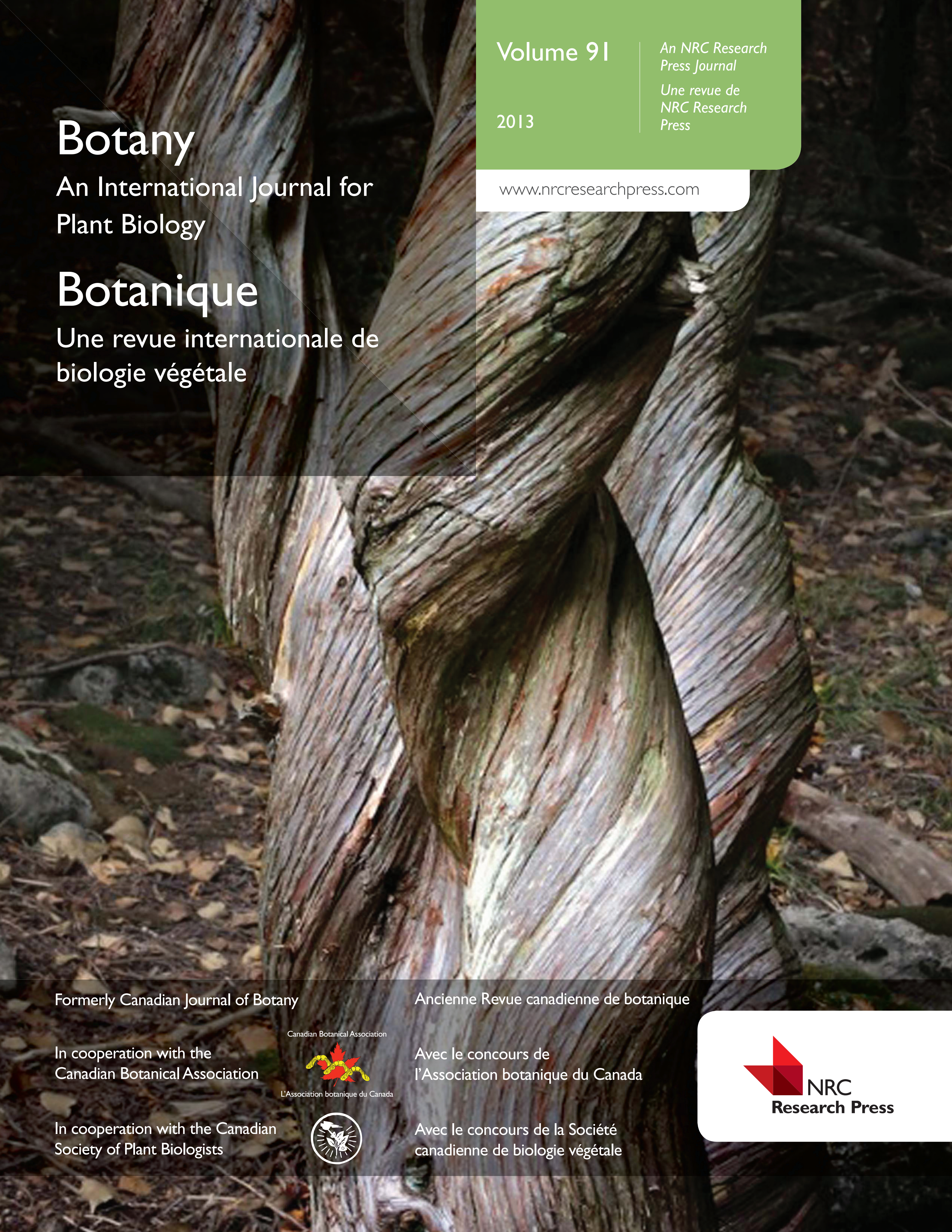

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ARTICLE

Patterns of moisture and temperature in canopy and terrestrial soils in a temperate rainforest, Washington

Dennis A. Aubrey, Nalini M. Nadkarni, and Casey P. Broderick

Abstract: The temperate rainforest on the Olympic Peninsula represents a biome that is characterized by unusually high epiphyte biomass and accompanying canopy soils. These canopy communities form thick mats that play important ecological roles: increasing ecosystem nutrient capital, fostering abundant invertebrates, and enhancing moisture retention. Little is known about the physical properties and microenvironmental conditions of these mats. We investigated seasonal patterns in temperature and moisture of canopy soils and compared them to O- and A-horizon terrestrial soils. Temperature tended to fluctuate more in canopy soils than in terrestrial soils. During the 4 months of highest precipitation, canopy soils also showed higher maximum saturation levels than terrestrial soils. Both soil types displayed sharp "dry-downs" during the summer dry season, which contrasts with results from similar research in a tropical cloud forest, where only canopy soils dried significantly during the dry season. In the late summer in the Olympic Rainforest, canopy soils remained dry until the first rainfall, whereas terrestrial soils began to rehydrate a month earlier, possibly through hydraulic redistribution. Regional climate models predict increased winter precipitation but drier summers for this area. Our results suggest that extended summer droughts may increase canopy drying, which may have negative impacts on epiphyte communities.

