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REGULAR ARTICLE

Effects of soil nitrogen availability on rhizodeposition in plants: a review

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Abstract
Background Soil contains the majority of terrestrial carbon (C), forming the foundation for soil fertility and nutrient cycling. One key source of soil C is root-derived C, or rhizodeposits, which signal and sustain microbes that cycle nutrients such as nitrogen (N). Although N availability can affect rhizodeposition both quantitatively and qualitatively, these effects remain poorly understood due to conflicting results among studies.
Scope Here, we review studies examining the influence of soil N availability on rhizodeposition. We conduct a quantitative analysis of the response of various rhizodeposition C pools to N availability, and assess methodological aspects potentially underlying the highly variable results among studies. We also review impacts of N availability on the composition and quality of rhizodeposits.
Conclusions Effects of N on rhizodeposition were strongly dependent upon the specific C pools considered and the units for reporting those pools. N additions increased nearly all rhizodeposit C pools when expressed on a per plant basis, and decreased rhizodeposition per unit fixed C for several C pools, while no rhizodeposition C pools were significantly altered when expressed per unit root mass. Nevertheless, N effects were generally mixed due to a combination of variation in experimental methods and species-specific responses. Overall, our review indicates several key challenges for better understanding the mechanistic links between N availability, plant physiology, and microbial function. Identifying such links would substantially improve our ability to predict C- and N-dynamics in changing ecosystems.

Keywords Isotope labeling · Nutrient cycling · Root-derived carbon inputs · Root exudation

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Introduction

Soil contains the majority of carbon (C) in the terrestrial biosphere, providing the foundation for soil fertility and nutrient cycling (Schimel 1995; Schlesinger and Andrews 2000). Plants are the major source of C inputs into soil, contributing C through litterfall and whole-plant senescence, as well as root-derived C losses from living plants. These root-derived C inputs, or rhizodeposits, constitute

approximately 0.5–10% of net fixed C (Farrar et al. 2003), with some estimates as high as 40% when root respiration and microbially-respired rhizodeposits are included (Lynch and Whipps 1990; Jones et al. 2009). Although specific definitions in the literature are diverse (Wichern et al. 2008), rhizodeposits can be broadly defined to include passively-released low molecular weight compounds (root exudates), active secretions such as secondary metabolites, proteins, or mucilage, gaseous compounds such as root-respired CO_2, sloughed root cap and border cells, and senesced root tissue (Uren 2001). Once released into the soil, organic C in rhizodeposits can then serve as a substrate for microbial growth and metabolism at the root-soil interface (Lynch and Whipps 1990; Hütsch et al. 2002), affecting both soil C sequestration and organic matter turnover (Schenck Zu Schweinsberg-Mickan et al. 2012). Thus, rhizodeposition is considered an important component of the feedback loop in which plants use nutrients to assimilate atmospheric C, and microbes use the assimilated C to power nutrient transformations in soil (Saggar et al. 1997; Jackson et al. 2008; Meier et al. 2017).

Nitrogen (N) is one of the most commonly limiting nutrients for plant productivity worldwide (Vitousek and Howarth 1991; Lebauer and Treseder 2014). Given the dependence of the N cycle on microbial transformations in soil, plant rhizodeposition is generally expected to play an important role in mediating soil N availability (Rovira 1965; Clarholm 1985; Biondini et al. 1988; Robinson et al. 1989; Qian et al. 1997; Paterson 2003; Bürgmann et al. 2005; Phillips et al. 2011; Finzi et al. 2015). In turn, N availability can influence plant rhizodeposition both quantitatively and qualitatively, altering the substrates available to microbes and further modifying nutrient transformations in soil. However, fertility-induced changes in plant rhizodeposition remain poorly understood (Aitkenhead-Peterson and Kalbitz 2005; Henry et al. 2005; Baptist et al. 2015; Ge et al. 2015; Gschwendtner et al. 2016), given the conflicting results (Zagal et al. 1993; Henry et al. 2005; Phillips et al. 2009) and variation in methodological approaches among studies (Johansson 1992; Darwent et al. 2003; Baptist et al. 2015).

This is a key point, considering recent global shifts in N deposition (Vitousek et al. 1997), an ongoing transition in agricultural practices towards precision fertilization and organic farming (Paterson 2003), and attempts to intervene in the N cycle through engineering enhanced N-fixing symbioses as well as interactions with other plant growth-promoting rhizobacteria (Geddes et al. 2015; Pii et al. 2015; Mus et al. 2016), all of which have uncertain effects on plant-soil C dynamics.

Here, we review studies examining the influence of soil N availability on rhizodeposition (i.e. root-derived C inputs to soils). Although numerous studies have investigated the impacts of N on overall soil C accrual and cycling (e.g., Neff et al. 2002; Khan et al. 2007; Tiemann and Billings 2011), here we specifically focus on studies in which these soil C flows can be directly attributed to root-derived C inputs in order to better understand the mechanisms underlying overall soil C dynamics. We first review the pools of C attributed to rhizodeposition and the methods by which those pools are measured. Next, we conduct a quantitative analysis of the response of rhizodeposition C pools to N availability in soil using data from a wide variety of species and experimental methodologies, and discuss factors which may underlie the wide variation in N effects among studies. We also review impacts of N availability on the composition and quality of rhizodeposits, and conclude with an assessment of outstanding questions and promising avenues for future research.

Root-derived C inputs: Methods for quantification and units of measurement

Before considering the effects of N on rhizodeposition, or root-derived C inputs, it is important to first consider the C inputs themselves and the methods by which they are measured. Of the total C fixed by plants, between 20 and 60% is translocated to the root system (Lynch and Whipps 1990; Kuzyakov and Domanski 2000). Up to a third of that root-translocated C is then lost to the soil through rhizodeposition of organic C (see recent reviews by Kuzyakov and Domanski 2000; Kuzyakov 2002b; Jones et al. 2009), which then has several possible fates: 1) it stays in the soil, either remaining in soil solution or incorporated into organo-mineral complexes; 2) it is assimilated into microbial biomass; 3) it is assimilated into microbial biomass and is subsequently respired (either by the microbes themselves or by their predators) or released into soil solution as those microbes turn over (Fig. 1).

The most common method by which each of the above pools is quantified is through isotope labeling, which can be used to track carbon flows through the plant-soil system and determine the fate of plant-derived

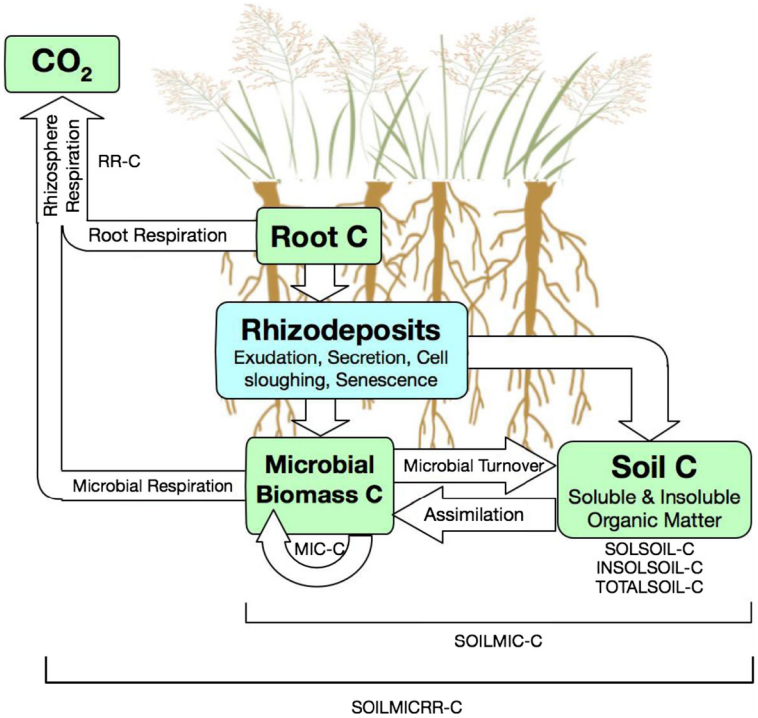


Fig. 1 Simplified diagram of the fates of rhizodeposited carbon (C) derived from living roots. Boxes correspond to C pools, while arrows correspond to processes and flows between C pools. Note that the arrows represent possible flows, as, for example, a portion of soil C could remain in recalcitrant forms rather than all soil C being converted to CO_2 through microbial respiration. See main text for details on the contrasting hypotheses for N effects on the rhizodeposit C pools illustrated here

C. Isotope labeling is conducted by exposing plants either for a short period (minutes to hours; i.e. 'pulse-chase labeling') or for a single, longer period (days to weeks; i.e. 'continuous labeling') to an isotope-enriched (^{13}C or ^{14}C) CO_2 atmosphere. Given that both ^{14}C- and ^{13}C–enriched atmospheres can be used to track carbon flows through plants, we refer to 'tracer-C' hereafter to include both ^{14}C and ^{13}C. After exposing plants to a tracer-C CO_2-labelled atmosphere, tracer-C can then be quantified in each plant-derived C pool (plant tissue, soil, microbial biomass, and respiratory losses from the soil), where tracer-C in the soil, microbial biomass, and respiration are all components of rhizodeposited C. For ^{14}C–based labeling studies, rhizodeposition is generally quantified by simply measuring and reporting ^{14}C activity (Bequerels or Bq) in each potential rhizodeposit C pool. However, some studies then attempt to quantify total rhizodeposition ($^{14}C + {}^{12}C$ rhizodeposition) by dividing each ^{14}C pool by the specific activity of ^{14}C (Bq per unit C) in the experimental atmosphere or in the plant tissues (e.g., Bushby et al. 1992), a method which assumes that $^{14}C/^{12}C$ ratios remain constant in the atmosphere-plant-soil continuum. Although this assumption may be valid in continuous labeling studies in which plants are exposed to a ^{14}C–enriched atmosphere for long periods, this assumption should be used with caution in pulse-chase studies, which can result in inhomogeneous distribution of isotope label across the plant (Meharg 1994). In comparison to ^{14}C–based methods, ^{13}C–based labeling studies often quantify rhizodeposition from the atom percent excess of tracer-C in the rhizodeposit C pools of labeled versus unlabeled replicate plants, a method which does not assume similar $^{13}C/^{12}C$ ratios in plants versus soil (e.g. Baptist et al. 2015). Regardless of the isotope used, an important consideration of pulse-chase versus continuous labeling studies is their ability to assess specific components of rhizodeposition. For example, pulse labeling biases towards recently-fixed carbon in non-structural pools, and therefore the rhizodeposits measured will largely be comprised of root-respired carbon, lysates from root cap and border cells, and low molecular weight C compounds lost through passive exudation (Meharg and Killham 1988; Lynch and Whipps 1990; Meharg 1994). On the other hand, continuous labeling results in more homogenously-labelled plant tissue, and therefore the isotope-labeled rhizodeposits examined in such studies are more representative of overall plant rhizodeposition (Whipps and Lynch 1983; Meharg 1994), likely including a greater proportion of senesced root tissue and other root debris. Similarly, duration of the pulse-chase periods, or duration of the labeling

periods in continuous studies, could affect the type of rhizodeposits measured, as longer studies may capture more root senescence and debris than shorter studies. Other considerations of pulse-chase and continuous labeling have been thoroughly reviewed elsewhere (Meharg 1994; Kuzyakov and Domanski 2000; Kuzyakov and Schneckenberger 2004).

Similar to isotope labeling is a method based on ^{13}C natural abundance. This method relies on the lower discrimination against the 'heavy' ^{13}C isotope in C_4 plants versus C_3 plants, which results in plant tissue $^{13}C/^{12}C$ isotope ratios ($\delta^{13}C$ values) of roughly −14‰ in C_4 species and −28‰ in C_3 species (O'Leary 1988). This lower discrimination against ^{13}C in C_4 versus C_3 species results in greater ^{13}C enrichment soil historically planted with C_4 species (Cerri et al. 1985; Balesdent et al. 1987; Cheng 1996). Therefore, when growing C_3 plants on a historically C_4-planted site, or vice versa, researchers can assess changes in the $\delta^{13}C$ in soil and obtain rough estimates of C inputs derived from the focal plants of the experiment (Cheng 1996; Kuzyakov and Domanski 2000). However, given that the difference in $\delta^{13}C$ between C_4 plants and C_3-conditioned soil (or vice versa) is a maximum of only approximately 14‰, and the $\delta^{13}C$ of soil organic matter fractions is naturally somewhat variable, this method is limited by poor sensitivity (Balesdent and Balabane 1992; Cheng 1996; Paterson et al. 1997). Therefore, pulse-chase and continuous labeling studies are considered more accurate than ^{13}C natural abundance studies in their estimates of rhizodeposition (Balesdent and Balabane 1992).

