

Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland

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ARTICLE INFO

Article history:

Received 2 February 2012

Received in revised form 8 June 2012

Accepted 28 July 2012

Keywords:

Air temperature

Climate change

Forest microclimate

Relative humidity

Seedling recruitment

ABSTRACT

Forest canopy generally moderates below-canopy air temperature and relative humidity and thus creates a specific microclimate for tree seedling growth. Climate change will alter the moderating capacity, which may render the below-canopy conditions unsuitable for recruitment of the hitherto dominant tree species. We assigned long-term meteorological data (1997–2010) recorded inside and outside of 14 different forest ecosystems in Switzerland to three forest types (broadleaved, non-pine conifer, pine), two altitudinal levels (low, high), the four seasons and general weather situations (normal, hot/dry, cold/wet) to compare moderating capacity of each of these classifiers. Our results confirmed a general moderating effect of canopy on below-canopy microclimate with a decrease of daily maximum air temperature of up to 5.1 °C (overall average: 1.8 °C) and an increase of daily minimum relative humidity of up to 12.4% (overall average: 5.1%) in the long-term average, respectively. Broadleaved and non-pine conifer forests moderated daytime microclimate about twice as much as pine forests, while at nighttime considerably less cooling down and even negative effects on levels of relative humidity compared to the open area were recorded at the pine forest sites. Moderating capacity was stronger at low altitude than at high altitude. It was strongest during the growing season, particularly in summer, and depended in a complex way on the general weather situation. Deviations from the general seasonal and weather condition patterns most likely occurred when soil moisture pools were depleted. Despite the moderating capacity, below-canopy microclimate did not lag behind open area microclimate. Based on our results we conclude that natural recruitment in pine forests and high-altitude forests may respond most sensitively to climate change.

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1. Introduction

Forest canopy creates a specific understory microclimate that differs from the surrounding local climate. This alteration of local climate is the result of a complex interplay of several stand characteristics and physiographic settings. Regardless of complexity, most studies about forest microclimate found a general moderating effect of forest canopy on common meteorological parameters (e.g., Grimmer et al., 2000; Mitscherlich, 1981; Renaud et al., 2011). Tree seedlings, which constitute the most vulnerable life stage within the life cycle of a tree (Niinemets, 2010), are adapted to and depend on the specific microclimatic conditions created by forest

canopy (Bertrand et al., 2011; Jemison, 1934). Increasing global temperature and frequency of extreme weather events will affect below-canopy microclimate with the potential to shape future structures of forest ecosystems, particularly where natural regeneration is common practice (Bertrand et al., 2011; Cunningham et al., 2006; Dulamsuren et al., 2009; Hunziker and Brang, 2005; Kharuk et al., 2009; Raymond et al., 2006). Forest ecosystems with different characteristics may show different sensitivities to these changes (Lindner et al., 2010). Quantitative data about spatio-temporal relationships between below-canopy microclimate and local open-area climate based on long time frames and a range of different forest ecosystems is scarce, yet important to improve models, optimize forest management, and, ultimately, secure future economical and ecological functioning of forest ecosystem.

The influence of forest canopy on understory microclimate is directly and indirectly related to the presence of canopy and stems. Branches, leaves and needles reflect and absorb part of the solar radiation during the day, allowing less energy to reach the ground below the canopy (Geiger et al., 2009). The degree of absorption is largely determined by stand structure and species composition (Geiger et al., 2009; Hunziker and Brang, 2005; Mitscherlich, 1981; Renaud et al., 2011). During the night, infrared heat released from

Abbreviations: T , air temperature; T_{mean-d} , daytime mean air temperature; T_{mean-n} , nighttime mean air temperature; T_{max} , daily maximum air temperature; T_{min} , daily minimum air temperature; RH , relative humidity; RH_{mean-d} , daytime mean relative humidity; RH_{mean-n} , nighttime mean relative humidity; RH_{max} , daily maximum relative humidity; RH_{min} , daily minimum relative humidity.

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both the ground and plants is partly held back by the canopy above (Geiger et al., 2009; Mitscherlich, 1981). As a consequence forested areas usually cool down less during the night and limit daytime air warming. Several authors showed that this smoothing effect on daily amplitudes of T is most pronounced on warm, sunny days and in dense stands (Holst et al., 2004; Ma et al., 2010; Renaud et al., 2011; Renaud and Rebetez, 2009), but also depends on physiographic settings such as elevation, slope and aspect (Ferrez et al., 2011; Mitscherlich, 1981), distance from forest edge (Chen et al., 1993; Heithecker and Halpern, 2007; Vanwallegem and Meentemeyer, 2009), ground vegetation layer and soil moisture (Fischer et al., 2007; Koster et al., 2004; Seneviratne et al., 2006). Within a stand, canopy and stems offer resistance to the mixing of air and the exchange of air with the surrounding atmosphere (Flemming, 1982; Geiger et al., 2009). Because of this insulating effect, and because evaporation from soil and wet plant surfaces and transpiration by leaves add water to the air while cooling and thus lowering the water holding capacity of the air, absolute and particularly relative humidity are generally increased below canopy (Geiger et al., 2009). The difference to the open area is greatest at noon and in the early afternoon, when daily minimum values are recorded (Geiger et al., 2009; Mitscherlich, 1981). Despite the generally higher RH , daily amplitudes below canopy are usually smaller than in the nearby open area (Abd Latif and Blackburn, 2010; Chen et al., 1993; Renaud et al., 2011).

These general near-ground trends and processes are accompanied by distinct diurnal dynamics of all forest microclimatic parameters relevant to plant growth (solar radiation, temperature, relative humidity, wind) across different stand layers (Geiger et al., 2009; Mitscherlich, 1981; Staudt et al., 2011). Near-ground conditions are generally more sheltered while conditions in the top canopy layer approach ambient conditions. These gradients result in vertical thermodynamic processes between the different layers of forest stands.

Air temperature (T) and relative humidity (RH), which are the focus of this study, are two key meteorological parameters influencing plant growth. T is directly linked to metabolic rates. A recent study by Bertrand et al. (2011) showed that even small warming of around 1°C over a few decades may lead to changes in species composition of forests. RH influences a plant's loss of water due to transpiration to fix a certain amount of CO_2 . More closely related to a plant's transpiration rate is vapor pressure deficit (VPD ; Ladjal et al., 2007; Leuschner, 2002; Maier-Maercker, 1998) that can be calculated from RH and T (ASHRAE, 1972; Buck, 1981; Prenger and Ling, 2001). Relatively small changes in RH and T may disproportionately influence VPD and hence plant water balance (Kramer and Boyer, 1995). Assuming, for instance, a constant RH of 60%, a reduction in T by 2°C from 15° to 13°C would reduce VPD by 12% (from 0.68 to 0.60 kPa); the same reduction of VPD would be attained when assuming constant T of 15°C and an increase in RH from 60% to 65%. However, under natural conditions, a decrease of T is usually linked to a concomitant increase of RH due to physical laws (see above), which thus additionally intensifies the influence of small changes in T and RH on VPD . From the forest regeneration and management perspective it is thus important to know the conditions during which the moderating effect of forest canopy on subjacent microclimate is stronger or weaker, and how this may be affected by ongoing and future climate change.

