

23. P. L. Munday, R. R. Warner, K. Monro, J. M. Pandolfi, D. J. Marshall, *Ecol. Lett.* **16**, 1488–1500 (2013).
 24. B. M. Riegl, S. J. Purkis, A. S. Al-Cibahy, M. A. Abdel-Moati, O. Hoegh-Guldberg, *PLOS One* **6**, e24802 (2011).

ACKNOWLEDGMENTS

The authors thank the following funding bodies: Australian Research Council Discovery Program grant DP130101421 (awarded to W.L. and T.D.A.); Australian Research Council Super Science Program grant FS110200046 (awarded to Terry P. Hughes, Director, Australian Research Council Centre of Excellence for Coral Reef Studies); Australian Research Council Centre of Excellence for Coral Reef Studies grant CE0561435; the Great Barrier Reef Foundation (Coral Health Grant); the NOAA National Environmental Satellite, Data, and Information Service; and the NOAA Coral Reef Conservation Program. The authors thank N. Wolff for providing SST projections and help in analysis of

ecosystem model components and M. De Freitas Prazeres for cell counts. The contents in this manuscript are solely the opinions of the authors and do not constitute a statement of policy, decision, or position on behalf of NOAA or the U.S. government. T.D.A., S.F.H., J.C.O., and W.L. designed the study. T.D.A., D.O., and W.L. conducted experimental procedures and physiological analyses. S.F.H. and C.M.E. conducted SST and oceanographic analyses. J.C.O. and P.J.M. conducted predictive modeling and model validation. T.D.A., S.F.H., J.C.O., P.J.M., A.G., C.M.E., and W.L. wrote and finalized the manuscript. Code for the analysis of SST data is available through contact and collaboration with S. Heron (scott.heron@noaa.gov). Code for the ecosystem model is available through contact and collaboration with J.-C. Ortiz (j.ortiz@uq.edu.au). The NOAA data and code are available from a dedicated web page: http://coralreefwatch.noaa.gov/publications/AinsworthEtAl_2016.php. All data and code are available at FigShare project number 12040: Ecosystems

model code and scripts (DOI 10.6084/m9.figshare.3081127); Bleaching on the GBR data release (DOI 10.6084/m9.figshare.3081127); Physiology and gene expression data (DOI 10.6084/m9.figshare.3081064). D.O. is currently employed by Boehringer Ingelheim, Fremont, CA. The authors declare no competing financial interests.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/352/6283/338/suppl/DC1
 Materials and Methods
 Supplementary Text
 Figs. S1 to S8
 Tables S1 to S8

10 September 2015; accepted 10 March 2016
 10.1126/science.aac7125

FOREST ECOLOGY

Belowground carbon trade among tall trees in a temperate forest

Tamir Klein,^{1,*} Rolf T. W. Siegwolf,² Christian Körner¹

Forest trees compete for light and soil resources, but photoassimilates, once produced in the foliage, are not considered to be exchanged between individuals. Applying stable carbon isotope labeling at the canopy scale, we show that carbon assimilated by 40-meter-tall spruce is traded over to neighboring beech, larch, and pine via overlapping root spheres. Isotope mixing signals indicate that the interspecific, bidirectional transfer, assisted by common ectomycorrhiza networks, accounted for 40% of the fine root carbon (about 280 kilograms per hectare per year tree-to-tree transfer). Although competition for resources is commonly considered as the dominant tree-to-tree interaction in forests, trees may interact in more complex ways, including substantial carbon exchange.

