

Controls over monoterpene emissions from boreal forest conifers

MANUEL LERDAU,¹ MARCY LITVAK,² PETER PALMER³ and RUSSELL MONSON²

¹ Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA

² Environmental, Population, and Organismic Biology Department, University of Colorado, Boulder, CO 80309-0334, USA

³ Department of Chemistry and Biochemistry, San Francisco State University, San Francisco, CA 94132, USA

Received June 17, 1996

Summary We investigated controls over the emission of monoterpenes from two species of boreal forest conifers, black spruce (*Picea mariana* Miller (B.S.P.)) and jack pine (*Pinus banksiana* Lamb). Monoterpenes are important in plants as carbon-based defensive compounds and in the atmosphere as photochemically reactive compounds that affect ozone and carbon monoxide concentrations. We examined ecological theories of plant allocation to defensive compounds in relation to emission rates of monoterpenes from the foliage of these two species. Monoterpene emission from plants is controlled by the vapor pressure of the monoterpenes within plant tissues, and vapor pressure is controlled by two parameters, air temperature and terpene concentration within the tissues. We measured the concentration of terpenes and nitrogen within foliage and the emission rate from foliage, and demonstrated that emission rate was linearly related to nitrogen concentration and exponentially related to air temperature. Current theories of plant allocation to carbon-based defenses predict an inverse relationship between foliar nitrogen and carbon-based defenses. We found that, under certain circumstances, these theories were sufficient to predict concentrations and emissions, but under other circumstances, the theories did not predict monoterpene concentrations or emissions. These results are discussed in the context of landscape/regional modeling of hydrocarbon emission from vegetation.

Keywords: carbon-nutrient balance hypothesis, concentration, emission, growth-differentiation balance hypothesis, Henry's Law, nitrogen, *Picea mariana*, *Pinus banksiana*.

Introduction

Monoterpenes are produced by many flowering plants and nearly all conifers (Banthorpe and Charlwood 1980) and are stored either within or on the surface of plant tissues (Croteau 1987). Monoterpenes serve a variety of roles involved with plant chemical defense, acting as feeding deterrents to some herbivores, toxins to fungal pathogens, and physical barriers to certain bark beetles. Because of their high vapor pressures, monoterpenes readily volatilize from plant tissues (Lerdau 1991). Once in the atmosphere, monoterpenes play critical

roles in determining concentrations of tropospheric ozone and carbon monoxide, in producing organic nitrates and weak organic acids, and in controlling the atmospheric lifetime of methane (Jacob and Wofsy 1988). In addition to knowledge of the atmospheric roles of monoterpenes, a strong body of ecological theory has developed concerning the impacts of resource availability on monoterpene production, but only recently have atmospheric science and plant ecology come together to test the effects of ecological parameters on monoterpene emissions from plants.

Monoterpene emission from plants is controlled by the vapor pressure of the monoterpenes within the plant tissues. Vapor pressure of monoterpenes is controlled by two parameters, air temperature and the concentration of terpenes within tissues (Lerdau et al. 1994a). Because of the control that monoterpene concentration exerts over its emission rate, ecological theories of plant allocation to defense can be applied to explain emission dynamics. Although the relative composition of monoterpenes within plant tissues is under genetic control, overall monoterpene concentrations are closely linked to the availability of resources (Gershenson 1994). This relationship between monoterpene concentration and resource availability has been studied extensively by scientists wishing to understand allocation to defense in an ecological context.

The two main ecological theories that have developed concerning the effect of resource availability on plant allocation to defensive compounds such as monoterpenes are the Carbon-Nutrient Balance Hypothesis (CNBH) and the Growth-Differentiation Balance Hypothesis (GDBH) (Herms and Mattson 1992). The CNBH and GDBH both predict that plants in environments where belowground resources are limited will allocate more of their carbon (an aboveground resource) to chemicals and structures that will protect the more rare resource. Thus, when a belowground resource such as nitrogen is rare, these theories predict that plants will allocate more to carbon-based defenses such as monoterpenes.

