100 YEARS Journal of Ecology British Ecological Society

Journal of Ecology 2013, **101**, 1201–1213 doi: 10.1111/1365-2745.12121

Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate

Georg von Arx[1]*, Elisabeth Graf Pannatier[1], Anne Thimonier[1] and Martine Rebetez[1,2]

[1] *Swiss Federal Institute for Forest Snow and Landscape Research WSL, Zuercherstrasse 111, 8903, Birmensdorf, Switzerland; and* [2] *Institute of Geography, University of Neuchâtel, Espace Louis-Agassiz 1, 2000, Neuchâtel, Switzerland*

Summary

1. Forest microclimate is crucial for the growth and survival of tree seedlings and understorey vegetation. This high ecological relevance contrasts with the poor functional and quantitative understanding of how the properties of forest ecosystems influence forest microclimate.

2. In a long-term (1998–2011) trial, we investigated how temporal patterns of microclimate below sparse and dense forest canopy related to those of nearby open areas and how this relationship was influenced by soil moisture and seasonality. Air temperature (T), vapour pressure deficit (VPD), soil matrix potential and leaf area index (LAI) were measured in a unique set-up of below-canopy and open-area meteorological stations at eleven distinct forest ecosystems, characteristic of subalpine and temperate climate zones. Data from these plots were analysed for the moderating capacity of the canopy, that is, the differences between below-canopy and open-area microclimate, with respect to (i) long-term means, (ii) dynamics within homogeneous moist- vs. dry-soil periods and (iii) diurnal patterns.

3. The long-term mean moderating capacity of the canopy was up to 3.3 °C for daily $T_{\max}$ and 0.52 kPa for daily $\mathrm{VPD}_{\max}$, of which soil moisture status alone accounted for up to 1.2 °C ($T_{\max}$) and 0.21 kPa ($\mathrm{VPD}_{\max}$). Below dense canopy ($\mathrm{LAI} > 4$), the moderating capacity was generally higher when soils were dry and increased during dry-soil periods, particularly in spring and somewhat less in summer. The opposite pattern was found below sparse canopy ($\mathrm{LAI} < 4$). At the diurnal level, moderating capacity below dense canopy was strongest in mid-afternoon and during dry-soil conditions, whereas peak moderation below sparse canopy occurred in mid-morning and during moist-soil conditions.

4. *Synthesis.* Our results suggest a threshold canopy density, which is probably linked to site-specific water availability, below which the moderating capacity of forest ecosystems switches from supportive to unsupportive for seedling establishment. Under supportive moderating capacity, we understand a stronger mitigation during physiologically most demanding conditions for plant growth. Such a threshold canopy density sheds new light on forest resilience to climate change. Climate change may alter forest canopy density in a way that precludes successful establishment of tree species and ultimately changes forest ecosystem structure and functioning.

Key-words: air temperature, forest ecosystems, leaf area index (LAI), plant–climate interactions, soil matrix potential, soil moisture, Swiss Long-Term Forest Research Programme LWF, temperate climate zone, vapour pressure deficit (VPD)

Introduction

Forest ecosystems have a distinct below-canopy microclimate, regulated by diverse biophysical processes, and of eminent importance to the growth and survival of understorey vegetation and seedlings. Canopy and tree stems partly shield near-ground areas from solar radiation and reduce mixing of air. As a consequence, below-canopy microclimate may substantially differ from comparable open areas (Geiger, Aron & Todhunter 2009). Inside forest stands, air temperature (T)

*Correspondence author. E-mail: georg.vonarx@wsl.ch

usually decreases less during the night and increases less during daytime, whereas the tightly coupled relative humidity (RH) shows the opposite pattern (Aussenac 2000; Morecroft, Taylor & Oliver 1998; von Arx, Dobbertin & Rebetez 2012b; Ma *et al.* 2010). This smoothing effect on daily *T* and RH amplitude is not uniform, but depends on the ambient weather situation and season (Renaud *et al.* 2011; von Arx, Dobbertin & Rebetez 2012b; Grimmond, Robeson & Schoof 2000; Morecroft, Taylor & Oliver 1998), forest structure and physiographic situation such as elevation, slope and aspect (Mitscherlich 1981; von Arx, Dobbertin & Rebetez 2012b; Ferrez, Davison & Rebetez 2011), and distance from forest edge (Chen, Franklin & Spies 1993; Heithecker & Halpern 2007; Meyer, Sisk & Covington 2001).

While shading by the canopy affects both soil and air temperature, the direct effect on air temperature is assumed to be smaller (Morecroft, Taylor & Oliver 1998; Porte, Huard & Dreyfus 2004), mainly because air is mobile, as well as partly mixed and exchanged with the open area. Consequently, forest soils generally warm up less than the open area (Mitscherlich 1981), leading to a diminished sensible heat flux. Furthermore, the colder below-canopy *T* results in a higher RH inside the forest, when assuming constant absolute air water content. An additional impact of soil on microclimate results from evaporative cooling or latent heat flux. Moist soils thus attenuate warming-up of the air and lowering of RH (Fischer *et al.* 2007; Hirschi *et al.* 2011; Seneviratne *et al.* 2006; Ferranti & Viterbo 2006; Jaeger & Seneviratne 2011). While basic principles of forest microclimate and the relationships with open-area microclimate therefore seem established, a more functional and quantitative view on how the properties of forest ecosystems influence below-canopy microclimate is largely missing. Particularly, interactions between canopy density and soil moisture throughout the year and their influence on dynamics of forest microclimate are unexplored.

The poor functional and quantitative understanding of forest microclimate contrasts with its high ecological relevance for many forest ecosystem processes (Breshears *et al.* 1997; Chen *et al.* 1999; Scharenbroch & Bockheim 2007; Vanwalleghem & Meentemeyer 2009; Closa, Irigoyen & Goicoechea 2010). For survival and growth of young tree seedlings, for instance, favourable *T*, air humidity and soil moisture are crucial determinants, especially until the root system is sufficiently developed and other factors such as light conditions and nutrient availability become limiting (Aussenac 2000; Wicklein *et al.* 2012; Lloret, Penuelas & Estiarte 2005). In fact, at the initial life stage, many seedlings die within hours if conditions are unfavourable (Harper & White 1974). *T* affects rates of metabolism and growth and influences plant water demand. Similarly, soil temperature has been shown to influence root water uptake and thus transpiration rates (Mellander, Bishop & Lundmark 2004). To reduce short-term water demand, stomata often close when soil moisture and/or air humidity are low (Aasamaa & Sõber 2011; Ladjal *et al.* 2007). Effectively, stomatal conductance is usually regulated by a simple negative feedback loop between demand and supply, that is, between vapour pressure deficit of the air (VPD) and soil moisture (Maier-Maercker 1998). The balance of this feedback loop varies among species depending on their specific eco-physiological requirements and strategies. Yet, some studies also report closed stomata in herbaceous plants and tree seedlings even when there was ample soil moisture, if the air was considerably dry and VPD consequently elevated (Leuschner, 2002; Lendzion & Leuschner, 2008; Kupper *et al.*, 2011). Stomatal control and therefore photosynthetic efficiency are also influenced by levels of CO_2 in the air (Kramer & Boyer 1995), which is additionally released from the forest floor by decomposition processes and root respiration (Neufeld & Young 2003), particularly when soils are moist and warm (Deng *et al.* 2010; Lloyd & Taylor 1994; Raich & Tufekciogul 2000).

The interplay of all above-mentioned microclimatic and microsite factors changes during the growing season and so does the impact of these factors on plant processes (Wu, Jansson & Kolari 2012; Ogle *et al.* 2012). Equally, the requirements and limitations of plant growth follow seasonal patterns. Early in the season, for example, germinating seeds and young seedlings may depend on the moderating capacity of canopy with respect to temperature extremes, whereas in summer, desiccation may pose a problem. While most species in forest ecosystems are largely adapted to the prevailing microclimatic conditions, manipulation experiments to simulate climate change showed differential seedling survival under altered conditions (Lloret *et al.* 2009; Classen *et al.* 2010). Since growing season is projected to be warmer and drier due to climate change in the study region (Appenzeller *et al.* 2011) and many regions of the world (IPCC 2007), it seems important to improve our understanding of how forest microclimate is influenced by the key determinants air temperature, vapour pressure deficit and soil moisture potential.

In this study, we wanted to quantify the relationships between the moderating capacity of the canopy, canopy density and soil moisture at different time frames. Moderating capacity of the canopy (henceforth simply referred to as 'moderating capacity') is defined here as the difference Δ between below-canopy and open-area microclimate. We deliberately focused on *T* and VPD. While *T* controls rates of many processes, VPD may be considered as the drying power of air (Kramer & Boyer 1995) and is therefore more directly related to plant water balance than the more frequently used RH. Our specific questions were as follows: (i) How do canopy density and soil moisture influence below-canopy *T* and VPD compared with the nearby open area? (ii) How does this moderating capacity in *T* and VPD change during dry-soil periods depending on canopy density? (iii) How are diurnal patterns of ΔT and ΔVPD influenced by canopy density and soil moisture? These questions were investigated for each season using long-term data from 11 distinct forest ecosystems in Switzerland. Our analyses revealed several important relationships and threshold effects between forest microclimate, soil moisture and canopy density. The results will be discussed with respect to their meaning for natural seedling establishment in the context of future climate change.

