

Open Access Articles

Changing forest water yields in response to climate warming: results from long-term experimental watershed sites across North America

The Faculty of Oregon State University has made this article openly available. Please share how this access benefits you. Your story matters.

Citation	Creed, I. F., Spargo, A. T., Jones, J. A., Buttle, J. M., Adams, M. B., Beall, F. D., & Yao, H. (2014). Changing forest water yields in response to climate warming: Results from long-term experimental watershed sites across North America. Global Change Biology, 20(10), 3191-3208. doi:10.1111/gcb.12615
DOI	10.1111/gcb.12615
Publisher	John Wiley & Sons Ltd.
Version	Version of Record
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse



Global Change Biology (2014) 20, 3191-3208, doi: 10.1111/gcb.12615

Changing forest water yields in response to climate warming: results from long-term experimental watershed sites across North America

IRENA F. CREED¹, ADAM T. SPARGO¹, JULIA A. JONES², JIM M. BUTTLE³, MARY B. ADAMS⁴, FRED D. BEALL⁵, ERIC G. BOOTH⁶, JOHN L. CAMPBELL⁷, DAVE CLOW⁸, KELLY ELDER⁹, MARK B. GREEN¹⁰, NANCY B. GRIMM¹¹, CHELCY MINIAT¹², PATRICIA RAMLAL¹³, AMARTYA SAHA¹⁴, STEPHEN SEBESTYEN¹⁵, DAVE SPITTLEHOUSE¹⁶, SHANNON STERLING¹⁷, MARK W. WILLIAMS¹⁸, RITA WINKLER¹⁹ and HUAXIA YAO²⁰ ¹Department of Biology, Western University, 1151 Richmond St., London, ON N6A 5B7, Canada, ²Department of Geography, College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA, ³Department of Geography, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada, ⁴USDA Forest Service, NRS, P.O. Box 404, Parsons, WV 26287, USA, ⁵Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen St. East, Sault Ste. Marie, ON P6A 2E5, Canada, ⁶Department of Civil and Environmental Engineering, University of Wisconsin-Madison, 1552 University Ave., Madison, WI 53726, USA, USA, USA Forest Service, 271 Mast Rd., Durham, NH 03824, USA, 8Colorado Water Science Center, US Geological Survey, MS 415 Denver Federal Center, Denver, CO 80225, USA, ⁹Rocky Mountain Research Station, USDA Forest Service, 240 West Prospect Rd., Fort Collins, CO 80526, USA, ¹⁰Center for the Environment, Plymouth State University, Plymouth, NH 03264, USA, 11 School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA, ¹²Coweeta Hydrologic Laboratory, Southern Research Station, USDA Forest Service, Otto, NC 28763, USA, ¹³Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada, ¹⁴Global Water for Sustainability Program, Florida International University, Miami, FL 33199, USA, ¹⁵Center for Research on Ecosystem Change, USDA Forest Service, 1831 Hwy 159 East, Grand Rapids, MN 55744, USA, 16Lands and Natural Resource Operations, BC Ministry of Forests, 1520 Blanshard St., Victoria, BC V8W 9C2, Canada, ¹⁷Department of Earth Science and Environmental Science, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4R2, Canada, ¹⁸Department of Geography, University of Colorado-Boulder, Boulder, CO 80309, USA, ¹⁹Lands and Natural Resource Operations, BC Ministry of Forests, 441 Columbia Street, Kamloops, BC V2C 2T3, Canada, ²⁰Dorset Environmental Science Centre, Ontario Ministry of the Environment, 1026 Bellwood Acres Rd., Dorset, ON POA 1E0, Canada

Abstract

Climate warming is projected to affect forest water yields but the effects are expected to vary. We investigated how forest type and age affect water yield resilience to climate warming. To answer this question, we examined the variability in historical water yields at long-term experimental catchments across Canada and the United States over 5-year cool and warm periods. Using the theoretical framework of the Budyko curve, we calculated the effects of climate warming on the annual partitioning of precipitation (P) into evapotranspiration (ET) and water yield. Deviation (d) was defined as a catchment's change in actual ET divided by P [AET/P; evaporative index (EI)] coincident with a shift from a cool to a warm period – a positive d indicates an upward shift in EI and smaller than expected water yields, and a negative d indicates a downward shift in EI and larger than expected water yields. Elasticity was defined as the ratio of interannual variation in potential ET divided by P (PET/P; dryness index) to interannual variation in the EI – high elasticity indicates low ddespite large range in drying index (i.e., resilient water yields), low elasticity indicates high d despite small range in drying index (i.e., nonresilient water yields). Although the data needed to fully evaluate ecosystems based on these metrics are limited, we were able to identify some characteristics of response among forest types. Alpine sites showed the greatest sensitivity to climate warming with any warming leading to increased water yields. Conifer forests included catchments with lowest elasticity and stable to larger water yields. Deciduous forests included catchments with intermediate elasticity and stable to smaller water yields. Mixed coniferous/deciduous forests included catchments with highest elasticity and stable water yields. Forest type appeared to influence the resilience of catchment water yields to climate warming, with conifer and deciduous catchments more susceptible to climate warming than the more diverse mixed forest catchments.

Keywords: Budyko curve, catchments, climate change, elasticity, evapotranspiration, forest, precipitation, resilience, water yield

Received 20 August 2013 and accepted 2 March 2014

Correspondence: Irena F. Creed, tel. + 1-519-661-4265, fax + 1-519-661-3935, e-mail: icreed@uwo.ca

Introduction

Since the Industrial Revolution, warmer air temperatures have been observed at continental scales (Jansen et al., 2007). The effects of climate warming on water yield from headwaters are of great concern given their key role as water supply source areas (National Research Council, 2008). Long-term meteorological and hydrological records in headwater catchments, initiated to investigate management effects on hydrological fluxes in the early 20th century, are increasingly valuable for exploration of the effects of climate warming on water supplies. These data indicate that water yield response to climate warming varies among biomes (Jones et al., 2012). This variability highlights the difficulties of predicting water yield response to climate change and its consequences for downstream water supplies (Bates et al., 2008).

Different responses among catchment water yields to climate warming may reflect differences in resilience. Resilience concepts in environmental studies were first introduced by Holling (1973), who defined a resilient ecosystem as one that is able to absorb change while maintaining ecosystem function. Holling (1996) went on to distinguish between the concepts of engineering vs. ecological resilience. Engineering resilience suggests that a system may exist in only one stable equilibrium state; to measure such a system's resilience, one must determine its resistance to change and the time needed to return to the equilibrium state. Ecological resilience suggests that a system may exist in multiple stable equilibrium states; resilience in this case is measured as the magnitude of change an ecosystem can absorb before it shifts from one stable state to another stable state. While humans may deem some equilibrium states more desirable or valuable than others, the assumption is that each stable state is ecologically functional. Therefore, the main difference is that engineering resilience implies a single state (the system may be displaced from that state but if it is resilient, it will return to it), whereas ecological resilience implies a system flip among two or more stable states, all of which reside in a landscape of possible alternatives, and different disciplines have adopted different definitions to describe resilience (Brand & Jax, 2007).

Catchment scientists have recently started to apply resilience concepts to hydrological sciences. In this article, we adopt the concept of hydrological resilience (Gerten *et al.*, 2005): the ability of a catchment to absorb change and maintain or quickly regain hydrological function. This definition effectively refers to engineering resilience, which is more appropriate than ecological resilience for exploring the impact of climate

warming on catchment water yields. Hydroloigcally resilient catchments are those with stable (operating within a range of natural variability, Poff *et al.*, 1997) and/or predictable water yields in face of changing environmental conditions. Catchments that lack hydrological resilience can be problematic. Human communities have often developed on the basis of historical water yields, and for this reason, substantial changes to water yields place these communities at risk.

Recent catchment hydrological studies have used a Budyko curve (Fig. 1, Budyko, 1974) approach to examine the interactions of climate, vegetation and water yield (e.g., Wang & Hejazi, 2011; Gentine et al., 2012; Williams et al., 2012; Troch et al., 2013), but none of these studies uses long-term data from forested headwater catchments to explore the hydrological resilience of water yields to changing climate. We use the Budyko curve to explore the concept of hydrological resilience. This well-known curve describes the relationship between a catchment's potential evapotranspiration (PET) and its actual evapotranspiration (AET), each normalized by precipitation (P) - i.e., the curve describes AET/P (evaporative index, EI) as a function of PET/P (dryness index, DI). Budyko defined two catchment states, with evapotranspiration (ET) being limited by either energy supply or water supply. Climate determines the drying power of the atmosphere (net radiation and vapor pressure deficit) and the supply of water in the catchment (intercepted by the canopy or stored on ground surface or in soil) both of which influence ET. A value of DI < 1 indicates a humid, energy-limited catchment, whereas a value of DI > 1 indicates a dry, water-limited catchment. A catchment can be plotted on the Budyko curve based

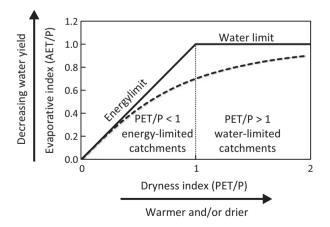


Fig. 1 A Budyko diagram (evaporative vs. dryness index). The solid lines represent energy and water limits to the evaporative index, and the dashed line represents the original theoretical Budyko curve (after Budyko, 1974).

on its DI and EI. Paired DI and EI values based on long-term monitoring data from North American forested headwater catchments place the catchments on or near the Budyko curve (Jones et al., 2012). Long-term offsets from the curve are likely due to unaccounted-for site characteristics such as vegetation type (Zhang et al., 2001), soil type (Wang et al., 2009), water storage capacity (Milly, 1994), or timing of water recharge (Potter et al., 2005). We conceive of forested headwater catchments as exhibiting hydrological resilience because they hover around an attractor state defined by the Budyko curve but occasionally deviate due to a climatic variability or climatic extremes. Ultimately, though, they return to that attractor.