These theories have been used to predict the effects of nitrogen resource availability on monoterpene emissions for plants growing under controlled conditions (Lerdau et al. 1995). These theories have not, however, been tested for their ability to predict monoterpene emissions under field condi-

tions. We studied the relationship among temperature, concentrations, and emissions as well as the relationship between nitrogen concentration and monoterpene concentration in the foliage of two conifers, black spruce (*Picea mariana* Miller (B.S.P.)) and jack pine (*Pinus banksiana* Lamb), growing in the boreal forest of Canada. A relationship between nitrogen concentration in the foliage and monoterpene emissions would enable the development of algorithms that relate remotely sensed information on foliar nitrogen to monoterpene emissions at large spatial scales. The results from this study also provide information on the utility of the CNBH and GDBH in predicting monoterpene concentrations and emissions across large spatial scales.

Materials and methods

Species

Black spruce and jack pine, common species in the boreal forest of North America (Barbour and Billings 1988), were studied. Black spruce is commonly associated with boggy habitats, although it can be found growing on many sites including dry ridge tops. Jack pine is found in sandy soils and is well known as one of the more drought-tolerant species of the boreal forest (Elliot-Fisk 1988).

Sites

The three research areas were in the Southern Study Area (SSA) of the BOREAS program (for full details, see Sellers et al. 1995). The first two areas were the Old Jack Pine (OJP) and Old Black Spruce (OBS) tower-flux locations of the BOREAS project and were the locus for the monoterpene emission measurements. These areas contained mature stands of jack pine and black spruce and were the focal sites in the BOREAS program for studies of biosphere-atmosphere exchange from these two habitat types. The OBS site is situated in a black spruce-sphagnum bog with the largest trees being 155 years old and 10–15 m tall. The OJP site is in a jack pine forest, 80–120 years old, that lies on a sandy bench of glacial outwash with the largest trees being 10–15 m tall. The third site consists of six bogs in the SSA that lie on an east-west transect between the OJP and the Old Aspen sites (Sellers et al. 1995). The data on tissue concentrations of nutrients and monoterpenes were collected from trees growing in these six bogs.

Each bog area had continuous vegetation going from the middle of the bog (open water) up a topographic gradient to a hilltop region that never had standing water. Because the altitudinal change per unit distance was not constant from bog to bog, we chose our sampling points by first deciding on the endpoints (the highest and lowest points included) and then sampled evenly between those points.

Sample selection

For the photosynthesis and hydrocarbon measurements, 10 trees of each species were chosen that had sunlit leaves accessible within 3 m of the ground. All measurements were conducted on sunlit leaves that had developed the previous year.

Tissue chemistry and gas exchange sampling on sunlit leaves from branches much higher in the canopy showed that there was no significant effect of branch height on photosynthetic rate or on tissue composition (ANOVA, $P > 0.05$, data not shown). The black spruce trees sampled for tissue chemistry measurements along the bog transect were chosen on the basis of accessibility of sunlit leaves within 2 m of the ground.

All hydrocarbon measurements were made on fully expanded needles that had developed during the previous growing season. Needles were placed in a cuvette so that only those needles that expanded during the previous growing season were included. Needle age in all cases was determined by marking needle cohorts before leaf expansion in the spring and by examining the branches for twig color change and bud scarring associated with each year's growth. Bog transect measurements were also all made on last year's fully expanded needles.

Sample procedure

Hydrocarbon emissions Samples were collected by enclosing branches in a temperature- and light-controlled cuvette connected to a plant gas exchange system (Campbell MPH 1000, Campbell Scientific, Logan, UT), and flowing hydrocarbon-free air over the needles. Temperature was controlled by use of thermoelectric coolers (Campbell Scientific), and light intensity was controlled by mounting a projector bulb at right angles to the top of the glass-topped cuvette. Light was then reflected by a cold mirror (Model 15-33233, OCLI, Santa Rosa, CA) mounted at a 45° angle to the cuvette. The mirror transmitted light at 720 nm and reflected light of shorter wavelengths. Hydrocarbon-free air was produced by pumping ambient air through a clean-air generator (Aadco 5L, AADCO Instruments, Silver Springs, FL) and adding CO₂ back to the entering air stream. All flows and environmental conditions were monitored by the sensors and mass flow controllers of the Campbell MPH 1000.

