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Influence of Light and Temperature on Monoterpene Emission Rates from Slash Pine

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ABSTRACT

There is a growing awareness of vegetation's role as a source of potentially reactive hydrocarbons that may serve as photochemical oxidant precursors. This study assessed the influence of light and temperature, independently, on monoterpene emissions from slash pine (*Pinus elliottii* Engelm.). Plants were preconditioned in a growth chamber, then transferred to an environmentally controlled gas exchange chamber. Samples of the chamber atmosphere were collected; the monoterpenes were concentrated cryogenically and measured by gas chromatography. Five monoterpenes (α-pinene, β-pinene, myrcene, limonene, and β-phellandrene) were present in the vapor phase surrounding the plants in sufficient quantity for reliable measurement. Light did not directly influence monoterpene emission rates since the emissions were similar in both the dark and at various light intensities. Monoterpene emission rates increased exponentially with temperature (*i.e.* emissions depend on temperature in a log-linear manner). The summed emissions of the five monoterpenes ranged from 3 to 21 micrograms C per gram dry weight per hour as temperature was increased from 20 to 46 C. Initially, emission rates from heat-stressed needles were similar to healthy needles, but rates decreased 11% per day. Daily carbon loss through monoterpene emissions accounted for approximately 0.4% of the carbon fixed during photosynthesis.

High levels of ozone have been measured in rural and remote locations, far from significant anthropogenic sources of oxidant precursors. Elevated oxidant concentrations in these areas could be the result of transport into these areas and/or photooxidation of locally produced biogenic hydrocarbons. Volatile organics, including monoterpenes, have been detected in the atmosphere (11, 15, 18, 25), and the reports suggested that the hydrocarbons had a biogenic origin. Robinson (17) proposed that hydrocarbon concentrations were governed by both long distance transport and local production. However, there are only limited data available concerning the biogenic emission rates of potential photochemically reactive hydrocarbons such as the monoterpenes.

The data used to estimate emission rates for monoterpenes were collected using a variety of experimental techniques ranging from static encapsulation chambers to profile measurements in the field. The degree of environmental control during the measurement period was highly variable making it difficult to establish a clear relationship between monoterpene emission rates and environmental conditions. The data base for monoterpene emission rates is limited almost exclusively to α-pinene. Only limited data are available concerning the influence of the environment, particularly light and temperature, on monoterpene emission rates. Apparently light does not directly influence monoterpene emissions even though photosynthate is required for biosynthesis (4, 13). The emissions of camphor (23) and α-pinene increase with temperature (1, 10, 13).

The objectives of this study were to (*a*) determine the monoterpene emission rates from intact plants under controlled environmental conditions using a dynamic mass balance gas exchange chamber; (*b*) determine the independent influence of light and temperature on monoterpene emission rates; (*c*) determine the emission rates of monoterpenes from dead needles; and (*d*) estimate the relationship between the monoterpene emission rate and the photosynthetic rate of slash pine.

MATERIALS AND METHODS

Plant Culture. Bare root seedlings of slash pine (*Pinus elliottii* Engelm.) were obtained from the Division of Forestry, Florida Department of Agriculture and Consumer Services. The seedlings were planted in 15-cm pots in a Jiffy Mix-Perlite (1:2, v/v) mixture. Plants were cultured in a greenhouse for approximately 14 months at maximum day/night temperatures of 28 and 20 C, respectively. Sunlight was supplemented and the photoperiod extended to 16 h/day with light from high intensity discharge sodium vapor lamps. The plants were watered daily with North Carolina State University phytotron nutrient solution (5). At least 4 weeks prior to sampling for monoterpene emissions, the trees were transferred into a controlled environment chamber. The plants were grown at day/night temperatures of 27 and 18 C, respectively; the light intensity, at canopy height, was approximately 400 $\mu E\ m^{-2}\ s^{-1}$ with a 16-h photoperiod. The trees were approximately 15 months old when sampled and appeared healthy. The plants had both mature and recently elongated needles, none of which appeared to be defective, and there were no significant bark lacerations or gum exudations.