An underlying assumption of the Budyko approach is that over the long-term, mean annual P can be predictably partitioned into ET and water yield (Q): P = ET + Q. The larger the DI (Fig. 1), the greater the proportion of precipitation that is partitioned to ET and the less that is available for discharge (water yield). A catchment that plots on the left-hand side of the curve will have greater water yield (smaller EI) than those catchments that plot on the right-hand side of the curve (larger EI). However, the Budyko curve may also provide a useful framework for developing a predictive understanding of how catchments respond to changing climatic conditions. For an individual catchment, we ask the questions: As DI (climate) changes, how does EI (water partitioning) respond? And do the DI and EI points move along the Budyko curve or do they deviate from the curve? A catchment that plots above (below) the curve is allocating more (less) water than predicted to ET and is yielding less (more) than predicted in the form of runoff. Relative to the Budyko curve, we define hydrological resilience as the ability of a catchment to absorb the effects of climate change and still maintain hydrological function as predicted by the curve. We suggest that hydrologically resilient catchments need not be fixed at a specific location on the Budyko diagram but that they do need to adapt to changing conditions such that their DI and EI points keep them near the Budyko curve.

To the extent that recent climate warming has manifested as increased atmospheric drying power (increased DI), we would expect that hydrologically resilient energy-limited catchments may be changing their allocations of P such that the proportion going into ET is increasing (increased EI) at the expense of water yield. A number of mechanisms operating over a range of scales could be involved, including (a) stomata closing in response to the increase in drying power; (b) forests accessing water stored in riparian areas, wetlands and lakes; or (c) forests reallocating water between evaporation (from intercepted or stored water)

and transpiration, with some tree species reallocating more toward one than the other. All of these, as well as other factors like changes in timing and magnitude of precipitation (including partitioning of rain vs. snow) and changes in vegetation and soil composition, might produce a catchment response to climate warming indicative of an 'adaptive capacity' of the forest (Gunderson, 2000).

In this study, we examined changes in a catchment's DI and EI coincident with climatic transitions from relatively cool to warm conditions. We looked specifically for deviations from the Budyko curve with time to determine whether the catchments shifted predictably in terms of their water balance. To that end, we developed quantitative metrics to express changes in a catchment's Budyko characteristics with time. Dynamic deviation (d) is a measure of change in a catchment's EI relative to the Budyko curve as climate varies - in other words, a measure of the extent to which the allocation of precipitation to ET vs. runoff matches theoretical expectations. Elasticity is a measure of a catchment's ability to maintain water partitioning consistent with the Budyko curve as climate varies (i.e., the ratio of a catchment's range in DI to its range in EI). Elasticity of water yield to changes in P has shown utility in quantifying hydrological sensitivity to climate change (Schaake, 1990; Sankarasubramanian et al., 2001); we apply elasticity to Budyko characteristics. A catchment has high elasticity if its DI changes with climate warming, but EI changes only slightly. In contrast, a catchment has low elasticity if EI responds substantially to changes in DI.

We used elasticity as an indicator of the hydrological resilience of catchments. Hydrological resilience is exhibited when a change in DI results in a corresponding change in EI such that the system moves along the theoretical Budyko curve – i.e., its water yields respond consistently with theoretical expectations (high elasticity and low deviation). A lack of hydrological resilience is exhibited when a change in DI results in a corresponding change in EI that pushes the system away from the theoretical Budyko curve – i.e., its water yields are larger or smaller than would be predicted from theoretical expectations (low elasticity and high deviation). A nonresilient state could lead to fundamental changes in forest structure and function and possibly shift the catchment into a permanent alternative state.

We investigated how water partitioning between ET and runoff has responded over time to climate warming in forested headwater systems, and how forest type and forest history affect hydrological resilience to climate warming. In answering this question, we tested two hypotheses. First, during climate warming, resilient catchments (high elasticity and low deviation) will

shift along the Budyko curve, but nonresilient catchments (low elasticity and high deviation) will deviate upward from the theoretical curve, indicating a decrease in water yield. The magnitude of decline in water yields (increasing EI) will be a positive function of the extent of warming but may be modified by the direction of precipitation change. Wetter conditions serve as a negative feedback (less deviation), while drier conditions serve as a positive feedback (more deviation). Second, elastic catchments will be characterized by relatively undisturbed conditions, with mixed forests being more elastic than either purely coniferous or deciduous forests and with older forests being more elastic than younger forests (recognizing that we may not have sufficient sample size to test the role of forest age as rigorously as we would like). The relatively short cool and warm periods used in this study (5 years) give us a basic understanding of catchment responses to changing climate, which can then give us an indication of what longer-term responses might be.

Our analysis uses long-term monitoring data from headwater catchments, including sites of the United States (US) Long Term Ecological Research (LTER), US Forest Service, US Geological Survey, and Canadian HydroEcological Landscape Processes (HELP) networks. Each site benefits from a generation or more of site studies of local processes and patterns. This analysis is one of the first to combine US and Canadian data from coast to coast to explore headwater catchment responses to changing environmental conditions across broad climatic gradients.

Materials and methods

Study sites

More than 100 potential catchments from the combined networks were examined as possible candidates for the analysis of catchment response to climate warming. We selected forested and alpine headwater catchments that were located within forest regions that had (a) no anthropogenic disturbances since 1950; (b) a minimum of 15 years since 1980 of consecutive and coincident records of daily air temperature $(T, ^{\circ}C)$, precipitation $(P, \text{mm yr}^{-1})$, and water yield $(Q, \text{L s}^{-1})$; and (c) detectable shifts from cooler to warmer air temperatures. These criteria resulted in the selection of 21 headwater catchments at 12 sites (Fig. 2; Tables 1 and 2; Table S1). At

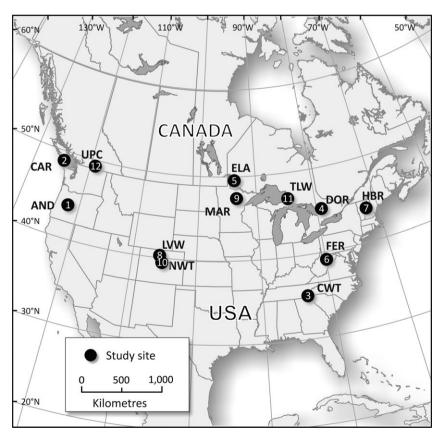


Fig. 2 Location of long-term monitoring catchments that met the selection criteria for this study (*n* = 12). Site identifiers are: 1, HJ Andrews; 2, Carnation; 3, Coweeta; 4, Dorset; 5, Experimental Lakes Area; 6, Fernow; 7, Hubbard Brook; 8, Loch Vale Watershed; 9, Marcell; 10, Niwot; 11, Turkey Lakes Watershed; 12, Upper Penticton.

