

Decreased photosynthetic efficiency in plant species exposed to multiple airborne pollutants along the Russian–Norwegian border

Ann Marie Odasz-Albrigtsen, Hans Tømmervik, and Patrick Murphy

Abstract: Photosynthetic efficiency was estimated by chlorophyll fluorescence measurements (Fv/Fm) in 11 plant species growing along a steep gradient of airborne pollution along the Russian–Norwegian border (70°N, 30°E). Photosynthetic efficiency was positively correlated with environmental variables including annual temperature and a maritime gradient and was negatively correlated with the airborne concentrations of Cu, Ni, and SO₂ from the Cu–Ni smelters. Photosynthetic efficiency in six plant species from the mixed forest, but not pine (*Pinus sylvestris* L.), and three species from the birch forest was inversely correlated with SO₂ and the concentrations of Ni and Cu in lichens. Measurement of fluorescence in these species was a sensitive indicator of pollutant impact. Plant cover at the 16 study sites and the photosynthetic efficiency of five target species correlated with normalized difference vegetation index (NDVI) values. This study demonstrated that it is possible to detect relations among field-measured ecophysiological responses in plants, levels of airborne pollutants, and satellite remote-sensed data.

Key words: chlorophyll fluorescence, smelters, sulfur dioxide, nickel, copper, normalized difference vegetation index (NDVI).

Résumé : Les auteurs ont estimé l'efficacité photosynthétique en mesurant la fluorescence de la chlorophylle (Fv/Fm), chez 11 espèces de plantes poussant le long d'un gradient accentué de pollution atmosphérique, le long de la frontière russo-norvégienne (70°N, 30°E). L'efficacité photosynthétique est positivement corrélée avec les variables du milieu, incluant la température annuelle et le gradient maritime, et montre une corrélation négative avec les teneurs de l'air en Cu, Ni, et SO₂ provenant des fonderies de Cu–Ni. L'efficacité photosynthétique de six espèces de plantes de la forêt mixte, mais non de pin (*Pinus sylvestris* L.), et trois espèces de la forêt de bouleaux, montrent des corrélations inverses avec le SO₂ de l'air et les teneurs en Ni et Cu des lichens. La mesure de la fluorescence chez ces espèces, constitue un indicateur sensible de l'impact des polluants. Le couvert végétal sur les 16 sites d'étude et l'efficacité photosynthétique de 5 plantes cibles montrent des corrélations avec les valeurs de l'indice de végétation différentielle normalisée (normalized difference vegetation index (NDVI)). Cette étude démontre qu'il est possible de déceler des relations entre les réactions écophysologiques des plantes mesurées sur le terrain, les teneurs en polluants dans l'air et les données obtenues à distance par satellites.

Mots clés : fluorescence de la chlorophylle, fonderies, bioxyde de soufre, nickel, cuivre, indice de végétation différentielle normalisée (NDVI).

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Introduction

In 1932, a Canadian–Finnish corporation established a Cu–Ni smelting plant on the Kola Peninsula, Russia (70°N, 30°E). Between 1933 and 1974 approximately 100 000 t of sulfur dioxide (SO₂) (Traaen 1991; Kalabin 1991) were emitted each year from the smelters operated at Nikel and

Zapolyarnij, 10 and 12 km, respectively, east of the Norwegian border (Fig. 1). The 1974 initiation of smelting Siberian Norilsk ores caused an escalation of SO₂ emissions to 400 000 t/year, which decreased to 354 000 t in 1985, 273 000 t in 1990, and 230 000 t in 1993. Additional airborne pollutants include Cu and Ni with annual emission of ca. 310 and 510 t, respectively (Sivertsen et al. 1992).

Vegetation close to the smelters has been severely damaged or killed (Tømmervik et al. 1998). Approximately 10% of the SO₂ emitted is blown by prevailing winds from the smelters and is deposited in Norway. The concentration of metals in the airborne dust is highest north and northwest of the smelters and decreases southeast towards Svanvik, Norway. The transport of these pollutants into the South-Varanger region, Norway, in summer results in the highest measured values of SO₂, Ni, and Cu for all of the Nordic countries (Sivertsen et al. 1992). Many environmental variables (e.g., prevailing winds, topography, exposure, eleva-

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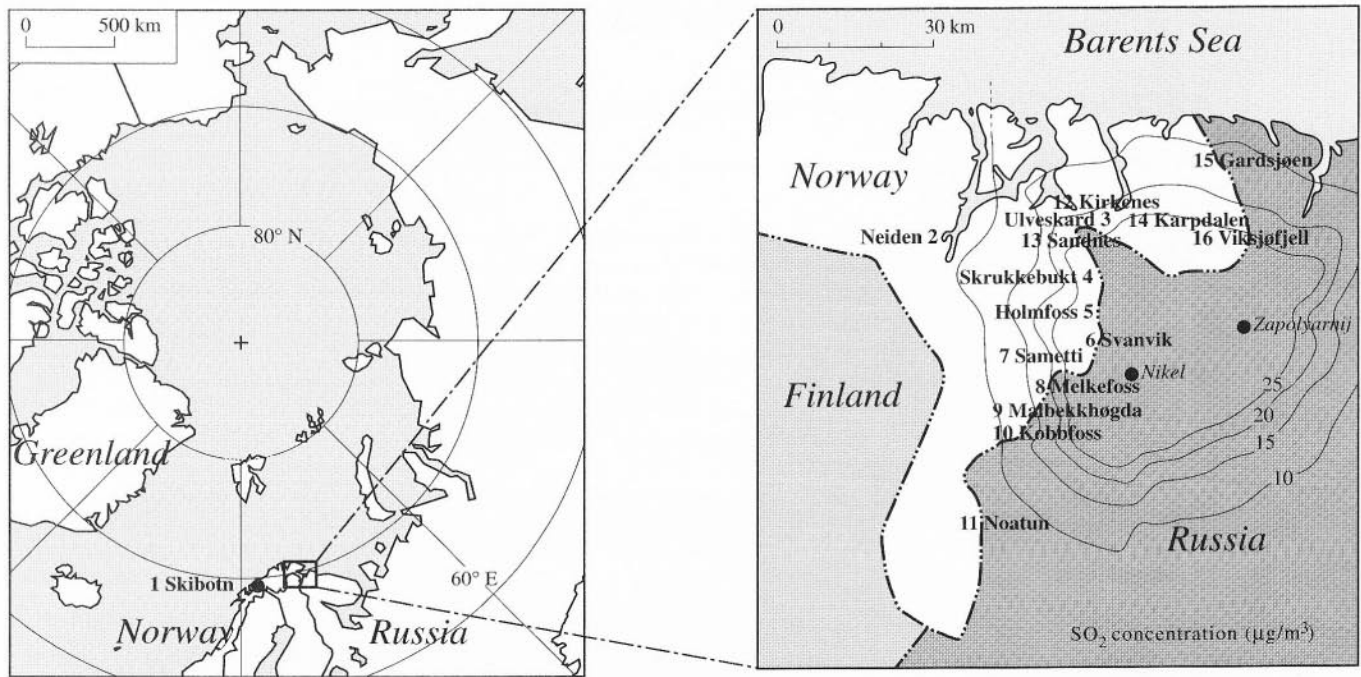
A.M. Odasz-Albrigtsen.¹ Department of Arctic Biology, Institute of Medical Biology, and Institute of Biology, University of Tromsø, N-9037 Tromsø, Norway.