Stable carbon isotope labeling at the canopy scale is a powerful tool for tracing carbon allocation in forest ecosystems (1, 2). In a dense forest, large quantities of photoassimilates may be exported to mycorrhiza and rhizosphere microbes (3–11), and hyphae of mycorrhizal fungi can form “underground highways” for carbon and nutrient exchange with and between plants (9). It has been suggested that because of the unpredictability of disturbance events and the divergence of responses among plant communities, mycorrhizal fungi and their host plant species are under selective pressure to evolve generality (9, 10). The groups of plants that are interlinked through a common mycorrhizal network are hence termed “guilds” (10). The identity and ensemble of fungal species may affect plant community structure and ecosystem productivity (12, 13), with mycorrhiza improving plant fitness by increasing phosphorus and nitrogen uptake (14). As a result, mycorrhizal networks are considered an integral

part of the autotrophic system (15, 16) and are essential components in ecosystem resilience to change. Yet, these benefits have traditionally been studied from a nutrient supply perspective, and the mycorrhiza “pipeline” was never shown to transfer considerable amounts (>1 g) of mobile carbon compounds among trees (4–10). In addition to mycorrhizal networks, carbon can be transferred through natural root grafts, which are anatomical fusions between two or more roots. Growth of interconnected trees in situ can be affected directly by the presence of root grafts—for example, by translocation of water and carbohydrates (17). Transport across root grafts has been demonstrated in numerous field studies using various methods, from dye injection to the use of radioactive tracers (18, 19), but these grafts are restricted to trees of the same species or, at most, of phylogenetically closely related species (17–20).

Using a tall canopy crane (1, 2), we continuously labeled five 40-m-tall Norway spruce trees (*Picea abies*) as part of a 5-year free-air CO₂ enrichment experiment (FACE) in a mixed forest in northwest Switzerland (3, 21, 22) (figs. S1 to S7). Five unlabeled *Picea* trees served as controls (fig. S8). We then measured $\delta^{13}\text{C}$ from “tip to toe,” including canopy twigs, stems, and fine roots of labeled and unlabeled individuals of *Picea* and of neighboring trees belonging to different taxa (*Fagus sylvatica*, *Pinus sylvestris*, and *Larix decidua*).

Except for the five labeled *Picea*, none of the trees were exposed to CO₂ labeling. Using industrial, ¹³C-depleted CO₂ gas, our canopy labeling made the $\delta^{13}\text{C}$ signal of labeled trees more negative by 5.3 per mil (‰) compared to unlabeled control trees: Twig $\delta^{13}\text{C}$ was –31.4‰ in labeled and –26.1‰ in unlabeled *Picea* (Fig. 1). New fine roots of labeled *Picea*, isolated from 90 ingrowth cores (figs. S9 and S10) had 2.6‰ lower $\delta^{13}\text{C}$ values than the control trees growing in ambient air (no ¹³C label) (Fig. 1). Almost the same isotopic signal was found among fine roots of similarly tall nonconspicuous trees in the neighborhood that were unlabeled and contributed about half of the fine roots recovered from ingrowth cores (Fig. 2A). To validate that fine roots of the other taxa were not confused with those of *Picea*, we excavated roots from *Picea* (control and labeled) and neighboring tree species and traced them to the trunk of origin (figs. S12 to S14). Again, fine roots of these non-*Picea* taxa showed a ¹³C signal similar to that of their neighboring *Picea* (either control or labeled) but jointly at a 2.6‰ less negative level when ¹³C-labeled *Picea* was present (Fig. 2B). Hence, both the root-ingrowth-core data (with multiple individuals’ input) and the data for intact root systems from three individuals belonging to three different tree genera yielded the same signals. Sapwood $\delta^{13}\text{C}$ of the 2010 to 2014 annual rings in stem cores taken at breast height from neighboring and nonneighboring non-*Picea* trees was –27.8 ± 0.1‰ and –26.9 ± 0.1‰, respectively—still a significant difference ($P = 0.019$).

Because our FACE system operated in the canopy only (20 to 40 m aboveground), tank CO₂, and thus the ¹³C label, were not present in the understory. This was ascertained first by ¹³C signals in understory plants, which are exclusively vesicular-arbuscular mycorrhizal: *Paris quadrifolia*, *Mercurialis perennis*, and *Rubus fruticosus*. $\delta^{13}\text{C}$ values in rhizomes/root stocks from these three species growing under both unlabeled and labeled *Picea* showed the typical, very negative signals for deep shade plants (from –30.2 to –34.5‰) (fig. S15). Besides differences among species, however, there was absolutely no signal difference between samples collected under unlabeled and labeled *Picea* and no difference between years. Second, we checked the canopy crowns of the trees neighboring the labeled *Picea* individuals for traces

¹Institute of Botany, University of Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland. ²Laboratory of Atmospheric Chemistry, Ecosystems Fluxes Research Group, Paul Scherrer Institute, PSI, 5323 Villigen, Switzerland.