Hydrocarbon emission samples were collected by diverting a fraction of the air exiting the leaf cuvette through a sampling tube packed with a solid sorbent (Supelco Carbotrap 300 cartridges (Bellafonte, PA) with dimensions of 18 cm in length and 6.5 mm in outer diameter). The sampling tubes were conditioned before each use at 220 °C for a minimum of 4 h at a flow of approximately 10 ml min⁻¹ of ultrahigh purity nitrogen by means of a Tekmar ThermoTrap unit (Cincinnati, OH). A blank from each set of conditioned cartridges was analyzed to ensure that they had been properly cleaned. The flow rate and volume of air passing over the sampling tube were controlled with a low-flow pump (Model-222, SKC, Inc., Eighty Four, PA). This sample volume was variable, but kept well below the typical breakthrough volumes for terpenes on this sampling tube (Anon 1986).

Foliar chemistry After the emissions samples were collected, we separated the branchlet and needles from the main branch. Total needle biomass was measured on fresh needles. We then separated the total needle biomass into two parts, half of which we placed in a 60 °C drying oven and weighed daily until no further change in weight was observed. These dried

needles were then stored for nitrogen analysis. The remaining needles were ground in liquid nitrogen and stored in 20-ml scintillation vials filled with pentane until they were analyzed for monoterpene concentrations. The pentane storage was never less than seven days and was more than sufficient to allow for complete solvent extraction of the monoterpenes (Lerdau et al. 1995). The fresh weight/dry weight ratio of the needles used in the nitrogen analyses was applied to each monoterpene sample to provide an estimated dry weight for the sample. All analyses are reported on a dry weight basis.

Analysis

Hydrocarbon emissions Samples were analyzed by thermal desorption followed by gas chromatography–mass spectrometry (GC–MS) using a modified form of the EPA TO-1 method (Anon. 1984). A Tekmar AeroTRAP unit (Cincinnati, OH), Tekmar Cryofocusing unit, and ultrahigh purity helium purge gas were used to desorb hydrocarbons off the cartridges thermally by a multi-step process. Cartridges were heated to 220 °C to desorb the sample onto glass-beads packed in an internal trap cooled with liquid nitrogen to –165 °C. Next, the sample was desorbed off the internal trap at 220 °C, passed through a moisture control system to remove water, and re-focused onto the head of the column which was held at –165 °C by means of liquid nitrogen. Finally, the sample was injected onto the column by flash heating the head of the column to 220 °C.

A gas chromatograph–ion trap mass spectrometer data system (Model ITS40, Finnigan, Inc., San Jose, CA) was used to analyze hydrocarbons in the samples. A 25 m, 0.25 mm ID DB-5ms column from J & W Scientific (Folsom, CA) was used to separate the terpenes. The temperature of the column was programmed to separate the terpenes of interest. This entailed holding the column at 40 °C for 5 min, increasing the temperature at 8 °C min⁻¹ to 220 °C, and then holding the temperature at 220 °C for 4 min. The transfer line to the ion trap mass spectrometer was held at 250 °C, and the ion trap manifold was set to 100 °C. The ion trap mass spectrometer was run through a daily auto-tune sequence before data acquisition of samples, standards, and blanks. This auto-tune sequence involved calibrating the mass scale and setting the emission current, multiplier voltage, automatic gain control target values. Mass spectra were acquired under electron ionization (EI) conditions at a scan range of *m/z* 50 to 200 and a scan rate of one scan s⁻¹.

Terpenes were identified by both retention time confirmation and matching experimental mass spectra against a custom library of mass spectra derived from a series of terpene standards. Terpenes were quantified against external standards, in which the most intense ion for the individual terpene (quantitation ion) was compared to the same ion from analyses of known amounts of terpene standards in hexane. Method blanks were used to correct for any response for terpenes on the conditioned cartridges. All emission rates are reported on a dry weight basis.

Foliar chemistry Monoterpenes were separated on an HP 5890 Series II gas chromatograph equipped with a split/split-

less injector, flame ionization detector (FID) and a 30 m DB-1 capillary column (0.32 mm i.d., 1 µm film thickness, J & W Scientific), 2 µl of sample was injected in the split mode (80:1 split) with an HP 7673 Auto Sampler, with He as the carrier gas at a flow rate of 2.2 ml min⁻¹. Column temperature was programmed to stay at 50 °C for 5 min, then increase at 6 °C min⁻¹ to 250 °C and hold for 5 min. Detector and injector temperatures were 300 and 275 °C, respectively.

