CO₂ Deficit in Temperate Forest Soils Receiving High Atmospheric N-Deposition

Evidence is provided for an internal CO₂ sink in forest soils, that may have a potential impact on the global CO₂-budget. Lowered CO₂ fraction in the soil atmosphere, and thus lowered CO₂ release to the aboveground atmosphere, is indicated in high N-deposition areas. Also at forest edges, especially of spruce forest, where additional N-deposition has occurred, the soil CO₂ is lowered, and the gradient increases into the closed forest. Over the last three decades the capacity of the forest soil to maintain the internal sink process has been limited to a cumulative supply of approximately 1000 and 1500 kg N ha⁻¹. Beyond this limit the internal soil CO₂ sink becomes an additional CO₂ source, together with nitrogen leaching. This stage of "nitrogen saturation" is still uncommon in closed forests in southern Scandinavia, however, it occurs in exposed forest edges which receive high atmospheric N-deposition. The soil CO₂ gradient, which originally increases from the edge towards the closed forest, becomes reversed.

INTRODUCTION

Root and microbial respiration implies that soils are a carbon dioxide (CO₂) source, constituting half of the CO₂ from respiration on the continents around the globe. An almost equivalent amount is released directly from terrestrial plants to the atmosphere (1, 2). CO₂ is transported to the atmosphere directly from the soil surface, or with drainage water to streams. The lowest CO₂ concentration in the soil atmosphere, even after total inhibition of CO₂ production in the soil, is considered to be that in the aboveground atmosphere, e.g. under frozen or dry conditions when no CO₂ is produced (3). However, low soil CO₂ concentrations during warm and wet conditions, even concentrations slightly below the aboveground atmospheric concentration, were recorded at some sites on the Swedish west coast where atmospheric N-deposition is high. These findings initiated the extensive 10-yr study reported here. In order to determine whether or not there was a soil process strong enough to decrease CO₂ emissions to the atmosphere, I collected 4594 soil atmosphere samples from 1992 through 2000, including one sampling occasion in June 2001 in the NW Pacific rainforest, Washington, USA.

MATERIALS AND METHODS

Sampling was carried out in (number of samples within parentheses): Sweden (4200), Denmark (232), The Netherlands (55), USA (31), Norway (17). In addition, samples were also taken in Argentina, Brazil, Canada, The Czech Republic, Germany, Greece, Italy, and Polen (altogether 59). Samples were taken in spruce forest (3243), pine forest (253), deciduous forest (588), clearcut forest (227), grassland (57), agricultural land (196), and different types of vegetation, e.g. heathland (30). Sampling depth was generally 0–20 cm, but at some sites deeper layers were sampled, but less frequently. A total of 785 analyses of CO₂ were carried out in soil or the above soil atmosphere at the laboratory. Air samples were also analyzed (4). Site descriptions (fertilizer supply, N-leaching) are given in several research reports

(5–12) and by I. Stjernquist (pers. comm. relating to the Konga experimental beech forest site).

Atmospheric N-deposition can be taken up by leaves/needles, leaving an unknown fraction that may reach the ground directly. This fraction (throughfall) is, among other conditions, dependent on whether the site has reached nitrogen saturation or not. Although easy to measure, it is not used as a measure of N-deposition in this study.

N-deposition refers to the EMEP (13, G. Lövblad, pers. comm.). The cumulative N-input over the last 30 yrs was estimated based on the same annual atmospheric N-deposition during 1970–2000, and a 10% lower deposition during the late 1960s (L. Granat, pers. comm, 14).

At fertilized sites N added is included. Thirty-year N-accumulation was chosen, to include in the study the well-defined

Figure 1. The consequence of thinning for soil CO₂ concentration. A) CO₂ in the soil atmosphere at 20 cm in a spruce stand on peatland at Amböke, SW Sweden. Thinning resulted in a rise in summer groundwater levels from about 90 cm to 50 cm. Concurrently with the drastic increase in surficial soil CO₂, CH₄ concentrations up to more than 12% (v/v) were recorded at 40 cm. B) CO₂ at 0–40 cm depth at the Mahult spruce site one year before (1996), and the first (1997) and second year (1998) after thinning. Annual averages from 6, 7, and 10 complete profiles, respectively. Annual precipitation is indicated. The increase in CO₂ the first year after thinning can not be related to increased precipitation, and in the second year the effect of thinning is decreasing despite increased precipitation that year.

southern Swedish research sites that were started during the late 1960s, and since then have been administered by the Swedish University of Agricultural Sciences.