Another consideration of isotope-based methods for quantifying rhizodeposition is that shifts in tracer-C/^{12}C ratios in rhizodeposits relative to roots (i.e. isotope fractionation) has been shown to occur in some, but not all studies (Cheng 1996; Werth and Kuzyakov 2010; Zhu and Cheng 2011). This is an important point for ^{13}C natural abundance studies, as well as some isotope labeling studies (see above), which assume that plant tissues and rhizodeposit C pools have equivalent tracer-C/^{12}C ratios in order to quantify rhizodeposition (Werth and Kuzyakov 2010). Equally as important, isotope fractionation in plants can be affected by nutrient supply, potentially leading to errors in estimates of N effects on rhizodeposition. For example, in a study by Werth and Kuzyakov (2010), exudates of high nutrient treated plants were enriched in $\delta^{13}C$ by 4–7‰ compared to roots, but exudates were not enriched in $\delta^{13}C$ compared to roots in low nutrient treated plants. In ^{13}C natural abundance studies, differential isotope fractionation of this magnitude between high and low N plants could lead to inaccurate estimates of N effects on rhizodeposition, given that differential fractionation of 4–7‰ is large relative to the maximum difference in $\delta^{13}C$ of roughly 14‰ between C_4 plants and C_3 soil (or C_3 plants and C_4 soil). In contrast, 4–7‰ is likely a much lower proportion of the difference in $\delta^{13}C$ (or ^{14}C) between plants and soil in pulse-chase and continuous labeling experiments, in which plant tissue $\delta^{13}C$ (or ^{14}C) is substantially higher. For example, after 16 h of pulse-labeling with an atmosphere in which ~50% of the CO_2 was ^{13}C, beech root tissue had $\delta^{13}C$ values of +969‰ and +417‰ for low N and high N treated plants, respectively, while soil $\delta^{13}C$ was approximately −20‰ (Gschwendtner et al. 2016). As a result, estimates of rhizodeposition using pulse-chase or continuous labeling should be much less influenced by isotope fractionation at the root-soil interface than those using ^{13}C natural abundance (Werth and Kuzyakov 2010).

Once rhizodeposits enter the soil, isotope fractionation by soil microbes can then influence quantification of rhizodeposit C pools in isotope-based studies. For example, the $\delta^{13}C$ of microbial biomass and microbially-respired CO_2 can sometimes differ by up to several parts per thousand relative to the organic matter which they are decomposing (reviewed in Werth and Kuzyakov 2010). Again, this level of fractionation could lead to biased estimates of rhizodeposit C pool sizes, particularly in ^{13}C natural abundance studies in which plant tissues differ a maximum of only roughly 14‰ from the background soil $\delta^{13}C$. Moreover, given that shifts in nitrogen availability can affect microbial community composition (e.g. Gschwendtner et al. 2016; Wang et al. 2016; Lv et al. 2017) and functioning (e.g. Frey et al. 2004; Fierer et al. 2012), it is possible that changes in N availability lead to differential C isotope fractionation in microbes, leading to biased estimates of the effects of N on rhizodeposition in isotope-based studies. Nevertheless, conflicting results among studies regarding the magnitude and direction of microbial carbon isotope fractionation during decomposition of organic substrates (reviewed in Werth and Kuzyakov 2010) suggest that this phenomenon is context dependent (Fernandez and Cadisch 2003). Additional study is needed to quantify the potential impacts of N availability on carbon isotope fractionation by microbes and the potential ramifications for assessing rhizodeposition under contrasting N availabilities using isotope-based methods.

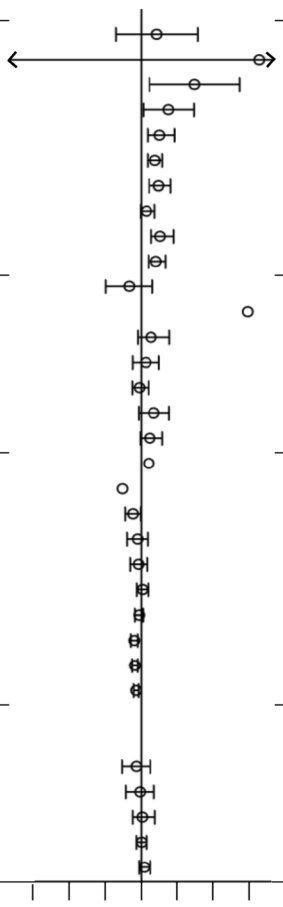
Although the isotope approaches described above are generally useful for *quantifying* root-derived C inputs, they do not allow for the *identification* of the specific C metabolites in those inputs (Aitkenhead-Peterson and Kalbitz 2005). For example, consider an isotope-labeling experiment in which plants are exposed to a $^{14}CO_2$ atmosphere, and at the conclusion of the experiment, total ^{14}C and ^{14}C–glucose are measured in the soil. Although the soil ^{14}C–glucose is indeed root-derived C, it is impossible to determine whether that ^{14}C–glucose was truly lost from roots as ^{14}C–glucose, or whether it was lost from roots as another metabolite (e.g. ^{14}C–fructose) that was then metabolized to ^{14}C–glucose by soil microbes (Aitkenhead-Peterson and Kalbitz 2005). This is an important point for studies attempting to identify the specific metabolites by which plants signal or sustain rhizosphere microbes (e.g., Rudrappa et al. 2008; Zhang et al. 2014; Yuan et al. 2015). Therefore, growing plants in sterile conditions is essential for studies assessing the composition of rhizodeposited C to ensure that any C metabolites in the soil were directly produced by plants and not modified by microbes (Aitkenhead-Peterson and Kalbitz 2005). On the other hand, the presence of soil microbes can affect rhizodeposition by stimulating the exudation of specific metabolites (Dakora et al. 1993). Additional considerations of sterile versus non-sterile culture are reviewed elsewhere (Paterson et al. 1997; Vranova et al. 2013; Kuijken et al. 2015).

Some isotope-based studies quantifying the influence of N availability on rhizodeposition report all of the C pools described above (tracer-C in soil, microbial biomass, and respiration) while others report only a subset of those pools (Fig. 2, Online Resource 1). In addition, the methods for delineating rhizodeposition C pools varies among studies in several important ways. First, soil tracer-C measurements often (e.g., Billes et al. 1993; Van Der Krift et al. 2001; Bazot et al. 2006; Butterly et al. 2015), but do not always (e.g., Bushby et al. 1992; Van Ginkel and Gorissen 1998), include soil microbial biomass tracer-C. Microbial biomass tracer-C can be measured separately from soil tracer-C using methods such as fumigation-extraction (Vance et al. 1987), in which soils are fumigated with chloroform to lyse microbial cells, then extracted with K_2SO_4. The additional extractable tracer-C (compared to that of non-fumigated soils) is considered to be from microbial biomass, and a correction factor can then be used to account for the proportion of the microbial biomass tracer-C that is insoluble in the extraction solvent. However, the proportion of isotope label that is in the soluble or the insoluble fractions of the microbial biomass can depend on the duration of the study (i.e. as microbes incorporate more of the soluble tracer-C in the cytoplasm into the cell wall or other insoluble components over time) (Bremer and van Kessel 1990). As a result, the fumigation-extraction method does not always allow for accurate estimates of microbial biomass C (Glanville et al. 2016), depending on the quantity of isotope label that is in insoluble fractions of the microbial biomass. Second, although studies occasionally attempt to quantify microbially-respired tracer-C separately from the tracer-C from root respiration (Kuzyakov et al. 2002b; Baptist et al. 2015), most studies report 'rhizosphere respiration', which includes both root- and microbially-respired tracer-C. Root respiration has been estimated to account for roughly 40–50% of rhizosphere respiration (Kuzyakov 2002a; Kuzyakov and Larionova 2005), although values from 17% (Kuzyakov et al. 1999) to 95% (Swinnen 1994) have been reported. This illustrates one of the challenges arising from the many definitions for rhizodeposition used in the literature: if only organic C released by roots is considered as rhizodeposition, studies assessing rhizosphere respiration always overestimate rhizodeposition by including root-respired CO_2. On the other hand, studies not assessing rhizosphere respiration in situations where microbial decomposition of rhizodeposits can occur (such as in nonsterile conditions) will always underestimate rhizodeposition by excluding microbially-respired rhizodeposits. It is also worth noting that measurement of rhizosphere/microbial respiration can impact assessments of N effects on other C pools. For example, consider an experiment in which plants are grown in a ^{14}C–enriched atmosphere, and are amended with either low N or high N. Greater ^{14}C in the soil of low N plants may not represent greater rhizodeposition from low N plants per se, but may represent lower decomposability of those rhizodeposits compared to plants under high N (Van der Krift et al. 2001). Disentangling these two scenarios is only possible when either explicitly measuring microbial respiration, or conducting studies in sterile culture, thereby eliminating the possibility of microbial decomposition of rhizodeposits. There are a variety of approaches for distinguishing microbially-respired from root-respired CO_2 thoroughly reviewed elsewhere (Hanson et al. 2000; Kuzyakov and Siniakina 2001; Kuzyakov 2002a; Kuzyakov and Larionova

2005; Kuzyakov 2006; Schuur and Trumbore 2006; Sapronov and Kuzyakov 2007; Hopkins et al. 2013), although each method has its respective assumptions and limitations (Kuzyakov 2006; Hopkins et al. 2013). Optimization and implementation of such methods is needed for more accurate estimates of N effects on rhizodeposition.

In addition to inconsistent approaches for quantifying and delineating rhizodeposition C pools, studies investigating the effects of N often differ in the units for reporting those inputs (Fig. 2, Online Resource 1). The most commonly-reported unit of measure is C inputs per plant (in mg or g C), which describes the actual quantity of C lost through rhizodeposition. Other units of measure, such as C inputs per unit root mass, describe whether and how plants shift C allocation in response to N and provide insight into possible regulatory processes (Hill et al. 2007). Similarly, isotope-based studies often report root-derived C inputs as a proportion of the total tracer-C detected in the plant-soil system, also referred to as 'total tracer-C fixed.' Most studies calculate the total tracer-C fixed as the sum of tracer-C in the plant, soil, microbial biomass, and rhizosphere respiration at the conclusion of the study (e.g., Bushby et al. 1992; Billes et al. 1993;

Units	Rhizodeposit C pool	n	Percent change in response to N	Min	Max
Plant^{-1}	SOLSOIL-C	6	44.1 (-69.8, 158.1)	-65.0	221.1
	INSOLSOIL-C	2	329.0 (-1983.5, 2641.5)	147.0	511.0
	TOTALSOIL-C	9	**149.0 (24.0, 274.1)**	-10.1	471.3
	MIC-C	11	**77.1 (6.4, 147.9)**	-42.9	316.7
	SOILMIC-C	24	**52.0 (18.8, 94.4)**[a]	-48.5	363.5
	RR-C	11	**39.1 (18.7, 59.5)**	-16.7	91.9
	SOILMICRR-C	11	**49.7 (22.6, 82.8)**[a]	5.0	209.1
	Total Root Mass	41	15.1 (-1.3, 38.1)[a]	-50.0	550.5
	Total Shoot Mass	33	**53.8 (28.5, 91.6)**[a]	-40.0	8158.2
	Total Biomass	33	**41.3 (21.3, 69.2)**[a]	-32.6	2693.2
Root Mass^{-1}	SOLSOIL-C	5	-33.0 (-98.2, 32.2)	-93.5	48.8
	INSOLSOIL-C	1	297.1	-	-
	TOTALSOIL-C	10	28.0 (-8.8, 79.8)[a]	-42.7	271.1
	MIC-C	9	13.0 (-23.9, 49.9)	-29.4	115.3
	SOILMIC-C	21	-4.4 (-24.6, 21.4)[a]	-67.9	201.4
	RR-C	9	36.0 (-6.5, 78.4)	-20.6	161.6
	SOILMICRR-C	9	24.8 (-2.3, 59.3)[a]	-20.3	145.5
Total tracer-C fixed^{-1}	SOLSOIL-C	1	22.2	-	-
	INSOLSOIL-C	1	-52.4	-	-
	TOTALSOIL-C	7	**-22.9 (-44.1, -1.7)**	-65.3	10.0
	MIC-C	8	-10.2 (-38.9, 18.6)	-45.8	41.7
	SOILMIC-C	14	-6.9 (-30.7, 16.9)	-61.5	78.1
	RR-C	20	3.7 (-12.8, 20.1)	-60.0	89.4
	SOILMICRR-C	14	-5.9 (-17.8, 5.9)	-43.6	36.4
	ROOT-C	15	**-19.3 (-28.4, -10.2)**	-42.9	6.9
	ROOTSOILMIC-C	14	**-17.8 (-25.6, -10.1)**	-49.4	4.9
	ROOTSOILMICRR-C	14	**-14.3 (-20.9, -7.7)**	-32.1	3.9
Tracer-C Below-ground^{-1}	SOLSOIL-C	0	-	-	-
	INSOLSOIL-C	0	-	-	-
	TOTALSOIL-C	4	-13.0 (-52.6, 26.6)	-49.1	7.9
	MIC-C	4	-2.9 (-42.1, 36.4)	-25.0	30.6
	SOILMIC-C	11	3.0 (-23.6, 39.0)[a]	-42.8	127.5
	RR-C	11	1.0 (-13.1, 15.0)	-51.7	26.1
	SOILMICRR-C	11	9.1 (-5.6, 26.0)[a]	-20.2	78.6