Key words: temperate rainforest, arboreal soil, epiphyte mats, canopy.

Résumé : La forêt tempérée ombrophile de la Péninsule Olympic représente un biome caractérisé par une biomasse épiphyte particulièrement abondante, accompagnée de sols de canopée. Ces communautés de la canopée forment des coussins épais jouant des rôles écologiques importants : augmentation de la réserve en nutriments de l'écosystème, encouragement d'une abondante prolifération d'invertébrés, augmentation de la rétention de l'humidité. On connaît peu de chose au sujet des propriétés physiques et des conditions micro environnementales de ces coussins. Les auteurs ont examiné les patrons saisonniers de la température et de l'humidité des sols de canopée avec celles des horizons O et A des sols terrestres. La température a tendance à fluctuer plus fortement dans les sols de canopée que dans les sols terrestres. Au cours des 4 mois les plus pluvieux, les sols de canopée montrent également un maximum de saturation plus élevé que les sols terrestres. Les deux types de sol montrent une nette dessiccation au cours de la saison sèche estivale, ce qui contraste avec les résultats de recherches similaires conduites dans la forêt tropicale ombrophile, où seuls les sols de canopée sèchent significativement au cours de la saison sèche. À la fin de l'été, dans la Péninsule Olympic, les sols de canopée demeurent secs jusqu'à la première pluie, alors que les sols terrestres commencent à se réhydrater un mois plus tôt, possiblement par redistribution hydraulique. Les modèles climatiques régionaux prédisent une augmentation des précipitations hivernales, mais des étés plus secs pour cette région. Les résultats suggèrent que la prolongation de la durée des sécheresses estivales pourrait augmenter la dessiccation de la canopée, ce qui pourrait avoir des impacts négatifs sur la communauté épiphyte. [Traduit par la Rédaction]

Mots-clés : forêt ombrophile tempérée, sol arboricole, coussins d'épiphytes, canopée.

Introduction

Old-growth temperate forests of the western slopes of the Olympic Mountains host extremely high epiphyte biomass and diversity (Franklin and Dyrness 1988; Kirk and Franklin 1992), supporting communities that are dominated by nonvascular plants. These reach their greatest accumulations in the canopy of big-leaf maples (*Acer macrophyllum* Pursh). On inner branches and trunks of these trees, beneath mats of living epiphytes, canopy soil can accumulate up to 10 cm thick (Nadkarni 1984; Rousk and Nadkarni 2009). Canopy soils have been described as arboreal histosols (Bohlman et al. 1995; Enloe et al. 2006). In the Olympic Rainforest, they are composed of dead and decaying bryophytes, lichens, Oregon spikemoss (*Selaginella oregana* D.C. Eaton), and other organic matter, interlaced with rhizomes of licorice fern (*Polypodium glycyrrhiza* D.C. Eaton) and adventitious roots from host trees themselves (Nadkarni 1981; Ellyson and Sillett 2003; Sillett and Van Pelt 2007). Inorganic nutrients derived from intercepted host-tree foliage and precipitation also contribute to canopy soil nutrient capital (Nadkarni and Matelson 1991).

Canopy soils also exist in a few other temperate and tropical forest types, and are of interest because of their unique soil properties (Ingram and Nadkarni 1993; Nadkarni et al. 2004; Enloe et al. 2006) and the critical ecological roles they play (Nadkarni 1984, 1986). Canopy communities foster abundant invertebrates (Nadkarni and Longino 1990; Ellwood and Foster 2004), and also increase total forest biodiversity (Nieder et al. 2001), moisture retention (Ozanne et al. 2003; Pypker et al. 2006), and nutrient capital derived from autochthonous inputs (Nadkarni 1984, 1986;

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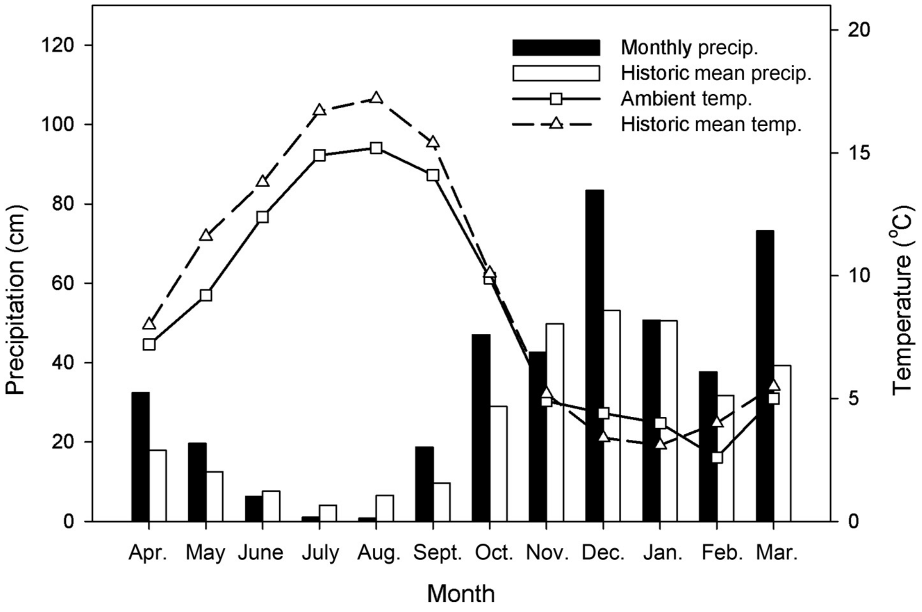
Fig. 1. Monthly precipitation and mean ambient temperature for the 2010–2011 research period and for the period of record (1999–2010) at a NOAA weather station (Bunch Field, Olympic National Park, National Park Service) ca. 5 km east of the study site. These data were assumed to be representative of conditions at the study site and are used to show the representativeness of the research period.



