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Review

Long-term hydrological response to forest harvest during seasonal low flow: Potential implications for current forest practices☆

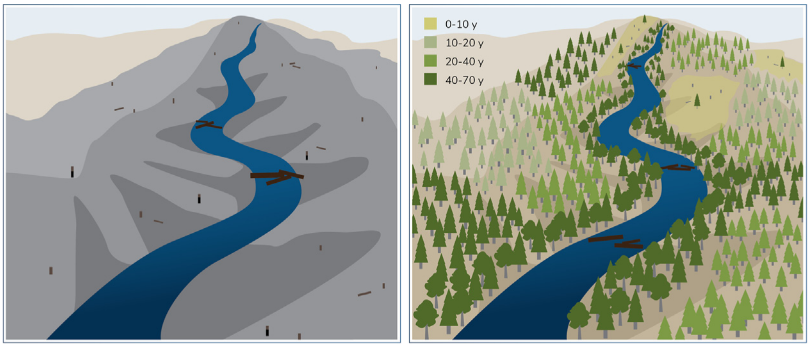
Ashley A. Coble [a,⁎], Holly Barnard [b], Enhao Du [c], Sherri Johnson [d], Julia Jones [e], Elizabeth Keppeler [f], Hyojung Kwon [g], Timothy E. Link [c], Brooke E. Penaluna [d], Maryanne Reiter [h], Mark River [h], Klaus Puettmann [g], Joseph Wagenbrenner [i]

[a] National Council for Air and Stream Improvement, Inc., 227 NW Third St., Corvallis, OR 97330, USA
[b] Department of Geography, Institute of Arctic and Alpine Research University of Colorado, Boulder, CO, USA
[c] College of Natural Resources, University of Idaho, Moscow, ID, USA
[d] USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR, USA
[e] Geography CEOAS, Oregon State University, Corvallis, OR, USA
[f] USDA Forest Service, Pacific Southwest Research Station, Fort Bragg, CA, USA
[g] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA
[h] Weyerhaeuser Company, Springfield, OR, USA
[i] USDA Forest Service, Pacific Southwest Research Station, Arcata, CA, USA

HIGHLIGHTS

- Climate-related low flow declines may also be influenced by forest management.
- Few studies describe multi-decade effects of forest management on streamflow.
- We assembled catchment studies of long-term effects of harvest (>10 years).
- We define 3 periods of expected low flow responses to forest regrowth after harvest.
- Decreased low flow was observed years after harvest in 16 of 25 catchments.

GRAPHICAL ABSTRACT



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ABSTRACT

Seasonal changes in the magnitude and duration of streamflow can have important implications for aquatic species, drinking water supplies, and water quality. In many regions, including the Pacific Northwest (U.S. and Canada), seasonal low flow is declining, primarily due to a changing climate, but is also influenced by urbanization, agriculture, and forestry. We review the responses of seasonal low flow, catchment storage, and tree-water relations to forest harvest over long timescales and discuss the potential implications of these responses for current forest practices and aquatic biota. We identify three distinct periods of expected low flow responses as regrowth occurs following forest harvest: in the first period an initial increase in low flow can occur as replanted stands regenerate, in the second period low flow is characterized by mixed and variable responses as forests become established, and in the third period, which follows canopy closure, low flow declines may occur over long

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☆ All authors contributed equally to this manuscript; author order is alphabetical (with exception of first author).Conceptualization: AAC, SJ, MR; Supervision: AAC; Writing- Original draft preparation: all authors drafted original text: Writing- Reviewing and Editing: all authors.

⁎ Corresponding author.
E-mail address: acoble@ncasi.org (A.A. Coble).

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timescales. Of 25 small catchments with ≥10 years post-harvest data, nine catchments had no change or variable low flow and 16 catchments experienced reduced low flow years after harvest. The retention of riparian buffers, limited size of harvest units, and adherence to reforestation requirements have altered the contemporary forest landscape relative to historical forest practices, but data documenting multi-decadal hydrological responses to current harvest practices is limited. Our review suggests that the magnitude of low flow responses attenuates downstream as a broader mosaic of stand ages occurs and multiple hydrological periods are represented. Declines were not observed in the seven large catchments reviewed. The consequences of low flow declines for aquatic biota are not well understood, but where data do exist aquatic biota have not been adversely affected. We identify priorities for future research that will aid in improving predictions of low flow responses to harvest as forests regenerate.

Contents

1. Introduction

Due to the growing concern of the consequences of declining low seasonal streamflows, there is a need to better understand the role of managed forest landscapes and the degree to which past and contemporary management practices may affect streamflow. The magnitude and duration of low seasonal streamflow can have direct and indirect effects on aquatic species, drinking water supplies, recreation and water quality (Power et al., 2008; Clifton et al., 2018). Climate change is expected to further reduce seasonal low flows in 1/3 of global rivers (van Vliet et al., 2013). Low flows in the Pacific Northwest have declined over recent decades primarily associated with changes in climate via declines in both summer precipitation and snowpack, acceleration of snowmelt, and increased irrigation and drinking water extraction (Luce and Holden, 2009; Kormos et al., 2016; Holden et al., 2018; Mote et al., 2018). While climate is considered the dominant control on the volume and timing of summer discharge (Burt et al., 2015; Li et al., 2018; Ficklin et al., 2018), land management from urbanization (Cuo et al., 2009), dam regulation (Asarian and Walker, 2016), agriculture (van Kirk and Naman, 2008) and forestry (Johnson, 1998; Perry and Jones, 2017; Gronsdahl et al., 2019) are also influential.

Much of our understanding of forest hydrology has been defined by paired catchment experiments (Bosch and Hewlett, 1982, $n > 166$) specifically designed to isolate the effects of forest cover change on hydrology by accounting for year to year variation in climate. This robust approach is feasible only for small catchment scales; paired catchment studies have ranged from 0.009 to 1272 km^2 (mean = 9.8 km^2, median = 0.4 km^2; Bosch and Hewlett, 1982; Brown et al., 2005). The smallest catchment scale is characterized by highly variable hydrological, chemical, and biological factors, is more coupled to hillslope and groundwater processes, and supports greater biodiversity than downstream systems (Gomi et al., 2002; Meyer et al., 2007; Rolls et al., 2019; Coble et al., 2019). However, a disconnect remains between the scale of small catchment experimental studies and the implications for downstream responses (i.e., Gomi et al., 2002; Blöschl et al., 2007). Hydrological responses are most sensitive at small spatial and temporal scales and cannot simply be scaled up (Gomi et al., 2002). Within large catchments (mean = 177,716 km^2, median = 8940 km^2, range = 1033 to 3,702,481 km^2; Li et al., 2017; Zhang et al., 2017), the initial direction of hydrological responses was consistent with that observed in smaller catchments (i.e., increased runoff after overstory removal), but the magnitude of the responses attenuated with increasing catchment size (Li et al., 2017; Zhang et al., 2017). Similarly, climate related changes in hydrology attenuate as water flows downstream to larger river networks (Chezik et al., 2017). This recent emphasis on larger catchments has greatly improved our understanding of scaling in the near-term after forest harvest (Li et al., 2017; Zhang et al., 2017), but how scaling and the distribution of successional stands at various forest ages influences longer-term hydrologic responses to the overstory removal and revegetation remains unclear.