Gas Exchange Chamber. A dynamic mass balance gas exchange chamber was used to determine monoterpene emission and photosynthetic rates (22). The gas exchange chamber was housed in a controlled environment chamber which regulated light intensity and cooling. Ambient air was pumped through an Aadco pure air generator to remove hydrocarbons and CO_2 and to reduce the dewpoint. CO_2 and water vapor were added back to the air stream to obtain the desired concentrations within the gas exchange chamber. CO_2, water vapor and hydrocarbons were measured at the gas exchange chamber's inlet and outlet ports, and air flow was measured at the chamber inlet. Photosynthetic and monoterpene emission rates were determined using the equations for calculating gas fluxes in an open gas exchange chamber (19). During experiments, the CO_2 concentration in the gas exchange chamber was $350 \pm 40\ \mu l\ l^{-1}$; the dewpoint of the air entering the chamber was constant during the experiment, at approximately −3–0 C, whereas the dewpoint of the air exiting the chamber ranged between 26 and 38 C depending on the light and temperature conditions of a given experiment. Air temperature within the gas exchange chamber was measured with a shielded ther-

mocouple, leaf temperature was measured with a thermocouple pressed against the shaded portion of a needle in midcanopy. Light intensity, at canopy height, was measured with a Lambda Instruments model LI-190SR quantum sensor.

Experimental Protocol. The influence of temperature on monoterpene emissions at various light levels was studied by increasing the temperature from 20 to 46 C in 4- to 6-degree increments at each of five light levels (approximately 0, 100, 200, 400, or 800 μE m^{-2} s^{-1}). To study the effect of light intensity on monoterpene emissions, light intensity was increased in a step by step manner (0, 100, 200, 400, and 800 μE m^{-2} s^{-1}) at each of four temperatures (29, 35, 40, or 46 C). After each change of light or temperature there was a 60-min equilibration period before collecting duplicate air samples for hydrocarbon analysis. Concurrent measurements of the CO_2 exchange rate of the plants were also made. A minimum of three plants was used to develop each temperature or light response curve. After each experiment, needles were removed, dried at 70 C for 72 h, and dry weight was measured.

To determine emission rates from dead needles, two pine trees were heat-stressed at 60 C for 7 h during the dark portion of their photoperiod. The heat-stressed plants were retained for approximately 3 months after stressing, during that period there was no bud break or other signs of plant growth. Also, the plants were not capable of photosynthesis. To estimate emission rates, plants were placed in the gas exchange chamber at a light intensity of 400 μE m^{-2} s^{-1} and the temperature increased from 20 to 46 C as in live plant studies. Gas exchange data were collected 2 days after the heat treatment and continued for 3 weeks. During that period, a total of nine data sets were collected on the two plants.

Monoterpene Sampling and Analysis. The monoterpenes were separated on a 15.2 × 0.5 mm i.d. stainless steel, support-coated open tubular (Scot) column coated with 4% Carbowax 20M (helium carrier, 4 cm^3 min^{-1}) and quantified with a flame ionization detector, and the resultant peaks were integrated electronically. Since a flame ionization detector responds linearly to the mass of organic carbon (3), a 1.01 μl l^{-1} isooctane external standard was used to calculate the mass of organic carbon emitted for each monoterpene. Three to six 1-ml isooctane standards were taken each day with a reproducibility of ± 2%. Standards of each monoterpene were used to determine their retention times.

For each analysis, 25- to 50-ml air samples were collected from the sample ports of the gas exchange chamber with a gas-tight syringe. Samples were injected through a K_2CO_3 filter (to remove water) and a six-port valve into a stainless steel loop (61 cm × 0.25 mm i.d.) immersed in liquid oxygen to concentrate the hydrocarbon samples (16). After the samples were injected the stainless steel loop remained in the cryogen for a 4-min period with a helium purge flow (13 cm^3 min^{-1}). The concentrated sample was volatilized onto the column by heating the loop rapidly in boiling water.

Positive identification of monoterpenes emitted from slash pine was made by a combination of GLC-MS using a Finnigan 1015. Air samples from the gas exchange chamber were collected, cryogenically concentrated and chromatographed as described above. The GLC line separator interface temperature was 200 C. The MS electron beam had a source temperature of 90 C and was operated at 70 ev and 270 μamps. Monoterpene mass spectra from the air samples were compared to spectra in the registry of mass spectral data (21) and spectra from monoterpene standards to confirm identification.

