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Measuring and modelling stomatal conductance and photosynthesis in mature birch in Sweden

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Abstract

Stomatal conductance (g_s), net photosynthesis (A_n) and twig water potential (Ψ_t) were measured in mature silver birch (*Betula pendula*) during 3 years in southern Sweden. Measurements from 2 years were used to parameterise three different g_s models and measurements from a 3rd year were used to validate these models. Two different multiplicative stomatal models were used. In one of these, the g_s response function for the water vapour pressure deficit (D) was fixed, while in the other the g_s sensitivity to D increased with the accumulated time after sunrise with D above a certain threshold value. Furthermore, one combined stomatal-photosynthesis model (L-model) was used. The L-model was run either by using observations of photosynthesis as input data, or by predicting g_s and photosynthesis simultaneously from environmental data. The model used to predict photosynthesis was parameterised from measurements of the photosynthetic responses to the photosynthetically active radiation, CO_2 and temperature. The stomatal response functions of the L-model were parameterised using observations of photosynthesis as input data in order to make them independent of the performance of the photosynthesis model. The difference in model performance between the two multiplicative models was relatively small. The multiplicative stomatal models and the L-model were similarly successful in predicting g_s when the L-model was driven by observations of photosynthesis. However, the L-model was considerably less successful when photosynthesis was predicted. Photosynthesis was systematically under- and overestimated at high and low Ψ_t, respectively, causing errors in the prediction of g_s. In most situations, measurements of photosynthesis are not available and g_s must be predicted from environmental data. In such cases, we conclude that the two multiplicative models are more successful in predicting g_s in mature silver birch than the combined stomatal-photosynthesis model.

Keywords: *Betula pendula*; Modelling; Photosynthesis; Stomatal conductance; Water potential

1. Introduction

Stomata regulate energy and gas exchange between the vegetation and the atmosphere, and vice versa.

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Estimates of stomatal conductance (g_s) are therefore important in research related to carbon sequestration, hydrology, micrometeorology and effects of elevated carbon dioxide (CO_2) and air pollution (Williams et al., 1997; Collins and Avissar, 1994; Medlyn et al., 2001; Fuhrer, 2000). Estimates of the g_s for large vegetation areas require the use of mathematical modelling. Currently, there are two main types of models commonly used to simulate g_s on large spatial scales. The first, outlined by Jarvis (1976), is based on direct stomatal responses to different driving variables that are assumed to regulate the g_s in a multiplicative manner and without any mutual interactions (denoted *multiplicative stomatal model* in the following). The second, denoted *combined stomatal-photosynthesis model* in the following, is based on the observed correlation between net photosynthesis (A_n) and g_s (Wong et al., 1978), and assumes a proportional and interactive relationship between g_s and A_n (Ball et al., 1987; Leuning, 1995). Models taking into account how the water relations in the soil–plant–atmosphere continuum regulate stomata (e.g., Williams et al., 1996) require many input parameters and are not applicable on a large spatial scale at present.

In the work within the Convention on Long-Range Transboundary Air Pollution, United Nations Economic Commission for Europe, efforts are now being made to relate the effects of ground-level ozone on plants to the amount of ozone taken up through the stomata, since this is regarded as a physiologically more relevant ozone index than indices based on the external exposure (Fuhrer, 2000). Estimates of the stomatal uptake of ozone are currently made by using the multiplicative stomatal model approach (Emberson et al., 2000). In studies with wheat (Danielsson et al., 2003), potato (Pleijel et al., 2002) and birch (Uddling et al., 2004a) reductions in yield or total biomass were more strongly related to the stomatal uptake of ozone than to indices based on external ozone exposure. Multiplicative stomatal models parameterised for different vegetation types were recently incorporated into the European Monitoring and Evaluation Programme (EMEP) photo-oxidant model that is used to provide estimates of ozone concentrations across Europe (Simpson et al., 2003). In order to establish stomatal ozone uptake–response relationships and to improve the EMEP estimates of ozone uptake it is necessary to improve the g_s model parameterisations for different species (Fuhrer, 2000).

The aim of this study was to parameterise, evaluate and compare different models for predicting g_s in mature silver birch that require few parameters and can be driven by environmental data readily available on a large spatial scale within the EMEP. Two multiplicative stomatal models and one combined stomatal-photosynthesis model were applied.

2. Materials and methods

2.1. Site description

The study was carried out in two stands with mature *Betula pendula* at the Asa Forest Research Station (57°10′ N, 14°47′ E, altitude 190 m; Swedish University of Agricultural Sciences) in southern Sweden. The mean annual temperature and rainfall in Asa during 1988–2002 were 6.2 °C and 710 mm, respectively. The textural soil types and soils were clayey-silty sediment and cambisol in stand 1 and sandy-silty till and podzol in stand 2. Tree characteristics in the two stands are summarised in Table 1. In stand 1, most of the roots were distributed at <0.2 m depth, but occasional fine roots were found at 1 m

Table 1
Tree characteristics and diurnal gas exchange measurements in the two *Betula pendula* stands at Asa

Year	Stand	No. of trees	Tree age (years)	Height (m)	BHD[a] (m)	No. of gas exchange measurements[b]	Use of measurements
2001	1 and 2	5 + 5	30–40	15–18	–	248	Validation
2002	1	4	35–40	16–22	0.21–0.36	393	Parameterisation
2003	1	4	35–40	16–22	0.22–0.37	322	Parameterisation

Different trees were measured in stand 1 in 2001 and in 2002–2003, while the same 4 trees were measured in 2002 and 2003.
[a] Brest height (1.3 m) diameter.
[b] The gas exchange measurements from the upper sun-exposed canopy used for g_s modelling.