The immediate flow responses (<5–10 years) have been well documented (Fig. 1) following harvest and typically demonstrate an increase in low flows(Harr and Krygier, 1972; Keppeler and Ziemer, 1990; Surfleet and Skaugset, 2013). Typical harvest rotations range from ~40

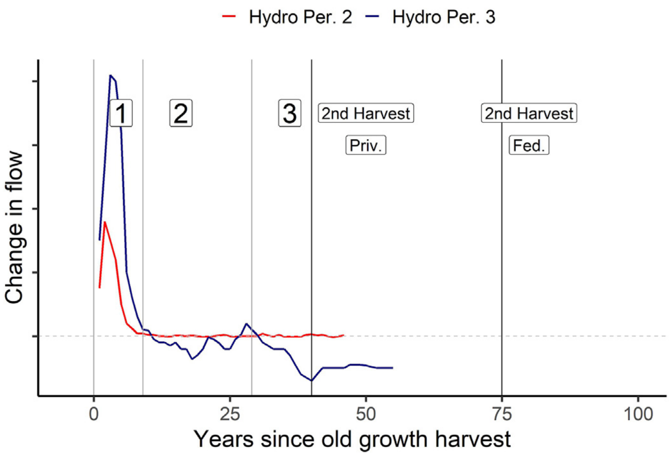

Fig. 1. Distinct low flow (Jul - Sep) hydrological periods as defined in Table 1 shown using theoretical responses based on previously published data (Jones and Post, 2004; Perry and Jones, 2017). The red line depicts a theoretical low flow hydrological response that remains in hydrological period 2 for the duration of the record. The blue line depicts a theoretical low flow hydrological response that experiences all three hydrological periods with gray vertical lines showing the transition among periods. Black vertical lines indicate approximate rotation age when harvest is expected on private and federal land. Horizontal dashed line represents no change with responses above indicating increases and responses below representing decreases. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to 60 y on private industrial forests and ~ 80 y on federal forests in the Pacific Northwest. Much less is known about the hydrological responses as forests regrow (Troendle et al., 2010). Where studies continue >10–20 years after harvest, variable low flow responses have been observed including: increases (Hicks et al., 1991; Jones and Post, 2004), no change or return to baseline (Troendle and King, 1985; Jones and Post, 2004; Zhang and Wei, 2014), and declines (Reid, 2012; Perry and Jones, 2017; Gronsdahl et al., 2019). Streamflow changes during forest regeneration have been attributed to reduced evapotranspiration (ET) rates immediately after harvest or greater transpiration rates of young, second growth trees relative to old-growth trees as forests regrow (Moore et al., 2004; Brown et al., 2005). Low seasonal streamflow responses may also be affected by shifts in tree species composition that affects ET rates (Hicks et al., 1991; Moore et al., 2004) or shifts in the timing of snowmelt (Gronsdahl et al., 2019).

Here, we describe low flow responses to past forest practices over long timescales by reviewing the long-term (>10 years) low flow responses across 25 catchments from the U.S. and Canada and presenting detailed results from three case studies (Section 2). In addition to streamflow, we review several hydrological relationships in the forest water budget to better understand the potential mechanisms that affect these low flow responses, and how they may vary with forest stand characteristics (Section 3). Specifically, within this section we review subsurface catchment storage (Section 3.1) and evapotranspiration at ecosystem scales (Section 3.2) as well as tree and stand levels (Section 3.3). We discuss consistencies and inconsistencies of prior treatments in low flow studies with current forest practices to better understand their potential effects (Section 4.1). Additionally, given the importance of the summer flow regime on biota, we discuss potential effects of low flow on in-stream biota (Section 4.2). We conclude by identifying next steps and remaining questions (Section 5).

2. Low flow hydrological responses over successional time

2.1. Defining periods of hydrological response

Low flow is often used interchangeably with the term baseflow. However, baseflow conditions are defined as streamflow primarily sourced from deep and shallow subsurface storage (Ward and Robinson, 1990) and can occur in between precipitation events at any time of the year. In the Pacific Northwest, low flow is defined as an annual phenomenon that occurs during the prolonged dry period, characteristic of the Mediterranean climate experienced in the region (WMO, 1974; Smakhtin, 2001). Elsewhere, the timing of the low flow season varies with local climatic conditions, and can occur in winter or summer (e.g., Cheng, 1989).

We define three distinct time periods following forest harvest to depict the expected low-flow hydrological responses as forest regrowth occurs (Table 1; Fig. 1; Brown et al., 2005; Du et al., 2016). Hydrological period 1 refers to the immediate response to forest harvest and is often a period of substantial baseflow enhancement as canopy leaf area index (LAI), ET, and canopy interception are all reduced following the removal of overstory vegetation. On intensively managed forests, tree planting and herbicide application occurs during this hydrological period to promote forest regrowth. These practices have replaced large broadcast burns and seeding that typically occurred decades ago in the Pacific Northwest. As planted trees, seeds, or naturally regenerating trees grow, and LAI increases, transpiration, canopy interception, and losses by evaporation and sublimation increase. These changes contribute to hydrological period 2, which can include small, mixed, and variable low flow responses as regenerating stands undergo rapid canopy development (Table 1). Continued growth creates dense overstory vegetation as canopy LAI reaches a maximum and ET is elevated, which can coincide with hydrological period 3. This period is defined by declines in low flow (Table 1). Pre-commercial thinning removes small trees, not yet of commercial size, to reduce stand density and improve growth of remaining trees, and may occur during hydrological period 2 or 3. Eventually subsequent harvest commonly occurs in stands approximately 40 to 60 years old on private industrial forests and up to 80 years old on federal land (Fig. 1). Harvest may include clearcuts on intensively managed forests or commercial thinning of large merchantable timber on federal land.

2.2. Literature review methods

To understand the occurrence of these three hydrological periods we performed a literature review of long-term hydrological responses to forest harvest. Long-term hydrological responses were not evaluated in earlier low flow reviews due to the limited duration of data at the

Table 1
Three distinct hydrological periods for each forest stage during the seasonal low flow period (e.g., Jul-Sep) as depicted in Fig. 1. Canopy characteristics (leaf area index (LAI) and evapotranspiration (ET)) of each period are based on successional metrics for annual responses as described by Brown et al. (2005) and Du et al. (2016) and may be particularly relevant when the growing season corresponds with the seasonal low flow period.

Period	Managed forest stage	Hydrological response	Canopy characteristics
1	Regeneration of stand (green up period and establishment)	Substantial low flow enhancement that declines as the period progresses	canopy LAI minimal, low ET, reduced canopy interception
2	Rapid canopy development	Small, mixed, variable low flow effects, initial return to baseline occurs within this transitional period but may not stabilize	canopy LAI increases, increasing ET
3	Continued growth of overstory canopy	Low flow declines	canopy LAI reaches a maximum, high ET
Harvest	Harvest of overstory canopy in uplands	Substantial low flow enhancement	

time (≤8 years post-harvest; Austin, 1999). To extend their findings, we searched for updates on low flow responses for the catchments where low flow responses were previously described (Austin, 1999; Pike and Scherer, 2003) as well as searching for keywords "forest harvest" and "low flow" in literature using search engines Google Scholar and Web of Science. Studies with a minimum of 10 years of post-harvest seasonal low flow responses for the U.S. and Canada were retained (Table 2).

