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Seasonal changes in the photosynthetic capacity of cones on a larch (*Larix kaempferi*) canopy

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Abstract

The seasonal changes of photosynthesis of cones of Japanese larch (*Larix kaempferi* Carr.) trees showed that gross photosynthetic rate of young cones (P_g) was 2-3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at surface area unit and P_g/R_{dark} (dark respiration of cones) peaked about 0.7 in the same period, indicating that 70% respiratory CO_2 is refixed. With maturation, P_g and P_g/R_{dark} sharply decreased. Chlorophyll content in cones was 3-20% of that in leaves, which made it a limiting factor for photosynthesis and its content was closely correlated with photosynthetic capacity. Although sunken and linearly arranged stomatal organs were found on the scale of young cones, differently from the significant regulation of leaf photosynthesis, these stomata tended to be non-function since CO_2 is not limiting factor for cone photosynthesis. In conclusion, photosynthesis of larch cones is an additional contribution to their development.

Additional key words: *Larix kaempferi*, photosynthesis, respiration, chlorophyll, stomata, seasonal changes, cone, refix ratio.

Introduction

Japanese larch (*Larix kaempferi*) produces large amount of cones in masting year, which need large quantity of photosynthates supply. It has been reported that the green of wings of seeds and peels of Satsuma orange and other various fruits may contribute photosynthates to the organ developments (Chen et al. 2002, Kenzo et al. 2003, Aschan and Pfanz 2003). Although young larch cones are green, little information is available on the significance of this green for cone development (Wang et al. 2001). If this green could fix CO_2 , questions such as, how large is its capacity at different stages of cone development and how much of the respiratory CO_2 could be refixed, are necessary to understand. A seasonal and annual study on cone gas exchange traits could answer these questions.

Furthermore, the two substrates for photosynthesis are the light captured by chlorophyll and the CO_2 supplied via stomata diffusion from atmosphere or respiratory internal cycling, which made these substrates could limit photosynthetic capacities. In health leaves, light capture by chlorophyll seldom affect photosynthesis (Larcher

2003) and significant stomatal regulation could be manifested by the close correlation between stomatal conductance (g_s) and photosynthetic rate (Farquhar and Sharkey 1982, Wang et al. 2001c, 2003a). However, cone structure and function are different from leaves. For example, although stomata exist on non-photosynthetic organs, its quantity is small comparing with that on leaves and also there are no reports on larch species (Blanke 1993, Peschel et al. 2003, Wang 2005). Chlorophyll in cone scale gradually degrades with development, while chlorophyll in leaves is quite stable during the same period. Moreover, respiratory activity of cones is much higher than that of leaves (Kozłowski and Pallardy 1997, Wang 2005). It is expected that these differences may influence the relations between chlorophyll, g_s and P_g .

For understanding the photosynthetic traits of Japanese larch cones, therefore, seasonal changes in P_g measured in situ, chemical analysis of chlorophyll content, anatomical structure of cone scale and g_s were examined.

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Material and methods

Study site and material: This study was carried out in a plantation of Japanese larch (49-yr-old in 2004) (*Larix kaempferi*) at the Sapporo Experiment Forest (43°44'N, 141°31'E) in Northern Japan. The altitude is ca. 60 m a. s. l., the average tree height was 18~20m, the soil is brown forest soil mixed with volcanic ash. Here, a 15 m step was erected for gas exchange measurement.

Gas exchange measurement: Respiration and photosynthetic rates of cones were measured by a LI-6400 portable photosynthesis system *in situ* with a conifer chamber. After at least five minutes balance of intact cones in chamber, photosynthetic rate was recorded at full sunlight, and dark respiration was measured after covering the chamber by aluminum foil. Five cones were measured in each time. P_g was computed as the difference between photosynthetic rate at saturation light and dark respiration rate. Under full sunlight, the role of photorespiration is important to avoid photoinhibition (Kozaki and Takeba 1996). Further study will be needed to access the role of photorespiration in cone development under field. Data recalculation was according to the surface area of the larch cone. This area was calculated by the formula of a cone-shape as following,

$$A = \pi a(a + \sqrt{a^2 + b^2}) \quad (1),$$

where, A is the surface area of cones, a is half of the cone width and b is height of cones.

Stomatal conductance: g_s of cones was simultaneously measured when photosynthesis measurement was carried out and recalculation was also carried out according to above equation 1).

Chlorophyll measurement: Chlorophyll content of cone scale and needles was measured by DMSO method as described by Barnes *et al.* (1992) and Shinano *et al.* (1996).

Anatomical observation: To check the cone scale structure and stomatal aperture, the transverse slices of the cone scale were prepared. The transverse slices were frozen in a drop of distilled water and sectioned with a sliding microtome. The cone scale structure on the transverse sections (about 30 μm thickness) by a conventional light microscope (Axioskop2 Plus, Zeiss, Germany).

