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ORIGINAL PAPER

Microclimate and ecological threshold responses in a warming and wetting experiment following whole tree harvest

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Abstract Ecosystem climate manipulation experiments (ECMEs) are a key tool for predicting the effects of climate change on ecosystems. However, the strength of inferences drawn from these experiments depends on whether the manipulated conditions mimic future climate changes. While ECMEs have examined mean temperature and moisture conditions, ecosystem processes may respond more to microclimatic thresholds (e.g., freeze–thaw events). We reported the mean and microclimatic thresholds from a post-clearcut ECME in a temperate, mixed deciduous forest. Target treatments were ambient, warmed (+~2 °C), wetted (+~20 % precipitation), and warmed+wetted. Wetted treatments increased mean monthly precipitation by 23 %, but did not change the amount of time the soil water potential was below the permanent wilting point. Relative to ambient, warmed treatments increased the mean temperatures of the surface and soil by 1.8 and 2.5 °C, respectively. Warming decreased the number of soil freeze–thaw events and increased the number of growing degree days, frost-free days, and amount of time leaf surface temperatures were in the optimal photosynthetic range. Our results showed that, even when ECMEs mimic mean predicted climate conditions, their effect on microclimatic thresholds can be variable. We suggest that measuring these and other microclimatic thresholds will be essential for interpreting ECME results and assessing their value in predicting ecosystem responses to future climate change.

Abbreviations

ECME	Ecosystem climate manipulation experiment
FC	Field capacity
FFD	Frost-free days
FoRCE	Forest Regeneration and Climate Change Experiment
F-Ts	Freeze–thaw events
GDD_5	Growing degree days above a base temperature of 5 °C
LTG_{35}	Leaf temperature >35 °C
OLT	Optimum leaf temperature
OWC	Optimum water content
PWP	Permanent wilting point
VWC	Volumetric water content

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1 Introduction

Global climate is predicted to change due to anthropogenic factors, with a possible 2 to 5 °C increase in global temperature within the next century (Solomon 2007). In that same time frame, precipitation regimes are expected to exhibit greater spatial variability, with a larger degree of uncertainty in the predictions (Solomon 2007). For northeastern USA, the predictions for changes in annual precipitation range from slightly negative to +30 % (Hayhoe et al. 2007).

Ecologists are using a suite of tools to predict ecosystem responses to climate change, and one of the key approaches is plot-scale ecosystem climate manipulation experiments (ECME). Some of the common methods used in ECMEs to manipulate temperature include infrared (IR) lamps (Harte et al. 1995), open top chambers (Norby et al. 1997), or buried cables (Melillo et al. 2002). Studies on the effects of precipitation changes to ecosystems include increases or decreases in the total amount of precipitation, changes in the frequency of precipitation events, and changes in the timing of large-scale precipitation events (Fay et al. 2000; Knapp et al. 2002; Wullschleger and Hanson 2006). More recently, ecologists are using ECMEs that cross temperature and precipitation treatments in order to test for interactive effects. A meta-analysis of 85 experiments (Wu et al. 2011) concluded that the few experiments crossing temperature with precipitation manipulations resulted in smaller interactive effects than predicted by additive interaction models and recommended more research be done. Additionally, it is known that temperature and moisture can have counteracting effects on each other. For example, Carlyle et al. (2011) found that decreasing precipitation in open top chambers increased temperature by 0.4 °C and that watering decreased temperature by 0.4 °C. Thus, the methods used in ECMEs do not act independently or exclusively on the variables that they are intended to target.

ECMEs often target fixed increases in climate variables (e.g., set increases in air or soil temperatures); however, the mean change in temperature or moisture conditions may not adequately describe treatment effects on microclimate if the manipulations also change the frequency or duration of time that climate extends beyond critical ecological thresholds. An ecological threshold can be defined as a nonlinear ecosystem response to an environmental driver (Groffman et al. 2006). In this manuscript, our goal is not to reveal thresholds, but rather, to take advantage of several well-established ecological thresholds (e.g., freezing) and quantify effects of climate change manipulations on the duration and frequency that thresholds are crossed.

An important temperature threshold for soil biogeochemical cycling is the freezing point of water (0 °C), below which soil microbial activity is dramatically reduced (Rivkina et al. 2000), although activity has been measured in soils as low as −39 °C (Panikov et al. 2006). The number of soil freeze–thaw events (F-Ts) or cycles has been linked to increased losses of both soil C and N (DeLuca et al. 1992; Groffman et al. 2001b; Grogan et al. 2004). The main mechanisms thought to be driving this increased cycling is the lysing of soil microbial cells or fine root dieback from the physical stress of freezing, followed by the metabolism or leaching of the available C and N during the thaw cycle (Matzner and Borken 2008).

Plant physiology is strongly influenced by ambient and leaf surface temperatures. Freezing temperatures can be regarded as an ecological threshold because plants can experience tissue damage when the temperature drops below 0 °C (Pearce 2001). Temperature regimes over the growing season can be represented by indices common in forestry and agriculture that relate surface temperature to plant growth such as the number of frost-free days (FFD) or growing degree days (GDD) (Sykes et al. 1996). It is widely thought that plants must experience a critical number of days with mean temperatures >5 °C (growing degree days above a base temperature of 5 °C [GDD_5]) for the regulation of phonological events such as leaf out (Lechowicz 1984). Because a day with an average temperature of 5 °C may still experience frost, GDD and FFD are complementary temperature-related thresholds used for studying plant growth responses to the environment (Körner and Basler 2010; van der Meer et al. 2002).

Actual leaf surface temperature is an important control on plant physiology, affecting both carbon fixation and water loss through evapotranspiration (Dreyer et al. 2001; Kobza and Edwards 1987). Helliker and Richter (2008) used stable oxygen isotopes in tree rings to show that most tree C is fixed when leaf temperatures are 19.2–23.6 °C across a broad range of ecosystems from the tropics to boreal forests. This suggests another temperature-related threshold range that could be useful for evaluating potential effects of an altered microclimate on plant success. In addition, leaf photosynthetic pathways have been shown to be negatively affected by temperatures above 35 °C (Schrader et al. 2004).

Both plant and soil microbial processes respond nonlinearly to well-established soil moisture thresholds. Plant physiological and morphological responses to water stress are also strongly controlled by thresholds in soil moisture, particularly in arid ecosystems (Schwinning and Ehleringer 2001). For instance, the permanent wilting point (PWP) is the lowest water potential at which a plant can access water from the soil (Veihmeyer and Hendrickson 1949). Although there is a wide range of soil water potential values over which plants can draw water (from −1.0 to −8.0 MPa), the conventional threshold of PWP is considered to be −1.5 MPa (Lambers et al. 2008). The PWP can serve as a measureable threshold to separate stressed and unstressed conditions of plants, as well as a measure of inhibited soil microbial activity and nutrient cycling (Porporato et al. 2004).

We established an ECME combining temperature and precipitation manipulations in 2007 in a recently harvested northeastern temperate forest in central Pennsylvania. The experiment was conducted in a postharvest environment because of our interest in early successional forest community responses to predicted changes in climate. The experimental design applied four treatments: warmed (+~2 °C), wetted (+~20 % precipitation), warmed+wetted, and ambient (control). Our objectives for this paper are to summarize how manipulations used to simulate predicted climate change affect the microclimate of the ecosystem and to highlight how a climate manipulation experiment may alter the frequency and duration of key ecological thresholds.