Calculations of seasonal low flow response to harvest use changes in the reference catchment to control for year to year climatic fluctuations. Therefore, any synthesis will be limited by the mathematical reality that relative changes among catchments cannot be calculated as flow in the reference catchment approaches zero (the denominator). When calculations are possible, large relative changes may represent a small absolute change (Austin, 1999; Pike and Scherer, 2003; Jones and Post, 2004). To address this challenge, multiple metrics have been developed to quantify low flow including: the number of low flow days each year (the number of days that daily discharge was less than a defined threshold) (Harr, 1980; Bultot et al., 1990; Keppeler and Ziemer, 1990; Stednick, 2008; Perry and Jones, 2017; Gronsdahl et al., 2019), water yield during a single, typically dry month or multiple dry months (Hicks et al., 1991), relative and/or absolute differences in daily minimum or mean values in relation to a reference or pre-treatment conditions (Harris, 1977; Jones and Post, 2004; Perry and Jones, 2017), and metrics derived from flow duration curves (e.g. Q95 or baseflow index (baseflow/annual flow); Smakhtin, 2001). Without consistent metrics or enough information in the original studies to calculate a similar metric, we cannot summarize low flow responses across studies. Rather, we focus on categorizing the type of hydrological response and its duration.

In addition to evaluating studies of small catchments, we also reviewed studies from larger catchments that rely on the use of advanced statistical methods in combination with graphical methods (flow duration curves) to evaluate the role of forest harvest, along with other disturbances (Zhang and Wei, 2012; Buttle and Metcalfe, 2000; Zhang et al., 2017). We extracted a list of large catchments within a recent review of annual hydrological response (Zhang et al., 2017) and then searched for catchments where long-term low flow responses to harvest were reported.

2.3. Results: long-term low flow hydrological responses

We identified 25 small harvested catchments ranging in size from 0.10 to 33.9 km^2, with 17 to 100% of overstory vegetation removed (Table 2). Stand age of reference catchments was older than 80 years in fourteen catchments, younger than 80 years in nine catchments, and was not reported in two catchments (Table 2). Riparian buffers were retained in only five catchments. Hydrological period 1 resulted in one or more years of increased low flow in 21 of the 25 small catchments reviewed. The duration of increased low flow ranged from 0 to 40 years, with a mean and median of 8.8 years and 8 years, respectively.

The duration of hydrological period 2, ranged from zero (H.J. Andrews; Perry and Jones, 2017) to 42 years (Harder et al., 2015). In 6 of 25 catchments evaluated, no detectable change occurred through the end of the record, with the longest record extending to 42 years post-harvest (Harder et al., 2015). Three of 25 catchments had variable responses through the end of the reporting period extending up to 35 years post-harvest (Keppeler, 1998; Jones and Post, 2004). Collectively, these 9 studies represent a range in catchment size from 0.16 to 33.9 km^2 with harvest area comprising 17 to 100% of the catchment (Table 2).

Low flow declines relative to the control catchment define hydrological period 3. These declines were observed in 16 harvested catchments of 25 evaluated (64%) and represent a relatively short duration (3 year duration occurring 43 to 46 y post-harvest, Coyote Creek; Perry and Jones, 2017) to a much longer duration (20 years occurring 27 to 47 years post-harvest, H.J. Andrews, Hicks et al., 1991; Perry and Jones, 2017). This response was observed in 0.10 to 4.5 km^2 catchments with 25 to 100% of the catchment harvested (Table 2).

We also identified and evaluated seven large-scale catchment studies from the U.S. and Canada that specifically evaluated the role of forest harvest on low flows. These catchments ranged in size from 401 to 3500 km^2 with 4.9 to 62.2% of the area affected by forest disturbance (Supplemental Table 1). In addition to harvest, the forest disturbances included harvesting, fire, and mountain pine beetle outbreaks, with disturbance areas often equated to equivalent cumulative clearcut area. Periods of record extended from six (Buttle and Metcalfe, 2000) to >50 years (Zhang and Wei, 2012; Zhang and Wei, 2014; Li et al., 2018). Three of these seven catchments reported an increase in low flow responses over time (6 y to 59 y records) while the other four reported no change in low flows (6 y to 50 y records). However, declines in seasonal low flow, which are characteristic of hydrological period 3, were not observed in any of these.

2.4. Case studies

2.4.1. Case study I: Caspar Creek, California, USA

Two Caspar Creek second-cycle harvest experiments enhanced summer low flows beginning the first year after the onset of logging (~80 year old stands), but the magnitude and duration of flow increases differed due to silvicultural methods. Low flow declines were observed 15 to 30 years after harvest in the South Fork catchment, while in the North Fork catchment increases remained 12 years after harvest. The Caspar Creek Experimental Watersheds are located along California's north coast (39.35° N, 123.73°W; Fig. 2) approximately 7 km from the ocean and occupy the headwaters of this coastal catchment. Elevations range from 40 to 322 m. The terrain is characterized by moderately steep hillslopes and steep inner gorges underlain by sandstones and shales of the Coastal belt of the Franciscan Complex. Mean annual precipitation (1962–2017) is 1200 mm, primarily received as rainfall, with approximately half becoming runoff. Mean minimum flows, from July through September, are 2.2 mm per month.

Rainfall and runoff gauging was initiated in 1962, six decades after the original coast redwood and Douglas-fir forest had been clear cut and burned. The 4.73 km^2 North Fork initially served as a reference catchment while second-cycle selection harvest occurred on the 4.24 km^2 South Fork from 1967 to 1973. Partial clearcutting occurred on sub-catchments in the North Fork from 1985 to 1992. Sub-catchments were either retained as controls or clearcut with 15 to 46 m wide riparian buffers retained along streams with aquatic organisms (Reid, 2012). Subsequent broadcast burning and pre-commercial thinning in the clearcut units as recently as 2001, reduced basal area by ~75% and enhanced low flow (Keppeler et al., 2009).

On the South Fork where selection harvest and tractor logging occurred, increased low flows persisted 5 years after harvest was completed (hydrological period 1) and were largest during and after drought years (Keppeler and Ziemer, 1990). During this period, days with flows <0.115 mm day^{-1} occurred 40% less frequently. The maximum proportional increase in summer flow volumes (55%, 0.079 mm day^{-1}) was observed 5 years post-harvest after the severe drought of 1976 to 1977. For the next decade (hydrological period 2), effects were mixed. Reid (2012) used an antecedent precipitation model to assess long-term low flow trends and found that August and September daily flows became consistently lower than expected 15 to 30 years after harvest with the largest decrease (48% of expected flow, 0.016 mm day^{-1}) occurring 21 years after harvest. Late-summer flows then returned to pre-treatment levels through post-harvest year 36 (Reid, 2012).