Individual monoterpenes were identified by comparison of their retention times with authentic monoterpene standards (purchased from Sigma/Aldrich Chemical Co., St. Louis, MO) that were analyzed under conditions identical to those used for the unknown samples. Monoterpenes were quantified with fenchone as an internal standard. Fenchone was added to the extract 24 h before analysis. The results are expressed as mg terpene per gram of needle dry weight.

Needle nitrogen concentration was measured as total Kjeldahl nitrogen (TKN; calculated as a percentage of needle dry mass) as described by Jaeger and Monson (1992). Needles were ground and digested in sulfuric acid with a copper sulfate catalyst at 360 °C for 3 h and then analyzed colorimetrically with a flow injection analyzer (LACHAT Instruments, Mequon, WI).

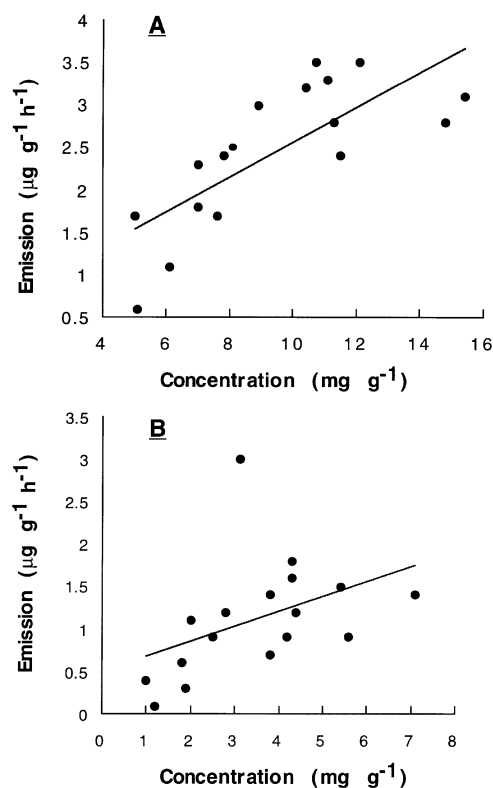


Figure 1. Monoterpene concentration versus emission for black spruce (A) and jack pine (B). Data collected at a temperature of 30 °C and an irradiance of 1000 µmol m⁻² s⁻¹. The lines through the points are least-squares regressions: the regression equation for spruce is $y = 0.2x + 0.3$ ($r^2 = 0.52$) and for pine it is $y = 0.1x + 1.3$ ($r^2 = 0.47$). Both slopes are significantly different from zero ($P < 0.05$) but neither intercept differs significantly from zero ($P > 0.05$).

Results and discussion

Monoterpene emissions

Monoterpene concentrations and emissions were closely correlated in both jack pine and black spruce (Figure 1). The emission versus concentration relationship was positive and linear for both jack pine and black spruce, but the slope of the relationship differed between the species. A positive, linear relationship between monoterpene concentrations and emissions has also been observed for ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Flyckt 1979, Lerdaу et al. 1994a, 1995). Thus, we conclude that, for any one taxon at a particular temperature, a linear relationship exists between concentration and emission. This relationship is consistent with emissions being governed by volatilization according to the Henry's Law effect on vapor pressure. Recent work has shown there may also be a light-dependent component to emissions from conifers (Lerdaу et al. 1997); however, the light-dependent component is exceedingly small and is probably seen in our data as noise about the regression line.

Monoterpene emissions increased exponentially with temperature for both species, and the curves for the two species were similar (Figure 2). An exponential rise in emissions with increasing temperature has been found in many studies (e.g., Tyson et al. 1974, Zimmerman 1979, Guenther et al. 1993,