	23	
,	Ξ	
	Ę	
	ä	
	a	
	ĭ	
	Ξ	
	5	
	~	
	2	
-	>	
•	g	
۶	η	
	he	
	듬	
	Ξ	
	ın the	
,	ರ	
	Ð	
	ă	
	٠.	
,	catchments	
	ᇁ	
	ue	
	Ξ	
,	듯	
,	$\stackrel{\smile}{}$	
	g	
,	ĭ	
	0	
	Ħ	
,	ᄗ	
	ξ	
	8	
	š	
	نة	
ſ	\Box	
,	_	
	c۵	
,	ĭ	
,	무	

	Sito	Catchment	Catchment	Area	Dominant enectes	Soils and geomorphology	Rodinok apology
1a	HJ Andrews	AND 2	WS02	09	Douglas fir and western hemlock	Holocene; steep (>30°) planar slopes with thin (1–2 m) soil; slump benches	Miocene volcanic breccia and sedimentary rocks capped by lava flows
116	HJ Andrews	AND 8	WS08	21	Douglas fir and western hemlock	and head scarps Holocene; Moderate (6–10°) slopes with thick soil (2+ m); irregular landslide	Miocene volcanic breccias and lava flows
7	Carnation	CAR	Sub-watershed WS C	146	Western hemlock, western red cedar, Amabilis fir, old growth	Virture of morainal veneer, colluvial veneer, and morainal blanket with minor rock outcrops	Jurassic volcanics of the Bonanza group consisting of basaltic to rhyolitic lava, tuff, beccia, minor argillite and graywacke, and Island intrusives consisting of granodiorite, quartdiorite,
3a	Coweeta	CWT 17	Watershed 17	14	Eastern white pine plantation	Holocene to Tertiary; Colluvial sediments, discontinuous; Discontinuous, or patchy in distribution; soils are in the Saunook series, a fine-loamy, mixed, mesic Humic Hapludult, found at streamside positions, and Cowee-Evard complex soils, fine-loamy, mixed-oxidic, mesic, Typic Hapludult, found	Basal coarse-grained quartz diorite gneiss (Persimmon Creek Gneiss), overlain with metasandstone and politic schist (Coleman River Formation), overlain by quartzose metasandstone and quartzite (Ridgepole Mountain Formation)
35	Coweeta	CWT 18	Watershed 18	13	Mixed oak hardwood	on ridge positions Holocene to Tertiary; Colluvial sediments, discontinuous; Discontinuous, or patchy in distribution; soils are in the Saunook series, a fine-loamy, mixed, mesic Humic Hapludult, found at	Basal coarse-grained quartz diorite gneiss (Persimmon Creek Gneiss), overlain with metasandstone and politic schist (Coleman River Formation), overlain by quartzose metasandstone and quartzite (Ridgepole Mountain Formation)

Table	Table 1 (Continued)						
	Site	Catchment code	Catchment name	Area (ha)	Dominant species	Soils and geomorphology	Bedrock geology
4a	Dorset	DOR HP3	Harp Lake 3	56	Sugar maple and red maple with some beech, birch, and hemlock; wetland areas dominated by black spruce	streamside positions, and Cowee-Evard complex soils, fine-loamy, mixed-oxidic, mesic, Typic Hapludult, found on ridge positions Till Veneer, thin and discontinuous till; may include extensive areas of rock outcrop; Coarse grained (Glacio)Lacustrine, sand, silt, and gravel; deposited as deltas, sheet	Precambrian; early Mesoproterozoic metamorphic rocks; orthogneiss
4b	Dorset	DOR HP 3A	Harp Lake 3A	20	Sugar maple and red maple with some beech, birch, and hemlock; wetland areas dominated by black spruce	sands, and lag deposits Till Veneer, thin and discontinuous till; may include extensive areas of rock outcrop; Coarse grained (Glacio)Lacustrine, sand, silt, and gravel; deposited as deltas, sheet sands, and lag	Precambrian; early Mesoproterozoic metamorphic rocks; orthogneiss
4c	Dorset	DOR HP 4	Harp Lake 4	123	Sugar maple and red maple with some beech, birch, and hemlock; wetland areas dominated by black spruce	deposits Thin (1–10 m thick) veneer of discontinuous till with extensive areas of rock outcrop; Coarse grained (Glacio)Lacustrine, sand, silt, and gravel; deposited as deltas, sheet sands, and lag	Precambrian; early Mesoproterozoic metamorphic rocks; granitized biotite and hornblende gneiss
4q	Dorset	DOR HP 5	Harp Lake 5	191	Sugar maple and red maple with some beech, birch, and hemlock; wetland areas dominated by black spruce	deposits Till Veneer, thin and discontinuous till; may include extensive areas of rock outcrop; Coarse grained (Glacio) Lacustrine, sand, silt,	Precambrian; early Mesoproterozoic metamorphic rocks; granitized biotite and homblende gneiss

Domest Catchment Catchment Area Ar								
Dorset DOR PC Plastic Lake 27 White pine eastern hemicok and fred maple and red maple and red maple and red maple beckersive thin and experimental ELA Watershed 239 400 Jackpine and black spruce discontinuous till: may include extensive areas of rock outerop areas		Site	Catchment code	Catchment name	Area (ha)	Dominant species	Soils and geomorphology	Bedrock geology
Experimental ELA Watershed 239 400 Jackpine and black spruce discontinuous till: In Jackpine areas of rock coutcropy: Colluvial sediments, discontinuous discontinuous Brook Watershed 4 39 Oak-hickory forest Steps slopes (20-40%), within soils (-1 m); Colluvial sediments, discontinuous Wisconsinan; glacial Il Jackpine and black outcrops on the upper watershed brook Hubbard HBR 6 Watershed 6 13 Sugar maple, beech and Pleistocene; late brook In Jackpine and border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden to the upper watershed border to over 5 m thick holden thin thin the upper watershed border to the upper watershed border to over 5 m thick holden thin thin thin thin thin thin thin thi	46	Dorset	DOR PC	Plastic Lake	27	White pine, eastern hemlock and red maple	and gravel; deposited as deltas, sheet sands, and lag deposits Till Veneer, thin and discontinuous till; may include extensive	Precambrian; early Mesoproterozoic metamorphic rocks; granitized biotite and hornblende gneiss
Fernow FER Watershed 4 39 Oak-hickory forest Steep slopes (20-40%), with thin soils (<1 m); Colluvial sediments, discontinuous discontinuous shook HBR 3 Watershed 3 42 Sugar maple, beech and Pleistocene; late Persock Hubbard HBR 6 Watershed 6 13 Sugar maple, beech and pomy: thickness ranges from 0 m at bedrock outcrops on the upper watershed brook HBR 6 Watershed 6 13 Sugar maple, beech and Pleistocene; late Brook Ucch Vale LVW Andrews Creek 183 Alpine tundra Holocene till, latus, and colluvium; Discontinuous, or patchy in distribution to pre-Illinoian; Glacial till mostly in distribution to pre-Illinoian; Glacial till pre-Personal distribution in the pre-Illinoian; Glacial till in the pre-Personal distribution in the personal distribution in the pre-Personal distribution in the personal distribution in the	rV	Experimental Lakes Area	ELA		400	Jackpine and black spruce	Till Veneer, thin and discontinuous till; may include extensive areas of rock outcrop; (Glacio)Lacustrine acidic brunisol, silt	Precambrian; undivided Neoarchean intrusive rocks and undivided granitoid rocks
Hubbard HBR 3 Watershed 3 42 Sugar maple, beech and Wisconsinan; glacial till, mostly sandy loam; thickness ranges from 0 m at bedrock outcrops on the upper watershed brook HBR 6 Watershed 6 13 Sugar maple, beech and border to over 5 m thick brook wisconsinan; glacial till, mostly sandy loam; thickness ranges from 0 m at bedrock outcrops on the upper watershed brook in thick prook brook watershed 6 13 Sugar maple, beech and wisconsinan; glacial till, mostly sandy loam; thickness ranges from 0 m at bedrock outcrops on the upper watershed brook in thick brook watershed brook in thick brook watershed brook 183 Alpine tundra Colluvium; Discontinuous, or patchy in distribution to pre-Illinoian; Clacial till to pre-Illinoian; Clacial till	9	Fernow	FER		39	Oak-hickory forest	Steep slopes (20–40%), with thin soils (<1 m); Colluvial sediments,	Paleozoic Devonian; predominantly interbedded sandstones and shale, some marine sediment layers
Hubbard HBR 6 Watershed 6 13 Sugar maple, beech and Pleistocene; late Wisconsinan; glacial till, mostly sandy loam; thickness ranges from 0 m at bedrock outcrops on the upper watershed border to over 5 m thick LVW Andrews Creek 183 Alpine tundra Holocene till, talus, and colluvium; Discontinuous, or patchy in distribution watershed S2 10 Aspen, birch, black spruce Pleistocene; late Wisconsinan to pre-Illinoian; Glacial till	7a	Hubbard Brook	HBR 3		42	Sugar maple, beech and yellow birch	Pleistocene; late Wisconsinan; glacial till, mostly sandy loam; thickness ranges from 0 m at bedrock outcrops on the upper watershed	Paleozoic Silurian; mica schist, quartzite and calc-silicate granulite
Loch Vale LVW Andrews Creek 183 Alpine tundra Holocene till, talus, and colluvium; Discontinuous, or patchy in distribution Marcell MAR 2 Watershed S2 10 Aspen, birch, black spruce Pleistocene; late Wisconsinan to pre-Illinoian; Glacial till	22	Hubbard Brook	HBR 6		13	Sugar maple, beech and yellow birch	Pleistocene; late Wisconsinan; glacial till, mostly sandy loam; thickness ranges from 0 m at bedrock outcrops on the upper watershed	Paleozoic Silurian; mica schist, quartzite and calc-silicate granulite
or patchy in distribution MAR 2 Watershed S2 10 Aspen, birch, black spruce Pleistocene; late Wisconsinan to pre-Illinoian; Glacial till	∞	Loch Vale	LVW	Andrews Creek	183	Alpine tundra	Holocene till, talus, and colluvium; Discontinuous,	Precambrian granitic and metamorphic rocks
	9a 	Marcell	MAR 2		10	Aspen, birch, black spruce	or patchy in distribution Pleistocene; late Wisconsinan to pre-Illinoian; Glacial till	Early Precambrian granitic rocks