Data Analysis. The relationship between the means and SDs of samples taken at each light and/or temperature indicated that monoterpene emission rates were distributed lognormally. Therefore, emission data were transformed to their respective natural logarithms for all statistical analyses. Means of duplicate samples collected at each light and temperature combination for each plant were used to estimate the monoterpene emissions.

Data graphs showed that $\log_e$ monoterpene emissions increased linearly with temperature for each plant. Since a series of monoterpene measurements were made on a given plant while temperature was varied, all data points collected from the same plant were correlated, violating the assumption of independent observations for regression analysis. Consequently, estimation of monoterpene emissions as a function of temperature could not be done simply by fitting a common regression line to the $\log_e$ data for all plants. Instead, a separate regression line was fitted to each plant. Since monoterpenes were measured at the same temperature levels for all plants, the averages of the intercepts and slopes of the individual plant regression lines were optimum estimates (maximum likelihood estimates) of the intercept and slope of the population regression line (7). By computing the variance and covariance of these slopes and intercepts, it was also possible to fit a confidence band about the estimated population response. Since the individual monoterpenes also responded in a log-linear manner to temperature, a regression line together with confidence bands was fitted for each monoterpene in the same manner as for the sum of the monoterpenes. To determine if monoterpene production depended on light, individual regression lines were fitted to each plant which had been exposed to varying light levels. The population intercepts and slopes were estimated as described above, and a t test was performed to test the hypothesis that the population slope was not significantly different from zero.

RESULTS

In the gas phase surrounding slash pine foliage, five monoterpenes were found in sufficient quantity to measure reliably. A sixth, camphene, was detected but at a level too low for reliable measurement. Selected physical properties of these monoterpenes are listed in Table I.

To determine the influence of light on monoterpene emission rates, light intensity was varied from 0 to 800 μE m^{-2} s^{-1} at each of four temperatures. A single regression line for $\log_e$ (sum of monoterpenes) *versus* light was fitted to the data of each plant (Table II). The slope parameter for each line was small, and half were negative. The average slope for all lines, the estimate of the population slope, was only -0.105×10^{-3}, indicating that monoterpene production changed less than 8% as light increased from 0 to 800 μE m^{-2} s^{-1}. According to a t test, the regression of monoterpene emissions on light was not significant (slope not significantly different from 0), confirming that the emission rate of the sum of the monoterpenes did not depend on light intensity. Similar results were obtained for the individual monoterpenes. In subsequent temperature studies, response curves developed at different light intensities were combined.

The influence of increasing temperature on monoterpene emission rates was determined by increasing temperatures from 20 to

Table I. *Major Monoterpenes Measured in the Gas Phase Surrounding Slash Pine Foliage*

Compound	Boiling Point	Vapor Pressure[a]	Average Emission at 35 C
	C	*mm Hg*	*μg C/g dry wt·h*
α-Pinene	156	8.8	4.46
β-Pinene	164	5.9	3.44
Myrcene	167	3.4	0.32
Limonene	178	3.3	0.16
β-Phellandrene	171	2.5	0.22

[a] Vapor pressures were based on data of Jordan (9). Because of the similarities in boiling points and molecular structures, the vapor pressure of β-phellandrene was assumed to equal α-phellandrene.

Table II. *Effect of Increasing Light Intensity on Monoterpene Emission Rates at Several Temperatures*

Temperature	Slope[a]
C	$b \times 10^3$
29	1.010
	−0.789
	−0.329
35	−0.859
	−3.868
	−1.798
40	−0.500
	2.818
	0.440
46	1.858
	0.670
	0.039
$\bar{x}$[b]	−0.105
SD	1.726

[a] The slopes are for the regression $\log_e$ (sum of monoterpenes) on light, with each slope computed from data for a single plant.

[b] This mean is the best estimate of the regression slope for the population of plants. The ratio of $\bar{x}$ to SD/$\sqrt{N}$ yields a t value to test if emissions are light dependent.