In this investigation we used long-term meteorological data to quantify the spatio-temporal relationships between below-canopy microclimate (T and RH) and local climate in dependence on a wide range of different forest ecosystems, different seasons and general weather situations. General weather situation here is arbitrarily defined as the prevailing weather conditions during one month, which is a period long enough to affect plant growth (Weber

et al., 2007). Other relevant parameters and determinants of plant growth than T and RH such as solar radiation, wind speed, soil characteristics and rooting depths are excluded from analysis, but partly considered when discussing the results. We hypothesized that (i) forest ecosystems characterised by a high density of canopy and crown would show a greater moderating effect on below-canopy microclimate than those characterised by a low density of canopy and crown; (ii) the moderating effect of forest canopy on below-canopy microclimate would be greater at low than at high altitudes, (iii) greater in summer than in winter, (iv) greatest during warm and dry general weather situations; (v) the previous individual factors would interact with each other, thus demonstrating the complexity of the relationship between below-canopy and open-area microclimate; and (vi) below-canopy T and RH would lag behind corresponding open-area microclimate, particularly in periods and settings experiencing great moderating effects of canopy. Results are discussed in the context of sensitivity of seedling recruitment in different forest ecosystems to future climate change.

2. Materials and methods

2.1. Study sites

The meteorological data used in this study were collected since 1997 at 14 of totally 17 sites within the Swiss Long-term Forest Ecosystem Research Programme LWF (Fig. 1; Innes, 1995) as described in a previous overview study by Renaud et al. (2011) that focused on general patterns of T , RH , photosynthetic active radiation (PAR) and wind speed. In brief, sites were deliberately chosen to include a wide range of forest ecosystems as to forest type and physiographic settings (Table 1) and may therefore represent most forest ecosystems within Central Europe. Each site is equipped with one meteorological station within a forest plot (hereafter referred to as “below canopy”) and one station in a nearby ($<2\text{ km}$) plot in a comparable physiographic setting outside of the stand (hereafter referred to as “open area”). T and RH sensors were placed two meters above ground according to the standards of ICP-Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests). Recording intervals were set at 10 min (T) and at 60 min (RH). All sensors were calibrated every two to three years by the Swiss company Rotronic with an uncertainty of $\pm 0.3^\circ\text{C}$ and $\pm 1.5\%$, respectively.

2.2. Data processing

The 14 sites were classified into the three forest types broadleaved, non-pine conifer and pine. This classification reflected fundamental differences in deciduousness and density of stand and crown, with broadleaved forests being deciduous and having a large basal area (BA; mean $\pm 1\text{ SE}$: 35.4 ± 3.2) and a high leaf area index (LAI; 5.7 ± 0.3), non-pine conifer forests being evergreen and having a large BA (42.7 ± 4.7) and a high LAI (4.2 ± 0.5), and pine forests being evergreen and having a small BA (19.9 ± 8.1) and a low LAI (1.6 ± 0.4 ; Table 1). Species setup within the forest types was variable and included shade-tolerant (e.g. *Fagus sylvatica*) and shade-intolerant species (e.g. *Quercus* sp.). Sites were furthermore classified into low-altitude (400–800 m asl) and high-altitude sites (1000–1900 m asl; cf. Table 1).

Months were grouped into growing season including spring (AM), summer (JJA), autumn (SO) and dormant season corresponding mostly to winter (NDJFM) to investigate differential responses to changes in water availability and demand. While real spring may start earlier than April and real autumn may end later than October

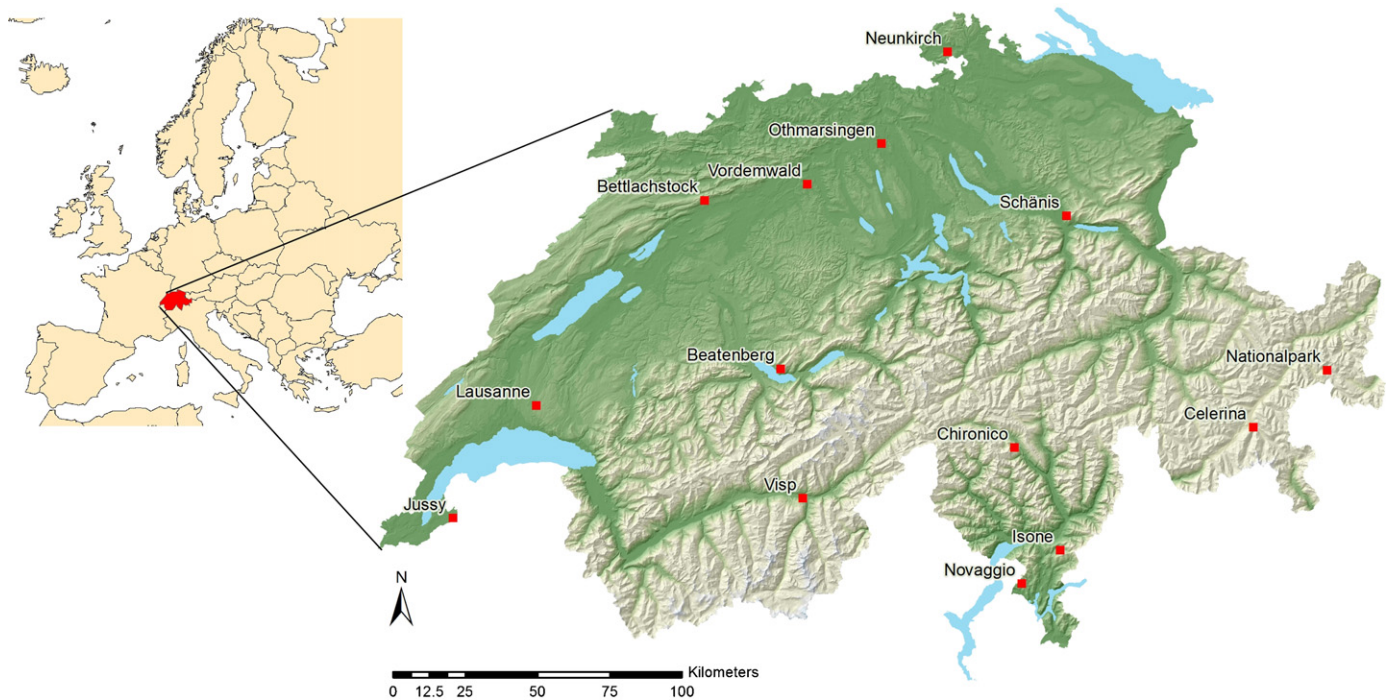


Fig. 1. Location of the 14 sites of the Swiss Long-term Forest Ecosystem Research Programme LWF where meteorological data used in this study was recorded since 1997. Each site is equipped with a meteorological station within a forest plot and a twin station in a nearby (<2 km) open-area plot. Map credit: F. Sutter.

at lower sites, this unvaried classification allowed consistent comparisons between sites.

General weather situations were derived from homogenized monthly long-term air temperature and precipitation data of the period 1961–2010 (Begert et al., 2005; MeteoSwiss, 2011) for all biogeographic regions of Switzerland. Therefore, each month was evaluated whether it was warm and/or dry (hereafter referred to as “hot/dry”), within ordinary ranges (“normal”) or cold and/or wet (“cold/wet”) referring to 0–20%, 20–80% and 80–100% long-term percentiles of the period 1961–2010. This classification was based on water availability and its interaction with temperature as one of the single most important determinants of forest ecosystem functioning besides radiation (Closa et al., 2010; Grimmond et al., 2000; Kharuk et al., 2009). Classes were chosen to represent a wide range of contrasting weather situations to allow estimating the impact of an increased weather variability in the wake of climate change. The effectiveness and effect of this and all other classifications of the data can be seen in Fig. 2.