Table 1 (Continued)

Table	Table 1 (Continued)						
	Site	Catchment code	Catchment name	Area (ha)	Dominant species	Soils and geomorphology	Bedrock geology
96	Marcell	MAR 5	Watershed S5	53	Aspen, birch, black spruce	over outwash sands, mostly silty, thick; 50 m Pleistocene; late Wisconsinan to pre-Illinoian; Glacial till over outwash sands, mostly silty, thick; 50 m	Early Precambrian granitic rocks
10	Niwot	NWT	Upper Green Lakes (GL4)	225	Alpine tundra	Holocene; accumulated since deglaciation about 12 000 years ago	Precambrian schists and gneisses, the Silver Plume quartz monzonite
11a	Turkey Lakes	TLW 35	Catchment c35	4	Sugar maple	Till Veneer, generally thin (<2 m) with areas of rock outcrop at higher elevations and steeper slopes	Precambrian; silicate greenstone with small outcrops of more felsic igneous rocks
11b	Turkey Lakes	TLW 38	Catchment c38	9	Sugar maple	Till Veneer, generally thin (<2 m) with areas of rock outcrop at higher elevations and steeper slopes	Precambrian; silicate greenstone with small outcrops of more felsic igneous rocks
12	Upper Penticton	UPC	Two Forty Creek	200	Lodgepole pine	Till mantle with minor glaciofluvial sands and gravels, includes extensive areas of rock outcrop at higher elevations	Cretaceous or Jurassic Okanagan Batholith; massive, medium-coarse-grained, light gray biotite granodiorite and granites

Table 2 Catchment 5-water-year (5-wyr) cool periods (period with lowest average temperature) and 5-wyr warm periods (period with highest average temperature), changes in temperature and precipitation during shift from cool to warm period, as well as components of catchment departures from the Budyko curve [static (*s*) and dynamic (*d*) deviations] and catchment abilities to maintain water partitioning consistent with the Budyko curve as climate varies (elasticity *e*). Catchment ecosystem type (alpine, coniferous, deciduous or mixed coniferous and deciduous forest) and age also provided

ID	Catchment	Cool period	Warm period	ΔT (°C)	$\Delta P~(\%)$	S	d	e	Forest type	Forest age (years)
1a	AND 2	1982–1986	1988–1992	0.57	-21	0.16	-0.01	1.61	Coniferous	450–500
1b	AND 8	1982-1986	1988-1992	0.57	-21	0.19	0.03	1.33	Coniferous	450-500
2	CAR	1985-1989	1990-1994	0.43	9	0.07	-0.18	0.23	Coniferous	>100
3a	CWT 17	1977–1981	1989-1993	1.13	13	0.17	0.02	2.08	Coniferous	60
3b	CWT 18	1977-1981	1989-1993	1.13	13	-0.04	0.01	1.61	Deciduous	80
4a	DOR HP3	1992-1996	1998-2002	1.65	-12	-0.04	0.04	1.04	Deciduous	>100
4b	DOR HP 3A	1992-1996	1998-2002	1.65	-12	-0.02	0.00	1.20	Deciduous	>100
4c	DOR HP 4	1992-1996	1998-2002	1.65	-12	-0.02	0.05	0.83	Deciduous	>100
4d	DOR HP 5	1992-1996	1998-2002	1.65	-12	-0.07	0.08	0.66	Deciduous	>100
4e	DOR PC	1992-1996	1998-2002	1.81	-8	-0.04	0.00	0.98	Mixed	>100
5	ELA	1993-1997	1998-2002	1.85	14	0.09	-0.01	1.68	Coniferous	>100
6	FER	1977–1981	1987-1991	1.44	-6	0.11	-0.02	1.24	Deciduous	90-100
7a	HBR 3	1992–1996	1998-2002	1.36	-4	-0.04	0.00	1.98	Deciduous	100
7b	HBR 6	1992-1996	1998-2002	1.36	-4	-0.03	-0.02	2.09	Deciduous	100
8	LVW	1995–1999	2000-2004	0.88	-27	0.04	-0.17	0.35	Alpine	>100
9a	MAR 2	1993-1997	1998-2002	2.12	-2	0.22	-0.05	2.91	Mixed	>80
9b	MAR 5	1993-1997	1998-2002	2.91	-2	0.31	-0.05	2.72	Mixed	>80
10	NWT	1992-1996	2000-2004	0.67	-17	0.20	-0.16	0.33	Alpine	>100
11a	TLW 35	1992-1996	1998-2002	1.95	-12	0.11	0.01	1.16	Deciduous	>140
11b	TLW 38	1992-1996	1998-2002	1.95	-12	0.14	-0.05	1.51	Deciduous	>140
12	UPC	1995–1999	2002–2006	0.59	-13	0.04	-0.08	0.72	Coniferous	125

some sites, multiple catchments were selected if they provided a contrast in catchment properties that could influence water partitioning. While these criteria resulted in a relatively small sample size and limits the detail of the analysis, there is enough variety in geographic area and site characteristics to make general observations about the effects of climate warming on different forest types and ages.

Dryness index (DI) and Evaporative index (EI)

For each catchment, T, P, and Q data were converted from daily to average monthly and annual T and total monthly and annual P and Q values (over water years, October through September). For sites with multiple T or P stations, the recommendations of local site researchers were followed in choosing either a representative single station record or some combination of the multiple station records.

Water-year PET was calculated for each catchment as a function of average monthly T according to the Hamon (1963) formula because only T data were available for all sites. The Hamon formula has a tendency to underestimate PET (Yao, 2009), but performs better than other T-based PET models and is comparable to common radiation-based PET models (Lu $et\ al.$, 2005). Water-year AET was estimated using a water balance approach and measurements of annual P and Q: AET = P — Q — ΔS , where ΔS is change in water storage volume. We assumed steady-state water storage (i.e., ΔS = 0) for

the time periods encompassed in this study. Both PET and AET estimates may be affected by variation in groundwater recharge and storage among sites due to different surficial and bedrock geologies (Table 1).

Budyko curve

The Budyko curve was developed as a theoretical expression to explain how annual water balance is partitioned as a function of the relative magnitude of water and energy supply. Several attempts have been made to derive theoretical equations that explain this relationship, and these equations have been applied and modified for catchments around the world. We used the equation from Zhang $\operatorname{et} \operatorname{al.}(2001)$, which accounts for plant-available water w that was tailored specifically for different catchments (i.e., $\operatorname{w}=2$ in forested catchments, $\operatorname{w}=0.5$ in grassland or cropland catchments, and $\operatorname{w}=1$ in mixed cover catchments). We used the Zhang $\operatorname{et}\operatorname{al.}(2001)$ model to give the theoretical relationship between DI and EI in our catchments using $\operatorname{w}=2$ for all catchments.

Climate warming shifts

For each catchment, a 5-water-year (5-wyr) moving average of the T time series was calculated. A catchment's 'cool period' was defined as the 5-wyr period with the minimum 5-wyr T. A catchment's 'warm period' was defined as the first 5-wyr

period after the cool period (no overlapping years) for which the 5-wyr T was (a) warmer than the previous 5-wyr T and (b) warmer than the subsequent three 5-wyr (moving-average) T values by more than 1 standard deviation. All such warming shifts were identified in the T record, and the largest shift was then selected as the basis for this analysis. The 'break point' is the last year of the designated cool period. The selected cool and warm periods did not necessarily include the temperature minima and maxima observed during the periods of record (Table 2).

Budyko metrics: deviation and elasticity

We developed several custom indices to describe the potential departure from the theoretical Budyko curve of a catchment's DI and EI points with time.

Deviation was characterized as a vertical departure from the Budyko curve – i.e., the difference between a catchment's measured EI (EI $_{\rm M}$) and its theoretical value (EI $_{\rm B}$, predicted as a function of DI according to the Budyko curve). Two components of deviation were calculated. Static deviation (s) results from inherent catchment characteristics that are assumed to be constant with time. Dynamic deviation (d) results from catchment changes over time – in this case, in response to climatic warming. Static deviation for each catchment was based on the cool-period observations; i.e., $s = {\rm EI}_{\rm M,cool} - {\rm EI}_{\rm B,cool}$ (Fig. 3a). Dynamic deviation was considered to be that portion of warm-period deviation, corrected for this static component; i.e., $d = {\rm EI}_{\rm M,warm} - {\rm EI}_{\rm B,warm} - s$ (Fig. 3a).

Elasticity (e) was calculated as the ratio of the range in water-year DI values to the range in water-year EI residual values experienced during the period encompassing the identified cool and warm periods; i.e., $e = (\mathrm{DI_{max}} - \mathrm{DI_{min}})/(\mathrm{EI_{R,max}} - \mathrm{EI_{R,min}})$ (Fig. 3b, c). The DI : EI relationship changes when moving right along the theoretical Budyko curve. We accounted for this by using the residuals of the EI values (EI_R) for each year for the period of record (EI_R = EI_M - EI_B) to calculate e. A catchment with high elasticity partitions P into Q and ET in a manner that produces smaller changes in EI_R values relative to changes in DI values and therefore varies predictably with the Budyko curve (Fig 3b). A catchment with low elasticity partitions water in a less predictable manner (Fig. 3c). We used e=1 as the defining threshold for elastic vs. inelastic catchments.