Materials and methods

STUDY SITES

We used meteorological and soil moisture data collected from 1998 to 2011 at 11 of 19 sites within the ongoing Swiss Long-term Forest Ecosystem Research Programme LWF (Innes 1995). Sites represent a wide range of forest ecosystems (Table 1) with respect to species composition, stand structure, altitude and climate and may therefore be representative for most forest ecosystems within central Europe and other temperate climate zones.

METEOROLOGICAL DATA

Each site is equipped with one meteorological station within a forest plot (hereafter referred to as 'below canopy') and one in a nearby (<2 km) plot in a comparable physiographic setting outside of the stand (henceforth referred to as 'open area'). Below-canopy stations were, on average, 185 m away from the closest forest edge, while open-area stations were, on average, 90 m apart from any forest edge. These distances should buffer sufficiently from edge effects (Davies-Colley, Payne & van Elswijk 2000; Heithecker & Halpern 2007), although some studies found edge effects extending >240 m into the forest when winds were high (Chen, Franklin & Spies 1995; Chen *et al.* 1999). The pairwise set-up was designed to investigate the influence of forest ecosystem properties on below-canopy microclimate.

Combined T and RH sensors of the type MP100A (Rotronic AG, Bassersdorf, Switzerland) were placed 2 m above ground according to the standards of ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests). While conditions at ground level may differ significantly from those measured at 2 m above ground, ground-level measurements are much more sensitive to small-scale heterogeneity in topography, soil properties and vegetation and therefore only representative for a few centimetres (Geiger, Aron & Todhunter 2009). Unlike below canopy, ground-level temperatures in the open area are usually higher than at 2 m (Mitscherlich 1981; Suggitt *et al.* 2011). Thus, the effective ground-level moderating capacity is potentially even greater than reported in this study. Recording intervals were set at 10 min (T) and at 60 min (RH). All sensors were calibrated every two to three years by Rotronic AG with an uncertainty of ±0.3 °C and ±1.5%, respectively. RH and T data were quality-checked and improved as described in the study by von Arx, Dobbertin & Rebetez (2012a,b). Precipitation, wind speed and global radiation, as well as other meteorological parameters were equally recorded (see Renaud *et al.* 2011; for details). Hourly VPD was calculated as the difference between saturated (P_{sat}) and effective water pressure of the air (P_{air}). P_{sat} [kPa] was calculated as follows (cf. Monteith & Unsworth 2008; WMO 2008):

$$P_{\mathrm{sat}} = 0.6112 \times \exp((17.62 \times T)/(T + 243.12)) \qquad \text{eqn 1}$$

P_{air} [kPa] was computed as (see Tetens 1930):

$$P_{\mathrm{air}} = P_{\mathrm{sat}} \times \mathrm{RH}/100 \qquad \text{eqn 2}$$

CANOPY DENSITY AND GROUND VEGETATION

Leaf area index (LAI; uncorrected for clumping, thus corresponding to effective LAI) was assessed at each site in summer 2004 (between

Table 1. Description of the study sites and forest stand properties

Site	Latitude (N)/ Longitude (E)	Altitude [m asl]	Mean T Apr–Oct* [°C]	Mean P Apr–Oct* [mm]	Basal area† [$\mathrm{m}^2\ \mathrm{ha}^{-1}$]	Tree height† [m]	Deciduous tree species†,‡ [%]	Dominant tree species†	LAI	LAI class	Ground vegetation cover [%]§
Bettlachstock	47° 13′/7° 25′	1050	11.9	789	41.7	22.2	50	*Fagus sylvatica*	6.5	High	41
Novaggio	46° 01′/8° 50′	1055	13.9	1303	23.4	14.7	100	*Quercus cerris*	4.9	High	67
Jussy	46° 14′/6° 17′	501	14.7	589	28.6	24.1	100	*Quercus sp.*	5.8	High	63
Lausanne	46° 34′/6° 39′	790	13.6	665	41.3	35.8	80	*Fagus sylvatica*	6.9	High	8
Othmarsingen	47° 24′/8° 14′	462	14.6	643	39.7	38.8	100	*Fagus sylvatica*	4.6	High	85
Schaenis	47° 10′/9° 04′	627	14.3	1303	49.4	37.5	90	*Fagus sylvatica*	5.5	High	52
Vordemwald	47° 16′/7° 54′	480	13.9	743	50.2	31.8	15	*Abies alba*	5.1	High	9
Beatenberg	46° 42′/7° 46′	1560	9.5	1002	34.1	26.7	0	*Picea abies*	3.8	Low	84
Celerina	46° 30′/9° 53′	1760	7.1	552	32.8	24.4	15	*Pinus cembra*	1.2	Low	94
Nationalpark	46° 40′/10° 14′	1914	6.8	597	22.0	14.5	0	*Pinus mugo*	1.3	Low	79
Visp	46° 18′/7° 51′	640	15.2	330	4.9	8.5	10	*Pinus sylvestris*	2.3	Low	64

*1998–2011.

†2000.

‡Based on basal area.

§Based on 5–7 vegetation relevé's of 500 m^2 using Braun–Blanquet method between 1994 and 2011 (Thimonier *et al.* 2011).

30 June and 30 August) using a portable LAI-2000 light sensor system (LI-COR, Inc, Lincoln, NE, USA) as described in the study by Thimonier, Sedivy & Schleppi (2010). On the basis of measured LAI values, sites were grouped into two LAI classes: low LAI (<4) corresponding to relatively sparse canopy and high LAI (>4) corresponding to dense canopy. Additional LAI measurements in 1997, 2001 and 2011 confirmed the consistency of this classification; despite some interannual variability of LAI in the range of 0.1–1.7, all sites remained within the attributed LAI class over these years. The high LAI forest ecosystems were mostly dominated by deciduous species (see Table 1). Consequently, canopy density was much lower in early spring and only reached high values after leaves were fully developed. Similarly, low-altitude sites were over-represented in the high LAI class, which reflects a natural linkage between these two variables (see Schleppi, Thimonier & Walthert 2011). Cover of ground vegetation in the forests was, on average, 46% below dense canopy and 80% below sparse canopy (Table 1).

SOIL MOISTURE

Soil matrix potential (SMP), a measure for how strongly water adheres to soil particles (Kramer & Boyer 1995), was determined manually on a bi-weekly basis at the below-canopy sites since 1998. Measurements were taken at five depths (15, 30, 50, 80 and 130 cm) using tensiometers composed of ceramic cups (highflow porous ceramic cups, Soilmoisture Equipment Corp. Santa Barbra, CA, USA) installed permanently in the field. For each depth, the tensiometers were installed at eight or more locations to get a spatially more robust average value (except the 130 cm depth where $n = 3$). The range of measurement was from water saturation until −900 hPa. At the dry site Visp (see Table 2), volumetric soil water content was recorded hourly at three depths (15, 50 and 70 cm) with four replicates per site using time domain reflectometry (TDR; Tektronix 1502B cable tester, Tektronix Inc., Beaverton, OR, USA). SMP and volumetric water content were measured according to the manual of ICP Forests (Raspe *et al.* 2013).

Daily SMP was modelled for the below-canopy sites using CoupModel, a coupled heat and mass transfer model for soil–plant–atmosphere systems (Jansson & Karlberg 2004). Model input parameters were meteorological data (precipitation, T, RH, wind speed, global radiation), stand characteristics (LAI, tree height, stand composition; see Table 1) and the water retention curves (WRC) for each soil horizon. The WRC were calculated using the van Genuchten parameters determined for different classes of bulk density and soil texture (Teepe, Dilling & Beese 2003). Table 2 gives an overview of the soil texture, the estimated water holding capacity and some other soil characteristics. The saturated hydraulic conductivity (K_{sat}) was derived from pedotransfer functions (Eckelmann 2006). The model was calibrated and validated with measured SMP (or, in the case of Visp, daily volumetric water content). The topmost soil layer interacts the most with the atmosphere and thus also shows great fluctuations in SMP. Nevertheless, only model outputs for the horizon 10–20 cm were considered for analysis, because measured data existed at a depth of 15 cm for quality control.

Every day each site was classified as having moist (≥−65 hPa) or dry (≤−350 hPa) soil. While the former threshold corresponds to field capacity, the latter was deliberately chosen to represent moderately dry soils to have sufficient data for the analysis. The quality control of modelled data revealed that 0.4% of the days falling into the 'moist' class according to biweekly measured SMP were classified as 'dry' in the corresponding modelled SMP. This percentage was 8.4% when comparing the 'moist' instead of 'dry' classification, meaning that soils were generally modelled too wet. The obtained classification was then smoothed by an algorithm that classified days with a modelled SMP between −65 and −350 hPa as 'dry' if both neighbouring days were 'dry' and as 'moist' if both neighbouring days were 'moist' to remove some high-frequency fluctuations.