The basic time intervals used for analysis were half-day aggregates including daytime (extending from 6:00 a.m. to <6:00 p.m. local winter time, i.e., UTC + 1 h) and nighttime (extending from 6:00 p.m. to <6:00 a.m. local winter time, i.e., UTC + 1 h). This time resolution was chosen to account for potentially differential effects of climate change on temperatures during day and night (Beier et al., 2004; Knappenberger et al., 2001; Rebetez and Reinhard, 2008; Revadekar et al., 2012). For each half-day, mean values were calculated (T_{mean-d} , T_{mean-n} , RH_{mean-d} , RH_{mean-n}). Additionally, daily minimum and maximum values (T_{min} , T_{max} , RH_{min} , RH_{max}) and point of time when peak values were reached were determined. Half-days and days that contained more than 5% missing 10 min- T data points were excluded from analysis. A half-day or day was excluded if any 60 min- RH data point was missing. Peak times were excluded if their lag recorded at the below-canopy and the corresponding open-area station was >360 min to exclude data that did not show clear diurnal patterns (e.g. during changing weather periods).

Table 1
Description of the study sites.

Site	Biogeographic region	Longitude (E)/Latitude (N)	Forest type	Dominant tree species	LAI Licor ^a	Basal area [m ² /ha]	Tree height [m]	Altitude [m]	Altitude class
Bettlachstock	Jura	47° 13' / 7° 25'	Broadleaved	<i>Fagus sylvatica</i>	6.5	41.7	22.2	1050	High
Isonne	Southern Alps	46° 08' / 9° 00'	Broadleaved	<i>Fagus sylvatica</i>	5.8	26	17.1	1150	High
Novaggio	Southern Alps	46° 01' / 8° 50'	Broadleaved	<i>Quercus cerris</i>	4.9	23.4	14.7	1055	High
Jussy	Jura	46° 14' / 6° 17'	Broadleaved	<i>Quercus</i> sp.	5.8	28.6	24.1	501	Low
Lausanne	Central Plateau	46° 34' / 6° 39'	Broadleaved	<i>Fagus sylvatica</i>	6.9	41.3	35.8	790	Low
Neunkirch	Central Plateau	47° 41' / 8° 32'	Broadleaved	<i>Fagus sylvatica</i>	5.2	33.3	29.8	463	Low
Othmarsingen	Central Plateau	47° 24' / 8° 14'	Broadleaved	<i>Fagus sylvatica</i>	4.6	39.7	38.8	462	Low
Schaenis	Northern Alps	47° 10' / 9° 04'	Broadleaved	<i>Fagus sylvatica</i>	5.5	49.4	37.5	627	Low
Beatenberg	Northern Alps	46° 42' / 7° 46'	Non-pine conifer	<i>Picea abies</i>	3.8	34.1	26.7	1560	High
Chironico	Southern Alps	46° 27' / 8° 49'	Non-pine conifer	<i>Picea abies</i>	3.7	43.7	32.8	1460	High
Vorderwald	Central Plateau	47° 16' / 7° 54'	Non-pine conifer	<i>Abies alba</i>	5.1	50.2	31.8	480	Low
Celerina	Eastern Central Alps	46° 30' / 9° 53'	Pine	<i>Pinus cembra</i>	1.2	32.8	24.4	1760	High
Nationalpark	Eastern Central Alps	46° 40' / 10° 14'	Pine	<i>Pinus mugo</i>	1.3	22	14.5	1914	High
Visp	Western Central Alps	46° 18' / 7° 51'	Pine	<i>Pinus sylvestris</i>	2.3	4.9	8.5	640	Low

^a Mean LAI (uncorrected for clumping = effective LAI) per plot in 2004 using a LAI-2000 instrument (Licor, Inc.; Thimonier et al., 2010).

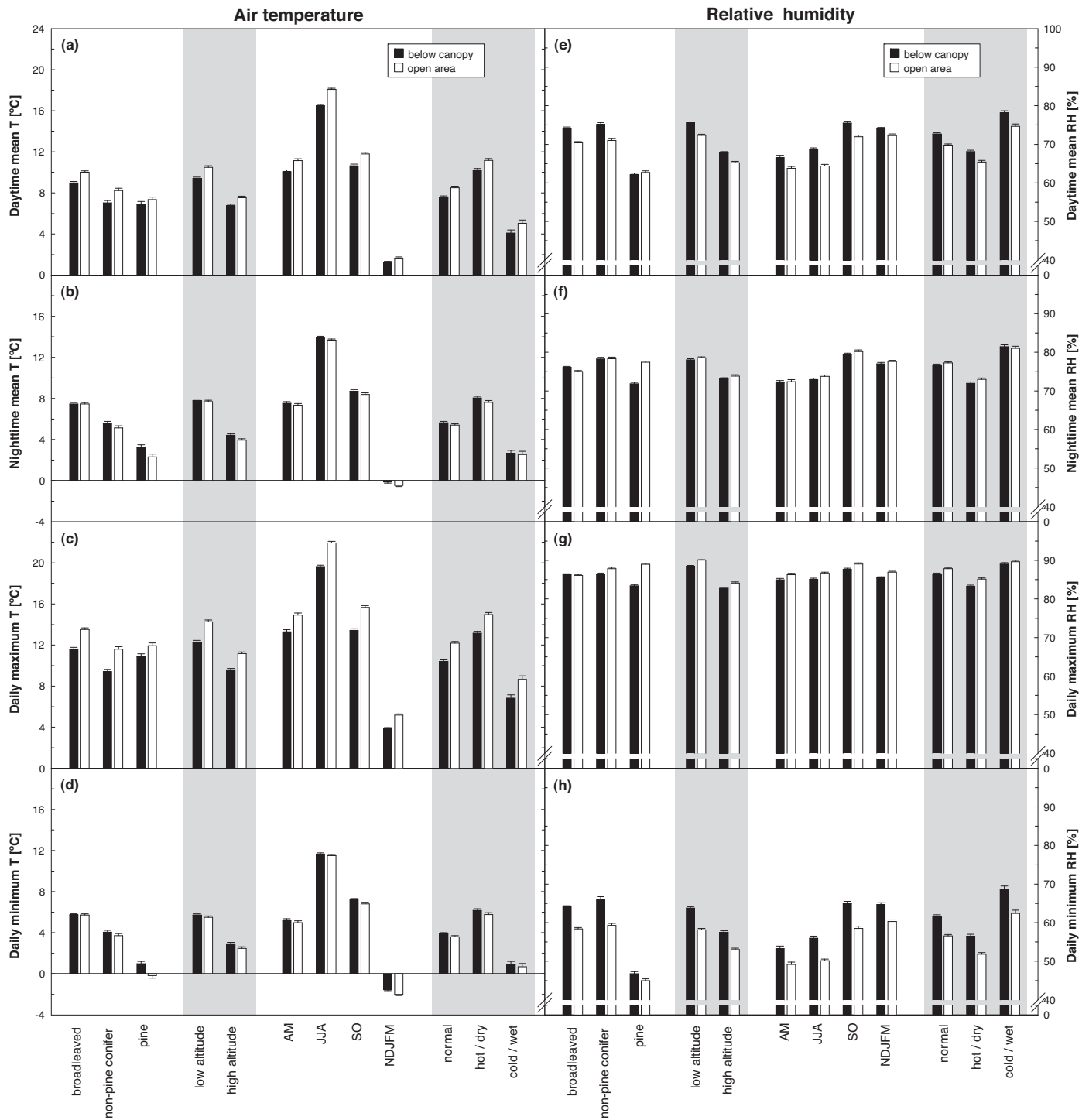


Fig. 2. Means (± 1 SE) of below-canopy and open-area daytime mean, nighttime mean, daily maximum and daily minimum air temperature (T ; a–d) and relative humidity (RH ; e–h) in dependence on forest type, altitude, season and general weather situation observed during the period 1997–2010 at 14 contrasting forest ecosystems in Switzerland.