Coxson and Nadkarni 1995). However, little is known about the physical properties and microenvironmental conditions of canopy soils in temperate rainforests.

Moisture and temperature regimes of canopy soils affect growth and nutrient uptake patterns of bryophytes (Busby et al. 1978; Proctor et al. 2007), vascular epiphytes (Criddle et al. 1994), canopy roots (Nadkarni 1994), and the distribution and activity of soil-dwelling organisms (Kühnelt 1976). A comparison of terrestrial and canopy soil temperature and moisture in a Costa Rican cloud forest documented that canopy and terrestrial soils shared many similar dynamics; however, canopy soils experienced sharp "dry-downs" during the dry season, whereas moisture content in O- and A-horizon terrestrial soils was generally constant (Bohlman et al. 1995). This pattern could affect the composition, life forms, and life cycles of organisms that live in canopy compared with terrestrial microhabitats (Longino and Nadkarni 1990; Nadkarni and Longino 1990; Basset et al. 2003). However, no comparison of canopy versus terrestrial soil water regimes has been carried out in the temperate rainforests of North America.

We investigated temperature and moisture patterns in canopy soil (C–O) of *A. macrophyllum* trees and O (T–O) and A (T–A) horizons of the surrounding terrestrial soil in the Olympic temperate rainforest. Our objective was to document the temperature and moisture regimes of canopy and forest floor soils and to compare these with patterns reported in Costa Rican cloud forest.

Materials and methods

Site description

This study was conducted in Olympic National Park, in the Upper Quinault River basin, adjacent to the North Shore road (47.32°N, 123.45°W), at 155 m elevation. This temperate rainforest is strongly influenced by Pacific maritime conditions (O'Connor et al. 2003). Fall, winter, and spring are characterized by heavy rains; summers are typically dry (Fig. 1). Mean annual precipitation (1931–2000) was 364 cm at the Quinault Ranger Station (WRCC 2000), 10 km to the southwest and 19 m lower in elevation than the study site. Temperatures ranged over the same period from a mean low of 0.7 °C in January to a mean high of 23.4 °C in August.

The forest at the site is in the Sitka spruce zone (Franklin and Dyrness 1988), Oxalis and sword fern associations (Henderson et al. 1989). Overstory species include Sitka spruce (*Picea sitchensis* (Bong.) Carrière), *A. macrophyllum*, red alder (*Alnus rubra* Bong.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn ex D. Don), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Epiphyte communities associated with *A. macrophyllum* are dominated by five mosses (isothecium moss (*Isothecium stoloniferum* Brid. = *Isothecium myosuroides* Brid.), splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp in B.S.G.), Oregon eurhynchium moss (*Eurhynchium oreganum* (Sull.) Jaeg.), leucolepis umbrella moss (*Leucolepis menziesii* (Hook.) Steere = *Leucolepis acanthoneuron* (Schwaegr.) Lindb.), and Menzies' metaneckera moss (*Metaneckera menziesii* (Hook. In Drumm.) Steere)), a liverwort (*Porella navicularis* (Lehm. & Lindenb.) Lindb.), *S. oregana*, lichens, and *P. glycyrrhiza*.

The forest is located in the floodplain of the Quinault River. No digital soils data exist for this site, but similar sites on the south side of the Quinault River (2 km south) have been classified as Hoh Sandy Loams (National Cooperative Soil Survey 2011). Terrestrial soils are heavily influenced by local hydrology and consist of a shallow O-horizon (<5 cm) overlying mineral (alluvial) soils (Fonda 1974; Van Pelt et al. 2006). They are deep, moderately well or well drained soils that formed in mixed alluvium (coarse–loamy, isotic, isomesic Andic Dystrudepts), occurring on low terraces and flood plains and have slopes of 0%–10%. The Oe horizon is 0–5 cm thick, composed of moderately decomposed leaves, needles, and wood fragments. The A horizon is 5–20 cm, dark reddish brown (5YR 2/2); moderate fine granular structure; friable, and strongly acid (pH 5.0).