Percent Change in Response to N

Fig. 2 Summary data for studies assessing rhizodeposition in response to increased nitrogen availability. Mean percent change in response to N is shown with 95% confidence limits. Means significantly different from zero are in bold. (n) indicates number of studies reporting each C pool; (a) indicates back-transformed data. Abbreviations for rhizodeposition C pools are: soluble soil C (SOLSOIL-C); insoluble soil C (INSOLSOIL-C); soluble + insoluble soil C (TOTALSOIL-C); microbial biomass C (MIC-C); rhizosphere respiration C (RR-C); soil + microbial biomass C (SOILMIC-C); soil + microbial + rhizosphere respiration C (SOILMICRR-C); root C (ROOT-C); root + soil + microbial biomass C (ROOTSOILMIC-C); root + soil + microbial + rhizosphere respiration C (ROOTSOILMICRR-C). See main text for additional information on C pools and units of measure

Bazot et al. 2006). Others calculate total tracer-C fixed as the difference between the tracer-C input into the experimental atmosphere and the tracer-C that is remaining in the experimental atmosphere at the end of the study: a method which assumes that all the 'missing' tracer-C has been taken up by the plant (e.g., Kuzyakov et al. 2002a, b; Gavrichkova and Kuzyakov 2008). Both approaches underestimate the total tracer-C fixed because they do not account for tracer-C that is fixed then respired by the shoot (Lynch and Whipps 1990), and as a result, they overestimate the proportion of total fixed tracer-C in each root-derived C pool (Kuzyakov and Domanski 2000). Nevertheless, these errors in estimates of total tracer-C fixed may be minor provided that the labeling and chase periods are relatively short. An alternative method is described in the study of Hill et al. (2007). The authors of that study used a pulse-chase labeling procedure on three consecutive days, and harvested several plants immediately following the final isotope pulse in order to minimize possible respiratory losses by the shoot. After a 48-h chase period, they then measured ^{14}C in soil, microbial biomass, and rhizosphere respiration for a second set of plants, and expressed each of these pools relative to the ^{14}C detected in the first set of plants harvested immediately after labeling. This presumably provided Hill et al. (2007) with more accurate values for the proportions of total fixed tracer-C in each root-derived C pool than if total fixed tracer-C had been assessed at the end of the experiment. However, such an approach could also result in underestimates of total fixed ^{14}C if labeling periods are relatively long in duration (thereby allowing for greater shoot respiratory losses). Still another approach is to report C inputs as a proportion of the total tracer-C belowground (sum of tracer-C in the roots, in the soil, in the microbial biomass, and in rhizosphere respiration).

Taken together, the different units by which rhizodeposition is reported drastically reduces the number of comparable studies that could be used for traditional meta-analyses of N effects (see further detail below). Although conversion between units is sometimes possible, studies do not always include the necessary data. For example, isotope-labeling studies reporting tracer-C rhizodeposition per plant also typically report total root mass, allowing calculation of tracer-C rhizodeposition per unit root mass. However, without also reporting data for shoot tracer-C, it is impossible to calculate rhizodeposition C pools as a proportion of total tracer-C fixed (given that shoot tracer-C is a component of total tracer-C fixed by the plant). Reporting rhizodeposition C in multiple units is important because each provides different insight into plant-soil C dynamics (Hill et al. 2007). For example, C inputs per plant inform on total C fluxes from plants and their contribution to soil C accrual, while C inputs per unit root mass inform on plant regulation of C allocation, both of which contribute to our understanding of the mechanisms underlying global C cycling. Thus, we recommend researchers report rhizodeposition in multiple units, or include raw data in an Appendix or Online Supplement where possible, to facilitate comparisons across studies and help determine generalities in N effects on rhizodeposition.

A variety of possible mechanisms generate conflicting predictions for effects of N on rhizodeposition

There are a variety of mechanisms by which N availability can either increase or decrease rhizodeposition (Henry et al. 2005). Root organic C losses result from a combination of root cap sloughing, passive leakage through the root epidermis, lysis of cortical cells and root hairs, senescing root fragments, active secretions such as mucilage, and direct C transfer to symbionts such as mycorrhizas (Jones et al. 2009). It should be noted that quantifying the relative contribution of these different rhizodeposition C sources is an outstanding challenge in rhizosphere research (Jones et al. 2009). In general, however, shifts in root system size, allocation, architecture, and/or morphology in response to N are likely to result in shifts in rhizodeposition as a passive consequence. For example, N fertilization can increase root branching and the number of root tips (Henry et al. 2005), the sites where root exudation tends to be highest (McDougall and Rovira 1970; Darwent et al. 2003), likely increasing the potential for root cap and border cell sloughing (Nguyen 2003). N fertilization can also increase total root system size and surface area for C loss (Henry et al. 2005; Phillips et al. 2009; Baptist et al. 2015), and rhizodeposition C has been positively associated with total root mass (Shamoot et al. 1968; Van der Krift et al. 2001; Baptist et al. 2015; Ge et al. 2015) and root length (Xu and Juma 1994). In addition, high N availability has been suggested to increase microbial growth by decreasing plant-microbe competition for N (Kuzyakov 2002b), leading to increased microbial consumption of exudates and therefore the concentration gradient for rhizodeposition (Nguyen 2003; Ge et al.

2015). Paradoxically, low N availability has also been suggested to increase rhizodeposition by similar passive mechanisms. For example, N limitation generally increases relative biomass allocation to roots (root:shoot ratio) (Poorter et al. 2012), and can result in increased root hair production and cortical cell death (Robinson and Rorison 1987; Gillespie and Deacon 1988). N limitation can also cause increased root length per unit mass (specific root length) (Paterson and Sim 1999; Paterson and Sim 2000), potentially resulting in a greater surface area for rhizodeposition relative to root mass (Johansson 1992). Potentially exacerbating these effects is the suggestion that N limitation increases root membrane permeability (Lee and Gaskins 1982; Phillips et al. 2009), a common response to other nutrient deficiencies (Graham et al. 1981; Cakmak and Marschner 1988).

In addition to the mechanisms affecting total C rhizodeposition described above, plants possess mechanisms through which rhizodeposition of specific metabolites can be actively regulated in response to N. For example, strigolactones, a diverse class of secondary metabolites, are transported by active mechanisms in plants (Kretzschmar et al. 2012), and have been shown to induce spore germination and/or hyphal branching in arbuscular-mycorrhizal fungi (Akiyama et al. 2005; Besserer et al. 2006). Exudation of several strigolactones has been shown to increase in response to N deficiency in some species, but not others (Yoneyama et al. 2007a, b, 2012), suggesting some species may up-regulate strigolactone exudation under N deficiency to initiate mycorrhizal symbioses and enhance N acquisition (Yoneyama et al. 2007a, 2012). In addition to active regulation of C export, plants can actively import common rhizodeposits, including amino acids (Jones and Darrah 1994; Lesuffleur and Cliquet 2010) and sugars (Mühling et al. 1993), making rhizosphere C flow a bidirectional process (Jones et al. 2009). For example, Farrar et al. (2003) calculated a hypothetical recapture efficiency of up to 80% for glucose lost from *Zea mays* roots via passive diffusion. On the whole, although it is likely that the re-uptake of rhizodeposited C is small relative to C export, given that soluble root exudates such as glucose comprise a small minority of total rhizodeposits (Uren 2001; Paterson 2003), it is nevertheless worth noting that plants can exert some level of active control on net rhizodeposition through C influx (Paterson and Sim 1999; Farrar and Jones 2000; Jones et al. 2009), and alter rhizodeposition in response to N. For example, Paterson and Sim (2000) applied ^{14}C–glucose to the soil of *Festuca rubra* grown under sterile conditions, and found that ^{14}C uptake was greater in high N than low N plants, potentially due to the greater C demand in high N plants for nutrient uptake and assimilation. In contrast, N had no effect on ^{14}C–glucose uptake in a similar study in *Lolium perenne* (Paterson and Sim 1999), although it should be noted that ^{14}C that was assimilated and subsequently respired was not accounted for in that study. These studies indicate that plants can actively (i.e., through re-uptake of rhizodeposit C) regulate the quantity and/or composition of rhizodeposits in response to N, and that such responses may be species-specific.

Finally, it should also be noted that 'low' and 'high' N are often used as discrete terms (including in this review), but in reality, only serve as relative points for comparison along a continuum of N availability. As such, morphological and physiological responses to N limitation (and therefore N effects on rhizodeposition) can depend on the severity of N deficiency it induces in the plant. For example, in *Arabidopsis thaliana*, moderate reductions in N availability generally led to an increase in the number of lateral roots, while severe reductions in N availability led to increased length of lateral roots (Remans et al. 2006). The complexity of plant physiological and morphological responses to varying N levels, and the molecular pathways regulating these responses, has been the subject of several recent reviews (Nacry et al. 2013; Kiba and Krapp 2016). It is also important to note that many of the above responses to N supply are directly or indirectly modulated by interactions with soil microbes. For example, diazotrophic bacteria which inhabit root nodules and fix atmospheric nitrogen (rhizobia), as well as plant growth-promoting rhizobacteria, can influence plant N nutrition and/or root growth and branching (reviewed in Kraiser et al. 2011), and therefore likely rhizodeposition.

In summary, there are a variety of mechanisms by which rhizodeposition can be altered in response to soil N availability, and in many cases, it has been argued that N additions can both increase and decrease the quantity of root-derived C inputs.

Literature search and data collection for N effects on rhizodeposition

In accordance with the contrasting arguments for N effects on rhizodeposition, previous literature summaries report that N additions have both positive and negative effects in experimental studies (Zagal et al. 1993; Nguyen 2003; Henry et al. 2005; Phillips et al. 2009). To determine

whether different patterns emerged across a wider range of studies, we conducted a literature search of studies experimentally manipulating N availability and quantitatively assessing rhizodeposition in soil. We included studies in which the only mineral nutrients manipulated were N (as nitrate or ammonium) and its counterions (K^+, Ca^{2+}, Cl^-, etc.), or where N was given as urea. In addition, we used the broadest definition of rhizodeposition, and considered as rhizodeposits any C inputs entering the soil through the living root system, which potentially includes root exudates, lysates, secretions, proteins, mucilage, root- and microbially-respired CO_2 (i.e. rhizosphere respiration), sloughed root cap and border cells, fine root fragments, and senesced root tissue (Uren 2001). Although root-respired CO_2 is not always considered a component of rhizodeposition (see Wichern et al. 2008 for a recent review of rhizodeposition definitions), we include it here (as a component of rhizosphere respiration) because of the challenges in separating root respiration from microbial respiration of plant rhizodeposits as described above.

