FORUM

Carbon balance gradient in European forests: should we doubt 'surprising' results? A reply to Piovesan & Adams

Jarvis, P.G.¹; Dolman, A.J.²; Schulze³, E.-D.; Matteucci, G.^{4*}; Kowalski, A.S.^{5,14}; Ceulemans, R.⁵; Rebmann, C.³; Moors, E.J.²; Granier. A.⁶; Gross, P.⁶; Jensen, N.O.⁷; Pilegaard, K.⁷; Lindroth, A.⁸; Grelle, A.⁹; Bernhofer, Ch.¹⁰; Grünwald, T.¹⁰; Aubinet, M.¹¹; Vesala, T.¹²; Rannik, Ü.¹²; Berbigier, P.¹³; Loustau, D.¹⁴; Guðmundsson, J.¹⁵; Ibrom, A.¹⁶; Morgenstern, K.¹⁶; Clement, R.¹; Moncrieff, J.¹; Montagnani, L.¹⁷; Minerbi, S.¹⁷ & Valentini, R.^{4*}

¹Institute of Ecology and Resource Management, University of Edinburgh, EH9 3JU Edinburgh; United Kingdom;

²Alterra, P.O. Box 47, 6700 AA Wageningen, The Netherlands; ³Max-Planck-Institut für Biogeochemie, D-07745

Jena, Germany; ⁴Department of Forest Environment and Resources, University of Tuscia, I-01100 Viterbo, Italy;

⁵Department of Biology; University of Antwerpen, Universiteitsplein 1; B-2610 Wilrijk, Belgium; ⁶Centre de
Recherches de Nancy, Unité d'Ecophysiologie Forestière, F-54280 Champenoux; France; ⁷Risø National
Laboratory; DK-4000 Roskilde; Denmark; ⁸Department of Physical Geography, Lund University, Box 118,
SE-22100 Lund, Sweden; ⁹Department of Production Ecology, Swedish University of Agricultural Sciences,
P.O. Box 7042, SE-75007 Uppsala, Sweden; ¹⁰Institut für Hydrologie und Meteorologie, Technische Universität
Dresden, D-01737 Tharandt, Germany; ¹¹Unité de Physique, Faculté Universitaire des Sciences Agronomiques de
Gembloux, B-5030 Gembloux, Belgium; ¹²Department of Physics; University of Helsinki; P.O. Box 9, FIN-00014
Helsinki, Finland; ¹³Unité de Bioclimatologie, INRA, Bordeaux, BP 81, F-33883 Villeneuve d'Ornon Cedex,
France; ¹⁴Unité de Recherches Forestières, INRA, Bordeaux, BP 45, F-33611 Gazinet, France; ¹⁵ Agricultural
Research Institute, Environmental Department, Keldnaholti, 112 Reykjavik, Iceland; ¹⁶Institut für Bioklimatologie,
Georg-August University of Göttingen, Büsgenweg 2, D-37077 Göttingen, Germany; ¹⁷Forest Services, Autonomous
Province of Bolzano, Bolzano, Italy; *Corresponding author; Fax +39 0761357389; E-mail rik@unitus.it

Abstract. This paper responds to the Forum contribution by Piovesan & Adams (2000) who criticized the results obtained by the EUROFLUX network on carbon fluxes of several European forests. The major point of criticism was that the data provided by EUROFLUX are inconsistent with current scientific understanding. It is argued that understanding the terrestrial global carbon cycle requires more than simply restating what was known previously, and that Piovesan & Adams have not been able to show any major conflicts between our findings and ecosystem or atmospheric-transport theories.

Keywords: Carbon flux; Decomposition; EUROFLUX; Respiration; Soil organic matter.

Abbreviations: LAI = Leaf area index; NEE = Net ecosystem exchange of carbon.

Piovesan & Adams (2000) criticize the results obtained by the EUROFLUX network on carbon fluxes of several European forests (Valentini et al. 2000) and also their interpretation. They consider that the reported results are 'surprising', since the reported latitudinal trend in carbon sequestration, with more uptake at lower than at higher latitudes, contrasts with the expectation that respiration will be higher in warmer climates and thus that the overall carbon uptake of the ecosystems will be less.