Partial clearcutting on the North Fork resulted in larger, more persistent low flow enhancements despite similar wet-season responses (Keppeler, 1998). Analysis of minimum mean daily flows demonstrated an increase in minimum flow after only 12% of the catchment was clearcut. The maximum increase in the North Fork

Table 2
Approximate duration of response (years post-harvest) for each low flow hydrological period. Catchments with at least 10 years of post-harvest data from the U.S. and Canada were included. Catchment responses are grouped by their long-term response: 1) variable response in hydrologic period 2, 2) no change in hydrological period 2, or 3) decrease in hydrologic period 3. Note different low flow metrics, different statistical analyses, and grouping of post-harvest years affect the duration of response for each study. The magnitude of response is not provided here because many different low flow metrics were used across the studies. *indicates additional harvesting occurred within the reported post-harvest record.

Catchment ID	Size (km^2)	Forest cover removed (%)	Riparian buffer (Y/N)	Stand age (y) at time of treatment		Hydrologic Period 1 Years of increase	Hydrologic Period 2 Years of no change or variable response	Hydrologic Period 3 Years of decrease	Citation
				Trt.	Ref.				
						Variable hydrologic period 2			
NC COW7	0.59	100	N (not described)	50	75	1 to 5	6 to 20 (variable)		Jones and Post (2004)
NH HBR2	0.16	100	N	27	64	1 to 10	11 to 35 (variable)		Jones and Post (2004)
CA Caspar* NF	4.73	12 (1985–6) 38 (1989–92)	Y; 15 to 46 m 50% retention (>10 ha)	80	–	1 to 12	TBD	TBD	Keppeler (1998)
						No change in hydrologic period 2			
NC COW37	0.44	100	N (not described)	35	75	1 to 5	6 to 35 (no change)		Jones and Post (2004)
OR COY2	0.68	30	N (not described)	150–350	150–350	1 to 9 - unable to determine from information available (large data gaps)	30 to 43		Perry and Jones (2017)
BC Camp Creek	33.9	27	not described	mature (>60)	40–60	1 to 6			Cheng (1989)
							1 to 18 (no change)		Moore and Scott, 2005
NH HBR4		100	Y; 10 m	32	64	1 to 15	16 to 35 (no change)		Jones and Post (2004)
AB Cabin Creek	2.12	21	n/a; cut blocks away from stream	not described		1 to 8			Swanson et al., 1986
							1 to 33 year record (no sig. change points or trends)		Harder et al., 2015
AB Twin Creek	2.80	17	n/a honeycomb treatment	not described			1 to 42 (no sig. change points or trends)		Harder et al., 2015
						Decrease in hydrologic period 3			
OR AND1	0.96	100	N	450	500	1 to 8	9 to 26	27 to 47	Perry and Jones (2017)
						1 to 5	6 to 30	31 to 35	Jones and Post (2004)
						1 to 3	4 to 5	6 to 22	Hicks et al. (1991)
OR AND6	0.13	100	N	125	150	1 to 20		21 to 38	Perry and Jones (2017)
						1 to 25	26 to 30 years	Not observed	Jones and Post (2004)
OR AND7*	0.15	60 (1974); 40 (1984)	N	125	150	1 to 5	6 to 17 (2nd harvest in year 9)	18 to 38 (thinning in year 26) since initial treatment)	Perry and Jones (2017)
OR AND10	0.10	100	N	125	500	1 to 12	5 to 21	22 to 38	Perry and Jones (2017)
						1 to 10			Jones and Post (2004)
OR AND3	1.01	33	N (not described): unclear - whether patch cut stream-adjacent	450	500	1 to 14	15 to 33	34 to 50	Perry and Jones (2017)
						1 to 15	16 to 25	Not observed	Hicks

(continued on next page)

Table 2 (*continued*)

Catchment ID	Size (km^2)	Forest cover removed (%)	Riparian buffer (Y/N)	Stand age (y) at time of treatment		Hydrologic Period 1 Years of increase	Hydrologic Period 2 Years of no change or variable response	Hydrologic Period 3 Years of decrease	Citation
				Trt.	Ref.				
									et al. (1991)
OR COY1	0.69	50	Not described	150–350	150–350	1 to 9		30 to 43 [no record from 10 to 29]	Perry and Jones (2017)
OR COY3	0.49	100	N	120	145	1 to 9	[no record from 10 to 29]	30 to 42	Perry and Jones (2017)
OR Needle Branch	0.71	100	N	110	110	1 to 10 1 to 5	[not evaluated]	41 to 44	Jones and Post (2004) Segura et al., 2020 Harr and Krygier, 1972
OR Deer Creek	3.04	25	Y; 15 to 30 m	110	110	2, 5	[not evaluated]	41 to 52	Segura et al., 2020 Harr and Krygier, 1972
CA Caspar SF	4.24	5 (1967); 67 (1971–73)	N	~85	~65	1 to 7	8 to 14	15 to 30	Reid (2012) Ziemer (1981)
NC COW13	0.16	100	N	12	75	–	1 to 20	21 to 25	Jones and Post (2004)
WV FER1	0.30	100	N	50	95	1 to 40	Not observed	41 to 45	Jones and Post (2004)
WV FER7	0.29	100	N	56	95	1 to 5	6 to 25	26 to 30	Jones and Post (2004)
NH HBR5	0.22	100	N	45	64	1 to 10	11 to 15	16 to 20	Jones and Post (2004)
BC Dennis	3.73	52	Y; 5 to 10 m on streams >1.5 m bankfull width	153	130		1 to 8 (no change)	9 to 17	Gronsdahl et al. (2019)
BC 241Cr	4.50	47	Y; 5 to 10 m on streams >1.5 m bankfull width	145	130			1 to 10 (ongoing logging for 15y prior)	Gronsdahl et al. (2019)

(287%, 0.04 mm day^{-1}) occurred 7 years after the onset of logging, which was also the year logging was completed. Comparatively, the 7-year mean increase for the South Fork was 28% (0.02 mm day^{-1}), which was much lower than the 148% (0.04 mm day^{-1}) increase for the North Fork during the initial 12-year period of stand regeneration.

In both harvest experiments, initial low flow increases after logging were attributed to reduced transpiration rates, while wet-season discharge increases were attributed primarily to reduced interception. We hypothesize that residual trees in the selectively-logged South Fork stands used local surplus soil moisture more readily than on North Fork sub-catchments where trees in uncut patches were not able to access elevated soil moisture in the clearcut areas, thus magnifying and prolonging the streamflow enhancements on the North Fork. A recent comparison of precipitation and streamflow anomalies suggests that timber harvest may have initially ameliorated drought effects in 1976–1977, but later regeneration intensified the magnitude of streamflow decreases during the 2014 drought (Keppeler and Wagenbrenner, 2018). Concurrently with this most recent drought, both North Fork and South Fork exhibited summer flow decreases relative to rainfall. Analyses are ongoing to determine how this apparent trend may be affected by forest conditions and climatic trends.

