Carbon dioxide exchange of larch (Larix gmelinii) cones during development

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Received March 17, 2005; accepted January 22, 2006; published online June 30, 2006

Summary  Larch (Larix gmelinii (Rupr.) Rupr.) cone scales are green, but little is known of their photosynthetic role in cone development or about how they differ in gas exchange characteristics from needle leaves. In contrast to leaf photosynthesis (Pleaf), we found that stomatal regulation of cone photosynthetic rate (Pcone) was marginal because the photosynthetic carbon came from internal recycling of respiratory carbon dioxide (CO2). Photosynthetic recycling of respired CO2 was confirmed by the finding that the intercellular CO2 concentration (Ci) in cone scales was much higher than ambient [CO2]; also, there was a positive correlation between Pcone and Ci, whereas Pleaf was almost constant as C i varied. Low chlorophyll (Chl) concentration was a limiting factor for Pcone, but not for Pleaf, as indicated by the correlation between Pcone and chlorophyll concentration. Moreover, chlorophyll utilization efficiency (Pcone/Chl a+b) for cone scales was lower than that for leaves. In both cones and leaves, nitrogen (N) was positively correlated with photosynthetic capacity (P), but the P/N value was much lower for cones than for leaves. For both organs, the ratio of respiration to N was broadly similar. Although mature cones have no photosynthetic capacity, Pcone of young cones was as high as 5.3 µmol m−2 s−1, about 1.26 times the value of Pleaf, and accounted for the refixation of 30–40% of the respiratory CO2 produced by cones, equivalent to the photosynthetic capacity of a bundle of short shoots near each cone. Thus, Pcone may be an important additional source of photosynthate for cones, given the weak assimilating capacity of leaves that are not fully expanded during cone development.

Keywords: chlorophyll, cones, larch, leaves, nitrogen, photosynthesis, stomatal regulation.

Introduction

Photosynthesis in organs such as stems, seed wings and the skin of fruits, which are not specialized for photosynthesis, may contribute significant quantities of carbon to organ development (Chen et al. 2002, Aschan and Pfanz 2003, Kenzo et al. 2003). Cones of larches, which are similar in shape to evergreen cones, may have a significant function in carbon acquisition (Wang et al. 2001a). However, there is no information on how much carbon dioxide (CO2) is photosynthetically assimilated by cones, where the CO2 assimilated by cones comes from (internal recycling or the atmosphere), or how the stomatal apparatus of cones scales functions. It has yet to be determined to what extent larch needles and cone scales differ in gas exchange and biochemical parameters such as chlorophyll (Chl), nitrogen (N), carbohydrate contents and stomatal characteristics. Comparative studies of cones and needle leaves of larch are needed to answer these questions.

We hypothesized that photosynthetic carbon assimilation by green larch cones contributes significantly in fulfilling the requirements of the cone. We also hypothesized that the photosynthetic features of larch cones differ from those of larch needles because of the difference in their functional specialization. To test these hypotheses, we examined gas exchange and the stomata of larch cones, and compared changes in the concentrations of chlorophyll, N, sugar and starch in larch cones and leaves during the period of cone maturation.

Materials and methods

Study site and plant materials

The stand of larch (Larix gmelinii (Rupr.) Rupr.) trees selected for study is located on a dark brown forest soil in Laoshan station in northeast China (45°20′ N, 126°34′ E). Mean height above sea level is about 160 m. We selected larch trees that were about 35–40 years old and had abundant seed cones. Measurements were made from May 25, 2004, about 15 days after cone formation, by which time scales were completely closed and pollination had already been completed, to August 25, 2004, by which time the cone scales had lost their green coloration. During this period, total rainfall was 300 mm (about half of the total annual precipitation), and mean daily temperature ranged from 12–30 °C, with a mean of 23 °C.
Mean daily air humidity was 60%, and at least 80% of the days were sunny (daily mean photosynthetic active radiation (PAR) > 500 µmol m\(^{-2}\) s\(^{-1}\)).