H. Tømmervik. Department of Arctic Ecology, Norwegian Institute of Nature Research, N-9296 Tromsø, Norway.

P. Murphy. Ecotone Corporation, 1554 North Street, Boulder, CO 80304-3514, U.S.A.

¹Author to whom all correspondence should be addressed (e-mail: annmarie@fagmed.uit.no).

Fig. 1. Location of smelters in Nikel and Zapolyarnij on the Kola Peninsula, Russia. The reference locality Skibotn (1), is shown on the overview map on the left. The locations of the investigation sites are also shown: 2, Neiden; 3, Ulveskard; 4, Skrukkebukt; 5, Holmfoss; 6, Svanvik; 7, Sametti; 8, Melkefoss; 9, Malbekkhøgda; 10, Kobbfoss; 11, Noatun; 12, Kirkenes; 13, Sandnes; 14, Karpdalen; 15, Gardsjøen; 16, Viksjøfjell. Isolines are modeled SO_2 concentrations (NILU 1993).



tion, soils, etc.) influence spatial deposition patterns and rates of chemical degradation of the airborne pollutants. The impact of airborne pollutants is especially relevant, because the vegetation in this area is grazed by semidomesticated herds of reindeer.

Airborne pollutants can limit the growth of plants especially at high latitudes where species are at the limits of their distribution and at the extreme of their habitat tolerance (Bliss 1962). Sustained reduction in efficiency of photosystem II (PSII) has been measured in many species after exposure to adverse conditions (Adams et al. 1989, 1995; Demmig-Adams and Adams 1992; Demmig-Adams et al. 1998). Multiple environmental stresses lower photosynthetic rates and increase the degree to which absorbed light energy can be excessive and potentially damaging to PSII. The lowered photosynthetic efficiency (Fv/Fm) of PSII in stressed plants is inversely related to the energy release from the conversion states in carotenoids of the xanthophyll cycle. The cycle, found in all examined (ca. 30) higher plant species, safely dissipates the potentially destructive excess energy (for a review, see Demmig-Adams and Adams 1996). This protective process termed "photoinhibition" (Demmig-Adams et al. 1998; Krause 1994) or "photoinhibition of PSII" (Osmond 1994) can be quantified from the ratio of variable to maximal chlorophyll fluorescence (Fv/Fm) (Kitajima and Butler 1975).

To evaluate if airborne pollutants that enter Norway from the Kola Peninsula decrease the photosynthetic efficiency of plants, we determined relationships among (i) the photosynthetic efficiency of plant species, natural environmental factors, and concentration of airborne pollutants (SO_2 , Ni, and Cu) at 16 sites along the steep gradient of airborne pollut-

ants; (ii) a satellite remote-sensed vegetation index, Fv/Fm, and plant cover at the sites; and (iii) the photosynthetic efficiency of the plant species and the concentrations of Ni and Cu in lichens. The widespread distribution of our analysed target species in the region allowed for spatial comparisons between in situ photosynthetic efficiency and Landsat satellite imagery.

Materials and methods

Investigation localities

Fifteen of the sixteen investigation localities (Fig. 1, Table 1) are in the South-Varanger region (7–45 km from the smelters in Nikel and Zapolyarnij, Russia). For comparison we selected a site at Skibotn, Norway, 386 km from the smelters, as a control. Selection criteria for investigation sites included (i) sites distributed along a gradient of airborne pollutants; (ii) sites included in either the Norwegian Institute of Air Research (NILU) (Sivertsen and Bekkestad 1995) or the Norwegian Institute of Forestry Research (NISK) (Aamlid and Venn 1993) monitoring programs; (iii) sites where Ni and Cu are measured in lichens (Meland 1992) and Ni, Cu, and SO_2 concentrations were measured at ground level and modeled by NILU (1993); and (iv) sites accessible by car for re-charging batteries for the fluorescence measurements. Site numbers 1–16, used in the tables and figures, represent each locality.

Field measurement sites were selected in the "mixed forest" vegetation type (with good cover of tree species, *Pinus sylvestris* L. (Scots pine) and *Betula pubescens* Ehrh. (mountain birch)), *Calamagrostio lapponicae*-Pinetum and in the "birch forest" vegetation types (without the *Pinus*), *Empetro*-Betuletum and *Myrtillo*-Betuletum (Fremstad and Elven 1987). The mixed forest and birch forest vegetation types were analysed separately.

Table 1. Site names and environmental variables for the study sites.

Site No. and name	Environmental variables														
	DIST	PREC	TEMP	CNX	MNX	SUN	TOPO	ELE	SLO	SO ₂	NiDE	CuDE	NiCO	CuCO	NDVI
Mixed forest															
1. Skibotn	386	475	275.0	24	38	114	4	90	5	—	—	—	—	—	0.468
2. Neiden	45	435	272.4	24	46	144	4	73	0	5.0	1.0	0.5	110	100	0.389
3. Ulveskard	30	365	272.3	22	39	130	3	80	5	22.5	5.0	3.0	452	369	0.367
4. Skrukkebukt	18	352	271.6	26	41	125	4	65	8	25.0	5.0	3.5	524	488	0.367
5. Holmfoss	13	352	271.6	26	41	161	4	50	3	30.0	7.5	5.0	738	651	0.367
6. Svanvik	7	352	271.6	28	41	148	4	50	4	30.0	8.0	5.0	712	620	0.508
7. Sametti	22	352	271.6	28	41	144	3	115	3	12.5	2.0	1.0	279	239	0.390
8. Melkefoss	18	352	271.6	30	41	134	4	70	3	17.5	2.0	1.5	436	374	0.446
9. Malbekkhøgda	25	352	271.6	30	41	149	1	150	8	12.5	1.5	1.0	322	246	0.446
10. Kobbfoss	30	341	271.9	32	38	143	4	80	5	10.0	1.0	0.5	214	172	0.446
11. Noatun	45	341	271.9	34	38	155	4	105	3	3.0	0.3	0.2	129	95	0.446
Birch forest															
12. Kirkenes	35	430	272.8	22	44	154	3	75	3	12.5	3.0	1.5	452	369	0.553
13. Sandnes	30	430	272.8	24	44	138	4	90	6	16.0	3.5	1.5	455	345	0.562
14. Karpdalen	31	365	272.3	22	39	143	4	90	6	25.0	6.0	3.5	449	365	0.424
15. Gardsjøen	33	365	272.3	22	39	137	4	105	3	17.5	3.5	1.5	438	327	0.286
16. Viksjøfjell	25	365	271.4	24	43	145	2	285	2	25.0	5.0	3.5	1295	910	0.161

Note: Skibotn is used as the clean reference site; it is 386 km from the smelters. DIST, distance from smelters (km); PREC, yearly precipitation (mm) (DNMI 1993; Førland 1993); TEMP, yearly mean temperature (K) (Aune 1993; DNMI 1993); CNX, Conrad's continentality index (Haapasaaari 1988); MNX, Martonnes maritime index (Tuhkanen 1980); SUN, sunrank (see text); TOPO, topography (see text); ELE, elevation (m.a.s.l.); SLO, slope (degrees); SO₂, sulfur dioxide (µg/m³) (see text); NiDE, nickel measured by NILU (mg/m²); CuDE, copper measured by NILU (mg/m²); NiCO, nickel concentration in *Cladina* (µmol) (Meland 1992); CuCO, copper concentration in *Cladina* (µmol) (Meland 1992), and NDVI, normalized difference vegetation index.

