

# Trends and methodological impacts in soil CO<sub>2</sub> efflux partitioning: A metaanalytical review

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## Abstract

Partitioning soil carbon dioxide (CO<sub>2</sub>) efflux ( $R_S$ ) into autotrophic ( $R_A$ ; including plant roots and closely associated organisms) and heterotrophic ( $R_H$ ) components has received considerable attention, as differential responses of these components to environmental change have profound implications for the soil and ecosystem C balance. The increasing number of partitioning studies allows a more detailed analysis of experimental constraints than was previously possible. We present results of an exhaustive literature search of partitioning studies and analyse global trends in flux partitioning between biomes and ecosystem types by means of a metaanalysis. Across all data, an overall decline in the  $R_H/R_S$  ratio for increasing annual  $R_S$  fluxes emerged. For forest ecosystems, boreal coniferous sites showed significantly higher ( $P < 0.05$ )  $R_H/R_S$  ratios than temperate sites, while both temperate or tropical deciduous forests did not differ in ratios from any of the other forest types. While chronosequence studies report consistent declines in the  $R_H/R_S$  ratio with age, no difference could be detected for different age groups in the global data set. Different methodologies showed generally good agreement if the range of  $R_S$  under which they had been measured was considered, with the exception of studies estimating  $R_H$  by means of root mass regressions against  $R_S$ , which resulted in consistently lower  $R_H/R_S$  estimates out of all methods included. Additionally, the time step over which fluxes were partitioned did not affect  $R_H/R_S$  ratios consistently. To put results into context, we review the most common techniques and point out the likely sources of errors associated with them. In order to improve soil CO<sub>2</sub> efflux partitioning in future experiments, we include methodological recommendations, and also highlight the potential interactions between soil components that may be overlooked as a consequence of the partitioning process itself.

*Keywords:* autotrophic respiration, carbon cycling, heterotrophic respiration, metaanalysis, partitioning techniques, root respiration, soil CO<sub>2</sub> flux

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## Introduction

In studies of the carbon (C) cycle of terrestrial ecosystems, soils have received considerable interest because of their critical role in the long-term storage of C sequestered from the atmosphere. The C balance of soils depends on the balance of C input and release, which show different temporal (i.e. seasonal or inter-annual) patterns and respond differently to environmental drivers. There is by now a considerable volume of studies quantifying soil carbon dioxide (CO<sub>2</sub>) efflux

( $R_S$ ) in a wide range of ecosystems, and investigating its temporal dynamics and abiotic controls (e.g. Raich & Schlesinger, 1992; Lloyd & Taylor, 1994; Raich *et al.*, 2002). However, while this knowledge has improved the general understanding of C cycling between plants, soil, and the atmosphere, it is of only limited use for the question of long-term C sequestration in the soil. Additionally, the need to separate individual components of  $R_S$  has emerged to better understand mechanisms underlying total  $R_S$ , and enabling predictions under changing environmental conditions (Ryan & Law, 2005).

Sources of CO<sub>2</sub> in the soil include (A) growth and maintenance respiration by roots (true root respiration), (B) rhizomicrobial respiration (i.e. heterotrophic decom-

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position of carbohydrates derived from live roots), (C) decomposition of fresh organic matter (surface and root litter), (D) decomposition of old soil organic matter (SOM), (E) priming of SOM decomposition by substrate input from live roots or plant litter, and (F) weathering of soil carbonates. The dynamics of these components are controlled by a range of biotic and abiotic factors, such as temperature, water availability, aboveground vegetation structure, photosynthetic activity, or plant phenological development. With regard to long-term storage of C in soils, there is an on-going debate whether the decomposition of old SOM shows the same response to temperature as fresh organic matter (e.g. Fang *et al.*, 2005; Knorr *et al.*, 2005; Reichstein *et al.*, 2005). The temperature sensitivity of root respiration had been reported to differ from that of heterotrophic decomposition (Boone *et al.*, 1998; Pregitzer *et al.*, 2000; Epron *et al.*, 2001), but more recent results suggest that there is no difference in the temperature sensitivity between autotrophic and heterotrophic CO<sub>2</sub> sources in the soil (e.g. Bååth & Wallander, 2003; Bhupinderpal-Singh *et al.*, 2003; Irvine *et al.*, 2005; Sulzman *et al.*, 2005). A number of recent publications suggest that acclimation occurs in response to increased temperatures both in soil CO<sub>2</sub> efflux (e.g. Kirschbaum, 2004; Eliasson *et al.*, 2005) and autotrophic respiration (e.g. Atkin *et al.*, 2000, 2005; Atkin & Tjoelker, 2003; Burton & Pregitzer, 2003; Loveys *et al.*, 2003; Cooper, 2004), but a better understanding of the underlying processes is needed before conclusive predictions are possible. The close link of root-derived CO<sub>2</sub> flux and substrate supply from aboveground (Ekblad & Höglberg, 2001; Ekblad *et al.*, 2005; Irvine *et al.*, 2005) mask a direct correlation with soil temperature, and increased fluxes because of increased substrate supply following higher canopy assimilation may be interpreted as an increase in temperature sensitivity. In a recent synthesis of forest free-air CO<sub>2</sub> enrichment (FACE) experiments, King *et al.* (2004) found a stimulating effect of elevated CO<sub>2</sub> concentrations on soil CO<sub>2</sub> efflux, with differential responses for species and stand age. Under a global change scenario, therefore, the fertilization effect on plants by higher CO<sub>2</sub> concentrations is likely to be at least as important to future root contributions (fractions A and B) to  $R_S$  as its response to an increase in temperature.

An unresolved question in this context is the possibility of soil priming (E), where older SOM is decomposed as a consequence of increased root activity (Kuzakov & Cheng, 2001; Kuzakov, 2002; Subke *et al.*, 2004b; Trueman & Gonzalez-Meler, 2005). While this priming effect may have the potential of accelerating SOM decomposition in the future, its relevance and magnitude has not been addressed sufficiently to make any firm predictions.

Dividing  $R_S$  broadly into autotrophic and heterotrophic flux components ( $R_A$  and  $R_H$ , respectively) means that differences between subcomponents within these groups (e.g. between fractions A and B for  $R_A$  and C and D for  $R_H$ ) are ignored. It is none the less a useful distinction, as it allows a separation and interpretation of relevant soil processes. Earlier reviews of global patterns in soil respiration have addressed this partitioning between  $R_A$  and  $R_H$  (Schlesinger, 1977; Singh & Gupta, 1977; Raich & Nadelhoffer, 1989; Raich & Tufekcioglu, 2000), but estimates of relative contributions were based on only a few studies from select ecosystems, or used a simplistic mass balance approach to obtain maximum C-allocation to roots from measured  $R_S$  and aboveground litter input. Hanson *et al.* (2000) reviewed partitioning methods and a range of observations from different biomes and ecosystems, indicating a mean contribution from autotrophic sources of 48% and 60% for forest and nonforest ecosystems, with a range of 10–90% contributions from different studies. However, these average estimates mask considerable variation because of the diversity of ecosystems, and potential biases because of different techniques and time scales.

To date, a variety of methods have been used to separate individual components of the overall soil CO<sub>2</sub> efflux, both under laboratory conditions or measured in the field. These methods act over a range of spatial scales, from the isolation of individual plant organs (roots) or soil components (e.g. surface litter), to input from aboveground plant parts at the stand level (trenching or forest girdling), as well as over a wide range of temporal scales (from hours or days in pulse label experiments to several years in long-term field studies). The results reported, therefore, only give limited insight into specific settings, and it is not clear if different (and sometimes conflicting) results are due to method-related artefacts, or to differences in the experimental setting. To date, no intercomparison of results obtained from different methods has been published, despite a wealth of studies reporting soil CO<sub>2</sub> efflux partitioning from almost all of the world's terrestrial biomes. The aim of this review is to provide the best estimate fluxes and their confidence limits based on a metaanalytic survey of the peer-reviewed literature. In particular, we critically review the methods commonly used to partition soil CO<sub>2</sub> efflux, and highlight method related biases in flux separation estimates from geographical, seasonal, or ecosystem related trends of flux contribution.

### Soil CO<sub>2</sub> efflux partitioning methods

We only list a brief description of techniques commonly used to separate root derived and microbial derived

components in soil CO<sub>2</sub> efflux, in order to define the categories used during the analysis. The reader is referred to Hanson *et al.* (2000) for an overview and more detailed descriptions of the different methodologies. Here, we distinguish between four principal ways in which soil CO<sub>2</sub> efflux has been separated into different components: (1) root exclusion, (2) physical separation of components, (3) isotopic techniques, and (4) indirect methods. The following section defines the different techniques within these groups, as we have categorized them for the purpose of this analysis.

#### *Root exclusion*

*Trenching.* This technique relies on severing all roots around the perimeter of the treatment plot in order to disrupt aboveground input from trees (e.g. Epron *et al.*, 1999). To exclude also any C input from subcanopy species, where present, these are generally removed. A trench is dug to a depth deeper than the main rooting zone, and any regrowth prevented by lining the trench with an impenetrable material (e.g. using polyethylene film). Some studies use deep soil collars which are inserted beyond the main rooting zone, and the surface CO<sub>2</sub> efflux from these collars is used as the heterotrophic flux components, and we classify these studies with the larger scale trenching approach.

*Girdling.* This technique applies to forest stands only. During stem girdling, the bark is removed over several centimetres around the circumference of all trees within the treatment plot. This treatment allow the trees to maintain water transport from the roots to the crown in the xylem, while disrupting the transport of assimilates from the crowns to the roots in the phloem, as the cambium is removed with the bark (e.g. Högberg *et al.*, 2001). While roots are not actually excluded from treatment plots, the disruption of substrate supply means that they are effectively removed from the active soil biota, and we place them therefore in this category.

*Clipping.* Applies to grassland and shrub communities, where all aboveground parts of the plants are clipped and removed, leaving the root system intact, but starved of aboveground input (e.g. Wan & Luo, 2003).

*Gap.* Several studies have compared the soil CO<sub>2</sub> efflux in mature stands to forest gaps created by clear-cuts, in order to estimate the amount of CO<sub>2</sub> from live root respiration (e.g. Nakane *et al.*, 1996). However, this comparison of efflux between gap and intact forest requires a number of corrections regarding altered

conditions in the gap beyond the exclusion of flux from roots (see Discussion).