Progress in science is made by discovering *surprising* phenomena, rather than by merely confirming the expected, particularly when new and advanced experimental techniques become available. Our results comprise the first large data set of direct measurements at the ecosystem scale of net ecosystem exchange of carbon (NEE) by closed-canopy forests located over the whole of the European continent. In this respect, we agree with Piovesan & Adams on some of the points that they raise: i.e.:

(1) determining the carbon sink capacity of any forested region is a very complex matter;

- (2) there is a need for a larger number of sites;
- (3) inter-annual variability is a key issue; and
- (4) temporal scales must be extended from annual to decadal variations. However, Piovesan & Adams raise a number of substantial other points with which we do not agree and these form the substance of this note.

The classic view on the increase of respiration with temperature is generally based on data collected at single sites and on local- or laboratory-based responses; there are few data from a number of sites measured directly with the same technique over the same period. The EUROFLUX data also show that soil and total ecosystem respiration analysed at individual sites increases with increasing temperature (Valentini et al. 2000; Janssens et al. in press). However, new data from a range of ecosystems, not only forests, suggest that the temperature response of respiration that holds at a particular site may not be generally applicable across a range of sites and to other ecosystems (Liski et al. 1999; Giardina & Ryan 2000; Janssens et al. in press).

In the short-term, soil-heating experiments have indeed shown an increase of soil respiration in heated plots compared with unheated control plots (Peterjohn et al. 1993; McHale et al. 1998). For example, in a northern hardwood forest, differences in annual respiration between the reference plot and soil plots 2.5, 5 and 7.5 °C warmer, were large and significant in the first year, but they were smaller, and mostly were not significant, in the second year. The largest difference was between the reference plot and the 2.5 °C heated plot, indicating some acclimation in responses to temperature and to duration of manipulation (McHale et al. 1998). In longer-term soil-heating experiments, reports are indicating that the differences become small or non-existent (Giardina & Ryan 2000; Jarvis & Linder 2000). The amount of soil organic matter that is readily decomposable is likely to limit the response of respiration to an increase in soil temperature unless, or until, the production of detritus is stimulated to increase (Jarvis & Linder 2000). At a larger spatial scale, annual soil and ecosystem respiration data of 18 forest ecosystems in Europe showed no significant relationship with mean annual temperature across the sites, while the supply of recently assimilated carbon (i.e. Gross Primary Production) turned out to be a significant driver of soil respiration across the sites (Janssens et al. in press).

The prediction of increased decomposition of soil carbon with increasing temperature is largely dependent on the assumption that the decomposition of all soil organic matter is as temperature-sensitive as that of fresh litter. However, several analyses do not support this assumption. A global review of published data on decomposition rates of organic carbon in mineral soil has recently argued that soil decomposition rates are remarkably constant, irrespective of average site temperature (Giardina & Ryan 2000). Furthermore, Liski et al. (1999) independently suggested that adaptation of soil respiration to temperature may result from the lower sensitivity of decomposition of old soil organic matter to temperature. Lloyd & Taylor (1994) developed an empirical model that coincidently partly accounts for adaptation of soil respiration to temperature. The model predicts that the coefficient representing the increase in soil respiration following an increase of 10 °C in temperature (the Q₁₀) would be expected to decline with increasing average soil temperature. Furthermore, respiration rates of vegetation grown in relatively warm environments are often lower than those in cooler environments, particularly when measured at the higher temperatures (Ryan 1991). These and other findings suggest that, while there could be a general capacity of the respiratory processes to adapt to gradual changes of temperature, respiration is likely to be linked to a combination of factors that may override a general across-site temperature relationship (Davidson et al. 2000).

