Journal of Hydrology 409 (2011) 371–381

Contents lists available at SciVerse ScienceDirect

Journal of Hydrology

journal homepage: www.elsevier.com/locate/jhydrol

Sap flux density and stomatal conductance of European beech and common oak trees in pure and mixed stands during the summer drought of 2003

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ARTICLE INFO

Article history:
Received 17 August 2010
Received in revised form 21 July 2011
Accepted 13 August 2011
Available online 22 August 2011
This manuscript was handled by Konstantine P. Georgakakos, Editor-in-Chief, with the assistance of Christa D. Peters-Lidard, Associate Editor

Keywords:
Sap flux
Stomatal conductance
Tree species mixture
Drought
Fagus sylvatica
Quercus petraea

SUMMARY

Sap flux density of European beech and common oak trees was determined from sap flow measurements in pure and mixed stands during the summer drought of 2003. Eight trees per species and per stand were equipped with sap flow sensors. Soil water content was monitored in each stand at different depths by using time-domain reflectometry (TDR). Leaf area index and vertical root distribution were also investigated during the growing season. From sap flux density (*SFD*) data, mean stomatal conductance of individual trees (G_s) was calculated by inverting the Penman–Monteith equation. Linear mixed models were developed to analyse the effects of species and stand type (pure vs. mixed) on *SFD* and G_s and on their sensitivity to environmental variables (vapour pressure deficit (D), incoming solar radiation (R_G), and relative extractable water (*REW*)). For reference environmental conditions, we did not find any tree species or stand type effects on *SFD*. The sensitivity of *SFD* to D was higher for oak than for beech in the pure stands ($P < 0.0001$) but the mixing of species reduced it for oak and increased it for beech, so that the sensitivity of *SFD* to D became higher for beech than for oak in the mixed stand ($P < 0.0001$). At reference conditions, G_s was significantly higher for beech compared to oak (2.1 and 1.8 times in the pure and mixed stand, respectively). This was explained by a larger beech sapwood-to-leaf area ratio compared to oak. The sensitivity of G_s to *REW* was higher for beech than for oak and was ascribed to a higher vulnerability of beech to air embolism and to a more sensitive stomatal regulation. The sensitivity of beech G_s to *REW* was lower in the mixed than in the pure stand, which could be explained by a better sharing of the resources in the mixture, by facilitation processes (hydraulic lift), and by a rainfall partitioning in favour of beech.

1. Introduction

Water transport in trees is required for a number of physiological processes. Among others, transpiration is coupled with photosynthesis through stomata functioning (Jarvis and Davies, 1998) and the water flux caused by transpiration is one of the processes involved in nutrient transport from soil to roots (Barber, 1995). In this context, canopy stomatal conductance for water vapour is defined as the mean value of the stomatal conductance of individual leaves added in parallel and weighted by leaf area (Baldocchi et al., 1991). This variable is particularly interesting since it reflects the stomatal control of transpiration. From transpiration measurements, canopy stomatal conductance can be derived by using the reverse form of the Penman–Monteith equation (Jarvis and McNaughton, 1986; Stewart, 1988). Several techniques have been developed to estimate transpiration, depending on the spatial and temporal scales (Smith and Allen, 1996; Köstner et al., 1998; Wullschleger et al., 1998). Common meteorological methods (e.g. eddy covariance) are suitable to measure transpiration at the stand level while the sap flux method is more adapted to estimate transpiration at the tree level (Granier and Bréda, 1996).

Stomatal conductance varies among individuals of a given tree species or of different tree species as a function of several tree characteristics depending on tree genetic, tree age, and growth conditions (site and competition): tree height, leaf area, sapwood area, root area, sapwood-to-leaf area ratio, and root-to-leaf area ratio (Addington et al., 2006). At the stand level, transpiration depends on the distribution of these tree characteristics that may vary greatly depending on species composition and stand structure. In multispecies stands, the spatial heterogeneity in water use is high and can partly be ascribed to physiological differences between tree species and to the variability in competition conditions (Hölscher et al., 2005). In addition, antagonistic or synergistic interactions between tree species may occur regarding water use in mixed stands; individuals of different species might reduce tree

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doi:10.1016/j.jhydrol.2011.08.032

competition for water in partitioning water uptake, either at a temporal or at a spatial level or both. Temporal partitioning occurs when species have a different phenological timing resulting in staggered water needs. Spatial partitioning may happen vertically due to differences in root distribution with depth and horizontally in relation with stand density and composition (Meinzer et al., 2001).

Stomatal conductance is also controlled by climatic variables, both on daily and sub-daily scales (McNaughton and Jarvis, 1991). The response of stomatal conductance to increasing vapour pressure deficit generally follows a logarithmic decrease. However, the magnitude of the decrease reflecting the stomatal sensitivity varies considerably both between and within tree species (Oren et al., 1999). Stomatal conductance is also affected by the soil water availability and is known to decrease when soil relative extractable water drops below a threshold of 0.4 (Granier et al., 1999). Bréda et al. (2006) analysed the ecophysiological responses of temperate forest trees and stands under the drought conditions of 2003 and concluded that there is a large inter and intra-specific diversity of hydraulic and stomatal responses to soil water deficit.

