Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 206 (2005) 153–166
Forest Ecology and Management
www.elsevier.com/locate/foreco

Variation in leaf conductance of silver birch: effects of irradiance, vapour pressure deficit, leaf water status and position within a crown

Arne Sellin*, Priit Kupper

Institute of Botany and Ecology, University of Tartu, Lai 40, 51005 Tartu, Estonia

Received 19 February 2004; received in revised form 4 October 2004; accepted 16 October 2004

Abstract

Responses of leaf conductance (g_L) to variation in photosynthetic photon flux density (Q_P), leaf-to-air vapour pressure difference (VPD), bulk leaf water potential (Ψ_x) and soil to leaf hydraulic conductance (G_T) were studied in silver birch (*Betula pendula* Roth) foliage with respect to leaf position within the canopy. The upper canopy leaves demonstrated 2.0–2.4 times higher ($P < 0.001$) daily maxima of g_L as compared to the lower-canopy leaves growing in the shadow of upper branches. Functional acclimation of the shade foliage occurred in the form of both a steeper initial slope of the light-response curve and a lower light-saturation point of g_L.

Leaf conductance decreased if Ψ_x fell below certain values after the noon, while the sun foliage experienced greater negative water potentials than the shade foliage. In a diurnal scale the influence of bulk leaf water potential on g_L altogether was rather weak. The lower-canopy foliage exhibited more conservative water-use behaviour, having lower maximum stomatal conductance and greater sensitivity to Ψ_x bringing about a smaller responsiveness to VPD than the upper canopy foliage. The mean G_T was 1.7–1.8 times bigger ($P < 0.001$) for the upper canopy, compared to the lower canopy; the shade foliage responded more sensitively to changes in G_T; there were steeper water potential gradients between the soil and lower-canopy leaves; g_L in the lower-canopy foliage was more strictly controlled by leaf water status—the evidence suggesting that the shade foliage may be hydraulically more constrained. We set up a hypothesis that stomatal conductance at the base of the live crown is limited not only by low light availability but also by plant's inner hydraulic constraints.

Keywords: *Betula pendula*; Hydraulic constraints; Leaf conductance; Leaf water potential; Photosynthetic photon flux density; Soil to leaf conductance

1. Introduction

Water transfer from the soil, through vegetation, to the atmosphere, takes place in a soil–plant-atmosphere continuum (SPAC) along water potential or hydro-

* Corresponding author. Tel.: +372 7376236; fax: +372 7376222.
E-mail address: arne.sellin@ut.ee (A. Sellin).

0378-1127/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2004.10.059

static pressure gradient. There is substantial resistance to water movement in roots, stems, and leaves, so, in a short-term time scale, stomatal conductance may be constrained by supply from the soil and resistance to transfer through the plant. However, a growing body of evidence suggests that, also in a longer time scale, trees hydraulic conductance may limit stomatal conductance and net photosynthesis, and therefore the growth of older and higher trees (Ryan and Yoder, 1997; Hubbard et al., 1999; Kolb and Stone, 2000; Schäfer et al., 2000). Meta-analysis performed across different plant life forms by Mencuccini (2003) indicated that whole-plant hydraulic conductance is inversely related to plant height, therefore, stature appears as a basic factor affecting gas exchange. As trees grow taller, the total hydraulic conductance of the soil to leaf pathway (G_T) declines, causing stomata to close earlier in the day to restrain water losses and prevent the development of damaging water potential gradients. This leads to lower intercellular CO_2 concentration and decreased net photosynthetic rate and net primary production during forest maturation. McDowell et al. (2002) suggested that the path length from bulk soil to leaf, rather than tree height per se, is the relevant term.

Overall, trees hydraulic capacity has undoubted implications for their performance, influencing also other aspects of plant life (e.g. duration of leaf growth; Nardini, 2002) besides stomatal conductance, net photosynthesis, and primary production. Drought tolerance (Sperry et al., 1998; Sperry, 2000; Martínez-Vilalta and Piñol, 2002), geographic distribution of species (Brodribb and Hill, 1999) and even type of photosynthetic pathway (Kocacinar and Sage, 2004) are considered to be associated with xylem hydraulic properties and with xylem vulnerability to cavitation in particular. At the same time, the relationships between leaf functioning within an individual crown and traits of the plant hydraulic architecture are still poorly understood (Gartner, 1995; Hubbard et al., 2002). Within the crown, the length of the water transport pathway does not necessarily determine the resistance to the flow of water, because both specific conductivity of xylem and leaf area to sapwood area ratio may vary considerably among different parts of the crown.

Our earlier studies (Sellin, 1994, 1996) in *Picea abies* (L.) Karst. revealed that low resistance to water flow throughout most of the trunk, except the very top, creates more equal prerequisites for water supply to branches situated at different heights in the crown. However, there is a remarkable systematic variation in xylem hydraulic capacity between the branches (Joyce and Steiner, 1995; Protz et al., 2000; Lemoine et al., 2002), and trees growing under low-light conditions produce sapwood with poor water conducting capacity (Sellin, 1993; Shumway et al., 1993). In *Pinus sylvestris* L., branches at the crown bottom had a lower proportion of sapwood area and a lower total hydraulic conductance than branches of the same diameter at the tree top (Mencuccini and Grace, 1996). Recently, both the specific and leaf-specific hydraulic conductivity (LSC) have been found to increase with branch insertion height (Protz et al., 2000; Clearwater and Meinzer, 2001; Lemoine et al., 2002), while in *Eucalyptus grandis* Hill ex Maiden, LSC declined as the branch grew larger (Clearwater and Meinzer, 2001).

A death of lower branches and vertical crown recession in closed-canopy trees are conventionally considered to be caused by carbon limitation because of insufficient light energy to drive photosynthesis (Sampson and Smith, 1993; Mäkelä, 1997). Protz et al. (2000) have proposed a modified explanation of crown recession based upon reduction in hydraulic conductivity of lower branches as a result of shading. According to their hypothesis, reduced photosynthesis because of low light availability at the bottom of crown results in the development of smaller xylem conduits and smaller earlywood proportion, increasing hydraulic resistance to the water flow. The reduced water supply for the foliage of branches in deep shade, in its turn, further limits carbon fixation in the subsequent years. This negative feedback intensifies over several growing seasons eventually leading to branch death.

The present study provides evidence for differential effects of plant hydraulic constraints on stomatal behaviour with respect to the crown position in silver birch (*Betula pendula* Roth). The goals of the paper were to: (1) establish the within-crown variation in leaf conductance depending on the level of irradiance, vapour pressure deficit, and leaf water status; (2) assess the contribution of the liquid-phase conductance to the control of leaf conductance in relation to the shoot position within a canopy. The results presented here may be used in further studies of trees water relations, gas exchange and canopy development.