2.4.2. Case study II: H.J. Andrews and South Umpqua Experimental Forests, Oregon, USA

Long-term streamflow records extending 38 to 50 years post-harvest from paired catchment experiments in the Cascade Range of Oregon demonstrate persistent summer low flow decreases resulting from the replacement of native mature and old-growth forest (reference catchments) with regenerating Douglas-fir plantations (treated catchments) (Perry and Jones, 2017). Relative differences in low streamflow were calculated for eight pairs of treated and reference catchments. Five paired treatments were located in the H.J. Andrews Experimental Forest (122.25°W, 44.2°N; Fig. 2) in the Willamette National Forest; these catchment pairs ranged from 0.10 to 0.96 km^2 in size, from 460 to 1190 m in elevation, and prior to treatments, all catchments contained 130 to 500 year old post-fire Douglas-fir forests. An additional three treatments were located in the South Umpqua Experimental Forest (Coyote Creek), (122.70°W, 43.22°N) in the Umpqua National Forest; these catchment pairs ranged from 0.49 to 0.69 km^2 in size, from 730

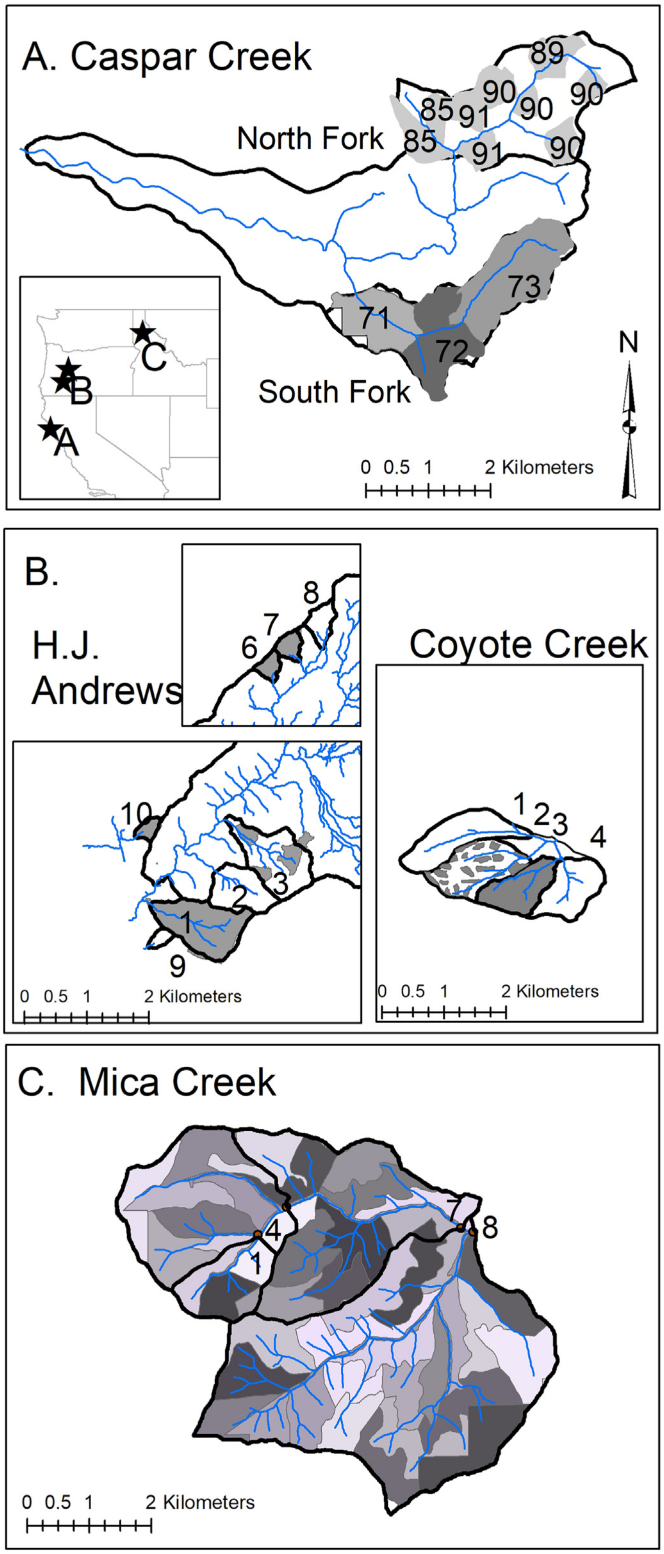

Fig. 2. Study site maps for the three case study catchments: A. Caspar Creek, California; B. H.J. Andrews and South Umpqua Experimental Forests, Oregon; C. *Mica* Creek Experimental Watershed, Idaho. Gray shading indicates locations of harvest. Year of harvest is identified in panel A. In panel B Coyote Creek 1 was a treated watershed (50% thinning). Shading in panel C represents modeled harvest units for a 40 year rotation for a privately managed working forest. Streams are shown in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to 1065 m in elevation, and prior to treatments, all catchments contained 200- to 300 year old post-fire mixed conifer forests. Roads were also installed for six of the eight treatments. Four treated catchments were entirely (100%) clearcut in a single entry with two of these subsequently broadcast burned. Two treated catchments included patch cuts that totaled 25 to 30% of the catchment area, with one also broadcast burned. A single treated catchment received 50% overstory selective cut in a single entry. One treated catchment included multiple entries with the entire catchment clearcut during the second entry, 10 years after the first entry. Broadcast burning followed the first entry, and 12% of the basal area was more recently thinned. No other catchments received additional management activities in the post-harvest period (i.e., pre-commercial thinning). No riparian buffers were retained in clearcut treatments, and following harvest all treated catchments were planted with Douglas-fir seed. As of the most recent measurement period (2007 to 2010), the forests in the reference catchments had basal area of 66 to 89 m^2 ha^{-1}, and the regenerating post-harvest Douglas-fir stands were 34 to 40 years old with basal areas of 27 to 35 m^2 ha^{-1}. Mean annual precipitation is 2300 mm at the H.J. Andrews and 1020 mm at the South Umpqua National Forest, with the majority (>75%) of precipitation received from November to April. The H.J. Andrews EF catchments have a seasonal snowpack above an elevation of 800 m, occurring in six of its eight catchments, but snow is rare in the South Umpqua catchments.

In the first 10 years after 150 to 500 year old forests were clearcut with no riparian buffers, large streamflow increases were recorded in the summer low flow period for the first 10 years after harvest (hydrological period 1). Summer streamflow decreases (hydrological period 3) appeared when plantation forests reached 15 years of age, and by 25 years of age, mean daily flow in summer (June through September) in catchments with plantation forests had declined by up to 50% (~0.06 mm d^{-1} Coyote Creek; ~0.32 mm d^{-1} HJ Andrews) relative to the reference catchments with 150- to 500-year-old forests. Only one catchment, which was 30% patch-cut, did not have long-term decreases in post-harvest years 30 to 43 (COY2, Table 2). The duration of summer streamflow decreases (defined as the difference in the number of days below the first percentile in catchments with plantations vs. reference catchments) was greater during dry compared to wet summers, at low compared to high elevation, and at the more southerly, drier South Umpqua compared to the H.J. Andrews (Perry and Jones, 2017). The 50% thinning treatment implemented in Coyote Creek WS1 decreased by 25% (~0.028 mm d^{-1}). Pre-commercial thinning (12% basal area removal) of the 15 to 25 year old plantation in Andrews WS7 did not affect summer streamflow declines.

