

Thomas R. Rambo¹, Department of Plant Sciences, University of California, Davis, California, 95616

and

Malcolm P. North, Sierra Nevada Research Center, 1731 Research Park Dr., Davis, California, 95618

Spatial and Temporal Variability of Canopy Microclimate in a Sierra Nevada Riparian Forest

Abstract

Past riparian microclimate studies have measured changes horizontally from streams, but not vertically through the forest canopy. We recorded temperature and relative humidity for a year along a two-dimensional grid of 24 data-loggers arrayed up to 40 m height in four trees 2 - 30 m slope distance from a perennial second order stream in the Sierra Nevada. Our objective was to quantify diurnal and seasonal changes in vertical and horizontal microclimate gradients. Our data suggest a dynamic zone of riparian influence on microclimate that fluctuates diurnally and seasonally. Stream influence on microclimate was limited (statistically significant < 5.0 m vertically, < 7.5 m horizontally). In summer and winter, mean daily temperature and vapor pressure deficit (VPD) increased horizontally and vertically from the stream. Maximum absolute differences in temperature and VPD between upland and streamside conditions were greater in summer than winter. Winter diurnal ranges of temperature and VPD were dampened near the stream, increasing with distance, while summer diurnal ranges were greater near the stream and decreased with distance. Microclimate change was markedly greater vertically above the stream than horizontally. Such steep gradients of air temperature and moisture through the vertical forest profile likely affect arboreal habitat conditions that influence epiphytes and their animal communities.

Introduction

Riparian areas are zones of transition between aquatic and terrestrial environments where microclimate is strongly influenced by the aquatic system (Gregory et al. 1991, FEMAT 1993, Meleason et al. 2003). Microclimate directly influences most plant and animal ecological and physiological processes (Xu et al. 1997, Chen et al. 1999, Zheng et al. 2000), and the steepness of riparian environmental gradients fosters distinct ecosystem characteristics and functions (Gregory et al. 1991, Malanson 1993). In the past, riparian boundaries have been defined by general hydrologic, topographic, edaphic, and vegetative criteria, such as the spatial extent of herbaceous plants adapted to moist soils, stream geomorphology, and areal extent of sediment generation or nutrient inputs to streams (Gregory et al. 1991, Naiman and Décamps 1997). More recently, forest management has shifted towards more structural approaches to defining riparian boundaries such as the site-potential tree height criteria called for in the Northwest Forest Plan (FEMAT 1993). Nevertheless, uncertainty in quantifying and defining riparian boundaries (Gregory 1997, Chen et al. 1999, Darveau et al.

2001, Meleason and Quinn 2004) will remain until research can provide a better understanding of environmental gradients and ecosystem dynamics in riparian forests (Brosofske et al. 1997, Gregory 1997, Chen et al. 1999, Anderson et al. 2007).

Although many aspects of forest microclimate have been well-studied, there has been less research on the effect and extent of riparian influences on within-stand climatic variables (Moore et al. 2005). Past riparian studies have either compared microclimate between riparian and upland forest environments (Janzen 1976, Meleason and Quinn 2004) or measured changes restricted to 0.2 - 2 m above ground along transects running from forested streams to more upland conditions (Ledwith 1996, Brosofske et al. 1997, Danehy and Kirpes 2000, Erman and Erman 2000, Chan et al. 2004, Welsh et al. 2005, Rykken et al. 2007). We know of no reported studies of riparian temperature or humidity gradients that extend upwards from the forest floor through the vertical forest profile.

Our objective was to extend previous riparian microclimate work vertically into the forest canopy to provide information on temperature and humidity gradients that are known to be important for the structure and composition of epiphyte communities (McCune 1993, Sillett and Rambo 2000) and could influence arboreal habitat for

¹Author to whom correspondence should be addressed.
E-mail: trambo@ucdavis.edu

animals (Dupuis et al. 1995, Danehy and Kirpes 2000). We had three goals: 1) to quantify vertical and horizontal temperature and vapor pressure deficit gradients, 2) to identify vertical and horizontal distances at which microclimate variables became statistically significant from streamside conditions, and 3) to compare changes in microclimate gradients between summer and winter seasons. Although our observations were limited to one stream system, they provide preliminary information for developing testable hypotheses in future research.

Methods

Study Site

The Teakettle Experimental Forest (36° 58'N, 119° 02'W) is in the Sierra National Forest above the North Fork of the Kings River, approximately 80 km east of Fresno, California. This 1300 ha old-growth forest spans the red fir (*Abies magnifica*) and mixed-conifer ecotone on the west side of the Sierra Nevada. The mixed-conifer overstory consists of red fir, white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*). Representative understory vegetation includes manzanita (*Arctostaphylos nevadensis* and *A. patula*), bush chinquapin (*Castanopsis sempervirens*), and whitethorn (*Ceanothus cordulatus*). Warm, dry summers (Fowells and Means 1990) contrast with the cooler, moist winters. Annual precipitation averages 112 cm and falls mainly as winter snow, which persists through May (Berg 1990). Precipitation for the year of our study was typical of a non- El Niño or La Niña year according to long-term California Data Exchange Center observations at nearby Wishon Dam (available online at <http://cdec.water.ca.gov>). Generally gradual slopes, with an aver-

age gradient of 136 m km⁻¹ (Keeler-Wolf 1990), surround our study site on the perennial West Fork of Teakettle Creek at 2,000 m elevation. In the area of our transect, this second order stream averaged a summertime width of 120 cm and a depth of up to 63 cm.