Both T and RH raw data series were quality-checked before analysis using tests for maximum range limits (physical and site-specific soft limits), minimum and maximum variability, spatial consistency among twin stations, data outliers, and homogeneity compared to nearby MeteoSwiss reference stations. Data points deemed unlikely were eliminated. Based on the results from homogeneity testing, 42% of the RH data series were detrended. The applied detrending procedure assumed linear drift during the two-to-three-year-long operation periods between calibration of each

sensor (Costa and Soares, 2009) and constant differences to nearby MeteoSwiss reference stations over time. Since drift rate depended on the absolute RH value, value-dependent drift rates were calculated (von Arx et al., in press).

2.3. Statistical analysis

All statistical analyses were performed in R version 2.12.2 (R Development Core Team, 2010). ΔT and ΔRH between the

below-canopy and open-area stations were compared using linear mixed models (package “lme4”, Bates et al., 2011) with forest type, altitude, season and general weather situation as fixed factors and site as a random factor (Crawley, 2007). A saturated model including all factors and two-way interaction was built as follows (exemplified by RH_{min}): $mMax \leftarrow \text{lmer}(dmin_rh \sim 1 + (fst + alt + ss + met)^2 + (1|site), REML = FALSE, data = RH_data)$, where $mMax$ denotes the saturated model, $dmin_rh$ the difference in RH_{min} , fst the forest type, alt the altitudinal level, ss the seasons and met the general weather situation. Four-way and three-way interactions were deliberately not considered because their interpretation is difficult. The saturated model was successively simplified using manual model reduction based on log-likelihood ratio tests to find the minimal adequate model for each target variable (Crawley, 2007). Since ΔT and ΔRH of consecutive days depended on each other time series analysis was used to determine the number of days after which auto-correlation disappeared (Cowpertwait and Metcalfe, 2009). This was the case after about ten days at all stations in both ΔT and ΔRH . Data series were thus partitioned into consecutive ten-day periods, and one randomly selected half-day mean and daily peak value from each period was used to perform statistical testing as described above. This randomized sampling procedure resulted in data sets of ΔT and ΔRH that contained 7168 records each when data from all 14 sites and all years was pooled.

3. Results

3.1. Below-canopy vs. open-area air temperature

3.1.1. Overall patterns

Forest type, altitude, season and general weather situation significantly influenced ΔT between below canopy and the nearby open area (Table 2). Significant interaction effects were similar in T_{max} and T_{mean-d} , and, to a lesser degree, in T_{min} and T_{mean-n} . Patterns of ΔT at broadleaved and non-pine conifer forest sites were generally more similar to each other than those at the pine forest sites (Fig. 3).

3.1.2. Effects of individual factors

Both T_{max} and T_{mean-d} were reduced, on average, by around 2.0°C (standard error here and in the following not reported because always equal to 0.0°C) and more than 1.0°C below canopy compared to the nearby open area in the broadleaved and non-pine conifer forests, respectively, but only about half as much at the pine forest sites (Fig. 3a and c). This relationship was reversed at nighttime and early in the morning with 1.0°C (T_{mean-n}) and 1.1°C (T_{min}) warmer conditions below pine canopy, but only half the attenuation of below-canopy air cooling at the non-pine conifer and even no effect at the broadleaved forest sites (Fig. 3b and d). Canopy thus generally lowered daytime warming irrespective of forest type with the exception of some situations at the only lowland pine forest site at Visp (Fig. 3a and c). At low altitudes, mean T_{max} was more strongly reduced under forest canopy (-2.0°C) than at high altitudes (-1.6°C), and the same was true for T_{mean-d} (-1.1°C vs. -0.8°C ; Fig. 3a and c). ΔT_{min} was slightly greater at high (0.4°C) than at low altitudes (0.2°C), and the same relationship was found in ΔT_{mean-n} (0.5°C vs. 0.1°C ; Fig. 3b and d). In summer, daytime warming (T_{max} and T_{mean-d}) was generally reduced the most (-2.3°C vs. -1.6°C), while the moderating effect reached a minimum in winter (-1.3°C vs. -0.4°C ; Fig. 3a and c). In contrast to daytime, there was no obvious seasonal pattern in the below-canopy and open-area differences in T_{min} and T_{mean-n} (Fig. 3b and d). Overall, the different general weather situations did not consistently influence patterns of ΔT despite the statistical significance

(cf. Table 2) because positive and negative effects occurred depending on context and balanced each other.

3.1.3. Interaction effects between different factors

At low-altitude broadleaved and non-pine conifer sites, the moderating effect was most pronounced in summer (JJA) and least in winter (NDJFM), while at the low-altitude pine forest site (Visp) it was strongest in autumn (SO) and even reversed under hot/dry conditions in summer (Fig. 3a and c). Equally striking is the pronounced attenuation of nighttime air cooling at the low-altitude pine forest site during hot/dry conditions compared to the other general weather situations, and the inconsistent response during cold/wet conditions (Fig. 3b and d). At high altitudes, the seasonal pattern was yet stronger at the broadleaved forest sites, where the overall greatest values were reached, with a 2.8°C (T_{mean-d}) and 5.1°C (T_{max}) reduction of daytime warming below the canopy compared to the open area (Fig. 3a and c). At high-altitude non-pine conifer sites, daytime warming was reduced the most under hot/dry conditions but hardly differed between seasons (Fig. 3a and c). The general seasonal pattern was inverted in ΔT_{max} at the high-altitude pine forest sites, i.e. the strongest moderating effect by the canopy was observed in winter (Fig. 3c).

3.1.4. Timing of diurnal patterns

T_{max} and T_{min} were reached almost at the same time below canopy and in the open area (Table 3). In non-pine conifer forests, T_{max} was reached 37 min before the nearby open area; all other differences were mostly in the range of a few minutes. Within factors, the greatest difference in the temporal occurrence of T_{max} was observed between altitudinal levels with a 70 min earlier peak time at high than at low altitudes, and within seasons with a 65 min earlier timing in winter than in summer. T_{min} was contrariwise reached 105 min later in winter than in summer.

3.2. Below-canopy vs. open-area relative humidity

3.2.1. Overall patterns

Similar to T , all considered factors significantly influenced the relationship between below-canopy and open-area RH (Table 2). However, the interaction effects were less consistent and depended on the specific aspect of RH . The influence of altitude and general weather situation was conspicuously larger, yet more complex, in RH than in T , whereas seasonal patterns were less consistent (Fig. 4). RH patterns showed only partly the inverse relationships to T as expected from the physical coupling of the two parameters.