2.4.3. Case study III. Mica Creek Experimental Watersheds, Idaho, USA

Eighty years of simulated low flow changes for an interior Pacific Northwest catchment indicate that the long-term trends and low-flow declines observed at the small catchment scale and in catchments with limited successive disturbances may not manifest at larger scales and instead may exhibit low flow increases over the long term. These responses would occur in landscapes comprised of a mosaic of stand ages, and actual changes in low flows would be primarily a function of the proportion of a given catchment in different age classes for fixed climate conditions. Simulated low flow changes reveal persistent low flow declines when the entire second-growth catchment is harvested at once. Conversely, physically-based simulations suggest persistent low flow increases for 40- and 80-year rotation harvests following second-growth harvest (Fig. 3). Low flow variability was greatest at smaller scales and attenuated at larger scales with a greater diversity of stand ages. Relative low flow differences were calculated for four nested catchments at the Mica Creek Experimental Watershed (MCEW) in northern Idaho (116.25°W, 47.17°N; Fig. 2). Catchments range from 1.39 to 26.82 km^2 in size, from 1008 to 1612 m in elevation (Hubbart et al., 2007), and prior to simulated treatments all catchments were assumed to contain ~70 year old second growth mixed conifer forests

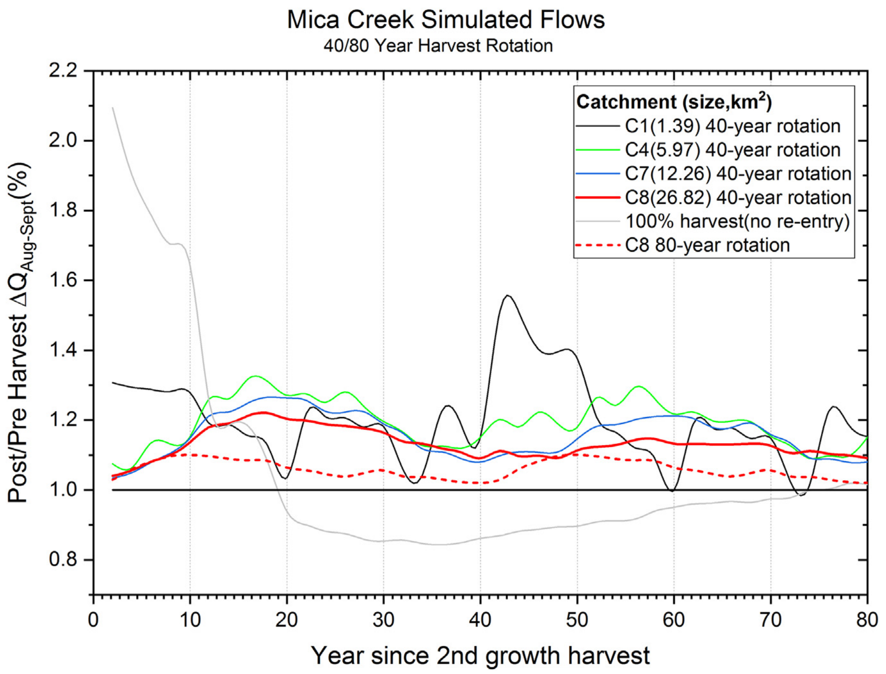

Fig. 3. DHSVM results for four Mica Creek catchments and modeled hydrological recovery for four catchment scales from a privately managed working forest including: 1 (small, 1.4 km^2), 4 (medium, 6 km^2), 7 (large, 12 km^2), and virtual 8 (WS6 + WS7, largest, 64 km^2), based on a 40 year rotation, and an 80 year rotation (for virtual 8). The y axis represents the change in August to September discharge (Q).

composed primarily of grand fir, Douglas-fir, western red cedar, and western larch (Du et al., 2014). The catchments are underlain by metamorphic bedrock with silt loam soils. Mean annual precipitation is approximately 1400 mm with roughly 2/3 occurring as snow between October and March. Mean pre-harvest runoff is ~550 mm with seasonal low flows of ~0.2 mm day $^{-1}$ typically occurring from August to September.

We used the Distributed Hydrology Soil Vegetation Model (DHSVM, Wigmosta et al., 1994) and Physiological Principles for Predicting Growth (3-PG, Landsberg and Waring, 1997; Wei et al., 2014) forest growth model to simulate changes in the low flow regime. The model was parameterized with extensive measurements collected throughout the catchment including streamflow at seven paired and nested gauging stations, snowpack dynamics, throughfall, soil water content, and sap flux (Du et al., 2014). The model was subsequently refined for this work using a quasi-Monte Carlo, stepwise optimization procedure to maximize water balance, model efficiency, and low flow simulations under a variety of both climate and landcover (pre- and post-harvest) conditions. To assess the potential effects of harvest and subsequent regeneration across forest age classes that commonly occur in industrial forestlands, one harvest unit was converted from mature forest to clearcut conditions each year. Fish-bearing streams lower in the network had simulated ~22.9 m riparian buffers, but non fish-bearing reaches higher in the catchment were unbuffered, reflecting state regulations and typical management practices in the region. The characteristics of regrowing vegetation were estimated based on previous 3-PG simulations (Du et al., 2016). The size of each harvest unit was similar to current regional harvest rates, representing approximately 50% of the 1.39 km^2 and 2.5% of the 26.82 km^2 catchment (Fig. 2). This results in two 40-year harvest rotations over the 80-year simulation, following initial harvest of second growth (80 year-old) timber. For comparison, 100% harvest (without re-entry) and an 80-year rotation were also simulated for the entire catchment.

When the entire catchment was harvested at once, low flows (August–September) increased by 0.244 mm day^{-1} immediately after harvest, returned to baseline after ~20 years, declined by 0.025 mm day^{-1} after ~35 years, and gradually returned to the baseline by ~75 years (Fig. 3). This low flow response was similar to trends observed in regional studies (e.g. Hicks et al., 1991; Perry and Jones, 2017; Gronsdahl et al., 2019; Fig. 1) and for annual hydrological yield and ET trends (Naranjo et al., 2011). Following repeated entries and harvest of smaller units (~0.7 km ^{2}), the smallest catchment (C1) had the largest and most variable low flow changes ranging from (<0.01 to 0.10 mm day^{-1}), with discrete increases approximately every 20 years resulting from harvests in the two main units that comprise the catchment. As the catchment size increased from 1.4 km^2 (C1) to 26.8 km^2 (C8) low flow increases became progressively smaller and more stable. Changes ranged from 0.01 to 0.04 mm day^{-1} at C8, where less of the catchment was recently harvested and a greater diversity of canopy ages occurred. An 80-year rotation, with smaller harvest units, exhibited the smallest low flow increase because less of the catchment was in recently harvested conditions.

3. Forest-water relationships

3.1. Accessible subsurface water storage for trees

In the Mediterranean climate of the Pacific Northwest, the growing season corresponds with the seasonally dry low flow period, when evaporative demand and solar irradiance are elevated. Elevated transpiration rates typically occur during this season, although these may not be sustained for its entire duration due to insufficient water supply (Irvine et al., 2004; Wharton et al., 2009). As a result, shallow and deep subsurface storage ultimately supplies water for both transpiration and streamflow during this low flow period (Rempe and Dietrich, 2018). Understanding how vegetation interacts with subsurface water sources, including allocation from deep vs. shallow subsurface storage (Brooks et al., 2010) and whether trees in proximity to the stream determines access to surface or subsurface water remains poorly understood (Bond et al., 2002; Barnard et al., 2010; Wondzell et al., 2007, 2010).