A soil depth of 0–20 cm was generally selected to make the unsaturated layers at the sites comparable. Samples from deeper layers were not collected from all sites. A stainless steel tube, outside diameter 6 mm, with a perpendicular hole on the side close to the closed bottom end, was used for sampling. With a hand-operated vacuum pump the soil atmosphere was transferred into a connecting polybutene tube. The dead volume was first pumped out, and the polybutene tube was instantly closed at both ends. Samples were analyzed within 2 days, but usually on the same day (overseas samples within 1 week). The sampled soil atmosphere was taken from the tube with a syringe and immediately analyzed by gas-solid chromatography, separation on Haye Sep Q with a Varian 3300 instrument, and a Varian 4400 Intergrator. Reference and carrier gases were from Air Liquide Gas Company.

RESULTS

To characterize the soil atmosphere that relates solely to N-deposition, long-term stable conditions were needed. Forest sites with anthropogenic disturbances other than high N-load, such as clearcutting, or even thinning—leading to higher groundwater

level as a result of decreased evapotranspiration, and manifesting methane production in the summer (15) (Fig. 1), as well as drained and limed sites—were treated separately.

Forest edges receive considerably higher N-depositions compared to closed forests (16–18). The latter study (18) was on the same site as that studied by me, i.e. a soil CO_2 -gradient from the forest edge (Stubbaröd in Fig. 4). Of the 45 sampling sites in undisturbed forests (Fig. 2) 5 were within 50 m from forest edges and N-depositions were adjusted to fit a gradient from 100% deposition at 50 m (closed forest) to 156% deposition 5 m from the forest edge (18).

The accumulated N-deposition on undisturbed sites showed a clear influence on CO_2 concentrations in the soil atmosphere (Fig. 2). However, high N-deposition does not only deplete soil CO_2 incidentally, but more importantly, soil CO_2 concentrations above the atmospheric concentration (the predominating situation) are lower than those resulting from respiration processes alone. In areas where cumulative atmospheric N-depositions—over the last 30 years—have reached $800\text{--}1000\text{ kg ha}^{-1}\text{ yr}^{-1}$, soil CO_2 concentrations are less than half of those in low deposition sites. These conditions are now widespread and the indicated sink may have large-scale implications.

I assumed that the indicated CO_2 -gradient in areas with low to high cumulative N-deposition should also occur locally where there is a similar N-deposition gradient. This deposition gradi-

Figure 2. A) Annual average CO_2 in the soil atmosphere as a function of the cumulative atmospheric N-deposition (30 yrs) at 45 nonfertilized temperate forest sites. The sites are sampled in frostfree conditions all over the year, depth 0–20 cm (unsaturated zone). The curve shown is a 2nd polynomial regression, adjusted $R^2 = 0.653$; $p < 0.001$; **B).** Logarithmic plot of the same relationship as in A). CO_2 at 4 nonfertilized Scandinavian arctic forest sites and at fertilized or otherwise anthropogenically (draining, clearcutting, agriculture) influenced sites is also shown. Breakdown of the CO_2 sequestration capacity was observed during the study period at the Skogaby experimental site. The slightly increased nitrate in soil solution (1992–1995 at the N-fertilized plots increased more than 30 times above the control plots, with subsequent drastic N-leaching (9). This change in N-cycling occurred simultaneously with the almost threefold increase in soil CO_2 indicated (1997–1998). At this site the available CO_2 data 1992–1995 were from July and the late autumn, and were compared with the same seasons 1997–1998. At the experimental site at Mellby, N is supplied to the reference plots solely as commercial fertilizer, while both commercial fertilizer and manure are added to plots receiving recommended N-supply and a double dose manure is added at the high N-treatment plots. Half the plots have/have not catch crops. The annual average from the NW Pacific mixed rainforest is indicated by a blue circle and is based on 3 sampling occasions in the Hoh River area (April, June and November) and one rainforest sampling at Victoria Island, BC (July).