Design and Analyses

Twenty-four Onset Hobo Pro 8 data-logging sensors were arrayed in a combined horizontal and vertical transect that ran perpendicular to and upland away from the stream (Figure 1). To reduce radiant heating, sensors were enclosed within naturally vented multiplate shields (however, see Nakamura and Mahrt 2005) and attached by brackets on northeast aspects of four tree boles. These two red and two white firs were approximately 2, 8, 22, and 30 m slope distance from the stream,

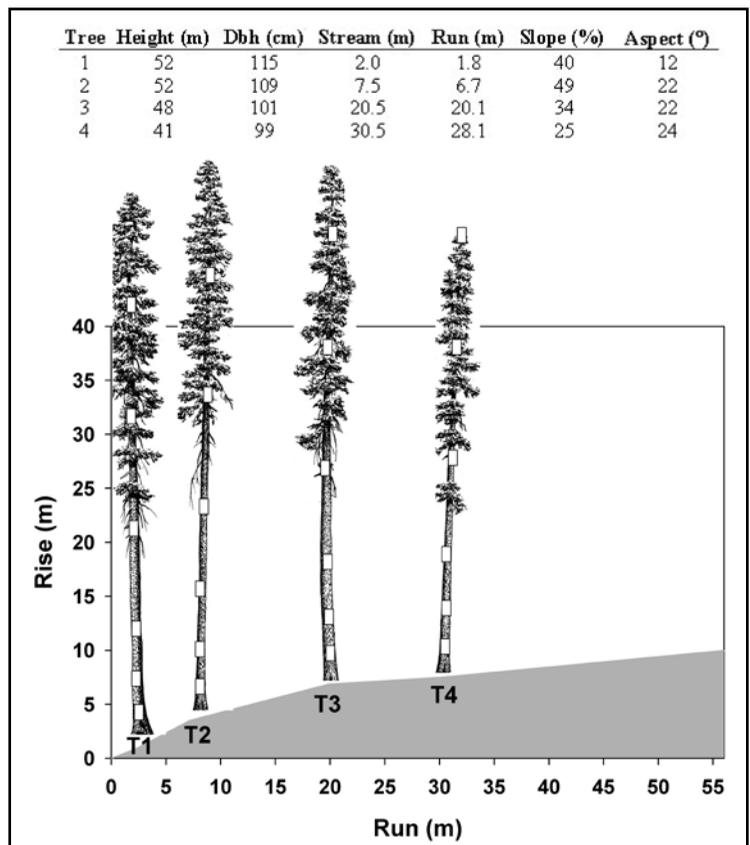


Figure 1. Study tree and environmental characteristics, and profile of the north-northwest facing slope of the study transect on the West Fork of Teakettle Creek. Approximate sensor locations are shown with white boxes in trees at 2, 5, 10, 20, 30, and 40 m above forest floor. Stream = slope distance to tree bole. The West Fork is located at the graph's origin.

and the sensors were mounted at 2, 5, 10, 20, 30, and 40 m (strata) above the forest floor. Sensors recorded temperature and relative humidity (RH) at 24 minute intervals for a year from September 2002 to September 2003. These sensors have accuracies of $\pm 0.2^\circ\text{C}$ and $\pm 3\%$ relative humidity ($\pm 4\%$ in condensing environments). Data from the sensor farthest from the stream (tree 4, 40 m height) was lost to lightning. Gap Light Analyzer software (Frazer et al. 1999) was used to calculate average canopy closure and transmittance of direct and diffuse light from hemispherical images taken from four cardinal directions around each tree.

Daily data from sensors in the 2 m stratum in the three more upland trees were averaged and smoothed using a moving average temperature approach (Liu et al. 1998) to determine starting and ending seasonal thresholds of temperature. Using threshold temperatures of 0 and 10°C , winter was defined as the time-period when daily mean temperatures were frequently $< 0^\circ\text{C}$ and summer when means were consistently $> 10^\circ\text{C}$ (Ma 2003). Because the transitional seasons of spring and fall are highly variable at this elevation of the Sierra, we focused our microclimate analyses on summer and winter seasons when temperature and humidity extremes are also likely to be most biologically important (Danahy and Kirpes 2000, Welsh et al. 2005).

The 24 minute observations of temperature and RH were used to calculate vapor pressure deficit (VPD, kPa), a measure of the drying power of the air more biologically relevant than RH to plant transpiration (Valigura and Messina 1994) and potential condensation especially important for epiphytic cryptogams. For practicality, we assumed $\text{VPD} = 0$ when temperature was $< 0^\circ\text{C}$. Because one goal was to assess changes in microclimate gradients relative to streamside conditions, rather than using absolute values, we calculated differences in mean daily temperatures and VPDs (Δ temperature and VPD) by subtracting the observation of the reference sensor nearest the stream (tree 1, 2 m height) from observations of each of the other arrayed sensors (Chen et al. 1995, Chen and Franklin 1997, Dong et al. 1998). These differences were assessed in two ways; mean daily differences were analyzed to quantify gradients in average temperature and VPD changes, and daily maxima differences were assessed to measure greatest differences between arrayed and streamside sensors. We also compared mean

daily temperature and VPD ranges to assess differences in microclimate buffering among sensor locations. Values were analyzed using repeated measures analyses of covariance (ANCOVAs, SAS 2002-2003) with time as a covariable and means compared with orthogonal contrasts ($P < 0.05$). Preliminary two-way analyses were run with Tukey's test for nonadditivity to test if the main effects of trees and strata were additive or multiplicative (Tukey 1949). Because main effects were consistently multiplicative, simple effects within trees and strata were examined. If power transformation of the response variable did not adequately achieve homoscedasticity and otherwise satisfy assumptions of normality, we resorted to nonparametric rank F tests. Lastly, mean temperature and VPD responses were regressed against horizontal, vertical, and direct hypotenuse distances from the stream to assess the relative amount of information explained by each.