Research approach and measurements

We gathered representative samples of canopy-held soils and compared them with terrestrial soil samples, following methods of previous studies of epiphyte biomass and composition in temperate rainforests (Nadkarni 1984) and tropical cloud forests (Bohlman et al. 1995). We selected nine *A. macrophyllum* to sample canopy soils, with criteria based on safe accessibility to the canopy, minimizing damage to the crown and soils, and maximizing

Table 1. Seasonal and overall mean temperature and gravimetric water content (wet mass basis) for canopy humus (C–O) and O- and A-horizon (T–O and T–A, respectively) terrestrial soils at the study area in the Quinault Rainforest, Washington.

	Seasonal				
Soil location	Spring	Summer	Fall	Winter	Overall
Soil temperature (°C)					
C-O	10.1±1.8 (6.6–13.6)	16.6±1.4 (13.3–19.0)	8.8±4.1 (3.6–15.0)	4.9±3.1 (0.5–8.2)	11.0±5.0 (0.5–19.0)
T–O	10.4±1.6 (6.6–13.5)	15.4±1.5 (12.7–18.1)	9.3±3.7 (4.2–14.8)	5.0±2.6 (0.6–7.8)	10.8±4.4 (0.6–18.1)
T–A	10.2±1.6 (7.1–12.7)	14.8±1.4 (12.2–16.8)	9.3±3.8 (4.3–14.6)	4.8±2.7 (0.7–7.5)	10.5±4.3 (0.7–16.8)
Soil moisture					
C–O	0.73±0.08 (0.38–0.84)	0.42±0.22 (0.13–0.75)	0.75±0.06 (0.59–0.83)	0.82±0.02 (0.75–0.86)	0.65±0.21 (0.13–0.86)
T–O	0.72±0.05 (0.54–0.81)	0.46±0.18 (0.12–0.73)	0.71±0.05 (0.64–0.81)	0.78±0.03 (0.69–0.83)	0.64±0.17 (0.12–0.83)
T–A	0.37±0.07 (0.26–0.54)	0.23±0.12 (0.06–0.51)	0.49±0.14 (0.26–0.64)	0.43±0.09 (0.31–0.61)	0.36±0.15 (0.06–0.64)

Note: Sampling period was April 2010 to March 2011, and spring, summer, fall, and winter are divided according to calendar seasons. Values are reported as means ± 1 SD, with ranges in parentheses.

the number of potential sampling branches. We climbed trees with single-rope techniques (Perry 1978), leaving temporary haul cords for the duration of the study. Data were collected between 1 April 2010 and 23 March 2011, with a mean sampling interval of 2 weeks during the dry season (April–November) and 3 weeks during the wet season (November–March). Samples were collected between the hours of 1100 and 1700.

With a random number generator, three of the nine trees were selected for sampling on each sample date. Each tree took ca. 90 min to sample, and nine C–O soil samples were collected from each tree: three samples per branch (within 5 m of the bole) from three different branches. Our fundamental unit of measure was an individual branch; nested triplicate samples were used to equalize microenvironmental variation for that branch. Likewise, each T–O data point represented a nested triplicate sample taken from one of three different zones beneath each tree. Nested triplicates were not used for T–A because (*i*) mineral soil tends to be more homogenous in moisture and temperature than the organic layer (Brady and Weil 2008), and (*ii*) to reduce the total duration of each sampling unit, thereby limiting the influence of changing environmental conditions over time.

In sampling C–O, the overlying live epiphytes were carefully moved aside and then samples were collected from the uppermost 5 cm of canopy soils. Concurrent with C–O collection, nine T–O and three T–A samples (one for each nested triplicate) were collected from under the same tree at random directions from the trunk, in three zones: at the base of the tree, at the outer canopy drip line, and at the midpoint between the two. T–O samples were taken from Oe and Oa horizons, which exclude undecayed leaves and litter (our sampling method excluded these from canopy samples because they were on top of live bryophytes), and T–A samples were taken from the top 5 cm of the A horizon.

All samples had a target fresh mass of ca. 20 g and were placed in Whirl-Pak® bags for transport to the Canopy Lab at The Evergreen State College. These samples were weighed for gravimetric moisture analysis (Black 1965) within 8 h of collection, and after being oven-dried at 65 °C for 36–48 h, to calculate percent gravimetric moisture content (wet mass basis).

Temperature data were collected concurrently with soil sampling. Two Comark® 300 digital thermometers were used, which were calibrated to each other at the beginning of each sampling date. One reading was taken within 10 cm of each sampling location, at a depth similar to soil sample depth.

Ambient temperature and rainfall data during the research period were collected from a National Oceanic and Atmospheric Administration (NOAA) weather station (Bunch Field; 47°32′9″N, 123°40′53″W; Olympic National Park, National Park Service), which is 24 m higher in elevation, 5 km to the east, and shares with the study site similar forest type, aspect, and position relative to the Quinault River. Temperature and rainfall data from Bunch Field were assumed to be representative of conditions at the study site. These data were also compared with historical mean values from Bunch Field (1999–2010) to assess the representativeness of our research period.