#### *Physical separation of components*

*Components.* This category includes all studies that have separated soil cores taken in the field to measure the respiration of some or all of its components (surface litter, roots, and SOM) in isolation in order to assess individual contributions (e.g. Thierron & Laudelout, 1996). Following their physical separation (superficial removal of litter, sieving of organic and mineral soil to separate roots), the components are commonly incubated at a standard temperature, and the CO<sub>2</sub> evolved under these conditions is taken as the true CO<sub>2</sub> flux contribution at this given temperature. We also include studies that measure root free soil in isolation and derive root contribution to  $R_S$  by subtracting this flux from field measurements of  $R_S$  (e.g. Lamade *et al.*, 1996).

*Root excising.* This technique relies on measuring the CO<sub>2</sub> produced by roots shortly after being recovered from a fresh soil core (e.g. Law *et al.*, 2001b). The root contribution to  $R_S$  is then calculated using this flux and estimates of root density in a stand, and measurements of undisturbed  $R_S$ . While this is analogous to the components methodology, it is widely used, and we decided on a separate category to investigate the effect of this particular technique without grouping it with other component studies.

*Live root respiration.* Following the careful excavation of entire roots (including fine roots), these are enclosed in a cuvette while still attached to the plant, to measure CO<sub>2</sub> production by roots directly (Kutsch *et al.*, 2001b). Again, this flux is scaled using root distribution to give an area-specific contribution to  $R_S$ .

#### *Isotope techniques*

*Isotopic labelling.* Isotopic labels (<sup>13</sup>C) introduced in CO<sub>2</sub> enrichment experiments (e.g. FACE, open top chambers or growth chambers), where atmospheric CO<sub>2</sub> concentrations are increased by adding CO<sub>2</sub> from fossil sources, have been used to separate plant-derived CO<sub>2</sub> within total  $R_S$  (e.g. Andrews *et al.*, 1999). Another possibility is to replace one or more soil components with isotopically labelled components (e.g. in soil transplant studies, where C4 plants are grown on soils previously dominated by C3 plants, or *vice versa*; e.g. Rochette & Flanagan, 1997). The basis of this approach is that the different photosynthetic pathways have specific isotopic fractionations, which

result in distinct  $\delta^{13}\text{C}$  values for C3- and C4-dominated plant communities for plants tissues, and consequently for litter, and SOM. By growing the respectively different plant type on a soil, it is possible to distinguish between the older (i.e. SOM and old litter)-derived  $\text{CO}_2$  and fresh plant-derived  $\text{CO}_2$ . Pulse labelling, or repeated pulse labelling using either  $^{13}\text{C}$  or  $^{14}\text{C}$  is also used to partition C assimilated by plants between plant and soil pools and respective respiratory fluxes (e.g. Meharg, 1994).

**Radiocarbon.** The radioactive decay of the  $^{14}\text{C}$  isotope allows organic matter to be dated as its  $\Delta^{14}\text{C}$  value reflects the atmospheric value at the time of photosynthetic assimilation. The elevated atmospheric  $^{14}\text{C}$  background values caused by nuclear weapons testing in the 1950s and 1960s ('bomb spike') allows sufficient resolution on the order of decades to distinguish different ages for different soil components, and consequently their respective contributions to  $R_S$  (e.g. Gaudinski *et al.*, 2000). As single measurements of the  $\Delta^{14}\text{C}$  value of soil respired  $\text{CO}_2$  reflect a mixture of sources, this technique requires additional modelling to disentangle individual components that have contributed to the overall efflux.  $^{14}\text{C}$  analysis of  $\text{CO}_2$  in soil air or soil  $\text{CO}_2$  efflux is also used in conjunction with other partitioning techniques in order to constrain otherwise unknown parameters such as fine root turnover (e.g. Trumbore *et al.*, 1995; Trumbore, 2000).

#### Indirect techniques

**Modelling.** We classified studies as *modelling* if they were strictly 'bottom-up' simulation of fluxes based on responses of ecosystem components to biotic and abiotic drivers (e.g. Eliasson *et al.*, 2005). Parameterization of models relies on either directly measured response functions and pool sizes, or literature values for estimates of C transfer between ecosystem pools and the atmosphere. This category does not include studies that use temperature response functions to derive annual flux sums (e.g. Bond-Lamberty *et al.*, 2004b), or 'top down' modelling studies where measured aboveground fluxes are used to estimate net plant or ecosystem productivity (net primary production (NPP) and net ecosystem production (NEP), respectively), and  $R_H$  is derived by difference (see *Subtraction*).

**Mass-balance.** This approach assumes that the fluxes of C into and out of the soil are balanced (i.e. that over the study period no net change C storage has occurred). If the rates of C input from above- and belowground litter

are known, the difference between these and the total soil  $\text{CO}_2$  efflux is attributable to root activity. While a simplistic approach using only aboveground litter input has been widely used to estimate total belowground C allocation (Schlesinger, 1977; Raich & Nadelhoffer, 1989), we only include studies where belowground litter input has been quantified (e.g. McDowell *et al.*, 2001).

**Subtraction.** This technique is similar to the mass-balance approach, but does not base estimates on direct measurements of above and belowground inputs. Rather, root contributions are derived by subtraction of other flux components computed by combinations of ecosystem NPP models and literature values (e.g. Arneeth *et al.*, 1998; Malhi *et al.*, 1999; Chambers *et al.*, 2004).

**Root mass regression.** Studies in this technique have correlated  $R_S$  at a given location with the root biomass at the same location. The variation in  $R_S$  is, thus, assumed to be due to the variation in root content (either fine or total root mass), and the  $y$ -intercept of the extrapolated regression line (i.e. the theoretical root content of 0) gives the portion of flux because of heterotrophic decomposition alone (e.g. Kucera & Kirkham, 1971).

#### Materials and methods

We identified studies from the literature of the past 30 years, in which soil  $\text{CO}_2$  efflux was partitioned into hetero- and autotrophic flux contributions by keyword searches on the ISI Web of Science database. We have attempted to keep this as inclusive as possible, while critically assessing the methods in which fluxes were obtained. Studies that did not include the total soil  $\text{CO}_2$  efflux, but only report subcomponent fluxes were not considered, as our analysis concentrates on the fraction of total efflux provided by individual components. Similarly, pulse labelling experiments that trace the fate of assimilated C in plants to plant components, including root respiration, while instructive, do not allow a partitioning into total root-, rhizomicrobial, and microbial respiration, and are, therefore, not considered. Wherever possible, we attempted to obtain original flux results from authors, when these were not reported in publications. Errors of flux estimates are unfortunately only rarely reported in the literature, and would be necessary to strengthen any rigorous metaanalysis. We recorded errors where they were reported, and propagated these to obtain the error of the estimated partitioning fractions. For studies that did not report errors,

the maximum error of that methodology was assumed for the purpose of the metaanalysis.

Methods for measuring soil CO<sub>2</sub> efflux have undergone a considerable evolution over the past 30 years, giving rise to what is today considered state-of-the-art measuring systems (e.g. Pumpanen *et al.*, 2004). Potential biases between different systems have received some attention, with several correction factors proposed for specific systems. It is beyond the scope of this analysis to assess the accuracy of measurements that have led to individual flux estimates, and we accept literature results at 'face value'. In the majority of cases, the ratio between treatment and control would be unaffected in any case, as the same measuring system is generally used in both.

### Metaanalysis

All the studies were categorized according to the biome and ecosystem in which they were carried out, the age of the stand (for forests), and the technique, time-step and experimental setting. The categorization by biome distinguished between Arctic, Boreal, Temperate, Mediterranean, and Tropical, and was applied according to Koeppen's climate classification (FAO-SDRN-Agrometeorology Group-1997), where Boreal and Temperate are, respectively, the cold temperate and the warm temperate climatic zones. Ecosystem categories covered agriculture, bare ground, coniferous forest, deciduous forest, grassland, lichen crust, peatland, and shrub, while stand age was simplified to young (<10 years), intermediate (10–40 years), and mature (>40 years) groups. The time step refers to the temporal resolution to which results apply. Results were classified as annual only if the experimental approach accounted for the full annual dynamics of a given ecosystem. Studies concentrating on growing season fluxes only were grouped with monthly studies, with short-term experiments being grouped into weekly or daily categories. A final distinction was made between studies measuring fluxes under field conditions, or in the laboratory.

The collected data set of all partitioning studies was analysed using Meta Win 2.1 software (Rosenberg *et al.*, 2000). For all literature results, we recorded the mean and variance of  $R_S$  and  $R_H$ . We decided to base the comparison on the  $R_H/R_S$  ratio rather than on the  $R_A/R_S$  ratio because the heterotrophic flux is recorded directly by the majority of techniques, while  $R_A$  is calculated by difference. Where  $R_A$  was recorded directly (e.g. in root excision or live root respiration), we calculated  $R_H$  and propagated errors on the basis of the errors reported for  $R_A$  and  $R_S$ . Wherever possible, we converted error estimates reported in primary studies, or estimated error terms from graphs, and assumed the

maximum error of any given partitioning technique, if no error terms were reported. The metric used in the metaanalysis was the natural logarithm of the individual response ratios ( $L$ ), and individual studies were weighted according to the reciprocal of the variance of  $L$ . MetaWin calculates the weighted mean of studies grouped by respective categories (e.g. biome, partitioning technique, time-step, etc.), and estimates 95% confidence intervals of mean estimates. A categorical random-effect model was used, which assumes a random component, in addition to the sampling variability, to the total variance of the group of studies. Significant differences between groups were identified on the basis of the within and between group heterogeneity ( $Q_W$  and  $Q_B$ , respectively), in a process analogous to ANOVA.  $Q_B$  is tested against a  $\chi^2$ -distribution at  $n-1$  degrees of freedom, where  $n$  is the number of groups being compared (Hedges *et al.*, 1999).

### Results and discussion

In Table 1, we list all studies to give a complete overview of experimental work conducted into  $R_S$  partitioning, even if not all studies were included in the metaanalysis (indicated in right-hand column of Table 1). As flux fractions were expressed in relation to total annual  $R_S$ , only studies reporting estimates of  $R_S$  were included in the statistical analysis. Other reasons for excluding studies are specified in the footnotes of Table 1. The reported flux partitioning for annual studies, show a clear correlation between the heterotrophic flux portion and the total soil CO<sub>2</sub> efflux (Fig. 1). This apparent influence of  $R_S$  on the  $R_H/R_S$  ratio across all biomes and ecosystem types, and including all techniques, has been reported in analogous form previously (Bond-Lamberty *et al.*, 2004a). The results indicate relatively wide range for the 95% confidence intervals, spanning about 60% of flux contributions throughout the range of  $R_S$ .

