allocation of C_{new} to aboveground sinks was slightly lower. These findings support the optimal partitioning theory by Bloom et al. (1985) stating that plants allocate C to the organ which is responsible for the uptake of the limiting resource—in our case water, most likely along with dissolved nutrients (Gessler et al., 2017).

Ectomycorrhizae of recovering spruce trees showed a similar C sink activity (Figure 3) and similar allocation of C_{new} as control trees (Figure 4a,b). This is in contrast to young beech trees, which preferentially allocated newly assimilated C to ECM during recovery from drought (Hagedorn et al., 2016). Species-specific root traits particularly under and following drought most likely explain these contrasting C allocation patterns. Beech forms fine-roots with a short lifespan and sustains fine-root formation under drought (Nikolova et al., 2020; Zwetsloot & Bauerle, 2021). Beech ECMs, thus, need to be continuously formed resulting in fast C turnover and a high C sink activity of ECMs immediately after drought release (Hagedorn et al., 2016). In contrast, spruce trees with long-lived fine-roots and slow C turnover, show a temporal dormancy during drought by suberization and reduced growth to prevent resource loss (Nikolova et al., 2020). Our findings on unaffected C allocation to vital ECM on trees that experienced long-term drought are in accordance with previous results on sustained functionality of the ectomycorrhizal symbiosis under drought (Fuchslueger et al., 2014; Nickel et al., 2018). In addition, the lack of an increased C allocation to ECM may reflect an asynchrony between fast fine-root growth after watering with the supply of C_{new} from day 7 on (Hikino et al., 2022) and slower ECM formation (duration around 4 weeks, Ineichen & Wiemken, 1992) on newly grown roots. Therefore, we suggest that C allocation in newly formed ECM peaked later in spruce and was not captured during this 4-week study period.

Root exudation was a negligible C sink with less than 1% of total C sink activity (Figure 3) and of C_{new} (Figure 4a), thus similar to Mediterranean conifer saplings (Rog et al., 2021), but somewhat lower than in other natural forest stands with 2%–6% of total C_{new} (Abramoff & Finzi, 2016; Gougherty et al., 2018) and saplings with up to 30% of total C_{new} (Liese et al., 2018). Allocation of C_{new} to root exudates, which was already small during the drought period (approx. 1%–2%, Brunn et al., 2022), remained small after drought release. Furthermore, allocation in the recovering trees tended to be

higher than in the controls, which is consistent with findings during the drought phase (Brunn et al., 2022).

The increased C sink activity and allocation of C_{new} to root growth in the recovering trees was not reflected in soil CO_2 efflux, that is, lower soil CO_2 efflux rates (Figure 3) and lower allocation of C_{new} to autotrophic soil CO_2 efflux compared with control trees even after drought release (Figure 4a,b), despite the similar soil water content between treatments after drought release (Grams et al., 2021). Sun et al. (2020) state that maintenance respiration of spruce fine-roots accounts for 70% of the total respiration (maintenance and growth). Due to increased suberization during drought (Nikolova et al., 2020; Zwetsloot & Bauerle, 2021), root maintenance respiration was likely decreased (Barnard & Jorgensen, 1977). This reduction cannot be compensated by increased root-growth, which only accounts for 30% of the initial fine-root biomass (Table 2, fine-root length growth rate). This result also suggests that soil microbial activity, which was potentially reduced during drought (Nikolova et al., 2009), did not increase immediately after drought release as observed in other Norway spruce forests (Muhr & Borken, 2009; Schindlbacher et al., 2012). During repeated drought, the microbial communities might have adapted to drought conditions leading to a higher C use efficiency and thus reduces respiration with the number of repetitive droughts (Canarini et al., 2021; de Nijs et al., 2019; Evans & Wallenstein, 2012). Therefore, in contrast to previous studies on young beech and slow-growing, mature pine trees (Gao et al., 2021; Hagedorn et al., 2016; Joseph et al., 2020), we assume that microbial biomass did not receive an enhanced amount of C_{new} after drought release, which is supported by the low allocation of C_{new} to root exudates.

