BRIEF COMMUNICATION

# Newly-formed photosynthates and the respiration rate of girdled stems of Korean pine (*Pinus koraiensis* Sieb. *et* Zucc.)

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## Abstract

A stem-girdling experiment was carried out on an evergreen conifer, the Korean pine (*Pinus koraiensis* Sieb. *et* Zucc.), in mid summer in Northeast China. A 50 % higher respiration rate at the upper part of the stem was observed 3 d after stem girdling, and a stable higher rate (1.2–2.8 times) one week later. However, no higher soluble sugar or starch contents were found in the upper bark of the girdled stems in measurements over three weeks. These findings indicate that most of the newly-formed photosynthates were consumed by the high respiratory activity; this is also implied by the strong correlation between the photosynthetic photon flux over the canopy (PPF) and respiration at the upper parts of girdled stems. Moreover, the maximum PPF and cumulative PPF one day before measurement (PPFmax-Y and CPPF-Y, respectively) were closely correlated with the respiratory difference between the upper and the lower parts, but no such correlation was found with the instantaneous PPF (PPF-I) and cumulative PPF on the current day from sunrise to measured time point (CPPF-C). This shows that photosynthates newly formed by canopy needles need at least one day for transportation in order to increase the stem respiration at tree breast height.

*Additional key words*: long-distance transport; photosynthetic photon flux; seasonal course; soluble sugar; starch.

Photosynthates are utilized mainly for synthesis of new organs, maintenance of the plant body, defence, and supporting symbiotic micro-organisms (Chapin *et al.* 1990). An important effect of tree-girdling is to stop the flow of newly-formed photosynthates to the lower part of the girdled stem; girdling can therefore be used to distinguish between the roles of newly-formed and stored photosynthates in respiration from stems and roots (Högberg *et al.* 2001). The issues are: how much of the newly-formed photosynthates from canopy photosynthesis are consumed in the enhanced respiratory activity resulting from girdling; and what is the functional difference between stored and newly-formed photosynthates in respiratory activity? From the girdling technique together with gas exchange measurements and photosynthate analysis, these questions may be answered.

Newly-formed photosynthates deriving from the canopy are determined by the total photosynthetic photon flux (PPF) impinging on a plant. If newly-formed photosynthates are more important for respiration (Högberg *et al.* 2001), the photosynthetic photon flux (PPF) will positively correlate with the respiratory differences between the upper and the lower parts of girdled stems. Moreover, long-distance transport of photosynthates from the canopy to low stems will take time, which will be observable in the processes of symplasmic and apoplasmic

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*Abbreviations*: CPPF-C, cumulative PPF on current day before measurement (from sunrise to the measurement); CPPF-Y: cumulative PPF of 'yesterday' (one day before measurement); PPF-I, instantaneous photosynthetic photon flux when stem respiration was measured; $PPF_{max}$-Y, maximum PPF values of 'yesterday' (one day before measurement); $R_{lower}$, respiration rate at the lower part of the girdled stem; $R_{upper}$, respiration rate at the upper part of the girdled stem.
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phloem loading as well as phloem unloading (Lambers *et al.* 1998).

Our aim was to clarify the importance of newly-formed photosynthates in respiration of girdled stems of the Korean pine (*Pinus koraiensis* Sieb. *et* Zucc.). We hypothesize that newly-formed photosynthates are responsible for the high rate of respiration at the upper parts of girdled stems ($R_{upper}$), so that the above-canopy PPF before the measurement should be closely correlated with the respiratory difference between $R_{upper}$ and that of the lower part ($R_{lower}$) of girdled stems.

The study site was located at Laoshan Station in Northeast China (45°20'N, 127°34'E). The mean height above sea level is *ca*. 340 m. The mean annual precipitation from 2001 to 2004 was 650 mm, of which about 70 % fell in the summer months of June to August. The soil is dark brown forest soil, which is fertile and mesic. The mean annual air temperature is about 2.8 $^{o}$C (NEFU 1984).