The influences of geology and topography on the movement of water in the subsurface have been studied extensively (Freeze and Witherspoon, 1967; Winter, 2001; Gleeson and Manning, 2008;

Rempe and Dietrich, 2014), but how tree water uptake affects surface flow paths and subsurface water storage remain open questions (Brooks et al., 2015; Brantley et al., 2017). Forest ecological and hydrological research over the last two decades has demonstrated that terrain and topographic complexity significantly influence plant-available water, groundwater recharge, and streamflow generation, with both communities calling for research focused on the importance of spatially and temporally variable water stores (Brooks et al., 2015; Fan, 2015). Complex topography drives the hydrologic and microclimatic dynamics of catchments and consequently, the spatial and temporal variation of forest ET and growth. Because surface topography is not always representative of subsurface conditions, it has been difficult to identify mechanisms that determine the spatial distribution of forest ET and its temporal feedbacks with groundwater storage and fluxes. The National Research Council identified understanding the interconnections between ET and groundwater fluxes to be one of the most important and emerging challenges in the past decade (NRC, 2012).

Tree physiology and ecohydrology observations suggest that forest ET and growth at the hillslope scale are more strongly related to subsurface storage than to local precipitation supply (McDonnell, 2003; Tromp-van Meerveld and McDonnell, 2006; Thompson et al., 2011; Pelletier et al., 2013). Dominant controls on subsurface moisture patterns often show substantial variability (Western and Blöschl, 1999; Penna et al., 2009) with spatial patterns of soil moisture controlled by lateral subsurface flow patterns that follow subsurface geologic features (Kampf et al., 2015). Recent work has highlighted the importance of terrain and deeper subsurface geophysical structure in controlling plant water availability (Swetnam et al., 2017; Hu et al., 2010). A growing number of studies have shown that land-atmosphere feedbacks depend on regional groundwater storage (Anyah et al., 2008; Kollet and Maxwell, 2008; Ferguson and Maxwell, 2010). For example, Maxwell and Kollet (2008) found that the depth of groundwater determines the relative sensitivity of areas to changes in temperature and precipitation. Similarly, another study (Tromp-van Meerveld and McDonnell, 2006) indicates that hillslope-scale transpiration and tree basal area are more strongly related to subsurface storage than surface water supply. Consequently, it is expected that subsurface storage dictated by terrain and subsurface complexity will contribute to forest resilience.

3.2. Evapotranspiration and interception by stand age in the Pacific Northwest

ET is the sum of evaporation from canopy, litter, and soil surfaces and transpiration from vegetation. Canopy interception of precipitation can be an important evaporative loss in the forest hydrological cycle, accounting for 10–50% of seasonal or annual precipitation (Carlyle-Moses and Gash, 2011; Link et al., 2004; Pypker et al., 2005; Roth et al., 2007). While precipitation events are limited during the low flow season, canopy interception of rain and snow from other times of the year can have important implications for catchment water storage, which sustains low flows. Across studies in the Pacific Northwest canopy interception loss ranged from 11 to 21% in young-, and 22 to 36% in old-growth Douglas-fir and 120 year-old coast redwood stands, respectively (Supplemental Table 2). Canopy interception in ponderosa pine stands was ~10% of annual precipitation (Rowe and Hendrix, 1951; Williams et al., 2001). Differences in canopy structure (i.e., epiphytes) and species composition can enhance water storage capacity in old-growth stands. However, despite this greater storage capacity, canopy interception loss between old-growth (450 years) and young (25 years) stands can also be similar because aerodynamic roughness can mitigate evaporative losses from canopy surfaces (Pypker et al., 2005).

Comparison of low flow responses across studies must also consider how ET varies with stand age because 1) transpiration rates of young versus old trees have been linked with low flow declines (Perry and Jones, 2017), 2) calculations of low flow responses have relied on reference catchments with different stand ages (i.e., old-growth or mature forest; Table 2), and 3) a mosaic of stand age occurs at larger catchment scales (Fig. 4). Within young to mature stands (< 60 years) ecosystem-scale ET rates measured using eddy covariance methods, typically increase with stand age in the Pacific Northwest (Jassal et al., 2009; Kwon et al., 2018; Table 3). Annual ET rates of Douglas-fir were similar between mature (58 years) and intermediate (19 years) aged stands but were lower in the youngest stand (7 years) in British Columbia (Jassal et al., 2009). Although stomatal dynamics limited transpiration in all three stands, the younger stands showed higher interannual variability in ET and sensitivity to soil water deficits as compared to the intermediate-age stand. In Oregon, ponderosa pine ET increased from 350 to 550 mm y^{-1} with stand age increasing from ~20 to ~60 years (Kwon et al., 2018). The effect of drought stress on ET was more pronounced in young pine than in mature pine due to a lower baseline soil water content and a shallower rooting depth.

Growing season and annual ecosystem-scale ET rates have yielded mixed results across young to old-growth stands revealing increases (Wharton et al., 2009), decreases (Chen et al., 2002, 2004), and no change (Irvine et al., 2002) with age (Table 3). Irvine et al. (2004) reported similar magnitude and pattern of ET between young (~25 years) and old (~250 years) ponderosa pine stands in Oregon. However, substantial differences were observed in tree transpiration (per leaf area), showing, at maximum, five times higher transpiration rates in the young ponderosa pine during a wetter season and three times lower during a drier season. These high rates of water use by the young stand can risk potential hydraulic dysfunction through cavitation and embolism formation in the xylem (Tyree and Sperry, 1988). A decline of Douglas-fir ET rates from young (0–15 years) to old-growth (450–500 years) was observed in Washington during the growing season (May to October; Wharton et al., 2009). Higher ET in the young stand was attributed to an inability to induce stomatal closure and conserve water under enhanced atmospheric evaporative demand until later in the dry season, while early stomatal closure to avoid cavitation led to lower ET in the old-growth stand.

Age-related ecosystem structure (root system and stem capacitance) can have important implications for seasonal drought responses, such that ET declines in early seral conifer stands as the summer progresses while mature or old-growth conifer stands maintain ET throughout the summer (Irvine et al., 2002; Wharton et al., 2009; Kwon et al., 2018). Young stands are likely to be more vulnerable to increased water stress than mature conifer stands if the Pacific Northwest experiences longer or more severe droughts, due to differences in age-related ecosystem structure. The timing of maximum ET of regenerating stands in relation to low flow declines may aid in determining the potential role of stand age in explaining low flow declines where they occur. For example, in British Columbia, declines observed in early summer in one catchment did not correspond with high rates of transpiration and instead were attributed to earlier snowmelt in the harvested catchment. Declines observed in late summer in the other treated catchment were, partly, attributed to recovery of transpiration and interception as forests regenerated (Gronsdahl et al., 2019). Expanding measurements of ET, and its individual components transpiration and evaporation, to encompass the spectrum of stand age classes present on the landscape will aid in understanding how forest hydrological processes contribute to low flow responses.