*Corresponding author. E-mail: tamir.klein@unibas.ch †Present address: Institute of Soil, Water, and Environmental Sciences, Agricultural Research Organization Volcani Center, Beit Dagan 50250, Israel.

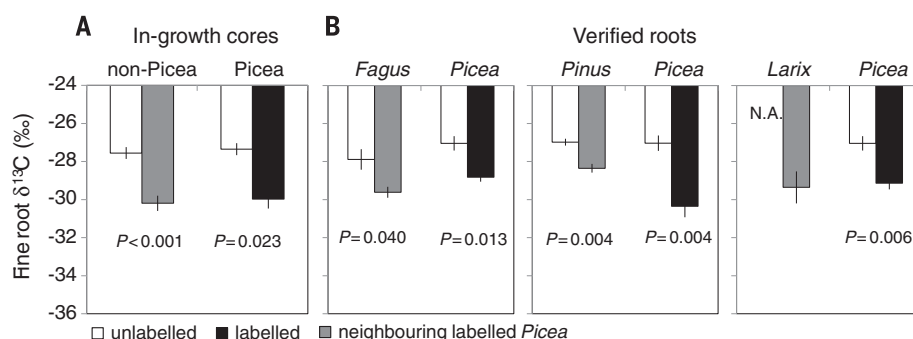
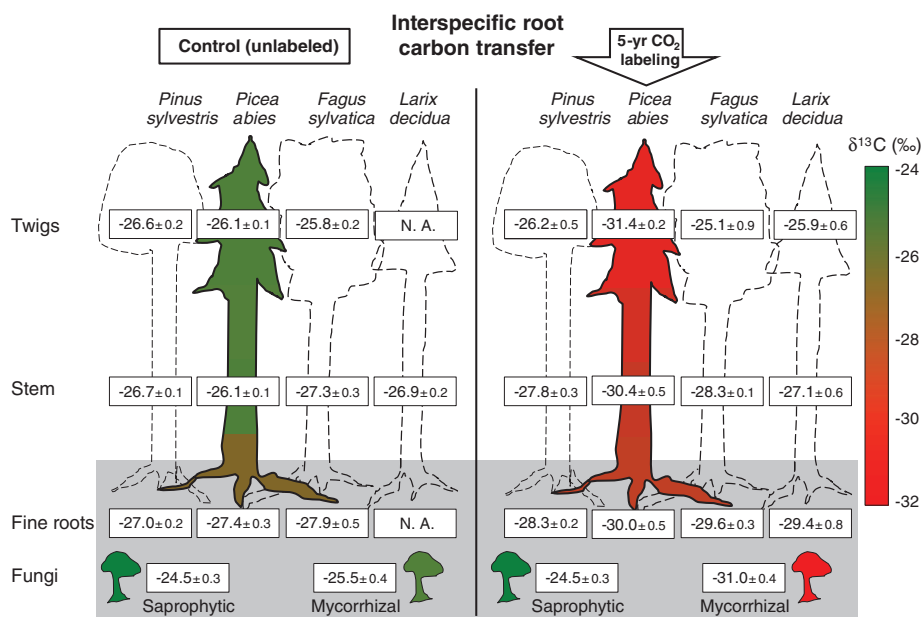


Fig. 1. Transfer of carbon from labeled spruce to fine roots of neighboring nonspruce trees. $\delta^{13}\text{C}$ gradients (means \pm SE; $N = 4$ to 5 samples from 1 to 5 trees) within tree compartments and fungal sporocarps in the studied mixed forest stand near Basel, Switzerland. The use of industrial, ^{13}C -depleted CO_2 gas for the FACE allowed for identifying carbon allocation in and from spruce trees exposed to labeled CO_2 ($\delta^{13}\text{C} \leq -30.0\text{‰}$), compared with other carbon in wood and fungi ($\delta^{13}\text{C} > -27.5\text{‰}$). Linear gradients were assumed between measurement points.