We included pulse-chase and continuous labelling experiments, as well as studies conducted in sterile culture, in which all C pools could be unequivocally identified as plant-derived. We also included several nonsterile studies which grew plants in media free of organic C (Uselman et al. 2000; Aitkenhead-Peterson and Kalbitz 2005; Phillips et al. 2009; Phillips et al. 2011; Yin et al. 2013) and filtered the solution in which rhizodeposits were collected to exclude microbes that may have colonized the pots during the course of the experiment. It is important to note that such a filtration step therefore excludes rhizodeposit C that may have been taken up microbes. We did not include ^{13}C natural abundance studies due to the greater possibility of differential isotope fractionation across N levels leading to experimental artifacts (described above). However, we did include studies that applied ^{13}C–enriched CO_2 (Baptist et al. 2015; Butterly et al. 2015; Atere et al. 2017; Ge et al. 2017). We excluded studies which examined rhizodeposition only in rhizosphere soil (soil adhering to the roots after removing the plant from the bulk soil), given that rhizosphere soil defined in this way can comprise a minority of root-derived C (Cotrufo and Gorissen 1997).

In total, our literature search resulted in 33 papers reporting 48 experiments (Online Resources 1, 2). Quantitative data for rhizodeposition C pools were either collected directly from tables and text, or from figures using WebPlotDigitizer (http://arohatgi.info/WebPlotDigitizer/). Of the 48 experiments for which data was collected, 16 examined the effects of N availability under both ambient and elevated CO_2. The majority of our analyses considered only N effects at ambient CO_2; however, we also collected data on rhizodeposition under elevated CO_2 for analysis of interactive effects between N and CO_2 availability (see statistical analyses below). For studies that assessed the effects of other factors (e.g. defoliation, high temperature), we collected data only for the 'control' conditions of those studies (e.g. no defoliation, ambient temperature). For studies that assessed rhizodeposition C pools at multiple dates, we collected data only for the latest date. Similarly, for studies that assessed rhizodeposition at three or more N levels, we collected data only for the highest versus the lowest N levels in each study. Where possible, we divided root-derived C inputs into different pools for comparison among studies: soluble soil C (defined as root-derived C in the soil that is water or K_2SO_4-extractable), insoluble soil C (defined as root-derived C remaining in the soil after removal of soluble soil C), total soil C (the total root-derived C in the soil excluding that in microbial biomass; also calculated as the sum of soluble and insoluble C), microbial biomass C, and rhizosphere respiration C (defined as the total CO_2 derived from root respiration plus microbial respiration of root-derived C). Several studies did not distinguish total soil C from microbial biomass C: we report this as soil + microbial C. Where possible, we also calculated total rhizodeposition as soil + microbial + rhizosphere respiration C. Lastly, when studies did not report values in all four of the major units for expressing rhizodeposition described above (rhizodeposition C per plant, per unit root mass, per unit total tracer-C fixed, or per unit belowground tracer-C), we converted between units where possible using mean values for C pools in the units that were reported.

Although rhizodeposition C was generally reported for most of the above categories for isotope-based studies, distinguishing C pools in non-isotope based studies was less straightforward. One study was conducted in nonsterile liquid culture, with the liquid medium assessed for organic C after excluding microbes using filtration (Aitkenhead-Peterson and Kalbitz 2005). This was considered as total soil C (the sum of soluble and insoluble soil C), given that any rhizodeposit C taken up by microbes (microbial biomass C) in the growth media was removed in the filtration step. Similarly, several other hydroponics studies used sand or glass beads as a growth medium to more closely approximate the mechanical impedance

of natural soils, and collected rhizodeposited C by leaching the growth medium (Paterson and Sim 1999; Paterson and Sim 2000; Uselman et al. 2000; Phillips et al. 2009, 2011; Yin et al. 2013). We considered sand leachate as soluble soil C, and glass bead leachate as total soil C (i.e. sum of soluble and insoluble soil C), given that sand has been suggested to more strongly adsorb low molecular weight organic acids than glass beads (Phillips et al. 2009).

Several studies conducted two or more experiments, of which we generally included only one to prevent pseudoreplication. The sole exception was (Gavrichkova and Kuzyakov 2008), which reported *Zea mays* responses to availability of both nitrate and ammonium: we retained both experiments given that the two N forms have different impacts on rhizodeposition across studies (see results of quantitative analyses below). For Henry et al. (2005), we excluded the sterile experiment in which low N and high N plants were harvested on separate dates, potentially confounding effects of N with sampling date. Two studies applied an isotope label at either early or late growth stages in separate experiments: for these studies, we collected data only for the later growth stage experiment (Kuzyakov et al. 2002b; Gavrichkova and Kuzyakov 2010). Hodge et al. (1996) conducted an experiment in which *L. perenne* was grown in sterile culture, and included both total C and ^{14}C pulse labeling. We included only the total C data, since the total C was collected over the final 36 days of plant growth while the ^{14}C pulse-chase component was only conducted over the final two days of plant growth. For Phillips et al. (2009), we retained only Experiment II, in which rhizodeposits were collected from plants grown on glass beads, as the authors of that study suggest strong adsorption of rhizodeposition C by the sand medium used in Experiment I. Liljeroth et al. (1990) used two different varieties of *T. aestivum* (wheat), which we averaged for our analysis. For Cotrufo and Gorissen (1997), we summed the values for C inputs in the rhizosphere and the bulk soil to obtain values for total rhizodeposition. Lastly, as described above, the majority of studies reporting C pools per unit total tracer-C fixed calculated total tracer-C fixed as the sum of tracer-C in the shoot, the root, the soil, the microbial biomass, and in rhizosphere respiration. An exception was the study of Hill et al. (2007), which accounted for shoot respiration, while the majority of studies did not. Therefore, we recalculated values for the Hill et al. (2007) study based on the total tracer-C recovered at the final harvest, similar to the majority of other studies.

Quantitative analysis of N effects on rhizodeposition

The studies selected in our literature search differed widely in a large number of methodological variables, including the types of C inputs measured, the units for reporting those inputs, the use of isotope labeling, the type of isotope labeling used (pulse-chase versus continuous), the number of isotope pulses used, pulse and chase duration and frequency, the species used, and the forms of N applied (Online Resource 1). In particular, the different units used for reporting rhizodeposition C pools across studies drastically reduced the statistical power necessary for a formal meta-analysis of the effects of N on rhizodeposition. Therefore, we instead focused on the direction and magnitude of N effects across studies to determine whether general trends existed, and assessed the influence of key experimental variables on N effects by sub-setting the data and using t-tests or ANOVAs as appropriate. First, for each C pool, we calculated the mean percent change in response to N additions as well as 95% confidence intervals using the *t*-distribution (Microsoft Excel 2016). This allowed us to determine for each C pool if the mean response to N was significantly different from zero across studies. When $n \geq 3$, data were transformed as needed in R (v. 3.4.1; R Core Team 2017) using $ln(x + 1)$, $1/(x + 1)$, square root, or cube root transformations to better approximate normality assessed using a Shapiro-Wilk test. Next, we assessed whether several experimental variables contributed to the variable N effects seen across studies. To examine whether the effects of N on rhizodeposition were dependent upon the labeling method used, we used t-tests to compare N responses in pulse-chase versus continuous labeling studies. We also tested whether the response to N additions is dependent upon the form of N used by comparing N responses in studies using nitrate versus ammonium versus ammonium nitrate. We used ANOVA when all three N forms were represented by at least two studies ($n \geq 2$), and a t-test when only two of the three N forms had $n \geq 2$. Finally, we compared N responses in annual versus perennial species using t-tests. For all statistical analyses, data were transformed as needed to meet assumptions of normality of residuals and homogeneity of variances; the latter of which was assessed using both

Bartlett's and Levene's tests (Levene 1960; Snedecor and Cochran 1989) in the 'car' package of R (Fox and Weisberg 2011). We used the Welch's t-test when the homogeneity of variance assumption was not met for t-tests, and the non-parametric Kruskal-Wallis rank sum test when ANOVA assumptions were not met.

Quantitative effects of increased N availability on rhizodeposition

When expressed on a per plant basis, N additions tended to increase rhizodeposition for nearly all C pools examined (Fig. 2). Total soil C, microbial biomass C, soil + microbial C, rhizosphere respiration C, and soil + microbial + rhizosphere respiration C all significantly increased in response to N, with an approximately 40–150% increase in these pools. Although it is difficult to extrapolate these findings to estimate the possible impacts of N additions on overall soil C sequestration, the result that N additions generally increase rhizodeposition of organic C (total soil C, microbial biomass C, and soil + microbial C), but also increase decomposition of those rhizodeposits (rhizosphere respiration C) are in agreement with previous reports that N fertilization can increase, decrease, or have no effect on overall soil C sequestration (Gregorich et al. 1996; Halvorson et al. 1999, 2002; Neff et al. 2002; Khan et al. 2007; Maaroufi et al. 2015). In contrast to rhizodeposition per plant, N additions decreased rhizodeposition per unit total tracer-C fixed for total soil C, root C, root + soil + microbial biomass C, and root + soil + microbial + rhizosphere respiration C (Fig. 2). This is in agreement with the general observation that plants increase relative allocation to the root system when soil resources are limiting (Poorter et al. 2012). No rhizodeposition C pools were significantly altered when expressed per unit root mass, or as a proportion of belowground tracer-C (root + soil + microbial + rhizosphere respiration C) (Fig. 2). Taken together, it is clear that the direction and magnitude of N effects are dependent upon the units reported in a given study. Nevertheless, despite these trends, a wide range of responses to increased N availability, including both increases and decreases in rhizodeposition, were reported for nearly all C pools and units reported (Fig. 2).

It is worth noting that the effects of N on total root mass were positively correlated with the effects of N on total rhizodeposition (soil + microbial + rhizosphere respiration C) per plant ($r = 0.81$, $n = 9$, $p = 0.009$). This suggests that rhizodeposition is at least somewhat dependent upon root system size, and therefore that passive processes play a role in regulating rhizodeposition (Billes et al. 1993). This is similar to the findings of Shamoot et al. (1968) that organic debris in rhizodeposits was correlated with root system size, likely because larger root systems result in greater root cap and border cell sloughing and surface area for C loss. In contrast, the effects of N on total root mass were negatively correlated with the effects of N on total rhizodeposition per unit root mass ($r = -0.79$, $n = 9$, $p = 0.012$). This indicates that increasing root system size in response to N addition leads to a decrease in rhizodeposition per unit mass, potentially due to a decrease in root surface area per unit mass in larger, thicker root systems. In any case, our findings support the assertion that rhizodeposition is dependent upon root system size (Pausch et al. 2013; Kanders et al. 2017).

We note that 16 of the 48 studies reviewed here assessed rhizodeposition in response to factorial manipulations of both N and CO_2 availability. Elevated CO_2 generally increases rhizodeposition (Nie et al. 2013), either through increasing root system size or activity (van Veen et al. 1991; Allard et al. 2006; de Graaff et al. 2007). Thus, N and CO_2 availability can potentially interact to influence rhizodeposition, as well as downstream nutrient cycling and soil C turnover. We tested this hypothesis using paired t-tests to compare responses to N additions in ambient CO_2 versus elevated CO_2, and found that soil + microbial C per plant, soil + microbial C per unit root mass (marginally significant; $p = 0.054$), and total soil tracer-C per unit belowground tracer-C (marginally significant; $p = 0.054$) all exhibited a greater increase in response to N under ambient than elevated CO_2 (Table 1). We also found several instances in which percent shifts in response to N were significantly different from zero under ambient but not elevated CO_2, and vice versa (Table 1). For example, N additions significantly increased soil + microbial C per plant and significantly decreased microbial biomass C as a proportion of total tracer-C fixed under ambient but not elevated CO_2. On the other hand, N additions decreased soil + microbial C as a proportion of total tracer-C fixed, and as a proportion of belowground tracer-C, under elevated but not ambient CO_2 (Table 1). Despite these differential N responses, studies varied widely in the C pools reported and the units for reporting those inputs, resulting in small sample sizes that limit our ability to confidently assess interactive

effects of N and CO_2 availability and its potential ecological consequences (Table 1, Online Resource 1). We therefore recommend that future studies report all rhizodeposit C pools (soluble and insoluble soil C, microbial biomass C, and rhizosphere respiration C), and in multiple units (rhizodeposition C per plant, per unit root mass, per unit total tracer-C fixed, and per unit belowground tracer-C), to facilitate comparisons across studies. Such studies are needed to improve our understanding of the mechanistic controls on C and nutrient cycling in soils, particularly in light of the projected shifts in both anthropogenic N deposition (Kanakidou et al. 2016) and atmospheric CO_2 concentrations (IPCC 2014) in the coming decades.