Figure 3. Soil CO_2 at 0–20 cm in transects from spruce forest edges into the closed forests, studied from mid-1999 to late-2000. The central Swedish sites Smedjebacken (average of 6 complete profiles) and Storfors (average of 7 complete profiles) have an annual atmospheric N-deposition to the closed forest of about 8 and 9 kg ha^{-1} , respectively.

ent occurs from the closed forest to the forest edge (18). Results from transects in central Sweden, where N-deposition to the closed forest is lower than in the south, support this hypothesis (Fig. 3).

A cumulative N-input of about 1000–1500 kg N deposited over a 30-yr period becomes critical. Beyond this N-accumulation level, soil CO₂ concentrations increase, concurrently with increasing nitrate leaching. During the course of the study this breakdown of the soil N- and CO₂-sequestration capacity was indicated at the Skogaby research site. Increased N-supply (from approx. 1500 to 1700 kg N deposited over 30 years) initiated a shift from low N-leaching into extreme leaching, simultaneously with an almost 3-fold increase in soil CO₂ (Fig. 2B). The same situation was also obvious for forest edges in a high N-deposition area in SW Sweden and in Denmark. Instead of the originally enforced soil CO₂ sink, the forest edge had become an increased CO₂ source (Fig. 4).

Low soil CO₂ concentrations were found even in the summer when intense soil respiration is expected. This could not be explained solely by decreased CO₂ production in the soil, as a result of, e.g. drying, or by day/night fluctuation of the above-ground CO₂, especially as the soil CO₂-depletion sometimes was more pronounced at deeper levels (19). Photosynthetic CO₂ consumption does not occur in the soil. To my knowledge, nitrification, a chemoautotrophic CO₂ consuming process, has not been considered as a potential CO₂ sink in forest soils. However, from wastewater-treatment processes it is well-known that nitrification alters alkalinity (CO₂ is removed and H⁺ is added) (20).

Soil N-fertilization studies in the laboratory supported the results, but did not result in CO₂ concentrations below the above-ground air (21). Reduced soil CO₂ release as a result of applied inorganic N has been observed earlier. Interpretations for this phenomenon have involved *i*) decreased microbial activity, explained by decreased C input or availability; *ii*) restriction of C-mineralization by high N-concentrations in the organic substrate; *iii*) disturbed balance between decomposers; *iv*) hampered production of enzymes; and *v*) formation of decomposing products being toxic or inhibitory (22–24). The impact of fertilization on soil respiration has also been reported as being low (25).

Nitrification has been demonstrated to occur even in acid forest soils (26–28). Nitrification in Swedish and Danish spruce forests was a chemoautotrophic process, with a high potential in the 10–50 cm soil layer (29). Liming stimulated nitrification, and reduced the CO₂ evolution rate, except when a nitrification inhibitor was used (23).

DISCUSSION

The present strong terrestrial, biospheric CO₂ sink, indicated by the ¹³C/¹²C ratio in atmospheric CO₂ (30) is located in temperate latitudes where it became significant during the late 1980s (31). At that time considerable atmospheric N-deposition with subsequent soil N-accumulation had occurred in extensive temperate areas. The “missing sink” was related to N or CO₂ fertilization in Russian forests and North American forest regrowth. Biospheric CO₂ sinks as a result of terrestrial N-fertilization, have so far been related to increased forest growth (32, 33), or to forest regrowth on abandoned agricultural land (34), but have recently been questioned as the putative CO₂ sink in temperate forests (35).

This imbalance of the global carbon budget is estimated as 0.4–3.4 · 10⁹ tonnes C yr⁻¹ (36–40). Estimates of the amount of CO₂ that could be assimilated, based on the energy yield from net nitrification (41), indicated that only a minor part of the missing CO₂ sink could be explained by this process. Recent findings from a study in western America (28) that gross nitrification in forest soils largely exceeds net nitrification, totally changed this view.