We have three categories of hypotheses regarding warming and wetting effects on ecological thresholds:

1. Direct effects of increased temperature and precipitation, without interactions. We hypothesize that warming alone will increase the number of FFD, GDD_5, surface temperatures in the optimum leaf temperature (OLT) range for C assimilation, surface temperatures >35 °C (leaf temperature >35 °C [LTG_{35}]) where photosynthesis is suppressed, and soil F-Ts. Wetting will decrease the frequency that soil moisture falls below the PWP and increase the time that soils are between PWP and field capacity (FC).
2. Interactive effects in which warming treatments cause drying. We hypothesize that warming will have a drying effect counteracting the wetting effect on moisture-dependent thresholds of PWP and PWP-FC.
3. Interactive effects in which wetting treatments cause cooling. We hypothesize that wetting will have a cooling effect counteracting the warming effect on temperature-dependent thresholds of FFD, GDD_5, OLT, LTG_{35}, and F-Ts.

These seven microclimatic parameters (FFD, GDD_5, OLT, LTG_{35}, F-Ts, PWP, and FC) exert strong control over ecosystem structure and function in a temperate forest ecosystem, especially in a secondary successional forest (Chen et al. 1999). Furthermore, the selected microclimatic parameters encompass those where the responses in ecosystem processes to temperature or precipitation may be either hindered (e.g., LTG_{35}) or enhanced (e.g., OLT).

2 Materials and methods

The Forest Regeneration and Climate Change Experiment (FoRCE) was located in the Pennsylvania State University's Stone Valley Forest in central Pennsylvania (40°40′32″ N, 77°54′00″ W). The average mean temperature in the region is 8.6 °C. The annual average maximum is 27 °C in July, while the average minimum is −8 °C in January. Mean annual precipitation was 1,046 mm from 1899 to 2006 (PSC 2010). The site was situated on a southeast-facing slope with a 14 % grade. The soils were a fine loamy, mixed, superactive, mesic Oxyaquic Fragiudalfs in the Clarksburg series derived from a Tuscarora sandstone parent material. Depth to bedrock is approximately 2.5 to 3 m. The mean particle size distribution of the A horizon was 17 % sand, 67 % silt, and 16 % clay. Prior to installing the study plots, the overstory canopy in a 2-ha area was removed by whole tree harvesting, leaving only advanced tree regeneration <0.5 m tall. Harvesting resulted in 34 % decrease in the mass of O horizon material and a 20 % increase in bulk density (Rollinson and Kaye 2012). Postharvest woody debris <2 cm thick was left on plots and evenly distributed. A 2-m high fence was installed around the study area to exclude deer and other large mammals.

The experimental design was a 2×2 factorial randomized complete block. Sixteen 2×4-m plots (Fig. S1) were arranged into 4 blocks with 1 plot of each of the following treatments: warmed, wetted, warmed+wetted, and ambient (or control). Each experimental plot was surrounded by a 0.5-m tall mesh fence spaced 1 m from the plot borders that was erected in spring 2009 to deter rodent herbivory. One half of each plot (2×2 m) was randomly selected as a "natural" subplot and vegetation was allowed to naturally regenerate (right side of Fig. S1). The other half of the plot was designated as the "planted" subplot and was planted with seeds from 11 eastern tree species and weeded on a regular basis (for vegetation responses to treatments, see Rollinson and Kaye 2012 and Rollinson et al. 2012).

2.1 Temperature and precipitation manipulations

Our goal was to increase daily canopy temperatures by approximately 2 °C and ambient precipitation by 20 % of the long-term average. The targeted temperature increases were based on general circulation models (GCMs) that predict warming from 2 to 5 °C and within the next century (Solomon 2007). Model predictions for precipitation changes in northeastern USA are far more variable than temperature (Hayhoe et al. 2007), but 20 % was chosen because it was on the wetter end of the predictions and greater than the historical coefficient of variation (16 % from 1882 to 2005).

Warmed treatments were achieved in plots using a proportional–integrative–derivative (PID) control system described in Kimball (2005). The PID system works by programming the IR heater controllers to maintain constant canopy temperature differentials between ambient and warmed plots. The PID system was programmed to maintain daytime and nighttime canopy temperatures by 1.5 and 3.0 °C above those of unheated reference plot temperatures, respectively. Over each warmed plot hung two 165×15-cm IR heaters with maxima of 100 W m^{-2} output (HS-2420, 240 V, 2,000 W Electric Radiant Infrared Heater with Modified Reflector, Kalglo Electronics Inc., Bethlehem, PA, USA) suspended 1.5 m above the ground on a steel cable supported by 2.4 m tall steel posts. Plots were warmed continuously from May 2008 through August 2010. Due to fire hazard from plant contact with the heaters, all heaters were raised to 2 m in April 2010. The shading effect and drip line caused by the heaters were mimicked in the wetted and reference plots by installing "dummy" heaters with the same physical dimensions and shading as the real heaters, but lacking a heating element.

The surface temperature in each plot was recorded by infrared radiometers (IRR; model IRR-P, Apogee Instruments Inc., Logan, UT, USA), CR1000 data logger (Campbell Scientific, Logan, UT, USA), and a multiplexer (model AM16/32; Campbell Scientific, Logan, UT, USA). The plot surface was either plant or soil, depending on the time of year and time since harvest, and temperature measurements were taken in the center of the 2×4-m plots (incorporating both "natural" and "planted" subplots). The IRRs were installed 2 m above the canopy and tilted 45° from parallel to the surface, so that they viewed an oval that was 2.3 m wide by 3.8 m long (ellipse area of 6.9 m^2). IRR temperature was averaged over 1-h periods and recorded by the CR1000 data logger. Every 15 s, IRR sensor temperatures in warmed plots were compared to ambient plots within the same block to calculate the heating needed to maintain the target warming. A signal was then sent to a dimmer switch (LCED-2484 Incandescent Light Dimmer 249 V Single Phase 60 Hz 8.5 KW; Kalglo Electronics Inc., Bethlehem, PA, USA) for each block that is in three voltage settings: "off" (0 V), quarter power (5 V), or full power (10 V). The dimmers use one of three signals (off, half, or full) to send to the four heaters in that block to maintain the target temperature difference. The Kalglo IR heaters have a maximum electrical requirement of 2,000 W and are 20 % efficient at low wind over 4 m^2 (Kimball 2005), so the maximum IR radiation impinging on the plots from the heaters was about 100 W m^{-2}. Similar methodology has been used in grassland and alpine experiments to study the effects of a warming climate (Price and Waser 2000; Wan et al. 2002; Morgan et al. 2011) and is currently employed in boreal forests and old field successional ecosystems (websites: http://forestecology.cfans.umn.edu/B4WARMED.html and http://www.ecosystems.umb.edu/bace.html).