Table 1 Summary data for studies assessing rhizodeposition in response to both CO_2 and nitrogen availability, subdivided according to CO_2 level

Units	Rhizodeposit C pool or Biomass	n	Ambient CO_2			Elevated CO_2			P-value
			Percent change in response to N	Min	Max	Percent change in response to N	Min	Max	
Plant^{-1}	SOLSOIL-C	1	221.1	–	–	245.8	–	–	–
	INSOLSOIL-C	1	147.0	–	–	9.3	–	–	–
	TOTALSOIL-C	5	129.5 (−26.4, 285.5)	16.6	337.1	166.5 (−65.4, 398.5)	−9.5	418.6	0.634
	MIC-C	3	89.4 (−90.0, 268.7)	42.7	172.5	59.5 (−182.0, 301.0)	−36.0	158.3	0.432
	SOILMIC-C	11	**83.3 (11.8, 154.8)**	−41.5	293.8	30.1 (−16.4, 76.7)	−58.9	159.9	**0.025**
	RR-C	5	32.8 (−20.6, 86.1)	−16.7	91.9	54.8 (−4.6, 114.3)	3.5	117.0	0.383
	SOILMICRR-C	5	75.0 (−27.3, 177.3)	5.0	209.1	43.2 (−7.9, 94.4)	2.1	89.0	0.528
	Total Root Mass	12	**86.9 (16.4, 200.4)**[a]	−28.6	550.5	**111.6 (31.4, 240.7)**[a]	−16.7	621.1	0.193
	Total Shoot Mass	12	**106.1 (39.1, 173.1)**	−27.8	297.1	**110.4 (45.6, 175.3)**	−14.8	276.5	0.610
	Total Biomass	12	**88.9 (31.7, 146.2)**	−32.6	221.6	**95.4 (41.1, 149.8)**	−13.1	215.7	0.622
Root mass^{-1}	SOLSOIL-C	0	–	–	–	–	–	–	–
	INSOLSOIL-C	0	–	–	–	–	–	–	–
	TOTALSOIL-C	4	10.3 (−51.2, 71.9)	−42.7	50.0	49.0 (−85.8, 183.8)	−40.0	121.4	0.494
	MIC-C	1	−12.5	–	–	−80.0	–	–	–
	SOILMIC-C	8	**−27.1 (−46.4, −7.7)**	−56.6	1.2	**−50.4 (−64.9, −30.0)**[a]	−69.2	0.0	0.054
	RR-C	3	24.9 (−61.1, 111.0)	−3.9	63.4	36.6 (−239.2, 312.4)	−50.7	161.5	0.830
	SOILMICRR-C	3	19.2 (−45.4, 83.8)	−3.1	47.7	24.1 (−209.5, 257.7)	−53.8	128.6	0.919
Total tracer-C fixed^{-1}	SOLSOIL-C	0	–	–	–	–	–	–	–
	INSOLSOIL-C	0	–	–	–	–	–	–	–
	TOTALSOIL-C	3	**−22.2 (−27.7, −16.8)**	−24.4	−20.0	**−39.7 (−50.2, −29.2)**	−43.8	−35.3	**0.042**
	MIC-C	3	**−28.3 (−46.8, −9.8)**	−36.8	−23.1	−37.6 (−137.3, 62.1)	−81.5	−2.8	0.672
	SOILMIC-C	7	−8.1 (−46.4, 30.1)	−60.0	72.5	**−39.8 (−50.7, −28.8)**	−61.5	−23.5	0.120
	RR-C	7	−18.4 (−37.6, 0.8)	−60.0	6.3	−16.1 (−44.9, 27.7)[a]	−45.8	104.4	0.735
	SOILMICRR-C	7	−5.4 (−24.9, 14.0)	−28.3	36.4	−21.1 (−46.7, 16.9)[a]	−47.9	78.8	0.709
	ROOT-C	7	**−19.2 (−36.8, −1.6)**	−42.9	6.9	11.1 (−42.2, 64.3)[b]	−20.0	141.1	0.386
	ROOTSOILMIC-C	7	**−18.0 (−34.6, −1.3)**	−49.4	4.9	−2.4 (−37.5, 32.8)[b]	−22.9	82.9	0.344
	ROOTSOILMICRR-C	7	**−16.4 (−27.0, −5.7)**	−32.1	−1.6	−6.5 (−27.9, 14.9)	−30.6	41.0	0.440
Tracer-C below-ground^{-1}	SOLSOIL-C	0	–	–	–	–	–	–	–
	INSOLSOIL-C	0	–	–	–	–	–	–	–
	TOTALSOIL-C	2	−1.0 (−86.5, 88.5)	−5.9	7.9	−35.8 (−83.5, 11.9)	−39.6	−30.1	0.054
	MIC-C	2	−12.5 (−171.3, 146.3)	−25	0	−32.1 (−655.2, 591.0)	−81.1	16.9	0.687
	SOILMIC-C	5	16.9 (−63.8, 97.5)	−41.1	127.5	**−35.2 (−59.3, −11.1)**	−61.4	−10.9	0.128
	RR-C	5	−5.4 (−39.4, 28.6)	−51.7	17.3	−2.5 (−44.0, 39.0)	−45.3	46.6	0.844
	SOILMICRR-C	5	14.8 (−16.5, 57.8)[a]	−6.7	78.6	−10.1 (−45.6, 25.4)	−47.5	27.8	0.266

Means with 95% confidence limits in parentheses. Means significantly different from zero, and p-values comparing N responses under ambient and elevated CO_2 that are significant at $a = 0.05$, are in bold. (n) number of studies reporting each pool; (−) no data available. (a) back-transformed data. (b) mean was significantly less than zero when excluding a single outlier. Abbreviations are as in Fig. 2

Methodological variation among studies may partially explain contrasting N effects on rhizodeposition

Although our analyses show that N effects on rhizodeposition described above were clearly dependent on the units of measure used, N effects on a given C pool were often mixed, even across studies using the same units. Therefore, we next investigated several key methodological variables which may underlie mixed results among studies.

One potential source of variation in N effects on rhizodeposition across studies is the use of pulse-chase versus continuous labeling, which can have important consequences for assessments of C flows in plant-soil systems (Meharg 1994). For example, senescing root tissues are likely not significantly labelled in pulse-chase studies since senescing tissues are poor sinks for C, but all tissues are expected to contain tracer-C in continuous labeling studies in which plants are exposed to tracer-C for a longer duration, thus generating a potentially large source of rhizodeposits that differs between the two methods and could affect quantification (Mikan et al. 2000; Henry et al. 2005). In the present review, pulse-chase and continuous labeling studies did not differ in the effect of N availability of any rhizodeposition C pools using t-tests, yet we found several instances in which responses to N were significantly different from zero for studies using one labeling method, but not the other (Table 2). For example, microbial C, soil + microbial C, rhizosphere respiration C, and soil + microbial + rhizosphere respiration C per plant all increased in response to N in continuous labeling but not pulse-chase studies. Greater increases in total rhizodeposition per plant in continuous labeling studies may be because N additions significantly increased total root mass in continuous labeling, but not pulse-chase studies (Table 2). Another possible explanation is the relatively short period of rhizodeposit collection (pulse plus chase periods) in pulse-chase studies compared to the weeks or months in continuous labeling studies in which tracer-C can be assimilated and translocated belowground (Nguyen 2003), although duration of rhizodeposit collection was not correlated with N effects on total rhizodeposition per plant (soil + microbial + rhizosphere respiration C) ($n = 9$, $p = 0.801$). Finally, as described above, due to the bias towards recently-fixed carbon in pulse-chase studies, and the more homogeneous labeling in continuous studies, the types of rhizodeposits detected in the two types of studies can differ, potentially affecting total rhizodeposition quantity and the detection of N effects. In any case, it is clear that the choice of labeling method contributed to the variation in N effects in studies reviewed here.

In addition to the methods by which root-derived C is measured, the species used in a given study can also affect the influence of N on rhizodeposition (Paterson and Sim 2000; Baptist et al. 2015). Studies reviewed here used both monocotyledonous and dicotyledonous plants, annuals and perennials, agricultural crops and wild species, graminoids and forbs, and legumes and non-legumes (Online Resource 1). Differences in the magnitude and/or direction of N responses among species could be due to a variety of underlying mechanisms, since plants exhibit a variety of different strategies for N acquisition, allocation, and storage (Chapin et al. 1990; Kraiser et al. 2011; Nacry et al. 2013). Indeed, in studies which assessed rhizodeposition in multiple species, differential responses to N among species were common (Van der Krift et al. 2001; Baptist et al. 2015; Butterly et al. 2015). For example, Baptist et al. (2015) investigated root-derived C inputs in four grass species, and reported species-by-N interactions for total rhizodeposited ^{13}C (sum of soluble soil ^{13}C, microbial ^{13}C, and microbially-respired ^{13}C), total rhizodeposited ^{13}C per unit root mass, microbial ^{13}C, and microbially-respired ^{13}C. Similarly, across all studies reviewed here, we found that annuals and perennials differed in the effects of N on soil + microbial biomass C per unit root mass, as well as soil + microbial biomass C and rhizosphere respiration C per unit tracer-C fixed (Table 3). Moreover, N additions led to a significant increase in root mass in perennials, but not annuals, indicating that differential growth responses to N availability could explain the differential rhizodeposition responses to N between the two life history strategies. To control for the influence of different species, we examined results of studies using ryegrass (*L. perenne*), the most frequently-used species in our literature review (used in 10 of the 48 studies). We found several instances in which N availability significantly affected rhizodeposition in some studies, but not others. For example, several studies reported responses to both N and CO_2 in *L. perenne*, and found either a significant main effect of N (Gorissen et al. 1995; van Ginkel et al. 1997; Bazot et al. 2006) or no main effect of N (Allard et al. 2006) on rhizosphere respiration tracer-C per unit total tracer-C fixed. Similarly, studies

Table 2 Summary data for studies assessing rhizodeposition in response to increased nitrogen availability, subdivided according to the type of isotope labeling used