Data analysis

Triplicate samples of branch and ground locations were averaged and used as single moisture content and temperature data points in the case of C–O and T–O to avoid pseudoreplication, giving us a sample size of three for each tree. Individual samples were used for T–A.

We plotted temperature (°C) and gravimetric water content and compared overall means among C–O, T–O, and T–A using repeated-measures ANOVAs (in JMP version 7; SAS Institute Inc. 1989–2007). Overall means were also compared pairwise using repeated-measures ANOVAs to separately compare values of C–O and T–O, and T–O and T–A. Means from individual sampling dates were also compared. Statistical significance for all tests was determined with $\alpha = 0.05$.

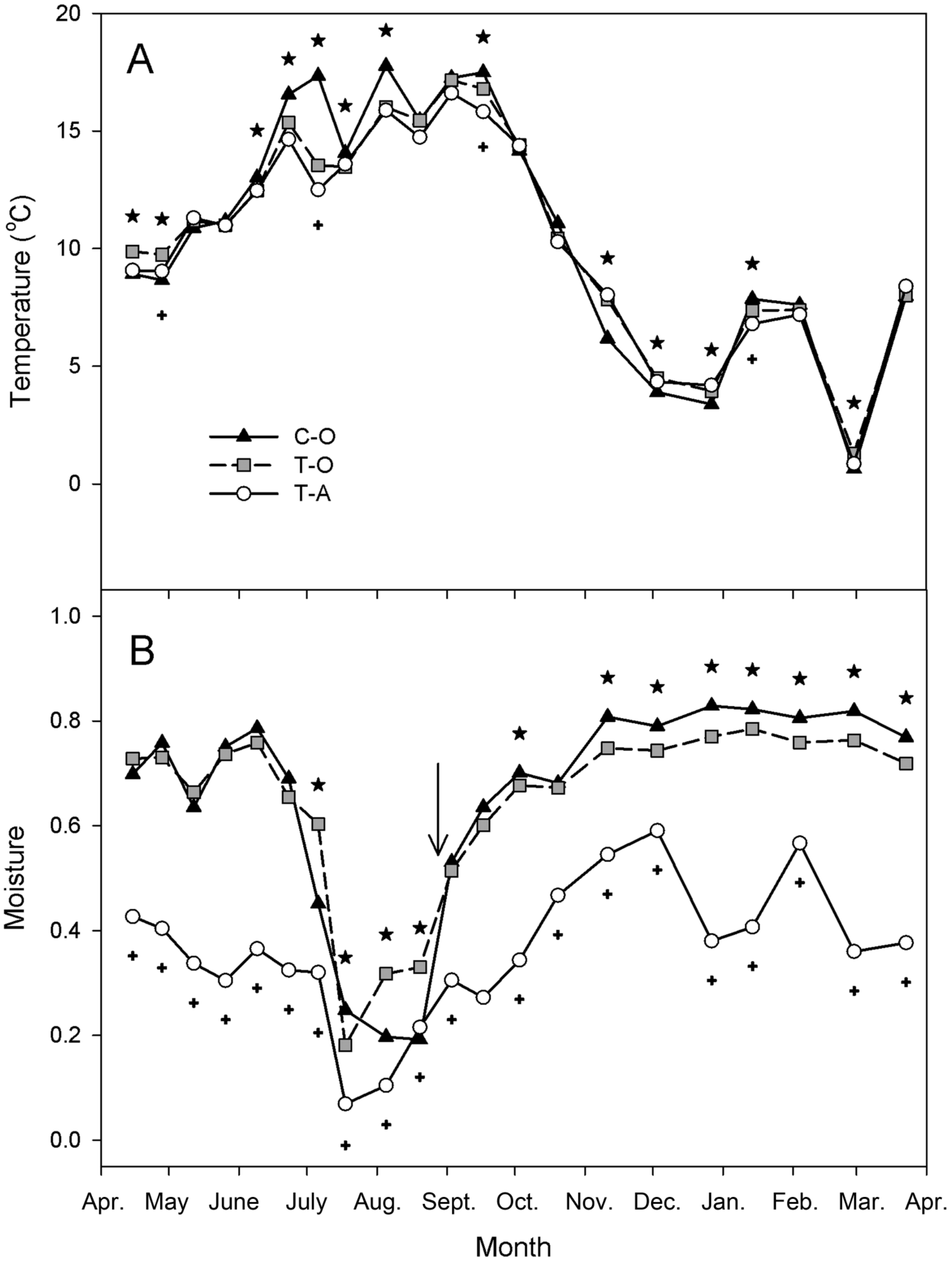
Results

Monthly precipitation and mean temperature showed some variance from historical mean values (Fig. 1). Precipitation was lower than normal during most of the already dry summer months (June–August), but higher than normal in September. Mean temperatures were lower than normal for every month of the sampling period except December and January.