Results

Seasonal changes in photosynthesis: Young cones had a quite high gross photosynthetic rate, even near 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in saturation light. With cone development, photosynthesis became less sensitive to increasing PPFD (photosynthetic photon flux density) (Fig. 1a). P_g peaked 2-3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in young cones, while it decreased sharply with cone maturation. It differed in 2001 and 2004 and showed about 0.1-0.5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in September, and completely no photosynthesis in October (Fig. 1b).

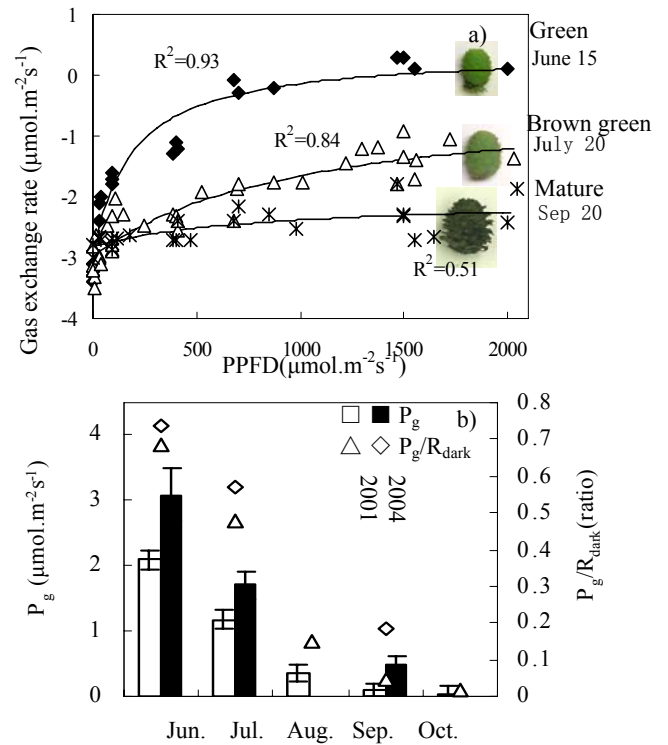


Fig. 1 Light response curves of cone gas exchange rate at different phase of development (a) and the seasonal changes in photosynthetic rate (P_g = difference of gas exchange rate at saturation light and dark environment) and ratio between P_g and dark cone respiration (b) measured in 2001 and 2004.

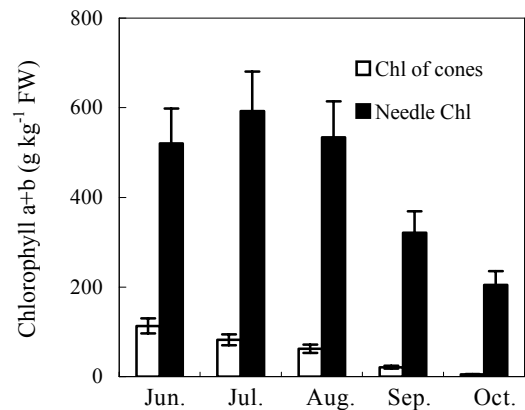


Fig. 2 Changes of chlorophyll content in cones and leaves during development of larch cones.

Ratio of P_g and R_{dark} was peaked about 0.7 in young cones; sharply decrease to zero in October.

Chlorophyll changes: Chlorophyll content in cone scale peaked at 113 $\text{g}\cdot\text{kg}^{-1}\cdot\text{FW}$ in young cone, which was 20% of that in leaves. It gradually decreased in July and August, was only 20 $\text{g}\cdot\text{kg}^{-1}\cdot\text{FW}$ in September (7% of that