Results

During our sample period, using the 0 and 10°C thresholds, winter was 143 days from 16 December through 7 May, and summer 130 days from 21 May through 27 September (Figure 2a). Over the summer period mean daily temperature (Figure 2b) ranged from 9.0°C (0630) to 21.7°C (1400) and over winter from -2.7°C (0700) to 3.8°C (1230). Summer mean daily RH ranged from 41.9% (1400) to 77.9% (0800), while winter RH ranged from 78.6% (1230) to 94.7% (2200 - 2400). Along our transect, the average canopy cover (76.8%) and transmitted diffuse light ($2.9 \text{ mol m}^{-2}\text{d}^{-1}$) calculated from 14 digital hemispherical photographs were not significantly different from the means (79.8% and $2.3 \text{ mol m}^{-2}\text{d}^{-1}$) calculated for nearby control plots in the Teakettle Experiment (Wayman and North 2007). However, those authors found higher levels of average transmitted direct light ($24.9 \text{ mol m}^{-2}\text{d}^{-1}$) beneath the canopy than we did ($8.2 \text{ mol m}^{-2}\text{d}^{-1}$), likely due to the patchy nature of mixed-conifer forest (Bonnicksen and Stone 1982) and the sloped northeast aspect of our transect (Figure 1).

Temperature

Summer mean daily temperatures increased with height and horizontal distance from the stream. However, maximum daily temperatures generally decreased with increasing distance, this

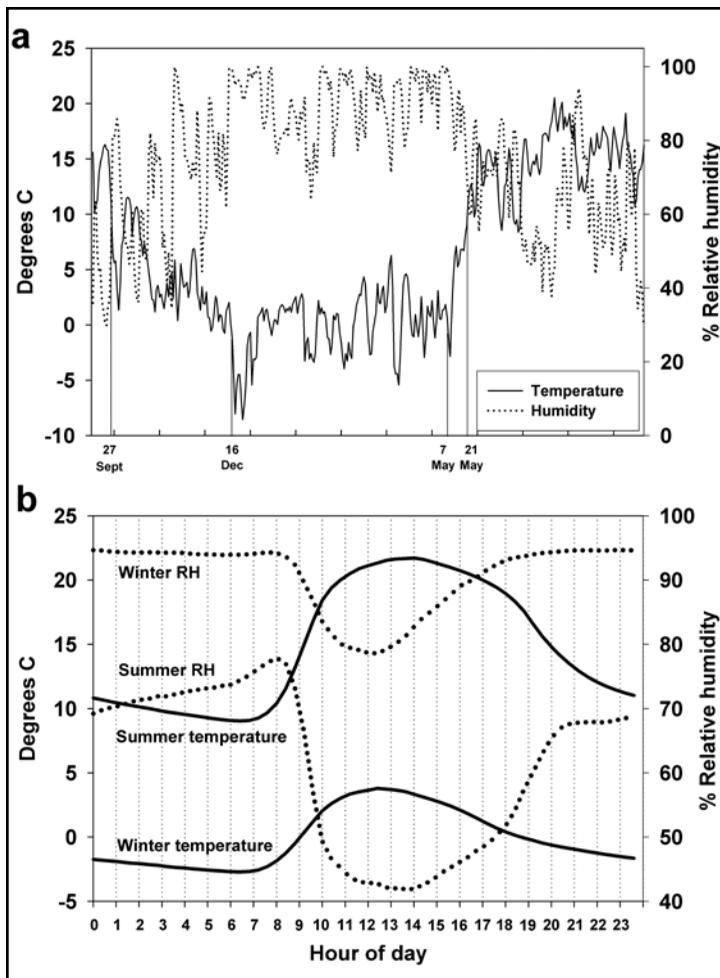


Figure 2. Mean humidities and temperatures 2 m above the forest floor averaged across the three most upland study trees (Trees 2, 3, 4), a) seasonally, September 15, 2002 – September 15, 2003, showing beginning and ending dates of summer and winter, and b) diurnally for summer and winter.

trend being most pronounced along diagonal, hypotenuse distances from the reference sensor. Statistically significant vertical declines occurred immediately between the 2 and 5 m strata across trees, and horizontally between trees 2 and 3 (7.5 and 20.5 m slope distance from stream, Figure 1). Daily ranges in temperature were greatest near the stream, and generally decreased vertically and horizontally away from it (Table 1a). These decreases became statistically significant from streamside conditions vertically between the 5 and 10 m strata across trees 1 and 2, and horizontally between trees 2 and 3.

Across sensors, daily mean and maximum summer temperature differences (Δ s) from the reference sensor generally increased with increasing distance from the stream vertically and horizontally (Figure 3). Maxima increased consistently above the stream. However, for both measures, horizontal increases noticeably weakened with height. Increases for both were immediately statistically significant vertically between the 2 and 5 m strata in tree 1 and horizontally between trees 1 and 2 (2 and 7.5 m slope distance).

Winter mean daily temperatures also increased consistently with distance from the stream. Winter mean temperature ranges (Table 1b) and Δ s increased vertically, and horizontally up to 20 m height, above which their horizontal trends of increase deteriorated. Maximum daily Δ s increased nearly consistently across heights and distances (Figure 3). Increases for both Δ measures and daily ranges became immediately statistically significant vertically between the 2 and 5 m strata in tree 1 and horizontally between trees 1 and 2.