Figure 4. Same soil CO₂ transect measurements in spruce forests as in Figure 3, sampling from late 1998 to late 1999. One Danish site (Draved in south Jutland, average of 7 complete profiles) and 2 southern Swedish sites (Åstorp, average of 6 complete profiles and Stubbaröd, average of 8 complete profiles). These forests receive about 3 times higher N-deposition than the forests in Figure 3.

From areas with low N-deposition on undisturbed forests in New Mexico and Oregon, USA, Stark and Hart (28) reported gross nitrification up to 304 mg N m⁻² day⁻¹ during spring. This is in the magnitude of twice the total annual atmospheric N-deposition cycled in one day. A discrete estimate based on one third of that value (100 mg N m⁻² day⁻¹), lasting for 250 days per year, implies that 250 kg N ha⁻¹ would be nitrified annually. However, high atmospheric N-deposition areas in Europe receive, and retain, 10–20 times more N every year than do the American sites studied by Stark and Hart. A 10-fold increase in the N-cycling rate in these high N-deposition areas would result in 159 kg C ha⁻¹ yr⁻¹ (41). The efficiency of the nitrification reaction was set to 10%. Providing that 100 kg of the C reassimilated within the soil is preserved as organic material, and this process occurs in areas corresponding to half of the world's moist temperate and boreal forest soils (only 8.4% of Haldridge's Life Zones), gross nitrification would account for an annual sink 0.11 · 10⁹ tonnes C (0.40 · 10⁹ tonnes CO₂).

The American study (28) showed that NO₃ produced by nitrification is effectively assimilated by microorganisms. In this way, NO₃ leaching is prevented, which explains the effective N-retention in most forest soils. In the mature forest ecosystem, nitrogen is rapidly remobilized from the organic material (dead microbial biomass) and the NH₄ released makes repeated nitrification possible. According to my results and those of the American study (28), a soil “CO₂ -pump” is operating, run by N-cycling in the forest soil. Every turn of the cycle implies CO₂-sequestration, resulting in the high potential soil CO₂-sink indicated where N-deposition has increased (Figs 2, 3).

High evapotranspiration is known to increase soil CO₂ production (3). However, the sites with highest evapotranspiration (Pacific rainforest) and lowest (two arctic sites in Scandinavia) all show high soil CO₂ concentrations (Fig. 2B). Atmospheric N-deposition is very low at these sites.

The results support the explanation that nitrogen cycling (nitrification, followed by microbial NO₃ uptake), causes the soil CO₂ sink. If production of CO₂ were disturbed or hampered by increased nitrogen supply, which was the alternative interpretation (22–24) this would probably enforce the sink, and not turn it into an increased CO₂ source when still more nitrogen is deposited. Whether the explanation is nitrification alone, or in combination with an inhibitory effect, N-deposition causes extensive reductions of forest soil CO₂ concentrations.

In summary, N-saturation causes increased N-leaching (42) and this coincides with loss of the internal soil CO₂ sequestra-

tion capacity, which implies increased CO₂ release from the soil. Effective N-cycling is still the most widespread process in forests (43). Therefore, the internal soil CO₂ sink still dominates. My results indicate that this sink can even be enforced extensively by additional N-deposition except in some very high deposition areas, e.g. in Europe, where N-saturation and subsequent increased CO₂ emissions from the soils are present. Support for this CO₂ sink in order to counteract the increase of CO₂ in the atmosphere, will need better knowledge of its areal distribution, and probably monitoring programs coupled with effective feedback measures. When other aspects such as biodiversity are considered, increased N-deposition may be undesirable.

Using my findings some results, published quite recently, may be re-interpreted. Soil warming experiments in Massachusetts (44) and in northern Sweden (45) did not result in the expected increase in CO₂ release from the soil. Acclimatization of soil res-

piration was suggested to occur under temperature increase. According to my findings, the alternative interpretation may be that increased temperature, as expected, enhances soil respiration but also the internal soil CO₂ consuming process discussed here.