Larch cones include ovuliferous scales and bract scales. Outside each ovuliferous scale is a much smaller bract scale (at most about one third of the size of the ovuliferous scale) (Chou 1986). Because of the overlapping of ovuliferous and bract scales, only a small portion of bract scales, or none, receive incident light. As a result, the photosynthetic capacity of the cones measured in this study was mainly attributable to ovuliferous scales. Measurements of chlorophyll, N, sugar and starch and stomatal density and conductance, were all made on ovuliferous scales. We use the term cone scales below with reference to both bract and ovuliferous scales.

**Gas exchange measurement and recalculation**

The respiration and photosynthetic rates of cones \( (R_{\text{cone}}, P_{\text{cone}}) \) were measured in situ with an LI-6400 portable photosynthesis system (Li-Cor, Lincoln, NE). An intact cone was placed in the chamber for 5 min; respiration was recorded first in darkness, and then in full sunlight (> 1000 µmol m\(^{-2}\) s\(^{-1}\)). Consistent with previous studies (Linder and Troeng 1981, Koppel et al. 1987, Ogawa and Takano 1997), we designated the difference between dark respiration and respiration at light saturation as \( P_{\text{cone}} \). For young cones, the subtending needles at the base of the cones were gently removed 7–10 days before measurement to prevent any influences on estimates of cone photosynthesis. The leaf scars were covered with vaseline to prevent CO\(_2\) leakage. We assumed that cone gas exchange was unaffected by photorespiration; an assumption that may have resulted in an underestimation of the photosynthetic capacity of the cone (Aschan and Pfanz 2003).

The interval for measurement was 7–10 days. At least five replicates were measured on each occasion. The sun-exposed needles of short larch shoots were also measured for comparison. After the gas exchange measurements, cone fresh mass (FM) and the projected area of the leaves was measured with a Li-Cor LI-3000 leaf area system. Chlorophyll was then extracted by the dimethylsulfoxide method described by Barnes et al. (1992) and Shinano et al. (1996) and quantified spectrophotometrically.

Soluble sugar and starch in cone scales and leaves were assayed as described by Li (2000). Oven-dried ground samples (100–200 mg) were placed in 10 ml of 80% ethanol in a water bath at 80 °C for 40 min. The extract was centrifuged and the supernatants were used for soluble sugar analysis. Active carbon (10 mg) was used to decolor the supernatant, and its volume was adjusted to 25 ml or 50 ml. One ml of this solution was mixed with 5 ml of anthrone solution and incubated at 90 °C for 15 min, and then cooled rapidly by immersing in cold water. A colorimetric assay was performed at 625 nm with a Unico-2000 spectrophotometer (Unico, Shanghai, China). Starch concentration was determined by the sulfuric acid oxidation method, together with the anthrone colorimetric method. A calibration curve was established with glucose as the standard.

The nitrogen concentrations of cone scales and leaves were determined with an NC analyzer (NC-900, Shimadzu, Kyoto, Japan). The N content was calibrated and checked against a standard (acetanilide: N = 10.36%, C = 71.09%; Wako, Osaka, Japan). The dry mass (DM) of the cone scales and leaves was determined after drying at 60 °C for 72 h.

Changes in stomatal density on the scale epidermis and leaves after each measurement were assessed by the SUMP method (Suzuki Universal Micro Printing method) (Koike et al. 1998).

**Calculation of \( P/N, R/N \) and \( P/\text{Chl a+b} \) in cones and leaves**

To calculate normalized rates of photosynthesis (\( P \)) and respiration (\( R \)) relative to tissue N content \( (P/N \) and \( R/N \), respectively), the observed values were converted from \( \text{µmol} \text{ m}^{-2} \text{ s}^{-1} \) to \( \text{µmol} \text{ kg}^{-1} \text{ s}^{-1} \), based on the specific cone surface area \( (0.32 \text{ m}^2 \text{ kg}^{-1} \text{ DM}) \) and the specific leaf surface area \( (18.2 \text{ m}^2 \text{ kg}^{-1} \text{ DM}) \), before dividing by nitrogen concentration \( (\text{mg} \text{ g}^{-1} \text{ DM}) \). Two methods were used to calculate \( P/\text{Chl a+b} \). In Method 1, we first converted chlorophyll concentration from \( \mu \text{g} \text{ cm}^{-2} \) to \( \mu \text{g} \text{ g}^{-1} \text{ DM} \) based on the water content of the cone and leaf (0.7 and 0.5 g g\(^{-1} \text{ DM} \), respectively; Wang 2005); then the ratio between photosynthetic rate \( (\text{µmol} \text{ kg}^{-1} \text{ s}^{-1}) \) and nitrogen per unit dry mass was computed. In Method 2, we converted chlorophyll concentration from \( \mu \text{g} \text{ cm}^{-2} \) (cone scale projection area) to \( \mu \text{g} \text{ cm}^{-2} \) (cone surface area, based on the measured ratio between the sum of the projection area of each scale of one cone and the intact cone surface area, 2.91 (0.28 SD), and then calculated the ratio between photosynthetic rate \( (\text{µmol} \text{ m}^{-2} \text{ s}^{-1}) \) and chlorophyll per unit cone surface area.