DATA ANALYSIS

Moderating capacity of canopies on forest microclimate was assessed at three different time levels. The dependence of long-term mean differences in daily maximum temperatures (ΔT_{max}) and vapour pressure deficits ($\Delta \mathrm{VPD}_{\mathrm{max}}$) between below-canopy and open-area sites on LAI and soil moisture, respectively, was determined using regression analysis. Third-order polynomial regressions were performed and

Table 2. Characteristics of soils at the study sites: soil depth, soil type and texture (Walthert *et al.* 2003), estimated water holding capacity from the surface to 100 cm depth and measured soil matrix potentials at 15 cm depth (1998–2011)

Site	Soil depth* [m]	Soil type†	Humus type	Soil texture sand-clay‡ [%]	Water holding capacity§ [L m^{-2}]	Soil matrix potential¶ [hPa], percentiles		
						5%	50%	95%
Bettlachstock	0.90	Rendzic Leptosol	Mull	11–53	138	−540	−43	−4
Novaggio	1.30	Dystric Cambisol	Moder	71–11	176	−422	−108	−37
Jussy	0.70	Eutric Gleysol	Mull	20–46	145	−673	−16	+7
Lausanne	3.00	Dystric Cambisol	Mull	51–18	198	−547	−49	−8
Othmarsingen	1.70	Haplic Acrisol	Mull	55–12	161	−577	−39	−9
Schaenis	1.60	Eutric Cambisol	Mull	45–20	232	−199	−22	−4
Vordemwald	>4.50	Dystric Planosol	Moder	19–20	199	−507	−42	−9
Beatenberg	0.65	Podzol	Raw humus	84–8	163	−50	−14	+1
Celerina	>1.00	Podzol	Mull	36–12	169	−274	−69	−21
Nationalpark	>0.10	Calcaric Fluvisol	Moder	27–10	127	−388	−65	−13
Visp	1.05	Calcaric Phaeozem	Moder	36–12	224	−3027	−863	−150

*Soil thickness down to parent material (C or R horizon).

†Following FAO (1988).

‡Soil texture between 10 and 20 cm depth.

§Estimated water holding capacity from 0 to 100 cm depth derived from pedotransfer functions (Teepe, Dilling & Beese 2003).

¶Summary for year-round bi-weekly measurements except for Visp, where modelled soil matrix potential is reported (from April to October, only, since modelled values are less reliable when soils are frozen).

reduced to second- or first-order polynomial regressions if the cubic or quadratic terms were not significant.

Combined effects of season, LAI and soil moisture class on long-term mean ΔT_{max} and ΔVPD_{max} were determined using *t*-tests and Wilcoxon tests. *T*-tests were applied when normality and homoscedasticity of residuals were met according to the Shapiro and Levene tests. Otherwise Wilcoxon tests were performed. In an effort to avoid transitional days between moist- and dry-soil status, only data from homogeneous soil moisture periods (see classification above) lasting at least 10 days and from these only data starting from the tenth day, were considered.

Linear regression analyses were performed to investigate how daily ΔT_{max} and ΔVPD_{max} changed over 20-day homogeneous dry- vs. moist-soil periods, depending on LAI and season. The same analyses were performed for the subperiods of days 1–10 and 11–20 to determine whether the response would change over time.

Furthermore, diurnal courses of ΔT and ΔVPD depending on soil moisture, LAI and season were determined using mean hourly data to look for differences in amplitudes, timing of peaks, changes from positive to negative effects of canopy and vice versa.

Statistical significance was assumed at $P = 0.05$. All statistical analyses were performed in R version 2.14.1 (R Development Core Team 2010).

Results

MEAN RESPONSES OF *T* AND VPD TO CANOPY DENSITY AND SOIL MOISTURE

Below-canopy vs. open-area differences in daily maximum temperature (ΔT_{max}) and vapour pressure deficit (ΔVPD_{max}) increased with increasing canopy density of the forest stand (LAI) and decreased with increasing desiccation of the soils (Fig. 1). Under sparse canopy (LAI < 4) or when soils were very dry, the difference between below-canopy and open-area microclimate levelled off. At the moist end of the SMP scale, ΔVPD_{max} stabilized between a soil moisture potential of −500 to 0 hPa (Fig. 1d).

The influence of LAI on below-canopy microclimate depended on soil moisture. The moderating capacity of dense canopy (LAI > 4) on T_{max} in summer was significantly larger when soils were moist than when they were dry (−3.3 vs. −2.8 °C). In contrast, for VPD_{max}, this effect was larger when soils were dry (−0.52 vs. −0.40 kPa; Fig. 2). Below sparse canopy (LAI < 4), the overall largest dependence of moderating capacity on soil moisture was observed in summer, when T_{max} was reduced by 1.3 °C with moist soils and only by 0.1 °C with dry soils (Fig. 2a). Similarly, VPD_{max} was reduced by 0.11 kPa when soils were moist and even increased by 0.06 kPa compared with the open area when soils were dry (Fig. 2b). Below dense canopy, the largest dependence of moderating capacity on soil moisture was observed in spring, with a reduction of T_{max} by 2.7 °C when soils were dry and 1.7 °C when soils were moist (Fig. 2a). Likewise, during periods of dry soils, VPD_{max} below dense canopy was reduced by 0.38 kPa compared with 0.17 kPa when soils were moist (Fig. 2b), which represented the overall largest dependence of VPD on soil moisture. The effects of LAI and soil moisture on below-canopy microclimate also interacted with and depended on season. In spring and summer, the strongest moderating capacity under sparse canopy (LAI < 4) on both *T* and VPD was observed when soils were moist, whereas under dense canopy, the strongest

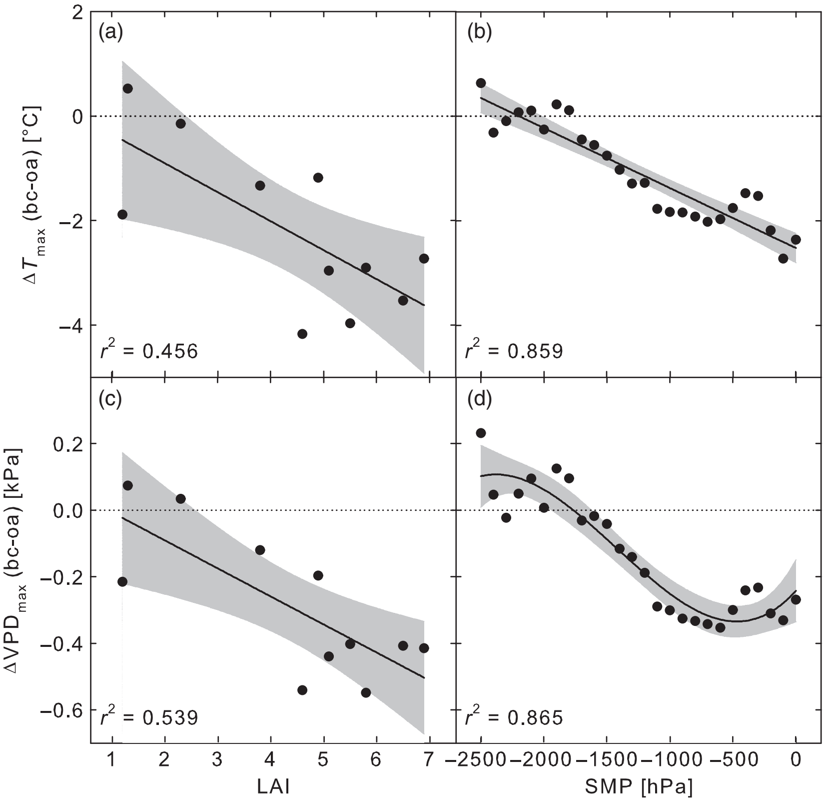


Fig. 1. Difference in maximum daily temperature (ΔT_{max}; a, c) and vapour pressure deficit (ΔVPD_{max}; b, d) between below-canopy (bc) and open-area (oa) plots depending on leaf area index (LAI) and soil matrix potential (SMP) during summer (JJA) based on long-term (1998–2011) data from 11 contrasting forest ecosystems in Switzerland. Third-order polynomial regressions were performed and reduced to second- or first-order polynomial regressions if the cubic or quadratic term was not significant. Significant regression curves ($P \leq 0.05$) and corresponding 95% confidence envelopes are given.