of ^{13}C label in 2-year old high-canopy twigs from all four compass directions in each crown. No influence of the ^{13}C label could be found. $\delta^{13}\text{C}$ in twig xylem of *Picea* was $-26.1 \pm 0.1\text{‰}$ and $-31.4 \pm 1.1\text{‰}$ in unlabeled and labeled trees, respectively. In twig xylems of the three neighboring tree species (*Fagus*, *Pinus*, and *Larix*), $\delta^{13}\text{C}$ was -25.1 ± 0.9 , -26.2 ± 0.5 , and $-25.9 \pm 0.6\text{‰}$, respectively, as previously observed in these trees (23). Only in twigs sampled in the small crown fraction immediately next to the crowns of the labeled *Picea* (<20% of the crown circumference), $\delta^{13}\text{C}$ was slightly lowered compared with the aforementioned values (-28.1 , -29.2 , and -28.8 in twigs of *Fagus*, *Pinus*, and *Larix*, respectively). The remainder of the crown periphery and the crown center showed no label, and hence the overall crown volume that was slightly influenced by the isotope label was <10%. Moreover, the $\delta^{13}\text{C}$ values in those proximal twigs were still 2.2 to 3.3‰ above those in the labeled *Picea* twigs.

The tree-to-tree transfer of labeled carbon was so strong in this study that roots of different tree taxa (of which only *Picea* was labeled) shared an

almost similar isotopic signature: -30.0‰ and -29.1‰ in labeled and neighbor trees, respectively (Fig. 1). The decrease in $\delta^{13}\text{C}$ of unlabeled neighbor roots, and the parallel increase in $\delta^{13}\text{C}$ of labeled roots relative to their source tissues (Fig. 1), indicate a bidirectional carbon exchange. To estimate the direction and magnitude of the carbon exchange, we compared the aforementioned $\delta^{13}\text{C}$ values with those prevailing without any labeled carbon transfer ("baseline" signatures). We then applied a simple carbon isotope mixing calculation between roots of labeled and neighbor trees using the equation $a \times n + (100 - a) \times m = p$, where a is the contribution of one of two sources to a mixture (in %), n is its isotopic signature, m is the isotopic signature of the other source, and p that of the mixed product. In the neighbor roots, the $\delta^{13}\text{C}$ value of -29.1‰ reflects a decrease by 1.7‰ from a mean baseline value of -27.4‰ observed in roots of the same tree species growing around unlabeled *Picea* (Fig. 1). However, a baseline signature in the labeled *Picea* roots is harder to estimate, because we had no reference observation of labeled *Picea* that did not exchange

carbon with non-*Picea* neighbors. To this mixing, one must add an intrinsic dilution by the contribution of older, unlabeled carbon to current fine root growth (3, 24). We do know that in control *Picea*, $\delta^{13}\text{C}$ of roots was 1.3‰ more negative than that of the canopy twigs (Fig. 1) (a common observation), and hence a premixed baseline for the labeled *Picea* root would be -32.7‰ (-31.4 minus 1.3‰). Thus, our isotope mixing calculation had to solve for a mixing ratio that would satisfy (i) a 2.7‰ increase in the labeled *Picea* root signal (-30.0 minus -32.7‰); (ii) a 1.7‰ decrease in the neighbor root signal; and account for (iii) the intrinsic dilution ratio with old stored carbon. We found that a 20% contribution of older, unlabeled carbon to current fine-root growth of labeled *Picea*, and an isotope-mixing ratio of 60% self and 40% exchanged carbon between fine roots of labeled and unlabeled trees, satisfied the ^{13}C signal changes at both sides of the transfer (Fig. 3).