Plant community and species

Five vegetation plots (1 m² each) were investigated at each locality. The proportional cover of plants, bare rocks, gravel, soil, and litter were recorded in each. Plant species with a high frequency of occurrence and cover selected for estimation of photosynthetic efficiency included two tree species, *Betula pubescens* and *Pinus sylvestris*; five shrubs, *Vaccinium myrtillus* L. (bilberry), *Empetrum hermaphroditum* Hagerup (crowberry), *Arctostaphylos alpinus* Spreng. (ptarmigan berry), *Betula nana* L. (dwarf birch), and *Salix lapponum* L. (lap willow); two epiphytic lichens on birch tree-trunks, *Hypogymnia physodes* (L.) W. Watson (branch lichen) and *Parmelia olivacea* (L.) Ach. (snow-level lichen); a mixed group of ground reindeer lichens, including *Cladina arbuscula* ssp. *mitis* (Sandst.) Hale & Culb., *Cladina rangiferina* (L.) Nyl., and *Cladina stellaris* (Opiz) Brodo, which grow in continuous or scattered mats; and one moss species, *Pleurozium schreberi* (Brid.) Mitt. (pine moss). Nomenclature for vegetation types follows Fremstad and Elven (1987), vascular plant species follows Elven (1994), moss species follows Hallingbäck and Holmåsén (1991), and lichen species follows Moberg and Holmåsén (1990).

Chlorophyll fluorescence/photosynthetic efficiency (Fv/Fm)

Chlorophyll fluorescence was measured in intact leaves, on the upper half of the thallus of the lichen clusters and on the upper half of the green leafy moss clusters under field conditions during the 1993 growing season with a portable plant stress meter (Biomonitor S.C.I. AB, Umeå, Sweden).

Some of the radiation trapped by chlorophyll is re-emitted as red and far-red light (fluorescence). The absorption and emission process takes only nanoseconds. Measurements of fluorescence were taken on whole leaves or needles. To ensure that the peak maximum level of fluorescence (Fm) was reached, we dark adapted the analysed plant material for 30 min with a lightweight leaf cuvette. The excitation treatment involved a photon flux density of actinic light of 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by a halogen lamp in combination with a 5-mm Schott glass filter BG 39 for 5 s (Öquist and Wass 1988). Our laboratory tests showed this excitation was bright enough to reach Fm. Minimal and maximal levels of fluorescence (Fo and Fm) were used to estimate peak field PSII efficiency from $(F_m - F_o)/F_m = F_v/F_m$ (Öquist and Wass 1988). Fv/Fm represents the ratio of variable to maximum fluorescence yielded under the actinic light treatment.

Chlorophyll fluorescence (Fv/Fm) was measured in 50–100 leaves per species per site. Initially 10 leaves of 10 plants of each species were measured, but little variation was detected so the number of replicates was reduced to 10 leaves of 5 plants of each species. New and green leaves were measured on the lower branches of pine and birch trees and on the lower parts of bushes. Leaves were selected at random, but damaged or discolored leaves were avoided.

Environmental variables

Sixteen environmental variables were recorded for each site (Table 1): PREC, mean annual total precipitation (mm) for 1961–1990 (DNMI 1993; Førlund 1993); TEMP, mean annual temperature (K) for 1961–1990 (Aune 1993; DNMI 1993); CNX, Conrad's continentality indices calculated from meteorological data for each site (Haapasaari 1988); MNX, de Martonne's maritime indices calculated from meteorological data for each site (Tuhkanen 1980); SUN, sunrank, a scalar variable reflecting the intensity of sunlight by combining the annual sun position and time of day; ELE, elevation (m a.s.l.); SLO, degrees of slope; DIST, distance from the smelters (km); and SO₂, modeled mean sulfur dioxide concentration ($\mu\text{g}/\text{m}^3$) of measurements taken at ground level for 1989–1992 by NILU (isolines in Fig. 1); TOPO, topography; WEA, weather;

NiDE and CuDE, nickel and copper concentrations measured in air (mg/m^3) and modeled by NILU (NILU 1993); NiCO and CuCO, measured nickel and copper concentration (μmol) for lichens *Cladina mitis* – *C. arbuscula*; and NDVI, normalized difference vegetation index. Measurements on predawn dark-adapted leaves are not possible during the growing season at the study sites because of the midnight sun. The low angle of the sun passing through the atmosphere at the latitude of almost 70°N results in less contrast between predawn and midday sun intensities than occurs at lower latitudes; thus, sunrank was developed to account for differences in temporal sunlight intensities. Two values are summed. The first value is based on the position of the sun with respect to the summer solstice, i.e., June 21, is given a value of 100 with a value of 1 subtracted for every day prior or subsequent to that date. The second component is time of day with a time of 13:00 EST (estimated time of maximum sun height and intensity) given a value of 100 with a reduction of 1:12 or about 8.33% for each hour prior or subsequent to this. Maximum possible score is 200. Topography scalar values relate to cold air drainage and inversions, which have a strong local effect on either flushing out or trapping pollution in a valley. Values ranged as follows: 1, ridge; 2, upper slope; 3, midslope, 4, lower slope; 5, valley bottom. Weather was given scalar values intending to increase with increased sunlight: 2, rain–fog; 3, overcast–rain, 4, overcast; 5, overcast – partly sunny; 6, partly sunny; 7, sunny–overcast; 8, partly cloudy; 9, sun – partly cloudy, 10, sunny. The SO₂ model is based on data from stations located in Norway and Russia (Sivertsen and Bekkestad 1995). The SO₂ values were interpolated by NILU using dispersion models for 483 locations, which gave a complete coverage of the South-Varanger – Nikel region. The cell size of the grid used in the coverage was 100 × 100 m. The model uses a multiple-source Gaussian plume formation for long-term average concentration estimates. The model calculated concentrations and dry depositions of gases and particles, respectively, with various sizes in a given grid net. The plume rise is calculated according to Briggs formulas (Larsen 1994; Bekkestad et al. 1995). Modeled and observed correlations for monthly data were high ($r = 0.74$) (Hellevik and Sivertsen 1991). Samples for NiDE, CuDE, NiCO, and NiDE were collected in South-Varanger during summer 1990. Localities sampled were in the lichen heaths and forests dominated by *E. hermaphroditum* – *B. nana*, the *Empetrum* heaths, and the pine and the oligotrophic birch forests (Meland 1992). The NDVI data were obtained by Landsat-5 thematic map (TM) satellite (Høgda et al. 1995).