The criticism by Piovesan & Adams is not based on original observations or experiments that contradict our findings: it merely contains a rather imprecise review of the literature. They say that our data are 'unusual' compared with those 'taken at many other broadly comparable sites around the world (Malhi et al. 1999)'. However, in that paper Malhi et al. report NEE values that are exactly in line with those measured in European forests by EUROFLUX. They report a NEE of 68 g C m⁻² yr⁻¹ for a boreal forest, 585 g C m⁻² yr⁻¹ for a temperate broadleaved forest, and 590 g Cm⁻² yr⁻¹ for a tropical forest (see Table 6, item 16 in Malhi et al. 1999). These values are of the same order of magnitude as our data and clearly also indicate a general latitudinal trend. The boreal forest data, for example, are coincident with our EUROFLUX data at the same latitude. The data are so clearly presented that we can only assume that Piovesan & Adams have made a mistake in their analysis!

A similar latitudinal trend is also evident in an independent data set from North America, collected between 1992 and 1998 over similar closed-forest ecosystems (Fig. 1). This similarity strongly suggests that our measurements are not biased by our selection of sites but that they are representative of a more general trend. It is interesting that the latitudinal trend of the North American sites shows less carbon sequestration at the same latitude than in Europe; this probably reflects the effects of a more

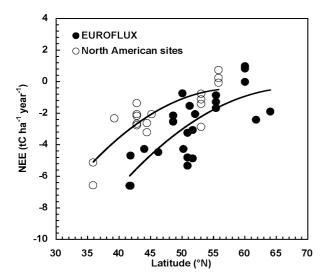


Fig. 1. Rates of Net Ecosystem Exchange (NEE) from European (Valentini et al. 2000) and North-American closed-forest ecosystems. The North American data are from Baldocchi et al. (2000), Black et al. (1996), Black et al. (2000), Goulden et al. (1996, 1998), Greco & Baldocchi (1996), Hollinger et al. (1999), Law et al. (2000), Schmid et al. (2000) and Wosfy et al. (1993).

continental climate on the length of the growing season and on drought.

In the analysis of the EUROFLUX data set, a multivariate statistical analysis on the effect of single factors (latitude, precipitation, ecosystem type, elevation, mean annual temperature, age, management type, LAI) in explaining variation in NEE, resulted in latitude as the most significant single variable model (Valentini et al. 2000). Nevertheless, in plotting our data against latitude, we do not wish to imply that latitude is a dominant, causative factor. Latitude is a surrogate for a number of possible driving variables, including length of growing season, site history and management practice, and the multiple variables that impact on soil decomposition processes (soil moisture, land-use, soil organic matter properties). As such, latitude provides a practical scale that takes these and other variables into account.

The eddy covariance technique, in contrast to other approaches, allows measurement and representation of the *net* carbon balance at a local scale. The technique is able to resolve small spatial and temporal changes and is a research tool for full-carbon-accounting at ecosystem scale (Baldocchi et al. 1996; Running et al. 1999; Valentini et al. 2000). In particular, when combined with traditional, ecophysiological techniques a new and coherent picture is obtained of the component processes that are relevant to carbon sequestration by ecosystems, as shown for forest stands by Malhi et al. (1999).

The results obtained lead to improved understanding of the variables driving the carbon uptake processes and of the functional ecology of forest ecosystems and, as Piovesan & Adams recognize, they can be used to validate ecosystem models and to provide, at local scale, realistic constraints on estimates of the global carbon balance (Running et al. 1999; Valentini et al. 2000). Nevertheless, it is not realistic simply to sum canopy flux data from a number of ecosystems to obtain a carbon budget at a larger scale, as Piovesan & Adams do when they identify a contribution by a particular biome to the missing carbon sink at global scale. In doing this, they neglect to recognise that closed-forest land cover differs widely from biome to biome. For example, the closed-forest cover of Mediterranean countries (23.9 Mha) is less than half that of temperate (52.8 Mha) or boreal (51.9 Mha) countries (Beckel 1995). It is for this reason that we confined our analysis to forest ecosystems, and did not extrapolate to regional areas of forest biomes and their roles as active carbon sinks.