Vapor Pressure Deficit

Summer mean daily VPDs increased (as RH decreased) with distance from the stream, though maximum VPDs showed no consistent pattern. Daily ranges decreased with increasing height and horizontal distance from the stream above 5 m (Table 1a). Thus, daily ranges were greatest nearest the stream and forest floor, with decreases becoming statistically significant vertically between 10 and 20 m in tree 1, 5 and 10 m in trees 2 and 4, and 2 and 5 m in tree 3.

Vertical and horizontal differences (Δ s) in summer mean and maximum (Figure 3) daily VPDs from the reference sensor generally increased with distance from the stream. Increases for both measures became immediately statistically significant

TABLE 1. Mean daily ranges (SD) in temperature (°C) and vapor pressure deficit (VPD, kPa) among sensors by tree (column) and stratum (row) for a) summer and b) winter. Within trees (columns), values with different letter superscripts are significantly different ($P < 0.05$). Within strata (rows), values in bold italics are significantly different from values in tree 1 ($P < 0.05$). Thick bold lines separate sensors that have significantly lesser (summer) or greater (winter) values ($P < 0.05$) from the reference sensor (tree 1, 2 m). The 40 m sensor in Tree 4 was lost to lightning.

a) Summer (n = 130 days)								
	Mean daily range temperature				Mean daily range VPD			
	1 2.0 m	2 7.5 m	3 20.5 m	4 30.5 m	1 2.0 m	2 7.5 m	3 20.5 m	4 30.5 m
40	11.5 ^e (1.8)	11.0^e (1.9)	10.7^e (1.7)		1.39 ^c (0.42)	1.32^f (0.44)	1.35^d (0.40)	
30	12.3 ^d (1.9)	12.0 ^d (2.0)	11.4^d (1.9)	11.0^e (1.9)	1.44 ^b (0.48)	1.37^e (0.49)	1.36^d (0.46)	1.31^e (0.45)
20	12.5 ^{cd} (2.0)	12.3 ^{cd} (2.0)	12.2 ^c (2.0)	11.8^d (2.0)	1.45 ^{ab} (0.50)	1.40^d (0.50)	1.40^c (0.49)	1.36^d (0.48)
10	13.0 ^{bc} (2.1)	12.8 ^{bc} (2.1)	12.4^{bc} (2.1)	12.4^c (2.1)	1.46 ^a (0.52)	1.44^c (0.52)	1.42^b (0.51)	1.41^c (0.51)
5	13.1 ^{ab} (2.1)	13.2 ^{ab} (2.1)	12.7 ^{ab} (2.1)	12.8 ^b (2.2)	1.46 ^{ab} (0.52)	1.48^b (0.53)	1.43^b (0.52)	1.47 ^b (0.54)
2	13.6 ^a (2.2)	13.7 ^a (2.2)	13.0^a (2.1)	13.4 ^a (2.2)	1.47 ^a (0.52)	1.52^a (0.54)	1.46 ^a (0.53)	1.51^a (0.55)

b) Winter (n = 143 days)								
	Mean daily range temperature				Mean daily range VPD			
	1 2.0 m	2 7.5 m	3 20.5 m	4 30.5 m	1 2.0 m	2 7.5 m	3 20.5 m	4 30.5 m
40	8.2 ^c (3.2)	8.2 ^c (3.2)	8.0^b (3.1)		0.40 ^c (0.36)	0.41 ^d (0.37)	0.42 ^d (0.37)	
30	8.4 ^c (3.1)	8.4 ^c (3.2)	8.1^{bc} (3.1)	8.0^c (3.0)	0.37 ^c (0.35)	0.38 ^{cd} (0.36)	0.40 ^{cd} (0.37)	0.40 (0.36)
20	8.1 ^c (3.0)	8.2 ^c (3.1)	8.3^c (3.2)	8.2^{ab} (3.2)	0.33 ^{bc} (0.32)	0.34 ^{bcd} (0.33)	0.37 ^{abcd} (0.35)	0.39 (0.37)
10	7.6 ^b (3.0)	7.8^b (3.0)	8.0^b (3.1)	8.3^b (3.3)	0.27 ^{ab} (0.28)	0.30 ^{abc} (0.30)	0.32 ^{abc} (0.31)	0.36 (0.34)
5	7.3 ^{ab} (2.8)	7.6^{ab} (3.0)	7.9^{ab} (3.1)	8.3^{ab} (3.2)	0.23 ^a (0.25)	0.27 ^{ab} (0.27)	0.30 ^{ab} (0.30)	0.35 (0.33)
2	7.0 ^a (2.9)	7.4 ^a (2.9)	7.7^a (3.0)	8.1^{ac} (3.2)	0.20 ^a (0.22)	0.23 ^a (0.24)	0.28^a (0.28)	0.31 (0.30)

between the 2 and 5 m strata in tree 1, and between trees 1 and 2 horizontally. However, the trend of increasing change with distance weakened with greater height.

Winter mean daily VPDs similarly increased as RH decreased with distance from the stream. However, opposite to the summer pattern, winter daily ranges in VPD increased with vertical and horizontal distance from the stream (Table 1b), becoming statistically significant vertically between

10 and 20 m in tree 1 and 5 and 10 m in tree 2, and horizontally between trees 2 and 3.