**Data analysis**

Differences between cones and leaves in gas exchange, chlorophyll concentration, N concentration and carbohydrate con-
Results

Temporal changes in P and R of cones and leaves

Respiration and photosynthetic rates were maximal in young cones. During cone development, \( R_{\text{cone}} \) decreased progressively from a maximum value of about 21.9 µmol m\(^{-2}\) s\(^{-1}\) to around 0.3 µmol m\(^{-2}\) s\(^{-1}\) in late August. Correspondingly, \( P_{\text{cone}} \) decreased gradually from 7.8 µmol m\(^{-2}\) s\(^{-1}\) to zero. Normalized per unit fresh mass and per unit cone surface area, changes in \( R_{\text{cone}} \) and \( P_{\text{cone}} \) during maturation showed broadly similar trends (Figure 1).

As shown in Table 1, \( P_{\text{cone}} \) was positively correlated with the total chlorophyll concentration in cone scales (\( r^2 > 0.82, P < 0.001 \)), whereas there was no correlation between foliar chlorophyll concentration and \( P_{\text{leaf}} \) (\( r^2 = 0.02, P > 0.1 \)). A good correlation was observed between \( P_{\text{cone}} \) and soluble sugar concentration in cone scales (\( r^2 = 0.85, P < 0.001 \)), but there was no significant correlation between starch concentration and \( P_{\text{cone}} \) (\( r^2 = 0.07, P > 0.1 \)). However, both soluble sugar and starch concentrations in leaves were positively correlated with \( P_{\text{leaf}} \) (\( r^2 > 0.22, P < 0.01 \)). Nitrogen concentration in cone scales and in leaves was positively correlated with the corresponding photosynthetic rate. A positive correlation was observed between stomatal density and \( P_{\text{cone}} \) (\( r^2 = 0.91, P < 0.001 \)), but no correlation was found between \( g_s \) and \( P_{\text{cone}} \). The \( C_i - P_{\text{cone}} \) relationship was statistically significant, whereas no such relationship was found in leaves. The water status of cone scales significantly influenced \( P_{\text{cone}} \) (\( r^2 = 0.51, P < 0.01 \)), whereas leaf water content did not affect leaf photosynthesis (\( r^2 = 0.07, P > 0.1 \)) (Table 1).

Gas exchange and biochemistry of cone scales and leaves

Chlorophyll concentration was higher in needles than in cone scales, both per unit surface area and per unit fresh mass. The Chl a/b ratio was 18% lower in cones than in leaves (\( P < 0.05 \)). Soluble sugar concentration in cone scales was only 70% of that in leaves; there was a similar trend in starch concentration. Nitrogen concentration was significantly lower in cone scales than in needles (Table 2). Dark respiration rates were higher in cones than in leaves, but only young cones had higher photosynthetic rates than leaves. Photosynthetic rate per unit chlorophyll was, on average, 1.60 times higher in leaves than in cones. Similarly, \( P_{\text{leaf}}/N \) was more than 30 times higher than \( P_{\text{cone}}/N \). The ratios \( R_{\text{cone}}/N \) and \( R_{\text{leaf}}/N \) were broadly similar for cones and leaves (Table 2). Stomatal density was about three times higher on leaves than on scales of young cones, and much higher than on scales of mature cones. The value of \( C_i \) (400–1000 µmol mol\(^{-1}\)) was about three times higher in cone scales than in leaves (about 220 µmol mol\(^{-1}\)), and was also higher than atmospheric [CO\(_2\)] (about 360 µmol mol\(^{-1}\)) (Table 2).