3.2.2. Effects of individual factors

Canopy of broadleaved and non-pine conifer forests considerably increased below-canopy RH_{mean-d} and RH_{min} by 3.8–6.8% (standard error here and in the following not reported, but always $\leq 0.3\%$) compared to the nearby open area, whereas this relationship was much less in ΔRH_{min} (1.8%) and even slightly negative in ΔRH_{mean-d} (-0.6%) at the pine forest sites (Fig. 4a and c). At the pine forest sites RH_{max} and RH_{mean-n} were noticeably reduced by around 5.5% below canopy, but only inconsistently differed at broadleaved and non-pine conifer sites, ranging from -1.5 to 1.1% (Fig. 4b and d). At low altitudes, below-canopy RH_{min} was more strongly increased (5.7%) than at high altitudes (4.4%), which was similar in RH_{mean-d} (3.2% vs. 2.5%; Fig. 4a and c). No meaningful altitudinal effect was detected in ΔRH_{mean-n} and ΔRH_{max} ($\Delta RH = 0.2\%$ throughout; Fig. 4b and d). In summer and autumn, ΔRH_{mean-d} and ΔRH_{min} were greatest (4.3% vs. 6.4%), while smallest humidifying effect of canopy were recorded in spring (ΔRH_{min} : 4.1%) and particularly winter (ΔRH_{mean-d} : 1.8%; Fig. 4a and c). ΔRH_{max} and ΔRH_{mean-n} were smallest in spring but differed between seasons only in the range of a few tenth of a percent ($\leq 0.6\%$; Fig. 4b and d).

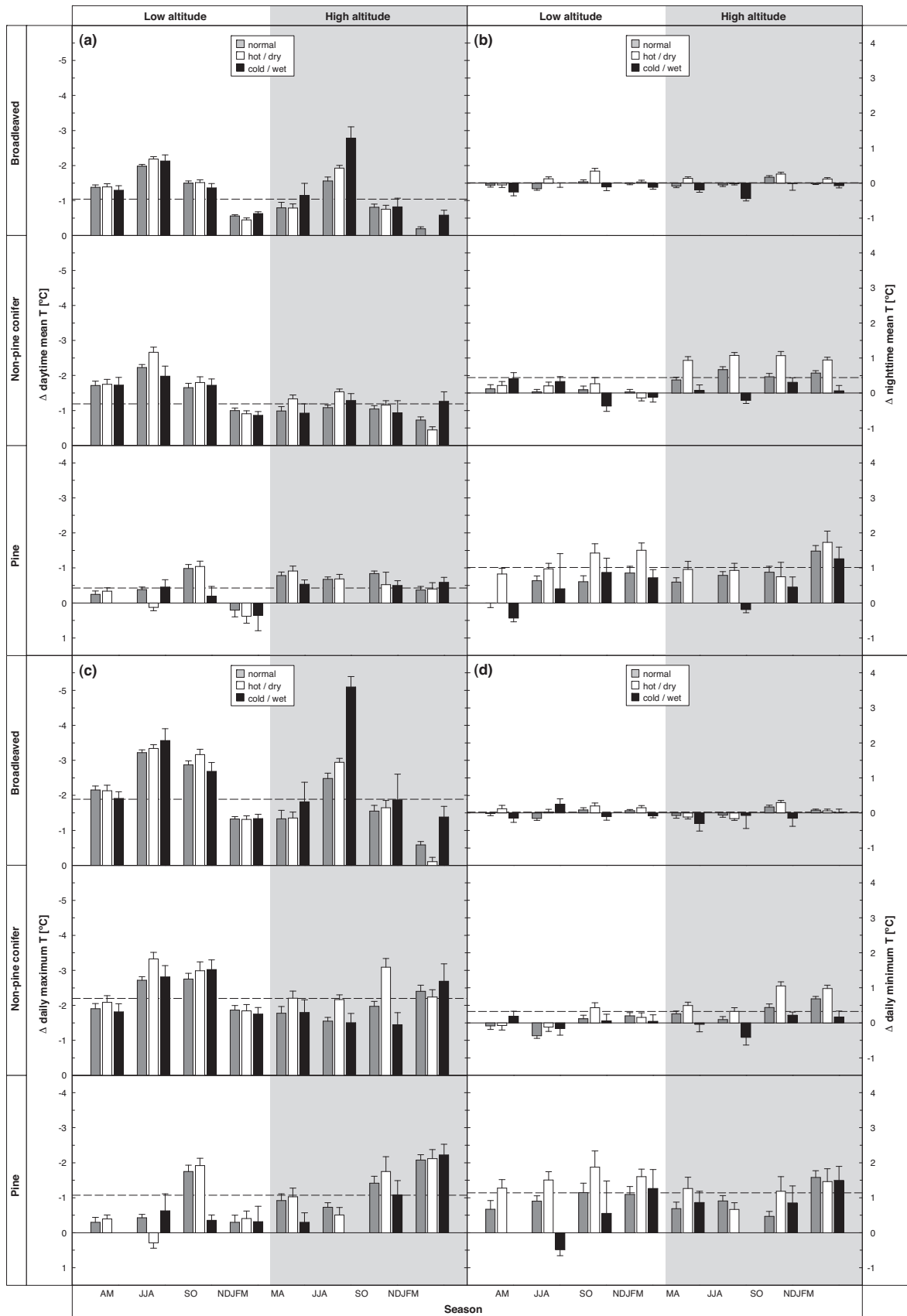


Fig. 3. Difference (mean \pm 1 SE) between below-canopy and nearby open-area (a) daytime and (b) nighttime mean and daily (c) maximum and (d) minimum air temperature (T) in dependence on forest type, altitude, season and general weather situation observed during the period 1997–2010 at 14 contrasting forest ecosystems in Switzerland. Dashed lines indicate mean difference within the respective forest type. Note the inverse vertical scales for daytime (a and c) vs. nighttime (b and d) panels that are intended to distinguish moderating (upward columns) from accentuating (downward columns) effects of forest canopy on T . Scales are identical in all charts to ease comparison of effect sizes; however, ranges are adjusted to match respective values. Only columns based on three or more data points are shown. See Table 2 for the significance of the specific factors and interactions.