An evergreen conifer plantation of *P. koraiensis* planted in 1969 was studied. The diameter at breast height (DBH) was 16.4 cm (2.7 SD) and the average height was *ca*. 13 m. In mid summer (July 1, 2004), girdling belts (*ca*. 2 cm in width) of the bark were made on seven trees. $R_{lower}$ and $R_{upper}$ as well as respiration rates in four un-girdled trees were measured using a *LI-6400* system (Lincoln, NE, USA) with a null balance chamber at an interval of one day or two days. After each measurement, samples (bark+phloem) were collected from each tree for laboratory analysis of soluble sugar and starch. The experiment ran from July 1 to July 31. Details of the stem respiration measurements and resulting data are given in Wang *et al.* (2003).

Soluble sugar and starch in barks were assayed by sulphuric acid oxidation and the anthrone colorimetrical method described by Li (2000). Colorimetric assay was performed at 625 nm by a *Unico-2000* spectrophotometer (*Unico*, Shanghai, China) with glucose as a standard chemical.

Rainfall during the measurement period was recorded twice per hour by a model *900ET* weather station (*Spectrum*, Illinois, USA). The PPF was measured 21 m up a $CO_2$ flux tower by a *PAR-02* sensor (*Prede*, Tokyo, Japan). Data were recorded twice per hour from July 1 to July 31, 2004. The cumulative PPF (CPPF) in one day is calculated as:

$$\mathrm{CPPF} = \sum_{i=1}^{48} \frac{(I_i + I_{i+1})}{2} \times 30 \times 60 ,$$

where $I_i$ is the PPF value at the *i*–th measurement (in 24 h there are 48 measurements), 30 represents min between measurements, and 60 means s min$^{-1}$. CPPF in current day before measurement (CPPF-C) was calculated from sunrise time to the measurement, while CPPF one day before measurement (CPPF-Y) was calculated from 00:00 to 24:00. The significance test for the regression equation is performed using *SPSS 11.5* (*SPSS*, Chicago, USA). In the case of power or exponential relations, the original data were first transformed by a logarithmic transformation.

During the measurement period, two-thirds of the days were sunny, and one-third was cloudy or rainy; the total precipitation in the period was about 200 mm (Fig. 1*A*). The observation that $R_{upper}$ was 50 % higher than $R_{lower}$ was first found three days after stem girdling. However, $R_{upper}$ decreased again on July 5 and July 6 because of the cloudy and rainy weather, and a continually and stable higher $R_{upper}$ than $R_{lower}$ was observed after July 8 (seven days after girdling). This difference increased with time, so that $R_{upper}$ was 2.8 times higher than $R_{lower}$ in later July (Fig. 1*B*).

The starch and soluble sugar contents in the bark did not differ obviously between the upper and lower parts of girdled stems during the three weeks after girdling (Fig. 1*C,D*). The starch content in the upper parts of girdled stems was 15–40 % (30 % average) higher than in the lower parts for three weeks after girdling (July 23) (Fig. 1*C*). Similarly, the soluble sugar content in the upper parts of girdled stems was 8–63 % (25 % average) higher than in the lower parts after July 21 (Fig. 1*D*).

Correlations between $R_{upper}$, $R_{lower}$, $R_{upper}$-$R_{lower}$, and instantaneous PPF and CPPF on the current day (PPF-I and CPPF-C, respectively) were not significant. However, these respiration statistics were closely correlated with the maximum PPF value and cumulative PPF one day before measurement ($PPF_{max}$-Y and CPPF-Y, respectively) (Table 1). Moreover, the $r^2$ and *p*-level for correlations between $R_{upper}$, $R_{lower}$, $R_{upper}$-$R_{lower}$, and the sum of CPPF and CPPF-Y were lower than for CPPF-Y alone (Table 1).

Photosynthates accumulate at the upper part of a girdled stem (Noel 1970, Taylor 1999). However, the time needed for significant accumulation is not clear (Wang 2005). Our experiment reveals that for both starch and soluble sugars this period is at least three weeks for Korean pine trees and the enhancement is still not so evident even one month after girdling (Fig. 1).