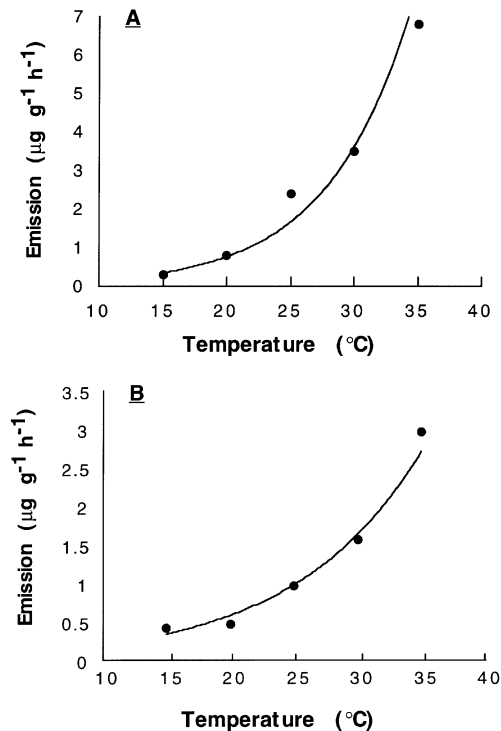


Figure 2. Monoterpene emission versus temperature for black spruce (A) and jack pine (B). Data are for branchlets measured at an irradiance of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. The lines through the points are simply best-fit exponential equations and do not differ significantly from the predicted vapor-pressure exponential equation of Tingey et al. (1991).

Lerdaу et al. 1994a). Monoterpene concentration in the needle tissue and needle temperature combine to control emission rate. At a given temperature, Henry's Law explains the existence of an equilibrium between monoterpene concentration and vapor pressure. As temperature increases, this equilibrium shifts to favor a higher vapor pressure at any given concentration. Thus, the gradient in vapor pressure between the internal needle tissue and the ambient atmosphere determines the driving force for the emission rate.

Monoterpene concentrations

Seasonality Monoterpene concentrations differed among seasons but did not show any consistent patterns; however, the

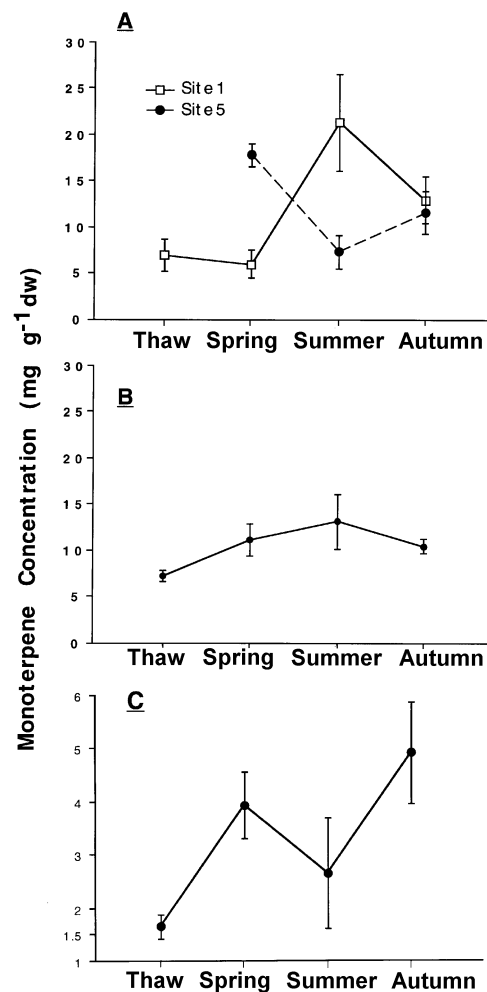


Figure 3. Monoterpene concentrations at different seasons for black spruce (A and B) and jack pine (C). The data in panel A show results from two sites (1 and 5) with $n = 5$ for each point and the bars represent one SE of the mean. The data in panel B are the combined results from all six bog sites, $n = 30$, and the bars represent one SE of the mean. Whenever possible the same trees were sampled so that samples across seasons are not independent. The points in panel C represent the mean values for 5–8 individuals growing at the OJP site, and the bars represent one SE of the mean.

pattern of seasonal variation differed between jack pine and black spruce (Figure 3). In jack pine, we observed large differences in monoterpene concentrations between seasons and also very large variances within a season. Black spruce trees at both the OBS site and the bog sites showed a slight rise during the year and then a decline in the autumn, and much smaller variances within a season than in jack pine.

We conclude that seasonal factors control monoterpene concentrations, but that these factors may be linked to environmental variation rather than to plant ontogeny or phenology, or both (see Bernard-Dagan 1988 for a detailed study of seasonal changes in monoterpene biosynthesis). It may well be that site-specific parameters such as changes in water availability, determined the observed patterns of seasonal variation. Black spruce trees, which grow in sites with high soil water content year round, showed small variances in their seasonal monoterpene concentration. Jack pine trees, in contrast, grow on sandy soils and may be exposed to severe seasonal water stress. In addition, the geomorphology of the sandy benches on which jack pine grows increases the probability of within-site heterogeneity because of differences in the depth of the sand substrate (Elliot-Fisk 1988). This increased intra-site heterogeneity may explain the increased variance in monoterpene concentrations found in jack pine.