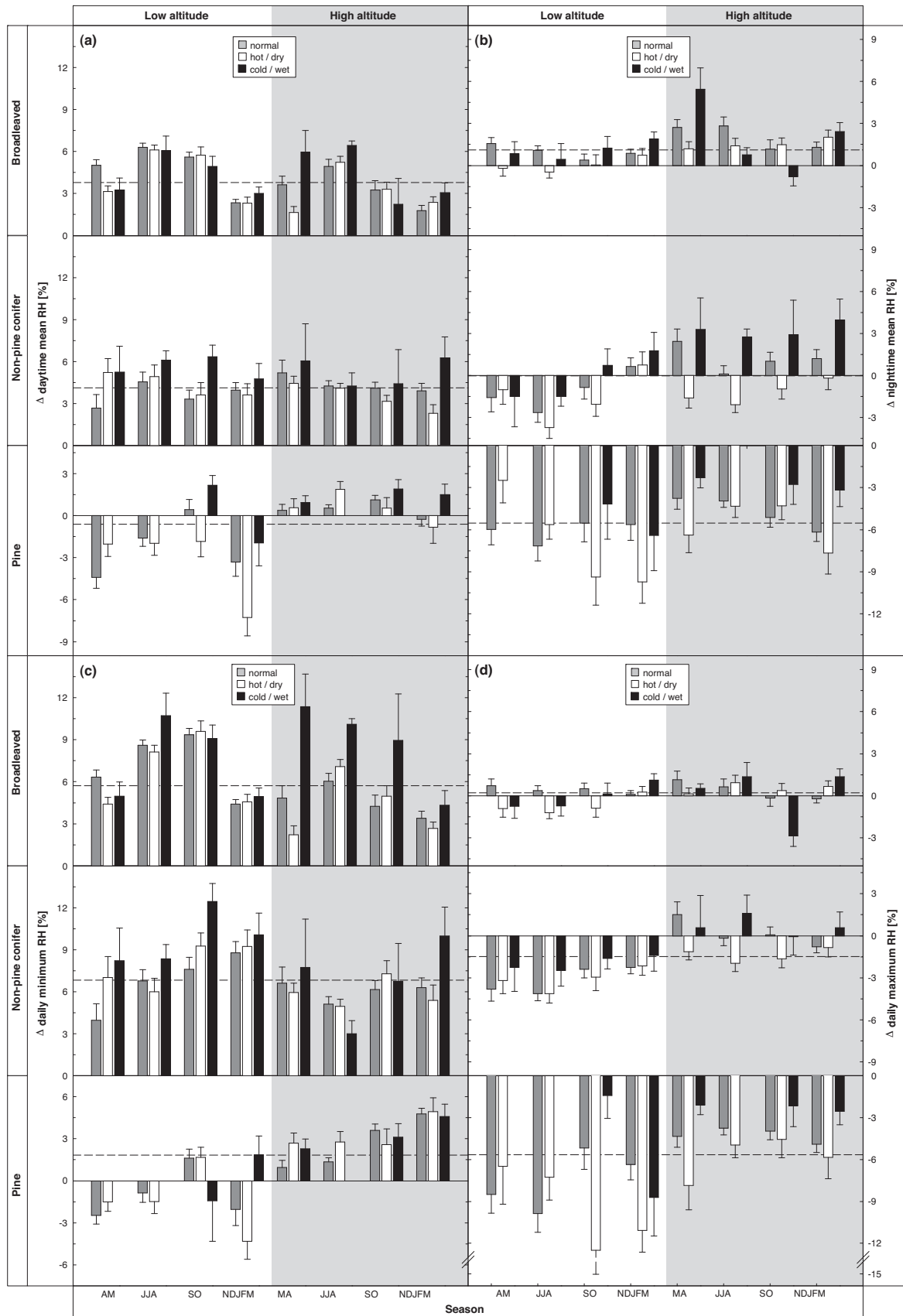


Fig. 4. Difference (mean \pm 1 SE) between below-canopy and nearby open-area: (a) daytime and (b) nighttime mean and daily (c) minimum and (d) maximum relative humidity (RH) in dependence on forest type, altitude, season and general weather situation observed during the period 1997–2010 at 14 contrasting forest ecosystems in Switzerland. Dashed lines indicate mean difference within the respective forest type. Note the inverse vertical scales for daytime (a and c) vs. nighttime (b and d) panels that are intended to distinguish moderating (upward columns) from accentuating (downward columns) effects of forest canopy on RH. Scales are identical in all charts to ease comparison of effect sizes; however, ranges are adjusted to match respective values. Only columns based on three or more data points are shown. See Table 2 for the significance of the specific factors and interactions.

Table 2

Minimum adequate models to describe differences in daytime mean (T_{mean-d} , RH_{mean-d}), daily maximum (T_{max} , RH_{max}), nighttime mean (T_{mean-n} , RH_{mean-n}) and daily minimum air temperature and relative humidity (T_{min} , RH_{min}), respectively, between below-canopy and open-area. frst – forest type, alt – altitude, ss – season, met – general weather situation.

Model terms	ΔT_{mean-d} (χ^2)	ΔT_{max} (χ^2)	ΔT_{mean-n} (χ^2)	ΔT_{min} (χ^2)	ΔRH_{mean-d} (χ^2)	ΔRH_{max} (χ^2)	ΔRH_{mean-n} (χ^2)	ΔRH_{min} (χ^2)
frst	260.22***	614.95***	144.01***	65.6***	59.42***	22.89***	60.31***	139.63***
alt	49.80***	82.99***	7.85*	12.42**	24.16**	18.00*	9.09 m	43.69***
ss	1700.40***	1263.30***	158.61***	12.38**	274.61***	9.17 ns	66.21***	278.21***
met	331.92***	785.52***	50.98***	59.54***	14.31**	33.72***	24.48***	6.89*
frst:alt	–	–	–	–	–	–	–	9.77**
frst:ss	256.23***	612.38***	128.81***	59.54***	48.01***	–	52.62***	121.03***
frst:met	–	–	11.41*	–	–	14.30**	–	–
alt:ss	48.53***	82.52***	–	–	17.98***	8.63*	9.00*	33.50**
alt:met	–	–	7.45*	12.38**	6.03*	7.21*	–	–
ss:met	43.19***	34.83***	–	–	–	–	–	–

m: $P \leq 0.100$; ns: not significant.

* $P \leq 0.050$.

** $P \leq 0.010$.

*** $P \leq 0.001$.

During hot/dry general weather situations the overall humidifying effect of forest canopy was less pronounced in RH_{mean-d} and RH_{min} (2.7% and 4.7%, respectively) than under cold/wet conditions (3.5% and 6.3%, respectively; Fig. 4a and c), and the same pattern showed in ΔRH_{mean-n} (–1.0% vs. 0.5%) and ΔRH_{max} (–1.8% vs. –0.6%; Fig. 4b and d).

3.2.3. Interaction effects between different factors

Daytime ΔRH at broadleaved forest sites showed a maximum in summer, whereas no consistent seasonal pattern was observed at the other sites (Fig. 4a and c). At high-altitude broadleaved forest sites, ΔRH_{min} was strikingly larger when it was cold/wet than during the other general weather situations (Fig. 4c). Furthermore, the effect of cold/wet conditions on ΔRH_{max} and ΔRH_{mean-n} changed from positive to negative during the growing season (Fig. 4b and d). At the non-pine conifer sites, the strongest positive and, where present, the least negative effect of canopy on ΔRH was generally observed during cold/wet conditions (Fig. 4a–d) – with the largest overall difference of 12.4% (Fig. 4c). The most remarkable pattern at the only low-altitude non-pine conifer forest site at Vordemwald was the drying-out effect of canopy during nighttime; at high-altitude sites this drying-out effect was confined to hot/dry conditions, while during cold/wet conditions it was considerably moister below canopy during the night (Fig. 4b and d). At pine forest sites, cold/wet conditions occurred only infrequently

during nighttime, particularly in spring and summer, but when such conditions occurred the drying-out effect of forest canopy was less (Fig. 4b and d). In contrast, drying-out below pine canopy tended to be intensified during hot/dry conditions (Fig. 4a–d), except for the high-altitude sites where hot/dry summer conditions were more humidifying at daytime than normal summer conditions (Fig. 4a and c).

3.2.4. Timing of diurnal patterns

Point of time when RH_{max} and RH_{min} were reached below canopy coincided more or less with those at open areas (Table 3). The difference was never larger than 25 min, regardless of forest type, altitude, season or general weather situation. In pine forests, RH_{max} was reached 110 min earlier than in non-pine conifer forests, and 40 min earlier at low than at high altitudes. RH_{min} was reached 85 min earlier at high than at low altitudes, and 50 min earlier in winter than in summer. All other lags were shorter.

4. Discussion

4.1. Spatio-temporal temperature and humidity patterns

In this study we used long-term meteorological data from 14 distinct forest ecosystems, which were classified into three different forest types and two altitudinal levels. Although these two

Table 3

Below-canopy (bc) peak times of daily maximum and minimum air temperature (T_{max} and T_{min} , respectively) and relative humidity (RH_{max} and RH_{min} , respectively) and time lag compared to open-area (oa) peak times in dependence on forest type, altitude, season and general weather situation.