The results for forest ecosystems in different biomes confirm the general decline of  $R_H/R_S$  with increasing annual  $R_S$  (Fig. 2). Of the groups included in this comparison, only boreal coniferous and temperate coniferous forest sites are significantly different from each other. To our knowledge, no statistically significant difference in flux fractions between ecosystem types and biomes have been reported previously, and it is somewhat surprising that the only difference was found between identical forest types in neighbouring biomes. As indicated by the regression line in Fig. 2, the higher fluxes observed in boreal forests are consistent with the global trend of forest biomes. While the predictive power of  $R_S$  for flux fractions of  $R_H$  and  $R_A$  is limited by the relatively wide confidence intervals, this statistically significant trend contradicts a frequently cited

**Table 1** Partitioning studies, listing (where available), total annual soil CO<sub>2</sub> efflux ( $R_S$ ) in g C m<sup>-2</sup> yr<sup>-1</sup>, heterotrophic flux fraction ( $R_H/R_S$ ), and its variance

Biome	Ecosystem	Method	Age	Step	$R_S$	$R_H/R_S$	Reference	Excl
Arctic	Shrub	Clip	M	d	44*	0.25*	Grogan <i>et al.</i> (2001)	*
		r exc	M	a	152	0.47	Nakatsubo <i>et al.</i> (1998)	
	Grassland	r exc	n/a	m	402	0.25	Billings <i>et al.</i> (1978)	
	Bare ground	r exc	n/a	d	47	0.99	Nakatsubo <i>et al.</i> (1998)	
Boreal	Lichen crust	r exc	n/a	d	103	0.87	Nakatsubo <i>et al.</i> (1998)	
		r exc	n/a	d	103	0.87	Nakatsubo <i>et al.</i> (1998)	
	Coniferous forest	Trench	M	a	540	0.73	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	M	a	338	0.86	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	M	a	375	0.88	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	M	a	375	0.94	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	425	0.67	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	337	0.71	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	551	0.70	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	570	0.62	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	484	0.78	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	397	0.83	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	Y	a	255	1.03	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	Y	a	137	0.98	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	Y	a	85	0.89	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	Y	a	513	0.97	Bond-Lamberty <i>et al.</i> (2004b)	
		Trench	I	a	858	0.58	Haynes and Gower (1995)	
		Trench	M	a	640	0.62	Lavigne <i>et al.</i> (2003)	
		Trench	M	a	1170	0.44	Lavigne <i>et al.</i> (2003)	
		Trench	M	a	1520	0.36	Lavigne <i>et al.</i> (2003)	
		Trench	M	a	564	0.78	O'Connell <i>et al.</i> (2003)	
		Trench	M	a	319	0.83	O'Connell <i>et al.</i> (2003)	
		Trench	M	a	496	0.42	Vogel <i>et al.</i> (2005)	
		Trench	M	a	415	0.59	Vogel <i>et al.</i> (2005)	
		Trench	M	a	377	0.52	Vogel <i>et al.</i> (2005)	
		Gird	M	m	563	0.54	Bhupinderpal-Singh <i>et al.</i> (2003)	
		Gird	M	m	657	0.58	Högberg <i>et al.</i> (2001)	
		Gap	M	m	857	0.65	Striegl & Wickland (1998)	
		r exc	M	m	470	0.43	Ruess <i>et al.</i> (2003)	
		r exc	M	m	1780	0.67	Widén & Majdi (2001)	
		r exc	M	m	1780	0.76	Widén & Majdi (2001)	
		r exc	I	m	1780	0.71	Widén & Majdi (2001)	
		<sup>13</sup> C	M	d		0.35	Ekblad & Högberg (2001)	
		<sup>14</sup> C	M	m	633	0.49	Czimczik <i>et al.</i> (2006)	
		<sup>14</sup> C	I	m	500	0.09	Czimczik <i>et al.</i> (2006)	
		<sup>14</sup> C	I	m	560	0.14	Czimczik <i>et al.</i> (2006)	
<sup>14</sup> C	Y	m	680	0.03	Czimczik <i>et al.</i> (2006)			
<sup>14</sup> C	M	m	533	0.65	Wang <i>et al.</i> (2000)			
Mod	M	m	438 <sup>†</sup>	0.34	Bonan (1993)			
Mod	M	m	967 <sup>†</sup>	0.11	Bonan (1993)			
Mod	M	m	1124 <sup>†</sup>	0.27	Bonan (1993)			
Mod	M	m	1050 <sup>†</sup>	0.38	Bonan (1993)			
Mod	M	m	1003 <sup>†</sup>	0.23	Bonan (1993)			
Mod	I	m	1215	0.39	Eliasson <i>et al.</i> (2005)			
m bal	I	a	858	0.53	Haynes & Gower (1995)			
m bal	M	m	470	0.61	Ruess <i>et al.</i> (2003)			
subtr	M	a	592	0.76	Malhi <i>et al.</i> (1999)			
Grassland	Clip	n/a	w	2274	0.81	Craine <i>et al.</i> (1999)		
	Clip	n/a	m	829	0.58	Silvola <i>et al.</i> (1996)		
	Shade	n/a	w	3364	0.61	Craine <i>et al.</i> (1999)		
	r exc	n/a	d	2274	0.60	Craine <i>et al.</i> (1999)		

Table 1 (Contd.)

Biome	Ecosystem	Method	Age	Step	R <sub>S</sub>	R <sub>H</sub> /R <sub>S</sub>	Reference	Excl
Temperate	Peatland	Trench	n/a	m	357	0.95	Silvola <i>et al.</i> (1996)	
		Trench	n/a	m	507	0.84	Silvola <i>et al.</i> (1996)	
		Trench	n/a	m	677	0.97	Silvola <i>et al.</i> (1996)	
		Trench	n/a	m	406	0.89	Silvola <i>et al.</i> (1996)	
		Trench	n/a	m	606	0.77	Silvola <i>et al.</i> (1996)	
		Trench	n/a	m	534	0.91	Silvola <i>et al.</i> (1996)	
		Trench	n/a	m	733	0.75	Silvola <i>et al.</i> (1996)	
	Coniferous Forest	Trench	n/a	m	1405	0.75	Silvola <i>et al.</i> (1996)	
		Trench	I	a	710	0.70 <sup>‡</sup>	Buchmann (2000)	
		Trench	Y	m	1703	0.45	Janssens <i>et al.</i> (1998)	
		Trench	M	a	564	0.50	Saiz <i>et al.</i> (2006)	
		Trench	I	a	686	0.43	Saiz <i>et al.</i> (2006)	
		Trench	I	a	556	0.43	Saiz <i>et al.</i> (2006)	
		Trench	Y	a	991	0.41	Saiz <i>et al.</i> (2006)	
		Trench	M	a	800	0.77	Sulzman <i>et al.</i> (2005)	
		Gird	I	m	1788	0.59	Subke <i>et al.</i> (2004b)	
		Gap	M	a	1299	0.54	Nakane <i>et al.</i> (1983)	
		Gap	M	a	987	0.49	Nakane <i>et al.</i> (1984) <sup>§</sup>	
		Gap	M	a	1255	0.54	Nakane <i>et al.</i> (1986)	
		Gap	I	a	618	0.43	Ohashi <i>et al.</i> (2000)	
		Comp	I	d	227	0.50 <sup>¶</sup>	Witkamp & Frank (1969)	
		r exc	M	a	597	0.46	Irvine & Law (2002)	
		r exc	I	a	427	0.52	Irvine & Law (2002)	
		r exc	M	m	780	0.52	Law <i>et al.</i> (2001b)	
		r exc	I	m	654	0.49	Law <i>et al.</i> (2001b)	
		r exc	I	a	1263	0.48	Maier & Kress (2000)	
		<sup>13</sup> C	I	a	1183 <sup>  </sup>	0.45	Andrews <i>et al.</i> (1999)	
		<sup>14</sup> C	M	m	1713	0.80	Wang <i>et al.</i> (2000)	
		mod	M	a	1400	0.47	Moncrieff & Fang (1999)	
		m bal	I	a	710	0.75	Buchmann (2000)	
		m bal	M	a	518	0.62	Cronan (2003)	
		m bal	I	a	811	0.65	Maier <i>et al.</i> (2004)	
		m bal	M	a	856	0.69	McDowell <i>et al.</i> (2001)	
		m bal	M	a	849	0.61	McDowell <i>et al.</i> (2001)	
		Subtr	Y	a	950	0.33	Arneth <i>et al.</i> (1998)	
		r reg	M	a	670	0.16	Rodeghiero & Cescatti (2006)	
		r reg	M	a	648	0.40	Rodeghiero & Cescatti (2006)	
		r reg	M	a	576	0.52	Rodeghiero & Cescatti (2006)	
		r reg	M	a	644	0.26	Rodeghiero & Cescatti (2006)	
		r reg	M	a	773	0.47	Rodeghiero & Cescatti (2006)	
	r reg	M	a	1015	0.58	Rodeghiero & Cescatti (2006)		
	r reg	M	m	592	0.73	Subke (2002)		
	Deciduous forest	Trench	M	m	371	0.67	Bowden <i>et al.</i> (1993)	
		Trench	I	a	660	0.39	Epron <i>et al.</i> (1999)	
		Trench	I	a	1290	0.37	Ewel <i>et al.</i> (1987)	
		Trench	Y	a	850	0.49	Ewel <i>et al.</i> (1987)	
		Trench	M	m	1123	0.48	Kelting <i>et al.</i> (1998)**	
		Trench	M	m	532	0.57	Lee <i>et al.</i> (2003)	
		Gird	I	a	420	0.94	Edwards & Ross-Todd (1979)	
		Gap	M	m	642	0.61	Brumme (1995)	
Gap		M	a	529	0.93	Edwards & Ross-Todd (1983) <sup>††</sup>	*	
Gap		M	a	940	0.49	Nakane <i>et al.</i> (1996)		
Gap		M	a	487	0.96	Toland & Zak (1994) <sup>††</sup>	*	
Gap		M	a	469	1.01	Toland & Zak (1994) <sup>††</sup>	*	
r exc		M	a	1627	0.45	Burton <i>et al.</i> (2004)		

(Continued)

Table 1 (Contd.)