The stem could enhance its respiratory activity after girdling in order to recover from its wound (Negisi 1977); this has been observed at both the upper and lower parts of girdled stems (Wang 2005). However, the upper parts of girdled stems displayed much higher respiration than the lower parts, by a factor of 1.2–2.8 at one week after girdling (Fig. 1*B*). Photosynthates in the stem showed no apparent accumulation of both soluble sugar and starch in the upper parts, even by three weeks after girdling (Figs. 1*C,D*). It follows that most of the newly formed photosynthates should be consumed by the high $R_{upper}$. The importance of newly-formed photosynthates has also been reported by Högberg *et al.* (2001). They found that root and mycorrhizal respiration decreased sharply within 5 d because of the lack of newly-formed photosynthates.

The over-canopy PPF determines the production of

Table 1. Correlations between stem respiration rates and photosynthetic photon flux (PPF), cumulative PPF(CPPF). PPF-I, photosynthetic photon flux when stem respiration was measured; $PPF_{max}$-Y, maximum PPF values 'yesterday' (one day before measurement); CPPF-C: cumulative PPF on current day before measurement; CPPF-Y: CPPF 'yesterday' (one day before measurement); CPPF-C+ CPPF-Y; sum of CPPF-C and CPPF-Y. $^{*}p<0.05$, $^{***}p<0.001$.

| Dependent factor X | Independent factor Y, stem respiration [μmol $m^{-2}$ $s^{-1}$] $R_{upper}$ | $R_{lower}$ | $R_{upper}$-$R_{lower}$ |
|---|---|---|---|
| PPF-I [μmol $m^{-2}$ $s^{-1}$] | Y = 1 E – 04 x + 2.225, $r^2 = 0.005$, $p>0.1$ | Y = –1 E – 05 x + 1.555, $r^2$ = 9 E – 05, $p>0.1$ | Y = 0.0001 x + 0.677 $r^2 = 0.004$, $p>0.1$ |
| $PPF_{max}$-Y [μmol $m^{-2}$ $s^{-1}$] | Y = 0.144 $x^{0.388}$, $r^2$=0.45, $p$=0.0009$^{***}$ | Y = –0.0004 x + 2.122 $r^2 = 0.20$, $p$=0.04$^{*}$ | Y = 0.972 ln(x) – 6.13 $r^2 = 0.59$, $p$=0.00005$^{***}$ |
| CPPF-C [mol $m^{-2}$] | Y = 0.006 x + 2.227, $r^2 = 0.01$, $p>0.1$ | Y = –0.004 x + 1.587 $r^2 = 0.007$, $p>0.1$ | Y = 0.0096 x + 0.644 $r^2 = 0.03$, $p>0.1$ |
| CPPF-Y [mol $m^{-2}$] | Y = 1.024$x^{0.239}$, $r^2 = 0.25$, $p$=0.02$^{*}$ | Y = –0.0114 x + 2.044 $r^2 = 0.27$, $p$=0.02$^{*}$ | Y = 0.712 ln(x) – 1.587 $r^2 = 0.46$, $p$=0.0008$^{***}$ |
| CPPF-C+CPPF-Y [mol $m^{-2}$] | Y = 0.990 $x^{0.227}$, $r^2 = 0.16$, $p$=0.07 | Y = –0.0102 x + 2.017 $r^2 = 0.22$, $p$=0.03$^{*}$ | Y = 0.667 ln(x) – 1.655 $r^2 = 0.29$, $p$=0.01$^{*}$ |