	T_{max}		T_{min}		RH_{max}		RH_{min}	
	Peak time [p.m.] ^a	$\Delta bc-oa$ [min]	Peak time [a.m.] ^a	$\Delta bc-oa$ [min]	Peak time [a.m.] ^a	$\Delta bc-oa$ [min]	Peak time [p.m.] ^a	$\Delta bc-oa$ [min]
Forest type								
Broadleaved	2:10	8	8:05	9	7:50	17	2:10	2
Non-pine conifer	1:55	37	8:05	7	8:25	20	1:35	8
Pine	1:50	5	7:25	4	6:35	10	2:15	5
Altitude								
Low	2:35	13	7:50	9	7:20	18	2:45	3
High	1:25	14	8:05	5	8:00	13	1:20	5
Season								
AM	2:25	7	7:05	6	7:05	11	2:25	0
JJA	2:35	5	7:05	8	7:10	25	2:30	–1
SO	2:10	21	7:45	12	7:45	21	2:00	7
NDJFM	1:30	18	8:50	6	8:10	10	1:40	9
General weather situation								
Normal	2:00	13	8:00	9	7:35	15	2:00	4
Hot/dry	2:15	15	7:40	5	7:45	20	2:10	4
Cold/wet	1:45	14	8:30	6	7:40	11	1:55	3

^a local winter time (UTC + 1 h)

classifications included great within-level variability and did not account for the diversity in species composition, aspect, slope, etc. among sites (cf. Table 1; Ferrez et al., 2011; Renaud et al., 2011; Renaud and Rebetez, 2009), they allowed to reveal fundamental differences between below-canopy and open-area air temperature (T) and relative humidity (RH) patterns with respect to seasons and contrasting general weather situations. Results from mixed effect models (cf. Table 2) showed that the different factors interacted, as hypothesized, in a complex way to produce a specific below-canopy microclimate.

Broadleaved and non-pine conifer forests generally showed, as hypothesized and observed in previous studies (e.g. Holst et al., 2004; Ma et al., 2010), more strongly moderated diurnal fluctuations of T and RH than pine forests (Figs. 3 and 4). However, this effect only showed during daytime hours, because pine forests cooled down less during the night than the other forest types. The associated lower nighttime RH in pine forests was likely a direct consequence of the T -driven increase in saturated vapour pressure (Geiger et al., 2009). More generally, a tighter coupling of RH to T at nighttime than at daytime is demonstrated by the stronger correlation of mean halfday values (T_{mean-n} vs. RH_{mean-n} and T_{mean-d} vs. RH_{mean-d}) over the entire study period (Pearson's $r_{nighttime} = -0.67$ vs. $r_{daytime} = -0.45$). An explanation for the differential diurnal T patterns can be found in the different stand structures (cf. Table 1). Broadleaved and non-pine conifer forests were characterized by a higher stand and crown density that prevented larger shares of (shortwave) solar radiation from reaching the ground than the comparably sparse pine stands. Consequently, daytime vertical air exchange was greater in the comparably sparse pine stands. At night, vertical air movement was less because of the absent (shortwave) solar radiation; however, (longwave) infrared radiation from soils that were more warmed up in the pine stands during daytime could not escape to the sky because of the canopy and reduced mixing of air, much as observed in a greenhouse (Geiger et al., 2009; Mitscherlich, 1981). While moderation of daytime temperature may often be beneficial for tree seedling recruitment (Jemison, 1934; Mitscherlich, 1981), the opposite may be true at nighttime, particularly during the growing season, due to greater metabolic rates that deplete carbohydrate reserves (Beier et al., 2004). Along the same lines, levels of daytime RH rather than nighttime RH may be more important for plant growth, because it determines the exchange rate of atmospheric CO_2 and plant H_2O when stomata are open during photosynthesis (Ladjal et al., 2007; Leuschner, 2002; Maier-Maercker, 1998).

High-altitude forest ecosystems are often more exposed to the ambient atmosphere. Consequently, greater moderating effects were hypothesized, and mostly observed, at low altitudes. An additional explanation for the (small) differences in moderating capacity depending on altitude comes from stand structure. LAI at the low-altitude sites generally was greater than at high-altitude sites (mean \pm 1 SE: 5.1 ± 0.5 vs. 3.9 ± 0.8 ; Table 1), meaning that crown density-related effects as discussed in the previous paragraph will likely have played a role. Some striking deviations from the general pattern were found at the pine forest sites. This may be due to the specifics of the only considered low-altitude pine stand at Visp that is located in a precipitation-poor inner-Alpine valley; there, two factors may have lowered or even reversed the common moderating effect of canopy: very low stand density (basal area) and tree height (cf. Table 1), and the generally low soil moisture content that poorly contributed to RH and evaporative cooling, particularly during hot/dry conditions (Fischer et al., 2007; Seneviratne et al., 2006). Support for this explanation comes from a study by Renaud and Rebetez (2009) at the same site, in which the identical pattern was found in the heat summer of 2003. A similar exception was recorded in RH_{mean-n} and RH_{max} at the low-altitude non-pine conifer site at Vordemwald. Since T did not show the inverse pattern

(Figs. 3d and 4d), other unknown factors than the general physical coupling with T (see above) have to be responsible.

When solar radiation is stronger, T generally rises. Consequently, a greater moderating effect of forest canopy in summer than in winter was hypothesized and has also been reported in previous studies by Morecroft et al. (1998), Renaud et al. (2011), and Renaud and Rebetez (2009), particularly when considering T_{mean-d} and T_{max} . Winter deciduousness in broadleaved forests amplified this seasonal pattern, particularly at high-altitude sites where solar radiation is more intense; and it was likely the most important factor responsible for the significant forest type \times season interaction (Table 2). Because of the general physical coupling with T a similar seasonal pattern was expected in RH , and confirmed (Figs. 3a, 3c, 4a and 4c). The effect of stand density-dependent shading (as expressed by LAI) also explains the similar patterns of the broadleaved and non-pine conifer forests, because their structure was more similar to each other than to the pine forests (cf. Table 1). The generally smaller differences in T_{mean-n} and T_{min} between below-canopy and open-area plots confirm the dominant role of solar radiation and shading; our findings thus match those of previous studies by Chen and Franklin (1997), and Renaud et al. (2011). Interestingly, ΔT_{max} in pine forests was not greatest in summer (Fig. 3c). Other factors must thus have overruled the typical seasonal patterns, such as depletion of soil moisture pools in summer and the concomitant smaller evaporative cooling effect (see above). Additional support for this explanation comes from RH data, since pine forests generally grew at dry locations (Table 2), and did also not show greatest ΔRH to the nearby open area in summer (Fig. 4c). Another noteworthy deviation from the prevailing seasonal pattern occurred at the non-pine conifer sites where, in summer, the smallest (high altitudes) or atypically small (low altitudes) humidifying effect (ΔRH_{min}) was observed (Fig. 4c).

General weather situation significantly influenced the difference between below-canopy and open-area microclimate, which was particularly true for daytime T (see great χ^2 values in Table 2). This influence is related to the high thermal capacity of water that makes water in the soil and the air efficient sinks of energy (Geiger et al., 2009). During hot/dry daytime conditions intense solar radiation (which was in our case $901 \pm 8 \text{ W m}^{-2}$ in JJA 2010 [daily maximum global radiation] compared to $794 \pm 12 \text{ W m}^{-2}$ during cold/wet conditions) promotes radiative warming and thus evaporative cooling, as long as water from soil and plants is available (Fischer et al., 2007; Seneviratne et al., 2006). Because of this latent heat flux the inverse RH to T relationship may be partly decoupled (Geiger et al., 2009). This mechanism may explain the generally increased daytime ΔT at high-altitude non-pine conifer sites (Fig. 3a and c). However, the mechanism is interrupted when soil moisture pools are depleted (e.g. during prolonged drought) as likely occurred at the low-altitude pine forest site Visp (see above). The strikingly greater ΔRH of high-altitude broadleaved forest canopy during cold/wet than hot/dry conditions may be mostly due to direct physical coupling with T , together with co-varying soil moisture pools (Figs. 3c and 4c). Altogether, the generally complex, context-dependent responses during different general weather situations probably explain their small overall net effect on ΔT .