Remote sensing

The NDVI is calculated from data collected by the Landsat-5 TM satellite that has monitored areas of vegetation in South-Varanger, Norway, since 1984 (Høgda et al. 1995; Tømmervik et al. 1995; 1998). Techniques of multispectral transformation of satellite image data are used to produce the NDVI indices (pixel size 30 m²). NDVI is calculated from the reflected solar radiation in the near-infrared (NIR) and red (RED) wavelength bands using the equation: $\text{NDVI} = (\text{NIR} - \text{RED})/(\text{NIR} + \text{RED})$. Values vary with absorption of red light by plant chlorophyll and the reflection of infrared radiation by water-filled leaf cells. It is correlated with intercepted photosynthetically active radiation (IPAR). In most cases (but not all) IPAR and hence NDVI is correlated with photosynthesis and the chlorophyll content. Because photosynthesis occurs in the green parts of plants the NDVI is normally used to estimate abundance and vigor of green vegetation (Tucker and Sellers 1986). Vegetation change, i.e., species composition and photosynthetic rates has been monitored over time using these indices (Pitblado and Amiro 1982; Prince 1991; Mikkola and Ritari 1992; Sellers and Schimel 1993). The NDVI from the Landsat-5 TM satellite sensed on 23 July 1994 were analysed in relation to photo-

synthetic efficiency and total plant and total nonplant cover percent for each of the study sites.

Data analysis

We used a canonical correspondence analysis (CCA) in the CANOCO program (canonical community ordination; Ter Braak 1988) for direct gradient analysis to determine the relative importance of multiple environmental factors including airborne pollutants on the photosynthetic efficiency of the plant species. We ordinated the 11 target species photosynthetic efficiency (Fv/Fm) with the environmental variables from each site, including the airborne pollutants and the NDVI. CCA combines within one algorithm a reciprocal averaging solution for a correspondence analysis of species-site data (with a detrending option) and a weighted multiple regression analysis on environmental variable-site data (Ter Braak 1986, 1988). The horseshoe effect was not observed in the ordination, so the detrending function was not selected. Correlations between the dependent variable species subset and the independent environmental variable subset are represented in the same canonical ordination. The resulting relative positions in the diagram define their interrelationships. The construction of ordination plots for CCA is described by Ter Braak (1986).

Plant fluorescence measurements were compared with measured (Meland 1992) and modeled (NILU 1993) plant concentration of heavy metals, Ni and Cu, and with parameters measured by scientists at the Norwegian Institute of Forestry Research (NISK) in the forest vitality monitoring program in South-Varanger in 1993. Tree vitality for birch and pine included crown density by percent cover and crown color using four classes designated by percentage of yellowed foliage: (1) 0–10%; (2) 11–25%; (3) 26–60%; and (4) >60% yellowed foliage (Aamlid and Venn 1993).

Pearson correlation analysis (significant relations based on r) (SPSS Inc. 1997; Abacus Concepts 1988) was used to detect relationships between photosynthetic efficiency and pollution variables and NDVI. Skibotn was used as a clean reference site and was included in correlation analyses for both the mixed forest and birch vegetation types.

Significant correlations were evaluated at the 5% level of probability.

Results

Photosynthetic efficiency (Fv/Fm)

The Fv/Fm values ranged between 0.3 and 0.8 (Table 2). Generally, plants growing closer to the smelters had lower Fv/Fm values than those at a distance. Site means of Fv/Fm for each species are population level values and the standard errors show the variation in range of influence of site-specific environmental variables (Table 2).

Environmental correlations

CANOCO ordinations of Fv/Fm values show the relationships between 16 environmental variables, Fv/Fm values in 11 plant species, and 15 localities (Skibotn excluded as an outlier) (Figs. 2A and 2B). Table 3 is the correlation matrix of the ordination axes and the environmental variables. Cumulative percent variance of species–environment relations totaled 86.8% for the first four axes. Eigenvalues for axes 1, 2, and 3 were 0.387, 0.204, and 0.137, respectively. Since the eigenvalue for axis 3 was not much less than axis 2 and the correlation between axes 1 and 3 was not significant, we were able to obtain meaningful ordinations using the first axis horizontally and third axis vertically (Fig. 2). This al-

lowed us to remove axis 2, which correlated with the variable SUN and not with the other variables (Table 3).

The most influential environmental factors, listed in order of relative importance and represented by the length of the vector in the ordinations are CNX, ELE, MNX, NiCO, CuCO, PREC, TOPO, TEMP, NiDE, CuDE, NDVI, and SO₂ (Table 3). SO₂, NiDE, CuDE, NiCO, and CuCO are all highly correlated with each other and inversely correlated with DIST from the smelters (Table 3). ELE and TOPO are highly inversely correlated (Table 3). PREC and TEMP vectors have approximately the same vector length in the lower right hand quadrant of the ordination. These are positively correlated with MNX and inversely correlated with CNX (Table 3). *Empetrum hermaphroditum* and *A. alpinus* are positioned along the warmer TEMP, PREC, MNX vectors, and high SO₂ vector (Fig. 2A).

Of the investigation localities, Kirkenes (site 12) is positioned at the extremes of TEMP, PREC, and MNX influence, and Viksjøfjell (16) is at the extreme of the ELE vector. Kobbfoss (site 10) and Noatun (site 11) are at the extreme on the CNX vector, and Karpdalen (site 14), Svanvik (site 6), and Kirkenes are extremes along the SO₂, CuDE, and NiDE pollution vectors (Fig. 2B).

Plant species responses

Six species in the mixed forest vegetation had weak but significant correlations between Fv/Fm and SO₂ (Fig. 3A). Simple regression lines for *E. hermaphroditum*, *V. myrtillus*, *H. physodes*, *B. pubescens*, *Cladina* spp., and *Parmelia olivacea* reveal the inverse relationship of Fv/Fm along the gradient of increased SO₂. *Pinus sylvestris* did not exhibit the decreased Fv/Fm but is included in the figures for later discussion. Results were similar in the birch forest vegetation, but the trends were based upon a limited number of data points. In the mixed forest, photosynthetic efficiency values in all the lichen species, *H. physodes*, *Parmelia olivacea*, and *Cladina* spp. were inversely correlated with Ni and Cu deposition and concentrations of Ni and Cu in lichens (Table 4).

Significant positive relationships were found between Fv/Fm in five species of the mixed forest vegetation and the NDVI (Fig. 3B). *Arctostaphylos alpinus* was located at only two sites; therefore, the line is broken in the figure, and no r was calculated.

Plant community

Characteristics of each vegetation layer are listed in Table 5. Target species cover (measured for chlorophyll fluorescence) by vegetation layer, and percent target species cover of total vegetation are given in Table 6. *Parmelia olivacea* represented almost no ground cover, because it grows on birch tree trunks and, therefore, is not included in the table. *Pinus sylvestris* and *H. physodes* were only found in the mixed forest vegetation type; *A. alpinus*, *S. lapponum*, and *Parmelia olivacea* were found in the birch type.

NDVI was positively correlated with the total plant cover ($r = 0.472$). Total percent plant cover was negatively correlated with percent cover of barrens (gravel, bedrock, bare soil, and litter) ($r = -0.533$).

Table 2. Fv/Fm mean values and standard errors for species at each study site.