Winter differences in daily mean VPDs from the reference sensor generally increased with vertical and horizontal distance from the stream, becoming statistically significant between the 5 and 10 m strata vertically, and between trees 1 and 2 horizontally. Maximum differences increased consistently with distance, becoming immediately statistically significant vertically between the 2

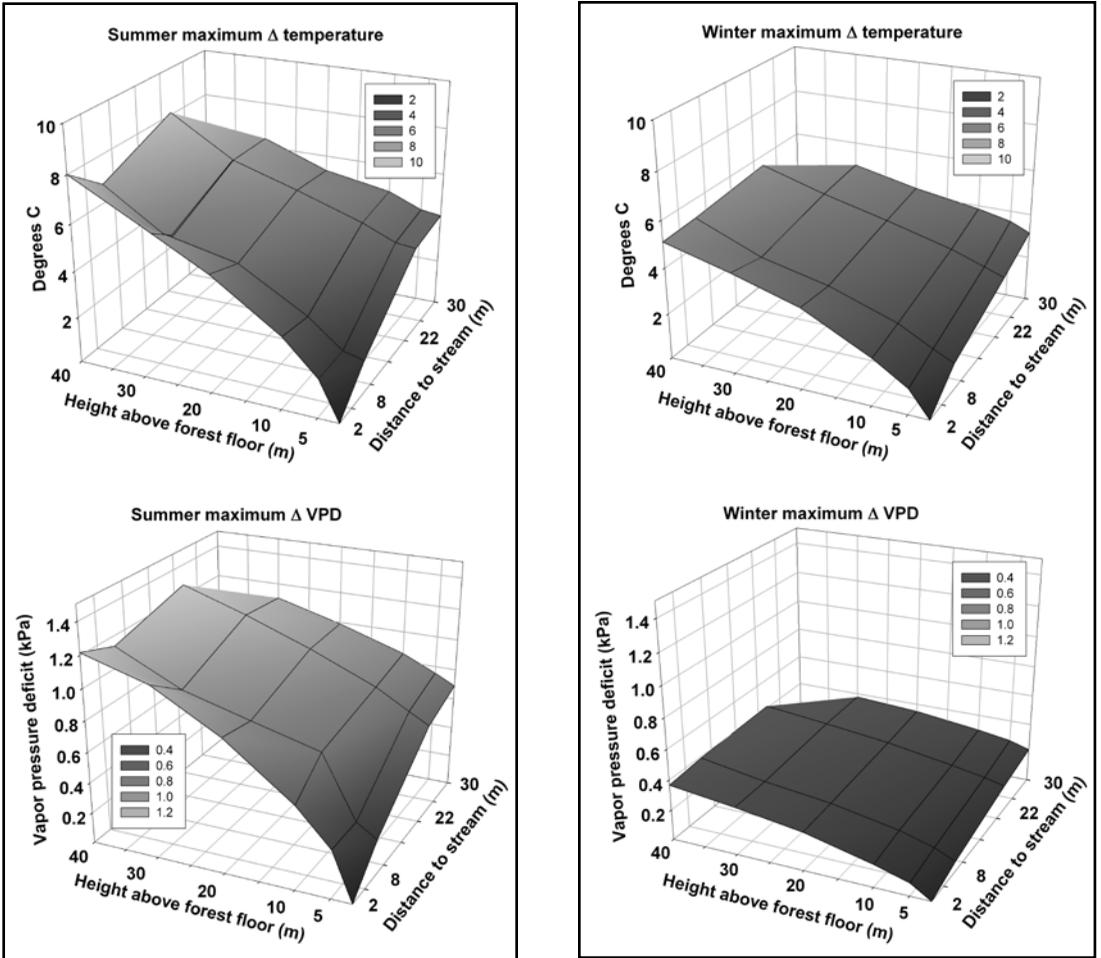


Figure 3. Summer and winter mean maximum Δ temperature ($^{\circ}$ C) and vapor pressure deficit (VPD, kPa) plotted for each sensor station ($n = 23$, data from sensor in tree 4, 40 m height was lost to lightning). Delta (Δ) is the difference between the reference sensor nearest the stream (tree 1, 2 m height) and each of the other arrayed sensors.

and 5 m strata in tree 1, and horizontally between trees 1 and 2.

Discussion

Our results show a two-dimensional zone of stream influence on air moisture and temperature that expanded and contracted diurnally and seasonally. In our ANCOVA analyses, the main effects of trees (horizontal distance from stream) and strata (vertical height) were consistently multiplicative for temperature and VPD responses, and in regression analyses the interactive effect of direct, hypotenuse distance from the stream accounted for 63.0, 70.7, 80.0, and 81.1 % (R^2 , $P < 0.0001$) of the variation in mean summer temperature and VPD, and winter

temperature and VPD, respectively. Though it is inexact where the dynamic boundaries of this zone passed through the coarse grid of our sensor array, quantification of temperature and VPD gradients over horizontal and vertical distances from the reference streamside sensor demonstrated a very restricted area of stream influence of < 7.5 m horizontally and < 5 m vertically (< 10 m for winter mean VPD).

Riparian surface microclimate studies in Pacific Northwest forests have generally found a greater extent of horizontal stream influence on temperature and humidity than we did. In western Washington, Brosofske et al. (1997) concluded that a minimum forested riparian buffer of 45 m

was necessary to maintain a natural streamside microclimatic environment, and Welsh et al. (2005) found markedly lower summer air temperatures and higher humidities up to 30 m from streams at their late-seral, mixed Douglas-fir (*Pseudotsuga menziesii*) and coast redwood (*Sequoia sempervirens*) sites. In contrast, in western Oregon to the interior of the Coast Range, Chan et al. (2004) saw the greatest change in RH from streamside conditions occurring within 15 m and not stabilizing until approximately 25 m distance, while Rykken et al. (2007) found small headwater streams provided cooler and moister environments upslope to 20 m.