Biome	Ecosystem	Method	Age	Step	R <sub>S</sub>	R <sub>H</sub> /R <sub>S</sub>	Reference	Excl
		r exc	M	a	1824	0.29	Burton <i>et al.</i> (2004)	
		r exc	M	a	1801	0.46	Burton <i>et al.</i> (2004)	
		r exc	M	a	2176	0.65	Burton <i>et al.</i> (2004)	
		r exc	M	a	1065	0.65	Edwards & Harris (1977) <sup>i</sup>	
		r exc	M	m	1662	0.65	Edwards & Sollins (1973)	
		r exc	M	a	660	0.61	Fahey <i>et al.</i> (2005)	
		r exc	M	m	650	0.77	Tate <i>et al.</i> (1993)	
		live r	M	a	1754	0.30	Kutsch <i>et al.</i> (2001b)	
		<sup>14</sup> C	M	a	630 <sup>SS</sup>	0.60	Dörr & Munnich (1987)	
		<sup>14</sup> C	M	a	840	0.41	Gaudinski <i>et al.</i> (2000) <sup>*†</sup>	
		Mod	M	a	538	0.57	Kutsch <i>et al.</i> (2001a)	
		Mod	M	a	1668	0.29	Kutsh <i>et al.</i> (2001a)	
		m bal	M	a	387	0.57	Coles & Yavit (2004)	
		m bal	M	a	660 <sup>   </sup>	0.77	Fahey & Hughes (1994)	
		m bal	M	a	494	0.57	Nakane (1980)	
		m bal	M	a	1100	0.48	Nakane (1980)	
		m bal	M	a	1000	0.80	Tate <i>et al.</i> (1993)	
		Subtr	I	a	660	0.48	Epron <i>et al.</i> (2001)	
		Subtr	M	a	754	0.48	Malhi <i>et al.</i> (1999)	
		r reg	M	a	1079	0.51	Rodeghiero & Cescatti (2006)	
	Grassland	Clip	n/a	a	1120	0.65	Wan & Luo (2003)	
		Clip	n/a	d	1779	0.58	Wan & Luo (2003)	
		Clip	n/a	d	3043	0.65	Wan & Luo (2003)	
		r exc	n/a	d		0.66	Herman (1977)	*
		<sup>14</sup> C	n/a	a	630 <sup>j</sup>	0.90	Dörr & Munnich (1987)	
		Mod	n/a	a	1425	0.59	Kutsch <i>et al.</i> (2001a)	
		r reg	n/a	a	468	0.72	Buyanovsky <i>et al.</i> (1987)	
		r reg	n/a	m	987	0.63	Kucera & Kirkham (1971)	
	Agriculture	<sup>13</sup> C	n/a	m	1594	0.56	Rochette & Flanagan (1997)	
		<sup>13</sup> C	n/a	d	1325	0.32	Søe <i>et al.</i> (2004)	
		<sup>13</sup> C	n/a	d	1325	0.27	Søe <i>et al.</i> (2004)	
		Mod	n/a	a	770	0.66	Kutsch <i>et al.</i> (2001a)	
		m bal	n/a	a	607	0.86	Buyanovsky <i>et al.</i> (1987)	
Mediterranean	Coniferous forest	r reg	Y	m	1408	0.53	Xu <i>et al.</i> (2001)	
	Deciduous forest	Trench	I	a	1097	0.77	Rey <i>et al.</i> (2002)	
		Gap	M	a	620	0.61	Tang & Baldocchi (2005)	
		<sup>14</sup> C	M	m	1395	0.48	Wang <i>et al.</i> (2000)	
	Agriculture	<sup>14</sup> C	n/a	m	1077	0.27	Wang <i>et al.</i> (2000)	
Tropical	Coniferous forest	Trench	I	a	850	0.44	Li <i>et al.</i> (2004)	
	Deciduous forest	Trench	I	a	971	0.30	Li <i>et al.</i> (2004)	
		Trench	M	a	1084	0.76 <sup>***</sup>	Silver <i>et al.</i> (2005)	*
		Trench	M	a	1084	0.65 <sup>†††</sup>	Silver <i>et al.</i> (2005)	
		gap	Y	a	1570	0.42	Epron <i>et al.</i> (2006)	
		<sup>13</sup> C	Y	a	2220	0.27	Giardina <i>et al.</i> (2004) <sup>†††</sup>	
		m bal	M	a	1430	0.51	Nakane (1980)	
		m bal	M	a	1084	0.73	Silver <i>et al.</i> (2005)	
		m bal	M	a	1363	0.62	Silver <i>et al.</i> (2005)	
		m bal	M	a	2400	0.37	Trumbore <i>et al.</i> (1995)	
		Subtr	M	a	1210	0.45	Chambers <i>et al.</i> (2004)	
		Subtr	M	a	1650	0.59	Malhi <i>et al.</i> (1999)	
		r reg	I	d	835	0.50	Behera <i>et al.</i> (1990)	
	Grassland	Clip	n/a	m		0.47	Robertson <i>et al.</i> (1995)	*
		m bal	n/a	a	1050	0.44	Trumbore <i>et al.</i> (1995)	
		m bal	n/a	a	1710	0.38	Trumbore <i>et al.</i> (1995)	
	Agriculture	Comp	I	m	1558	0.31	Lamade <i>et al.</i> (1996)	

Table 1 (Contd)

Biome	Ecosystem	Method	Age	Step	R <sub>S</sub>	R <sub>H</sub> /R <sub>S</sub>	Reference	Excl	
Laboratory studies	None	Comp	n/a	d		0.03	Bååth & Wallander (2003)	*	
		Comp	M	m		0.90	Coleman (1973)	*	
		Comp	n/a	m		0.83	Coleman (1973)	*	
		Comp	I	d		1.06	Fang <i>et al.</i> (2005) <sup>§§§</sup>	*	
		Comp	M	a		2079	Thierron & Laudelout (1996) <sup>†††</sup>	*	
		<sup>13</sup> C	n/a	w			0.11	Cheng (1996) <sup>    </sup>	*
		<sup>13</sup> C	n/a	d			0.70	Cheng & Johnson (1998)	*
		<sup>13</sup> C	M	d			0.57	Formánek & Ambus (2004)	*
		<sup>13</sup> C	n/a	w			0.25	Kuzyakov & Cheng (2001)	*
		<sup>13</sup> C	n/a	w			0.18	Kuzyakov & Cheng (2004)	*
		<sup>13</sup> C	Y	m		1211	0.78	Lin <i>et al.</i> (1999)	
		<sup>14</sup> C	n/a	d			0.71	Herman (1977)	*
		<sup>14</sup> C	n/a	w			0.60	Warembourg & Paul (1973) <sup>****</sup>	*

\*Fluxes are for ecosystem respiration under snow, assumed to be soil CO<sub>2</sub> efflux only.

†Modelled fluxes not always well matched by measured fluxes.

‡Rough estimate based on trenching shallow fine roots only.

§Cited in Nakane *et al.* (1996).

††Rough estimate based on assumption that roots are found in mineral soil only, and that they dominate CO<sub>2</sub> flux from that layer.

‡‡R<sub>S</sub> from Andrews & Schlesinger (2001) for the same year.

\*\*\*Measurements under ozone treatment.

†††Study not included in meta-analysis, as results are deemed an artefact of altered temperature and moisture conditions or changed in C pools following harvest.

‡‡‡Authors assume root Q<sub>10</sub> of two for calculation of R<sub>A</sub>.

§§§Rough regional estimate; R<sub>S</sub> integrated over different vegetation forms.

††††Estimate of R<sub>A</sub> includes unknown fraction of heterotrophic litter decomposition.

||||R<sub>S</sub> from Fahey *et al.* (2005).

\*\*\*\*Ratio assumes complete mineralisation of C lost from root litter ('low estimate'); only 'high estimate' (following row) included in statistical analysis to avoid repetition of study results.

†††††Ratio assumes no mineralisation of C lost from root litter ('high estimate').

‡‡‡‡Only fluxes from unfertilized plots considered.

§§§§Authors consider disturbance following sampling behind R<sub>H</sub>/R<sub>S</sub> ratio > 1.00.

†††††Excluded from meta-analysis, as measurements consider R<sub>S</sub> from top 10 cm only, and R<sub>H</sub>/R<sub>S</sub> ratio applies to specific temperature only.

|||||Study reports measurements of soil [CO<sub>2</sub>], not CO<sub>2</sub> efflux.

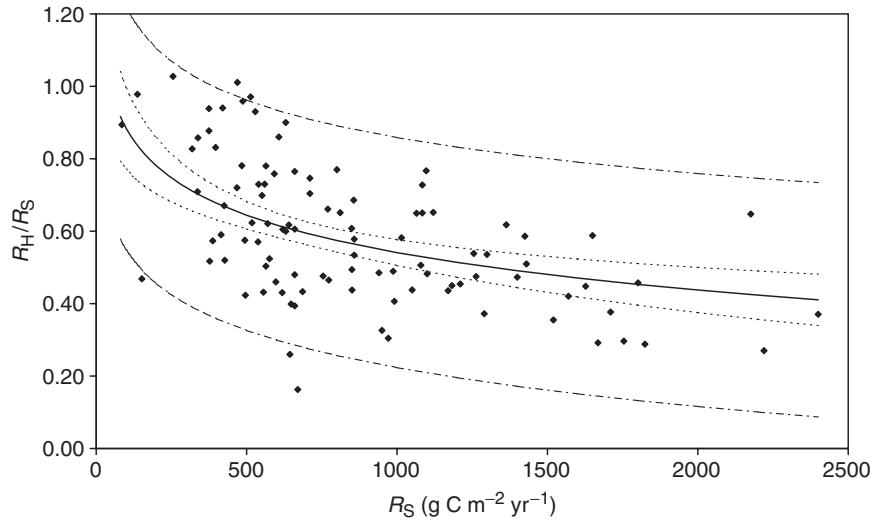
\*\*\*\*†Study reports an approximate estimate of R<sub>A</sub> only.

Clip, clipping; comp, component integration; Gird, girdling; <sup>13</sup>C, <sup>13</sup>C labelling; <sup>14</sup>C, radiocarbon; live r, live root respiration; m bal, mass balance; Mod, modelling; Subtr, subtraction; r reg, root mass regression; r exc, roots excised; Shade, shading; Trench, trenching. Forest stands are classified as either young (Y) intermediate (I), or mature (M), and the time step for which data are applicable is either annual (a), monthly to seasonal (m), 1–3 weeks (w), or daily or less (d). Flux values are given on an annual basis irrespective of time step. Asterisks indicate studies that were not included in the meta-analysis.