Site No. and name	D	Fv/Fm \pm S.E. ($\times 10^3$) ^a										
		P.s.	B.p.	V.m.	E.h.	B.n.	A.a.	S.l.	P.s.	H.p.	P.o.	C.s.
Mixed forests												
1. Skibotn	386	710 \pm 5	706 \pm 7	791 \pm 2*	795 \pm 3*				563 \pm 6*	537 \pm 5	441 \pm 7	505 \pm 6*
2. Neiden	45	537 \pm 9	718 \pm 7	711 \pm 3*	755 \pm 3*	675 \pm 9	669 \pm 5*		325 \pm 9*		425 \pm 6	531 \pm 4*
3. Ulveskard	30	583 \pm 8	667 \pm 9	705 \pm 5								
4. Skrukkebukt	18	645 \pm 7		659 \pm 8								
5. Holmfoss	13	613 \pm 12	732 \pm 9	692 \pm 4*	731 \pm 6*	717 \pm 6			662 \pm 6*	387 \pm 7*	435 \pm 8*	513 \pm 5*
6. Svanvik	7	673 \pm 9	691 \pm 7	715 \pm 3*	771 \pm 4*	659 \pm 6	715 \pm 3*		636 \pm 9*		366 \pm 9	511 \pm 6*
7. Sametti	22	648 \pm 6	744 \pm 8	748 \pm 7	769 \pm 7				558 \pm 14		506 \pm 5	572 \pm 7
8. Melkefoss	18	648 \pm 8	730 \pm 5	702 \pm 6								
9. Malbekkhøgda	25	606 \pm 9	679 \pm 9	648 \pm 8								
10. Kobbfoss	30	626 \pm 10	722 \pm 8	712 \pm 4*	734 \pm 4*				658 \pm 4*	480 \pm 13	485 \pm 8	587 \pm 5*
11. Noatun	45	645 \pm 12	775 \pm 4	719 \pm 4*	746 \pm 3*				629 \pm 12*	462 \pm 8	505 \pm 6	605 \pm 3*
Birch forests												
12. Kirkenes	35		699 \pm 7	780 \pm 3*	799 \pm 3*	719 \pm 7	736 \pm 5*	695 \pm 6				419 \pm 10
13. Sandnes	30		675 \pm 8	705 \pm 7								
14. Karpdalen	31		663 \pm 7	680 \pm 5*	770 \pm 4*	643 \pm 7	673 \pm 5*	594 \pm 8			379 \pm 11	451 \pm 8*
15. Gardsjøen	33		672 \pm 7	667 \pm 8								
16. Viksjøfjell	25		697 \pm 5	649 \pm 6*	732 \pm 3*	716 \pm 8	664 \pm 4*	694 \pm 6				

Note: Sites are included in the mixed forest (*Calamagrostio lapponcae* Pinetum vegetation type) or in the birch forest (*Empetro-Betuletum*/*Myrtillo-Betuletum* vegetation types) (Fremstad and Elven 1987). D, distance from smelters (km); P.s., *Pinus sylvestris*; B.p., *Betula pubescens*; V.m., *Vaccinium myrtillus*; E.h., *Empetrum hermaphroditum*; B.n., *Betula nana*; A.a., *Arctostaphylos alpinus*; S.l., *Salix lapponum*; P.s., *Pleurozium schreberi*; H.p., *Hypogymnia physodes*; P.o., *Parmelia olivacea*; C.s., *Cladina* spp. (see text for details).

^an = 50 except where indicated by asterisks, n = 100.

Fig. 2. CCA ordination (CANOCO) of Fv/Fm values for 11 plant species (A) and 15 investigation localities (B) along the 16 environmental vectors, with the first axis horizontally and the third axis vertically. Numbers refer to the investigation localities as listed in Fig. 1 and Tables 1–6. ○, mixed forest sites; ●, birch forest sites.

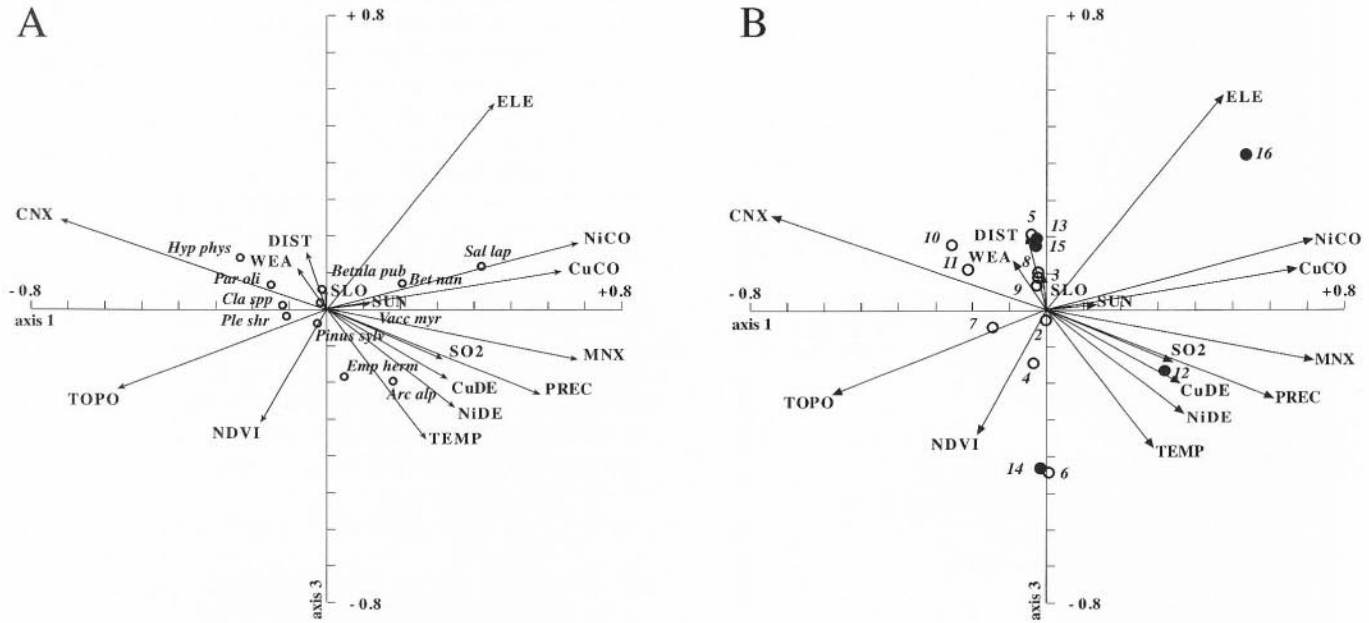


Fig. 3. Fv/Fm decreased as SO₂ increased (A) and NDVI decreased (B) in plant species in the mixed forest. Simple regression lines are shown with a broken line for *Arctostaphylos alpinus*, which is present at only two of the sites. Significant correlation coefficients are shown.