Soil temperature was measured with Decagon ECH_2O EC-TM soil probes (Decagon Devices, Inc., Pullman, WA, USA) installed 3 cm below the mineral soil surface approximately 50 cm from the plot center in the "natural" subplots. The ECH_2O EC-TM probes were installed parallel to the longer side of the plots (4 m side). Effective soil temperature was measured at 5 cm depth. Soil moisture and temperature were recorded every hour within each plot. Starting in fall of 2009, a handheld temperature probe (model 9847N made by Taylor) was used to verify ECH_2O EC-TM temperature data in the natural subplots every 2 weeks during the growing season. The Taylor probe integrates temperature readings from 0 to 8 cm depth. Three temperature readings from the Taylor probe were taken after the probe had been inserted into the soil surface for approximately 1 min and averaged. A climate station with a thermistor (CR107-L; Campbell Scientific, Logan, UT, USA) and anemometer were used to record air temperature and wind speed at one location near the center of the harvested area throughout the experiment.

The wetted treatments received weekly water additions that totaled 20 % of the average long-term precipitation received in the nearby state college (~10 km NE of the study site). Mean monthly precipitation from 1882 to 2005 was calculated from the US Historical Climatology Network data (Easterling et al. 1996). The calculated 20 % monthly precipitation was divided into weekly watering amounts. During the growing season (April–November), water was applied weekly by hand with watering cans and water collected in on-site precipitation catchments. Five precipitation catchments were constructed adjacent to the study plots using a wooden frame covered with clear corrugated roofing that drained into 55-gal opaque barrels through roofing gutters. The barrels were wrapped with reflective insulation to limit passive solar heating and reduce algal growth in the stored water. In the winter months (December–March), open top containers were installed near the study plots to capture snow, ice, and precipitation. Precipitation caught in the containers was manually distributed on the plots weekly as snow, ice, or water. If the precipitation was in liquid form, we delivered the volume equivalent of 20 % of the long-term mean. If the collected precipitation was snow or ice, we modified the delivery of the wetted treatment by adding the snow and ice collected in containers that represent 20 % of the area of a study plot. The mass of the snow or ice inside the containers was recorded and used to calculate water equivalent in millimeters of wet precipitation.

A tipping bucket rain gauge within the study area measured ambient precipitation. The quantity of water (whether liquid, snow, or ice) applied weekly to the watered plots was recorded and percent effective watered treatment was calculated by week, month, year, and experiment duration by dividing the wetted treatment amount by the ambient precipitation. Soil volumetric water content (VWC) was measured between 3.5 and 6.5 cm using the same Decagon ECH_2O EC-TM soil probes recording hourly temperature. Starting in summer of 2009, additional soil VWC measurements were collected every 2 weeks with a Theta Probe-type ML2x (Delta-T Devices, Cambridge, England). The Theta Probe integrates VWC along 0 to 5 cm depth. In each natural subplot, three Theta Probe measurements were taken within the inner 25 cm boarder, and each of the three measurements was the median of three readings from that specific location. Finally, gravimetric soil water content (in grams H_2O per gram OD soil) was measured every season.

2.2 Climate-driven ecological thresholds

The six thresholds addressed by our hypotheses are (1) cumulative GDD_5 and FFD, (2) optimal leaf temperature for photosynthesis (OLT), (3) LTG_{35}, (4) soil F-Ts, (5) soil water content below PWP, and (6) volumetric soil water content between PWP and FC or optimum water content (OWC).

Total GDD_5 were calculated from May 2008 to August 2010 with the equation $\sum([(T_{\max}+T_{\min})/2]-T_{\text{base}})$ with $T_{\text{base}}=5$ °C. We used the dominant method for calculating

GDD, where if $[(T_{max}+T_{min})/2]<T_{base}$, then $[(T_{max}+T_{min})/2]=T_{base}$ (McMaster and Wilhelm 1997). FFD were the number of days between March and November where the minimum daily IRR temperature was >0 °C. Optimal leaf surface temperature for carbon fixation was identified as 19.2–23.6 °C (Helliker and Richter 2008). The number of hourly surface temperature measurements that fell between 19.2 and 23.6 °C during daylight hours were summed for each plot and then averaged within treatments. Likewise, the LTG_{35} was calculated in the same manner but for all the data since temperatures rarely exceeded this value at night.

The number of F-Ts was summed for each plot for the duration of the experiment. Soil F-Ts were identified with 5-cm depth soil temperature data from the Decagon ECH_2O EC-TM soil probes. F-Ts occurred each time temperature fell below 0 °C and then returned above 0 °C. Not only is the frequency of soil F-Ts biogeochemically important, but also the duration (Henry 2007). Therefore, we also calculated the duration between a freezing and thawing event for each plot.

The OWC was defined as any soil VWC between PWP and FC after converting these moisture thresholds from matrix potentials to VWC. Water retention curves for five soil cores and bulk densities were used to make this conversion. For the water retention curves, a combination of raised water columns for potentials −0.001 to −0.01 MPa and pressure plates for potentials −0.01 to −1.5 MPa were used. The water retention curve was modeled using the van Genuchten (1980) equation. The average VWC for each of the five soil cores at −1.5 MPa was 0.11 $m^3\ m^{-3}$, which we used as the threshold value for PWP (Lambers et al. 2008). The average VWC when soil cores were at −0.01 MPa was 0.28 $m^3\ m^{-3}$, which we used as the threshold value for FC (Brady and Weil 2000).

2.3 Data analysis

Temperature and soil moisture data were presented and analyzed in histograms. Histogram bins were created according to a modified method of Freedman and Diaconis (1981). We used the equation $h=2\times[Q1-Q3]/n^{1/3}$, where h is the bin size, n is the total number of data points, and Q1 and Q3 are quartile 1 (25 %) and quartile 3 (75 %), respectively. The number of bins (k) was calculated by using $k=[Max-Min]/h$, where Max and Min are the maximum and minimum values, respectively. Bivariate histograms of soil temperature and moisture were created by crossing 1 °C intervals in temperature with 0.010 $m^3\ m^{-3}$ intervals in VWC in order to achieve greater resolution. All data analyses were conducted with Statistical Analysis Software version 9.1 (SAS Institute Inc., Cary, NC, USA). Repeated-measures analysis of variance (ANOVA) was used to test treatment effects on soil moisture and temperature with *proc mixed*. The data used in these repeated-measures ANOVA were pooled by month. For ANOVAs on ecological threshold histogram data, post hoc tests were performed to compare treatment means using *ls means* in SAS. An alpha value of 0.05 was used to determine significance. Data losses in the Decagon ECH2O EC-TM probes due to damage from animals were gap-filled using the most recent 200 or more values in a simple linear regression against other plots from the same treatment. These regressions had R^2 values >0.75. Data for VWC were trimmed to the time period between the months of April to October because the data were not as reliable during months with freezing temperatures.

3 Results

Mean annual air temperature at our site in 2009 (the only full year with microclimate data) was 9.1 °C; the mean air temperature for the region from 1971 to 2000 was 8.7 °C (Fig. 1). From May 2008 until August 2010, the greatest deviation of the monthly mean air temperature from the historical mean was during 2010 (Fig. 1). The annual precipitation was 883 mm for 2009, compared to the historical mean for the region of 1,046 mm. Precipitation at the site fell below historical means approximately 17 out of 25 months, and above historical means for 5 months (Fig. 1). Thus, we conducted our experiment in a drier than normal time period. The target wetted treatment was 20 % of the long-term mean precipitation, while the effective wetted treatment over the duration of the experiment was 23 % above ambient precipitation. Monthly increases in precipitation ranged from 12 to 43 % of ambient precipitation, with weekly additions ranging from 0 (winter weeks where no precipitation was collected) to 6.6 mm $week^{-1}$.