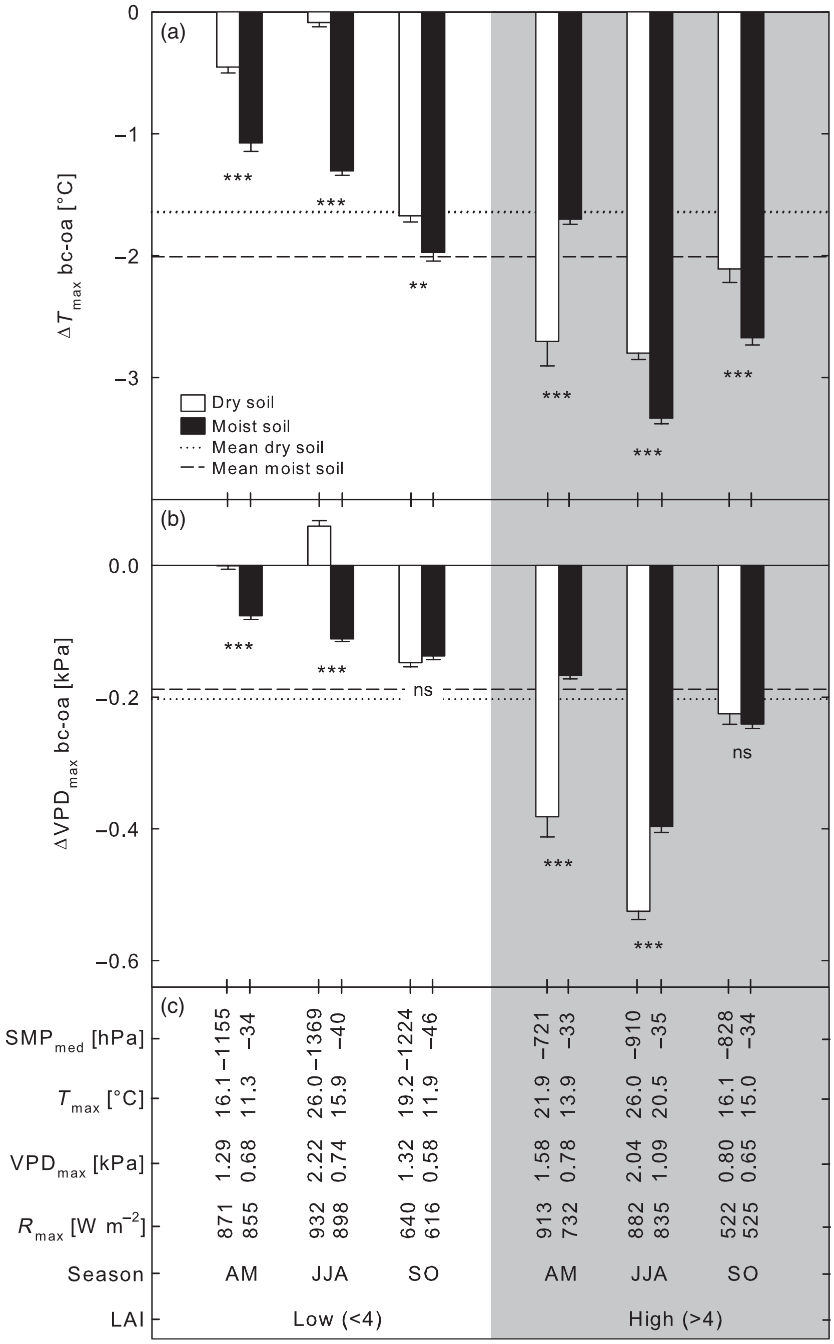


Fig. 2. Mean differences in daily maximum temperature ($\Delta T_{\max}$, a) and vapour pressure deficit ($\Delta VPD_{\max}$, b) between below-canopy (bc) and open-area (oa) plots depending on soil moisture status and leaf area index (LAI) class based on long-term (1998–2011) data from 11 contrasting forest ecosystems in Switzerland. Panel (c) reports the corresponding long-term baseline data of several relevant determinants of $\Delta T_{\max}$ and $\Delta VPD_{\max}$. Only days ≥10 within homogenous soil moisture periods were considered. SMP_{med} – median daily soil matrix potential at bc plots; $T_{\max}/VPD_{\max}/R_{\max}$ – mean daily maximum *T*/VPD/global radiation at oa plots. ns, not significant; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.

moderating capacity was generally recorded when soils were dry (Fig. 2). In fall, soil moisture had no significant impact on $\Delta VPD_{\max}$, regardless of canopy density (Fig. 2b).

DYNAMICS OF *T* AND VPD DURING HOMOGENEOUS PERIODS

Daily differences of $T_{\max}$ and $VPD_{\max}$ over 20-day homogeneous periods of dry and moist soils showed some linear trends that depended on LAI. Significant trends were most frequent in spring and below dense canopy and only partly present in fall and below sparse canopy (Fig. 3). The most conspicuous dynamics occurred below dense canopy in spring. While there was only a weak increase in the moderating capacity when forest soils were moist, moderating capacity when soils were dry increased strongly and even more so in the second half of the considered period (Fig. 3d,j). This is in contrast to low-canopy-density forests. There, moderating capacity in periods of dry soils slightly decreased and approached zero, particularly in the second half of the considered period (Fig. 3a,g). In summer, the moderating capacity decreased also below dense canopy when soils were dry (Fig. 3e,k). An example of how the moderating capacity of canopy on VPD interacted with absolute VPD values and soil moisture is given in Fig. S1 in the Supporting Information for the site at Jussy. While $\Delta VPD_{\max}$ during the moist growing season 2007 co-varied with $VPD_{\max}$, $\Delta VPD_{\max}$ decreased in the dry summer 2006 when $VPD_{\max}$ increased.

DIURNAL COURSE OF ΔT AND ΔVPD

Diurnal patterns of ΔT and ΔVPD showed systematic range shifts that were largely consistent with mean differences with regard to LAI and soil moisture (Fig. 4). However, daily amplitudes were larger in both climatic parameters when soils were dry. There were also changes from positive to negative effects of canopy on night-time understorey *T* and VPD compared with the open area when soils were dry, but hardly so when soils were moist. During daytime, maximum values were always more moderate below canopy than in the open area regardless of soil moisture and LAI. Timing when the maximum differences between below-canopy and open-area *T* and VPD were observed (not to be confused with $\Delta T_{\max}$ and $\Delta \mathrm{VPD}_{\max}$, the differences of daily maximum values) depended consistently on LAI. Below sparse canopy, the diurnal maximum moderating capacity was already reached at around 9 AM in the morning, while it was only reached at around 3 PM below dense canopy. Timing of maximum moderating capacity below dense canopy therefore approximately matched with timing of daily maximum *T* and VPD. In contrast, moderating capacity below sparse canopy was comparably small at the time of daily maximum *T* and VPD.

Discussion

The aim of this study was to quantify the relationships between below-canopy vs. open-area air temperature (*T*) and vapour pressure deficit (VPD) depending on canopy density (LAI) and soil moisture at different time-scales. While the moderating capacity of forest canopy on these two important microclimatic parameters generally increased, as expected, with increasing LAI and soil moisture content, we also observed some unforeseen interactions between these two determinants. The patterns and dynamics of ΔT and ΔVPD were mostly similar, which is an effect of the temperature dependence of VPD. The influence of soil moisture on moderating capacity was strongest in spring and summer and weakest in fall.

INTERACTIVE INFLUENCE OF LAI AND SOIL MOISTURE ON BELOW-CANOPY *T* AND VPD

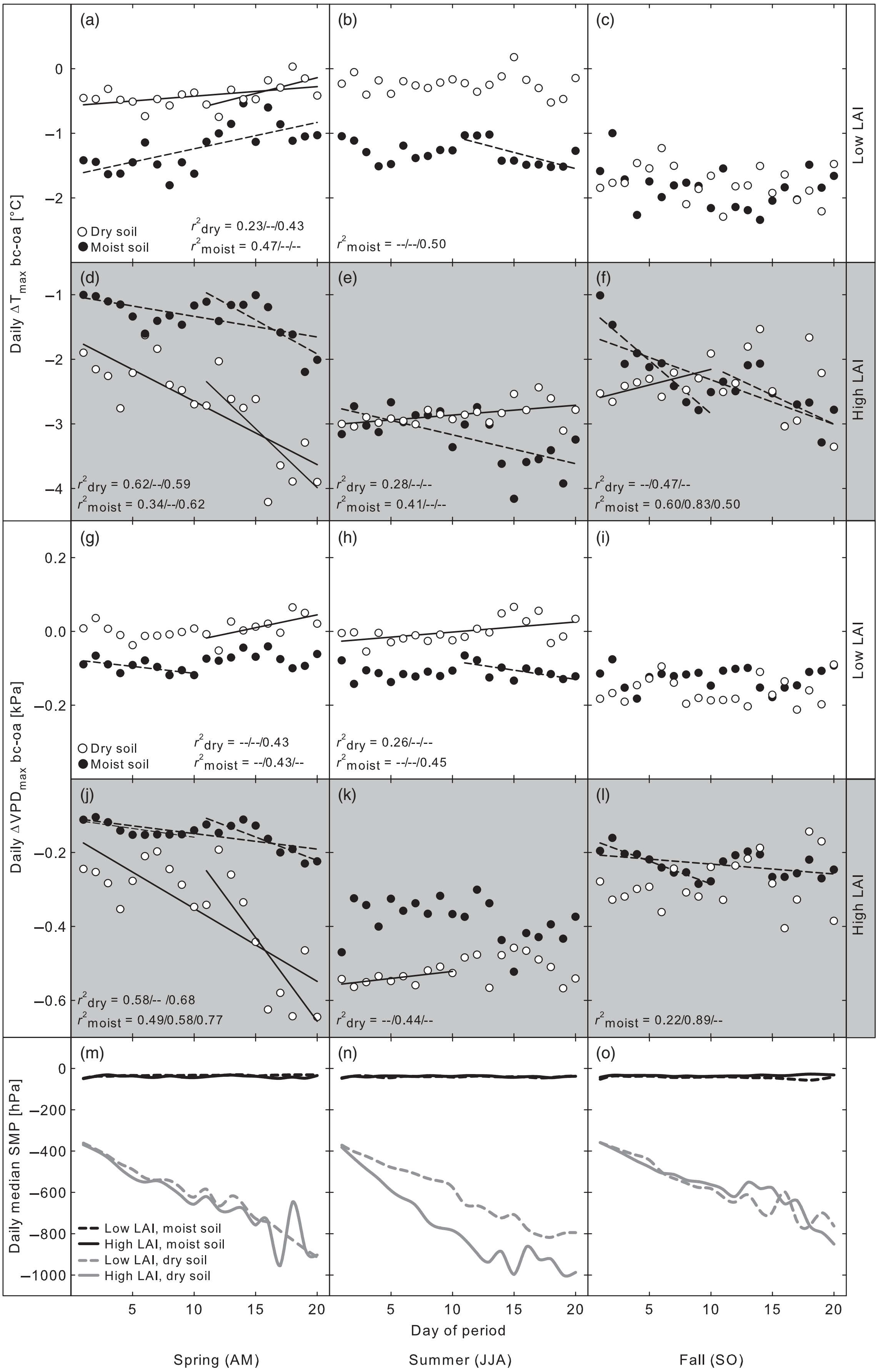
Canopy density and soil moisture are partly coupled: everything else being equal, forest stands with a dense canopy transpire more water and therefore deplete soil moisture faster than areas having a sparse or no canopy (Aussenac 2000; Breshears *et al.* 1997; Peck, Zenner & Palik 2012; Scharenbroch & Bockheim 2007; cf. Fig. 3n). Conversely, dense-canopy forests usually grow in less water-limited regions (Breshears *et al.* 1997; Schleppi, Thimonier & Walthert 2011) where soils are mostly re-wetted before soil moisture drops below a critical threshold.