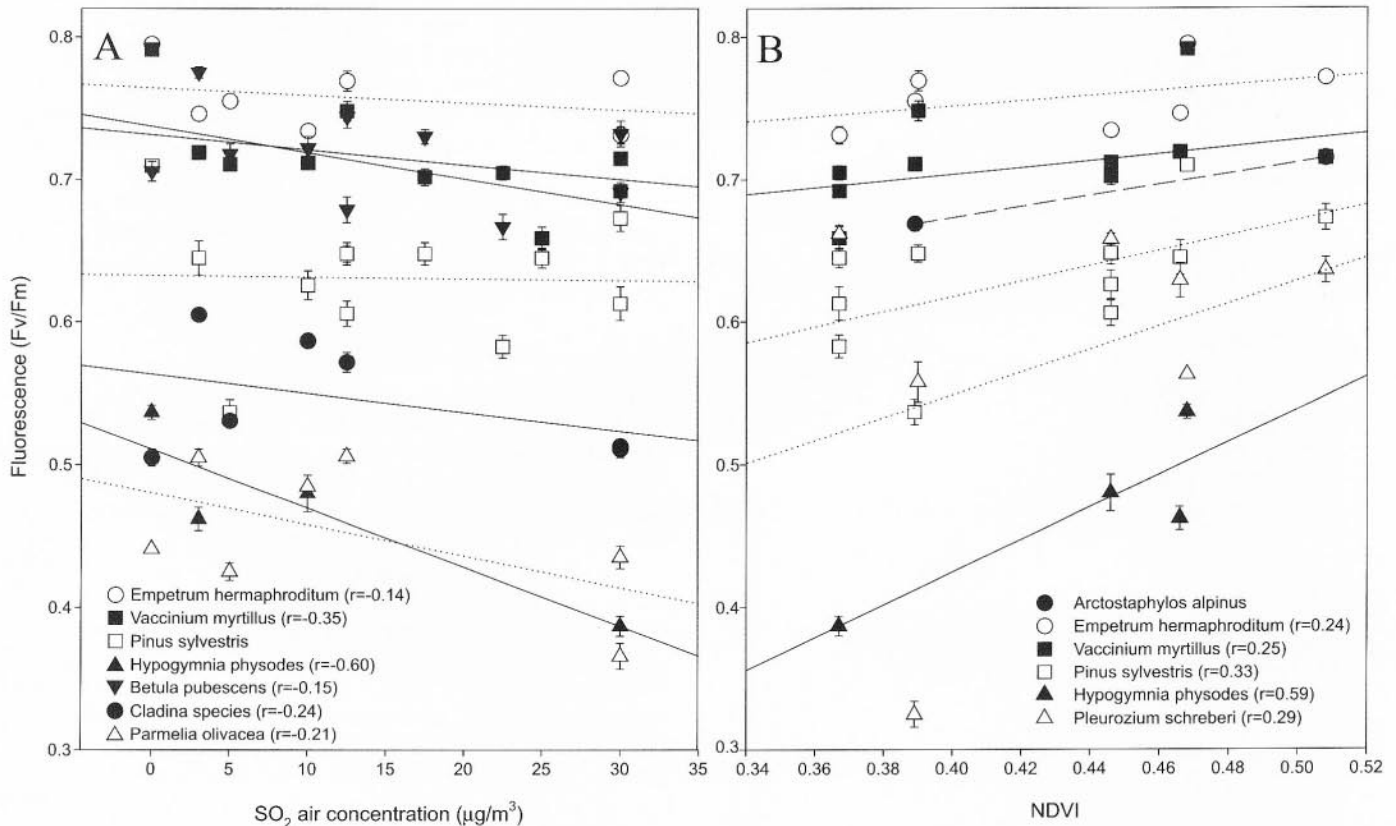


Table 3. Weighted correlation coefficients for species axes 1, 2, and 3 and environmental variables.

	Axis 1	Axis 2	Axis 3	DIST	PREC	TEMP	CNX	MNX	SUN	TOPO	WEA	ELE	SLO	SO ₂	NiDE	CuDE	NiCO	CuCO	
Axis 2	0.005																		
Axis 3	-0.004	-0.001																	
DIST	-0.058	-0.124	0.165																
PREC	0.568*	0.087	-0.257	0.407															
TEMP	0.264	0.099	-0.336	0.598*	0.818*														
CNX	-0.709*	-0.217	0.249	0.046	-0.696*	-0.521*													
MNX	0.673*	0.076	-0.142	0.062	0.853*	0.400	-0.658*												
SUN	0.127	-0.628*	0.023	0.025	0.046	0.023	0.110	0.059											
TOPO	-0.572*	-0.166	-0.236	0.010	-0.145	0.078	0.266	-0.308	0.010										
WEA	-0.082	-0.178	0.107	-0.350	-0.068	-0.219*	0.018	0.096	0.530*	0.447									
ELE	-0.529*	-0.079	0.568*	0.085	0.086	-0.321	-0.097	0.122	-0.119	-0.667*	-0.344								
SLO	-0.001	0.335	0.046	-0.305	-0.400	-0.216	0.057	0.427	-0.335	0.301	-0.313	0.250							
SO ₂	0.317	0.118	-0.147	-0.846*	-0.228	-0.384	-0.388	0.020	0.002	-0.005	0.435	0.052	0.359	0.966*					
NiDE	0.331	0.130	-0.275	-0.773*	-0.115	-0.258	-0.433	0.086	0.149	0.076	0.519*	-0.057	0.235	0.971*	0.989*				
CuDE	0.319	-0.011	0.195	-0.788*	-0.186	-0.358	-0.360	0.060	0.166	0.062	0.566*	-0.004	0.236	0.813*	0.759*	0.789*			
NiCO	0.685*	-0.007	0.188	-0.615*	-0.073	-0.368	-0.412	0.230	0.095	-0.355	0.261	0.541*	0.292	0.878*	0.836*	0.864*	0.987*		
CuCO	0.632*	-0.001	0.104	-0.703*	-0.090	-0.383	-0.410	0.225	0.127	-0.272	0.353	0.410	0.267	0.878*	0.836*	0.864*	0.987*		
NDVI	-0.169	0.071	-0.319	0.394	0.491	0.525*	-0.152	0.318	-0.047	0.178	-0.189	-0.525*	-0.622*	-0.551*	-0.495	-0.546*	-0.673*	-0.632*	

Note: Significant correlations are indicated by asterisks.

Discussion

Photosynthetic efficiency (Fv/Fm)

Many of the widespread target species had reduced photosynthetic efficiency in the more polluted sites. In general, healthy plants have photosynthetic efficiency (Fv/Fm) of 0.8–0.9, whereas plants suffering stress have ratios ca. 0.3–0.7 (Öquist and Wass 1988). In the present study, we confirmed that plants closer to the smelters had lower values of Fv/Fm than plants in the clean reference site at Skibotn and the study sites with greatest distance from the source of the airborne pollutants (Table 2). Most plants with low photosynthetic efficiencies were not visibly stressed or damaged. This suggests that the measurement of photosynthetic efficiency using chlorophyll fluorescence can provide “early warning” of stress levels of plants before visible plant damage occurs. Lauenroth and Dodd (1981) suggested that chronic exposure to even low concentrations of SO₂ can destroy chlorophyll function without subsequent visible necrosis.

Low Fv/Fm values measured for many plant species under stressed conditions in the field coincide with increased energy dissipation rates by the xanthophyll cycle and reduced photosynthetic efficiency (Demmig-Adams and Adams 1996; Verhoeven et al. 1999).

The predawn dark adaptation of PSII, although suggested as best for estimating photosynthetic efficiency (Adams and Demmig-Adams 1994), was not possible in our investigation area because of the continual light during the growing season. In addition, measuring the efficiency of PSII can be complicated by local climate conditions; for example, cloudy weather affects dark adaptation and leads to greater excitation of fluorescence. High light intensities in sunny weather can also result in excitation, because light–photosynthesis relations can metabolize the SO₂ that may otherwise cause damage (Lauenroth and Dodd 1981). These factors were partially filtered out of our ordination by removing axis 2, which correlated with the influence of sunlight intensity, the SUN scalar variable, on the estimation of photosynthetic efficiency.