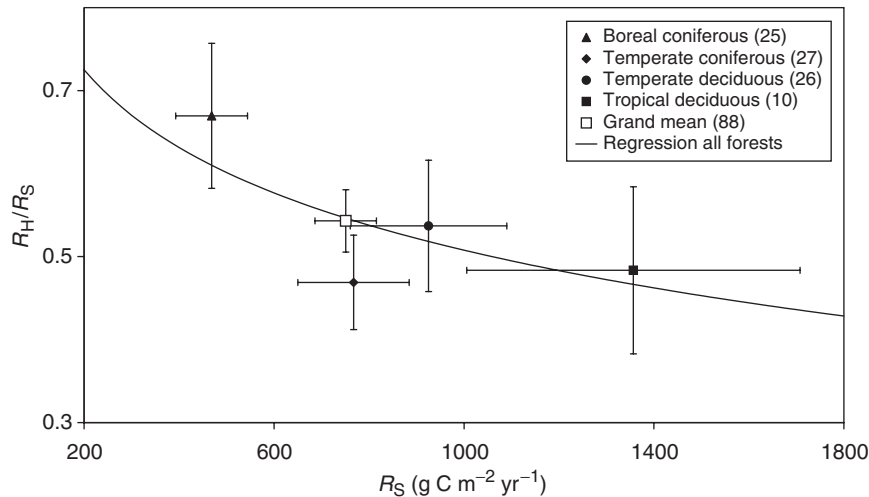
review by Schlesinger (1977), in which the R<sub>A</sub> contribution to R<sub>S</sub> is a constant fraction of soil CO<sub>2</sub> efflux across all latitudes.

One possible explanation for the pattern of declining R<sub>H</sub>/R<sub>S</sub> for increasing annual R<sub>S</sub> values is that allocation patterns belowground change with ecosystem productivity. Direct correlations between productivity and R<sub>S</sub> have been proposed (e.g. Raich & Tufekcioglu, 2000; Janssens *et al.*, 2001) and the results in Fig. 1 could mean that a relatively greater amount of assimilated C is allocated to R<sub>A</sub> in more productive ecosystems. Results

from a long-term FACE experiments in deciduous forests (Körner *et al.*, 2005) and a mesocosm study in greenhouses (Heath *et al.*, 2005) indicate that an increase in gross plant productivity following the increase in [CO<sub>2</sub>] does not result in an increase in plant biomass. Instead, C appears to be 'pumped' through plants belowground, where R<sub>S</sub> was found to significantly increase. While R<sub>S</sub> was not partitioned as part of these particular studies, it supports the hypothesis that high aboveground gross productivity increases R<sub>S</sub> through increases in R<sub>A</sub>, with no increase in R<sub>H</sub> through biomass



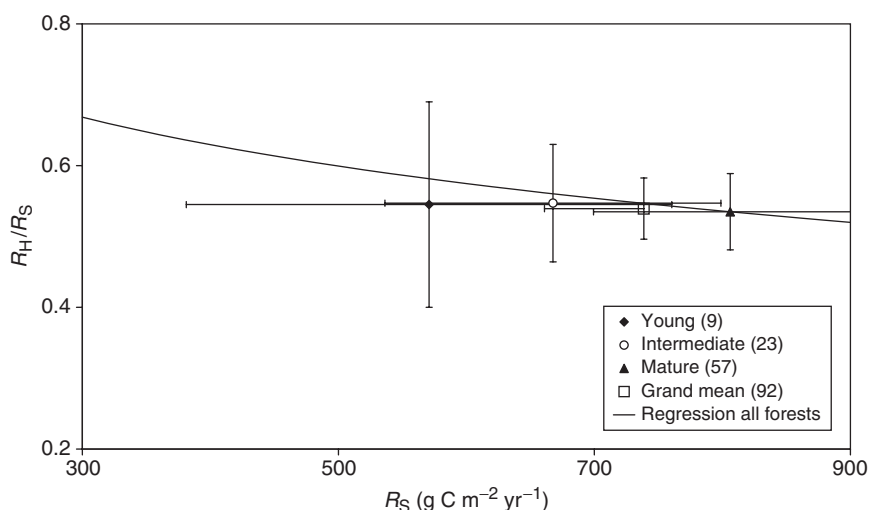
**Fig. 1** Heterotrophic flux contribution ( $R_H/R_S$ ) in relation to total soil carbon dioxide efflux ( $R_S$ ) for all studies reporting annual flux sums. The regression line is weighted by the reciprocal of the variance of  $\ln(R_H/R_S)$  of individual estimates; regression line:  $R_H/R_S = -0.138 \ln(R_S) + 1.482$ ,  $R_2 = 0.302$ ,  $P < 0.001$ . The dotted line gives the 95% confidence zone for the regression, while the hatched lines show 95% confidence limits for individual estimates.



**Fig. 2** Weighted mean heterotrophic flux contributions to total efflux in different forest types, in dependence of total soil  $\text{CO}_2$  efflux ( $R_S$ ) for all studies reporting annual flux sums. Mediterranean sites are grouped with temperate forests for the purpose of this comparison. Error bars are 95% confidence intervals, and numbers of primary studies per group are indicated in the legend. The regression line is analogous to Fig. 1, but calculated for forest sites only. Between-group difference was significant at  $P = 0.012$  ( $Q_B = 18.7$  at 3 df).

production, thus reducing the  $R_H/R_S$  ratio. An increase in microbial soil respiration under elevated  $[\text{CO}_2]$ , as observed by Heath *et al.* (2005) is likely to be due to enhancement of root exudation. Bond-Lamberty *et al.* (2004a) found that across ecosystems  $R_A$  is not correlated to NPP (either aboveground, belowground, or total), indicating that there is no proportional allocation of assimilates to growth and autotrophic respiration. It is,

therefore, suggested that during periods of high primary productivity, plant growth is not limited by the supply of assimilates, resulting in a disproportional allocation of C between growth and maintenance requirements on the one hand, and C release from roots (e.g. as exudations) on the other. Generally, this C loss from roots is likely to be passive, following an increase in the concentration of C compounds in the root tissue during times of high



**Fig. 3** Effect of stand age ('young' <10 years, 'intermediate' = 10–40 years, and 'mature' <40-year-old stands) on heterotrophic flux contributions ( $R_H/R_S$ ) in dependence of total soil carbon dioxide efflux ( $R_S$ ) at forest sites. Only studies reporting annual flux sums are included, the number of studies per group is indicated in the legend. Results are weighted mean values for both  $R_H/R_S$  and  $R_S$ , and error bars are 95% confidence intervals, indicating no significant difference between any of the groups. The regression line is analogous to Fig. 1, but calculated for forest sites only.

photosynthesis, while there is also some indication of active upregulation in C release from roots in some plants (Jones *et al.*, 2004).

#### Age trends in forest ecosystems

No significant difference emerged from the comparison of flux contributions for forest stands of different age (Fig. 3). Increasing stand age corresponded to smaller confidence intervals, and generally higher annual flux sums for  $R_S$ . The size of the confidence intervals in Fig. 3 is strongly affected by the larger number of studies in intermediate and mature age groups. The variance of  $R_H/R_S$  ratios reported in young stands is, however, four times larger than that of intermediate and mature stands. This higher variance is likely to be due to the disturbance caused before the establishment of a stand, which is mostly because of harvest or forest fires. Our 'young' category includes stands aged between 2 and 9 years, so that the impact of this disturbance varies considerably also within this category. Additionally, this grouping averages over a small numbers of studies from a wide range of forest types, adding to the uncertainty of results. Excluding the 'young' age group from other comparisons had only a small impact on mean results, and did not affect any significant differences reported, thus we decided to include all age groups for the purpose of all analyses.

To our knowledge, there are only three studies that investigated the age-related contributions of  $R_H$  to  $R_S$ , of which two studied chronosequences at the same

location. Using the trenching technique to separate flux portions, Bond-Lamberty *et al.* (2004b) indicate a decrease of  $R_H$  contributions from young to intermediate age groups, with a subsequent increase in mature stands for a chronosequence of black spruce in Canada, while Saiz *et al.* (2006) report a moderate decline in  $R_H$  contributions for a Sitka spruce chronosequence in Ireland. Czimeczik *et al.* (2006), working at the same location as Bond-Lamberty *et al.* (2004b), but using radiocarbon measurements to estimate flux portions, indicate a consistent increase throughout the age range. The authors speculate that the unusually low- $R_H$  contributions in young stands are caused by the removal of the litter layer by fire. However, given that the results of Bond-Lamberty *et al.* (2004b) and Czimeczik *et al.* (2006) are partly obtained from the same locations and show contrasting partitioning results points to a method related bias. The estimates of Czimeczik *et al.* (2006) with contributions of  $R_H$  below 10% form the absolute minimum of all field studies reviewed here, and in contrast to the other two chronosequence studies, there is no consistent trend between  $R_S$  and  $R_H/R_S$ .