Units	Rhizodeposit C pool or Biomass	Pulse-chase labeling				Continuous labeling				P-value
		n	Percent change in response to N	Min	Max	n	Percent change in response to N	Min	Max	
Plant^{-1}	SOLSOIL-C	0	–	–	–	2	175.6 (−401.6, 752.9)	130.2	221.1	–
	INSOLSOIL-C	0	–	–	–	2	329.0 (−1983.5, 2641.5)	147.0	511.0	–
	TOTALSOIL-C	1	90.6	–	–	6	149.5 (−35.5, 334.5)	−10.5	471.3	–
	MIC-C	1	52.9	–	–	10	**79.5 (0.4, 158.7)**	−42.9	316.7	–
	SOILMIC-C	6	13.5 (−46.5, 140.5)[a]	−41.5	293.8	18	**89.5 (40.3, 138.6)**	−48.5	363.5	0.162[b]
	RR-C	4	30.5 (−41.9, 102.9)	−16.7	91.9	7	**44.0 (24.9, 63.1)**	12.4	72.4	0.508
	SOILMICRR-C	4	81.4 (−65.7, 228.5)	5.0	209.1	7	**42.5 (24.4, 60.5)**	13.3	72.9	0.464
	Total Root Mass	14	−11.9 (−28.9, 9.2)[a]	−50.0	83.3	21	**55.4 (17.3, 105.9)[a]**	−37.0	550.5	**0.004[b]**
	Total Shoot Mass	10	30.6 (−1.3, 62.5)	−27.8	114.3	17	**83.6 (32.4, 154.6)[a]**	−40.0	825.0	0.047[b]
	Total Biomass	10	9.4 (−14.0, 39.1)[a]	−32.6	100.0	17	**57.0 (29.0, 91.1)[a]**	−13.1	202.1	**0.020[b]**
Root mass^{-1}	SOLSOIL-C	0	–	–	–	1	48.8	–	–	–
	INSOLSOIL-C	0	–	–	–	1	297.1	–	–	–
	TOTALSOIL-C	1	14.3	–	–	4	46.2 (−46.9, 302.1)[a]	−7.5	271.1	–
	MIC-C	1	−12.5	–	–	8	16.2 (−25.8, 58.3)	−29.4	115.3	–
	SOILMIC-C	5	−4.5 (−31.1, 55.4)[a]	−21.3	100.4	16	−5.9 (−30.5, 27.4)[a]	−67.9	201.4	0.806[b]
	RR-C	3	80.1 (−105.2, 265.3)	59.9	161.6	6	13.9 (−17.5, 45.2)	−20.6	61.6	0.088
	SOILMICRR-C	3	68.7 (−101.9, 239.3)	47.7	145.5	6	12.2 (−11.8, 36.2)	−20.3	45.5	0.095
Total tracer-C fixed^{-1}	SOLSOIL-C	1	22.2	–	–	0	–	–	–	–
	INSOLSOIL-C	1	−52.4	–	–	0	–	–	–	–
	TOTALSOIL-C	3	**−25.5 (−35.5, −15.6)**	−30.0	−22.2	4	−20.9 (−71.9, 30.2)	−65.3	10.0	0.792
	MIC-C	4	−15.0 (−76.1, 46.0)	−40.0	41.7	4	−5.3 (−60.9, 50.3)	−45.8	25.9	0.721
	SOILMIC-C	6	−7.8 (−55.0, 39.3)	−60.0	72.5	8	−6.2 (−40.9, 28.5)	−61.5	78.1	0.945
	RR-C	12	11.2 (−16.0, 38.4)	−60.0	89.4	8	−7.7 (−20.9, 5.6)	−35.9	10.9	0.185
	SOILMICRR-C	6	−3.1 (−27.0, 20.9)	−28.3	36.4	8	−8.1 (−24.7, 8.5)	−43.6	17.7	0.667
	ROOT-C	7	**−23.1 (−40.9, −5.3)**	−42.9	6.9	8	**−15.9 (−27.5, −4.2)**	−32.4	1.3	0.415
	ROOTSOILMIC-C	6	−18.3 (−37.0, 0.4)	−49.4	4.9	8	**−17.5 (−26.3, −8.7)**	−27.2	0.0	0.919
	ROOTSOILMICRR-C	6	**−14.6 (−27.8, −1.4)**	−32.1	0.5	8	**−14.1 (−23.5, −4.7)**	−30.6	3.9	0.934
Tracer-C below-ground^{-1}	SOLSOIL-C	0	–	–	–	0	–	–	–	–
	INSOLSOIL-C	0	–	–	–	0	–	–	–	–
	TOTALSOIL-C	1	−5.9	–	–	3	−15.3 (−89.7, 59.0)	−49.1	7.9	–
	MIC-C	1	−25.0	–	–	3	4.5 (−55.5, 64.6)	−17.1	30.6	–
	SOILMIC-C	3	23.6 (−202.3, 249.4)	−41.1	127.5	8	9.4 (−27.2, 46.0)	−42.8	101.4	0.726
	RR-C	3	−13.2 (−100.5, 74.1)	−51.7	17.3	8	6.3 (−4.0, 16.6)	−11.1	26.1	0.180
	SOILMICRR-C	3	26.1 (−88.2, 140.3)	−6.7	78.6	8	6.1 (−8.0, 20.2)	−20.2	30.8	0.291

Means are shown with 95% confidence limits in parentheses. Means that are significantly different from zero, and p-values comparing responses to N in pulse-chase versus continuous labeling that are significant at $a = 0.05$, are in bold. (n) indicates number of studies reporting each C pool; (−) indicates no data available. (a) indicates back-transformed data. (b) indicates *p*-value based on transformed data. Abbreviations for C pools are as in Fig. 2

reported either a significant main effect of N (van Ginkel et al. 1997; Allard et al. 2006) or no main effect of N (Bazot et al. 2006) on total soil tracer-C per unit total tracer-C fixed. Based on these results, it is clear that, although there are definite species-specific effects, differential responses to N among species do not completely explain the variation in N effects across studies seen here.

Table 3 Summary data for studies assessing rhizodeposition in response to increased nitrogen availability, subdivided according to plant life history

Units	Rhizodeposit C pool or Biomass	Annuals				Perennials				P-value
		n	Percent change in response to N	Min	Max	n	Percent change in response to N	Min	Max	
Plant^{-1}	SOLSOIL-C	1	130.2	–	–	5	26.9 (−112.0, 165.8)	−65.0	221.1	–
	INSOLSOIL-C	1	511.0	–	–	1	147.0	–	–	–
	TOTALSOIL-C	3	234.7 (−318.6, 788.1)	29.0	471.3	6	106.2 (−26.1, 238.5)	−10.5	337.1	0.293
	MIC-C	3	89.0 (−96.1, 274.2)	29.9	172.7	8	72.7 (−26.9, 172.2)	−42.9	316.7	0.832
	SOILMIC-C	12	**58.1 (6.1, 135.5)**[a]	−32.3	363.5	12	**65.9 (15.6, 116.1)**	−48.5	182.0	0.747[b]
	RR-C	7	**29.3 (4.1, 54.6)**	−16.7	72.4	4	**56.2 (6.6, 105.7)**	16.0	91.9	0.169
	SOILMICRR-C	7	**46.0 (16.6, 95.3)**[a]	13.2	209.1	4	48.4 (−7.3, 104.1)	5.0	88.9	0.863[b]
	Total Root Mass	18	1.5 (−16.9, 23.9)[a]	−50.0	136.4	23	**70.7 (26.5, 130.3)**[a]	−47.7	550.5	**0.005**[b]
	Total Shoot Mass	14	**39.3 (14.6, 69.3)**[a]	−12.1	180.0	19	**32.7 (13.2, 60.3)**[a]	−40.0	8158.2	0.129[b]
	Total Biomass	14	**27.4 (4.1, 55.9)**[a]	−15.6	161.5	19	**21.0 (2.8, 46.9)**[a]	−32.6	2693.2	0.074[b]
Root mass^{-1}	SOLSOIL-C	1	48.8	–	–	4	**−53.4 (−101.0, −5.9)**	−93.5	−26.3	–
	INSOLSOIL-C	1	297.1	–	–	0	–	–	–	–
	TOTALSOIL-C	3	101.0 (−266.2, 468.2)	3.4	271.1	7	18.8 (−13.7, 51.3)	−42.7	57.0	0.437
	MIC-C	3	14.0 (−52.0, 80.0)	−15.1	37.0	6	2.3 (−36.7, 65.4)[a]	−29.4	115.3	0.769[b]
	SOILMIC-C	11	24.2 (−7.4, 66.8)[a]	−21.3	201.4	10	−21.5 (−44.2, 1.2)	−67.9	14.3	**0.012**[b]
	RR-C	6	20.0 (−22.8, 86.7)[a]	−20.6	161.6	3	46.7 (−21.0, 114.4)	15.3	63.4	0.496[b]
	SOILMICRR-C	6	20.2 (−19.7, 80.0)[a]	−20.3	145.5	3	35.4 (−12.9, 83.7)	13.0	47.7	0.652[b]
Total tracer-C fixed^{-1}	SOLSOIL-C	0	–	–	–	1	22.2	–	–	–
	INSOLSOIL-C	0	–	–	–	1	−52.4	–	–	–
	TOTALSOIL-C	2	0.9 (−114.9116.6)	−8.2	10.0	5	**−37.9 (−81.5, 13.6)**[a]	−65.3	−20.0	0.367[b]
	MIC-C	3	2.6 (−89.1, 94.3)	−40.0	25.9	5	−17.8 (−60.7, 25.0)	−45.8	41.7	0.460
	SOILMIC-C	7	14.8 (−26.5, 56.0)	−39.3	78.1	7	**−28.6 (−51.3, −5.9)**	−61.5	4.1	**0.044**
	RR-C	13	13.0 (−11.0, 37.1)	−60.0	89.4	7	−13.8 (−27.5, 0.1)	−35.9	6.3	**0.045**
	SOILMICRR-C	7	4.1 (−14.4, 22.6)	−21.1	36.4	7	**−16.0 (−31.3, −0.8)**	−43.6	2.4	0.063
	ROOT-C	8	**−23.0 (−36.5, −9.4)**	−42.8	0.0	7	−15.0 (−30.6, 0.6)	−42.9	6.9	0.371
	ROOTSOILMIC-C	7	**−15.3 (−24.3, −6.3)**	−26.6	0.0	7	**−20.4 (−36.0, −4.9)**	−49.4	4.9	0.496
	ROOTSOILMICRR-C	7	**−11.6 (−20.4, −2.7)**	−23.4	3.9	7	**−17.0 (−29.1, −5.0)**	−32.1	0.5	0.389
Tracer-C below-ground^{-1}	SOLSOIL-C	0	–	–	–	0	–	–	–	–
	INSOLSOIL-C	0	–	–	–	0	–	–	–	–
	TOTALSOIL-C	1	−4.8	–	–	3	−15.7 (−89.6, 58.2)	−49.1	7.9	–
	MIC-C	1	30.7	–	–	3	−14.0 (−45.8, 17.7)	−25.0	0.0	–
	SOILMIC-C	7	33.9 (−20.1, 87.9)	−28.1	127.5	4	−22.8 (−61.3, 15.7)	−42.8	8.3	0.102
	RR-C	7	−0.4 (−23.6, 22.8)	−51.7	26.1	4	3.4 (−18.4, 25.1)	−11.1	17.3	0.791
	SOILMICRR-C	7	19.4 (−8.1, 46.9)	−6.3	78.6	4	−2.2 (−24.0, 20.4)	−20.2	11.7	0.211

Means are shown with 95% confidence limits in parentheses. Means that are significantly different from zero, and p-values comparing responses to N in annuals versus perennials that are significant at $a = 0.05$, are in bold. (n) indicates number of studies reporting each C pool; (−) indicates no data available. (a) indicates back-transformed data. (b) indicates p-value based on transformed data. Abbreviations for C pools are as in Fig. 2

Another possible source of variation contributing to the range of N effects seen here is the form and strength of the N treatments used, as studies reviewed here used N as nitrate such as KNO_3 (14 studies), ammoniacal N

such as $(NH_4)_2SO_4$ or urea (10 studies), and N as ammonium nitrate (NH_4NO_3; 23 studies), while one study did not report the form of N used (Online Resource 1). Given differential uptake capacities and growth responses to nitrate versus ammonium nutrition across species (Falkengren-Grerup 1995), these different N forms could have important consequences for rhizodeposition. For example, pulse-chase ^{14}C–labeled wheat had higher soil ^{14}C under NH_4NO_3 or NH_4SO_4 nutrition compared to $Ca(NO_3)_2$ nutrition (Lodhi et al. 2009). This could potentially be due to the higher energetic costs of nitrate assimilation, leading to higher respiratory losses from roots and lower rhizodeposition into soil (Henry et al. 2005; Gavrichkova and Kuzyakov 2008; Gavrichkova and Kuzyakov 2010). To examine whether the form of N used in a given study can influence the effects of N availability on rhizodeposition, we compared the response to N additions in studies using N as nitrate, N as ammonium nitrate, and N as ammonium/urea. Although the response of each rhizodeposit C pool to N availability differed among N forms only for rhizosphere respiration C using ANOVA/t-tests, we found several instances in which the response to N was significantly different from zero for some N forms but not others (Table 4). For example, N additions led to increased soluble soil C and microbial biomass C in studies using ammonium/urea but not ammonium nitrate, while N significantly impacted soil + microbial C per plant in studies using ammonium nitrate or ammonium/urea, but not those using nitrate (Table 4).

In addition to the form of N used, the different N treatment levels used could have contributed to the variation in N effects among studies. For example, Ge et al. (2015) treated rice (*Oryza sativa*) plants with either 0, 10, 20, or 40 mg N kg^{-1} soil, and found that ^{14}C in microbial biomass increased from low to intermediate N, then decreased from intermediate to high N. Studies reviewed here used a wide variety of N treatment levels, and the soils used in these studies varied in initial (background) N levels (Online Resource 1), which could have contributed to the variation in N effects across studies. Even similar N treatments in different soil types can result in different levels of available N, given variation in physical and biological properties across soils. Likewise, given that plant species differ in their N demands, similar N treatments may result in non-limiting N availability for some species, but limiting N availability for others. In order to account for all of these factors, yet obtain estimates of the importance of the strength of N treatments on rhizodeposition, we compared the effects of N additions on whole plant biomass (used as a biological indicator of total N availability) versus the effects of N additions on rhizodeposition. We found that the effect of N on plant biomass was strongly positively correlated with the effect of N on rhizodeposition ($r = 0.86$, $n = 9$, $p = 0.003$). This suggests that the strength of the N treatments applied (in terms of the biomass response to N additions) has a strong impact on the effects of N on total rhizodeposition. Altogether, it is clear that different levels and forms of N exert differential effects on rhizodeposition, indicating that the variety of different N treatments in studies reviewed here can partially explain their mixed results. The most appropriate solution in our view is to justify the use of specific N treatments (levels and form of N) based on ecologically-relevant conditions in the study species' field sites (Jensen and Christensen 2004; Bradford et al. 2008; Baptist et al. 2015).