During the total research period, temperature of C–O had the largest overall range of the three soil types at 0.5–19.0 °C and tended to be higher during summer sampling visits than T–O (Table 1). The temperature means for the three soils were significantly different from one another during the year ($F_{[2,18]} = 1.05$, $p = 0.002$), even though the trends were generally similar (Fig. 2). The temperature of C–O samples tended to be the warmest of the three soil types when ambient temperatures were increasing and colder when they decreased.

Percent gravimetric water content of soils decreased markedly during the summer months (C–O minimum = 13%; T–O = 12%.) At other times of the year, soils reached a maximum saturation at 82% for C–O and 78% for T–O (Table 1). Samples taken after two periods of heavy rainfall (27 December 2010 and 14 January 2011, 5-day totals >20 cm) showed no additional increases in water content (Fig. 2). The means of water content for the three soil types were significantly different from one another over the course of the year ($F_{[2,18]} = 72.2$, $p < 0.0001$). However, the means of C–O and T–O were not different ($F_{[1,16]} = 0.063$, $p = 0.332$). Some individual points, however, showed differences, particularly during the winter saturation period (November–March) and also the summer dry-down (July–August). In summer, C–O began drying earlier and continued drying out until the return of the rainy season in September. In contrast, T–O dried out more quickly, but then began rehydrating in early August.

Fig. 2. Temperature (A) and moisture content (B) of canopy humus (C–O) versus terrestrial O and A horizon (T–O and T–A, respectively) soils at the study area in the Quinault study area, Washington. Stars and plusses indicate statistical significance ($p < 0.05$) between C–O and T–O, and T–O and T–A, respectively. During the research period, temperature means for the three soil types were significantly different from one another ($F_{[2,18]} = 1.05$, $p = 0.002$). In B, the arrow indicates a significant rain event (>5 cm) following the dry season. Gravimetric moisture content (wet mass basis) means for all three soil types were significantly different from one another ($F_{[2,18]} = 72.2$, $p < 0.0001$), but the means of C–O and T–O were not different ($F_{[1,16]} = 0.063$, $p = 0.332$).



Discussion

Mats of C–O tend to be coarse and fibrous due to the high proportion of dead bryophytes (C. Tejo, unpublished data). C–O tends to be relatively open to air exchange and is thus more exposed to ambient temperatures than T–O. C–O is also not moderated by contact with T–A. Accordingly, we found that C–O tended to be more influenced by changes in ambient temperature than T–O and T–A. When ambient temperatures were higher than they were on the previous sampling visit, C–O tended to be the warmest of the three soil types. When ambient temperatures were lower, C–O tended to be the coldest. We also observed that on warm days, C–O temperature tended to rise more during the course of the ca. 4–5 h while samples were collected than did T–O and T–A.

In the winter, C–O and T— tended to remain saturated, even during dry spells. In summer, all soils showed a pronounced drydown, in contrast to patterns in a tropical montane forest where T-O remained moist throughout the dry season (Bohlman et al. 1995).

We also found that at the end of summer, C–O continued to lose moisture until the first significant rainfall, whereas T–O soils began rehydrating a month earlier. This pattern may be explained by hydraulic redistribution, a process by which trees draw moisture from deep roots and passively redistribute it in drier areas, often near the surface (Emerman and Dawson 1996; Horton and Hart 1998; Brooks et al. 2002). Hydraulic redistribution has been documented in Pacific Northwest forests (Brooks et al. 2002, 2006), and maple trees (Dawson 1993; Emerman and Dawson 1996), and is thought to occur in most situations involving a significant water potential gradient in terrestrial soils (Brooks et al. 2006). Hydraulic redistribution may be influential on terrestrial soil moisture during late summer owing to increased water potential gradients.

One reason to document soil temperature and moisture in canopy and terrestrial substrates is that most regional climate models predict a future increase in winter precipitation and more protracted summer drought conditions (Mote and Salathé 2010, Bachelet et al. 2011). Observational and experimental studies of epiphyte mats in tropical montane cloud forests have documented that canopy biota are vulnerable to the changes in rainfall, warming temperatures, and decreased cloud water predicted by climate change models (Foster 2001; Nadkarni and Solano 2002), but little research has been done on the subject in temperate rainforests. Patterns in tropical canopy soils may be similar to temperate rainforest canopy soils because (*i*) relative epiphyte abundance is often used as a general moisture gradient indicator (Häger and Dohrenbusch 2011), (*ii*) poikilohydric epiphytes are especially dependent upon moisture regimes (Sillett and Antoine 2004), (*iii*) bryophytes are sensitive to small microclimatic shifts (Gignac 2001; Kimmerer 2003), and (*iv*) once disturbed, epiphytes recolonize disturbed areas slowly (Nadkarni 2000; Cobb et al. 2001). For these reasons, canopy communities in the Olympic rainforest could be disproportionately affected by regional climate change; an effect that may be increased by canopy soil mat microenvironmental conditions during summer drought. Further studies are needed to ascertain the links between canopy soil moisture and the viability and health of epiphytes and their associated microbial and invertebrate biota.