#### Time scale aspects

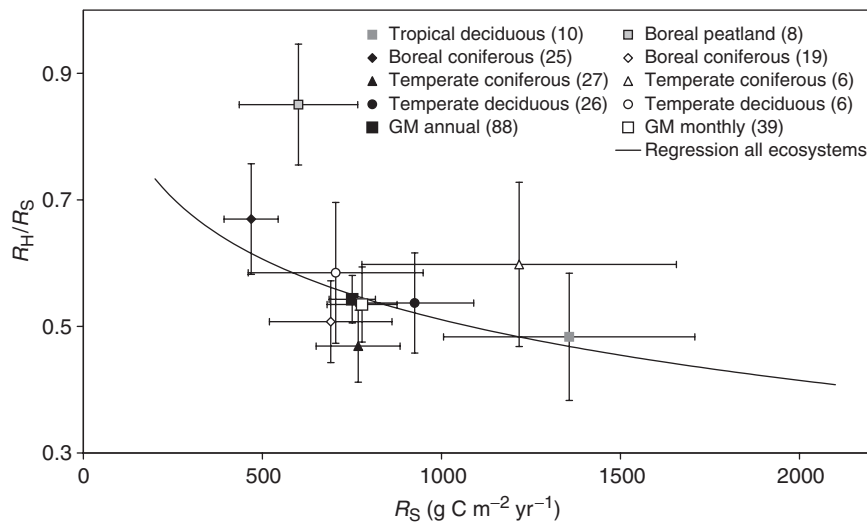
The majority of field studies have attempted to quantify flux contributions to  $R_S$  on an annual time scale. During the assembly of data, we critically assessed whether time scales had been reported realistically. Root mass regressions studies, for example, were only considered as annual studies if the root biomass had been collected

throughout the year, as a single sampling date would misrepresent the annual development of root biomass, and resulting contributions of  $R_A$ – $R_S$ . Similarly, studies reporting fluxes for time scales ranging from one to several months (commonly up to a full growing season) are likely to introduce a bias, if fluxes are extrapolated to the whole year. Certainly in biomes with distinct growing and dormant seasons, such studies would be expected to over-estimate annual  $R_S$ , and under-estimate  $R_H$ , which dominates during the dormant season. To test this hypothesis, we grouped studies according to ecosystem and biome, and time scale. A direct grouping according to time step, and irrespective of ecosystem did not produce significant results, and we considered this grouping not relevant, as a wide range of factors would be confounded within it. Daily to weekly time scales are predominantly used in artificial laboratory experiments, where total efflux does not represent a real spatial average of any ecosystem. For those ecosystems where both ‘annual’ and ‘monthly’ studies were available, there was no consistent trend for either  $R_S$  or  $R_H/R_S$  (Fig. 4). Boreal coniferous sites alone, which had the highest numbers of monthly studies compared with other sites, did show a small and not significant change towards higher  $R_S$  and lower  $R_H/R_S$  ratios for a change from annual to monthly time steps. However, for the grand mean of studies included in this comparison, no significant change was observed, and the small sample size for monthly studies in other forest biomes may account for a strong bias in this comparison. Figure 4

also includes data from boreal peatland sites, for which no annual data were available. Even if a bias because of the time scale is accepted, these results do indicate the difference of this particular ecosystem type to forest ecosystems. All results in this category are from the study by Silvola *et al.* (1996) and sites were dominated by *Pinus sylvestris*, with different mixtures of grasses and shrubs as understorey. These relatively high estimates indicate that for vegetation on deep peat soil,  $R_S$  is strongly dominated by heterotrophic contributions, possibly caused by the decomposition of peat, because of better aeration following drainage, as well as low root density in this particular ecosystem. However, more studies are needed in order to corroborate these conclusions.

#### Methodological impacts

As most techniques used to separate  $R_H$  and  $R_A$  from  $R_S$  are associated with disturbance of the soil system, it is inevitable that a bias is introduced by the choice of technique to achieve the flux separation. In addition to the physical disturbance, there are a range of assumptions or corrections that are not implemented in a uniform way, complicating further a direct comparison of results obtained with different techniques. The attempt to separate methodology-related effects in published partitioning results is complicated by the confounding effects of natural variability between, as well as within, different ecosystems (Figs 1 and 2). Despite the large



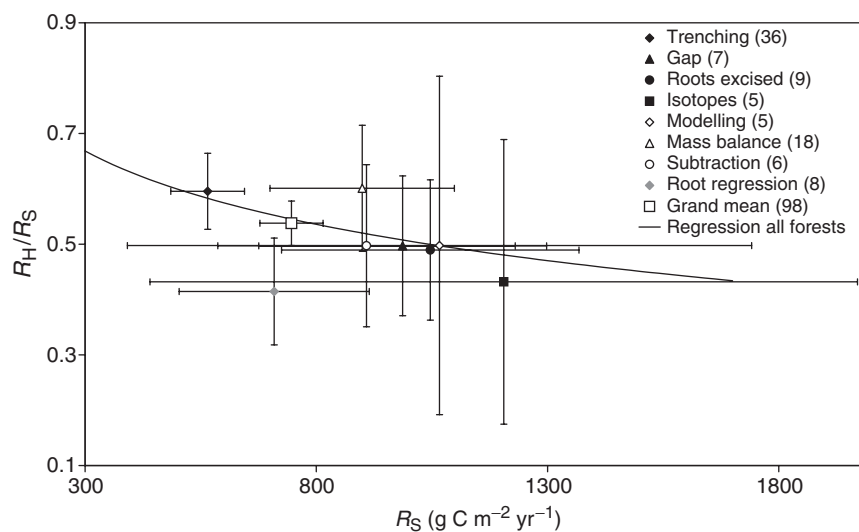
**Fig. 4** Results obtained by studies using annual (solid symbols), or monthly to seasonal (open symbols) time steps in different ecosystems. Values of heterotrophic flux contributions ( $R_H/R_S$ ) and for soil carbon dioxide efflux ( $R_S$ ) are weighted means, error bars are 95% confidence intervals. The numbers of studies in each group is indicated with the legend. Please note that the grand mean (GM) for either time scale is calculated for boreal coniferous and both temperate forest types, and that monthly estimates were extrapolated to calculate annual fluxes to allow a comparison between time scales; it is not implied that the  $R_H/R_S$  ratio remains constant throughout the year in monthly studies. The regression line is identical to Fig. 1.

number of studies attempting the partitioning of  $R_S$  into  $R_H$  and  $R_A$  (Table 1), it was not possible to aggregate values in sufficient numbers according to ecosystem type, stand age, method used, and time step applicable to allow a statistically meaningful comparison between partitioning techniques. Figure 5 shows weighted means of  $R_H/R_S$  ratios and respective means of  $R_S$  for studies using annual time steps, again using the overall regression line calculated for all studies as a reference. Please note that the regression line does not imply any 'true'  $R_H/R_S$  ratio from which particular methodologies deviate, but it is used as a relative guide to judge deviations between the different techniques. In the following sections, we discuss general strengths and weaknesses of specific techniques in relation to the trend observed in Fig. 5.

#### Root exclusion experiments

Root exclusion experiments form the largest group within the data set, with 40% of all studies (45% of studies reporting annual fluxes) using this approach. Compared with all other techniques, trenching has been more widely employed in boreal forests than in warmer biomes, resulting in a slight bias towards smaller  $R_S$  situations in the global comparison (Table 1, Fig. 3). The main concern associated with this technique, as well as with gap, clipping and girdling studies, is that it results in a considerable increase in dead root biomass in the treatment plots, which contribute to  $R_H$  and lead to an under-estimation in  $R_A$  when comparing soil CO<sub>2</sub> efflux from treatment and control plots. This issue is generally acknowledged by authors, but there is no consistent

methodology for implementing corrections. Epron *et al.* (1999) measured root decay in trenched plots by sampling root biomass of coarse (>2 mm) and fine ( $\leq 2$  mm) roots at the time of trenching, and after 2 years, and were thus able to calculate root decay constants for each size class. Decay constants are obtained by fitting a simple exponential decay function to the mass loss:  $M_1 = M_0 e^{-kt}$ , where  $M_1$  and  $M_0$  are the remaining and initial root biomass, respectively,  $k$  is the decay constant and  $t$  is the time over which decay was measured. Published values for root decay in root exclusion studies average at around 0.34 year<sup>-1</sup>, with a considerable range from 0.21–0.96 year<sup>-1</sup> (Table 2). These values have either been measured directly by litter-bag incubation in the field or repeated sampling, or authors have used decay constants published in the literature for corrections. Some authors make further assumption about the fraction of this mass (and therefore C), loss that is mineralized and contributes to the surface CO<sub>2</sub> efflux. In a sensitivity analysis of this parameter, Silver *et al.* (2005) compared  $R_A$  estimates in tropical forests if either 100% or 0% of decaying root C was converted to CO<sub>2</sub>. For this particular case, where a relatively high decomposition rate of 0.96 yr<sup>-1</sup> in a sandy loam soil was assumed, the difference in  $R_A$  contributions for this extreme range of C conversion to CO<sub>2</sub> was 11%. Of those trenching studies that calculate root decay, only about half estimate this fraction, which is commonly set to a narrow range of between 0.60 and 0.78 (Table 2). Applying this more constrained range of C conversion factors to the example of Silver *et al.* (2005),  $R_A$  flux estimates would have been over-estimated by between 6% and 8%.



**Fig. 5** Weighted means of total soil CO<sub>2</sub> efflux ( $R_S$ ) and heterotrophic flux contributions ( $R_H/R_S$ ) for studies reporting annual fluxes, with the number of studies per technique indicated in the legend. Means are weighted by reciprocal of the variance of  $\ln(R_H/R_S)$ , and error bars indicate 95% confidence intervals. The regression line is calculated for all ecosystem types, and includes all techniques.

**Table 2** Studies in which root decay caused by experimental treatment was considered before flux fractions were calculated

Reference	Technique	$\Delta R_H/R_S$	$k$ (year <sup>-1</sup> )	Mass loss (year <sup>-1</sup> )	Decomposition fraction
Bowden <i>et al.</i> (1993)	Trenching	-0.16	0.22*	0.20	1.00
Epron <i>et al.</i> (1999)	Trenching	-0.24	0.30 <sup>†</sup>	0.26	0.78 <sup>‡</sup>
Epron <i>et al.</i> (2006)	Gap	-0.16	0.38 <sup>§</sup>	0.32	0.60 <sup>¶</sup>
Lavigne <i>et al.</i> (2003)	Trenching	-0.21	0.30 <sup>  </sup>	0.26	1.00
Lavigne <i>et al.</i> (2003)	Trenching	-0.23	0.30 <sup>  </sup>	0.26	1.00
Lavigne <i>et al.</i> (2003)	Trenching	-0.17	0.30 <sup>  </sup>	0.26	1.00
Lee <i>et al.</i> (2003)	Trenching	-0.02	0.70 <sup>§</sup>	0.50	0.67**
Nakane <i>et al.</i> (1983) <sup>††</sup>	Gap	-0.04	0.20	0.18	1.00
Nakane <i>et al.</i> (1986) <sup>††</sup>	Gap	-0.13	0.14	0.13	0.64
Ohashi <i>et al.</i> (2000)	Gap	-0.08	0.21 <sup>‡‡</sup>	0.13	0.71 <sup>‡‡</sup>
Rey <i>et al.</i> (2002)	Trenching	-0.03 <sup>§§</sup>			1.00
Saiz <i>et al.</i> (2006)	Trenching	-0.03	0.20 <sup>¶¶</sup>	0.18	1.00
Saiz <i>et al.</i> (2006)	Trenching	-0.05	0.20 <sup>¶¶</sup>	0.18	1.00
Saiz <i>et al.</i> (2006)	Trenching	-0.05	0.20 <sup>¶¶</sup>	0.18	1.00
Saiz <i>et al.</i> (2006)	Trenching	-0.02	0.20 <sup>¶¶</sup>	0.18	1.00
Silver <i>et al.</i> (2005)	Trenching	-0.11	0.96 <sup>   </sup>	0.62	1.00

\*Value from McClaugherty *et al.* (1982), but not implemented in final calculation.