The magnitude of the exchange can be estimated: *Picea* fine-root biomass production estimated from our ingrowth cores (II) was $60 \text{ g m}^{-2} \text{ a}^{-1}$

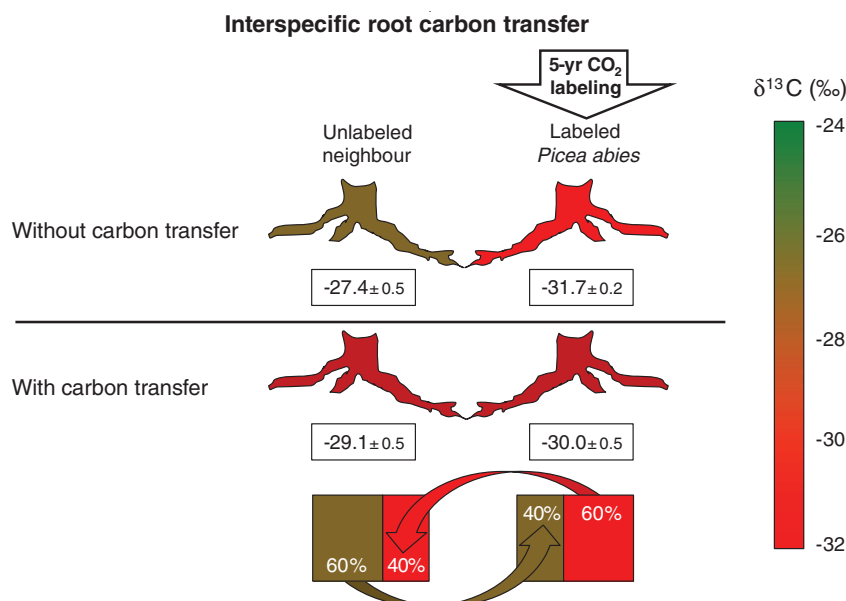


Fig. 3. Bidirectional root carbon transfer between mature forest trees. Estimation of the magnitude of the interspecific root carbon exchange in the studied mixed forest stand based on the observed $\delta^{13}\text{C}$ values. An isotope mixing ratio of 60% self and 40% exchanged carbon between fine roots of labeled and unlabeled trees satisfies the ^{13}C signals in both.

at 1- to 12-cm depth, upscaled linearly to $150 \text{ g m}^{-2} \text{ a}^{-1}$ for the entire 30-cm soil profile. Assuming an average root carbon concentration of 46%, this corresponds to a fine-root production of $69 \text{ g carbon m}^{-2} \text{ a}^{-1}$. If 40% of this fine-root carbon came from an exchange via mycorrhiza, this carbon transfer flux equals $28 \text{ g carbon m}^{-2} \text{ a}^{-1}$ —i.e., $280 \text{ kg ha}^{-1} \text{ a}^{-1}$, which is equivalent to 4% of the forest net carbon uptake (net primary production).

The carbon transfer that we observed most likely occurred through common ectomycorrhizal networks, which are very abundant at this site (table S1), and also exhibited the labeled carbon in their “fruit” bodies near labeled *Picea* (3) and are a substantial carbon sink in Norway spruce forests (16). Host specificity is a known trait among ectomycorrhizal taxa, yet common networks and the formation of trophic guilds play a crucial role in forest dynamics (25). For example, in a mixed Central European forest, 75 ectomycorrhizal taxa were identified on *Fagus sylvatica* roots (26); 29% and 10% of the ectomycorrhizal species were shared with one or two other tree species, respectively; however, it is noteworthy that the 61% host-specific ectomycorrhizal species colonized only 20% of the root tips (24). The ectomycorrhizal species *Russula ochroleuca* (Pers.) has been previously identified on roots of all four tree species studied here (27), and a *Russula* species was identified in our forest site (table S1). A taxonomic search in the ectomycorrhizal database (www.deemy.de) (28) revealed three other genera found at our site that are common symbionts to our four study tree species—namely, *Cortinarius*, *Lactarius*, and *Tricholoma*.

