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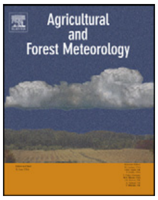

Up-scaling of water use efficiency from leaf to canopy as based on leaf gas exchange relationships and the modeled in-canopy light distribution

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A B S T R A C T

The aim of this study was to evaluate the extent to which water use efficiency (WUE) at leaf scale can be used to assess WUE at canopy scale, leaf WUE being assumed to be a constant function of vapor pressure deficit and to thus not be dependent upon other environmental factors or varying leaf properties. Leaf WUE and its variability and dependencies were assessed using leaf gas-exchange measurements obtained during two growing seasons, 1999 and 2000, at the Soroe beech forest study site on Zealand in Denmark. It was found that the VPD-normalized leaf WUE, $WUE_{normleaf}$, although dependent on incoming PAR below $500\,\mu mol\,m^{-2}\,s^{-1}$ is independent, both of the canopy levels and of variations in the environmental parameters. The average $WUE_{normleaf}$ for PAR above $500\,\mu mol\,m^{-2}\,s^{-1}$ was found to be $5.5\,\mu mol\,CO_2\,(mmol\,H_2O)^{-1}$ hPa and, for the full range, $2.3\,\mu mol\,CO_2\,(mmol\,H_2O)^{-1}$ hPa. These results showed that WUE can be up-scaled from leaf to canopy on the basis of $WUE_{normleaf}$ and the PAR distribution within the canopy. The up-scaling conducted was based on this $WUE_{normleaf}$ – PAR relationship, the light distribution being assessed using the MAESTRA model, parameterized in accordance with measurements obtained for the Soroe forest. The up-scaled WUE was then compared with WUE as estimated from turbulent flux data measured above the forest with the eddy-covariance technique. The modeled daily canopy WUE obtained for daytime fluxes (6:00 AM–6:00 PM) was found to be in agreement with corresponding canopy WUE estimates based on the turbulent fluxes observed and to be dependent on VDP and light intensity alone, its thus being independent of other environmental factors. Accordingly, canopy WUE can be estimated on the basis of the up-scaled WUE relationships, provided incident PAR and VPD within the canopy are known.

1. Introduction

The most powerful approach for measuring net ecosystem carbon and water exchange involves use of micrometeorological techniques, such as eddy correlation methods (Aubinet et al., 2000; Baldocchi et al., 2000). Methods of this sort, since they require both large homogeneous areas and only minor topographic variations, are thus not well suited for the measurement of small forest stands, which is needed in order to adequately study variable stand and management conditions. The fluxes of interest are the result of omnidirectional component fluxes that needs to be assessed within the ecosystems in question in order to adequately understand the interactions between the vegetation and the atmosphere. Although chamber measurements are often used in performing flux measurements on leaves, branches and stems (Lindroth and Cienciala, 1996; Stokes et al., 2010; Acosta et al., 2008) as well as for the soil (Janssens and Pilegaard, 2003) and on low vegetation (Larsen et al., 2007; Bahn et al., 2010), the internal variation within a stand is considerable, so that several simultaneous measurements are needed in order to make correct up-scaling possible. This limits the value of chamber measurement for quantifying the net ecosystem exchange. Net stand assimilation can also be assessed by use of biogeochemical modeling, relying on the parameterization of photosynthesis at the leaf level. Such an approach requires that one take the non-linear responses of assimilation to light into consideration (de Pury and Farquhar, 1997), thus that one can accurately, in spatial terms, describe the canopy structure and the light distribution, distinguishing, on the basis of observations, which leaves are shaded and which are sunlit. Biogeochemical models used to estimate the net ecosystem exchange also require that soil and biomass respiration be parameterized.

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In the present study, water use efficiency, WUE, i.e. the unit carbon gain per unit water lost, was evaluated in order to assess carbon uptake by the canopy from water flux measurements. The use of the concept of WUE relies on the strong link between the carbon uptake of plants by means of photosynthesis and by water use by plants through transpiration, there being a common pathway – through the stomata – for the two fluxes. WUE has been widely used in agriculture for plant development purposes, particularly in connection with irrigation need and assessment of water stress tolerance for evaluation of the seasonal plant performance (Bacon, 2004; Linderson et al., 2007; Morison et al., 2008; Boutraa, 2010). The relationship in question, which applies to instantaneous gas exchange, has been expressed by Bierhuizen and Slayter (1965), for example, as

$$\mathrm{WUE} = \frac{F_c}{F_w} = \frac{k}{\mathrm{VPD}} \quad (1)$$

where F_c is the net carbon uptake rate (μmol CO_2 m^{-2} s^{-1}), F_w is the transpiration rate (mmol H_2O m^{-2} s^{-1}), VPD is the vapor pressure deficit (Pa), estimated from $e_s - e_a$, where e_s is the saturated vapor pressure for the leaf temperature at the moment and e_a is the accompanying water vapor pressure of the adjacent air. The factor k is a constant representing the ratio of the resistances involved to the degree of transport of CO_2 and water vapor. The resistances consist of aerodynamic resistance, stomatal resistance, and internal resistance within the leaves to the transport of water vapor and of CO_2 respectively. At canopy scale, the inverted sum of the resistances for each of the constituents being termed the bulk canopy conductance. If the ratio which k represents is constant, the ratio of the conductance of water vapor to that of CO_2 is also constant.