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References

Bachelet, D., Johnson, B.R., Bridgham, S.D., Dunn, P.V., Anderson, H.E., and Rogers, B.M. 2011. Climate change impacts on western Pacific Northwest prairies and savannas. Northwest Sci. **85**(2): 411–429. doi:10.3955/046.085.0224.

Basset, Y., Novotny, V., Miller, S.E., and Kitching, R.L. 2003. Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge.

Black, C.A. 1965. Methods of soil analysis: Part I. Physical and mineralogical properties including statistics of measurement and sampling. American Society of Agronomy, Soil Science Society of America, Madison, Wisc.

Bohlman, S.A., Matelson, T.J., and Nadkarni, N.M. 1995. Moisture and temperature patterns of canopy humus and forest floor soil of a montane cloud forest, Costa Rica. Biotropica, **27**(1): 13–19. doi:10.2307/2388898.

Brady, N.C., and Weil, R.R. 2008. The nature and properties of soils. Pearson Prentice Hall, Upper Saddle River, N.J.

Brooks, J.R., Meinzer, F.C., Coulombe, R., and Gregg, J. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. Tree Physiol. **22**(15–16): 1107–1117. doi:10.1093/treephys/22.15-16.1107. PMID:12414370.

Brooks, J.R., Meinzer, F.C., Warren, J.M., Domec, J.-C., and Coulombe, R. 2006. Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations. Plant Cell Environ. **29**: 138–150. doi:10.1111/j.1365-3040.2005.01409.x. PMID:17086760.

Busby, J.R., Bliss, L.C., and Hamilton, C.D. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. Ecol. Monogr. **48**(2): 95–110. doi:10.2307/2937294.

Cobb, A.R., Nadkarni, N.M., Ramsey, G.A., and Svoboda, A.J. 2001. Recolonization of bigleaf maple branches by epiphytic bryophytes following experimental disturbance. Can. J. Bot. **79**(1): 1–8. doi:10.1139/b00-134.

Coxson, D.S., and Nadkarni, N.M. 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems. *In* Forest canopies. *Edited by* M.D. Lowman and N.M. Nadkarni. Academic Press, Inc., San Diego, Calif. pp. 495–543.

Criddle, R.S., Hopkin, M.S., McArthur, E.D., and Hansen, L.D. 1994. Plant distribution and the temperature coefficient of metabolism. Plant Cell Environ. **17**(3): 233–243. doi:10.1111/j.1365-3040.1994.tb00289.x.

Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. Oecologia, **95**: 565–574. doi:10.1007/BF00317442.

Ellwood, M.D.F., and Foster, W.A. 2004. Doubling the estimate of invertebrate biomass in a rainforest canopy. Nature, **429**: 549–551. doi:10.1038/nature02560. PMID:15175749.

Ellyson, W.J.T., and Sillett, S.C. 2003. Epiphyte communities on Sitka spruce in an old-growth redwood forest. Bryologist, **106**(2): 197–211. doi:10.1639/0007-2745(2003)106[0197:ECOSSI]2.0.CO;2.

Emerman, S.H., and Dawson, T.E. 1996. Hydraulic lift and its influence on the water content of the rhizosphere: an example from sugar maple, *Acer saccharum*. Oecologia, **108**(2): 273–278. doi:10.1007/BF00334651.

Enloe, H.A., Graham, R.C., and Sillett, S.C. 2006. Arboreal histosols in old-growth redwood forest canopies, northern California. Soil Sci. Soc. Am. J. **70**(2): 408–418. doi:10.2136/sssaj2004.0229.

Fonda, R.W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology, **55**(5): 927–942. doi:10.2307/1940346.

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth-Sci. Rev. **55**(1–2): 73–106. doi:10.1016/S0012-8252(01)00056-3.

Franklin, J.F., and Dyrness, C.T. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis.

Gignac, L.D. 2001. Bryophytes as indicators of climate change. Bryologist, **104**(3): 410–420. doi:10.1639/0007-2745(2001)104[0410:BAIOCC]2.0.CO;2.

Häger, A., and Dohrenbusch, A. 2011. Hydrometeorology and structure of tropical montane cloud forests under contrasting biophysical conditions in northwestern Costa Rica. Hydrol. Process. **25**(3): 392–401. doi:10.1002/hyp.7726.

Henderson, J., Peter, D., Lesher, R., and Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. R6 Ecology Technical Paper, United States Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, Oreg.

Horton, J.L., and Hart, S.C. 1998. Hydraulic lift: a potentially important ecosystem process. Trends Ecol. Evol. **13**(6): 232–235. doi:10.1016/S0169-5347(98)01328-7. PMID:21238277.

Ingram, S.W., and Nadkarni, N.M. 1993. Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. Biotropica, **25**(4): 370–383. doi:10.2307/2388861.

Kimmerer, R.W. 2003. Gathering moss: a natural and cultural history of mosses. Oregon State University Press, Corvallis.

Kirk, R., and Franklin, J.F. 1992. The Olympic rain forest: an ecological web. University of Washington Press, Seattle.