Nitrogen For black spruce, the relationship between monoterpene concentration and nitrogen concentration tended to be consistent within a bog site, but differed greatly among sites (Figure 4). The trees at Site 1 showed a positive relationship between monoterpene concentration and N concentration, but trees at the other sites showed either a negative relationship or no relationship at all. When these data were pooled and the overall relationship between monoterpene and N concentrations examined, no significant relationship was observed (Figure 5).

These results suggest that resource-based theories of plant allocation to defense such as the Carbon-Nutrient Balance Hypothesis (Bryant et al. 1983) or the Growth-Differentiation Balance Hypothesis (Lorio 1993) adequately explain the con-

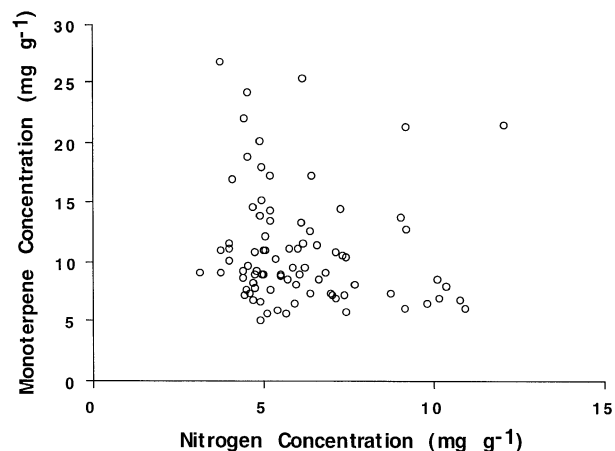


Figure 5. Monoterpene concentration versus nitrogen concentration for the black spruce from the bogs for all data combined. These data give a nonsignificant regression ($P > 0.05$).

controls over monoterpene concentrations in foliage for certain sites, but that other factors may be affecting concentrations at the other sites. At the sites with significant negative correlations between tissue N concentration and monoterpene concentration, allocation to the production of monoterpenes may be controlled by tissue carbon/nitrogen ratio. At sites without such patterns (e.g., Site 1), water availability and folivore density may have more important controls on monoterpene concentration than nitrogen. Thus resource-based theories need to consider a range of relevant resources rather than only one, and they may also need to consider the role of herbivores and pathogens with respect to allocation to defense. The Growth-Differentiation Balance Hypothesis as formulated by Loomis (1932) explicitly considers multiple resources and thus offers a potentially more useful model than the Carbon-Nutrient Balance Hypothesis. There is still no adequate mathematical model of the interaction of both resources and sinks as potential control factors over allocation (Lerdau et al. 1994b).

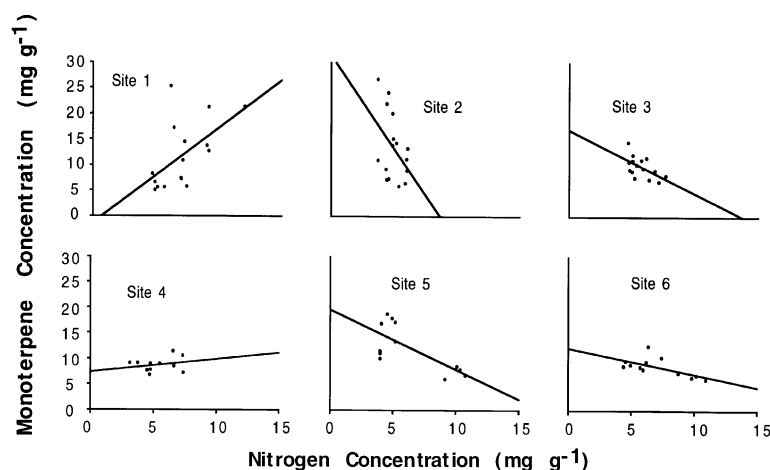


Figure 4. Monoterpene concentration versus nitrogen concentration for the black spruce at each bog site. The sample sizes, regression equations, and P values are given below:

Bog site	n	Equation	r^2	P
1	16	$y = 1.8x - 1.3$	0.3	0.2
2	16	$y = -3.6x + 31.5$	0.2	0.1
3	16	$y = -1.2x + 17.0$	0.3	0.02
4	12	$y = 0.2x + 7.4$	0.07	0.5
5	12	$y = -1.2x + 19.7$	0.5	0.01
6	12	$y = -0.5x + 12.2$	0.4	0.03

Implications for landscape emissions modeling and carbon balance

We have demonstrated that monoterpene emissions from both jack pine and black spruce can be adequately predicted from air temperature and the concentration of monoterpenes in foliage. Unfortunately, there do not appear to be any environmental correlates, such as seasonality or nitrogen availability, that can be used to predict foliar monoterpene concentrations. Estimates of monoterpene emissions from similar forest sites have a range of more than 200% (Fehsenfeld et al. 1992). Much of this variation could be the result of differences in foliar monoterpene concentrations. Current regional models of monoterpene emission such as that of Guenther et al. (1995) estimate terpene emission based on a single emission-temperature relationship. The accuracy of such models could be improved if they were modified to take into account the effect of monoterpene concentration on emission for those sites where data on monoterpene concentrations have been obtained. The next step, relating monoterpene concentrations to ecological parameters that can be detected by remote sensing (such as tissue nitrogen, Wessman et al. 1988) is complicated by our lack of an adequate theory of the ecological controls over allocation to monoterpenes by plants. Development and testing of such a theory is the next step in understanding monoterpene emissions at the scale of whole ecosystems or landscapes.

Although hydrocarbon emissions from boreal forest trees play important roles in tropospheric chemistry (Guenther et al. 1995), they represent only a small fraction of the ecosystem carbon balance. Photosynthetic and respiratory exchanges of CO₂ tend to be more than three orders of magnitude greater than the monoterpene fluxes reported here (Baldocchi and Vogel 1996). These results emphasize that the importance of fluxes of photochemically active gases is often out of proportion to their contribution to carbon mass balance. Thus, biological processes controlling hydrocarbon production and emission have a significance for atmospheric functioning that is much greater than is suggested by their magnitudes.

Acknowledgments

This research was supported by NASA Grant NAG 5-2287 and is a contribution to the NASA BOREAS program. M.T.L. acknowledges the support of an NRC Post-Doctoral Fellowship, and M.E.L. the support of a NASA Pre-Doctoral fellowship. We thank E. Allwine, D. Baldocchi, D. Bowling, P. Jarvis, B. Lamb, T. Raab, J. Randerson, C. Vogel, and H. Westberg for assistance with the data collection. We thank D. Gilbert, E. Kelly, T. Lynn, and L. Duran for assistance in the monoterpene and nitrogen tissue analyses, J. Solomon and Z. Cardon for assistance with the monoterpene emission analyses, and D. Taub for assistance with the statistical analyses. D. Peterson and C. Wong of the NASA Ames Research Center provided much logistical and legal support.