This natural interrelationship between canopy density and soil moisture may provide the background for understanding the consistently lower springtime moderating capacity on daily maximum *T* and VPD observed below sparse canopy when soils were dry, while the opposite applied below dense canopy. The small (*T*) and absent (VPD) moderation below sparse canopy probably reflects the exclusive shading effect by canopy, whereas during moist-soil conditions evaporative cooling and sensible heat flux added to the moderating capacity of canopy (Geiger, Aron & Todhunter 2009). Two different effects probably explain the contrasting larger moderating capacity generally observed below dense canopy during dry- vs. moist-soil condition. The first explanation is provided by the generally stronger radiation, warmer *T* and increased VPD in those periods (see Fig. 2), which is commonly associated with increased moderating capacity (Renaud & Rebetez 2009; Geiger, Aron & Todhunter 2009). Secondly, soil water content may only have been depleted to a point where a certain moderating effect remained.

The contrast in springtime moderating capacity between sparse- and dense-canopy forest sites also prevailed during periods of contrasting soil moisture. During periods of dry soils, the moderating capacity below sparse canopy tended to decrease and cancel out, particularly during the second half of the 20-day periods. The opposite pattern was found below dense canopy, where the progressive leafing of the dense-canopy forest ecosystems led to rising shading from solar radiation. The magnitude of this progressively increasing shading most probably corresponds to the observed increasing moderating capacity during the moist-soil period. Note that this effect is missing at the sparse-canopy sites because they were dominated by evergreens.

There was also a contrasting seasonal pattern of moderating capacity depending on canopy density. Unlike below dense canopy and as commonly reported (e.g. Geiger, Aron & Todhunter 2009; Renaud & Rebetez 2009; Grimmond, Robeson & Schoof 2000; Morecroft, Taylor & Oliver 1998), the moderating capacity below sparse canopy was nearly absent (*T*) or even negative (VPD) during periods of dry soils in summer, when conditions were physiologically most demanding for plant growth. This seasonal divergence may be explained by the high solar altitude in summer, when radiation was more vertical and therefore reached the soil through gaps in the sparse canopy more easily than in the other seasons (Geiger, Aron & Todhunter 2009; Mitscherlich 1981). The effect is amplified because the crown geometries of conifers dominating in our sparse-canopy sites are generally conical as opposed to the more widespread, horizontally distributed crowns of broadleaved species dominating at our dense-canopy sites (Baldocchi & Collineau 1994). In addition, soil moisture reached lowest levels at sparse-canopy sites in summer, thus contributing less to evaporative cooling. During summer, *T* and VPD also showed the most notable divergence, particularly at the dense-canopy sites. Because of the coupling of VPD with *T* (see eqn 1), this divergence must be due to differences in air humidity.

On a diurnal level, moist soils displayed more constant moderating capacity than dry soils irrespective of canopy density. This contrast was probably a consequence of energy absorption by the water vapour in the air and evaporative cooling (Monteith & Unsworth 2008), which were both more pronounced during moist-soil conditions. The observed early peak of moderating capacity at the sparse-canopy sites – well before


(a)
(b)
(c)
Low LAI
Daily ΔT$_{max}$ bc-oa [°C]
0
−1
−2
○ Dry soil
● Moist soil
r^2_{dry} = 0.23/--/0.43
r^2_{moist} = 0.47/--/--
r^2_{moist} = --/--/0.50
(d)
(e)
(f)
High LAI
−1
−2
−3
−4
r^2_{dry} = 0.62/--/0.59
r^2_{moist} = 0.34/--/0.62
r^2_{dry} = 0.28/--/--
r^2_{moist} = 0.41/--/--
r^2_{dry} = --/0.47/--
r^2_{moist} = 0.60/0.83/0.50
(g)
(h)
(i)
Low LAI
Daily ΔVPD$_{max}$ bc-oa [kPa]
0.2
0.0
−0.2
○ Dry soil
● Moist soil
r^2_{dry} = --/--/0.43
r^2_{moist} = --/0.43/--
r^2_{dry} = 0.26/--/--
r^2_{moist} = --/--/0.45
(j)
(k)
(l)
High LAI
−0.2
−0.4
−0.6
r^2_{dry} = 0.58/-- /0.68
r^2_{moist} = 0.49/0.58/0.77
r^2_{dry} = --/0.44/--
r^2_{moist} = 0.22/0.89/--
(m)
(n)
(o)
Daily median SMP [hPa]
0
−200
−400
−600
−800
−1000
Low LAI, moist soil
High LAI, moist soil
Low LAI, dry soil
High LAI, dry soil
5
10
15
20
Day of period
Spring (AM)
Summer (JJA)
Fall (SO)

daytime peaks of *T* and VPD were reached – no doubt goes back to the same interaction of canopy structure, crown geometry and solar altitude as detailed in the previous paragraph. This explanation is further supported by the quite consistent cancelling-out peak observed at noon. Following this argument, one would expect a second peak of elevated moderating capacity in the afternoon. While such a peak indeed occurred, its comparably small magnitude is likely due to sensible heat flux: solar radiation during the first half of the day warmed up the top layers of forest soils, and this stored energy was released to the atmosphere later in the day (Geiger, Aron & Todhunter 2009).

SIGNIFICANCE FOR FOREST ECOSYSTEMS IN THE WAKE OF CLIMATE CHANGE

When moving from dense- to sparse-canopy forests, the moderating capacity on microclimate deteriorated in three different ways. First, the mean moderating capacity decreased. Secondly, moderation was smallest or absent under low-soil-moisture conditions, as well as at times of the day and the growing season when conditions for growth of tree seedlings were most challenging. Thirdly, moderating capacity tended to decrease during dry-soil periods (Fig. 5). The seemingly unsupportive properties of sparse canopy on understorey microclimate may not be considered a serious issue, because seedlings growing in such forest ecosystems usually belong to species adapted to these conditions (Ellenberg 1986). However, if climate change leads to an identical drop of moderating capacity, the time above an assumed critical threshold during a dry period will be much longer at a moist than a dry site (Fig. 6). In other words, the safety margin in a sparse-canopy forest ecosystem may be narrower, should drought events become more frequent, severe and/or prolonged. Climate change scenarios for the study region and additional regions in the temperate climate zones predict just that (Appenzeller *et al.* 2011; IPCC 2007). A decrease in the moderating capacity of forest ecosystems, together with anticipated general warming, prolonged dry spells in summer and greater climate variability, may overstrain the resilience of tree seedlings, especially those growing in physiologically marginal habitats.

On a more long-term perspective, crown defoliation in dense-canopy forest ecosystems as direct (e.g. drought stress; Carnicer *et al.* 2011; Seidling, Ziche & Beck 2012; Rood *et al.* 2000) and indirect responses (e.g. increased attacks by insects and pathogens; Allen *et al.* 2010; Mattson & Haack 1987; Daniels *et al.* 2011) of climate change may alter their moderating capacity towards that of sparse-canopy forest ecosystems. Such a shift could probably expose young seedlings from current tree species to conditions detrimental for successful establishment, as a manipulation experiment by Lloret *et al.* (2009) in Mediterranean shrublands showed. Furthermore, sparser canopies often feature greater ground vegetation cover (see Table 1), which may increase competition by herbaceous species (Crunkilton, Pallardy & Garrett 1992; Plamboeck, North & Dawson 2008). While a greater share of precipitation reaches the ground through sparser canopies, more direct solar radiation will counteract this potential advantage by faster desiccating the top soil layer where the young seedlings root (Castro *et al.* 2004).