<sup>†</sup>Measured by repeated sampling in trenched plots.

<sup>‡</sup>Value from Jenkinson (1990).

<sup>§</sup>Measured using litter bags.

<sup>¶</sup>Value from Parton *et al.* (1987).

<sup>||</sup>Value from Epron *et al.* (1999).

\*\*Value from Nakane *et al.* (1996).

<sup>††</sup>Use compartmental model to estimate contributions from root decay, surface litter etc. after felling.

<sup>‡‡</sup>Value from Nakane (1995).

<sup>§§</sup>Estimate root decay to contribute 3% to annual efflux based on values from Silver & Miya (2001), but no correction implemented.

<sup>¶¶</sup>Value from Silver & Miya (2001).

<sup>|||</sup>Value from Silver *et al.* (2000).

$\Delta R_H/R_S$  is the result in efflux fraction change following the root decay correction,  $k$  is the exponential decomposition constant, and the decomposition fraction indicates the fraction of additional root decay that is assumed to be mineralized to CO<sub>2</sub> rather than entering the humified soil C pool.

Corrections for the additional decay of trenched roots have led to decreases in  $R_H$  contribution estimates by, on average, 12% (range from 2% to 24%; Table 2). The considerable range of decay constants and, to a lesser extent, also the range in constants reported indicate that root decay is strongly dependent on C lost as CO<sub>2</sub>, suggesting that these parameters are strongly dependent on local conditions (e.g. soil type, climate, or litter quality). Vogt *et al.* (1996) found no consistent trend of root NPP, root turnover, or SOM accumulation across different climatic forest types, or soil orders, and it is likely that the decay of roots is similarly site specific, which limits the applicability of literature results for estimations of root decay. It is advisable that the fine and coarse root biomass per area is recorded at the beginning and at the end of any root exclusion experiment, and that root decay is measured independently (e.g. using litter bags).

In order to avoid the complication of additional efflux from decomposing roots as an artefact of the experimental treatment, most researchers commence with soil CO<sub>2</sub> efflux measurements several months or in some cases even years after trenching. However, the approximate estimate of error introduced by the additional decay of trenched roots by Bond-Lamberty *et al.* (2004b) for the second year following trenching indicates that  $R_H$  may be overestimated by as much as 20%. Bhupinderpal-Singh *et al.* (2003) report an increase in apparent root derived respiration, in the second year of forest girdling from 56% to 65%, which may be partly attributable to the decomposition of roots in girdled plots during the first year. While a delay following the experimental treatment may mean that the disturbance related additional respiration and root decomposition may have subsided, there are other uncertainties that increase over time. Treatment plots not only lack input

of photosynthates from aboveground, but also lack litter input and turnover from roots (and in the case of gap studies also from aboveground). For a tropical plantation, Epron *et al.* (2006) found that  $R_H$  would have been underestimated by about 25% if the change in litter input and turnover following the first year after forest felling had not been considered. Similarly, Nakane *et al.* (1996) found that the changes in respiration rate in the upper mineral soil following clear-cutting accounted for about 17% of the estimated  $R_H$  flux. The treatment of surface residue is also critical, as highlighted by Edwards & Ross-Todd (1983), who showed that clear felled sites showed about twice the increase in  $R_S$  if harvesting residues remained on the soil compared with sites where harvest residues were removed. The lack of belowground litter input is not generally corrected for in root exclusion studies. Depending on the turnover rate of fine roots and litter, this error may become more significant than that of additional respiration from the decomposition of roots severed or starved by the experimental treatment after about 1 year. A survey of the mass-balance studies listed in Table 1 showed that root production averages at around 28% of annual soil CO<sub>2</sub> efflux for temperate and tropical forest ecosystem, with a higher ratio of 39% reported by Ruess *et al.* (2003) for a boreal coniferous site. Vogt *et al.* (1996), report a wide range in the ratio of belowground productivity to total ecosystem productivity which, in turn, is known to correlate strongly with soil CO<sub>2</sub> efflux (Janssens *et al.*, 2001), with no pattern of climatic forest type or soil order. If it is assumed that the net increase in root biomass is small between years, this ratio is close to that of annual root biomass turnover (i.e. it equals belowground litter input). Trenching studies where soil CO<sub>2</sub> efflux measurements are delayed by between 1 and 7 years (Bond-Lamberty *et al.*, 2004b; Li *et al.*, 2004; Sulzman *et al.*, 2005; Vogel *et al.*, 2005) do not take account of this reduction in belowground litter input, despite the considerable potential for the underestimation of  $R_H$ .

With the exception of girdling, all root exclusion techniques also have profound impacts on the abiotic soil environment. As no soil water is extracted from treatment plots following trenching, clipping, or gap formation, there is inevitably a difference in soil water availability for biological processes between treatment and control conditions. The absence of canopy interception of precipitation in gap studies further heightens this difference in soil water status. This is particularly problematic in locations that experience periodic drought stress, as either treatment will be affected quite differently. Gap formation and clipping in grasslands lead further to a dramatic change in the radiation balance of the soil surface, with considerable alterations

to mean soil temperature and diurnal temperature fluctuations (e.g. Edwards & Ross-Todd, 1983). Likely drying out of the top-soil may off-set the previously mentioned general increase in soil water status, but both processes follow quite different temporal and spatial controls. In order to control for the soil moisture effect, it is advisable that soil moisture be monitored at frequent intervals throughout the experimental period. If  $R_S$  is measured on both treatment and control plots, general dependencies of  $R_S$  on soil temperature and soil moisture may allow for a correction of the difference in soil moisture and temperature. In the same tropical plantation mentioned above, Epron *et al.* (2006) found that the moisture effect alone led to  $R_H$  being overestimated by about 27%. Combining the underestimation because of lack of litter turnover and the overestimation because of soil moisture differences meant that in this particular case, the two effects nearly cancel each other out (corrected  $R_H$  is about 3% higher than uncorrected  $R_H$ ).

#### *Physical separation techniques*

For this group, our classification of studies differs from the two previous reviews of  $R_S$  partitioning. All studies in which any soil component was isolated from other were grouped in one category as 'component integration' by Hanson *et al.* (2000), and as 'extraction' by Bond-Lamberty *et al.* (2004a). Both of these publications include studies classified here as either *mass-balance* or *root regression* approach. The reasoning in our classification is that the mentioned techniques differ significantly in their disturbance of the soil environment, and in the basis on which flux fractions are calculated. The broader definition of this group would, therefore, mask any systematic error introduced by any of the techniques. The distinction between the *components* and *roots excised* techniques is motivated by the difference in which total efflux is derived. For studies in the roots excised group, total efflux is that measured in the field by soil CO<sub>2</sub> efflux chambers. Any error introduced by the separation of components is therefore limited to the measurements of  $R_A$  on excised roots. Total  $R_S$  in studies in the components category is calculated by multiplying the specific respiration terms of soil components by the spatial average of respective components, and summing these component fluxes. The calculated flux fraction therefore contains errors derived from component separation in  $R_S$ , as well as in  $R_H$  and  $R_A$ , which we see as a fundamental difference compared with the roots excised approach. This more graded classification for component flux studies meant that only few studies were actually identified as components, and for annual time steps, this group was too small to give meaningful results in the metaanalysis of flux fractions.

The separation of soil components, that forms the basis of the techniques in this group, is also its biggest disadvantage. The effects of separating soil components such as litter, organic layer, mineral soil, and roots is that the natural aggregate of components in the soil is disrupted, with significant changes to the physical and biological environment of each of the components. Root free soil samples, for example, can only give an approximate estimate of the heterotrophic flux in a given horizon, because gradients between areas of high and low activity by the soil biota in this naturally heterogeneous environment have been homogenized by sieving.

There are conflicting views in the literature concerning the sensitivity of excised root CO<sub>2</sub> production to cuvette CO<sub>2</sub> concentration. Ryan *et al.* (1996) found a change in root respiration in response to [CO<sub>2</sub>], and quantified this error empirically, indicating an exponential increase in root respiration with an artificial decrease in surrounding CO<sub>2</sub> concentration. Following their example of roots measured at 400 µmol mol<sup>-1</sup> CO<sub>2</sub>, the actual efflux at the assumed concentration in the soil of 1500 µmol mol<sup>-1</sup> CO<sub>2</sub> would be overestimated by a factor of 4.5. Other authors also report marked impacts of cuvette [CO<sub>2</sub>] (Qi *et al.*, 1994; Burton *et al.*, 1997), while Burton & Pregitzer (2002) and Burton *et al.* (2004) report that there is no influence, suggesting that the sensitivity of measured root respiration to cuvette [CO<sub>2</sub>] may differ according to tree species (Burton & Pregitzer, 2003).

Rakonczay *et al.* (1997a) investigated the effect of timing between isolating excised root from soil and measuring the CO<sub>2</sub> production, and found that for the three tree species investigated (i.e. *Acer rubrum*, *Quercus rubra*, and *Pinus strobus*), measured CO<sub>2</sub> production rates dropped within 1 h to between 30% and 50% of values measured within 1 min of separation. In a separate study, Rakonczay *et al.* (1997b) compared specific root respiration rates measured *in situ* with that of excised and found that the agreement was better for excised roots 30 min after separation than for roots measured immediately after removal from the soil. As can be seen from Table 3, there is no uniform procedure regarding the time between root isolation and respiration measurement, the cuvette CO<sub>2</sub> concentration, or whether roots should be separated by washing or dry sieving. Given the conflicting evidence on [CO<sub>2</sub>] influence in root respiration, it is advisable to conduct respiration measurements of excised roots at concentrations close to those in the soil. The results of Rakonczay *et al.* (1997b) suggest that fluxes measured about 30 min after excising are more similar to live root respirations, and the rapid change in CO<sub>2</sub> evolution rate following the initial 30 min after root separation means that if the delay is not standardized, repeated measurements are prone to a considerable error. There is to our knowledge no rigorous examination of the effects of storage length and storage temperature and moisture for root or soil samples, which may have considerable influence over the measured rates.