Discussion

It is generally assumed that, in green tissues that are not specialized for photosynthesis, respiratory CO\(_2\) is internally recycled; however, direct evidence for this assumption has rarely been provided (Ogawa et al. 1988, Ogawa and Takano 1997, Aschan and Pfanz 2003). If \( C_i \) is much lower than ambient [CO\(_2\)] (360 µmol mol\(^{-1}\)), as is the case for most leaves, atmospheric CO\(_2\) will diffuse into intercellular spaces to replace CO\(_2\) consumed in photosynthesis. The \( C_i \) of larch needles was
220 µmol mol\(^{-1}\), indicating that CO\(_2\) from the atmosphere is an important source of carbon for photosynthesis. However, as shown in Table 2, \(C_i\) for cones (400–1000 µmol mol\(^{-1}\); mean 665 µmol mol\(^{-1}\)) was much higher than ambient [CO\(_2\)], and so atmospheric CO\(_2\) cannot diffuse from the atmosphere into intercellular spaces of cones. The strong correlation between \(R_{cone}\) and \(C_i\) (Wang 2005) indicates that this CO\(_2\) results from the high respiratory activity of the cone, and the positive correlation between \(P_{cone}\) and \(C_i\) indicates that photosynthesis mainly fixes CO\(_2\) produced during respiration, not atmospheric CO\(_2\).

Figure 1 and Table 2 show that \(P_{cone}\) peaks during the early stage of cone development, and that the maximum \(P_{cone}\) is on average twice that of \(P_{leaf}\). As a result of their high photosynthetic capacity, the cones were capable of refixing 30–40% of respiratory CO\(_2\). The refixation ratio is within the range reported for a wide variety of evergreen and deciduous species, including evergreen pine cones (50–85%) (Linder and Troeng 1981, Aschan and Pfanz 2003), olive fruits (40–80%) (Proietti et al. 1999) and orchid fruits (10–60%) (Zotz et al. 2003). In spring from May to June, corresponding to the young cone stage shown in Figure 1, larch needles begin, but do not com-

### Table 1. Relationships between photosynthetic rate per unit surface area (\(P\)) and physiological parameters in cones and leaves during cone maturation (\(y = \beta + \alpha x\) and \(x = \gamma\)).

<table>
<thead>
<tr>
<th>Parameters ((x))</th>
<th>Cones</th>
<th>Leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chl a+b ((\mu g cm^{-2}))</td>
<td>(y = 0.076e^{0.316x})</td>
<td>(y = 1.5e^{-5x} + 1.670)</td>
</tr>
<tr>
<td>Soluble sugars concentration ((\mu g g_{DM}^{-1}))</td>
<td>(y = 0.283x - 2.610)</td>
<td>(y = 0.092x - 0.0271)</td>
</tr>
<tr>
<td>Starch concentration ((\mu g g_{DM}^{-1}))</td>
<td>(y = 0.177x - 0.094)</td>
<td>(y = 0.0497x + 0.871)</td>
</tr>
<tr>
<td>Nitrogen concentration ((\mu g g_{DM}^{-1}))</td>
<td>(y = 0.070x - 0.1)</td>
<td>(y = 0.24, P &lt; 0.001)</td>
</tr>
<tr>
<td>Stomatal density ((\text{no. mm}^{-2}))</td>
<td>(y = 0.0148x + 0.028)</td>
<td>(y = 0.975x - 6.601)</td>
</tr>
<tr>
<td>Stomatal conductance ((\text{mol m}^{-2} s^{-1}))</td>
<td>(y = 0.19, P &lt; 0.001)</td>
<td>(r^2 = 0.11, P &gt; 0.1)</td>
</tr>
<tr>
<td>Intercellular [CO(_2)] ((\mu mol mol^{-1}))</td>
<td>(y = 0.010x - 4.218)</td>
<td>(y = 0.0003x + 2.449)</td>
</tr>
<tr>
<td>Water content ((g g_{FM}^{-1}))</td>
<td>(y = 0.456x - 0.054)</td>
<td>(y = -10.911x + 8.903)</td>
</tr>
</tbody>
</table>