Over the 2.5-year duration of the experiment, the warmed treatments significantly increased surface temperatures an average of 1.8 °C and soil temperatures of 2.5 °C at 5 cm depth ($p<0.001$; Table 1). Wetting had a slight cooling effect, as indicated by the lower temperatures in the two-factor treatment of 1.7 and 1.8 °C for surface and soil temperatures, respectively, but not significantly different from the warmed. Warming and wetting effects on mean monthly soil temperature both showed significant interactions with time of year (Table S1). The magnitude of soil warming (relative to the controls) depended upon the month (warmed × month, $p<0.0001$) and wetting (warmed × wetted, $p=0.0122$). Monthly means for surface and soil temperatures were significantly different among treatments except for the month of June (Table 1). Watering decreased surface temperatures, but not significantly (Table 2).

There were no individual treatment effects on soil moisture; however, there was a significant warmed × month interaction ($p=0.0170$). Three measures of soil water content indicate that warmed and warmed+wetted treatments

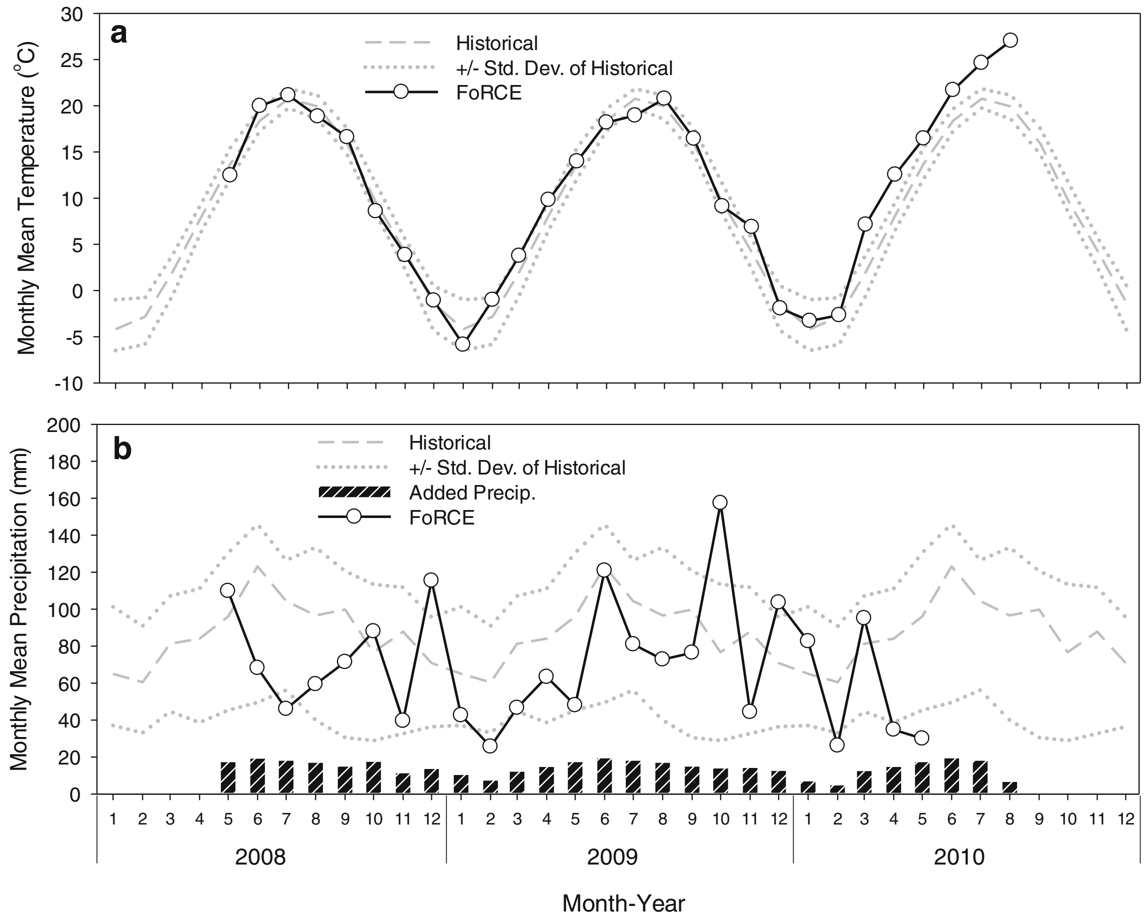

Fig. 1 **a** Historical monthly mean air temperature (*dashed line*) and ±standard deviations (*dotted lines*), and FoRCE air temperature (*solid line*) from 2008 to 2010. **b** Precipitation historical monthly means (*dashed lines*) and ±standard deviations (*dotted lines*), measured precipitation at the FoRCE site (*solid line*), and amount of additional precipitation added to the wetted treatment plots (*bars*). Historical temperature and precipitation data were retrieved from Penn State Climatologist (PSC 2010, http://climate.met.psu.edu)

decreased soil moisture, but not significantly (Table 2). Wetted treatments showed no significant overall long-term increases in soil water content measured volumetrically or gravimetrically (Table 1). However, we observed pulses in VWC after wetting events that typically lasted several hours (data not shown).

To validate soil temperature and moisture data collected with the Decagon ECH$_2$O probes, we compared soil temperature and moisture data collected independently with handheld probes. Buried sensors and handheld probes were well-correlated for soil temperature (R^2=0.97), but not for VWC (R^2=0.40) (Fig. 2). Buried Decagon VWC tended to underestimate VWC compared to the handheld Theta Probe under VWC of 0.3 and, conversely, to overestimate VWC above 0.3 (Fig. 2). We also used handheld probes to compare soil temperature and moisture between the “planted” and “natural” subplots. The soil moisture data were similar between subplots, falling along a 1:1 line (Fig. S2), but the soil temperature was often greater in the “planted” subplots. On average, “planted” subplots were 2.7±0.2 °C warmer than “natural” subplots.

Surface temperatures in warmed plots showed a significant increase in frequencies of 18–30 °C hourly measurements compared to nonwarmed plots, although this treatment effect diminishes for temperatures >33 °C (Fig. 3). The greatest effect of warming in both the single-factor and two-factor treatments was seen in the temperature ranges of less than −6 to 0 °C, where frequencies in these bins were much higher than ambient and wetted (Fig. 3a). As expected, warmed treatments also experienced fewer hourly measurements below 0 °C than ambient or wetted. Warmed treatments significantly increased the number of GDD$_5$ (Fig. 3b; p<0.0001) and FFD (Fig. 3c; p<0.0001). Warmed treatments recorded a greater number of hourly measurements within the range of optimal leaf temperature for C assimilation (19.2–23.6 °C based on Helliker and Richter 2008) than ambient and wetted (Fig. 3d; p<0.0001).

