Dependence of the Aboveground CO₂ Exchange Rate on Tree Size in Field-Grown Hinoki Cypress (Chamaecyparis obtusa)

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The CO₂ exchange of the aboveground parts for five different-sized 17-year-old (as of 1991) hinoki cypress (Chamaecyparis obtusa) trees growing in the field was non-destructively measured over one year, using an open CO₂ exchange system. The CO₂ exchange of individual trees decreased with decreasing tree sizes, such as aboveground phytomass, leaf mass and leaf area. However, the CO₂ exchange abruptly decreased near the smallest-suppressed sample tree. The size dependence was well described by a generalized power function. The annual gross photosynthesis of individual trees was proportional to the square root of leaf mass or leaf area. The size dependence of CO₂ exchange on annual phytomass increment was described by a simple power function with an exponent value less than unity, suggesting that CO₂ exchange per unit of phytomass increment was lower in larger-sized trees than in smaller-sized trees. The mean photosynthetic activity of a tree, i.e., gross photosynthesis per unit of leaf area, slightly increased to its highest value with decreasing leaf area and then decreased abruptly near the smallest sample tree. The maximum value of mean photosynthetic activity was estimated to be 2.85 kg CO₂ m⁻² year⁻¹ for a leaf area of 1.56 m² tree⁻¹. The ratio of mean photosynthetic activity to the maximum photosynthetic activity was the highest in an intermediate tree and decreased gradually toward larger-sized trees by ca. 60% and also decreased toward the smallest suppressed tree by ca. 35%.

Key words: Chamaecyparis obtusa — Gross photosynthesis — Individual trees — Photosynthetic activity — Respiration — Tree size dependence

For understanding the environmental feedback of forest stands, and when we predict the consequence of environmental changes, it has become widely accepted that process-based models provide a useful way (Jarvis 1993). Although some models scaling up to the stand level from leaves have been developed (e.g., Monsi and Saeki 1953, Kira et al. 1969, Hozumi and Kirita 1970, Kurachi et al. 1989, Mori and Hagihara 1991, Beyschlag et al. 1994, Holbrook and Lund 1995, Stenberg et al. 1995), the model scaling up from individual trees is restricted. Because the structure and function of forest stands are affected by the physiological characteristics of the composing individual trees, the models of forest dynamics based on the changes in individual trees are important for understanding the ecophysiological functions of forest stands (Shugart et al. 1992). Moreover, forest stands are composed of various sized trees, therefore, it is potentially important to clarify the relationship between the ecophysiological function of individual trees and their size (Hozumi and Shinozaki 1974, Peters 1983, Niklas 1994).

The ecophysiological function - tree size relationships were obtained on the whole-tree level for litterfall (Miyaura and Hozumi 1985, 1986, 1989, 1993), attached dead leaves and branches (Tange et al. 1987), cone production (Seki 1994), water-use efficiency (Donovan and Ehleringer 1992, 1994) and respiration (Ninomiya and Hozumi 1981, 1983a, Ogawa et al. 1985, Yokota et al. 1994). The relationship between photosynthetic production and tree size has not been confirmed yet, though the clear size dependence of photosynthetic production was obtained by scaling up to the whole-tree level from the leaf level (Mori and Hagihara 1991) or scaling down to the whole-tree level from the canopy level (Hagihara and Hozumi 1986).

To estimate the photosynthetic production of a tree, Mori and Hagihara (1991) used the traditional light - photosynthesis curves of leaves. Because their results were confined to a short period of a season, there was no information on the size dependence of photosynthetic production over a year. Is this size relation of photosynthetic production the same configuration throughout the year? On the other hand, Hagihara and Hozumi (1986) used a special function for the vertical distribution of foliage. Does the photosynthetic production really correspond to the vertical distribution of foliage? Is this method reasonable for discussing the characteristics of photosynthetic production on the individual tree level? In order to answer these questions, direct measurement of CO₂ exchange on the individual tree level is necessary. Concerning the direct measurement of whole-tree photosynthesis, difficulties existed due to methodological problems arising from the huge size inherent in trees. Matsumoto (1985) and Hagihara et al. (1987) constructed measuring systems for the aboveground parts of CO₂ exchange, which opened the way for measuring photosynthetic production on the individual tree level.

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In this paper, we non-destructively examine the CO$_2$ exchange, i.e., photosynthesis and respiration, on the aboveground parts of hinoki cypress (Chamaecyparis obtusa) trees over a one-year-period, using an open gas-exchange system (Hagihara et al. 1987, Paembonan et al. 1991, 1992). On the basis of the data, the dependence of CO$_2$ exchange on tree sizes, such as stem volume, aboveground phytomass, leaf mass and leaf area is confirmed. Finally, the photosynthetic production in relation to leaf area is discussed together with the published data.