Climate change is also associated with increasing atmospheric CO_2 concentrations, which may stimulate growth and productivity (Neufeld & Young 2003) and therefore increase canopy density. However, this only applies to regions where there is adequate moisture or growth is currently limited by cold (Chmura *et al.* 2011; Wertin, McGuire & Teskey 2012). Moreover, higher growth would also increase competition for nutrients between established trees and understorey vegetation (Neufeld & Young 2003). Increasing temperatures also affect phenology; specifically, a significant advancement of spring has been observed (Menzel *et al.* 2006). Prolonged spring growth activity may deplete soil moisture and therefore decrease moderating capacity in summer, besides other known risks of earlier phenology such as damage by late frost (Neufeld & Young 2003) and inappropriate root-to-shoot ratio to sustain dry summer periods (Richter *et al.* 2012).

There were some characteristics and limitations of potential relevance in our study. In the subset of sparse-canopy forests, data from the dry site Visp and the moist site Beatenberg were naturally overrepresented in the analyses of prolonged, homogeneous dry, respectively, moist spells. Furthermore, sparse-canopy forests were dominated by evergreen conifer species and dense-canopy forests by deciduous broadleaved species. Deciduous broadleaved tree species usually have more fine roots (Alvarez-Uria & Körner 2011 and references therein) and close stomata later than evergreen conifer species (Marshall & Waring 1984). Species identity of overstorey trees may thus alter the temporal and spatial patterns of water depletion and therefore affect forest microclimate and establishment of seedlings. Finally, besides *T* and VPD, overstorey tree species composition usually also influences abiotic (soil pH, texture, nutrient levels, litter amounts, etc.) and biotic (cover and composition of herbaceous vegetation) conditions in the forest floor (Gilliam & Roberts 2003; George & Bazzaz 2003; Monnier *et al.* 2012), which all affect the survivability of seedlings in the understorey.

Conclusion

In this study, we used a unique set-up of below-canopy and open-area meteorological reference stations replicated at a wide

Fig. 3. Dynamics of differences in daily maximum temperature ($\Delta T_{\max}$; a–f) and vapour pressure deficit ($\Delta \mathrm{VPD}_{\max}$; g–l) between below-canopy (bc) and open-area (oa) plots depending on leaf area index (LAI) during homogeneous 20-day periods of dry vs. moist soil based on long-term (1998–2011) data from 11 contrasting forest ecosystems in Switzerland. Corresponding dynamics of daily soil matrix potential (SMP) are given in m-o. Significant linear regression lines ($P \leq 0.05$) are depicted for the entire 20-day period, days 1–10 and days 11–20 of each period. The corresponding r^2-values are reported in that order. Note that scales between low and high LAI panels are shifted, while depicted scale ranges are identical.

range of distinct forest ecosystems to investigate the influence of canopy density and soil moisture on understorey microclimate. We demonstrated that canopy density and soil moisture interact in a complex way that depends on time-scale (seasons, multiday periods, diurnal cycles) to create a distinct understorey microclimate. Our results suggest that there is a threshold

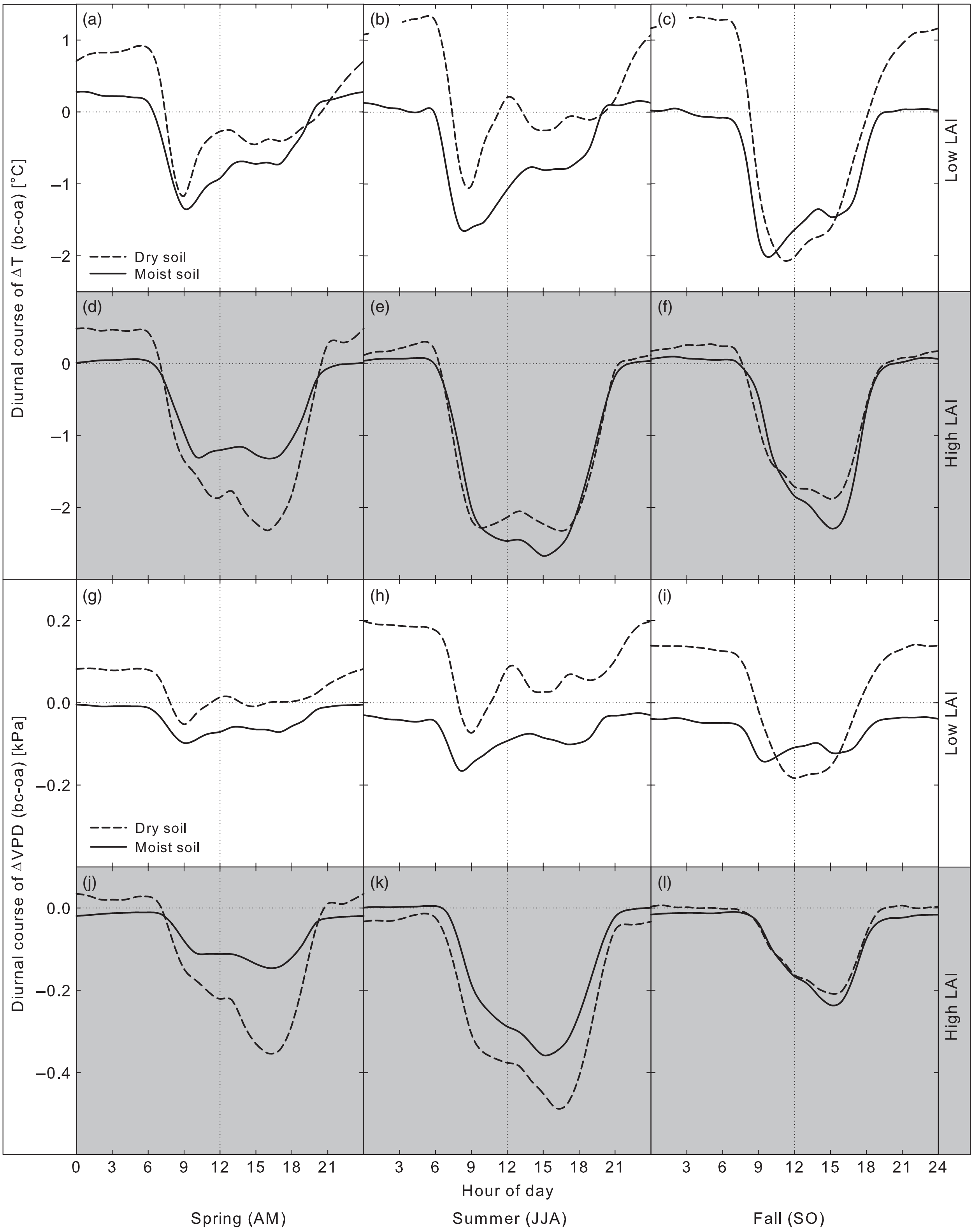


Fig. 4. Diurnal patterns of differences in temperature (ΔT; a–f) and vapour pressure deficit (ΔVPD; g–l) between below-canopy (bc) and open-area (oa) plots depending on leaf area index (LAI) during dry- vs. moist-soil periods based on long-term (1998–2011) data from 11 contrasting forest ecosystems in Switzerland. Note that scales between low and high LAI panels are shifted, while depicted scale ranges are identical.

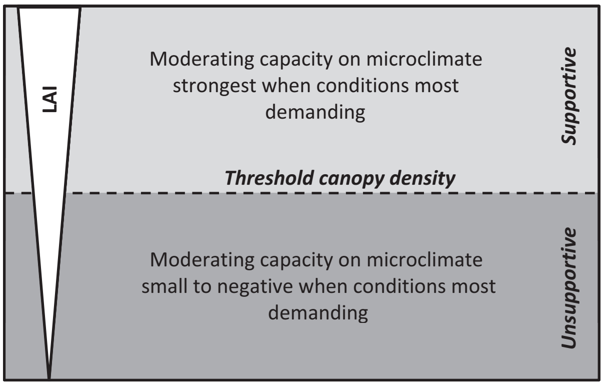


Fig. 5. Threshold canopy density for moderating capacity of forest canopy on understorey microclimate. Above the threshold, the moderating capacity was strongest at times (i) of the day, (ii) within periods and (iii) of the year when conditions were physiologically most demanding for establishing seedlings (‘supportive’). Below the threshold, the timing of strongest moderating capacity and most demanding conditions did not match (‘unsupportive’).