4.2 | Use of the stored C is essential for fine-root growth during recovery

Despite the preferential allocation of C_{new} to fine-root recovery, less than half of the increased fine-root growth in recovering trees was supported by C_{new} (Figure 5), which was lower than in control trees (61%) and what had been reported for other species (c. 75%; Lynch et al., 2013; Matamala et al., 2003). This suggests that the relative contribution of C_{new} decreases with high C sink activity belowground, which was also observed in autotrophic soil CO_2 efflux of controls (Figures 3 and 5). Likewise for coarse-root growth, around 86% of the present C was comprised of stored C (Figure 5), indicating the importance of stored C for root growth during drought recovery. Increased suberization and reduced respiration of fine-roots in recovery plots during drought (Nikolova et al., 2020; Zwetsloot & Bauerle, 2021) was accompanied by twice the starch concentration stored in these fine-roots before watering compared with the controls (data not shown). Reduction of these starch concentrations to the level of control trees within the first 7 days after watering indicates that they were most likely used for initial fine-root growth after drought release, which is similar to observations by Yang et al. (2016) in Chinese fir saplings. Lack of complete depletion might indicate an existence of regulation mechanism through enzymes degrading starch (Tsamir-Rimon et al., 2021). Furthermore, in addition to the starch conversion, reversal of osmotic potential in leaves (Hikino et al., 2022) and also in other organs likely released large amounts of osmolytes during first 4 weeks after watering, which became available for other C sinks (Tsamir-Rimon et al., 2021). Indeed, a reduced contC_{new} allocated to branches and upper stem growth in the recovering trees compared with controls might indicate a direct incorporation of C derived from the released osmolytes to sinks in the crowns, allowing C_{new} to bypass towards belowground sinks. C storage pools of the spruce trees (in leaves, branches, stem, and roots) had significantly decreased during the drought period (Hesse et al., 2021), and thus remobilized C from osmolytes also likely played a significant role as a C source.

5 | CONCLUSION

Restoring water uptake is crucial for long-term drought recovery of whole-tree functionality and preparation for upcoming drought periods. Following drought release, we found recovering spruce trees prioritized root growth by preferential allocation of new photoassimilates (i.e., C_{new}). The high belowground C sink activity was not entirely met by C_{new} and was largely subsidized by stored C. This highlights the role of both, the availability of C stores and the allocation of new photoassimilates to support repair and regrowth of functional tissues. It remains an open question whether (and how) the belowground C sink activity can be met over longer periods, even years, following drought release. Our findings also highlight the importance of belowground C sinks for analyses of post-drought growth increment and C stores of trees. If the altered C allocation towards belowground sinks persists in the following growing seasons, the drought effect on stem growth may remain for years. Thus, long-term observation of above- and belowground biomass partitioning is necessary to elucidate the longstanding consequences of altered C allocation upon drought release for forest productivity and C storage dynamics.

AUTHOR CONTRIBUTIONS

Thorsten E. E. Grams and Karin Pritsch originally designed the experiment. Kyohsuke Hikino, Vincent P. Riedel, and Thorsten E. E. Grams prepared and performed the ^{13}C labeling. Kyohsuke Hikino, Jasmin Danzberger, Vincent P. Riedel1, Benjamin D. Hesse, Benjamin D. Hafner, Timo Gebhardt, Romy Rehschuh, Nadine K. Ruehr, Melanie Brunn, Simon M. Landhäusser, Marco M. Lehmann, Thomas Rötzer, Franz Buegger, Fabian Weikl, Karin Pritsch, and Thorsten E. E. Grams collected and processed the samples/data. Kyohsuke Hikino and Jasmin Danzberger finalized the experimental design, analyzed and interpreted the data with supports from Thorsten E. E. Grams, Karin Pritsch, Benjamin D. Hesse, Benjamin D. Hafner, Franz Buegger, Fabian Weikl, Romy Rehschuh, Nadine K. Ruehr, Simon M. Landhäusser, Marco M. Lehmann, Timo Gebhardt, Thomas Rötzer,

Hans Pretzsch, and Taryn L. Bauerle. Kyohsuke Hikino and Jasmin Danzberger wrote the manuscript and all authors revised and edited the manuscript. Kyohsuke Hikino and Jasmin Danzberger contributed equally.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in mediaTUM (doi: 10.14459/2022mp1663853).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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