Warming with precipitation feedbacks

Shifts to warmer conditions were often accompanied by a change in precipitation (ΔP). To elucidate potential interactions among ΔT , ΔP , d, and e, we classified catchments based on both the degree of warming (i.e., the magnitude of ΔT) and the degree of drying or wetting (i.e., the magnitude of negative or positive ΔP). Data for any year following an extreme annual P occurrence (defined as >1.5 standard deviations from the long-term mean annual P) were removed because extreme P years resulted in 'legacy effects' that amplified d of the following year. Catchments were classified into one of six

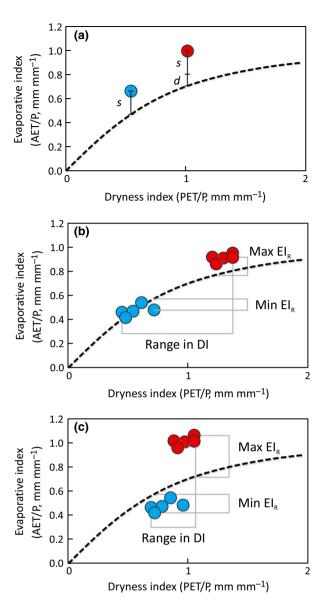


Fig. 3 Graphical representation of Budyko resilience metrics. Each dot shows a catchment's paired dryness index (DI) and evaporative index (EI) values: blue for the cool period and red for the later warm period. The dashed line represents the theoretical Budyko curve. (a) Static deviation (s) was calculated as the difference between measurement-based and theoretical evaporative indices during the catchment's cool period: $s = EI_{M,cool} - EI_{B,cool}$. Dynamic deviation (d) was calculated as the analogous warmperiod quantity, corrected for the previously determined s: $d = EI_{M,warm} - EI_{B,warm} - s$. Points that fall above the theoretical curve indicate smaller-than-predicted water yields; points that fall below the curve indicate larger-than-predicted yields. Elasticity (e) was calculated as the ratio of a catchment's range in DI to its range in EI during the two contrasting climate periods: $e = (DI_{max} - DI_{min})/(EI_{R,max} - EI_{R,min})$. (b) This example catchment exhibited a high degree of elasticity (e > 1) (i.e., approximating theoretical behavior). (c) This example catchment exhibited low elasticity (e < 1) (i.e., deviating from theoretical behavior).

different climate-shift categories, first by dividing ΔT into two categories according to whether the catchments experienced relatively little warming ($\Delta T < 1.5$ °C) or greater warming $(\Delta T > 1.5 \, ^{\circ}\text{C})$. Catchments were further subdivided according to whether the catchments became appreciably wetter ($\Delta P > 10\%$), experienced relatively little change $(-10\% < \Delta P < 10\%)$, or became appreciably drier (ΔP < -10%). Deviations from the Budyko curve as a function of both warming (and associated wetting or drying) and elasticity were examined by conducting regression analyses using SPSS version 20.0. (IBM Corp., Armonk, NY, USA).

Results

Static deviations inherent during cool period

Static deviation (s) describes the vertical displacement of a 5-wyr cool-period (DI, EI) point from the theoretical Budyko curve caused by inherent characteristics of a catchment (Fig. 4; Table 2). Vertical deviations from the Budyko curve ranged from -0.07 to 0.31 (Table 2). Catchments with s < 0 exhibited prewarming water yields that were higher than expected based on Budyko's theoretical predictions; catchments with s > 0exhibited lower water yields than expected. Catchment points falling in close proximity to the curve (|s| < 0.05) indicated prewarming water yields that were consistent with the theoretical predictions of the Budyko curve. For the eight catchments that fell below the curve, the magnitude of s was small (range of -0.02to -0.07), indicative of water yields marginally greater than expected. In contrast, for the 13 catchments that fell above the curve, the magnitude of s was comparatively large (range of 0.04-0.31), indicative of water yields marginally to substantially smaller than expected (Table 2). Local experts at some sites assisted with the identification of factors that may have influenced s, including forest disturbance legacies, surface storage mechanisms, surface water/ground water interactions, as well as imperfect measurement or inadequate characterization of *P*, *T*, or *Q* in the catchment (Table S1).

Dynamic deviation coincident with warming

Dynamic deviation (*d*) is given by the vertical departure of the 5-wyr warm-period (DI, EI) point from the Budyko curve once s has been removed (Fig. 5). Of the 21 catchments, 11 had warm-period water yields greater than predicted by the Budyko relation (d < 0), three had warm-period water yields that were as expected (d = 0), and seven had warm-period water yields smaller than expected (d > 0). Values of dynamic deviation ranged from d = -0.18 (below the curve) to d = 0.08(above the curve) (Table 2). For catchments below the curve, the magnitudes of dynamic deviation were often

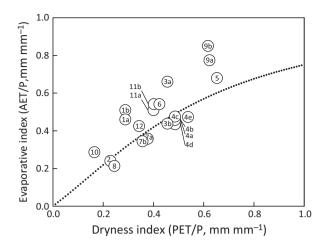


Fig. 4 Mean annual dryness index and evaporative index values for headwater catchments during the 5-water-year cool period. The dotted line represents the Zhang et al. (2001) modification of the Budyko curve (w = 2). The vertical displacement of each point from the Budyko curve is the static deviation s. Key to site IDs (the numbers within the circles) is given in Table 1.

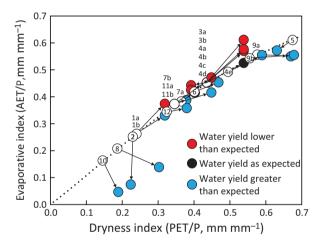


Fig. 5 Mean cool-period and warm-period dryness index (DI) and evaporative index (EI) values for headwater catchments showing catchment transitions from 5-water-year (5-wyr) cool period (numbered circles) to 5-wyr warm period (colored circles) with static deviation (s) removed from both periods. Arrows denote the direction of movement from cool to warm period. Red circles denote catchments with decreases in expected water yield (increasing EI); blue circles denote catchments with increases in expected water yield (decreasing EI); and black circles denote catchments with expected water yield. The dotted line represents the Zhang et al. (2001) modification of the Budyko framework (w = 2). Key to site IDs (the numbers within the circles) is given in Table 1. (Color in the online version)

larger (range of d = -0.18 to -0.01), indicating relatively larger increases in water yield (Table 2). For catchments above the curve, the magnitudes of dynamic deviation were smaller (range of d = 0.01-0.08), indicating a smaller range of decreases in water yield (Table 2). No obvious patterns emerged in terms of why a specific catchment's water yield would respond with a negative, neutral, or positive response to climate warming (Table 1).

Elasticity

Figure 6 shows the interannual variability in DI and EI points for representative catchments for the period of record. Elasticity (e) ranged from 0.23 to 2.91 (Table 2). Seven catchments exhibited a broad range in EI but not DI [i.e., vertical variation dominated, yielding a low elasticity (e < 1)]; the remaining 14 catchments exhibited a broad range in DI but not EI [i.e., horizontal variation dominated, yielding a high elasticity (e > 1)]. Catchments ELA (ID #5) and MAR (ID #9b) exhibited relatively high DI and tended to show broad interannual ranges in DI but not EI (Fig. 6). Catchments CAR (ID #2), LVW (ID #8) and NWT (ID #10), in contrast, exhibited relatively low DI and tended to show broad interannual ranges in EI but not DI (Fig. 6). At intermediate

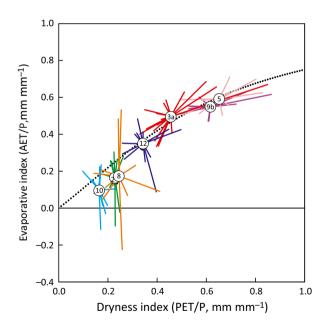


Fig. 6 Year-to-year variability in mean annual dryness index and evaporative index values for selected headwater catchments during period of record with static deviation (s) removed from each value. The numbered circles represent the mean annual values over the period of record. The radiating lines indicate annual excursions from that mean. The longer the line, the greater the departure from the long-term mean value. The dotted line represents the Zhang $et\ al.\ (2001)$ modification of the Budyko framework (w=2). Key to site IDs (the numbers within the circles) is given in Table 1.

DI values, both patterns of interannual variability were found.

Budyko metrics vs. dynamic deviation

Our first hypothesis was that elastic catchments (e > 1, our metric for resilience) would shift along the Budyko curve under warming conditions, but that inelastic catchments (e < 1, our metric for nonresilience) would deviate away from it. We predicted that inelastic catchments would deviate upward from the theoretical curve, indicating a decrease in water yield coincident with warming. We also predicted that the magnitude of this deviation would be a positive function of the degree of warming, but that wetter conditions would serve as a negative feedback (leading to less deviation), while drier conditions would serve as a positive feedback (leading to more deviation).