Generally, significant differences in soil temperature among treatments were at lower and higher temperature ranges (Fig. 4a). Warming significantly increased the number of hourly soil temperatures recorded between 24 and

Table 1 Monthly averages for surface and soil temperatures and VWC from May 2008 to August 2010

	Month	Ambient		Warmed		Wetted		Warmed+Wetted	
Surface temperature (°C)	January	−4.9	(0.1)	*−2.8*	*(0.2)*	−4.9	(0.1)	*−2.6*	*(0.2)*
	February	−2.1	(0.0)	*0.5*	*(0.1)*	−2.3	(0.1)	*0.1*	*(0.1)*
	March	5.8	(0.1)	*8.0*	*(0.2)*	5.7	(0.1)	*7.8*	*(0.1)*
	April	11.2	(0.2)	*12.9*	*(0.1)*	11.2	(0.0)	*12.9*	*(0.3)*
	May	15.5	(0.1)	*17.0*	*(0.0)*	15.3	(0.0)	*16.8*	*(0.2)*
	June	21.1	(0.2)	21.9	(0.3)	21.0	(0.1)	21.9	(0.3)
	July	22.0	(0.3)	*23.5*	*(0.1)*	21.5	(0.1)	*23.2*	*(0.3)*
	August	21.0	(0.2)	*23.0*	*(0.2)*	20.7	(0.3)	*22.5*	*(0.3)*
	September	17.1	(0.2)	*18.9*	*(0.2)*	16.7	(0.4)	*18.9*	*(0.5)*
	October	9.4	(0.2)	*11.1*	*(0.4)*	9.0	(0.1)	*11.4*	*(0.5)*
	November	5.4	(0.2)	*7.5*	*(0.4)*	5.0	(0.1)	*7.5*	*(0.4)*
	December	−1.5	(0.1)	*0.5*	*(0.1)*	−1.8	(0.1)	*0.6*	*(0.2)*
Soil temperature (°C) at 5 cm depth	January	0.5	(0.1)	*2.2*	*(0.5)*	0.7	(0.0)	*1.8*	*(0.3)*
	February	0.5	(0.2)	*2.4*	*(0.4)*	0.6	(0.1)	*2.0*	*(0.3)*
	March	5.2	(0.1)	*8.4*	*(0.4)*	5.3	(0.2)	*8.2*	*(0.3)*
	April	11.6	(0.2)	*14.2*	*(0.4)*	11.6	(0.2)	*13.7*	*(0.2)*
	May	15.5	(0.2)	*17.4*	*(0.4)*	15.3	(0.1)	*16.8*	*(0.1)*
	June	20.0	(0.3)	*21.8*	*(0.3)*	20.4	(0.2)	20.7	(0.1)
	July	21.1	(0.1)	*23.5*	*(0.3)*	21.6	(0.3)	*22.6*	*(0.1)*
	August	21.0	(0.1)	*23.8*	*(0.3)*	21.5	(0.3)	*22.9*	*(0.2)*
	September	18.0	(0.1)	*20.8*	*(0.3)*	18.5	(0.2)	*20.1*	*(0.4)*
	October	11.8	(0.3)	*14.1*	*(0.7)*	12.1	(0.1)	*14.2*	*(0.5)*
	November	8.0	(0.2)	*10.8*	*(0.8)*	7.9	(0.1)	*10.4*	*(0.6)*
	December	2.3	(0.3)	*5.1*	*(0.6)*	2.4	(0.1)	*4.5*	*(0.3)*
Soil moisture (m^3 m^{-3}) at 5 cm depth	January								
	February								
	March								
	April	0.336	(0.032)	0.333	(0.016)	0.340	(0.024)	0.324	(0.017)
	May	0.333	(0.035)	0.323	(0.017)	0.354	(0.021)	0.306	(0.021)
	June	0.264	(0.039)	0.253	(0.011)	0.272	(0.019)	0.235	(0.025)
	July	0.207	(0.037)	0.195	(0.005)	0.209	(0.015)	0.192	(0.023)
	August	0.193	(0.035)	0.149	(0.006)	0.165	(0.024)	0.172	(0.028)
	September	0.220	(0.032)	0.180	(0.012)	0.177	(0.020)	0.179	(0.026)
	October	0.335	(0.033)	0.278	(0.019)	0.288	(0.028)	0.262	(0.033)
	November								
	December								

Standard errors (n=4) are in parentheses, and treatments significantly different than ambient are in italics

30 °C compared to ambient and wetted treatments (Fig. 4a). Warmed treatments did not greatly decrease the number of hourly measurements recorded below 0 °C compared to nonwarmed, but did significantly decrease measurements of soils between 0 and 6 °C. Warmed treatments had significantly less F-Ts (p=0.0006) than ambient and wetted treatments (Fig. 4b). There was also a significant warmed×wetted effect on the duration of F-Ts (p=0.0402), but no significant difference among treatments.

There were no discernible trends in the distribution of VWC measurements compared among treatments (Fig. 5a), although there was one bin (0.15–0.20 range) with significant treatment effects on VWC. Warmed and wetted treatments did not significantly affect the number of measurements when soils were below PWP (<0.11 VWC) or extremely wet (>0.5 VWC), nor did the treatments significantly alter the frequency of measurements between PWP and FC (Fig. 5b).

Table 2 Mean deviations from ambient (i.e., treatment minus ambient) for soil temperature and moisture from May 2008 to August 2010

		Warmed		Wetted		Warmed+Wetted	
Soil temperature or moisture measurement	*n*	Difference from ambient temperature (°C)					
Surface temperature—infrared radiometer	19,255	*1.8*	*(0.0)*	−0.3	(0.0)	*1.7*	*(0.0)*
Soil temperature—Decagon ECH$_2$O	20,588	*2.5*	*(0.0)*	0.2	(0.0)	*1.8*	*(0.0)*
Soil temperature—Taylor	10	1.8	(0.2)	0.3	(0.2)	1.4	(0.3)
		Difference from ambient water content (m^3 m^{-3})					
Volumetric water content—Decagon ECH$_2$O	17,010	−0.029	(0.000)	−0.013	(0.000)	−0.026	(0.000)
Volumetric water content—Theta	22	−0.022	(0.020)	0.003	(0.004)	−0.017	(0.009)
Gravimetric water content	9	−0.060	(0.019)	0.034	(0.016)	−0.005	(0.047)

Mean deviations of treatments (n=4) and standard errors are shown in parentheses. Values significantly different than ambient are shown in italics

Binned frequencies of combined soil temperature and moisture intervals (e.g., 9–10 °C and 0.22–0.23 VWC) showed different patterns in warmed versus wetted soils (Fig. 6). Each panel in Fig. 6 plots the mean (n=4) frequencies for each treatment. Warming shifted the inverted L-shaped bivariate frequency figures in ambient and wetted to a more diagonal shape. The ambient and wetted treatments appeared to have a wider distribution in both temperature and moisture directions. The warmed treatment has less wet-hot measurements than all the other treatments. Ambient and wetted treatments show distinct vertical lines across the left side of the graphs between freezing and ~2 °C, whereas warmed and warmed+wetted graphs do not have as distinct vertical lines, but do have large, high-frequency wet-cold areas (upper left corners).