In our opinion, it is their incorrect interpretation of the scaling potential of the ecosystem flux data which leads to their second criticism, based on their comparison of the results in the *Nature* paper with those appeared in a previous paper that used data produced by the same research community (Martin et al. 1999). The analysis by Martin et al. is based on up-scaling our site data to European scale, using biomass as the scaling factor for NEE together with the European databases of forest cover and biomass, as is clearly stated in the paper. Martin et al. presented two European maps of regional NEE, ranging from a minimum to a maximum possible estimate. These up-scaled values represent a first attempt at scaling up the EUROFLUX data, and are not directly comparable with the site-based estimates presented in the *Nature* paper.

Piovesan & Adams also state that other data sets, (e.g. Miglietta & Peressotti 1999) show carbon sequestration rates that are lower than those of our Mediterranean and other forest ecosystems. The data they quote are for a particular shrub ecosystem with a very sparse canopy and a small leaf area index (LAI), whereas our data are for closed-canopy forests throughout Europe, with LAI ranging from 2.8 to 5.6 m² m⁻² (Valentini et al. 2000).

Piovesan & Adams consider that for some sites, particularly in the Mediterranean region, the reported values of NEE would imply a carbon sink that is larger than would usually be expected. We would like to point out that a project aimed at estimating net ecosystem production (NEP = NEE) of *Fagus* and *Picea* forest ecosystems along a north-south transect across Europe by measuring and summing the component processes and

fluxes (NPP, soil and litter carbon mineralization, etc.) obtained NEP values even higher than those measured in EUROFLUX by eddy covariance for the same species (CANIF; Schulze2000). The two projects had one site in common, the beech forest of Collelongo (site Italy 1 in Valentini et al. 2000). For this site, the average values of NEP by summation of component processes and by eddy covariance over a period of up to three years agreed to within 10% (Schulze et al. 2000). Thus the very surprising results to which Piovesan & Adams refer are consistent with results obtained by at least four different research groups working at the same site. For this site, in 1996, 50% of the carbon sink was estimated to be allocated to above-ground growth of wood and 50% to below-ground processes (Valentini et al. 1996), and not solely to the soil carbon reservoir, as stated by Piovesan & Adams.

Piovesan & Adams also write that "regenerating forests are slow to attain their high carbon densities and usually these stands take more than a century to reach maximum biomass after tree planting or natural forest regeneration after cutting (and a much longer time to reach maximum soil carbon density)". They fail to take into consideration that 14 out of the 17 forests (i.e. 82%) in our study are less than 80 yr old and the rest are around 100 yr old (see Table 1 in Valentini et al. 2000), i.e. they are not "mature late-successional forest stands". Furthermore, practically all the forest ecosystems in the study are actively managed and are certainly representative of the generally increasing growth trend of European forests (Kauppi et al. 1992; Spiecker et al. 1996).

Another criticism by Piovesan & Adams relates to uncertainties in the eddy covariance methodology. Like all techniques, eddy covariance is subject to errors of measurement and analysis. Such errors have been identified and quantified in a number of papers in which appropriate methods for correction are also presented (see citations in Piovesan & Adams 2000). We would point out that the literature the authors use to justify their statement that our results "are largely or entirely the result of errors in the eddy covariance method" has been very largely produced by scientists from within the EUROFLUX consortium. We assume that Piovesan & Adams have carefully read those papers, the results of which have been used to make considered corrections to our datasets (see Aubinet et al. 2000). We are surprised that Piovesan & Adams do not refer to the supplementary information that we provided in association with the *Nature* paper (Valentini et al. 2000). This information clearly states that the same stateof-the-art corrections were applied to the eddy covariance data throughout the whole network, so as to ensure comparable results.

Currently, nobody knows if, or how, the overall

picture that we have presented will change when data from more sites become available. At the moment, the existing data, both in Europe and in North America, show the same significant trend. We have already acknowledged that the variation is high at mid-latitudes (Valentini et al. 2000) and that we need more data from the Mediterranean and boreal regions. On a longer time scale, climatic anomalies, such as those regulated by the North Atlantic Oscillation and by the El Niño/La Niña cycles, as well as the consequences of global climatic change, may change the picture. Currently, the global carbon cycle is being added to General Circulation Models (GCMs) (e.g. Cox et al. 2000) and it is then crucial that the appropriate driving variables and feedbacks are included. Furthermore, in view of recent projections that current carbon sinks may become carbon sources within the next 50 years (Cox et al. 2000), continued, widespread investigation of the inter-annual variability and long-term trends in carbon fluxes from terrestrial ecosystems is urgently needed.