Dynamic deviation in water yield during the cool-to-warm climate shift was not explained by the degree of warming (Fig. 7a). Wetter conditions could conceivably counterbalance the effects of warmer temperatures, but when we removed from consideration those catchments where $\Delta P > 10\%$ [i.e., CWT 17 (ID #3a), CWT 18 (ID #3b), and ELA (ID #5)], dynamic deviation was still not explained by the extent of warming (data not shown).

Dynamic deviation in water yield during the cool-towarm climate shift varied with elasticity (Fig. 7b). Catchments with relatively low elasticity (e < 1) were more likely to experience a negative deviation (increase in water yield) in response to warming $(r^2 = 0.34,$ P < 0.01; line not shown). However, when we classified the catchments into two rates of warming ($\Delta T < 1.5$ °C and $\Delta T > 1.5$ °C), stronger relationships emerged. Catchments that experienced a relatively small degree of warming ($\Delta T < 1.5$ °C; yellow circles in Fig. 7) showed a significant exponential decrease in dynamic deviation as elasticity declined ($r^2 = 0.91$, P < 0.001). In contrast, catchments that experienced relatively high rates of warming ($\Delta T > 1.5$ °C; red circles) showed a significant exponential increase in dynamic deviation as elasticity declined ($r^2 = 0.81$, P < 0.001). For catchments with low elasticity (e < 1), the relationships between elasticity and dynamic deviation exhibited slopes of different signs, depending on the degree of warming (Fig. 7b). Classifying catchments according to whether they became appreciably wetter ($\Delta P > 10\%$), experienced relatively little change $(-10\% < \Delta P < 10\%)$, or became appreciably drier $(\Delta P < -10\%)$, did not have an effect on the relationship between dynamic deviation and either warming or elasticity (data not shown).

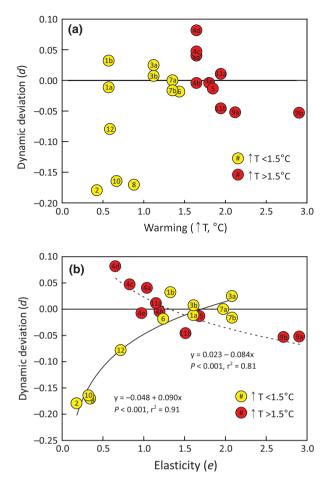


Fig. 7 Dynamic deviations of headwater catchments as a function of (a) warming and (b) elasticity. The color of the circle represents the extent of warming over the cool-to-warm transition (yellow = <1.5 °C warming; red = >1.5 °C warming). The longdash line in (b) represents the relationship between d and e for catchments that experienced <1.5 °C warming. The short-dash line in (b) represents the relationship between d and e for catchments that experienced >1.5 °C warming. Key to site IDs (the numbers within the circles) is given in Table 1.

Influence of forest type and age on elasticity

Our second hypothesis was that elastic catchments were characterized by forests that contained a diversity of forest types and ages, and that EI reflected the capacity of the ecosystem to adapt to changing climatic conditions. We predicted that mixed forests would be more elastic than either coniferous or deciduous forests. We also predicted that older forests would be more elastic than younger ones.

In our data set, dynamic deviation varied among forest types and perhaps forest ages (Table 2; Fig. 8). The alpine catchments (IDs # 8 and #10) experienced small increases in T ($\Delta T < 1.5$ °C) and large (>10%) decreases

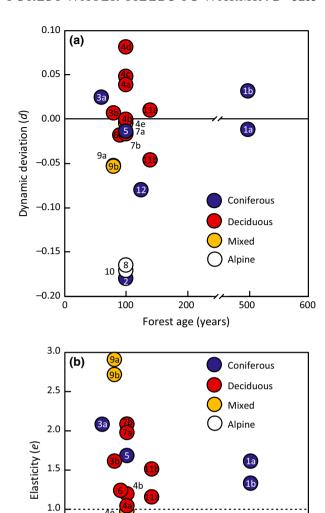


Fig. 8 Catchment properties as a function of forest type (colored circles) and forest age: (a) dynamic deviation d and (b) elasticity e. Key to site IDs (the numbers within the circles) is given in Table 1. (Color in the online version)

200

Forest age (years)

500

600

100

0.5

0.0

in P (Table 2; Fig. 7). Elasticity was low (e < 0.5) and dynamic deviation was substantial and negative (d < -0.15). These catchments had larger-than-expected water-yield increases associated with warming, perhaps due to glacier or permafrost melt.

Conifer catchments were generally situated in western North America and experienced slight warming (mostly $\Delta T < 1$ °C, with the exception of CWT17 (ID #3a) and ELA (ID #5), the two conifer catchments that were situated in eastern North America, which experienced $\Delta T > 1$ °C) with either decreases or increases in P (Table 2). They had a wide range of elasticity (e < 0.5–2.0) and wide-ranging but mostly negative dynamic deviation (d = -0.2 to 0.0). Those with the lowest elasticity [CAR (ID #2) and UPC (ID #12)] had the most negative dynamic deviation with larger-than-expected water yields. In contrast, those with greater elasticity (e > 1) had near-zero dynamic deviations (no change in water yields).

The deciduous catchments were all situated in eastern North America and experienced intermediate increases in T (1–2 °C) with either decreases or increases in P (Table 2). They had a slightly narrower range of elasticity (e = 0.5–2.0), and near-zero to mostly positive dynamic deviation (d = -0.05–0.1). Those with the lowest elasticity [DOR HP3 (ID #4a), HP4 (ID #4c), and HP5 (ID #4d)] had the highest positive dynamic deviation with smaller-than-expected water yields. The one exception was TLW38 (ID #12b), a sugar maple forest in the Turkey Lakes Watershed of central Ontario (d = -0.05). Some 20% of this catchment area is wetland, which may have provided a water supply to sustain water yields when climate shifted to warmer conditions.

The mixed deciduous-conifer forest sites, which were all situated in eastern North America, experienced the largest changes in T (mostly $\Delta T > 2$ °C) and also decreasing P (Table 2). These exhibited a wide range of elasticity, including sites with the highest elasticity (e=1.0–3.0) and slightly negative to near-zero dynamic deviation (d=-0.05 to 0). Catchments with this type of forest stayed the closest to the Budyko curve despite experiencing the greatest climate warming.

The range of forest ages among our sites was admittedly limited (Table 2, Fig. 8). This is partly due to our selection criteria, which required undisturbed forest since 1950 (older forests were often disturbed) and to a general lack of experimental catchments with older forests. However, there is a suggestion of convergence in dynamic deviation values to near zero and convergence of elasticity toward 1 with forest age (Fig. 8a, b). The magnitude of dynamic deviation (positive or negative) was closest to zero and elasticity was closest to 1 for the two catchments with the oldest forests [AND2 (ID #1a) and AND8 (ID #1b), which were 450–500 years in age].

Discussion

Climate change is expected to affect forest water yields (Aber *et al.*, 1995). However, not all forest ecosystems are expected to respond in a uniform manner. Rates of climate change vary geographically (Walther *et al.*,

2002; Karl et al., 2009; Loarie et al., 2009), and forests of different types and ages may influence catchment responses (Brown et al., 2005; Ewers et al., 2005). The results of our study investigating the responses of forested catchments to relatively short-term transitions from cool to warm conditions provide a conceptual basis for understanding and predicting the direction and magnitude of forest headwater yield response to climate change.

Ponce Campos et al. (2013) observed that the wateruse efficiency (the ratio of above-ground net primary production to ET) in forests was sensitive to water availability. Higher water-use efficiencies observed in drier years, and lower (native) water-use efficiencies were observed in wetter years. This flexibility in water-use efficiency suggests a resilience of the ecosystem to climate variability and in particular to climatic extremes observed in recent decades. Holling (1973, 1996) identified two distinct resilience concepts – engineering and ecological resilience. The hydrological responses of our headwater catchments exhibited engineering resilience because they hovered around an attractor state (mapped in EI vs. DI space), occasionally deviating from the attractor state defined by the Budyko curve (not necessary along the curve) due to a climatic variability or climatic extremes but ultimately returning to the Budyko curve. An ecological resilience would have occurred if, for example, the vegetation resisted change or if the vegetation community composition changed and shifted the weighted average stomatal conductance. We do not think we have evidence of ecological resilience in the data presented in this study. Ponce Campos et al. (2013) urged that the development of a predictive understanding of climatic threshold beyond which resilience will break down is needed to predict consequences of anticipated future climate change on water yields.