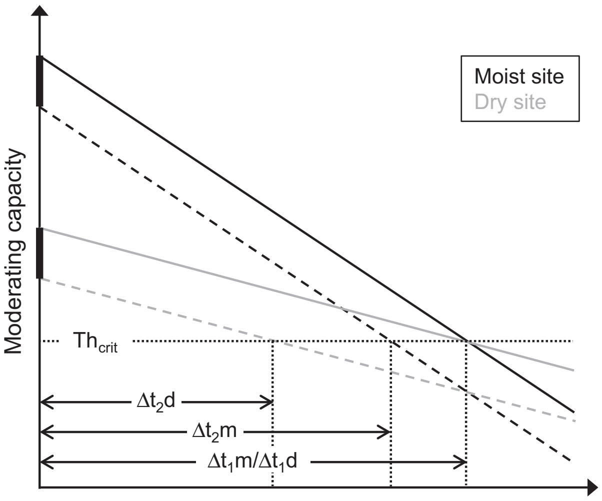


Fig. 6. Conceptual model of how climate change may affect below-canopy microclimatic moderating capacity in a moist vs. dry forest ecosystem during a dry spell in summer. Moderating capacity at a moist site is initially greater, but may decrease quicker (solid black line) than at a dry site (solid grey line). After continued drought (Δt_1m/Δt_1d), moderating capacity at both sites may cross a hypothetical threshold ($\mathrm{Th_{crit}}$) below which conditions for seedling growth may turn detrimental. An identical scale shift in moderating capacity through climate change would shorten the time that below-canopy microclimate remains above $\mathrm{Th_{crit}}$ much more at the dry (Δt_2d) than the moist site (Δt_2m).

canopy density, likely linked to site-specific water availability, below which the moderating capacity switches from supportive (strongest during physiologically most demanding conditions) to unsupportive (weakest or absent during physiologically most demanding conditions) for seedling establishment. It is possible that crossing of such canopy-density thresholds as induced by climate change alters below-canopy microclimate in a way that precludes successful establishment of some tree species or limits establishment to particularly favourable years, ultimately changing forest ecosystem structure and functioning. Our results demonstrate the importance of quantifying below-canopy microclimate depending on different functional aspects and time frames. Furthermore, we substantiate the need to improve the knowledge of physiological requirements of tree seedlings of different species to adjust management and mitigation plans in response to climate change.

Acknowledgements

This paper is dedicated to the memory of Matthias Dobbertin (deceased abruptly 31 October 2012), who contributed conceptually, as did Sonia Seneviratne and Heidi Mittelbach. Gustav Schneiter collected the meteorological data, and Peter Jakob helped handling the associated data base. Lorenz Walthert contributed to soil moisture modelling. Julian Helfenstein improved language and consistency. This project was supported by a grant within the program ‘Forest and Climate Change’ from the Swiss Federal Office for the Environment FOEN and Swiss Federal Research Institute for Forest, Snow and Landscape Research WSL.

References

Aasamaa, K. & Sõber, A. (2011) Responses of stomatal conductance to simultaneous changes in two environmental factors. *Tree Physiology*, **31**, 855–864.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Alvarez-Uria, P. & Körner, C. (2011) Fine root traits in adult trees of evergreen and deciduous taxa from low and high elevation in the Alps. *Alpine Botany*, **121**, 107–112.

Appenzeller, C., Bey, I., Croci-Maspoli, M., Fuhrer, J., Knutti, R., Kull, C. & Schaer, C. (2011) *Swiss Climate Change Scenarios CH2011*. C2SM, MeteoSwiss, ETH Zurich, NCCR Climate and OcCC, Zurich.

von Arx, G., Dobbertin, M. & Rebetez, M. (2012a) Detecting and correcting sensor drifts in long-term weather data. *Environmental Monitoring and Assessment*, **185**, 4483–4489.

von Arx, G., Dobbertin, M. & Rebetez, M. (2012b) Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agricultural and Forest Meteorology*, **116–167**, 144–155.

Aussenac, G. (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, **57**, 287–301.

Baldocchi, D.D. & Collineau, S. (1994) The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. *Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above and Belowground* (eds M.M. Caldwell & R.W. Pearcy), pp. 21–72. Academic Press, San Diego, CA.

Breshears, D.D., Rich, P.M., Barnes, F.J. & Campbell, K. (1997) Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications*, **7**, 1201–1215.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G. & Penuelas, J. (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 1474–1478.

Castro, J., Zamora, R., Hódar, J.A. & Gómez, J.M. (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, **92**, 266–277.

Chen, J.Q., Franklin, J.F. & Spies, T.A. (1993) Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, **63**, 219–237.

Chen, J.Q., Franklin, J.F. & Spies, T.A. (1995) Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**, 74–86.

Chen, J.Q., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L. & Franklin, J.F. (1999) Microclimate in forest ecosystem and landscape ecology - Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, **49**, 288–297.

Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shaw, D.C. & St Clair, J.B. (2011) Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. *Forest Ecology and Management*, **261**, 1121–1142.

Classen, A.T., Norby, R.J., Campany, C.E., Sides, K.E. & Weltzin, J.F. (2010) Climate change alters seedling emergence and establishment in an old-field ecosystem. *PLoS ONE*, **5**, 1–8.

Closa, I., Irigoyen, J.J. & Goicoechea, N. (2010) Microclimatic conditions determined by stem density influence leaf anatomy and leaf physiology of beech (*Fagus sylvatica* L.) growing within stands that naturally regenerate from clear-cutting. *Trees-Structure and Function*, **24**, 1029–1043.

Crunkilton, D.D., Pallardy, S.G. & Garrett, H.E. (1992) Water relations and gas exchange of northern red oak seedlings planted in a central Missouri clearcut and shelterwood. *Forest Ecology and Management*, **53**, 117–129.

Daniels, L.D., Maertens, T.B., Stan, A.B., McCloskey, S.P.J., Cochrane, J.D. & Gray, R.W. (2011) Direct and indirect impacts of climate change on forests: three case studies from British Columbia. *Canadian Journal of Plant Pathology-Revue Canadienne De Phytopathologie*, **33**, 108–116.

Davies-Colley, R.J., Payne, G.W. & van Elswijk, M. (2000) Microclimate gradients across a forest edge. *New Zealand Journal of Ecology*, **24**, 111–121.

Deng, Q., Zhou, G., Liu, J., Liu, S., Duan, H. & Zhang, D. (2010) Responses of soil respiration to elevated carbon dioxide and nitrogen addition in young subtropical forest ecosystems in China. *Biogeosciences*, **7**, 315–328.

Eckelmann, W. (2006) *Bodenkundliche Kartieranleitung. 5. Verbesserte und Erweiterte Auflage ["Pedological Mapping Guidelines. 5th Improved and Extended Edition"]*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Ellenberg, H. (1986) *Vegetation Mitteleuropas mit den Alpen in Ökologischer Sicht ["Vegetation of Central Europe and the Alps From an Ecological Perspective"]*. Ulmer, Stuttgart.

FAO (1988) *FAO/Unesco Soil Map of the World, Revised Legend, With Corrections and Updates. World Soil Resources Report 60*. Reprinted with updates as Technical Paper 20, ISRIC, Wageningen 1997. FAO, Rome.

Ferranti, L. & Viterbo, P. (2006) The European summer of 2003: sensitivity to soil water initial conditions. *Journal of Climate*, **19**, 3659–3680.

Ferrez, J., Davison, A.C. & Rebetez, M. (2011) Extreme temperature analysis under forest cover compared to an open field. *Agricultural and Forest Meteorology*, **151**, 992–1001.

Fischer, E.M., Seneviratne, S.I., Vidale, P.L., Luthi, D. & Schar, C. (2007) Soil moisture - Atmosphere interactions during the 2003 European summer heat wave. *Journal of Climate*, **20**, 5081–5099.

Geiger, R., Aron, R.H. & Todhunter, P. (2009) *The Climate Near the Ground*. Rowman & Littlefield, Lanham, MD.

George, L.O. & Bazzaz, F.A. (2003) The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 265–282. Oxford University Press, Oxford, UK.

Gilliam, F.S. & Roberts, M.R. (2003) Interactions between the herbaceous layer and overstory canopy of eastern forests. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 198–223. Oxford University Press, Oxford, UK.

Grimmond, C.S.B., Robeson, S.M. & Schoof, J.T. (2000) Spatial variability of micro-climatic conditions within a mid-latitude deciduous forest. *Climate Research*, **15**, 137–149.

Harper, J.L. & White, J. (1974) The demography of plants. *Annual Review of Ecology and Systematics*, **5**, 419–463.

Heithecker, T.D. & Halpern, C.B. (2007) Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. *Forest Ecology and Management*, **248**, 163–173.

Hirschi, M., Seneviratne, S.I., Alexandrov, V., Boberg, F., Boroneant, C., Christensen, O.B., Formayer, H., Orlowsky, B. & Stepanek, P. (2011) Observational evidence for soil-moisture impact on hot extremes in southeastern Europe. *Nature Geosciences*, **4**, 17–21.

Innes, J.L. (1995) Theoretical and practical criteria for the selection of ecosystem monitoring plots in Swiss forests. *Environmental Monitoring and Assessment*, **36**, 271–294.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Summary for Policymakers*. IPCC, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jaeger, E. & Seneviratne, S. (2011) Impact of soil moisture–atmosphere coupling on European climate extremes and trends in a regional climate model. *Climate Dynamics*, **36**, 1919–1939.

Jansson, P.E. & Karlberg, L. (2004) *Coupled Heat and Mass Transfer Model for Soil-Plant-Atmosphere Systems*. Royal Institute of Technology, Stockholm.

Kramer, J.P. & Boyer, J.S. (1995) *Water Relations of Plants and Soils*. Academic Press, San Diego, CA.