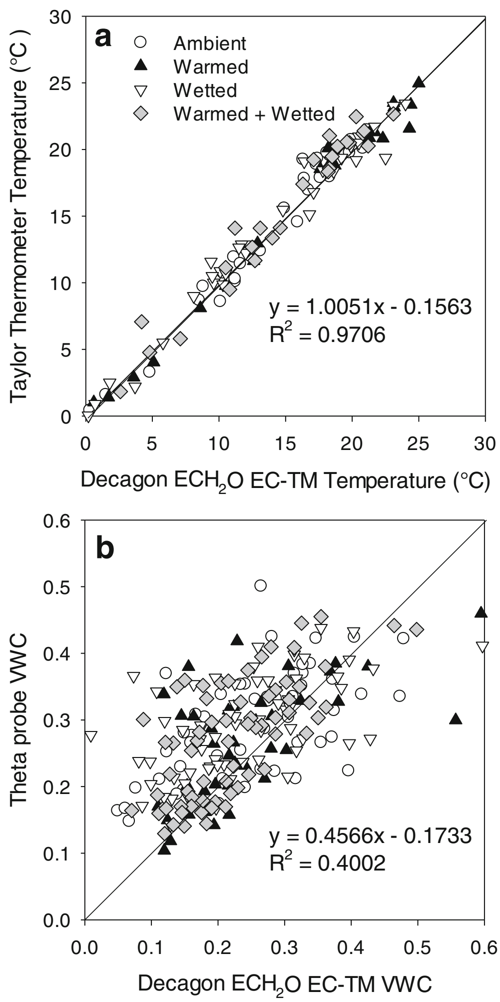

Fig. 2 **a** Soil temperature regression as measured by the Decagon ECH$_2$O EC-TM probes at 5 cm depth and Taylor thermometers integrating 0–8 cm depth. **b** Soil moisture regression as measured by the Decagon ECH$_2$O EC-TM probes at 5 cm depth and Theta Probes integrating soil moisture from 0 to 5 cm depth

4 Discussion

One important question that arises from this research and other ECME results is: Do the climate manipulations actually represent what is predicted to occur by GCMs? Warming with IR heaters has sparked a debate as to whether or not they realistically mimic future terrestrial microclimate conditions (Aronson and McNulty 2009; Kimball 2011). Kimball (2005) mentions that vapor pressure deficits caused by the IR heaters can be one of the main unintended warming effects, but that this can be overcome by adding supplemental water. Carlyle et al. (2011) found that using open top chambers and rainout shelters to manipulate temperature and precipitation created unintended "crossover" effects. In other words, manipulating temperature will affect a precipitation response variable (soil moisture) and vice versa. We observed this in our experiment as supplemental precipitation had a cooling effect on soil temperatures. The inextricable link between these two microclimate variables was further emphasized in this study.

Suspended IR heaters simulated the increases in mean temperature by raising surface temperatures an average of 1.8 °C. This increase in surface temperature was accompanied by a mean increase in soil temperature of up to 2.5 °C.

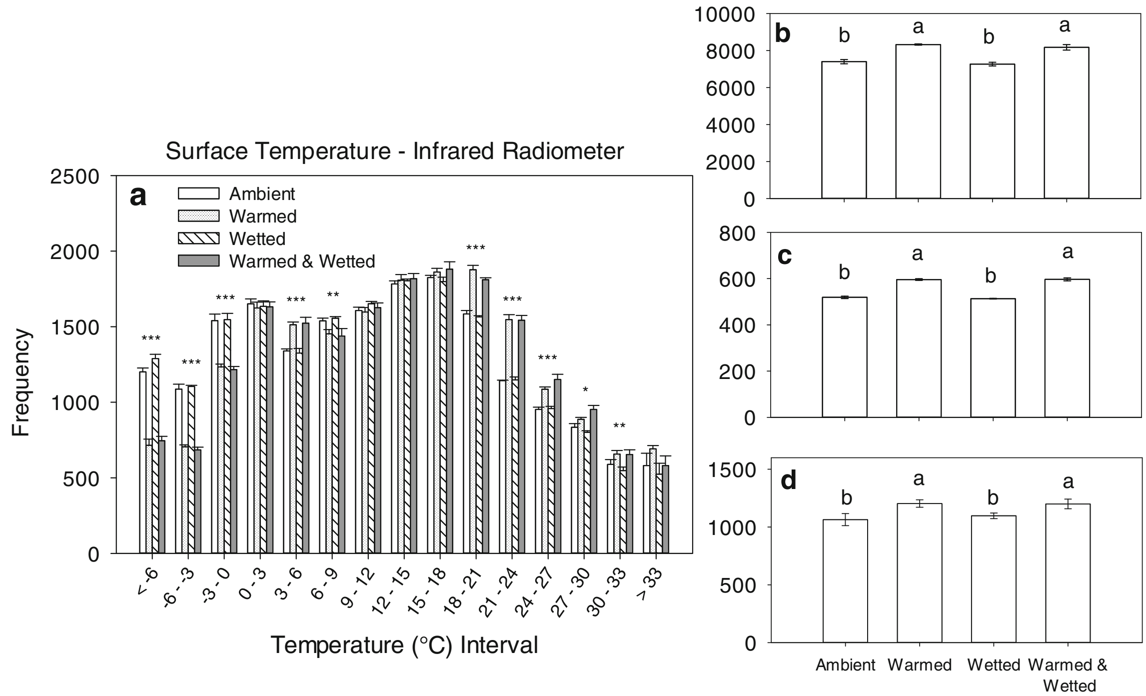

Fig. 3 Surface temperatures (in degrees Celsius) measured with Apogee IRR. **a** Frequency of readings from May 2008 to August 2010. *$p<0.05$, **$p<0.01$, ***$p<0.001$, significance levels. **b** GDD_5. **c** FFD. **d** Frequency of events with leaf temperatures in optimum C fixation range (OLT, 19.2 to 23.6 °C). *Bars* represent treatment means and *error bars* are ±1 standard error (n=4). Post hoc tests were least squared means with significance set at $\alpha<0.05$, and *lowercase letters* indicate significance

Other studies have observed similar heating effects using the same IR heaters (Harte et al. 1995; Kimball 2005; Wan et al. 2002). The interactive effects of warming and wetting had little effect on surface temperatures, but decreased soil warming by over 25 %, from an average of +2.5 °C in warmed plots to +1.8 °C in warmed+wetted plots. This interaction was likely due to the cooling effects of greater evapotranspiration in warmed+wetted plots. Vapor pressure

