

Interspecific variability of stem photosynthesis among tree species

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Summary The photosynthetic characteristics of current-year stems of six deciduous tree species, two evergreen tree species and ginkgo (*Ginkgo biloba* L.) were compared. Gas exchange, chlorophyll concentration, nitrogen concentration and maximum quantum yield of PSII were measured in stems in summer and winter. A light-induced decrease in stem CO₂ efflux was observed in all species. The apparent gross photosynthetic rate in saturating light ranged from 0.72 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (ginkgo, in winter) to 3.73 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (*Alnus glutinosa* (L.) Gaertn., in summer). Despite this variability, a unique correlation (slope = 0.75), based on our results and those reported in the literature, was found between gross photosynthetic rate and dark respiration rate. Mass-based gross photosynthetic rate decreased with stem mass per area and correlated to chlorophyll concentration and nitrogen concentration, both in summer and winter. The radial distribution of stem chlorophyll differed among species, but all species except ginkgo had chlorophyll as deep as the pith. In summer, the maximum quantum yield of stem PSII (estimated from the ratio of variable to maximal fluorescence; F_v/F_m) of all species was near the optimal value found for leaves. By contrast, the values were highly variable in winter, suggesting large differences in sensitivity to low-temperature photoinhibition. The winter values of F_v/F_m were only 31–60% of summer values for the deciduous species, whereas the evergreen conifer species maintained high F_v/F_m in winter. The results highlight the interspecific variability of gross photosynthesis in the stem and its correlation with structural traits like those found for leaves. The structural correlations suggest that the selection of photosynthetic traits has operated under similar constraints in stems and leaves.

Keywords: chlorophyll, F_v/F_m , nitrogen, stem gas exchange.

Introduction

In contrast with leaves, stems are not obviously specialized for photosynthesis. Their surface to volume ratio is low, as is transmittance to light through the bark layer (Pfanz et al. 2002). Nevertheless, these conditions, although a priori unfavorable, do not prevent chlorophyll synthesis and carbon assimilation in stems. Kharouk et al. (1995) calculated that 45%

of total tree chlorophyll is present in the twig and branch chlorophyll of aspen. Compared with leaves, stems have some photosynthetic advantages. For example, the measured CO₂ concentration in stems is high enough (up to 260,000 ppm) to inhibit photorespiration, increasing quantum yield. The lack of stomata inhibits transpiration, increasing water-use efficiency over that of leaves.

Stem photosynthesis has been studied in legume species, such as broom (Nilsen et al. 1993, 1996), and in various tree species (see review by Pfanz et al. 2002). Compared with the maximal net photosynthetic rate of leaves, which may reach up to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in temperate trees, e.g., some species of the genus *Quercus*, the photosynthetic rate of stems is much lower (Cernusak and Marshall 2000, Aschan et al. 2001, Wittmann et al. 2001). For this reason, gross photosynthesis is usually calculated to characterize the stem photosynthesis. Gas-exchange measurements of stems are generally achieved instantaneously, over short periods, and most studies provide only a snap-shot in time. Studies in which gas exchange was monitored during an entire season, however, have revealed that gross stem photosynthesis may be higher than the dark respiration rate, particularly during the stem growth period (April to September) and in winter (Foote and Schaedle 1976, Damesin 2003). A current-year stem of beech can potentially assimilate 0.13 g of carbon during the growth period, corresponding to 68% of the total carbon assimilated over one year (Damesin 2003).

Leaf gas exchange has often been related to leaf structural traits, both within and among species (Reich et al. 1997). Leaf mass per area (LMA) and nitrogen concentration are important leaf traits that are associated with variations in carbon assimilation. Expressed in mass-based units, the light-saturated assimilation of leaves is negatively correlated to LMA (Wright et al. 2004). Leaf photosynthetic capacities are positively correlated to leaf nitrogen concentration because proteins of the Calvin-Benson cycle and of thylakoids represent the major part of leaf nitrogen (Evans 1989). This relationship has also been observed for stem photosynthesis of the legume species *Spartium junceum* L. and *Cytisus scoparius* L. (Nilsen 1992, Nilsen and Karpa 1994) and of the tree species *Pinus monticola* Dougl. ex D. Don (Cernusak and Marshall 2000). To our knowledge, the relationship has never been compared