Our earlier study on this site (3) also showed zero $\delta^{13}\text{C}$ labeling in saprophytic fungi (Fig. 1) and decreasing mycorrhizal $\delta^{13}\text{C}$ with decreasing

distance from the labeled *Picea*. Our results indicate a bidirectional carbon exchange (Fig. 3) rather than a one-way transfer (17), which is not along a demand-supply gradient as previously reported (10, 17). Considering that all studied trees were dominant, healthy, and tall individuals, growing without obvious carbon limitation, no a priori source-sink gradients might be expected here (29). It has been suggested that carbon transfer between trees via mycorrhiza is rather regulated to satisfy the needs of the mycorrhiza itself (7). In our case, it is still possible that labeled *Picea* transferred excess carbon belowground (3) and, in turn, enhanced mycorrhizal activity and proliferation.

The mild, yet significant increase in sapwood $\delta^{13}\text{C}$ at the base of trees neighboring the labeled *Picea* (Fig. 1) indicates slight aboveground allocation of imported carbon. So far, root carbon uptake was shown in “green-to-ground” corn and in willow cuttings using labeled carbonate ($\text{NaH}^{14}\text{CO}_3$ and $\text{H}^{13}\text{CO}_3^-$) (31), as well as in pine seedlings (30), but not in mature trees in the field.

Finally, the observed interspecific carbon transfer among tall trees in our study can become increasingly important for forests under stress conditions (e.g., drought or spring frost) or after disturbance such as wildfire, when divergence in species’ responses come into play (5–10, 14, 20, 23). The magnitude, direction, and control of these transfer fluxes and their importance are yet to be resolved, and they add a new dimension and level of complexity to known ecosystem processes.

REFERENCES AND NOTES

- S. Pepin, C. Körner, *Oecologia* **133**, 1–9 (2002).
- C. Körner et al., *Science* **309**, 1360–1362 (2005).
- M. Mildner, M. K. F. Bader, S. Leuzinger, R. T. W. Siegwolf, C. Körner, *Oecologia* **175**, 747–762 (2014).

- M. C. Hirrel, J. W. Gerdemann, *New Phytol.* **83**, 731–738 (1979).
- R. Francis, D. J. Read, *Nature* **307**, 53–56 (1984).
- C. P. P. Reid, F. W. Woods, *Ecology* **50**, 179–187 (1969).
- A. H. Fitter, J. D. Graves, N. K. Watkins, D. Robinson, C. Scrimgeour, *Funct. Ecol.* **12**, 406–412 (1998).
- D. Robinson, A. Fitter, *J. Exp. Bot.* **50**, 9–13 (1999).
- D. A. Perry, T. Bell, M. P. Amaranthus, in *The Ecology of Mixed-Species Stands of Trees*, M. G. R. Cannell, D. C. Malcolm, P. A. Robertson, Eds. (Blackwell, Oxford, 1992), pp. 151–179.
- S. W. Simard et al., *Nature* **388**, 579–582 (1997).
- P. Högberg et al., *New Phytol.* **177**, 220–228 (2008).
- M. G. van der Heijden, T. Boller, A. Wiemken, I. R. Sanders, *Ecology* **79**, 2082–2091 (1998).
- M. G. van der Heijden et al., *Nature* **396**, 69–72 (1998).
- N. C. Johnson, G. W. Wilson, M. A. Bowker, J. A. Wilson, R. M. Miller, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2093–2098 (2010).
- N. A. Hynson, S. Mambelli, A. S. Amend, T. E. Dawson, *Oecologia* **169**, 307–317 (2012).
- H. Wallander, A. Ekblad, J. Bergh, *For. Ecol. Manage.* **262**, 999–1007 (2011).
- E. C. Fraser, V. J. Lieffers, S. M. Landhäusser, *Tree Physiol.* **26**, 1019–1023 (2006).
- B. F. Graham, *Ecology* **41**, 56–64 (1960).
- F. W. Woods, K. Brock, *Ecology* **45**, 886–889 (1964).
- B. F. Graham, F. H. Bormann, *Bot. Rev.* **32**, 255–292 (1966).
- M. Mildner, M. K. F. Bader, C. Baumann, C. Körner, *Biogeochemistry* **124**, 95–111 (2015).
- Materials and methods are available as supplementary materials on Science Online.
- V. S. Chevillat, R. T. W. Siegwolf, S. Pepin, C. Körner, *Basic Appl. Ecol.* **6**, 519–534 (2005).
- R. Vargas, S. E. Trumbore, M. F. Allen, *New Phytol.* **182**, 710–718 (2009).
- E. Bent, P. Kiekel, R. Brenton, D. L. Taylor, *Appl. Environ. Microbiol.* **77**, 3351–3359 (2011).
- C. Lang, J. Seven, A. Polle, *Mycorrhiza* **21**, 297–308 (2011).
- A. Pillukat, R. Agerer, *Z. Mykol.* **58**, 211–242 (1992).
- R. Agerer, G. Rambold, DEEMY: An Information System for Characterization and Determination of Ectomycorrhizae [first posted 2004-06-01; most recent update: 2011-01-10] (Munich, 2004); www.deemy.de.
- C. Körner, *J. Ecol.* **91**, 4–17 (2003).
- C. R. Ford, N. Wurzbarger, R. L. Hendrick, R. O. Teskey, *Tree Physiol.* **27**, 375–383 (2007).
- D. M. Matarese, thesis, Portland State University, Oregon (2011).