Tree species effects on transpiration and stomatal conductance have generally been analysed by comparing pure stands or patch of different species (Granier et al., 2000a; Gartner et al., 2009) or by comparing different species in a mixed stand (Pataki et al., 2000; Oren and Pataki, 2001; Wullschleger et al., 2001; Raftoyannis and Radoglou, 2002; Leuzinger et al., 2005; Keel et al., 2007). When trees species are compared based on pure stands located at different sites, the species effects can be confounded with spatial effects. The inter-species comparisons within a mixed stand do not present this disadvantage but are only valid for the particular competition conditions occurring in this stand. Comparing tree species in pure and mixed stands on a same site would allow to evaluate the species effect in different competition conditions and to test for the mixture effect. To the best of our knowledge, it has never been done until now.

The objective of this study was (i) to compare European beech and common oak tree sap flux density (*SFD*) and mean stomatal conductance (G_s) in pure stands located at a same site and within a mixed stand and (ii) to evaluate the mixture effect by comparing tree *SFD* and G_s of a same species in pure and mixed stands. Linear mixed models were developed to describe the response of *SFD* and G_s to environmental variables, which allowed us to test for the species and mixture effects on a reference *SFD* and G_s (at fixed environmental conditions) and on their sensitivity to the environmental variables. As the measurements were carried out during the 2003 vegetation period characterized by a severe drought, large ranges of atmospheric and soil moisture conditions were available.

2. Materials and methods

2.1. Study site

The study site is located in the western part of the Belgian Ardennes at 300 m elevation (50°01′N, 4°24′E). Mean annual rainfall is about 1044 mm with 411 mm falling during leaf cover period (May–September). Mean annual temperature is around 8 °C. However, in 2003, the year of concern for this study, rainfall was 836 mm with 344 mm during leaf cover period and mean annual temperature was 9.8 °C. The site consists of a 60 ha oak (*Quercus petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica* L.) forest lying on an acid brown earth soil, classified as Dystrochrepts (USDA soil taxonomy), with a moder-type humus and a A_hB_wC profile. The soil has been developed on a loamy and stony solifluxion sheet in which weathering products of the bedrock (Lower Devonian: sandstone and schist) were mixed with added periglacial loess.

By the end of the 19th century, the stand was probably an oak coppice with a few standards. Taking advantage of a massive oak regeneration in 1880, the stand was progressively converted to a high forest and then was invaded by beech. In 2003, the area was covered by even-aged (~120 years) oak trees and uneven-aged beech trees.

2.2. Experimental plots

Three experimental plots were installed in stands dominated either by oak (0.25 ha) or by beech (0.35 ha) and in a 1:1 mixture of both species (0.51 ha). These plots are all situated on the same tableland (305–312 m) and were selected in such a way that stand species composition was the main varying factor. The beech plot is located 600 m away from the oak plot and the mixed plot is located halfway between them. Soil homogeneity was evaluated on the

Table 1
Selected physical and chemical properties of a soil profile per experimental plot.

Plot	Horizon	Depth (cm)	Stone content (m^3 100 m^{-3})	Sand (%)	Silt (%)	Clay (%)	MO[a] (g 100 g^{-1})	pH (H_2O)
Oak stand	Ah	0–6	5	10	62	28	21.43	3.96
	Bw1	6–27	30	11	54	35	4.66	4.28
	Bw2	27–42	30	11	56	33	4.02	4.38
	2Bw3	42–55	30	9	47	44	5.21	4.40
	2Bg1	55–75	30	10	47	43	3.43	4.49
	2Bg2	75–119	30	11	48	41	4.13	4.67
	2Bg3	119–160	30	6	51	42	4.25	4.76
Mixed stand	Ah	0–6	8	15	74	11	18.46	3.82
	Bw1	6–20	8	14	61	25	4.71	4.37
	Bw2	20–36	8	14	60	26	4.06	4.41
	2Bw3	36–50	8	10	49	40	4.39	4.33
	2Bg1	50–81	10	11	42	47	4.51	4.41
	2Bg2	81–110	23	16	37	47	4.32	4.53
	2Bg3	110–160	75	12	47	42	3.96	4.95
Beech stand	Ah	0–8	8	14	62	24	15.87	4.15
	Bw1	8–20	8	15	60	25	5.69	4.27
	2Bw2	20–50	28	16	55	30	4.35	4.39
	2Bw3	50–80	60	18	61	21	3.78	4.46
	2Bw4	80–112	70	NA	NA	NA	NA	NA
	BC	112–160	80	NA	NA	NA	NA	NA

NA: not available.

[a] Organic matter determined by loss on ignition.