The dependency of WUE on VPD has been verified in many forest studies on both the leaf and the canopy scale, there having been shown to be a non-linear decreasing relationship between WUE and VPD (Baldocchi et al., 1987; Tang et al., 2006; Herbst et al., 2002; Morén et al., 2001; Lindroth and Cienciala, 1996). Early ecosystem flux measurements of WUE indicated the ratio of the conductance of CO_2 to the water vapor flux to be constant (e.g. Verma et al., 1986; Baldocchi et al., 1987; Tanner and Sinclair, 1983). The photosynthetic activity, and thus the internal CO_2 concentration, varies with the availability of light, however. Low light intensity reduces the carbon uptake by the leaf, which represents the driving process involved. As a consequence, the gradient between the atmospheric and the internal CO_2 concentration decreases, thus reducing WUE. This light dependency of the WUE–VPD relationship, already noted at leaf level by Bierhuizen and Slayter (1965), was observed later in studies of within-canopy variations in WUE caused by differences in light distribution (e.g. Le Roux et al., 2001). At low light intensities, the stomata may react to the decreased photosynthetic activity by closing (e.g. Kang et al., 2007), which can lead to a lowering of the transpiration as well and thus to WUE remaining constant even when the light intensity is decreased. Another light-dependent factor to be taken into account is that the leaf properties of sunlit and shaded leaves generally differ (Masarovicova and Stefancik, 1990; Fleck et al., 2003; Uemura et al., 2000; Ibrom et al., 2006), which can also be a reason for WUE varying within the canopy.

The water transport within the xylem and the soil water availability, both of which affect the leaf water potential, can also affect WUE due to their affecting the availability of water that can be transpired. A low leaf water potential is generally considered to reduce the size of the stomata (e.g. Knapp and Smith, 1988), thus lowering both CO_2 and water vapor flux. Such matters are affected by climatological factors, by drought in particular (e.g. Beer et al., 2009; Grassi and Magnani, 2005), and can also vary within the tree since the water potential decreases with height. Herbst et al. (1999) found beech trees to have the ability to exploit soil water from deep layers, this making them less sensitive to drought.

The various factors just considered may either amplify the sensitivity of WUE to environmental conditions or dampen the effects these have on the separate fluxes, in this way making WUE fairly stable and reducing environmental influence. Few studies of leaf WUE have been carried out under ambient conditions and most of those that have been concern rather short periods of time, but do indicate WUE to be fairly stable, its being determined by VPD alone, as already indicated.

The aim of the present study was to evaluate the extent to which leaf WUE can be used to assess canopy WUE, provided leaf WUE is a constant function of vapor pressure deficit and is thus not dependent on other environmental factors or varying leaf properties. The specific objectives of the study were to determine leaf WUE and its variability and dependencies on the basis of gas exchange measurements, to perform up-scaling from leaf to canopy WUE on the base of the relationships obtained and compare the up-scaled results to eddy flux data measured over the forest.

2. Materials and methods

The approach to WUE used in the study involves obtaining instantaneous measurements and is in the following named WUE. The distinction is made between $\mathrm{WUE_{leaf}}$, concerned with leaf scale fluxes and $\mathrm{WUE_{can}}$, concerned with fluxes on a canopy scale. One way that WUE can be expressed is as the ratio of the net assimilation to the conductance, in this form its being termed the intrinsic WUE ($\mathrm{WUE_i}$), which in practice is similar to WUE × VPD since the transpiration to VPD ratio corresponds approximately to the conductance of water vapor. $\mathrm{WUE_i}$ indicates the effect of the internal CO_2 concentration on WUE and is also a measure that can be assessed by isotope discrimination. A measure corresponding to $\mathrm{WUE_i}$, using ambient gas exchange measurements, is thus WUE × VPD, which can be regarded as a normalization of WUE by the use of VPD. In the following it will be termed normalized WUE, or $\mathrm{WUE_{norm}}$, which can be subdivided into $\mathrm{WUE_{normleaf}}$ and $\mathrm{WUE_{normcan}}$ for the leaf and canopy fluxes respectively. $\mathrm{VPD_{leaf}}$ is estimated on the basis of $e_s - e_a$, e_s being the saturated vapor pressure at the current leaf temperature and e_a the current water vapor pressure of the adjacent air. For $\mathrm{VPD_{can}}$, e_s within the canopy is estimated at 10 m on the basis of the air temperature and e_a is derived from the relative humidity in the top of the canopy (25 m) using e_s as estimated from the air temperature (T_a) at 37 m, since T_a at 25 m and at 37 m were assumed to be rather similar whereas, within the canopy, the values for T_a, and thus e_s as well differ from the canopy values given above. The current vapor pressure, e_a, is normally about the same at tree tops as within the canopy due to intensive mixing of air (Jarvis and McNaughton, 1986). PAR estimated adjacent to the leaf is termed here PAR, IPAR referring to the incident PAR above the canopy.

The leaf flux measurements were made in a forest called "Lille Boegeskov" near Soroe on the island of Zealand at 55°29′13″N, 11°38′45″E, 40 m above mean sea level. At the time, it was an 80-year old beech (*Fagus sylvatica,* L.) forest with an average tree height of 25 m and a wood increment of 11 m^3 ha^{-1} yr^{-1}. The average ecosystem carbon uptake of the forest during the years 1996–2009 was 157 g C m^{-2} yr^{-1} (Pilegaard et al., 2011). The terrain is flat with scattered stands of conifers constituting 20% of the source area of the flux measurements (Pilegaard et al., 2011). At the time that the leaf measurements were performed, the stand density of the forest was 283 stems ha^{-1}. Conventional meteorological profile measurements and turbulence measurements carried out at a single level using the eddy covariance method were performed at a height of 43 m on a 57 m tall mast (Pilegaard et al., 2011, 2003). A 24 m high scaffold tower was located next to the mast, serving as a platform for plant physiological studies and various experiments.