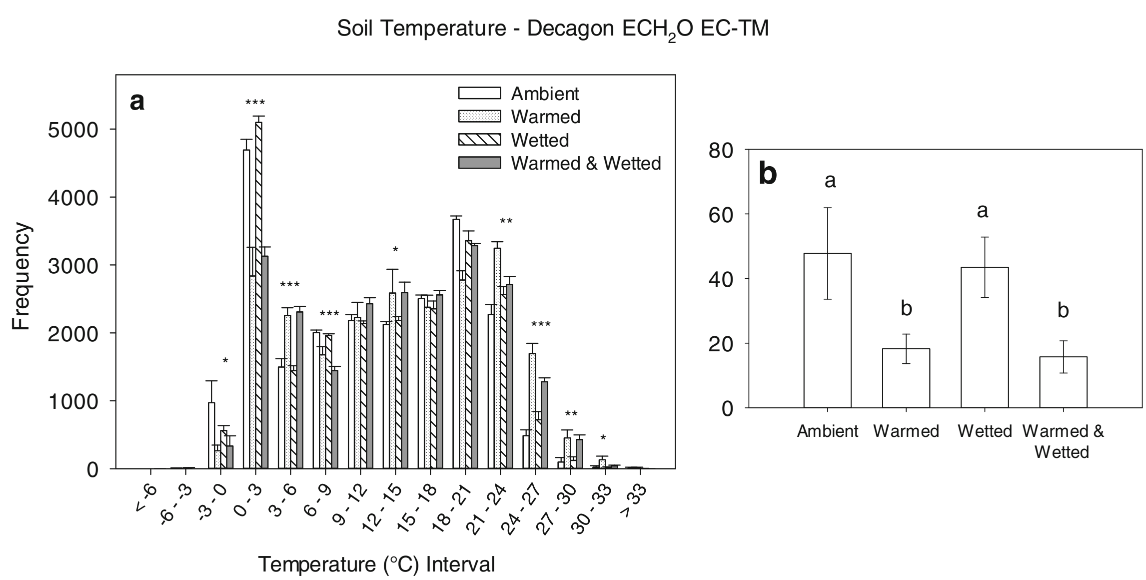

Fig. 4 Soil temperatures (in degrees Celsius) measured with Decagon ECH_2O EC-TM probes. **a** The frequency of temperature readings at 5 cm depth. *$p<0.05$, **$p<0.01$, ***$p<0.001$, significance levels. **b** The frequency of soil F-Ts from May 2008 to August 2010. *Bars* represent treatment means and *error bars* are the standard error (n=4). Post hoc tests were least squared means with significance set at $\alpha<0.05$, and *lowercase letters* indicate significance

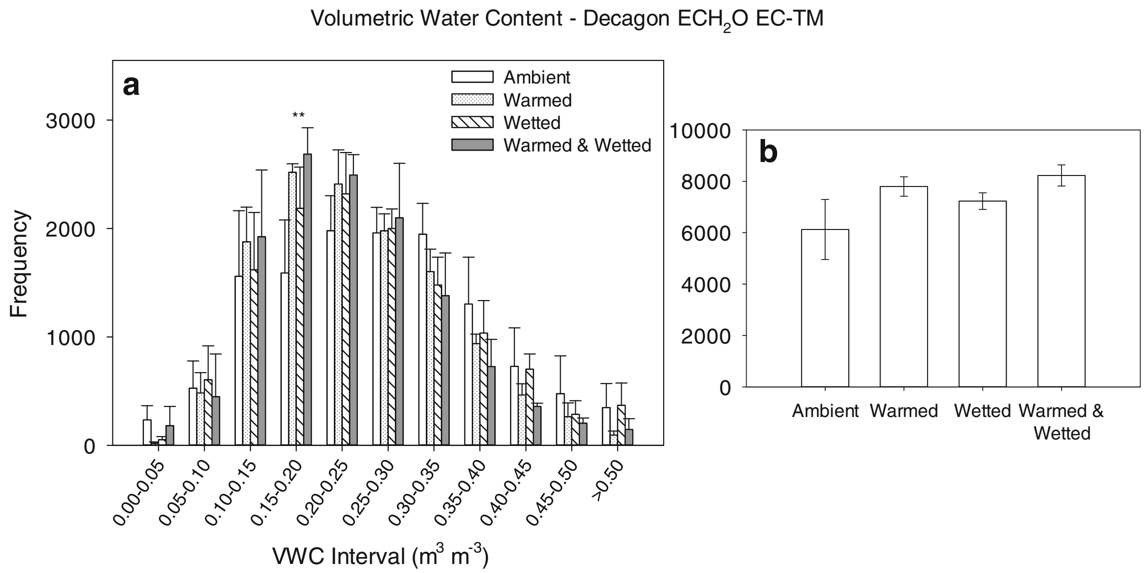

Fig. 5 Soil VWC measured with Decagon ECH$_2$O EC-TM probes. **a** The frequency of VWC readings at 5 cm depth from May 2008 to August. *$p<0.05$, **$p<0.01$, ***$p<0.001$, significance levels. **b** Frequency of readings between PWP, determined at a value of −15 MPa, and FC (−0.01 MPa). *Bars* represent treatment means and *error bars* are the standard error ($n=4$). Post hoc tests were least squared means with significance set at $\alpha<0.05$, and *lowercase letters* indicate significance

gradients and evapotranspiration have been shown to change under warming simulated by these IR heaters, and adding water could alleviate this artifact (Kimball 2005).

We hypothesized that the warming treatment would lengthen the growing season by increasing the number of GDD$_5$ and FFD. Our data support this hypothesis; warmed and warmed+wetted plots had more FFD and GDD than ambient or wetted only plots. Even though wetted treatments generally depressed surface temperatures over the course of the experiment, wetting had little effect on GDD$_5$ and FFD. In temperate forests, the mean annual temperature is below the OLT range for C fixation (Helliker and Richter 2008).

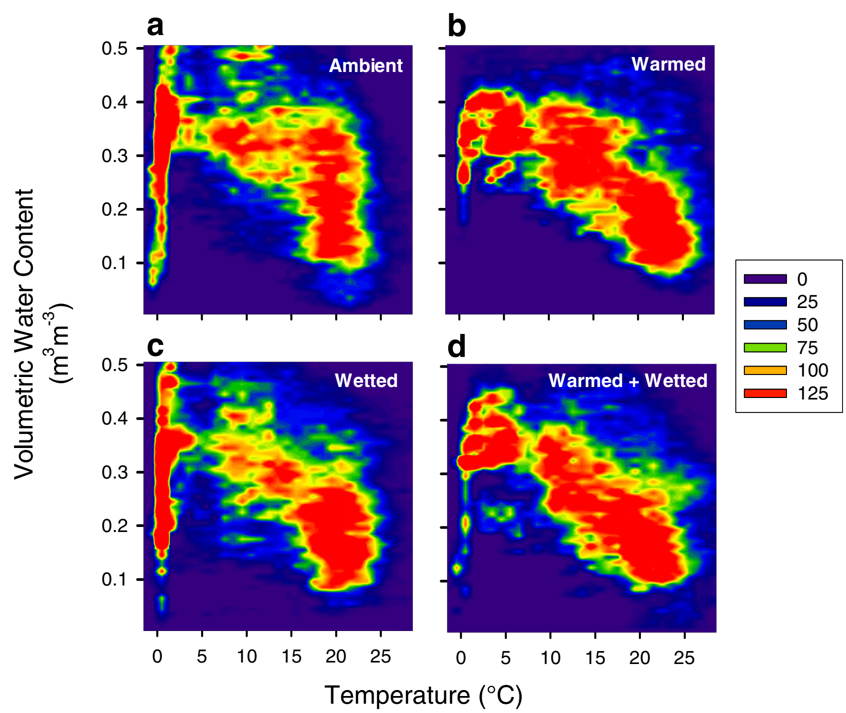

Fig. 6 Bivariate contour histograms with soil temperature and VWC frequencies at 5 cm depth shown for **a** ambient, **b** warmed, **c** wetted, and **d** warmed+wetted treatments. Frequencies, shown in the colors, are the means ($n=4$) from each treatment. The histogram bins were created by crossing 0.01 intervals in VWC with 0.5 intervals in temperature