1 Values are in units of mg dm\(^{-2}\).

### Table 2. Parameters determining gas exchange and biochemical characteristics in cones and leaves. Within a row, values followed by different letters are significantly different \((P < 0.05)\). Abbreviation: \(R_{dark}\) = dark respiration; \(P\) = photosynthetic capacity; and \(N\) = nitrogen.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Cone</th>
<th>Leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chlorophyll a+b ((\mu g cm^{-2}))</td>
<td>12.9(0.8) a(^1)</td>
<td>23.0(4.0) b</td>
</tr>
<tr>
<td>Chlorophyll ((\mu g g_{FM}^{-1}))</td>
<td>137.5(13.7) a</td>
<td>1977.6(295.5) b</td>
</tr>
<tr>
<td>Chl a/b</td>
<td>3.0(0.5) a</td>
<td>3.8(0.6) b</td>
</tr>
<tr>
<td>Stomatal density ((\text{no. mm}^{-2}))</td>
<td>21.9(6.0) a</td>
<td>66.5(8.2) b</td>
</tr>
<tr>
<td>Intercellular [CO(_2)] ((\mu mol mol^{-1}))</td>
<td>665(221.1) b</td>
<td>220.0(22.1) a</td>
</tr>
<tr>
<td>Soluble sugars ((\mu g g_{DM}^{-1}))</td>
<td>18.7(7.7) a</td>
<td>21.3(4.8) b</td>
</tr>
<tr>
<td>Starch concentration ((\mu g g_{DM}^{-1}))</td>
<td>15.8(5.6) a</td>
<td>31.4(5.5) b</td>
</tr>
<tr>
<td>Nitrogen concentration ((\mu g g_{DM}^{-1}))</td>
<td>12.93(3.69) c</td>
<td>19.5(4.6) b</td>
</tr>
<tr>
<td>(R_{dark}) ((\mu mol m^{-2} s^{-1})) Young:</td>
<td>16.9(3.69) c</td>
<td>0.70(0.5) a</td>
</tr>
<tr>
<td>Mature:</td>
<td>1.1(0.4) b</td>
<td></td>
</tr>
<tr>
<td>(P) ((\mu mol m^{-2} s^{-1})) Young:</td>
<td>5.22(1.8) c</td>
<td>4.2(1.7) b</td>
</tr>
<tr>
<td>Mature:</td>
<td>0.4(0.1) a</td>
<td></td>
</tr>
<tr>
<td>(P/N) ((\mu g g^{-1} N s^{-1})) Young:</td>
<td>0.12</td>
<td>3.92</td>
</tr>
<tr>
<td>Mature:</td>
<td>0.38</td>
<td>0.65</td>
</tr>
<tr>
<td>(R_{dark}/N) ((\mu mol g^{-1} N s^{-1})) Young:</td>
<td>9.2–13.9</td>
<td>18.3–19.3</td>
</tr>
</tbody>
</table>

1 Value is based on the projected area of measured cone scales; other units of cone photosynthesis and respiration were based on cone surface area and leaf surface area.
plete their expansion. Leaves during this period have a relatively low photosynthetic capacity, but have a high requirement for photosynthate for their own growth. During the same period, cone development generates a high demand for carbohydrate. There may therefore be a shortage of leaf-synthesized carbohydrates in larch trees during development of young cones. Based on the average surface area of a cone (3.2 cm²) and maximum P_{cone} (7.8 µmol m⁻² s⁻¹), refixation of CO₂ by a single cone is equal to the photosynthetic capacity of 21.5 needles (the mean area of one sunny short needle is about 14 mm²) or one bundle of short shoot leaves (a bundle of short shoot leaves generally has 19–29 needles from shade to sunny canopy; see Wang 2005). Refixation of CO₂ by cone scales appears, therefore, to be an important source of carbon acquisition that contributes significantly to cone formation (Aschan and Pfanz 2003).