Within the comprehensive Skogaby project in southern Sweden, run from 1988 to 2001, the C and N soil pools were calculated. Instead of expected C/N ratios of 25 at the N-fertilized plots, and 30 at the control plots which received solely atmospheric deposition, the ratios calculated were unexpectedly high, 37 and 145, respectively. Overestimation of the soil carbon content, or underestimation of organic material mineralization was suggested (46). My hypothesis, implying repeated soil CO₂ uptake as a result of N-cycling, supports considerable soil carbon sequestration. It also appears that soil respiration is not equivalent to CO₂ released from the soil, especially where the internal soil CO₂ uptake is high as a result of high N-deposition.

References and Notes

- Schlesinger, W.H. 1991. *Biogeochemistry. An Analysis of Global Change*. Academic Press, San Diego. 443 pp.
- IPCC 1994. *Report of the Scientific Assessment Working Group*.
- Brook, G.A., Folkoff, M.E. and Box, E.O. 1983. A world model of soil carbon dioxide. *Earth Surf. Process. Landforms* 8, 79–88.
- On 252 occasions, from 29 June 1992 till 18 January 2002, air from one meter above the ground was sampled from outside the Halmstad Castle (within the City center) and immediately analysed (in total 885 analyses). Mean summer (April–Sept.) CO₂ concentration was 0.0358 % by volume, the median 0.0358% (n = 138 days). Mean winter (Okt.–March) concentration was 0.0365%, median 0.0365% (n = 114 days).
- Eriksson, H. and Karlsson, K. 1997. Effects of different thinning and fertilization regimes on the development of Scots pine (*Pinus sylvestris* (L.)) and Norway spruce (*Picea abies* (L.) Karst.) stands in long-term silvicultural trials in Sweden. *Swedish University of Agricultural Sciences. Report 42*. (Summary in English).
- Persson, O.A., Eriksson, H. and Johansson, U. 1995. An attempt to predict long-term effects of atmospheric nitrogen deposition on the yield of Norway spruce stands (*Picea abies* (L.) Karst.) in southwestern Sweden. *Plant Soil* 168/169, 249–254.
- Hallgren Larsson, E., Knulst, J.C., Löfblad, G., Malm, G., Sjöberg, K. and Westling, O. 1997. Report on 10 years of regional monitoring in south Sweden 1985–1995. *Swedish Environmental Research Institute*. (In Swedish).
- Bergholm, J., Jansson, P.-E., Johansson, U., Majdi, H., Nilsson, L.-O., Persson, H., Rosengren-Brinck, U. and Wiklund, K. 1995. Air pollution, tree vitality and forest production—the Skogaby project. General description of a field experiment with Norway spruce in South Sweden. In: Nilsson, L.-O., Hüttle, R.F., Johansson, U.T. and Mathy, P. (eds). *European Commission, Ecosyst. Res. Rep.* 21, 69–88.
- Bergholm, J. 2001. *Long-Term Effects of Enhanced Nitrogen and Sulphate Additions on Soil Acidification and Nutrient Cycling in a Norway Spruce Stand*. PhD Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden. ISSN 1401-6230.
- van Dobben, H.F., Mulder, J., van Dam, H. and Houweling, H. 1992. *Impact of Atmospheric Deposition on the Biogeochemistry of Moorland Pools and Surrounding Terrestrial Environment*. Pudoc Scientific Publishers, Wageningen.
- Torstensson, G. and Aronsson, H. 2000. Nitrogen leaching and crop availability in manured catch crop systems in Sweden. *Nutr. Cycl. Agroecosyst.* 56, 139–152.
- Nohrstedt, H.-Ö., Sikström, U., Ring, E., Näsholm, T., Högborg, P. and Persson, T. 1996. Nitrate in soil water in three Norway spruce stands in southwest Sweden as related to N-deposition and soil, stand, and foliage properties. *Can. J. Forest Res.* 26, 836–848.
- EMEP is the Cooperative Program for Monitoring and Evaluation of Long Range Transmissions of Air Pollution in Europe. Grid size 50x50 km. Mean values for 1993 and 1994, for spruce forest and pine/mixed forest, respectively, were used.