Materials and Methods

Study site and plant materials

This study was made on a 17-year-old (as of 1991) hinoki cypress (Chamaecyparis obtusa (Sieb. et Zucc.) Endl.) plantation at the experimental field (820 m$^2$), School of Agricultural Sciences, Nagoya University, Japan, from November 1991 to October 1992. The general features of the study site during the experimental period were as follows: annual mean temperature, annual precipitation, tree density, mean tree height and mean stem volume were 15C, 1543 mm year$^{-1}$, 9091 trees ha$^{-1}$, 5.10 m and 9.77 dm$^3$ (as of February 1992), respectively. Monthly measurements were made of tree CO$_2$ exchange measurement. The general features of the study site during the experimental period were as follows: annual mean temperature, annual precipitation, tree density, mean tree height and mean stem volume were 15C, 1543 mm year$^{-1}$, 9091 trees ha$^{-1}$, 5.10 m and 9.77 dm$^3$ (as of February 1992), respectively.

Five different-sized sample trees were selected for the CO$_2$ exchange measurement. The general features of the sample trees in July 1992 are listed in Table 1. Tree No.5, the minimum size of the sample trees, was suppressed by canopy trees. Tree height and stem volume of the sample trees ranged from 4.12 to 6.72 m and 2.38 to 20.1 dm$^3$, respectively. Monthly measurements were made of tree height and stem girth at 50 cm intervals. The calculation of stem volume was based on Smallian’s equation (e.g., Avery and Burkhart 1994).

The aboveground phytomass $w_t$ (kg tree$^{-1}$), the leaf mass $w_l$ (kg tree$^{-1}$) and the leaf area $u$ (m$^2$ tree$^{-1}$) were estimated from the stem volume $v$ (dm$^3$ tree$^{-1}$) and stem diameter at the base of the live crown $D_b$ (cm tree$^{-1}$), using an allometric relationship, i.e., $w_t = 0.626v^{0.704}$, $w_l = 0.0226D_b^{2.40}$ and $u = 0.130D_b^{2.39}$, respectively (Hagihara et al. 1993). We define “leaves” as the “green parts of the branches”. The annual aboveground phytomass increment $\Delta w_t$ (kg tree$^{-1}$ year$^{-1}$) was calculated from the annual change in $w_t$. The leaf area ratio (LAR, ratio of leaf area to aboveground phytomass) was 1.00, 1.07, 0.70, 0.74 and 0.53 m$^2$ kg$^{-1}$, for Tree numbers 1 to 5, respectively. The suppressed smallest sample tree (No.5) obviously had a smaller leaf mass ratio.

CO$_2$ exchange measurement

The CO$_2$ exchange of trees under field conditions was measured in an open gas-exchange system (Hagihara et al. 1987, Paembonan et al. 1991, 1992). The two chamber systems were rotated at intervals of 10-15 days to perform the CO$_2$ exchange of all the sample trees within a month.

The aboveground parts of a sample tree were enclosed in an assimilation chamber, which was cylindrical except for a conical upper part with small ventilators. The chamber was made of polyvinyl chloride films (Takafuji Chem. & Syn. Co., Ltd.) 0.2 mm thick with a transmissivity of more than 90% of photosynthetically active radiation. The skirt of the chamber was tied around the base of the stem. No visible morphological abnormality on the leaves or branches of the sample trees was observed during the experimental period.

Air temperature inside and outside the chamber was monitored with platinum resistance thermometers (SHT-01; Koito Ind., Ltd.). Inside air temperature was adjusted to that of the outside with a temperature controller (MC-A3K; Koito Ind., Ltd.). Ambient air was mixed in 8.0 m$^3$ buffer tanks using fans (VFC404P; Fuji Elect. Co., Ltd.) to minimize short-term fluctuation in CO$_2$ concentration before introduction into the chamber. Air flow rate was monitored with a thermal flow meter (TH-1200; Tokyo Keiso Co., Ltd.). To maintain a difference in CO$_2$ concentration between the inlet and outlet within 10% of ambient, the air flow was set to be 100, 70, 45, 30 and 10 m$^3$ h$^{-1}$ during the daytime and 35, 30, 20, 15 and 10 m$^3$ h$^{-1}$ during the nighttime, according to tree size.

Air inside the chamber was stirred with a mixing fan at a flow rate of 480 m$^3$ h$^{-1}$. The measurement of solar illumination was made using illuminance sensors (IKS-15; Koito Ind., Ltd.), which were installed above the canopy surface and the crown top of the sample tree. The measured solar illumination (kx) was converted into photosynthetic photon flux density (PPFD, $\mu$mol m$^{-2}$ s$^{-1}$) with a conversion factor of 18 $\mu$mol m$^{-2}$ s$^{-1}$ kx$^{-1}$ (McCree 1981). Sample air at the inlet and outlet of the chamber was sucked through vinyl tubes into an infrared gas analyser (IR21; Yokogawa Elect. Works, Ltd.). Data from this equipment were corrected at intervals of three minutes on a microcomputer (PC-9801; Nippon Elect. Co., Ltd.). The CO$_2$ exchange rate was calculated from the difference in CO$_2$ concentration between inlet and outlet air, and the flow rate.

Data analysis

In this study, CO$_2$ exchange refers to photosynthesis and respiration of the aerial parts of trees. All the experimental results were dealt with as hourly-averaged values of 20 measurements. Discrimination between daytime and nighttime was based on positive illumination at the canopy top.