Our results, however, are more consistent with those of other studies done in similarly more open forests with less mesic climates. In relatively dry open forests of eastern Oregon and Washington, Danehy and Kirpes (2000), found a 5–10 m horizontal streamside zone of influence on RH at 0.5 m above ground. At a Sierra Nevada site similar to ours with relatively little recent human disturbance, Erman and Erman (2000) examined summer air temperatures and relative humidity up to 2 m above ground along horizontal transects from streams to as far as 176 m upland in mixed-conifer forest. Beneath undisturbed, closed canopy, near-stream (0.1–5 m) temperatures were significantly lower than farther from the stream. However, openings in the canopy were directly related to higher summer temperatures and lower humidity, and large enough openings overwhelmed any microclimate amelioration provided by streams. Forest canopies reduce diurnal air temperature ranges (Moore et al. 2005), and summertime streamside vegetation can form an insulating layer adjacent to the stream, keeping humidity higher, daytime temperatures cooler, and slowing the rate of nighttime cooling (Bilby 1988, Welsh et al. 2005).

Maximum absolute differences in temperature and VPD from streamside conditions were greater (more extreme) in summer than in winter (Figure 3). Summer temperature and VPD daily ranges were also more extreme, decreasing with vertical and horizontal distance from the stream, while winter ranges increased away from the stream (Tables 1a, b). Winter daily fluctuations were dampened with proximity to the stream.

Winter buffering of daily temperature and VPD fluctuations is not surprising at this elevation in the Sierra Nevada. Once snow begins to accumulate,

it covers the forest floor for most of winter, while many perennial streams such as ours continue to run openly. When winter solar radiation begins to warm the air in the forest canopy, low-lying drainages act as perpetual cold sinks throughout the day, and temperature inversion occurs with temperatures becoming warmer with height. This inversion, acting with the general buffering effect of snowpack on temperature and humidity nearer to the forest floor and stream, results in greater variability in winter temperature and humidity regimes throughout the day farther from the stream and higher in the forest canopy. Moreover, winter precipitation events are commonly accompanied by relatively stable temperatures and humidities that fluctuate very little for the duration of the storm. In their Sierra Nevada work, Erman and Erman (2000) noted that for weeks at a time, periods of rainy weather would overwhelm and neutralize the microclimate gradients that existed in drier weather. Similarly, Janzen (1976) observed that temperature and humidity differences between riparian forest and adjacent upland deciduous forest largely disappeared during the rainy season.

Not as intuitive was the pattern of greater summertime temperature and VPD ranges nearer the stream. However, topography near the interface between terrestrial and aquatic systems can modify local riparian microclimate (Barnes et al. 1998, Chen et al. 1999, Naiman et al. 2000, Geiger et al. 2003), and in small headwater streams the riparian zone may be narrowed by steep slopes that decrease direct solar radiation (Moore et al. 2005, Rykken et al. 2007). Drainages warmer than upland ridges during the day can normally be cooler at night because of downslope air flow from surrounding higher terrain. Nightly accumulation of cold air can result in a local inversion with temperatures increasing with height rather than decreasing. This creates more variable temperature fluctuations throughout an entire day near drainage low points than occur more upland or at greater heights above the forest floor.

Soil evaporation and plant transpiration can be major contributors to local air moisture content in forests (Danehy and Kirpes 2000). In dense forests, the great preponderance of evapotranspiration is attributable to transpiration (Barnes et al. 1998). However, in more open forests such as in this study (North et al. 2004), evaporation from the forest floor plays a larger role (Barnes et al.

1998, Geiger et al. 2003). Thus in summer, more variable temperatures near the stream and forest floor can combine with soil evaporation bolstered by the hyporheos to create conditions of greater variability in humidity and VPD throughout a day nearer the stream than occur more upland or in the forest canopy.

Perhaps the most biologically important result of this study was the steepness of the vertical microclimate gradients in comparison to the traditionally studied horizontal gradients of riparian influence. The more rapid change of the vertical microclimatic environment is most apparent in the differences in maximum daily temperature and humidity between sensors and streamside conditions (Figure 3). Slopes of the maximum Δ value surfaces across seasons were markedly steeper through the vertical profile than in the horizontal direction from the stream. While regression analyses of mean summer temperature, summer VPD, winter temperature, and winter VPD against height above the plane of the stream explained 89.8, 96.2, 97.1, and 98.2% of their respective variation (R^2 , $P < 0.0001$), horizontal distance regressions were not significant. Microclimate gradients play key roles in determining riparian vegetation composition (Brosnoff et al. 1997, Naiman et al. 2000), and the steepness of the vertical gradients found in this study may influence the structure and composition of canopy epiphyte communities and in turn those animals that use epiphytes for habitat or forage. The vertical stratification of arboreal epiphyte communities has been well established (e.g., Hale 1952, McCune et al. 1997, Sillett and Rambo 2000), and change in composition from one stratum to another generally reflects the sensitivity of individual species to desiccation and their consequent ability to achieve positive net photosynthesis in low moisture environments (Hosokawa et al. 1964, Tobiessen et al. 1977). Poikilohydric organisms such as lichens and mosses are strongly affected by moisture and temperature regimes (Proctor 1982, Kershaw 1985), and particularly sensitive to microclimate changes (Renhorn et al. 1997).