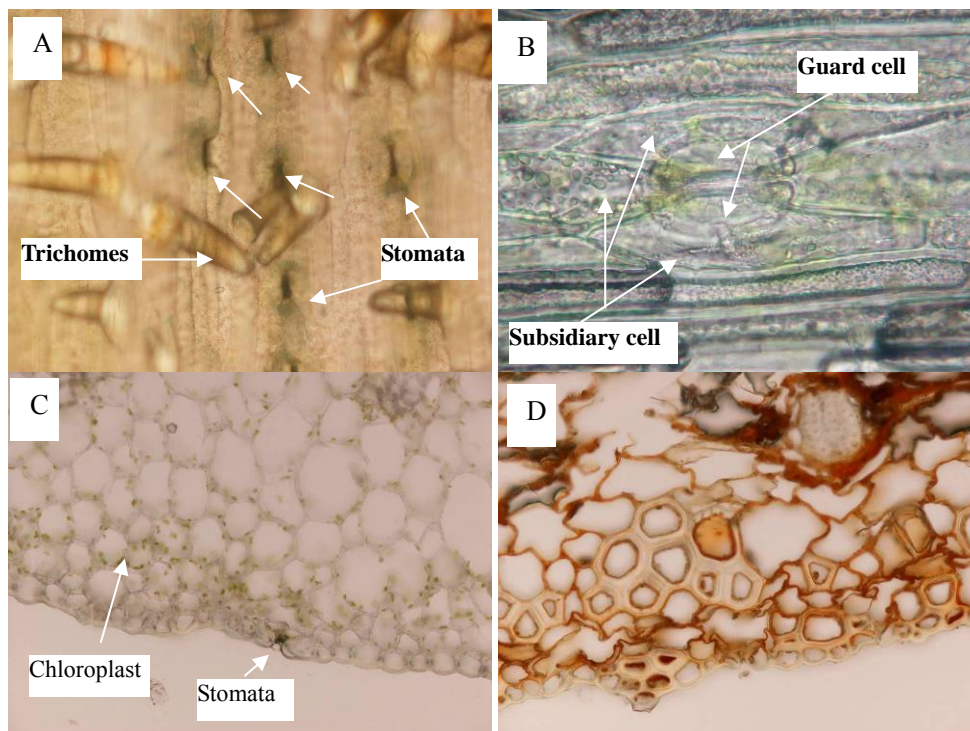


Fig. 3. The structure of stomata on cone scale.

A, C, D $\times 200$ and B $\times 500$. A: sunken stomata linearly distributed on the scale of young cone (Jun. 2004); B: Guard cells and subsidiary cells of the stoma; C: Cross section of stomata, most chloroplasts only distributed in surface layer of cone scale; D: Chloroplasts disappeared and stomata were also difficult to recognize when cone was mature (Sep. 2004).

in leaves), and almost no chlorophyll was observed in October (Fig. 2).

Anatomical structure: “Stomata-like” apparatus was observed on cone scale. Moreover, these sunken stomata were linearly arranged and trichomes were frequently observed (Fig. 3a). Typical stomata on cone scale include two guard cells and four subsidiary cells (Fig. 3 b). In the cross section of stomata, two guard cells were clearly observed and chloroplasts were also observed in other cells (Fig. 3c). However, when the cone became mature, chloroplasts disappeared and stomata were also hardly recognized.

Table 1. The correlation between photosynthesis and g_s , chlorophyll content

Parameters	Equation	R^2 and p-level
P_g vs g_s	$y = 2.532x + 1.001$	$R^2 = 0.10$, $p > 0.01$
P_g vs Chlorophyll	$y = 0.0226x - 0.302$	$R^2 = 0.90$, $p < 0.0001$

#: coefficient of linearly correlation.

Relations between g_s , Chlorophyll content and photosynthesis: Chlorophyll contents were closely

correlated with photosynthetic capacity ($R^2=0.90$, $p<0.0001$), while no correlation was found between g_s and photosynthesis ($R^2=0.10$, $p>0.01$) (Table 1).

Discussion

Contribution of cone photosynthesis and CO_2 refixation during its development: Many reproductive organs have the photosynthetic capacity. Ogawa et al.(1988) found that cones of hinoki (*Chamaecyparis obtusa*) could refix 55-57% of their daily respiratory CO_2 , while fruits of *Cinnamomum camphora* could refix 17% to 51% over the growth period (Ogawa and Takano 1997). Some evergreen pine cones could refix 50-85% (Linder and Troeng 1981, Aschan and Pfanz 2003), olive fruits 40-80% (Proietti et al. 1999) and similar to orchid fruits 10-60% (Zotz et al. 2003). Our studies showed that maximum P_g was $2-3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which took ca.70% of respiratory CO_2 , while in mature cones, no photosynthesis was observed. This value is within the range of previous reports. Therefore, the green of cone scale made the cone a better utilization of respiratory CO_2 , which may devote to the cone development (Aschan and Pfanz 2003).

Chlorophyll content determines photosynthetic capacity: Chlorophyll is a light receptor for photosynthesis. Although it is not a limiting factor in most of the health leaves in nature (Larcher 2003), the chlorophyll in young cone scale is only 20% of that in leaves, which significantly limit the photosynthetic capacity of cones (Fig. 2, Table 1). Trichomes and compact and waxy surface of cone scale may also decline the penetration of light into the internal space. Thus, the photosynthesis of cone scale is limited by the light reaction of the photosynthetic process via chlorophyll deficiency.

Marginal function of stomata in photosynthesis: The stomatal regulation of leaf photosynthesis is owing to the shortage of substrate CO₂ via stomata diffusion when the conductance of stomata is too small (Jones 1992), which can be manifested by the close correlation between gs and photosynthesis (Farquhar and Sharkey 1982, Wang *et al.* 2001c, 2003a). However, no this kind of correlation was found in cone photosynthesis (Table 1). Hence, stomata of cone can not regulate cone photosynthesis. The fact that almost no positive net photosynthetic rate (Fig. 1) manifests that the maximum state for cone photosynthesis is to internally recycle the respiratory CO₂. Thus, there is no need for income atmosphere CO₂ via stomatal diffusion. Therefore, CO₂, as a substrate for cone photosynthesis, is not a limiting factor for cone photosynthesis, which made non-function of stomatal regulation on cone photosynthesis.

In conclusion, the green of cone scale could recycle as most as 70% of total respiratory CO₂, which may contribute photosynthates for the cone development. Chlorophyll, as a light receptor strongly limited cone photosynthesis, while CO₂, as another substrate for photosynthesis, did not limit photosynthesis. This made the stomata non-function in regulating photosynthesis of cones.

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