We used elasticity as a metric for resilience. We hypothesized that elastic catchments (e > 1) would shift along the Budyko curve and that inelastic catchments (e < 1) would deviate upward from the curve, yielding less water than predicted by the theoretical relationship between DI and EI. We also hypothesized that elastic catchments would have a diversity of forest types and ages such that they would have the capacity to adapt to changing climatic conditions and therefore would have small changes in EI. We found that different forest types responded differently to climate warming. Catchments with high elasticity experienced little to no changes in water yields, whereas catchments with low elasticity experienced unpredictably larger or smaller water yields.

Our results are distinct from recent papers that use a Budyko curve approach to examine climate change and its influence on water yield (e.g., Wang & Hejazi, 2011; Williams et al., 2012; Troch et al., 2013). We used existing empirical datasets from forested headwater catchments that were not affected by land cover or land use changes to draw inferences about how forest type and age influence water yield. For this reason, we could attribute changes in water yield to changes in water use by the forested ecosystem. These unique aspects of our study design permitted us to draw inferences about resilience of headwater forested catchments to climate warming and environmental and ecological factors that may influence this response.

Factors that influence elasticity

Both hydrological and ecological mechanisms may potentially contribute to forest expressions of elasticity in response to climate warming (i.e., an increase in the DI). Hydrological mechanisms involve changes in the accessibility of water storages for ET, whereas ecological mechanisms involve changes in forest composition, structure, and function that affect water use. Future research should focus on which mechanisms are likely to dominate under different conditions.

Hydrological factors influencing elasticity include P and ET. Total annual changes in precipitation were variable among the catchments (with some showing an increase, a decrease or no change); however, partitioning catchments according to the degree of change in precipitation did not have an effect on the relationship between dynamic deviation and either degree of warming or elasticity. In contrast, the timing or seasonality of P and ET within a year did have an effect. Gentine et al. (2012) and Williams et al. (2012) used a Budyko framework to show that strongly seasonal precipitation contributed to higher evaporative indices. Based on the geographic distribution of headwater catchments in this study, our findings suggest that the seasonality of P and ET may also explain elasticity in water-yield responses to climate, with smaller responses of EI to DI in catchments where precipitation has less seasonality. For example, the eastern catchments (CWT, DOR, ELA, FER, HBR, KEJ, MAR, TLW) generally had summer P, synchronized P and ET (Yokoo et al., 2008), transpiration limited more by atmospheric evaporative demand than by soil water availability, and/or shallow slopes with deeper soils where water residence times are relatively long (Voepel et al., 2011). These eastern catchments tended to have small changes in water yields relative to variation in energy inputs (especially CWT, ELA, HBR, MAR). A potential change in ET could have been masked by deep soils and high baseflow, but there did not seem to be a consistent pattern in properties among the eastern catchments (e.g., FER has shallow

soils, MAR has substantial loss of water to regional groundwater aquifers). The western catchments (AND, CAR, LVW, NWT, UPC) generally had winter-dominated P, desynchronized P and ET, transpiration limited more by soil water availability than by atmospheric evaporative demand, and/or steep slopes with shallow soils where water residence times are relatively short (McGuire et al., 2005). These western sites tended to have more water-yield change in response to variation in energy inputs (especially CAR, NWT, LVW, UPC).

Another hydrological factor influencing elasticity was altered access to physical storages of water (in ice, groundwater, etc.). The alpine sites (e.g., NWT and LVW) had among the lowest elasticity values and the most negative dynamic deviation values, indicating that these ecosystems had low resilience. Water yield at these sites likely responded strongly to climate warming through increased melting of the water stored in glaciers, permafrost, and seasonal snowpacks (Baron et al., 2009; Caine, 2011), as suggested by many studies (Barnett et al., 2008; Stewart, 2009; Trujillo et al., 2012).

Ecological factors also influence elasticity and water yield responses to climate warming. Our study catchments varied in their ecological properties, including phenology and the sensitivity of stomatal resistance to soil water availability and atmospheric evaporative demand (e.g., Ewers et al., 2006; Grant et al., 2009). In general, water yield tended to increase with warming at conifer catchments [Fig. 8; Table 1, but see comment on CWT 17 (ID #3a) below], perhaps because of stomatal control of transpiration or lagged phenologic response to increased soil moisture from snow/ice melt (Grier & Running, 1977; Chabot & Hicks, 1982). In contrast, water yield tended to decrease with warming at deciduous catchments, perhaps because trees were able to leaf out earlier in response to warming or because of species-specific responses of transpiration to atmospheric evaporative demand (Swank et al., 2001; Ford et al., 2011; Polgar & Primack, 2011). Mixed forests responded to warming in a manner consistent with the combined responses of conifer and deciduous forests.

We recognize the potential importance of forest age (e.g., Cornish & Vertessy, 2001), but we were constrained in our ability to assess the role of forest age in conferring hydrologic resilience because our catchments included few old forests. However, the oldest forest (~500 years) and younger more diverse forests had larger elasticity (e > 1), whereas the younger and less diverse forests exhibited smaller elasticity (e < 1). Among these younger forests, conifer forests appeared less able to adapt and take advantage of warmer conditions by increasing ET (thereby leading to larger water

yields), and deciduous forests appeared more able to adapt (therefore leading to smaller water yields) in these energy-limited sites. Carbon dioxide fertilization effects may also have influenced transpiration (Bolker *et al.*, 1995).

Forest catchments varied in their water-yield (EI) responses to changes in available energy (DI). In the alpine catchments, EI varied a great deal relative to changes in energy inputs (showing low elasticity) because transpiration is limited by dry, short summers. In these catchments, climate warming led to increased water yield because the ecosystems could not adjust over the short term and because stored water melted (we define this as no resilience). The conifer forests included catchments with the widest variation in EI, which varied considerably in response to changes in DI (showing low elasticity) perhaps because transpiration is limited by reduced vapor pressure gradients and/or soil water availability, and therefore is unresponsive to changes in temperature (less resilient). The deciduous forests included catchments where EI varied relatively little despite changes in energy inputs (showing high elasticity). Most of these forests experience wet summers, so transpiration is not limited by water, and leaf area, timing of leaf out and leaf fall can respond to interannual variation in temperature (more resilient). Counter to the general trend, the coniferous catchment at CWT [CWT 17 (ID #3a)] had greater elasticity than the deciduous catchment [CWT 18 (ID #3b)], likely because it had been cut and replanted with a conifer plantation 60 years ago and was still relatively young. Young conifer forests are less able to regulate water use than older conifers (Moore et al., 2004; Ford et al., 2011). In mixed forests, EI varied the least in response to changes in energy inputs (highest elasticity and resilience). Diverse forest types and older forest systems appeared to show greater hydrologic resilience, perhaps because older forests have been acclimated by past climate variations in DI and associated biophysical responses.

Management implications

A significant proportion of the water supply for human consumption originates from forested catchments (e.g., 53% in the US; Brown *et al.*, 2008), and these supplies are likely to be impacted by climate warming (Aber *et al.*, 1995). In addition to climate change effects, forest management activities (i.e., deforestation, reforestation and afforestation) may have significant consequences on the hydrological resilience of water yields (Fischer *et al.*, 2006). The direction of impact has been debated. For example, some argue that additional forest cover will reduce

water yield, whereas others suggest it will increase water yield by intensifying the hydrological cycle (Ellison *et al.*, 2012). Greater insight to links between climatic variability and forest water yields may help inform this debate.

We observed a significant nonlinear relationship between elasticity and dynamic deviation of water yield in response to climate warming at the 21 study sites. We found that sites with relatively modest climate warming had low elasticity and large negative dynamic deviations. Water yields from forested headwater catchments responded nonuniformly to climate warming. Elastic catchments (e > 1) that remained close to the theoretical Budyko curve in response to climate warming had predictable water-yield changes. In contrast, inelastic catchments (e < 1) showed substantial deviations from the Budyko curve in response to climate warming and had unpredictable water yield changes.

Our novel application of the Budyko curve suggests a direction for improving forest management strategies in the face of changing climatic conditions. For example, forest managers will likely want to prioritize forested catchments that are hydrologically resilient to climate warming because replicating naturally resilient ecosystems is so difficult. Furthermore, forest managers will likely need to consider forest type and age as factors that influence hydrologic resilience; further analysis is needed to detect and discriminate the influences of forest type and age on catchment water yields.

Conclusion

This study indicates that the Budyko framework, using meteorological and discharge data from gauged headwater catchments, may help predict changes in water balance partitioning in response to climate warming. Expert knowledge of the individual catchments indicates that both environmental factors (e.g., summer precipitation, summer length, and water residence time) and ecological factors (forest type and age) contributed to the observed variability in water yield responses to climate warming. Further research into these factors with longer datasets that include a broader range of forest types and age, factors that appear to influence elasticity, would help extend the findings of this article to ungauged headwater catchments.

Acknowledgements

We thank the University of Western Ontario International Research Award, NSERC Discovery Grant, and Canadian Network of Aquatic Ecosystem Services NSERC Strategic Network Grant for grants to IFC; the Network of Centres of Excellence Sustainable Forest Management for support that led to the creation of the HELP database for Canadian catchments; and the Long Term Ecological Research Network, US Forest Service, and US Geological Survey for access to the databases for US catchments. We also thank the US National Science Foundation and Long Term Ecological Research Network for support of the workshops that led to this collaboration. We gratefully acknowledge Robin Pike for insights about Carnation and Jennifer Knoepp for insights about Coweeta.