Although our study should be viewed as a preliminary investigation of microclimate trends influenced by the forest and physiographic char-

acteristics of a single stream system, it quantifies a steep vertical microclimate gradient that can be broadly examined in different riparian conditions. At our Sierra Nevada site, stream influence on riparian microclimate was generally very restricted, especially in summer. In summer and winter, mean daily temperatures and VPDs increased with increasing distance from the stream. The diurnal ranges of summertime temperature and VPD decreased with increasing vertical and horizontal distance from the stream, while in winter, those ranges increased. Daily maximum absolute differences in temperature and VPD from streamside conditions were greater (more extreme) across sensors in summer than winter, and in both seasons temperature and humidity changes were markedly greater vertically above the stream than in the horizontal direction. This study demonstrates that riparian influence of a headwater stream can be narrowly constrained in a mesic, more open forest, and the relative steepness of the vertical microclimate gradient suggests riparian influence on forest canopy epiphyte community structure and composition may be particularly limited.

Acknowledgements

This study was associated with research funded by a U.S. Environmental Protection Agency STAR Graduate Fellowship. Direct funding support for sensors and other equipment came from the USDA Forest Service Sierra Nevada Research Center. Further funding for transportation expenses came from the UC Davis Public Service Research Program. Jiquan Chen of the University of Toledo provided the algorithms and SAS code to calculate vapor pressure deficits, and Jerome Braun of the UC Davis Statistical Laboratory helped with the analytical approach and further SAS programming. Trees in Figure 1 were adapted from drawings courtesy of Bob Van Pelt of the College of Forest Resources, University of Washington. Constructive reviews of the manuscript were provided by Kimberley Brosnoff of the School of Forest Resources and Environmental Science, Michigan Technical University, and Rob Davies-Colley of the National Institute of Water and Atmospheric Research, New Zealand.

Literature Cited

- Anderson, P. D., D. J. Larson, and S. S. Chan. 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. *Forest Science* 53:254-269.
- Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. 1998. *Forest Ecology*. John Wiley and Sons, New York.
- Berg, N. H. 1990. Experimental forests and ranges. Field research facilities of the Pacific Southwest Research Station. USDA Forest Service General Technical Report PSW-GTR-119. Pacific Southwest Research Station, Albany, CA.
- Bilby, R. E. 1988. Interactions between aquatic and terrestrial systems. In K. J. Raedeke (editor), *Streamside Management: Riparian Wildlife and Forestry Interactions*. University of Washington Institute of Forest Resources Contribution No. 59. Pp. 13-29.
- Bonnicksen, T. M., and E. C. Stone. 1982. Reconstruction of a presettlement giant Sequoia-mixed conifer forest community using the aggregation approach. *Ecology* 63:1134-1148.
- Brosfokske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* 7:1188-1200.
- Chan, S., P. Anderson, J. Cissel, L. Larsen, and C. Thompson. 2004. Variable density management in riparian reserves: Lessons learned from an operational study in managed forests of western Oregon, USA. *Forest Snow and Landscape Research* 78:151-172.
- Chen, J., and J. F. Franklin. 1997. Growing season microclimate variability within an old-growth Douglas-fir forest. *Climate Research* 8:21-34.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5:74-86.
- Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosfokske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288-297.
- Danehy, R. J., and B. J. Kirpes. 2000. Relative humidity gradients across riparian areas in eastern Oregon and Washington forests. *Northwest Science* 74:224-233.
- Darveau, M., P. Labbe, P. Beauchesne, L. Belanger, and J. Huot. 2001. The use of riparian forest strips by small mammals in a boreal balsam fir forest. *Forest Ecology and Management* 143:95-104.
- Dong, J., J. Chen, K. D. Brosfokske, and R. J. Naiman. 1998. Modelling air temperature gradients across managed small streams in western Washington. *Journal of Environmental Management* 53:309-321.
- Dupuis, L. A., J. N. M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conservation Biology* 9:645-653.
- Erman, D. C., and N. A. Erman. 2000. Testing variability of riparian temperatures in Sierra Nevada stream basins. Final Report to the Tahoe National Forest, Nevada City, CA.
- FEMAT (Forest Ecosystem Management Assessment Team). 1993. *Forest ecosystem management: An ecological, economic, and social assessment*. U.S. Government Printing Office, Washington, DC.
- Fowells, H. A., and J. E. Means. 1990. The tree and its environment. In R. M. Burns and B. H. Honkala (editors), *Silvics of North America, Vol 2. Hardwoods*. USDA Forest Service Agriculture Handbook 654, Washington, DC. Pp. 1-11.
- Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. *Gap Light Analyzer 2.0*. Simon Fraser University, Burnaby, BC, and Institute of Ecosystem Studies, Millbrook, NY.
- Geiger, R., R. H. Aron, and P. Todhunter. 2003. *The Climate Near the Ground*. Rowman and Littlefield Publishers, Lanham, MD.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41:540-551.
- Gregory, S. V. 1997. Riparian management in the 21st century. In K. A. Kohm and J. F. Franklin (editors), *Creating a Forestry for the 21st Century*. Island Press, Covelo, CA. Pp. 69-85.
- Hale, M. E. 1952. Vertical distribution of cryptogams in a virgin forest in Wisconsin. *Ecology* 33:398-406.
- Hosokawa, T., N. Odani, and H. Tagawa. 1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. *Bryologist* 67:396-411.
- Janzen, D. H. 1976. The microclimate difference between a deciduous forest and adjacent riparian forest in Guanacaste Province, Costa Rica. *Brenesia* 8:29-33.
- Keeler-Wolf, T. 1990. Ecological surveys of Forest Service Research Natural Areas in California. USDA Forest Service General Technical Report PSW-GTR-125. Pacific Southwest Research Station, Albany, CA.
- Kershaw, K.A. 1985. *Physiological ecology of lichens*. Cambridge University Press, Cambridge, UK.
- Ledwith, T. 1996. Effects of buffer strip width on air temperature and relative humidity in a stream riparian zone. M.S. Thesis, Humboldt State University, Arcata, CA.
- Liu, X., A. K. S. Huda, F. M. Kelleher, and P. S. Cornish. 1998. Temperature variability assessment in relation to crop sowing and harvest date. In D. Michalk and J. E. Pratley (editors), *Proceedings of the 9th Australian Agronomy Conference*. Australian Society of Agronomy, Wagga Wagga, Australia. Pp. 645-648.
- Ma, S. 2003. Interactions between microclimate, soil respiration, and disturbance in a forest ecosystem: Lessons from the Teakettle Experimental Forest in California's Sierra Nevada. Ph.D. Dissertation, University of Toledo, OH.
- Malanson, G. P. 1993. *Riparian Landscapes*. Cambridge University Press, Cambridge, UK.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. *Bryologist* 96:405-411.
- McCune, B., K. A. Amsberry, F. J. Camacho, S. Clery, C. Cole, C. Emerson, G. Felder, P. French, D. Greene, R.