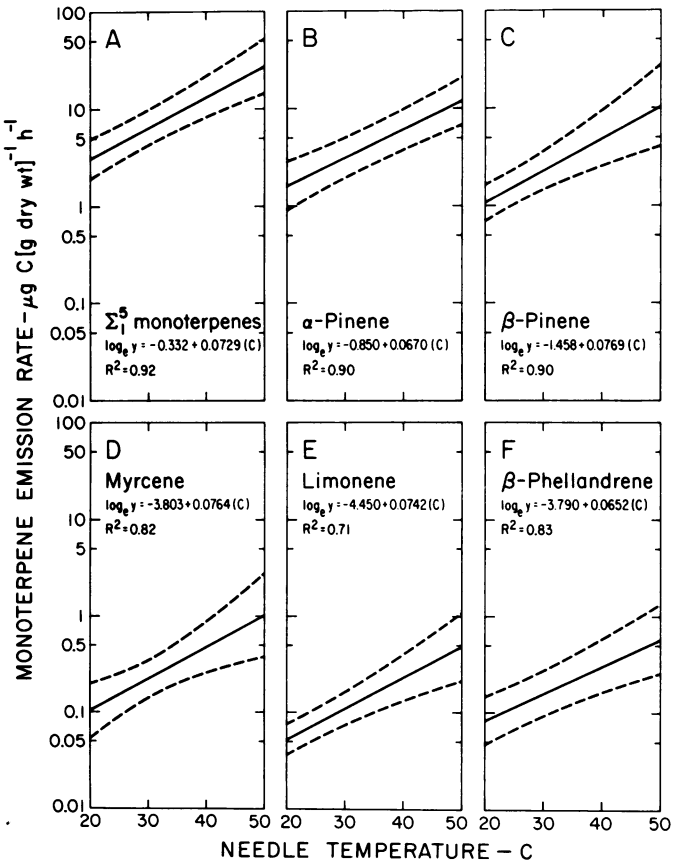

FIG. 1. Influence of increasing temperature on monoterpene emission rates in slash pine. Data from 14 plants were used to develop the temperature response curves. (---): 95% confidence bounds for the regression line.

46 C in the dark or at fixed light levels. The sum of the five monoterpenes and each individual monoterpene was log-linearly related to temperature even though there were large differences in the magnitudes of the individual components emitted (Fig. 1).

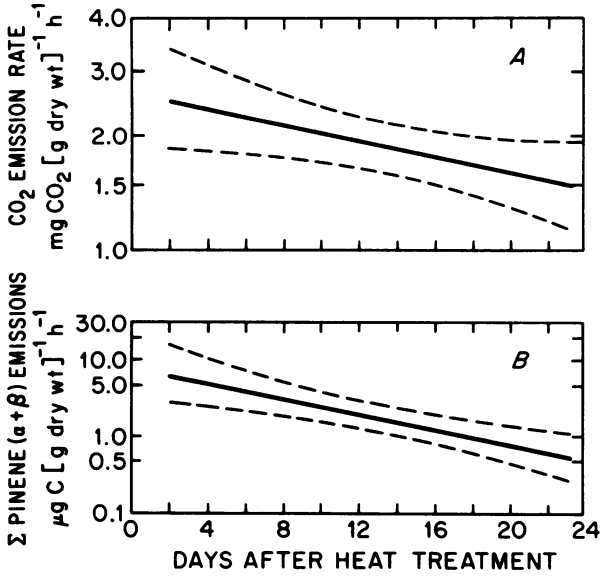

FIG. 2. Changes in the estimated (30 C) emission rates for CO_2 and α- and β-pinene in heat-stressed needles over time.

This log-linear relationship indicates that emissions increased exponentially with temperature. The per cent variation (R^2) accounted for by the log-linear model was greater than 0.80 for all components except for limonene (0.71). At 35 C, α- and β-pinene were emitted in the largest quantities (4.46 and 3.44 μg C g dry weight^{-1} h^{-1}), whereas limonene, myrcene, and β-phellandrene were only minor contributors to the total emissions (0.70 mg C g dry weight^{-1} h^{-1}, for the sum of the three components). The slope parameters (Fig. 1) were approximately equal indicating that the relative proportion of each component was approximately constant over the temperature range studied. The $\bar{x}$[1], SD, and CV were computed for the average monoterpene emission rates (35 C) and the slopes for the lines that related monoterpene emissions to temperature to show plant to plant variation. The plants showed large differences in their individual emission rates with a $\bar{x}$, SD, and CV of 11.38 μg C g dry weight^{-1} h^{-1}, 8.78, and 77%, respectively. The range of the individual emissions was 3.74–35.10 μg C g dry weight^{-1} h^{-1}; however, the individual observations were positively skewed, with 11 of the 14 observations being less than the mean. In constrast, the $\bar{x}$, SD, and CV of the slopes were 0.073, 0.031, and 42%, respectively, indicating that the slopes for the individual plants were similar. This agreement among slopes, together with the distinctly linear response seen for each plant in the data plots of $\log_e$ emission *versus* temperature, suggested a common response to temperature among plants despite large differences in average emission levels.