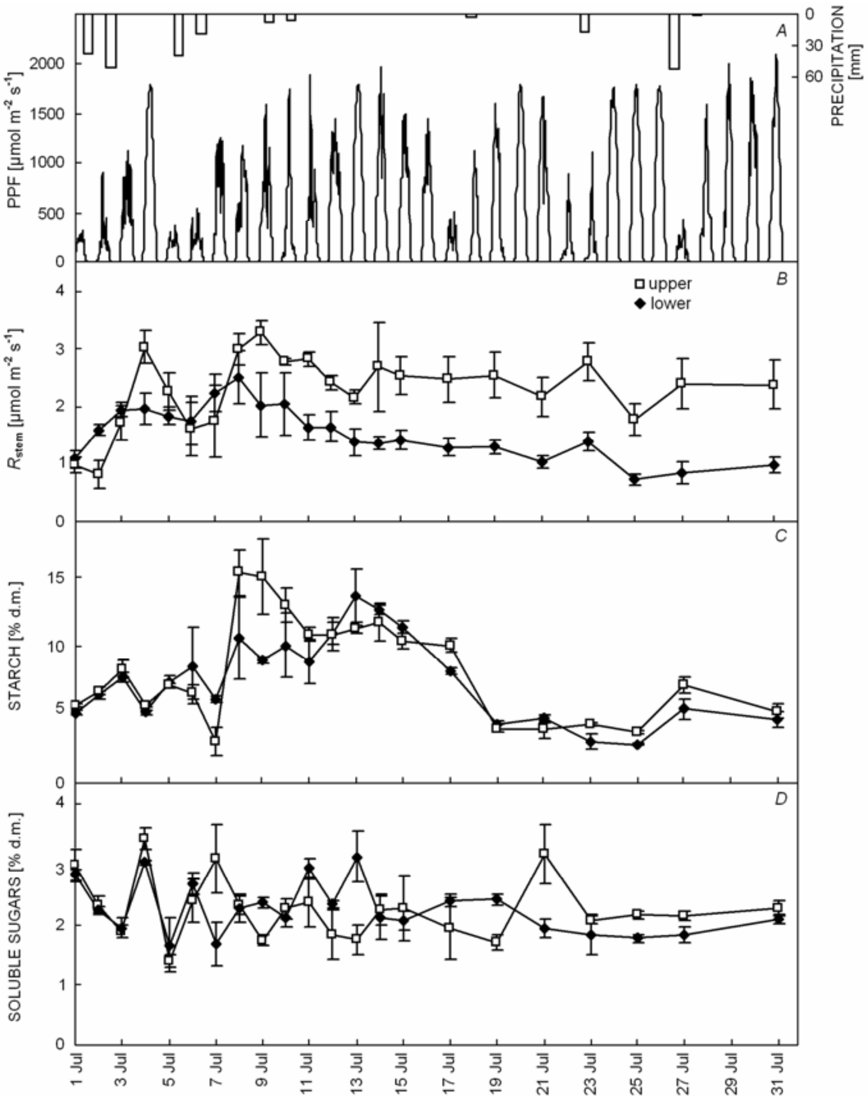


Fig. 1. Daily changes in (*A*) photosynthetic photon flux (PPF) and precipitation, (*B*) respiration rate at upper and lower part of girdled stem and un-girdled stem, (*C*) starch, and (*D*) soluble sugars in phloem region of bark. *Vertical bars* show the standard error.

newly-formed photosynthates by canopy photosynthesis (Kozlowski and Pallardy 1997, Larcher 2003). Although the shortage of precipitation in northeast China may also affect photosynthesis (Wang 2005), the frequent rainfall (200 mm, which is about one third of total annual precipitation) and cloudy weather (over 10 d) during the measuring period (July) may have eliminated any limitation of photosynthesis by the water supply (Fig. 1). Thus, if the newly-formed photosynthates are responsible for the high $R_{upper}$, the above-canopy PPF should be correlated with the respiratory difference between the upper and the lower parts of girdled stems. Moreover, the long-distance transport of photosynthates from canopy needles to the stem at breast height is time-consuming for phloem loading and unloading (Lambers *et al.* 1998). Thus, the respiratory difference might be correlated with previous PPF values rather than the instantaneous value. Just as shown in Table 1, our results clearly showed the close correlation between PPF and differences between $R_{upper}$ and $R_{lower}$. Particularly, the cumulative PPF and the maximum PPF for one day before the measurement were strongly correlated with both $R_{upper}$ and $R_{upper}$-$R_{lower.}$ Therefore, the relation of newly-formed photosynthates and stem respiration shows a time lag, which we estimate to be at least one day.

In conclusion, within the one month girdling treatment, most of newly-formed photosynthates at the upper part of the girdling stem were consumed by the high respiratory activity. Moreover, photosynthates formed one day before measurement functioned to the respiratory difference between the upper and the lower part of girdling stems, showing that the duration for photosynthates translocation from canopy to the stem at breast height is at least one day.

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