A host of other methodological factors could also contribute to the variation in N effects seen here. For example, factors such as the age or developmental stage of plants in a given study could impact N effects on rhizodeposition, as ontogenetic shifts in biomass allocation, root turnover, and root physiological processes can strongly impact the magnitude of rhizodeposition (Nguyen 2003). Of the studies reviewed here which reported plant age at the start of rhizodeposit collection, 90% (36 out of 40) used plants <100 days old (median age = 30 days; mean = 133.8 days ±469.6 S.D.), indicating a bias towards young plants, similar to the findings of Jones et al. (2009). Although plant age was not correlated with N effects on total rhizodeposition (soil + microbial + rhizosphere respiration C) per plant, per root mass, per tracer-C fixed, or per belowground tracer-C ($n \geq 7$, all p-values >0.05), potentially due to the strong bias towards young plants, additional study of mature plants would be useful to determine whether N effects at early growth stages are representative of N effects throughout the life cycle. Other factors such as pot size could also have contributed to the variation in results seen here: the majority of studies reviewed here conducted experiments on potted plants, which could have potentially restricted root system growth and therefore the magnitude of rhizodeposition. Nevertheless, pot volume was not correlated with the effects of N on total rhizodeposition (soil + microbial + rhizosphere respiration C) in any of the units measured ($n \geq 8$, all $p > 0.05$).

Table 4 Summary data for studies assessing rhizodeposition and plant biomass in response to increased nitrogen availability, subdivided according to the form of nitrogen used

Units	Rhizodeposit C pool or Biomass	Nitrate				Ammonium nitrate				Ammonium/Urea				P-value
		n	Percent change in response to N	Min	Max	n	Percent change in response to N	Min	Max	n	Percent change in response to N	Min	Max	
Plant^{-1}	SOLSOIL	2	−15.4 (−73.4, 42.6)	−20.0	−10.9	2	−27.8 (−500.4, 444.8)	−65.0	9.4	2	**175.6 (−232.6, 583.8)**	130.2	221.1	0.180[c]
	INSOLSOIL	0	–	–	–	0	–	–	–	2	329.0 (−1306.2, 1964.2)	147.0	511.0	–
	TOTALSOIL	0	–	–	–	3	127.6 (−323.4, 578.5)	16.7	337.1	5	173.6 (−32.7, 379.9)	−10.5	471.3	0.744
	MIC	0	–	–	–	5	66.5 (−116.6, 249.7)	−42.9	316.7	5	**72.8 (25.5, 176.9)**[a]	29.9	172.7	0.238[b]
	SOILMIC	7	22.2 (−34.9, 79.3)	−48.5	123.5	10	**83.1 (7.4, 158.8)**	−41.5	293.8	6	**137.4 (8.6, 266.1)**	0.4	363.5	0.143[b]
	RR	1	72.4	–	–	7	**21.3 (3.0, 39.6)**	−16.7	42.5	2	**58.4 (42.7, 74.1)**	56.7	60.1	**0.040**
	SOILMICRR	1	72.9	–	–	7	**28.9 (8.5, 61.5)**[a]	5.0	209.1	2	49.8 (−29.8, 129.5)	41.0	58.7	0.783
	Total Root Mass	13	21.6 (−8.9, 52.0)	−47.7	119.7	19	**73.0 (20.0, 149.4)**[a]	−50.0	550.5	8	−0.9 (−29.0, 43.3)[a]	−39.5	136.4	0.052[b]
	Total Shoot Mass	7	37.3 (−7.7, 82.3)	−12.1	129.0	19	**66.3 (23.9, 152.6)**[a]	−40.0	8158.2	6	77.1 (6.8, 147.4)	−3.3	180.0	0.210[c]
	Total Biomass	7	30.9 (−14.6, 76.4)	−12.3	127.0	19	**53.6 (20.7, 111.2)**[a]	−32.6	2693.2	6	52.1 (−10.8, 115.1)	−13.1	161.5	0.296[c]
Root Mass^{-1}	SOLSOIL	2	−31.0 (−90.7, 28.7)	−35.7	−26.3	2	−75.9 (−300.4, 148.7)	−93.5	58.2	1	48.8	–	–	0.221
	INSOLSOIL	0	–	–	–	0	–	–	–	1	297.1	–	–	–
	TOTALSOIL	0	–	–	–	6	21.3 (−17.6, 60.3)	−42.7	57.0	3	97.4 (−209.9, 404.7)	−7.5	271.1	0.477
	MIC	0	–	–	–	5	15.0 (−62.5, 92.6)	−29.4	115.3	3	18.2 (−47.5, 83.9)	−15.1	49.6	0.939
	SOILMIC	7	−14.8 (−40.5, 11.0)	−67.9	14.3	9	−0.1 (−42.3, 42.1)	−56.6	100.4	4	72.7 (−49.6, 195.0)	3.5	201.4	0.097
	RR	1	−20.6	–	–	6	44.5 (−21.2, 110.3)	−3.9	161.6	1	61.6	–	–	–
	SOILMICRR	1	−20.4	–	–	6	33.3 (−5.8, 88.6)[a]	−3.1	145.5	1	45.5	–	–	–
Total tracer-C fixed^{-1}	SOLSOIL	1	22.2	–	–	0	–	–	–	0	–	–	–	–
	INSOLSOIL	1	−52.4	–	–	0	–	–	–	0	–	–	–	–
	TOTALSOIL	1	−30.0	–	–	2	−16.3 (−119.0, 86.4)	−24.4	−8.2	3	−25.1 (−102.0, 51.8)	−65.3	10.0	0.781
	MIC	2	0.8 (−518.0, 519.7)	−40.0	41.7	2	−1.6 (−298.6, 295.3)	−25.0	21.7	3	−14.3 (−88.7, 60.1)	−45.8	25.9	0.911
	SOILMIC	2	−14.7 (−81.0, 51.5)	−20.0	−9.5	8	3.7 (−37.5, 45.0)	−60.0	78.1	3	−22.5 (−98.4, 53.4)	−61.5	13.1	0.706[b]
	RR	5	25.9 (−25.5, 77.3)	−21.1	89.4	8	−11.3 (−30.3, 7.8)	−60.0	10.9	6	9.2 (−29.2, 47.7)	−35.9	80.9	0.208[b]
	SOILMICRR	2	−9.3 (−159.2, 140.5)	−21.1	2.4	8	0.9 (−15.9, 17.7)	−28.3	36.4	3	−16.5 (−68.9, 36.0)	−43.6	7.9	0.476
	ROOT	2	−9.6 (−43.1, 23.9)	−12.2	−7.0	9	**−22.1 (−36.4, −7.7)**	−42.9	6.9	3	−19.6 (−56.7, 17.5)	−32.4	1.3	0.634[c]
	ROOTSOILMIC	2	**−10.8 (−13.7, −7.8)**	−11.0	−10.5	8	**−16.6 (−30.7, −2.6)**	−49.4	4.9	3	**−26.9 (−27.5, −26.4)**	−27.2	−26.6	0.111[c]
	ROOTSOILMICRR	2	−7.3 (−107.8, 93.1)	−15.3	0.5	8	**−12.3 (−22.5, −2.1)**	−32.1	3.9	3	**−23.4 (−39.2, −7.6)**	−30.6	−15.1	0.280

Table 4 (continued)

Units	Rhizodeposit C pool or Biomass	Nitrate				Ammonium nitrate				Ammonium/Urea				P-value
		n	Percent change in response to N	Min	Max	n	Percent change in response to N	Min	Max	n	Percent change in response to N	Min	Max	
Tracer-C below-ground^{-1}	SOLSOIL	0	–	–	–	0	–	–	–	0	–	–	–	–
	INSOLSOIL	0	–	–	–	0	–	–	–	0	–	–	–	–
	TOTALSOIL	0	–	–	–	1	−4.8	–	–	2	−20.6 (−276.7, 235.4)	−49.1	7.9	–
	MIC	0	–	–	–	1	30.6	–	–	2	−8.5 (−85.2, 68.2)	−17.1	0.0	–
	SOILMIC	1	−5.4	–	–	6	28.1 (−45.1, 101.3)	−41.1	127.5	3	−0.4 (−79.0, 78.2)	−42.8	33.2	0.540
	RR	1	−6.8	–	–	6	0.5 (−18.3, 32.7)[a]	−51.7	17.3	3	9.2 (−29.0, 47.4)	−11.1	26.1	0.811[b]
	SOILMICRR	1	−6.3	–	–	6	**10.2 (0.2, 35.8)**[a]	0.8	78.6	3	6.3 (−42.8, 55.3)	−20.2	27.2	0.467[b]

Means are shown with 95% confidence limits in parentheses. Means significantly different from zero, and p-values comparing responses to N availability among the different N forms that are significant at $\alpha = 0.05$, are in bold. (n) indicates number of studies reporting each C pool; (−) indicates no data available. (a) indicates back-transformed data. (b) indicates p-value based on transformed data. (c) indicates p-value from Kruskal-Wallis test. Abbreviations for C pools are as in Fig. 2

Only a small minority of the studies reviewed here (4 of 48 studies) were conducted in the field; additional field studies are needed to better understand the applicability of experiments assessing N effects on rhizodeposition using potted plants. Another factor likely contributing to the variable N effects on rhizodeposition is the wide variety of methods for separating roots from soil. For example, some studies use mesh sieves with or without washing to remove roots from soil, while others use hand-picking with or without the aid of a dissecting microscope, potentially leading differential inclusion of root fragments in rhizodeposition calculations across studies (Online Resource 1). This may be particularly important for studies assessing N effects on rhizodeposition, as N can affect root system size, and therefore also likely affects the level of root fragments and debris in the soil. Finally, as described above, differential isotope fractionation across N levels by both plants and microbes is another potential source of variation leading to the variable N effects on rhizodeposition reported here.

Although we assess the impacts of several key experimental variables above, the generally small number of studies reporting comparable rhizodeposit C pools, and in similar units, precluded a formal meta-analysis. Thus, reporting data in multiple units is imperative for future studies to improve our understanding of the influence of N on rhizodeposition. Another step towards advancing the field would be determination of the effects of key methodological variables such as those described above in studies assessing the effects of N on rhizodeposition. This would involve factorially manipulating variables such as pulse versus continuous labeling, as well as pulse and chase duration and frequency. Such studies would help to establish whether a standardized set of experimental parameters is necessary, and to inform on what those parameters should be. Next, incorporating multiple N levels and N forms, determined based on conditions in the study species' field sites, would improve confidence in the relevance of each study for natural conditions (Bradford et al. 2008). We also suggest such studies include multiple species, which could potentially reveal taxonomic patterns in N effects not currently identifiable in the literature due to confounding different species with different experiments. Conducting studies directly in the field would be the most advantageous, and systems for isotope-labeling in the field have been recently used to assess N effects on rhizodeposition (Hill et al. 2007; Butterly et al. 2015). Lastly, the majority of studies reviewed here collected data at only a single harvest date,

potentially obscuring patterns that would have been detected at earlier or later dates. For example, several studies reported significant interactions between N and sampling date, or significant effects of N at some dates but not others (Kuzyakov et al. 2002b; Bazot et al. 2006; but see Butterly et al. 2015). Future studies should consider multiple sampling dates to assess N effects that may not be captured in experiments with a single sampling event.