- Harris, M. Hutten, B. Larson, M. Lesko, S. Majors, T. Markwell, G. G. Parker, K. Pendergrass, E. B. Peterson, E. G. Peterson, J. Platt, J. Proctor, T. Rambo, A. Rosso, D. Shaw, R. Turner, and M. Widmer. 1997. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. *Northwest Science* 71:145-152.
- Meleason, M. A., and J. M. Quinn. 2004. Influence of riparian buffer width on air temperature at Whangapoua Forest, Coromandel Peninsula, New Zealand. *Forest Ecology and Management* 191:365-371.
- Meleason, M. A., S. V. Gregory, and J. P. Bolte. 2003. Implications of riparian management strategies on wood in streams of the Pacific Northwest. *Ecological Applications* 13:1212-1221.
- Moore, R. D., D. L. Spittlehouse, and A. Story. 2005. Riparian microclimate and stream temperature response to forest harvesting: A review. *Journal of the American Water Resources Association* 41:813-834.
- Naiman, R. J., and H. Décamps. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Naiman, R. J., R. E. Bilby, and P. A. Bisson. 2000. Riparian ecology and management in the Pacific Coastal rain forest. *BioScience* 50:996-1011.
- Nakamura, R., and L. Mahrt. 2005. Air temperature measurement errors in naturally ventilated radiation shields. *Journal of Atmospheric and Oceanic Technology* 22:1046-1058.
- North, M., J. Chen, B. Oakley, B. Song, M. Rudnicki, and A. Gray. 2004. Forest stand structure and pattern of old-growth western hemlock/Douglas-fir and mixed-conifer forest. *Forest Science* 50:299-311.
- Proctor, M.C.F. 1982. Physiological ecology: water relations, light and temperature responses, carbon balance. *In* A.J.E. Smith (editor), *Bryophyte Ecology*. Chapman and Hall, London. Pp. 333-381.
- Renhorn, K.-E., P.-A. Esseen, K. Palmqvist, and B. Sundberg. 1997. Growth and vitality of epiphytic lichens 1. Responses to microclimate along a forest edge-interior gradient. *Oecologia* 109:1-9.
- Rykken, J. J., S. S. Chan, and A. R. Moldenke. 2007. Headwater riparian microclimate patterns under alternative forest management treatments. *Forest Science* 53:270-280.
- SAS. 2002-2003. *SAS System for Windows V. 9.1.3*. SAS Institute Inc., Cary, NC.
- Sillett, S. C., and T. R. Rambo. 2000. Vertical distribution of dominant epiphytes in Douglas-fir forests of the central Oregon Cascades. *Northwest Science* 74:44-49.
- Tobiessen, P. L., K. A. Mott, and N. G. Slack. 1977. A comparative study of photosynthesis, respiration and water relations in four species of epiphytic mosses in relation to their vertical distribution. *Bryophytorum Bibliotheca* 13:253-277.
- Tukey, J. W. 1949. Dyadic anova, an analysis of variance for vectors. *Human Biology* 21:65-110.
- Valigura, R. A., and M. G. Messina. 1994. Modification of Texas clear-cut environments with loblolly pine shelterwoods. *Journal of Environmental Management* 40:283-295.
- Wayman, R., and M. North. 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *Forest Ecology and Management* 239:32-44.
- Welsh, H. H. Jr., G. R. Hodgson, and N. E. Karraker. 2005. Influences of the vegetation mosaic on riparian and stream environments in a mixed forest-grassland landscape in "Mediterranean" northwestern California. *Ecography* 28:537-551.
- Xu, M., J. Chen, and B. L. Brookshire. 1997. Temperature and its variability in oak forests in the southeastern Missouri Ozarks. *Climate Research* 8:209-223.
- Zheng, D., J. Chen, B. Song, M. Xu, P. Sneed, and R. Jensen. 2000. Effects of silvicultural treatments on summer forest microclimate in southeastern Missouri Ozarks. *Climate Research* 15:45-59.

Received 23 March 2008

Accepted for publication 11 September 2008