**Table 3** Overview of experimental conditions in studies using the *roots excised* technique

	Cuvette [CO <sub>2</sub> ] (ppm)	Time after root isolation	Separation method	Comment
Billings <i>et al.</i> (1978)	n/a	24 h	Wet	
Burton <i>et al.</i> (2004)	1000	15 min	Dry	Found no effect of 350 vs. 1000 ppm CO <sub>2</sub>
Craine <i>et al.</i> (1999)	370	12 h	Wet	Roots cooled during transportation to lab
Edwards & Harris (1977)	n/a	'Immediate'	n/a	Measure O <sub>2</sub> uptake rather than CO <sub>2</sub> production
Edwards & Sollins (1973)	n/a	'Immediate'	Wet	Measure O <sub>2</sub> uptake rather than CO <sub>2</sub> production
Fahey <i>et al.</i> (2005)	Ambient	15 min	Wet	
Herman (1977)	n/a	> 1 h	Wet	
Irvine & Law (2002)	n/a	'Immediate'	Dry	
Law <i>et al.</i> (2001a)	n/a	'Immediate'	Dry	
Law <i>et al.</i> (2001b)	n/a	'Immediate'	Dry	
Maier & Kress (2000)	380	60		Roots cooled before Measurements;
Nakatsubo <i>et al.</i> (1998)	350	1–9 days	Wet	
Ruess <i>et al.</i> (2003)	1000	'Immediate'	Dry	Some organic matter remained attached to roots
Tate <i>et al.</i> (1993)	n/a	19 days	n/a	Samples incubated at field temperatures over 14 days before measurements
Widén & Majdi (2001)	800–1400	30 min	Wet	Whole root, with 'some' mycorrhizae attached

Where authors did not specify cuvette CO<sub>2</sub> concentration ('n/a' in table), ambient concentrations are likely to have been used.

In contrast to most other techniques described earlier, physical separation techniques do generally produce  $R_A$  estimates that represent the actual autotrophic respiration (i.e. growth and maintenance respiration by roots), and not the sum of autotrophic and rhizomicrobial respiration. Nguyen (2003) estimates that about 50% of C allocated belowground is lost from roots as root cap cells, secretions of mucilage and exudations, and subsequently respired heterotrophically in the rhizosphere. It would, therefore, be expected that studies using the excised root technique would report relatively high  $R_H/R_S$  ratios, as the autotrophic component of  $R_S$  would be underestimated. However, Fig. 5 places this technique below the overall regression derived for all techniques, while the considerable error of this mean value means that there is no significant difference to any of the other techniques. It is, therefore, likely that this technique produces  $R_A$  estimates that are too high, and considerable care should be taken to maintain conditions surrounding the roots as close as possible to those *in situ*, in order to minimize this error.

In spite of the considerable problems posed by component isolation techniques, they are none, the less widely employed. The reason for this is that this kind of partitioning does not require the expensive equipment needed for isotopic studies, and is less complex than large-scale manipulation approaches as in root exclusion techniques.

#### Isotopic techniques

Isotopic techniques allow a mostly noninvasive measurement of flux fractions within  $R_S$ . Atmospheric labelling techniques, however, have been confined either to laboratory experiments (see Table 1 for references), or as a result of atmospheric CO<sub>2</sub> enrichment (in FACE or open top chamber experiments). The isotopic labelling is, therefore, confounded with increased photosynthesis following the atmospheric enrichment, and does not represent present natural conditions. While this is a useful set up to investigate the response of ecosystems under likely future conditions, care has to be taken when soil C dynamics are evaluated. Van Groenigen *et al.* (2005) found that the decomposition of root litter from plants grown under elevated CO<sub>2</sub> was slower (i.e. showed negative priming) in stands under FACE treatment, while older SOM showed an increase in decomposition under the same treatment (positive priming). Additionally, the label introduced into the atmosphere will over time become incorporated into plant and subsequently soil pools, so that corrections need to be applied when using the tracer to identify  $R_A$  within  $R_S$  (e.g. Hanson *et al.*, 2000).

Variations in the natural <sup>13</sup>C abundance in assimilates have been used to investigate the link between photosynthesis and  $R_A$ . Ekblad & Höglberg (2001) and Ekblad *et al.* (2005) made use of the fact that the  $\delta^{13}\text{C}$  value of leaf assimilates is correlated with stomatal openness, which varies according to the difference in leaf to air water vapour pressure. The consequential linear relationship between  $\delta^{13}\text{C}$  in soil-respired CO<sub>2</sub> and relative air humidity (after incorporation of a time lag corresponding to the time of transport of assimilates from the crown to roots) allows the calculation of  $R_A$  contributions on a daily time scale. A quantification of flux contributions is more difficult and only feasible for short (daily) time steps (Ekblad & Höglberg, 2001).

By measuring the  $\Delta^{14}\text{C}$  value of soil respired CO<sub>2</sub>, it is possible to divide SR into recently (<1 year) assimilated C and a flux portion representing sources of C fixed more than 1 year before measurements, using the change in atmospheric <sup>14</sup>CO<sub>2</sub> over time following the 'bomb spike'. However, this distinction into 'recent' and 'older' C only approximates  $R_A$  and  $R_H$ , respectively, as the 'recent' group not only includes C directly derived from roots, but also portions of decomposing surface and root litter. Gaudinski *et al.* (2000) estimated that the recent portion of soil CO<sub>2</sub> efflux (i.e.  $R_A$  + an unknown fraction of recent plant litter) comprised 59% of annual  $R_S$ .

Given the diversity of approaches described in the previous paragraphs, all of which we grouped as *isotopic* techniques, there is likely to be a range of technique related biases confounded with this categorization, and this group does in fact show the highest level of variation for  $R_H/R_S$  ratios of all techniques (Fig. 5).

#### Indirect methods

Within this category, the *root regression* method suffers from the most significant error source associated with the underlying assumptions. Figure 5 indicates that the root mass regression approach yields consistently lower results than the other techniques. The technique assumes that all variation in  $R_S$  in space is due to the activity of roots, while  $R_H$  is constant at all measuring points. However, spatial heterogeneity of  $R_S$  can be quite significant, with coefficients of variations of commonly up to 40% (e.g. Subke *et al.*, 2004a), and the correlation of  $R_S$  and root mass may be governed by soil parameters (e.g. rock content, changes in physical structure of soil horizons) that similarly affect  $R_H$ , so that the extrapolation of a root mass vs.  $R_S$  regression does not produce the true, spatially invariable  $R_H$ . Rodeghiero & Cescatti (2006) modified the simple regression function, so that  $R_S$  was regressed simultaneously to total root content, and to total C in the soil, assuming that the

**Table 4** Summary of methodological biases leading to either over-estimation (↑), under-estimation (↓), or no change (–) in the observed  $R_H/R_S$  ratio

Method	Reason for bias	Effect on $R_H/R_S$ ratio
Root exclusion	Increase in dead root biomass	↑
	Lack of litter input	↓
	Lack of water uptake by roots	↑
	Change in radiation and throughfall ( <i>gap</i> and <i>clipping</i> )	↑, ↓
Physical separation	Homogenizing of soil samples following separation	↑, ↓
	Low cuvette CO <sub>2</sub> concentration ( <i>roots excised only</i> )	↓, –
	Timing of measurement for excised roots	↓, –
Isotopic methods	Incorporation of isotopic label into biomass (continuous labelling and radiocarbon studies)	↓
Indirect methods	Spatial co-variance of $R_H$ and $R_S$ ( <i>root regression only</i> )	↓

Where the effect on the  $R_H/R_S$  ratio is ambivalent, the effects show different biases in short- and long-term responses, or more than one response was reported in the literature. Please see details in the discussion for a full descriptions of observed patterns, and possible corrections.

former correlates with  $R_A$ , and the latter with  $R_H$ . Other soil parameters further influence the relationship between  $R_S$  and root and C contents, as was evidenced by the correlation between  $R_A$  per root mass correlated with soil N content found by the same authors.

#### Interactions of $R_A$ and $R_H$

In the previous sections we have tried to show strengths and weaknesses of different techniques used to partition  $R_S$ , and Table 4 gives a brief summary of method-related biases introduced by different techniques. As partitioning studies by nature attempt to separate flux contributions, some of the interactions taking place belowground may go unnoticed. Over recent years, however, increasing numbers of studies have indicated interactions between different soil components may have either promoting or inhibiting effects on respective flux contributions (termed positive or negative priming effect, e.g. Kuzyakov, 2002). These results indicate that increases in NPP predicted as a consequence of higher global CO<sub>2</sub> concentrations and temperatures do not necessarily translate into higher C storage in soil, as the increase in plant activity simultaneously increases decomposition of recent and older SOM both in forest (e.g. Hoosbeek *et al.*, 2004; Subke *et al.*, 2004b; Sulzman *et al.*, 2005; Trueman & Gonzalez-Meler, 2005) and grassland studies (e.g. van Groenigen *et al.*, 2005; Xie *et al.*, 2005). Isotopic tracers have been particularly useful in elucidating the interactions between soil components both in laboratory situations and in the field (e.g. Hoosbeek *et al.*, 2004; Subke *et al.*, 2004b; Trueman & Gonzalez-Meler, 2005), but mechanisms of priming remain poorly understood (see Kuzyakov *et al.*, 2000

and Lafontaine *et al.*, 2003 for discussions of priming mechanisms), and there are insufficient studies attempting a quantification of priming under natural conditions to allow an analysis in the context of this metaanalysis.

#### Conclusions

The results of this metaanalysis clearly show the close link between relative flux contributions of  $R_H$  or  $R_A$  and total  $R_S$ . With a view to global change, this finding may indicate that higher C assimilation in the canopy does not translate into higher sequestration of C in ecosystems, but simply a faster transport through plants to return to the atmosphere via the roots. More work is needed to arrive at a better understanding of the effects that changed environmental conditions are likely to have on the partitioning of assimilated C into biomass and autotrophic respiration (including the rhizomicrobial route). The understanding of soil-priming processes at field scale is also just emerging, but critical to any prediction of future C storage of soils. If enhanced assimilation in a warmer and CO<sub>2</sub>-richer world will lead to increases in root exudations, priming of older SOM by roots will be of increased importance to the soil C budget.

While the comparison of methodologies in soil CO<sub>2</sub> efflux partitioning studies shows generally good agreement, there are numerous assumptions masked within these results, and we have tried to indicate where potential biases arise and corrections are needed. Interest in soil CO<sub>2</sub> efflux partitioning has seen a considerable increase over recent years, and new developments will hopefully help to validate some of the underlying assumptions for different approaches, and allow a

better understanding of belowground C dynamics in the light of global change.

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