The timing of T_{min} , T_{max} , RH_{min} and RH_{max} below canopy and at the nearby open areas more or less coincided, i.e., the hypothesis that microclimate below canopy would track open area conditions with some time lag was not confirmed. The hypothesis was founded in the assumption that more strongly fluctuating open-area conditions would penetrate forest canopy by exchange of air. The synchronous daytime peaks suggest, however, that horizontal convection/exchange of air from the open to the forested area is rather unimportant, and that solar radiation and vertical air exchange (see above) are the main drivers of T increase and concomitant RH decrease during the day. This explanation is supported

by the mostly absent influence of forest type, altitude, season and general weather situations on lag times. Holst et al. (2004) equally found no lag in a Central European beech forest when comparing diurnal T patterns in February within and above the stand, nor did Morecroft et al. (1998) in an oak stand in England on a single day in July.

4.2. Sensitivity of forest ecosystems to climate change

The sensitivity of forest ecosystems to climate change as discussed in the following refers to the impact of climate change on seedling recruitment. Potential changes of species composition and canopy density (LAI) that both would alter moderating capacity are disregarded. Other studies about forest sensitivity to climate change rather investigated whether a specific region would still be favourable to forest growth no matter of anticipated shifts in species composition, and focused on mature trees and their productivity (e.g. Griesbauer et al., 2011; Lasch et al., 2002; Lexer et al., 2002; Lindner et al., 2010).

The forest sensitivity according to our definition may be assessed from different points of view. According to a first approach, forest ecosystems with an changeless moderating capacity irrespective of season may be most sensitive, because they may not be able to attenuate the expected increase in mean T (Appenzeller et al., 2011) as simulated by the transition from a colder to a warmer season. In this scheme, pine forests may be most sensitive, because they did hardly show consistent changes in ΔT and ΔRH throughout the year. Furthermore, the generally stronger moderating effect of pine forest canopy on ΔT_{min-n} may be a disadvantage during the growing season because of increased metabolic rates (see above). In this scheme, broadleaved forests would thus be least sensitive to climate change. Similarly, high-altitude forests would be generally more sensitive than low-altitude forests, because high-altitude forests generally showed less consistent seasonal patterns (cf. Figs. 3 and 4 and interaction terms in Table 2).

According to a second approach, forest ecosystems that did not increase or even decrease in moderating capacity during hot/dry general weather situations may be most sensitive, because such conditions may simulate the behaviour during extreme events such as dry spells that are expected to become more frequent (Appenzeller et al., 2011; Schaer et al., 2004). In this framework, a great moderating capacity may be particularly important in summer, when tree seedlings may run close to physiological limits, but rather unimportant in winter. Pine forests would again be most sensitive, followed by the more or less equally sensitive broadleaved and non-pine conifer forests. The altitude of a forest ecosystem would not matter in a consistent way in this framework, although there were some significant interactions with general weather situation (cf. Table 2).

According to a third approach, the sensitivity of a forest ecosystem depends rather on the moderating capacity in the context of the specific physiological requirements of the seedlings of the dominant tree species. A shade-tolerant species may require a greater moderating capacity for successful recruitment, particularly in summer, than a shade-intolerant species that generally requires more light and tolerates greater VPD (Givnish, 1988). In this respect, the forest types as classified in this study were only partly suitable, because the broadleaved forests included both shade-tolerant (*Fagus sylvatica*) and shade-intolerant (*Quercus* sp.) dominant species, the non-pine conifer forests included shade-tolerant (*Abies alba*) and semi-shade-tolerant (*Picea abies*) dominant species, and only the pine forests included solely shade-intolerant dominant species (Ellenberg, 1986; cf. Table 1). Employing this approach, seedlings in pine forests may be expected to suffer less from the small to absent moderating capacity than suggested by the first

two approaches, provided that they are not already growing at their physiological limit. At least for one of the dominating pine species, *Pinus sylvestris* (cf. Table 1), current conditions have been reported to be physiologically limiting in the corresponding region, however (Dobbertin et al., 2007; Eilmann et al., 2011; Rebetz and Dobbertin, 2004). High-altitude forests may again be more sensitive than low-altitude forests, because of the smaller moderating capacity while there was no clear trend towards more or less shade-intolerant vs. shade-tolerant species at either altitude in our study.

Altogether, recruitment in pine forests and high-altitude forests may respond most sensitively to future climate change based on our analysis of T and RH patterns. With respect to pine seedlings, there is indeed evidence from other studies that physiological limitations due to more frequent extreme growing conditions may already hamper successful recruitment (Dulamsuren et al., 2009; Galiano et al., 2011; Rebetz and Dobbertin, 2004). In their review on climate change impacts and vulnerability of European forest ecosystems, Lindner et al. (2010) concluded that eastern and southern forest ecosystems might be most sensitive, mostly as a consequence of water limitation. This matches with the hypothesized stronger sensitivity of pine forests, because they grew in drier habitats in our study (Fig. 2e and h). Lexer et al. (2002) modelled impact of climate change on Austrian forest ecosystems and found that an increase of $\geq 1^\circ\text{C}$, which is well in the range of context-dependent fluctuations found in this study, would severely impact many forests.

5. Conclusions

This study compared long-term below-canopy microclimate to local climate in a wide range of forest ecosystems that are representative for large parts of Central Europe and other forest ecosystems in temperate latitudes. Forest canopy lowered daily maximum air temperature by up to 5.1°C (overall average: 1.8°C) and increased daily minimum relative humidity by up to 12.4% (overall average: 5.1%), respectively, which are ranges that will significantly affect growth of understory tree seedlings. The moderating capacity was generally stronger in broadleaved and non-pine conifer forest ecosystems than in pine forests, stronger at low than at high altitudes and stronger in summer than in winter. General weather situation significantly influenced these patterns in a complex way that putatively depended on soil water status. Despite the moderation of microclimate by forest canopy, there was no lag in the diurnal course compared to local open-area climate. The sensitivity of seedling recruitment in the three forest types to climate change was evaluated with respect to a general warming trend, increased frequency of extreme weather periods and physiological requirements of dominant tree species seedlings. In two of the three criteria, pine forests and high-altitude forests turned out to be most sensitive to climate change. The long time series (1997–2010) of meteorological data and the wide range of different forest ecosystems used in this study are quite unique and both add to the reliability and wider relevance of the results. By reducing the complexity of the 14 distinct forest ecosystems to a few tangible categories we were able to crystallize some fundamental differences in the way forest canopy moderates understory microclimate. Quantitative results of this study may help to improve models into forest dynamics and contribute to optimize forest management in the wake of future climate change.

Acknowledgements

We thank E. Graf Pannatier and A. Thimonier for valuable discussions and LAI data, G. Schreiner for meteorological data collection and sharing his expertise of local situation, P. Jakob

for help with the database, F. Sutter for technical support, M. Begert for advice on quality control of meteorological data and A. Drewek for statistical consulting. Three anonymous reviewer are acknowledged for valuable comments to an earlier version of this manuscript. This project was supported by a grant within the programme "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.

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