Heat-stressed trees were used to estimate monoterpene emission rates from nonliving tissue. All data were adjusted to 30 C using the log-linear model and the parameter estimation procedure as with the live plants. When the heat-stressed plants were placed in the light, there was no net CO_2 fixation. The needles emitted CO_2 in both the light and the dark, but the rate of emission decreased with time (Fig. 2A). During the same period, plants lost water at an average rate of about 24 mg H_2O g dry weight^{-1} h^{-1} (estimated at 30 C) which changed less than 10% during the 3-week period. Increasing temperature intensified monoterpene emissions at similar rates in both healthy and heat-stressed plants. Two days after heat-stressing, emission rates at 30 C for the sum of α- and β-pinene were approximately 6.2 μg C g dry weight^{-1} h^{-1} (Fig. 2B) which is similar to the emission rate of 5.4 μg C g dry weight^{-1} h^{-1}

[1] Abbreviations: $\bar{x}$: mean; CV: coefficient of variation.

(Fig. 1) from live needles for the same two monoterpenes. The monoterpene emission rate declined about 11% per day and decreased to one-half of the initial rate (day 2) within 6 days.

To model typical diurnal patterns for monoterpene emission and photosynthetic rates, environmental conditions for an average of summer days in Tampa, Florida, were used. Climatic summaries (12, 24) indicated an average daily solar radiation of approximately 45 E m^2 and average maximum and minimum air temperatures of 32 and 20 C, respectively, during the summer. The hourly values for the solar radiation flux were estimated by assuming the flux varied sinusoidally with a maximum (1,650 μE m^{-2} s^{-1}) at local noon and 0 at 0600 and 1800 h, respectively. The average air temperature (Fig. 3) was inferred from the observed maximum and minimum temperatures and what was known about typical diurnal temperature cycles. Needle temperature was assumed to equal air temperature (6). It was assumed that only temperature (Fig. 1) and not light (Table II) directly influenced monoterpene emissions. Photosynthesis was measured as a function of light and temperature, and these data were used to develop the daily curve of photosynthesis (Fig. 3).

Estimated hourly photosynthetic and monoterpene emission rates for slash pine in the vicinity of Tampa, Florida, are shown in Figure 3. The predicted photosynthetic rate increased rapidly in the light, reaching its maximum between 1000 and 1200 h, and then decreased. The negative photosynthetic rates indicated dark respiration during the dark phase. The predicted monoterpene emission rate increased more slowly, reaching its maximum about 1400 h and declined to a minimum shortly before sunrise. The monoterpene emission pattern was similar to the daily temperature cycle. Approximately 55% of the total daily monoterpene emissions occurred during the daylight hours (0600 to 1800) with an additional 25% being emitted between sunset (1800 h) and midnight (2400 h).

The estimated hourly photosynthetic and monoterpene emission rates from Figure 3 were used to determine the proportion of carbon lost as monoterpenes to that fixed in photosynthesis. Integration of the areas under the two curves (Fig. 3) indicated that approximately 0.4% of the carbon fixed daily in photosynthesis is lost through monoterpene volatilization.