References

- Anonymous. 1984. Method for determination of volatile organic compounds in ambient air using Tenax adsorption and gas chromatography/mass spectrometry (GC/MS). EPA-600/4-84-041, US EPA Environmental Monitoring Systems Laboratory, Research Triangle Park, NC, 38 p.
- Anonymous. 1986. Carbotrap—an excellent adsorbent for sampling many airborne contaminants. Supelco GC Bulletin 846 C, Bellefonte, PA, 4 p.
- Baldocchi, D. and C. Vogel. 1996. A comparative study of water vapor, energy and CO₂ flux densities above and below a temperate broadleaf and a boreal pine forest. *Tree Physiol.* 16:5–16.
- Banthorpe, D. and B. Charlwood. 1980. The terpenoids. *In* Encyclopedia of Plant Physiology, Vol. 12. Eds. E. Bell and B. Charlwood. Springer-Verlag, Berlin, pp 185–219
- Barbour, M. and W. Billings. 1988. North American terrestrial vegetation. Cambridge University Press, Cambridge, U.K., 434 p.
- Bryant, J., F. Chapin III and D. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–368.
- Croteau, R. 1987. Biosynthesis and catabolism of monoterpenes. *Chem. Rev.* 87:929–954.
- Elliot-Fisk, D. 1988. The boreal forest. *In* North American Terrestrial Vegetation. Eds. M. Barbour and W. Billings. Cambridge University Press, Cambridge, U.K., pp 34–62.
- Fehsenfeld, F., C. Calvert, R. Fall, P. Goldan, A. Guenther, C. Hewitt, B. Lamb, S. Liu, M. Trainer, H. Westberg and P. Zimmerman. 1992. Emission of volatile organic compounds from vegetation and the implications for atmospheric chemistry. *Global Biogeochem. Cycles* 6:389–430.
- Flyckt, D. 1979. Seasonal variation in the volatile hydrocarbon emissions from ponderosa pine and red oak. M.S. Thesis, Washington State University, Pullman, WA, 52 p.
- Gershenson, J. 1994. Metabolic costs of terpenoid accumulation in higher plants. *J. Chem. Ecol.* 20:1281–1328.
- Guenther, A., P. Zimmerman, P. Harley, R. Monson and R. Fall. 1993. Isoprene and monoterpene emission rate variability: model evaluation and sensitivity analysis. *J. Geophys. Res.* 98:12609–12617.
- Guenther, A., C. Hewitt, D. Erickson, R. Fall, C. Geron, T. Graedel, P. Harley, L. Klinger, M. Lerdau, W. McKay, T. Pierce, B. Scholes, R. Steinbrecher, R. Tallamraju, J. Taylor and P. Zimmerman. 1995. A global model of natural volatile organic compound emissions. *J. Geophys. Res.* 100:8873–8892.
- Hermis, D. and W. Mattson. 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* 67:283–335.
- Jaeger, C. and R.K. Monson. 1992. The adaptive significance of nitrogen storage in *Bistorta bistortoides*, an alpine herb. *Oecologia* 92:578–585.
- Jacob, D. and S. Wofsy. 1988. Photochemistry of biogenic emissions over the Amazon forest. *J. Geophys. Res.* 93:1477–1486.
- Lerdau, M. 1991. Plant function and biogenic terpene emission. *In* Trace Gas Emissions by Plants. Eds. T. Sharkey, E. Holland and H. Mooney. Academic Press, San Diego, CA, pp 121–134.
- Lerdau, M., S. Dilts, H. Westberg, B. Lamb and G. Allwine. 1994a. Monoterpene emission from ponderosa pine. *J. Geophys. Res.* 99:16609–16615.
- Lerdau, M., M. Litvak and R. Monson. 1994b. Monoterpenes and the growth-differentiation balance hypothesis. *Trends Ecol. Evol.* 9:58–61.
- Lerdau, M., P. Matson, R. Fall and R. Monson. 1995. Ecological controls over monoterpene emission from Douglas-fir. *Ecology* 76:2640–2647.
- Lerdau, M., A. Guenther and R. Monson. 1997. Plant production and emission of volatile organic compounds. *Bioscience*. In press.

- Lorio, P. 1993. Environmental stress and whole-tree physiology. *In* Beetle-Pathogen Interactions in Conifer Forests. Eds. T. Schowalter and G. Filip. Academic Press, London, pp 81-101
- Sellers, P., F. Hall, H. Margolis, B. Kelly, D. Baldocchi, G. Hartog, J. Cihlar, M. Ryan, B. Goodison, P. Crill, K. Ranson, D. Lettenmaier and D. Wickland. 1995. The Boreal Ecosystem-Atmosphere Study (BOREAS): an overview and early results from the 1994 field year. *Bull. Am. Meteorol. Soc.* 76:1549-1577.
- Tingey, D., D. Turner and J. Weber. 1991. Factors controlling the emissions of monoterpenes and other volatile organic compounds. *In* Trace Gas Emissions by Plants. Eds. T.D. Sharkey, E. Holland and H. Mooney. Academic Press, San Diego, CA, pp 93-119.
- Tyson, B., W. Dement, and H. Mooney. 1974. Volatilization of terpenes from *Salvia mellifera*. *Nature* 252:119-120.
- Wessman, C., J. Aber, D.L. Peterson and J. Melillo. 1988. Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. *Nature* 335:154-156.
- Zimmerman, P. 1979. Testing of hydrocarbon emissions from vegetation, leaf litter, and aquatic surfaces and development of a methodology for compiling biogenic emission inventories. US EPA, Tech. Rept. EPA-450/4-79-004, 71 p.