Indeed, the scientific communities in both Europe and North America considered it important to continue investigation of the carbon sequestration processes and, after rigorous peer-review of proposals, the funding agencies have decided to fund continuation of research like that carried out within EUROFLUX for the next three to five years, focussing on long-term forest stand carbon fluxes, their driving variables and inter-annual variability.

This critical discussion initiated by Piovesan & Adams has given us the opportunity to clarify points of concern and misunderstanding, and to add new evidence to the conclusions presented by Valentini et al. (2000). The major point of criticism was that the data provided by the scientific community of EUROFLUX (and also by implication AMERIFLUX) appeared to be inconsistent with current scientific understanding. However, understanding the terrestrial global carbon cycle requires more than simply restating what was known previously: it requires a willingness to accept new techniques and to understand and interpret surprising and unusual results. Despite their focussed criticisms, Piovesan & Adams (2000) have not been able to show any major conflicts between our findings and ecosystem or atmospheric-transport theories. This encourages us to reaffirm that our work has resulted in new knowledge and has contributed to recent scientific progress in a very complex field that is both scientifically and politically important: the assessment and prognosis of current and future sequestration rates of atmospheric carbon dioxide by the terrestrial biosphere.

References

- Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A.S., Martin, P.H., Berbigier, P., Bernhofer, Ch., Clement, R., Elbers, J., Granier, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R. & Vesala, T. 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Adv. Ecol. Res. 30: 113-175.
- Baldocchi, D.D., Finnigan, J., Wilson, K., Paw, U.K.T. & Falge, E. 2000. On measuring net ecosystem carbon exchange over tall vegetation on complex terrain. *Boundary-Layer Meteorol*. 96: 257-291.
- Baldocchi, D.D., Valentini, R., Running, S., Oechel, W. & Dahlman, R. 1996. Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biol.* 2: 159-167.
- Beckel, L. 1995. Satellite remote sensing forest atlas of Europe. Justus Pether Verlag, Gotha.
- Black, T.A., den Hartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nesic, Z., Lee, X., Chen, S.G., Staebler, R. & Novak, M.D. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol*. 2: 219-229.
- Black, T.A. Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nesic, Z., Hogg, E.H., Neumann, H.H. & Yang, P.C. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophys. Res. Letter* 27: 1271-1274.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408: 184-187.
- Davidson, E.A., Trumbore, S.E. & Amindson, R. 2000. Soil warming and organic carbon content. *Nature* 408: 789-790.
- Giardina, C.P. & Ryan, M.G. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404: 858-861.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C. & Wosfy, W.C. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271: 1576-1578.
- Goulden, M.L., Wosfy, W.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, F.A. & Munger, J.W. 1998. Sensitivity of Boreal forest carbon balance to soil thaw. *Science* 279: 214-217.
- Greco, S. & Baldocchi, D.D. 1996. Seasonal variation of CO₂ and water vapour exchange rates over a temperate deciduous forest. *Global Change Biol.* 2: 183-197.
- Hollinger, D.Y., Goltz, S.M., Davidson, E.A., Lee, J.T., Tu, K. & Valentine, H.T. 1999. Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biol.* 5: 891-902.
- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S.,

Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T, Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guðmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, Ch., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.-D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R. & Valentini, R. In press. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.*