Kühnelt, W. 1976. Soil biology, with special reference to the animal kingdom. Faber and Faber, London.

Longino, J.T., and Nadkarni, N.M. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. Psyche J. Entomol. **97**: 81–93. doi:10.1155/1990/36505.

Mote, P.W., and Salathé, E.P. 2010. Future climate in the Pacific Northwest. Clim. Change, **102**(1–2): 29–50. doi:10.1007/s10584-010-9848-z.

Nadkarni, N.M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. Science, **214**(4524): 1023–1024. doi:10.1126/science.214.4524.1023. PMID:17808667.

Nadkarni, N.M. 1984. Biomass and mineral capital of epiphytes in an *Acer macrophyllum* community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. Can. J. Bot. **62**(11): 2223–2228. doi:10.1139/b84-302.

Nadkarni, N.M. 1986. The nutritional effects of epiphytes on host trees with special reference to alteration of precipitation chemistry. Selbyana, **9**(1): 44–51.

Nadkarni, N.M. 1994. Factors affecting the initiation and growth of aboveground adventitious roots in a tropical cloud forest tree: an experimental approach. Oecologia, **100**(1–2): 94–97. doi:10.1007/BF00317135.

Nadkarni, N.M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. Biotropica, **32**(2): 358–363. doi:10.1111/j.1744-7429.2000.tb00479.x.

Nadkarni, N.M., and Longino, J.T. 1990. Invertebrates in canopy and ground organic matter in a neotropical montane forest, Costa Rica. Biotropica, **22**(3): 286–289. doi:10.2307/2388539.

Nadkarni, N.M., and Matelson, T.J. 1991. Fine litter dynamics within the tree canopy of a tropical cloud forest. Ecology, **72**(6): 2071–2082. doi:10.2307/1941560.

Nadkarni, N.M., and Solano, R. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. Oecologia, **131**(4): 580–586. doi:10.1007/s00442-002-0899-3.

Nadkarni, N.M., Schaefer, D., Matelson, T.J., and Solano, R. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. For. Ecol. Manage. **198**(1–3): 223–236. doi:10.1016/j.foreco.2004.04.011.

National Cooperative Soil Survey. 2011. Hoh series. Available from https://soilseries.sc.egov.usda.gov/OSD_Docs/H/HOH.html [accessed 11 May 2013].

Nieder, J., Prosperí, J., and Michaloud, G. 2001. Epiphytes and their contribution to canopy diversity. Plant Ecol. **153**(1–2): 51–63. doi:10.1023/A:1017517119305.

O'Connor, J.E., Jones, M.A., and Haluska, T.L. 2003. Flood plain and channel dynamics of the Quinault and Queets Rivers, Washington, U.S.A. Geomorphology, **51**(1–3): 31–59. doi:10.1016/S0169-555X(02)00324-0.

Ozanne, C.M.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Körner, C., Meinzer, F.C., Mitchell, A.W., Nakashizuka, T., Dias, P.L.S., Stork, N.E., Wright, S.J., and Yoshimura, M. 2003. Biodiversity meets the atmosphere: a global view of forest canopies. Science, **301**(5630): 183–186. doi:10.1126/science.1084507. PMID:12855799.

Perry, D.R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica, **10**(2): 155–157. doi:10.2307/2388019.

Proctor, M.C.F., Oliver, M.J., Wood, A.J., Alpert, P., Stark, L.R., Cleavitt, N.L., and Mishler, B.D. 2007. Desiccation tolerance in bryophytes: a review. Bryologist, **110**: 595–621. doi:10.1639/0007-2745(2007)110[595:DIBAR]2.0.CO;2.

Pypker, T.G., Unsworth, M.H., and Bond, B.J. 2006. The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage. Can. J. For. Res. **36**(4): 809–818. doi:10.1139/X05-298.

Rousk, J., and Nadkarni, N.M. 2009. Growth measurements of saprotrophic fungi and bacteria reveal differences between canopy and forest floor soils. Soil Biol. Biochem. **41**(4): 862–865. doi:10.1016/j.soilbio.2009.02.008.

SAS Institute Inc. 1989–2007. JMP. Version 7 [computer program]. SAS Institute Inc., Cary, N.C.

Sillett, S.C., and Antoine, M.E. 2004. Lichens and bryophytes in forest canopies. *In* Forest canopies. *Edited by* M.D. Lowman and H.B. Rinker. Elsevier Academic Press, Burlington, Ma. pp. 151–174.

Sillett, S.C., and Van Pelt, R. 2007. Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy. Ecol. Monogr. **77**(3): 335–359. doi:10.1890/06-0994.1.

Van Pelt, R., O'Keefe, T.C., Latterell, J.J., and Naiman, R.J. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. Ecol. Monogr. **76**(2): 277–298. doi:10.1890/05-0753.

WRCC. 2000. 1971–2000 Monthly climate summary, Quinault Ranger Stn, Washington (456864). Western Regional Climate Center, Reno, Nev.