References

- Aber JD, Ollinger SV, Federer CA et al. (1995) Predicting the effects of climate change on water yield and forest production in the northeastern United States. Climate Research, 5, 207-222.
- Barnett TP, Pierce DW, Hidalgo HG et al. (2008) Human-induced changes in the hydrology of the western United States. Science, 319. 1080-1083.
- Baron JS, Schmidt TM, Hartman MD (2009) Climate-induced changes in high elevation stream nitrate dynamics, Global Change Biology, 15, 1777-1789.
- Bates BC, Kundzewicz ZW, Wu S, Palutikof JP (eds) (2008) Climate Change and Water. Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secre-
- Bolker BM, Pacala SW, Bazzaz FA, Canham CD, Levin SA (1995) Species diversity and ecosystem response to carbon dioxide fertilization; conclusions from a temperate forest model. Global Change Biology, 1, 373-381.
- Brand FS, Jax K (2007) Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object. Ecology and Society, 12, 23.
- Brown AE, Zhang L, McMahon TA, Western AW, Vertessy RA (2005) A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. Journal of Hydrology, 310, 28-61.
- Brown TC, Hobbins MT, Ramirez JA (2008) Spatial distribution of water supply in the coterminous United States. Journal of the American Water Resources Association, 44 1474-1487
- Budyko MI (1974) Climate and Life. Academic Press, New York.
- Caine N (2011) Recent hydrologic change in a Colorado alpine basin: an indicator of permafrost thaw? Annals of Glaciology, 51, 130-134.
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. Annual Review of Ecological and Systematics, 13, 229-259.
- Cornish PM, Vertessy RA (2001) Forest age-induced changes in evapotranspiration and water yield in a eucalypt forest. Journal of Hydrology, 242, 43-63
- Ellison D, Futter MN, Bishop K (2012) On the forest cover-water yield debate: from $demand-\ to\ supply-side\ thinking.\ \textit{Global\ Change\ Biology},\ \textbf{18},\ 806-820.$
- Ewers BE, Gower ST, Bond-Lamberty B, Wang C (2005) Effects of stand age and tree species composition on transpiration and canopy conductance of boreal forest stands. Plant, Cell and Environment, 28, 660-678.
- Ewers BE, Mackay DS, Samanta S (2006) Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. Tree Physiol-
- Fischer J, Lindenmayer DB, Manning AD (2006) Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment, 4, 80-86,
- Ford CR, Hubbard RM, Vose M (2011) Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. Ecohydrology, 4,
- Gentine P, D'Odorico P, Lintner BR, Sivandran G, Salvucci G (2012) Interdependence of climate, soil, and vegetation as constrained by the Budyko curve. Geophysical Research Letters, 39, L19404.
- Gerten D, Lucht W, Schaphoff S, Cramer W, Hickler T, Wagner W (2005) Hydrologic resilience of the terrestrial biosphere. Geophysical Research Letters, 32. L21408.
- Grant RF, Barr AG, Black TA et al. (2009) Interannual variation in net ecosystem productivity of Canadian forests as affected by regional weather patterns - a Fluxnet-Canada synthesis. Agricultural and Forest Meteorology, 149, 2022-2039.
- Grier CG, Running SW (1977) Leaf area of mature northwester coniferous forests: relation to site water balance. Ecology, 58, 893-899

- Gunderson LH (2000) Ecological resilience in theory and application. Annual Review of Ecological and Systematics, 31, 425-439.
- Hamon WR (1963) Computation of direct runoff amounts from storm rainfall. International Association of Scientific Hydrological Publication, 63, 52-62.
- Holling CS (1973) Resilience and stability of ecological systems. Annual Review of Ecological and Systematics, 4, 1-23.
- Holling CS (1996) Engineering resilience versus ecological resilience. In: Engineering Within Ecological Constraints (ed. Schulze P), pp. 31-44. National Academy Press, Washington, DC
- Jansen E, Overpeck J, Briffa KR et al. (2007) Palaeoclimate. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 433-497. Cambridge University Press, Cambridge, UK and New York, NY.
- Jones JA, Creed IF, Hatcher KL et al. (2012) Ecosystem processes and human influences regulate discharge response to climate change at long-term ecological research sites. BioScience, 62, 390-404.
- Karl TR, Melillo JM, Peterson TC (eds) (2009) Global Climate Change Impacts in the United States. Cambridge University Press, Cambridge, UK.
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature, 462, 1052-1055.
- Lu J, Sun G, McNulty SG, Amatya DM (2005) A comparison of six potential evapotranspiration methods for regional use in the southeastern United States. Journal of the American Water Resources Association, 41, 621-633
- McGuire KI, McDonnell II, Weiler M, Kendall C, McGlynn BL, Welker IM, Seibert I (2005) The role of topography on catchment-scale water residence time. Water Resources Research, 41, W05002.
- Milly PCD (1994) Climate, soil water storage, and the average annual water balance. Water Resources Research, 30, 2143-2156.
- Moore GW, Bond BJ, Jones JA, Phillips N, Meinzer FC (2004) Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA. Tree Physiology, 24, 481-491.
- National Research Council (2008) Hydrologic Effects of a Changing Forest Landscape. Committee on Hydrologic Impact of Forest Management (Barten PK (Chair), Achterman GL, Brooks KN, Creed IF, Ffolliott P, Hairston-Strang A, Jones JA, Kavanaugh MC, Macdonald L, Smith RC, Tinker DB, Walker SB, Wemple BC, Weyerhaeuser GH). Water Science and Technology Board, Division of Earth and Life Studies, National Research Council of the National Academies. The National Academies Press, Washington, DC.
- Poff NL, Allan JD, Bain MB et al. (1997) The natural flow regime: a paradigm for river conservation and restoration. BioScience, 47, 769-784.
- Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. New Phytologist, 191, 926-941.
- Ponce Campos GE, Moran MS, Huete A et al. (2013) Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature, 494, 349-352
- Potter NJ, Zhang L, Milly PCD, McMahon TA, Jakeman AJ (2005) Effects of rainfall seasonality and soil moisture capacity on mean annual water balance for Australian catchments. Water Resources Research, 41, W06007.
- Sankarasubramanian A, Vogel RM, Limbrunner JF (2001) Climate elasticity of streamflow in the United States, Water Resources Research, 37, 1771-1781
- Schaake JC (1990) From climate to flow. In: Climate Change and U.S. Water Resources (ed. Waggoner PE), pp. 177-206. John Wiley, New York.
- Stewart IT (2009) Changes in snowpack and snowmelt runoff for key mountain regions. Hydrological Processes, 23, 78-94.
- Swank WT, Vose JM, Elliott KJ (2001) Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. Forest Ecology and Management, 143, 163-178.
- Troch PA, Carrillo G, Sivapalan M, Wagener T, Sawicz K (2013) Climate-vegetationsoil interactions and long-term hydrologic partitioning: signatures of catchment co-evolution. Hydrology and Earth System Sciences, 17, 2209-2217.
- Trujillo E, Molotch NP, Goulden ML, Kelly AE, Bales RC (2012) Elevation-dependent influence of snow accumulation on forest greening. Nature Geoscience, 5,
- Voepel H, Ruddell B, Schumer R et al. (2011) Quantifying the role of climate and landscape characteristics on hydrologic partitioning and vegetation response. Water Resources Research, 47, W00J09.
- Walther G, Post E, Convey P et al. (2002) Ecological responses to recent climate change. Nature, 416, 389-395

- Wang DB, Hejazi M (2011) Quantifying the relative contribution of the climate and direct human impacts on mean annual streamflow in the contiguous United States. Water Resources Research, 47, W00]12.
- Wang T, Istanbulluoglu E, Lenters J, Scott D (2009) On the role of groundwater and soil texture in the regional water balance: an investigation of the Nebraska Sand Hills. USA. Water Resources Research, 45, W10413.
- Williams CA, Reichstein M, Buchmann N et al. (2012) Climate and vegetation controls on the surface water balance: synthesis of evapotranspiration measured across a global network of flux towers. Water Resources Research, 48, W06523.
- Yao H (2009) Long-Term study of lake evaporation and evaluation of seven estimation methods: results from Dickie Lake, South-Central Ontario, Canada. *Journal of Water Resource and Protection*, 2, 59–77.
- Yokoo Y, Sivapalan M, Oki T (2008) Investigating the roles of climate seasonality and landscape characteristics on mean annual and monthly water balances. *Journal of Hydrology*, 357, 255–269.
- Zhang L, Dawes WR, Walker GR (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. Water Resources Research, 37, 701–708.

Supporting Information

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

Table S1. Temperature (T), precipitation (P), potential evapotranspiration (PET, estimated using the Hamon method) and discharge (Q) from catchment 5-water-year cool periods (period with lowest average temperature) and 5-water-year warm periods (period with highest average temperature).