Kupper, P., Sõber, J., Sellin, A., Lõhmus, K., Tullus, A., Räim, O., Lubenets, K., Tulva, I., Uri, V., Zobel, M., Kull, O. & Sõber, A. (2011) An experimental facility for free air humidity manipulation (FAHM) can alter water flux through deciduous tree canopy. *Environmental and Experimental Botany*, **72**, 432–438.

Ladjal, M., Deloche, N., Huc, R. & Ducrey, M. (2007) Effects of soil and air drought on growth, plant water status and leaf gas exchange in three Mediterranean cedar species: *Cedrus atlantica*, *C. brevifolia* and *C. libani*. *Trees – Structure and Function*, **21**, 201–213.

Lendzion, J. & Leuschner, C. (2008) Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. *Forest Ecology and Management*, **256**, 648–655.

Leuschner, C. (2002) Air humidity as an ecological factor for woodland herbs: leaf water status, nutrient uptake, leaf anatomy, and productivity of eight species grown at low or high vpd levels. *Flora - Morphology, Distribution, Functional Ecology of Plants*, **197**, 262–274.

Lloret, F., Penuelas, J. & Estiarte, M. (2005) Effects of vegetation canopy and climate on seedling establishment in Mediterranean shrubland. *Journal of Vegetation Science*, **16**, 67–76.

Lloret, F., Penuelas, J., Prieto, P., Llorens, L. & Estiarte, M. (2009) Plant community changes induced by experimental climate change: seedling and adult species composition. *Perspectives in Plant Ecology Evolution and Systematics*, **11**, 53–63.

Lloyd, J. & Taylor, J.A. (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Ma, S.Y., Concilio, A., Oakley, B., North, M. & Chen, J.Q. (2010) Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. *Forest Ecology and Management*, **259**, 904–915.

Maier-Maercker, U. (1998) Dynamics of change in stomatal response and water status of *Picea abies* during a persistent drought period: a contribution to the traditional view of plant water relations. *Tree Physiology*, **18**, 211–222.

Marshall, J.D. & Waring, R.H. (1984) Conifers and broadleaf species: stomatal sensitivity differs in western Oregon. *Canadian Journal of Forest Research*, **14**, 905–908.

Mattson, W.J. & Haack, R.A. (1987) The role of drought in outbreaks of plant-eating insects. *BioScience*, **37**, 110–118.

Mellander, P.-E., Bishop, K. & Lundmark, T. (2004) The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *Forest Ecology and Management*, **195**, 15–28.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R. *et al.* (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976.

Meyer, C.L., Sisk, T.D. & Covington, W.W. (2001) Microclimatic changes induced by ecological restoration of ponderosa pine forests in northern Arizona. *Restoration Ecology*, **9**, 443–452.

Mitscherlich, G. (1981) *Waldklima und Wasserhaushalt ["Forest Climate and Water Relations"]*. Sauerländer, Frankfurt am Main.

Monnier, Y., Prevosto, B., Ripert, C., Corbani, A.C. & Fernandez, C. (2012) Forest microhabitats differentially influence seedling phenology of two co-existing Mediterranean oak species. *Journal of Vegetation Science*, **23**, 260–270.

Monteith, J. & Unsworth, M. (2008) *Principles of Environmental Physics*. Academic Press, Burlington, MA.

Morecroft, M.D., Taylor, M.E. & Oliver, H.R. (1998) Air and soil microclimates of deciduous woodland compared to an open site. *Agricultural and Forest Meteorology*, **90**, 141–156.

Neufeld, H.S. & Young, D.R. (2003) Ecophysiology of the herbaceous layer in temperate deciduous forests. *The Herbaceous Layer in Forests of Eastern North America* (eds F.S. Gilliam & M.R. Roberts), pp. 38–90. Oxford University Press, Oxford, UK.

Ogle, K., Lucas, R.W., Bentley, L.P., Cable, J.M., Barron-Gafford, G.A., Griffith, A. *et al.* (2012) Differential daytime and night-time stomatal behavior in plants from North American deserts. *New Phytologist*, **194**, 464–476.

Peck, J.E., Zenner, E.K. & Palik, B. (2012) Variation in microclimate and early growth of planted pines under dispersed and aggregated overstory retention in mature managed red pine in Minnesota. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **42**, 279–290.

Plamboeck, A.H., North, M. & Dawson, T.E. (2008) Conifer seedling survival under closed-canopy and manzanita patches in the Sierra Nevada. *Madrono*, **55**, 191–201.

Porte, A., Huard, F. & Dreyfus, P. (2004) Microclimate beneath pine plantation, semi-mature pine plantation and mixed broadleaved-pine forest. *Agricultural and Forest Meteorology*, **126**, 175–182.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Development Core Team, Vienna, Austria.

Raich, J. & Tufekciogul, A. (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry*, **48**, 71–90.

Raspe, S., Beuker, E., Preuhsler, T., Bastrup-Birk, A., Raspe, S., Bastrup-Birk, A. *et al.* (2013) Meteorology. *Forest Monitoring. Methods for Terrestrial Investigations in Europe With an Overview of North America and Asia* (eds M. Ferretti & R. Fischer), pp. 319–336. Elsevier, Amsterdam.

Renaud, V. & Rebetez, M. (2009) Comparison between open-site and below-canopy climatic conditions in Switzerland during the exceptionally hot summer of 2003. *Agricultural and Forest Meteorology*, **149**, 873–880.

Renaud, V., Innes, J.L., Dobbertin, M. & Rebetez, M. (2011) Comparison between open-site and below-canopy climatic conditions in Switzerland for different types of forests over 10 years (1998−2007). *Theoretical and Applied Climatology*, **105**, 119–127.

Richter, S., Kipfer, T., Wohlgemuth, T., Calderón Guerrero, C., Ghazoul, J. & Moser, B. (2012) Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia*, **169**, 269–279.

Rood, S.B., Patiño, S., Coombs, K. & Tyree, M.T. (2000) Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees - Structure and Function*, **14**, 248–257.

Scharenbroch, B.C. & Bockheim, J.G. (2007) Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. *Plant and Soil*, **294**, 219–233.

Schleppi, P., Thimonier, A. & Walthert, L. (2011) Estimating leaf area index of mature temperate forests using regressions on site and vegetation data. *Forest Ecology and Management*, **261**, 601–610.

Seidling, W., Ziche, D. & Beck, W. (2012) Climate responses and interrelations of stem increment and crown transparency in Norway spruce, Scots pine, and common beech. *Forest Ecology and Management*, **284**, 196–204.

Seneviratne, S.I., Luthi, D., Litschi, M. & Schar, C. (2006) Land-atmosphere coupling and climate change in Europe. *Nature*, **443**, 205–209.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. & Thomas, C.D. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, **120**, 1–8.

Teepe, R., Dilling, H. & Beese, F. (2003) Estimating water retention curves of forest soils from soil texture and bulk density. *Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde*, **166**, 111–119.

Tetens, O. (1930) Ueber einige meteorologische Begriffe ["About some meteorological terms"]. *Journal of Geophysics*, **6**, 297–309.

Thimonier, A., Sedivy, I. & Schleppi, P. (2010) Estimating leaf area index in different types of mature forest stands in Switzerland: a comparison of methods. *European Journal of Forest Research*, **129**, 543–562.

Thimonier, A., Kull, P., Keller, W., Moser, B. & Wohlgemuth, T. (2011) Ground vegetation monitoring in Swiss forests: comparison of survey methods and implications for trend assessments. *Environmental Monitoring and Assessment*, **174**, 47–63.

Vanwalleghem, T. & Meentemeyer, R.K. (2009) Predicting Forest Microclimate in Heterogeneous Landscapes. *Ecosystems*, **12**, 1158–1172.

Walthert, L., Blaser, P., Lüscher, P., Luster, J. & Zimmermann, S. (2003) *Langfristige Waldökosystem-Forschung LWF in der Schweiz. Kernprojekt Bodenmatrix. Ergebnisse der Ersten Erhebung 1994-1999 ["Long-Term Forest Ecosystem Research LWF in Switzerland. Core Project Soil Matrix. Results of the First Survey 1994–1999"]*. Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zurich.

Wertin, T.M., McGuire, M.A. & Teskey, R.O. (2012) Effects of predicted future and current atmospheric temperature and [CO_2] and high and low soil moisture on gas exchange and growth of *Pinus taeda* seedlings at cool and warm sites in the species range. *Tree Physiology*, **32**, 847–858.

Wicklein, H.F., Christopher, D., Carter, M.E. & Smith, B.H. (2012) Edge effects on sapling characteristics and microclimate in a small temperate deciduous forest fragment. *Natural Areas Journal*, **32**, 110–116.

WMO (2008) *Guide to Meteorological Instruments and Methods of Observation, Appendix 4B. WMO-No. 8 (CIMO Guide)*. WMO, Geneva.

Wu, S.H., Jansson, P.-E. & Kolari, P. (2012) The role of air and soil temperature in the seasonality of photosynthesis and transpiration in a boreal Scots pine ecosystem. *Agricultural and Forest Meteorology*, **156**, 85–103.

Received 9 January 2013; accepted 20 May 2013
Handling Editor: Frank Gilliam

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Comparison of below-canopy daily maximum vapour pressure deficit and the difference to open-area vapour pressure deficit at the site Jussy in two contrasting years.