Environmental correlations

Kirkenes (site 12) is at the extreme along the SO₂ in air at the ground-level vector (Fig. 2B). This might partially be explained by the influence of the other strong environmental variables, such as TEMP, PREC, and MNX, and by the closeness of a small smelter in Kirkenes, which emitted less than ca. 600 t of SO₂ annually until ca. 1994.

The relatively unimportant (short) environmental vector of distance (DIST) in the ordination indicates that topographical factors confounded the direct decrease in photosynthetic efficiency with increasing distance from the smelters (Fig. 2). Aamlid and Venn (1993) reported that the effects of airborne pollutants decrease with increasing distance from the emission sources in Russia. However, heavy metal damage on vegetation is asymptotically distributed and apparently falls off more rapidly than SO₂ with distance from the smelters (Meland 1992; Richardson and Nieboer 1981). Tyler et al. (1989) reported that irregular topography and prevailing winds confounded patterns of heavy metal deposition.

Table 4. Pearson coefficients, r , for significant correlations between species Fv/Fm and pollution variables at the mixed forest sites.

Species	Pollution variable				
	SO ₂	NiDE	CuDE	NiCO	CuCO
<i>Betula pubescens</i>	-0.15	-0.15	-0.14	-0.11	-0.10
<i>Empetrum hermaphroditum</i>	-0.14	-0.09	-0.10	-0.15	-0.15
<i>Vaccinium myrtillus</i>	-0.35	-0.26	-0.27	-0.35	-0.34
<i>Hypogymnia physodes</i>	-0.60	-0.60	-0.60	-0.62	-0.62
<i>Parmelia olivacea</i>	-0.21	-0.29	-0.29	-0.20	-0.22
<i>Cladina</i> spp.	-0.25	-0.31	-0.32	-0.23	-0.25

Table 5. Total percent plant cover (summed for all canopy layers) and total nonplant cover (bare rocks, gravel, soil, and litter) at each investigation site, and plant cover (total %) and number of species of each vegetation stratum.

	Site No.															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Total nonplant cover	0	15	5	5	16	45	10	5	4	13	7	32	2	27	2	37
Total plant cover	169	190	149	159	176	188	158	164	158	203	176	212	193	211	173	130
Total no. of species	29	35	26	36	37	36	22	26	23	42	22	39	25	40	23	31
Tree canopy cover	19	13	14	20	14	17	18	25	18	15	30	8	22	9	19	0
No. species	2	2	2	2	2	3	2	2	2	3	2	2	1	1	1	0
Bush canopy cover	1	3	4	3	20	9	4	4	2	11	2	25	3	4	3	8
No. species	2	2	3	2	4	4	3	3	2	6	2	3	2	3	2	2
Low shrubs – herb cover	61	61	61	53	57	41	66	50	65	57	65	78	68	83	69	52
No. species	12	7	5	7	6	5	5	8	5	7	6	11	9	6	11	12
Lichen cover	38	72	13	22	17	58	13	9	12	60	40	14	7	35	3	17
No. species	7	18	12	19	18	19	8	7	10	17	9	14	7	21	4	10
Moss cover	50	25	52	57	52	16	47	71	57	47	32	56	91	53	76	16
No. of species	6	6	4	6	7	5	4	6	4	9	3	9	6	9	5	7

Note: See Table 1 for the names of the study sites.

Arctic cold air masses, especially during summer, can create inversions by overriding the warmer layers at ground level and forcing the warm polluted air northward along the river drainages. Prevailing high-elevation cold winds can “pump” the lower elevation warm-air pollution from the Nickel smelter stacks, which are 150 m high on lower slopes, in a northward direction confined between 200 and 400 m high mountains and onto the coast. The pollution is pumped and blown into the Viksjøfjell areas, where inversions can intensify and prolong the impact of the polluted air at the lower elevations. The Zapolyarnij smelter is located in the valley bottom, where winter winds from the south channel emissions along the drainages of the Grense Jakobselv River at the Norwegian–Russian border.

Plant species responses

Photosynthetic efficiency of six species in the mixed forest vegetation was reduced in locations where SO₂ values were highest (Fig. 3A). Sublethal exposures of airborne pollutants including SO₂ can alter plant growth, and other variables (e.g., light, pH, and tissue age) can determine the final effect on the individual plant (Lauenroth et al. 1979). Air pollutants can influence seasonal changes in cold tolerance in pine (Sutinen 1993). Intense light combined with SO₂ can lead to photoinhibition (Adams et al. 1989). SO₂ can irreversibly damage stomatal mechanisms, reduce chlorophyll, and cause leaf discoloration or death of vascular plants (Lauenroth and Dodd 1981). Plant stress from SO₂, heavy

metals, and nitrogen compounds can reduce a plant’s response to other environmental stress factors (e.g., frost tolerance or inhibit cold hardening). Resulting damage can be intense on poor soils close to Cu–Ni smelters (Freedman and Hutchinson 1980).

Species’ responses to environmental stress are often consistent within a growth form. Evergreen species like *Pinus sylvestris* and *E. hermaphroditum* receive long-term chronic exposure to SO₂ by accumulating contaminants over many seasons. In contrast, deciduous species, like *B. pubescens* and *V. myrtillus*, produce and lose all their leaves each season, thereby removing accumulated pollutants from the plant. Northern plant species differ in drought, cold, and heat resistance (Gauslaa 1984), and some alpine plants have mechanisms such as leaf cuticular protection, which reduce diffusion and which may also decrease sensitivity to airborne pollutants. Thick, leathery leaves, a concentration of sunken stomates on the bottom of leaves, and decreased gas exchange may decrease uptake of airborne pollutants and thereby decrease plant sensitivity to the pollutants. Cuticular diffusion resistance (for the four species with available data) decreases from 85.5 s·cm⁻¹ in *E. hermaphroditum*, 58.9 s·cm⁻¹ in *B. nana*, 25.0 s·cm⁻¹ in *A. alpinus*, and to 19.9 s·cm⁻¹ in *S. lapponum* (Gauslaa 1984). *Empetrum hermaphroditum* had the highest photosynthetic efficiency of all species measured in the two forest vegetation types (Table 2), a result that might reflect high cuticular diffusion resistance. High diffusion resistance in alpine plants may be

Table 6. Ground cover (%) of each target species (measured for chlorophyll fluorescence) by vegetation layer, and total target species as a percentage of total plant cover by site.