- Granat, L. 1998. Rise and decline of acid precipitation in Sweden as seen from long term measurements. In: *Abstracts of Papers Presented at the Rossby-100 Symposium 8–12 June 1998, Stockholm*. Dept of Meteorology, Univ. of Stockholm and International Meteorological Institute in Stockholm, Sweden.
- Granberg, G., Mikkilä, C., Sundh, I., Svensson, B.H. and Nilsson, M. 1997. Sources of spatial variation in methane emission from mires in northern Sweden—A mechanistic approach in statistical modelling. *Global Biogeochem. Cycles* 11, 135–150.
- Grennfeldt, P. 1987. Deposition processes for acidifying compounds. *Environ. Technol. Lett.* 8, 515–527.
- Beier, C. and Gundersen, P. 1989. Atmospheric deposition to the edge of a spruce forest in Denmark. *Environ. Pollut.* 60, 257–271.
- Balsberg, A.-M. and Bergqvist, B. 1995. Acid deposition and soil acidification at a south-west facing edge of Norway spruce and European beech in south Sweden. *Ecol. Bull.* 44, 43–53.
- Occasionally, low CO₂-concentrations below the surficial soil layer, which could not be explained by prolonged drying, frost or day/night fluctuations, were recorded. The Skällås Norway spruce site was a weak CO₂ source 13 June 1994, with 0.045, 0.038 and 0.038% at 10, 20 and 30 cm, respectively. Two days later the site was almost no CO₂ source, with 0.037, 0.032 and 0.032%, and three days more 0.039, 0.037 and 0.034% was recorded. Two years later, 6–8 June 1996 were hot days, up to 30°C, followed by rainy days. 13 June 1996, at the Mahult spruce site, the following CO₂ concentrations were found at 10, 20, 30 and 40 cm depth, respectively: 0.076, 0.041, 0.032 and 0.036 percent. The same day at the Gårdshult spruce site 0.033, 0.033, 0.033 and 0.034 percent were recorded at the same depths, respectively. This site was no CO₂ source to the aboveground atmosphere, rather a weak sink.
- Changes in alkalinity according to NH₄ + 1.86 O₂ + 0.10 CO₂ = 0.021 CH₃H₂O₂N + 0.941 H₂O + 0.98 NO₃ + 1.98 H⁺ are used as a measure of nitrification in the wastewater-treatment process. Net nitrification is also an important acidifying process. However, only net nitrification results in acidification, but every turn of the N-cycle, implying repeated nitrification (8), adds to the cumulative CO₂ sequestration in soils.
- Closed soil cores in the laboratory repeatedly showed decreased CO₂-concentrations in the soil or above-soil atmosphere when inorganic-N corresponding to 1–10 annual depositions per area unit in SW Sweden were added, compared to references with no additional nitrogen.
- Kowalenko, C.G., Ivarson, K.C. and Cameron, D.R. 1978. Effect of moisture content, temperature and nitrogen fertilization on carbon dioxide evolution from field soils. *Soil Biol. Biochem.* 10, 417–423.
- Nohrstedt, H.-Ö., Arnebrant, K., Bååth, E. and Söderström, B. 1989. Changes in carbon content, respiration rate, ATP content, and microbial biomass in nitrogen-fertilized pine forest soils in Sweden. *Can. J. Forest Res.* 19, 323–328.
- Persson, T., Karlsson, P.S., Seyferth, U., Sjöberg, R.M. and Rudebeck, A. 2000. Carbon mineralization in European Forest Soils. *Ecol. Stud.* 142, 257–275.
- Raich, J.W. and Schlesinger, W.H. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44 B, 81–99.
- Martikainen, P.J. and De Boer, W. 1993. Nitrous oxide production and nitrification in acidic soil from a Dutch coniferous forest. *Soil Biol. Biochem.* 25, 343–347.
- Persson, T. and Wirén, A. 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. *Plant Soil* 168/169, 55–65.
- Stark, J.M. and Hart, S.C. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385, 61–64.