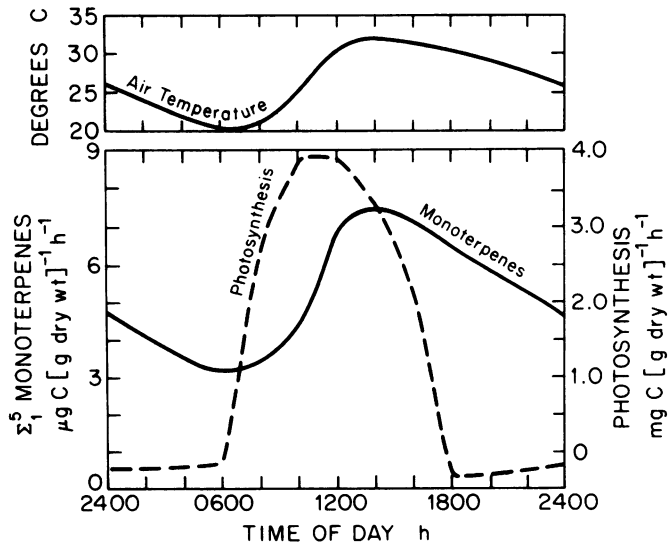

FIG. 3. Estimated diurnal photosynthetic and monoterpene emission rates for slash pine in Tampa, Florida, for an average of summer days. Needle temperature was assumed to equal air temperature and the photoperiod was from 0600 to 1800 h.

DISCUSSION

The qualitative composition of the monoterpenes in the vapor phase surrounding the slash pine foliage was similar to that reported for cortical oleoresins (20). Hanover (8) showed that the monoterpene composition in the cortical oleoresins and the foliage of pine was quite similar. He (8) also reported that foliage and vapor phase monoterpene compositions were qualitatively similar. However, the per cent vapor phase concentration of monoterpenes with low boiling points was frequently higher than the per cent foliar concentration (8). Monoterpenes emitted in the highest quantity from slash pine were those with the lowest boiling point (Table II).

Dement *et al.* (4) proposed that the monoterpene volatilization rate from *Salvia* depended on both the vapor pressure and the monoterpene pool in the tissue. Our monoterpene emission rates increased in a log-linear manner with temperature (Fig. 1): *i.e.* emission rates increased exponentially with temperature. This log-linear relationship ($\log_e$[monoterpene] = a + b [temperature]) for emissions is expected since monoterpene vapor pressures are also log linearly related to temperature (9). The slope of the $\log_e$ (vapor pressure) *versus* temperature curve is essentially equal for the monoterpenes listed in Table I and indicates a relative increase in vapor pressure of approximately 5.4%/C (9). This figure is similar to the 7.3%/C rate of increase for the sum of monoterpene emission rates from slash pine (Fig. 1A) indicating that vapor pressure is a significant factor in controlling monoterpene emissions. Pine needles contain a large pool of monoterpenes available for volatilization into the atmosphere. The concept of a large pool is supported by the observations that monoterpene emission rates from dead needles were initially similar to healthy ones and the emissions from dead needles decreased only 11%/day. The above data indicate that monoterpene emissions from pine needles are controlled by both vapor pressure and pool size. This suggests that only monoterpenes with appreciable vapor pressures at ambient temperatures and a sufficient pool size will occur in significant concentrations in the atmosphere.

The increase in monoterpene emissions with temperature (Fig. 1) is similar to results from other species (1, 10, 13, 23). When data from the above studies were recalculated using the log-linear model, α-pinene emissions increased at a relative rate of 12.2%/C (average of three pines and one fir species), 9.0%/C for loblolly pine and 8.1%/C for *Cryptomeria.* Our data (Fig. 1) indicate that α-pinene emissions would increase at a relative rate of 6.7%/degree.

The monoterpene emissions from slash pines are similar in the dark and at various light intensities. This response is similar to reports for other species (13, 23). The lack of light influence on monoterpene emissions contrasts with the light-dependent emissions of the hemiterpene, isoprene (14, 22).

Monoterpene emissions reported in Figure 1 and estimated from the model (Fig. 3) are similar to emission rates measured on slash pine in the Tampa, Florida area (26). The α-pinene emission rates presented for slash pine and loblolly pine (1) were similar when expressed in the same units and similar to the values reported for *Cryptomeria* (10).

The carbon loss from slash pine, as monoterpenes, was approximately 0.4%/day of the carbon, as CO_2, assimilated. This carbon loss in slash pine is higher than the 0.06%/day carbon loss as monoterpenes from *Salvia* (23). These differences in the carbon loss ratio can, in part, be explained by the lower monoterpene emission rate for *Salvia.* Using the data of Tyson *et al.* (23), the monoterpene emission rate from *Salvia* is 1.09 mg (m^2 ground area)$^{-1}$ h^{-1} at 30 C. When the monoterpene emission rate for slash pine at 30 C is converted to a unit ground area basis using the biomass value from Bayley (2), the emission rate is 4.23 mg C m^{-2} h^{-1}

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