	Site No.															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Target % of total cover	76.8	52.2	81.9	74.9	60.6	44.6	75.9	79.1	84.8	63.5	72.8	46.4	66.6	57.7	63.1	30.1
Tree canopy																
<i>Betula pubescens</i>	5.4	7	2	2.2	3.4	1.8	5.4	14	7.2	2.4	3	7.4	16.6	9	16	0
<i>Pinus sylvestris</i>	13.6	6.2	11.6	18	5.6	15.6	13	6.6	10.6	11.6	27	0.2	0	0	0	0
Bush canopy																
<i>Betula pubescens</i>	0.4	0	1.2	0	1.4	0.8	1.2	2.4	1.4	1.4	1.2	5	2.4	0.4	2	0
<i>Betula nana</i>	0	3	0.6	0.4	1.4	2.4	0	0	0	4	0	8	1	3	0	5
<i>Pinus sylvestris</i>	0.4	0.2	1.4	2.2	8.2	1.4	0	1	0.4	2	0.6	0	0	0	0	0
Low shrubs/herbaceous																
<i>Salix lapponum</i>	0	0	0	0	0	0	0	0	0	1.6	0	2	0	1	0	2.8
<i>Arctostaphylos alpinus</i>	0	11	0	0	0	3	0	0	0	0	0	10	0	10	0	2.6
<i>Empetrum hermaphroditum</i>	27	26.4	35	32	37	22	38	28	41	28	24	44	35	47	22	23
<i>Vaccinium myrtillus</i>	8.6	6.6	12.6	8.2	4.8	4.6	16	14	12.6	11.6	7.2	5.4	20	10.8	19	4.2
Lichen																
<i>Hypogymnia physodes</i>	0.2	0	0	0.6	1.2	0	0.6	0	0	1.8	0	0	0	0	0	0
<i>Cladina</i> spp.	34.2	30.8	10	10.8	5.6	20.4	8.6	5	8.8	41.6	35.4	3.4	3.4	15.8	2.2	1
Moss																
<i>Pleurozium schreberi</i>	40	8	48	45	38	11.6	37	59	52	23	30	13	50	25	48	0.4

Note: See Table 1 for the names of the study sites.

an adaptation to the abrasive effect of blowing ice crystals or water stress during the winter when soils are frozen (Sowell et al. 1982).

Plant sensitivity to SO_2 and heavy metals increases at low pH (Hill 1971), a common feature of soils and waters in Arctic regions and areas influenced by acid rain. Organic particulate matter rapidly binds most heavy metals deposited in soil–water systems. Vascular plants absorb metal cations primarily through their roots and to a lesser extent through their leaves, whereas terrestrial lichens take up metals directly from the air. SO_2 acidifies the environment and enhances bioaccumulation of the metals (AMAP 1998).

The snow-level lichen, *Parmelia olivacea*, as well as other epiphytic lichens, no longer occur in the vicinity of the Russian smelters (Aamlid 1992; Aamlid and Venn 1993). Elevated concentrations of SO_2 in lichens can cause chlorophyll degradation by exerting deleterious effects on the symbiosis between the fungal partner and its photobiont (LeBlanc and Rao 1973). The bedrock in the South-Varanger region, termed Polmak-Pasvik-Pechenga greenstone belt, is a basic volcano–sedimentary assemblage. It contains the Cu–Ni ore deposits of the Nikel–Zapolyarnij area. Ironically, this bedrock increases the buffer capacity in local freshwater lakes (Nøst et al. 1992) and may have similar influence on local soil types.

Although potentially buffered by the basic soil layers, the cover of *Cladina* reindeer lichens might be extra sensitive to the airborne particles, because they lack a cortex to protect the medulla from the atmosphere and the rough surface has greater area for trapping airborne particles. Lichens are long lived and accumulate heavy metals by trapping insoluble particles and by ion exchange into cell walls and cells (Richardson 1992). Generally, the lichen–heath vegetation, originally growing on exposed ridges, is now uncompetitive with dwarf shrubs like *E. hermaphroditum* and is transformed into a more barren habitat with an apparently more resistant and robust vegetation including *V. myrtillus* and *Deschampsia flexuosa* (L.) Trin. (Deyeva and Maznaja 1993). This pattern agrees with similar smelter pollution problem studies in Sudbury, Ont., Canada (Freedman and Hutchinson 1980), and Kokkola, Finland (Väisänen 1986).

Photosynthetic efficiency in *E. hermaphroditum* was significantly reduced in both mixed forest and birch forest vegetation (Fig. 3A). Much of the historical distribution of *E. hermaphroditum* has been replaced by *V. myrtillus* (Tømmervik et al. 1998) possibly because of the biological consequences of reduced photosynthetic efficiency or reduced competitive advantage in soils where the lichen ground cover has died and blown away. This removal of the protective lichen mat, which maintains the humidity at the soil surface and shades the soil and shallow rooting structures, may contribute to scorching of the exposed soil surface during summer in this continental region, where growing seasons can be hot and dry.

Pine exhibited no difference in photosynthetic efficiency along the SO_2 pollution gradient (Fig. 3A). Fv/Fm measurements were made in the lower pine canopy, where influence from the branches above appeared to mitigate air pollution impacts while inflicting its own influences, (e.g., acid needle fall, rain drip, shade, competition for moisture, etc.) on itself and on other species in the understory. Photosynthetic effi-

ciency increased along increasing canopy cover density in the mixed forests understory species, especially in *E. hermaphroditum*, *H. physodes*, *Parmelia olivacea*, and *Cladina* spp. Possibly the pine canopy buffers the understory species from the impact of airborne pollutants (Aamlid 1992). Furthermore, damage in the canopy measured on a color scale by NISK (Aamlid 1992) paralleled the decreased photosynthetic efficiency in the same four mixed forest species. Similarly, in the birch forest vegetation, photosynthetic efficiency in *V. myrtillus* and *Cladina* spp. increased with canopy cover and also decreased along the birch canopy damage gradient.

The photosynthetic efficiency of six species in the mixed forest was reduced where the NDVI was lowest (Fig. 3B). This relationship is likely because we are comparing several plant species in the same geographical area and NDVI is an estimate of vigor or health of several trees and field vegetation in the area of a pixel (30 m²).

Plant community

NDVI is calculated from vegetation representing the same phenological stage as Fv/Fm and ground cover measurements in the field because Fv/Fm was measured during late July 1993 and the cloud-free satellite image was from 23 July, 1994. The index represents chlorophyll per unit area because near infrared (NIR) reflectance is sensitive to the vegetation structure and red reflectance (RED) decreases as chlorophyll absorption increases (Waring et al. 1995). The correlations between NDVI and plant cover percent ($r = 0.472$; Table 5), and between NDVI and the species Fv/Fm (Fig. 3B), represent a likely covariation between biomass or plant cover characteristics and general vegetation health. Higher values of NDVI indicate greater vigor and plant cover, which is in correspondence with Sellers and Schimel (1993).

Conclusions

We showed that photosynthetic efficiency is reduced in vascular plant species along the gradient of increased airborne pollution (SO_2 , Ni, and Cu) emanating from smelters on Kola Peninsula. Measurements of photosynthetic efficiency in many target species were a sensitive indicator of airborne pollutant impact on plants, and these patterns correlated with Ni and Cu concentrations in lichens. Fv/Fm in five target species correlated with NDVI. Whole plant community cover also correlated with NDVI. As technology improves and smaller pixel size allows for better remote sensing resolution, plant responses should be more easily detected.

Photosynthetic efficiency was reduced in more than 50% of the investigated species. However, the new practice of reducing emissions when the dominant wind direction is towards Norway, implemented in 1991, may encourage recovery of photosynthetic efficiency and stabilize the vegetation changes. The impact of this new procedure is not yet estimated. Sulfur emissions in western Europe, the former USSR, and North America are currently decreasing (Lövlblad et al. 1992; EMEP 1994); thus, SO_2 deposition is likely to continue to decrease.

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