ACKNOWLEDGMENTS

Research at the Swiss canopy crane site was funded by the Swiss National Fund project FORCARB (31003A_14753/1 to C.K.). T.K. was cofunded by the Plant Fellows program of the Zürich-Basel Plant Science Center (PSC) through the EU FP7 Marie Curie action. We thank J. Grünzweig (Hebrew University of Jerusalem, Israel) and R. Milo (Weizmann Institute of Science, Israel) for providing comments on an earlier version of the paper; M. Saurer and L. Schmid at the Paul Scherrer Institute for stable isotope analyses; S. G. Keel, R. Keller, and M. Wilhelm for collection and taxonomic classification of mycorrhizal fungi; E. Amstutz and L. Rizzelli for crane operation; and G. Grun for electronics and CO₂ control. Data showing the experimental set-up, mycorrhiza species list, supplementary figs. S1 to S15, and materials and methods are available in the supplementary materials. The authors declare no conflict of interest and that there are no material transfer agreements or patent applications involved in the study. Author contributions: C.K. designed the experiment, T.K. initiated the fine-root study, C.K. and T.K. sampled the plant materials, and R.T.W.S. did the isotope analyses. All authors wrote the paper jointly.

SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/352/6283/342/suppl/DC1
Materials and Methods
SupplementaryText
Figs. S1 to S15
Table S1
References

11 October 2015; accepted 2 March 2016
10.1126/science.aad6188



Belowground carbon trade among tall trees in a temperate forest

Tamir Klein, Rolf T. W. Siegwolf and Christian Körner (April 14, 2016)

Science Translational Medicine **352** (6283), 342-344. [doi: 10.1126/science.aad6188]

Editor's Summary

Carbon trading between adult trees

Competition between individual plants for resources is well known, but sharing of resources may also occur. Klein *et al.* observed tree-to-tree carbon shuttling between roots of tall trees in a mixed temperate forest in Switzerland (see the Perspective by van der Heijden). By applying stable carbon isotope labeling to individual tree canopies, they show that up to 40% of the carbon in the fine roots of one individual may be derived from photosynthetic products of a neighbor. Carbon transfer of this kind, mediated by plant-associated fungi, or mycorrhizae, in the soil, has been reported on a smaller scale in seedlings, but not before in trees.

Science, this issue p. 342; see also p. 290

This copy is for your personal, non-commercial use only.

Article Tools

Visit the online version of this article to access the personalization and article tools:

<http://science.sciencemag.org/content/352/6283/342>

Permissions

Obtain information about reproducing this article:

<http://www.sciencemag.org/about/permissions.dtl>

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright 2016 by the American Association for the Advancement of Science; all rights reserved. The title *Science* is a registered trademark of AAAS.