- Persson, T., Wirén, A. and Andersson, S. 1990/91. Effects of liming on carbon and nitrogen mineralization in coniferous forests. *Water Air Soil Pollut.* 54, 351–364.
- Cias, P., Tans, P.P., Trolier, M., White, J.W.C. and Francey, R.J. 1995. A large northern hemisphere terrestrial CO₂ sink indicated by the ¹³C/¹²C ratio of atmospheric CO₂. *Science* 269, 1098–1102.
- Craig, S., Holmén, K. and Björkström, A. 1997. Net terrestrial carbon exchange from mass balance calculations: an uncertainty estimate. *Tellus* 49 B, 136–148.
- Wisniewski, J. and Lugo, A.E. (eds). 1992. Natural sinks of CO₂. Reprinted from *Water Air Soil Pollut.* 64, 466 pp.
- Hudson, R.J.M., Gherini, S.A. and Goldstein, R.A. 1994. Modeling the global carbon cycle: Nitrogen fertilization of the terrestrial biosphere and the “missing” CO₂ sink. *Global Biogeochem. Cycles* 8, 307–333.
- Falkowski, P., Scholes, R.J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Högborg, P., Linder, S., Mackenzie, F.T., Moore III, B., Pedersen, T., Rosenthal, Y., Seitzinger, S., Smetacek, V. and Steffen, W. 2000. The global carbon cycle: a test of our knowledge of earth as a system. *Science* 290, 291–296.
- Nadelhoffer, K.J., Emmet, B.A., Gundersen, P., Kjönas, O.J., Koopmans, C.J., Schleppig, P., Tietemal, A. and Wright, R.F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature* 398, 145–148.
- Sedjo, R.A. 1993. The carbon cycle and global forest ecosystem. *Water Air Soil Pollut.* 70, 295–307.
- Sundquist, E.T. 1993. The global carbon dioxide budget. *Science* 259, 934–941.
- Rotmans, J. and Den Elzen, M.G.J. 1993. Modelling feedback mechanisms in the carbon cycle: balancing the carbon budget. *Tellus* 45B, 301–320.
- Fan, S.M., Blaine, T.L. and Sarmiento, J.L. 1999. Terrestrial carbon sink in the Northern Hemisphere estimated from the atmospheric CO₂ difference between Mauna Loa and the South Pole since 1959. *Tellus* 51B, 863–870.
- Lenton, T.M. 2000. Land and ocean carbon cycle feedback effects on global warming in a simple Earth system model. *Tellus* 52 B, 1159–1188.
- ΔG is –348 KJ for NH₄-oxidation to NO₃, and 469 KJ for CO₂ reduction to organic material.
- Rosén, K., Gundersen, P., Tegnhammar, L., Johansson, M. and Frogner, T. 1992. Nitrogen enrichment of Nordic forest ecosystems. The concept of critical loads. *Ambio* 21, 364–368.
- Binkley, D. and Högborg, P. 1997. Does atmospheric deposition of nitrogen threaten Swedish forests? *Forest Ecol. Mgmt* 92, 119–152.
- Luo, Y., Wan, S., Hui, D. and Wallace, L.L. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413, 622–625.
- Strömberg, M. 2001. *Soil-Surface CO₂ Flux and Growth in a Boreal Norway Spruce Stand. Effects of Soil Warming and Nutrition*. PhD Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Persson, T. and Nilsson, L.-O. (eds) 2001. *The Skogaby Experiment*. Swedish Environmental Protection Agency. Report 5173, 220 pp. (In Swedish).
- This study was supported by the Brita and Sven Rahmn foundation and by the WWF. I thank Gunnar Jacks and Jan Pokorny for their critical review of the manuscript, and Jonas Svensson and Lars Stibe for re-counting.
- Further information, including site descriptions, is available from the author.
- First submitted 19 April 2002, accepted for publication 12 Sept. 2002.

Siegfried Fleischer is professor of limnology at the Wetland Research Center, Halmstad University, Sweden. Nitrogen cycling and its coupling to greenhouse gas production in the aquatic and terrestrial environment have been emphasized in his research, as well as interdisciplinary approaches to environmental problems. His address: County Administration Board, SE-301 86 Halmstad, Sweden. E-mail: sifl@n.lst.se