Developing reproductive organs generally act as carbon sinks that preferentially mobilize current photosynthates in leaves (Kozlowski 1992, Ogawa 2004). Our comparisons between leaves and cones revealed differences both in the relationships between gas exchange and biochemical traits and in the function of stomata in regulating photosynthetic capacity (Table 1). For example, chlorophyll concentration was a limiting factor for photosynthesis in cones, but not leaves. Chlorophyll utilization efficiency in photosynthesis was lower in cones than in leaves. The scales of cones are much thicker than leaves, and there is also more wax and lignin at the surface. This may make it difficult for light to penetrate to the cone scale mesophyll, so that chloroplasts of the mesophyll (Wang 2005) receive insufficient light to fully exploit the high [CO₂] in the intercellular space. This appeared to reduce the efficiency of chlorophyll in cone scales. As end-products of photosynthesis, soluble sugar and starch concentrations in cones were both much lower than in leaves, indicating a larger sink capacity for cones. The absence of end-product inhibition of photosynthesis in both organs is indicated by the positive correlation between soluble sugar and photosynthesis. However, the starch concentration in cones was not correlated with photosynthesis, although a significant correlation existed in leaves. Starch in cones is derived from synthesis by cone scales and transport from leaves, whereas starch in leaves is derived solely from synthesis, which may account for this difference.

Many studies have shown a positive correlation between leaf N concentration and leaf net photosynthetic rate (Field and Mooney 1986, Evans 1989), which is attributed to the involvement of N in the photosynthetic machinery (Lambers et al. 1998, Shinano et al. 2001). Although the R/N and P/N relationships for cones are consistent with the findings for leaves, the r² value for P/N was higher for cones than for leaves (0.88 versus 0.38; Table 1). Moreover, P/N was much lower in cone scales than in leaves, though R/N in cone scales was more nearly similar (Table 2). The function of cones is to produce seed, which requires a large amount of protein and presumably a large amount of N. Consequently, it is likely that less N was available for photosynthesis in cones than in leaves, leading to the lower P/N ratio in cone scales compared with leaves. Therefore, because of the difficulty in determining N allocation to the cone photosynthetic apparatus, unlike P_{leaf}/N, P_{cone}/N may underestimate photosynthetic N-use efficiency.

Stomatal regulation of leaf photosynthesis has been the subject of many studies (e.g., Farquhar and Sharkey 1982, Wang et al. 2001b, 2003), and a positive correlation between g, and photosynthesis has generally been found across species (Zu et al. 2005). We also found that g was correlated with photosynthesis of larch needles (Table 1). There are only a few reports on the effects of stomatal structure and function on non-photosynthetic organs (Blanke 1993, Blanke et al. 1999, Peschel et al. 2003) or on larch cone scales. We found a low stomatal number on cone scales compared with leaves. Stomatal density of young cone scales (20 mm⁻²) was about one third that of needle leaves (Table 2). However, cone stomatal density was much higher than that of mature berries of currant (Ribes rubrum L. and R. nigrum L.) or sweet cherry fruit (Prunus avium (L.) L.), which have less than one stoma mm⁻² (Blanke 1993, Peschel et al. 2003). Aschan and Pfanz (2003) found that stomata on young fruit are as sensitive as leaves, but Blanke (1993) and Peschel et al. (2003) found that the regulatory function of stomata on berry fruits disappeared with maturation. Our results with larch cones are consistent with the results of these studies; the function of stomatal regulation in cone gas exchanges was marginal, in contrast to stomatal regulation in leaves. For example, there was an insignificant correlation between g, of cones and P_{cone} (Table 1). Furthermore, the high C₅ (> 400 µmol m⁻² s⁻¹) made it unnecessary for stomata to adjust their aperture to control CO₂ diffusion into intercellular spaces (Table 2).

In conclusion, green cone scales serve an important role in cone formation. Young cones of L. gmelinii refixed about 35% of their respiratory CO₂ production, which is equivalent to the photosynthetic production of a bundle of short shoots. The functional difference between cones and leaves has resulted in modifications in the relationships between cone photosynthesis and cone biochemical traits compared with leaves. For example, chlorophyll concentration limits cone photosynthesis, but not needle photosynthesis; soluble sugar concentration in both cones and leaves was positively correlated with photosynthesis, whereas starch concentration was correlated with photosynthesis only in leaves; P/N was much lower in cones than in leaves and stomata did not regulate cone photosynthesis.

Acknowledgments

This study was supported financially by the National Natural Science Foundation of China (No. 30300271), the State Key Basic Research and Development Plan of China (2004CCA02700) and the Ministry of the Environment, Japan (S1, B053).

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