N effects on composition and quality of root-derived C inputs

Our review has thus far focused on the quantitative impact of N of rhizodeposition, which is likely an important determinant of soil C and nutrient cycling (Kuzyakov 2002b, 2010; de Graaff et al. 2014). In addition to quantity, however, substrate quality is an important prerequisite for microbial utilization in soil (Hobbie 2000; Tiemann and Billings 2011), yet surprisingly few studies have investigated the influence of N availability on the composition of rhizodeposits. The studies that have examined this agree that N deficiency results in lower rhizodeposition of a variety of amino acids (Bowen 1969; Carvalhais et al. 2011), potentially due to lower amino acid concentrations in the roots of N-deficient plants (von Wirén et al. 2000). Carvalhais et al. (2011) also reported lower rhizodeposition of the disaccharide maltose under N deficiency.

An intriguing question is whether such shifts in the composition of rhizodeposits in response to low N will alter microbial nutrient transformations in ways that enhance local N availability (Dijkstra et al. 2013). For example, the soil of low N-treated plants sometimes, but not always, exhibits greater decomposition of extant soil organic matter (SOM) compared to high N-treated plants (Liljeroth et al. 1990; Billes et al. 1993; Zagal et al. 1993; Liljeroth et al. 1994; van Ginkel et al. 1997; Cheng and Johnson 1998; van Ginkel and Gorissen 1998; Van der Krift et al. 2001; Fontaine et al. 2004; Hoosbeek et al. 2006). This suggests a priming effect, defined broadly as an increase in extant SOM decomposition due to the addition of labile substrates (Bingeman et al. 1953; van der Wal and de Boer 2017), by which plants can increase N availability in low N soils. When N availability is low, rhizodeposits may shift towards higher C:N ratios (Blagodatskaya et al. 2010), which may in turn cause soil microbes to shift towards decomposing extant SOM to a greater extent to satisfy their demand for N (Zagal et al. 1993; van Ginkel et al. 1997; van Ginkel and Gorissen 1998; Kuzyakov 2002b, 2010; Lloyd et al. 2016). In the short term, this may lead to N immobilization in microbes, but in the longer term, may lead to greater N availability for plants as those microbes turn over (Darwent et al. 2003; Paterson 2003). This hypothesis received mixed support from a recent study which found that application of sucrose (containing no N) to soil led to greater priming effects over time than maize root extracts (containing N) in a clay soil, as predicted. However, both substrates led to similar priming effects in a sandy soil, suggesting no impacts of rhizodeposit C:N on SOM decomposition (Lloyd et al. 2016). Nevertheless, it is unlikely that plants ever completely eliminate the loss of N through their roots, even in low N conditions, limiting the applicability of sucrose as a realistic representative for rhizodeposition. Along those lines, a recent study coupling computer modeling and synthetic exudate applications found that some level of N loss from roots (rhizodeposition of N-containing metabolites) may actually be beneficial for maximizing priming effects, since C-only exudates can constrain microbial biomass and exoenzyme synthesis (Drake et al. 2013).

In contrast to low N conditions, N fertilization often decreases microbial decomposition of extant SOM, and increases decomposition of more easily degradable carbon sources (Fog 1988; Tiemann and Billings 2011), such as the soluble, labile C compounds in root exudates which are a component of rhizodeposits. Soil microbes have been proposed to preferentially decompose such labile substrates compared to extant SOM under high N conditions (Cheng and Johnson 1998), potentially because N fertilization tends to increase total rhizodeposition as seen in our quantitative analyses above, and/or because the N in the rhizodeposits is sufficient to meet microbial N demand. This hypothesis is in agreement with the recent finding that increased input of synthetic root exudates leads to lower decomposition of plant residues in soil (de Graaff et al. 2010). Nevertheless, the mixed effects of low and high N-treated plants on extant SOM decomposition, and their many possible interactions with other factors such as temperature, CO_2, and light availability, warrant further investigation of how N availability can impact the composition of rhizodeposits and the resulting impacts on N cycling in soil (Dijkstra et al. 2013; Cheng et al. 2014).

It is worth noting that the effects of N on decomposition of rhizodeposits versus extant SOM described above can reflect shifts in the quality and quantity of

those rhizodeposits (Liljeroth et al. 1990; Liljeroth et al. 1994), but could also reflect shifts in the diversity and activity of rhizosphere microbial communities (Van der Krift et al. 2001; Bazot et al. 2006; Dijkstra et al. 2013; Cheng et al. 2014; Geisseler and Scow 2014; Geisseler et al. 2016). For example, a recent meta-analysis (Treseder 2008) showed that N fertilization tends to reduce overall soil microbial biomass, although there was no effect in studies considering only bacteria. This is somewhat surprising, given that our quantitative analyses found that N additions tend to increase total C rhizodeposition and therefore the C available for microbial growth and metabolism; however, the findings of Treseder (2008) could simply reflect the great variation in N effects on C rhizodeposition seen here. Similarly, some studies report shifts in rhizosphere community composition in response to N availability (Gschwendtner et al. 2016; Wang et al. 2016; Lv et al. 2017), while others report that these shifts are dependent upon the duration of the chase period following labeling (Li et al. 2016). Finally, soil amendments such as organic fertilizers and biochars can potentially influence the abundance and diversity of soil bacteria involved in N transformations (*Nitrosomonas, Nitrospira*) (Zhang et al. 2017). These studies raise an important question from a mechanistic standpoint: are shifts in microbial community diversity in response to N mediated by the effects of N on the quantity and composition of rhizodeposits, or do such shifts represent direct N effects on microbes? Separating plant effects on microbes from direct effects of N on microbes can be accomplished, for example, by comparing microbial diversity in non-sterile planted soil treated with high or low N to microbial diversity in non-sterile plant-free soil treated with high or low N. An alternative method could include collection of root exudates under sterile conditions, followed by application of those exudates to microbes in plant-free soil at low and high N.

Key challenges and future directions for understanding N effects on rhizodeposition

Our review of studies experimentally manipulating N availability indicates several key challenges and outstanding questions in the literature regarding the influence of N availability on rhizodeposition. The most obvious challenges are the limitations associated with the currently-available methods for investigating root-derived C inputs. Although isotope-labeling techniques are useful for determining N effects on total C inputs, they do not allow for the identification of the specific C compounds produced by roots, except when conducted in sterile culture which renders isotope labeling unnecessary. Sterile culture, on the other hand, allows for both quantification of soil C inputs as well as identification of the specific metabolites comprising those inputs. However, sterile culture is limited in that soil microbes can strongly influence rhizodeposition through their effects on root morphology, C allocation to roots (such as for mycorrhizal symbioses, or for root nodules in leguminous plants), and root-soil concentration gradients (Nguyen 2003), and in any case does not realistically represent conditions that plants experience. It is difficult to envision a non-sterile method in which the composition of rhizodeposits could be accurately assessed, although the use of biosensors (microbial strains engineered to display a measurable signal in the presence of a specific metabolite) may be one possible route (Jaeger et al. 1999; Bringhurst et al. 2001). For example, Jaeger et al. (1999) report the use of two strains of *Erwinia herbicola* engineered to exhibit ice nucleation activity (measured as the catalysis of ice formation at temperatures > −10 °C) in the presence of tryptophan and sucrose, respectively. Although neither strain exhibited significant ice nucleation signal in bulk soil, both strains did so in the rhizosphere of the grass *Avena barbata,* indicating the presence of tryptophan and sucrose. In addition, the two strains exhibited different spatial patterns along the root system, suggesting differential localization of tryptophan and sucrose rhizodeposition from roots (Jaeger et al. 1999). However, such approaches are still limited in that they cannot distinguish tryptophan (or sucrose) that came directly from plant roots from tryptophan (or sucrose) produced by rhizosphere microbes. The field would benefit from the further development of approaches that sidestep the logistical challenges associated with isotope labelling, as well as the limitations of growing plants in sterile, unnatural conditions (discussed in further detail below).

A related challenge is in establishing mechanistic links between plant traits and root-derived C inputs (Jones et al. 2009). Such links are needed for improved predictions of global C dynamics (Rasse et al. 2005; Kell 2012). For example, Henry et al. (2005) showed that a model including both the number of root apices and the concentration of soluble C in the roots explained over half of the variation in root-derived soil C for

Lolium multiflorum, both within and among N treatments. Other studies reviewed here reported correlations between root mass or root soluble C and rhizodeposition C pool sizes (Liljeroth et al. 1990; Van der Krift et al. 2001; Baptist et al. 2015; Ge et al. 2015). These studies illustrate the necessity for assessing root traits accurately and in realistic conditions. Additional studies examining whether such relationships are generalizable within and among species, developmental stages, and environments would be an important step towards determining the mechanisms of C losses to soil. Such studies would also allow the use of commonly-measured roots traits for predicting root C losses in the field, thereby avoiding the difficulties associated with isotope-based systems.

We also note several outstanding questions regarding N effects on rhizodeposition. The first, as described above, is whether more definitive generalities can be made regarding whether and how N affects rhizodeposition. This requires additional studies reporting comparable rhizodeposit C pools in multiple units (as described above) for more traditional meta-analyses than reported here. The next question is how the composition of rhizodeposits responds to varying N availability. Surprisingly few studies have attempted to address this question, despite the widely-assumed importance of rhizodeposition for N cycling in soils. A logical follow-up question is to ask which of those rhizodeposits are metabolized by microbes, and whether this is affected by N levels. Experimental incubations with synthetic exudates in which one or more constituents are isotopically-labeled could help determine the specific compounds microbes are assimilating. Such studies are essential for determining the specific metabolites by which plants signal and sustain ecologically-important soil microbes. The next step would be to ask which microbes are consuming those specific rhizodeposits, and whether this is affected by N levels. One recent and powerful strategy for addressing this question is combining DNA, RNA, or phospholipid fatty acid (PLFA) profiling of soil microbes with stable isotope probing (DNA/RNA/PLFA-SIP). This method involves either growing plants in an isotopically-enriched CO_2 atmosphere, or applying isotopically-labeled synthetic exudate mixes to soil, followed by analyses of isotopically-labeled microbial DNA, RNA, or PLFA in order to identify the microbes that utilized the exudates (Radajewski et al. 2000; Singh et al. 2004; el Zahar Haichar et al. 2008; Li et al. 2016). Caveats of these methods which limit the researcher's ability to determine the organisms which initially consumed the rhizodeposits include: the relatively poor phylogenetic resolution of PLFA-based studies, the relatively low sensitivity of DNA/RNA-SIP studies in which both unlabeled C (^{12}C) and tracer-C are available to soil organisms, as well as the fact that tracer-C taken up directly by microbes may then be assimilated by organisms that consume them (Radajewski et al. 2000; Singh et al. 2004). A similar type of study applied sucrose with varying $^{13}C/^{12}C$ ratios, and assessed shifts in relative ^{13}C abundance in fungal specific (glucosamine) and bacterial specific (muramic acid) metabolites to ascertain the relative utilization of sucrose by the two microbial groups (Indorf et al. 2015). However, few studies have used the above methods while also manipulating N availability, particularly in agricultural soils (but see Wang et al. 2016; Ge et al. 2017) where anthropogenic N deposition can be most effectively managed. A final question concerns the effects of rhizodeposition at varying N levels on microbial function in the rhizosphere, and whether plants manipulate the N cycle in the rhizosphere according to N demand. Both these questions require the separation of plant effects on microbial function from direct effects of N on microbial function, as described above. Answers to all of the interlinked questions outlined here are needed to bridge the gap between N-mediated impacts on root morphology, physiology, and metabolism, and downstream microbial nutrient cycling and ecosystem function.

Conclusions

Rhizodeposition is considered to be of vital importance for plant mineral nutrition, microbial activity, and ecosystem function (Grayston et al. 1996; Hütsch et al. 2002; Paterson 2003; Jones et al. 2009; Kuzyakov 2010; Phillips et al. 2011). Given the dependence of soil N availability on microbial transformations, it is often assumed that alteration of rhizodeposition is an important mechanism by which plants regulate N availability in the rhizosphere. Here, we reviewed studies assessing impacts of N on rhizodeposition, and found surprisingly large variation in the C inputs reported as well as the units for reporting those inputs. Although our analyses indicate that the effects of N were dependent on the units of measure used, N effects on rhizodeposition were often mixed, due to a combination of variation in experimental methods and species-specific effects. Our

review and quantitative analyses also revealed several key challenges and outstanding questions for better understanding the mechanistic links between N availability, plant function, and microbial activity. Identifying such links would substantially improve our ability to predict C- and N-dynamics in changing ecosystems.

Data availability statement All data generated or analyzed during this study are included in this published article [and its supplementary information files].

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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