- Jarvis, P.G. & Linder, S. 2000. Constraints to growth of boreal forests. *Nature* 405: 904-905.
- Kauppi, P.E., Mielikäinen, K. & Kuusela, K. 1992. Biomass and carbon budget of European forests, 1971 to 1990. Science 256: 70-74.
- Law, B.E., Williams, M., Anthoni, P.M., Baldocchi, D.D. & Unsworth, M.H. 2000. Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biol.* 6: 613-630.
- Liski, J., Ilvesniemi, H., Mäkelä, A. & Westman, C.J. 1999.
 CO₂ emissions from soil in response to climatic warming are overestimated. The decomposition of old soil organic matter is tolerant of temperature. *Ambio* 28: 171-174.
- Lloyd, J. & Taylor, J.A. 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8: 315-323.
- Malhi, Y., Baldocchi, D.D. & Jarvis, P.G. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ*. 22: 715-740.
- Martin, P.H., Valentini, R., Jacques, M., Fabbri, K., Galati, D.,
 Quaratino, R., Moncrieff, J.B., Jarvis, P., Jensen, N.O.,
 Lindroth, A., Grelle, A., Aubinet, M., Ceulemans, R.,
 Kowalski, A.S., Vesala, T., Keronen, P., Matteucci, G.,
 Granier, A., Berbingier, P., Loustau, D., Grelle, A., Schulze,
 E.-D., Tenhunen, J., Rebman, C., Dolman, A.J., Elbers,
 J.E., Bernhofer, Ch., Grünwald, T. & Thorgeirsson, H.
 1998. New estimates of the carbon sink strength of EU
 forests integrating flux measurements, field surveys, and
 space observations: 0.17-0.35 Gt C. Ambio 27: 582-584.
- McHale, P.J., Mitchell, M.J. & Bowles, F.P. 1998. Soil warming in a northern hardwood forest: trace gas fluxes and leaf litter decomposition. *Can. J. For. Res.* 28: 1365-1372.
- Miglietta, F. & Peressotti, A. 1999. MEDEFLU Summer drought reduces carbon fluxes in Mediterranean forest. Global Change NewsLetter 39: 15-16.
- Peterjohn, W.T., Melillo, J.M., Bowles, F.P. & Steudler, P.A. 1993. Soil warming and trace fluxes: experimental design and preliminary flux results. *Oecologia* (*Berl.*) 110: 18-24.
- Piovesan, G. & Adams, J.M. 2000. Carbon balance gradient in European forests: interpreting EUROFLUX. *J. Veg. Sci.* 11: 923-926.
- Running, S.W., Baldocchi, D.D., Turner, D.P., Gower, S.T., Bakwin, P.S. & Hibbard K.A. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modelling and EOS satellite data. *Remote Sens. Environ.* 70: 108-127.
- Ryan, M.G. 1991. Effects of climate change on plant respira-

- tion. Ecol. Appl. 1: 157-167.
- Schmid, H.P., Grimmond, C.S.B, Cropley, F., Offerle, B. & Su, H.-B. 2000. Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States. *Agricult. For. Meteorol.* 103: 357–374.
- Schulze, E.-D. (ed.) 2000. Carbon and nitrogen cycling in European forest ecosystems. Ecological Studies 142, Springer Verlag, Heidelberg.
- Schulze, E.-D., Högberg, P., Van Oene, H., Persson, T., Harrison, A.F., Read, D., Kjøller, A. & Matteucci, G. 2000. Interactions between the carbon- and nitrogen cycle and the role of biodiversity: A synopsis of a study along a north-south transect through Europe. In: Schulze, E.-D. (ed.) *Carbon and nitrogen cycling in European forest ecosystems. Ecological Studies* 142, pp. 468-491. Springer Verlag, Heidelberg.
- Spiecker, H., Miellikänen, K., Köhl, M. & Skovsgaard, J.P. 1996. *Growth trends in European forests*. Springer-Verlag, Heidelberg.

- Valentini, R., De Angelis, P., Matteucci, G., Monaco, R., Dore, S. & Scarascia Mugnozza, G.E. 1996. Seasonal net carbon dioxide exchange of a Beech forest with the atmosphere. *Global Change Biol.* 2: 199-207.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, Ch., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Gu∂mundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S. & Jarvis, P.G. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404: 861-865.
- Wosfy, S.C., Goulden, M.L., Munger, J.W., Fan, S.-M., Bakwin, P.S., Daube, D.C., Bassow, S.L. & Bazzaz, F.A. 1993. Net exchange of CO₂ in a mid-latitude forest. *Science* 260: 1314-1317.