Thus, we predicted that the warmed treatments would increase the number of hours that plant surface temperatures are within the optimal photosynthetic range of 19.2 to 23.6 °C. This hypothesis was also supported; we found that warmed plots experienced significantly more time in the optimum temperature range than nonwarmed plots. Biochemical processes, such as photosynthesis and respiration, are increased at higher temperatures because of changes in activation energy and enzyme function (Way and Oren 2010); however, these effects will not be experienced similarly by all plant species. For instance, in some regions, plants are already at or near their growing season optima temperatures and they could be negatively impacted by climate change. Therefore, the consequences of a warmer world on plant-level physiology could scale up to have regional to global impacts on species success and distribution (Hamann and Wang 2006; Iverson and Prasad 1998). We found that temperatures above 35 °C occurred in all treatments, which is a temperature threshold where plant biochemical pathways are adversely affected (Schrader et al. 2004). Warmed plots only had slightly (nonsignificant) greater frequency of measurements above 35 °C.

The freezing point of soil water is a critical temperature threshold in soils and can exert controls on ecosystem functioning. Based on prior research (Fitzhugh et al. 2001; Groffman et al. 2001a), we hypothesized that warming would reduce snowpack that insulates soils, leading to an increase in soil F-Ts (Hardy et al. 2001). In contrast to our expectation, warmed plots had fewer soil F-Ts than ambient plots or wetted plots. A major difference between snow removal experiments and our experiment is that, after melting, thermal inputs from the IR heaters prevented exposed soils from dropping below 0 °C. One explanation for these results is that the PID system controlling the warming is quick enough to warm before soil temperatures reach 0 °C. In contrast, a system that has a slower feedback mechanism may warm soils, next allow them to cool below 0 °C, and then warm them again, thereby creating more F-Ts. Soil F-Ts are an important threshold for determining soil microbial processes and root dynamics (Fitzhugh et al. 2001; Groffman et al. 2001a; Matzner and Borken 2008), and our results show that this threshold is very sensitive to details of heater programming.

The direct effect hypothesis that wetting increases soil moisture was not supported. We did not show that wetting increased the time that soil moisture is between PWP (−1.5 MPa) and FC (−0.01 MPa). Our data trend in this direction, but the treatments were not significantly different. The lack of a prolonged soil moisture effect seen in the watered treatments was unexpected, as was the lack of soil drying in the warmed plots (Harte et al. 1995; Kimball 2005). Possible explanations for the lack of soil moisture response to climate manipulations include soil probe limitations (e.g., high variability) and possible effects of plant communities on the physical soil conditions or water movement from soils.

Decagon ECH$_2$O probe readings have been found to be temperature dependent, with every 1 °C increase in temperature relating to a 0.1 % decrease in the VWC estimate (Czarnomski et al. 2005). However, this artifact of warming on VWC would cause warmed treatments to have lower VWC, which is opposite to the trend we observed (Fig. 5b). Additionally, forest harvesting disturbs soil hydrologic processes (Huang et al. 1996), which could in turn affect both soil water content and probe efficacy. Indeed, soil moisture as measured with the Decagon probes was much more variable than temperature (Figs. 4 and 5) and did not correlate as well with an independent measure of surface soil moisture (Fig. 2).

Another factor affecting soil temperature and moisture probe operation could be the large amount of regenerative root growth resulting from the postharvest environment of our study site. Roots were observed growing around the Decagon soil moisture probes, which could have affected soil moisture readings by either interference or plant drawdown of soil water. The lack of soil drying effect by warming may have been due to water transported by plants from deeper to shallower depths in the soil profile, which we cannot confirm because we only have moisture data to 5 cm depth. Tree species' composition measured in these plots were different among treatments (Rollinson et al. 2012), and individual tree species are known for differences in soil water uptake and hydraulic lift (Aranda et al. 2012; Jackson et al. 1999). However, we found that overall root biomass in the upper 15 cm was not different among plots (unpublished data). Thus, concomitant changes in plant communities with wetting may have been responsible for the lack of a wetting effect on soil moisture, but we were unable to confirm this.

The interactions of the treatment effects on soil temperature and moisture were apparent in the altered distributions in the bivariate histograms (Fig. 6). Observing soil temperature and moisture frequency data in these bivariate histograms can be more helpful than the individual microclimate histograms alone (Figs. 4 and 5) because these two variables have interacting effects on ecosystem structure and function. First, the vertical lines between 0 and ~2 °C are indicative of unreliable VWC readings during this time because of soil water freezing. The warmed treatments, while lacking this vertical line, show an increase in frequency of data in the wet and just-above-freezing regions, which is due to the IR heaters preventing freezing and keeping the soils moist. The overall shift in distributions from more of an "inverted L" shape in the nonheated to a diagonal shape in the warmed treatments reflects a warming-induced drying at higher temperatures. These data suggest that we have ultimately changed the soil temperature–moisture regimes, but that there are anomalies missed (e.g., high variability in nonheated plots at lower temperatures) when analyzing each microclimate variable separately.

The seven climate-driven ecological thresholds we examined in this manuscript impact ecosystem functioning and structure. Added precipitation did not noticeably affect the number of extremely dry or wet measurements. Warmed treatments often resulted in less snowpack (from observation), but the IR heater warming was great enough to prevent soil freezing. Warmed treatments also increased the GDD_5, FFD, and the time leaf temperatures spent in the optimal photosynthetic range. PWP was used as an indicator of water stress; watered and warmed treatments did not show any significant effect on frequency of readings below PWP. Thus, some of the climate-driven, ecologically important thresholds followed predictable patterns (direct warming hypotheses); however, some of our hypotheses were not supported, meaning that unpredictable threshold responses are possible in the use of ECMEs intended to study the effects of climate change on ecosystem structure and function.

5 Conclusion

Mean warming predicted by GCMs for northeastern USA was successfully mimicked in a postharvest forest climate manipulation experiment in central Pennsylvania. This warming was expected to lead to changes in the regenerating forest ecosystem's structure and function. Despite augmenting precipitation by 23 %, we did not observe a prolonged response in soil moisture with the Decagon probes. Interactive effects between the two climate variables (wetting-induced cooling of surface and soil temperatures) emphasize the importance of conducting multivariate climate change experiments. On the whole, the microclimate in this regenerating forest ecosystem showed significant responses to what are low-level to mid-level predicted changes of climate in the northeastern USA. We found that some of the hypotheses regarding critical, climate-driven ecological thresholds from a warmed and wetted experiment were supported. However, the increase of F-Ts and lack of prolonged VWC increase due to wetted treatments contrasted with our initial hypotheses.

Ecosystem climate manipulation studies often report only mean responses in microclimatic variables (e.g., mean temperature increases), and our data are consistent with these findings. However, we evaluated thresholds that are likely as important, if not more, to ecological functioning as means of microclimatic variables. We suggest that future ECMEs, especially those crossing multiple treatments, also report microclimatic thresholds that are known to impact ecological functioning.

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