3.3. Tree and stand water use

Tree growth is closely related to transpiration rates. More productive trees transpire more water, and this appears to hold within and among species (Lesch and Scott, 1997; Moore et al., 2011). Despite differences in species' water usage (Chan et al., 2003; Moore et al., 2004), the relationship between productivity and transpiration rates did not differ in monoculture and various mixtures of young red alder and Douglas-fir in western Oregon (Moore et al., 2011). The variability in transpiration

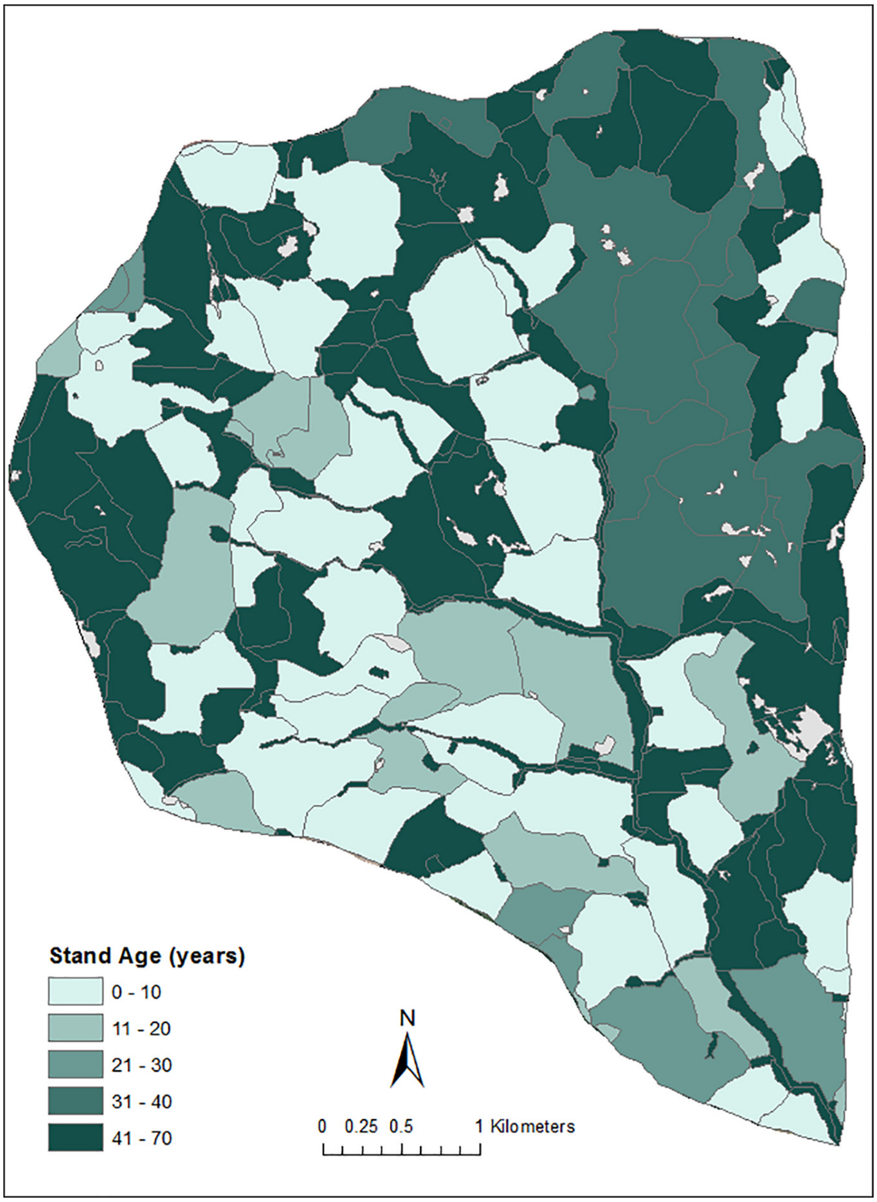

Fig. 4. Example of an actively managed private industrial catchment located in the western Cascades in Oregon USA. Individual harvest units of different ages and retention of riparian buffers contribute to a mosaic of stand age.

was influenced by biomass productivity, which was determined by site conditions (e.g., soil moisture and nutrient; Moore et al., 2011). The influence of growth rate on transpiration is also reflected in tree responses to drought. A review of thinning studies in North America and Europe found significant reductions in tree growth of thinned and unthinned stands during drought, indicating a decline in tree transpiration (Sohn et al., 2016). However, tree growth rates in thinned stands rapidly recovered within 1 year of the drought due to their increased foliage and fine-root biomass.

Stand water use is a function of the species, densities, and sizes of trees and other vegetation. Lowering tree density by thinning has been suggested repeatedly as an option to improve individual tree vigor by providing each tree with more resources, especially water (Chmura et al., 2011; Puettmann, 2011; Grant et al., 2013). Similarly, overstory thinning has been hypothesized to enhance water availability to streams and potentially alleviate low flow declines when they occur (i.e., Sun et al., 2018). The literature shows several hydrological response patterns, including no responses in catchments with low intensity thinning operations (e.g., ≤ 25% of stems or basal area removed; Lesch and Scott, 1997; Perry and Jones, 2017) and increased annual water yield and low flows in catchments with higher thinning intensities (e.g., greater than one-third and up to three-quarters of the overstory removed; Lesch and Scott, 1997; Hubbart et al., 2007; Keppeler et al., 2009; Dung et al., 2012; Webb and Kathuria, 2012; Hawthorne et al., 2013; Sohn et al., 2016). The absolute amount of rainfall was also influential with less evident responses in years with high precipitation (Lesch and Scott, 1997). Several mechanisms may be responsible for these trends following thinning. First, removal of overstory vegetation by thinning or gap creation immediately leads to reduced water interception (Vanclay, 2009; Nanko et al., 2016). Second, for heavier thinnings lower stand-level transpiration due to reduced leaf area (Hawthorne et al., 2013) appear to be overriding increased transpiration demands of the remaining trees due to their more exposed crowns (Bladon et al., 2007). Opening of overstory vegetation can increase understory ET (Lechuga et al., 2017), which is typically considered to be minor (< 10% of total transpiration; Price et al., 1986) but can be significant (up to 70% of total transpiration; Tan et al., 1978).

Table 3
Evapotranspiration (ET) rates across stand age-gradients measured across the Pacific Northwest (U.S. and Canada) measured with an eddy co-variance methodology.

Location		Site name	Dominant Species	Maximum stand age	ET (mm/d)	P/ET	Duration of record	Citation
Vancouver Island, BC		DF49	PSME	58	1.11	3.73	annual; 7 year mean (2002 to 2007)	Jassal et al., 2009
		HDF88	PSME	19	1.12	3.93		
		DF00	PSME	7	0.73	5.29		
Coast Range, OR		DF = Douglas-fir	PSME	45	1.23	3.03	annual; 4 year mean (2007 to 2010)	Kwon et al., 2018
Cascade Range near Sisters, OR		MP = mature pine	PIPO	60	1.52	0.86	annual; 10 year mean (2003 to 2012)	
		YP = young pine	PIPO	20	1.00	1.02	annual; 4 year mean (2005 to 2008)	
eastern Cascade Range near Sisters, OR		O = Old	PIPO	250	1.69	0.85	summer; 4 month mean (May to Aug)	Irvine et al., 2002
		Y = Young	PIPO	14	1.78	0.85		
Wind River, WA	Year 2 (1999)	20YR	PSME	20	1.35	5.01	summer; 3 month mean (Jul to Sep)	Chen et al., 2004
	Year 2 (1999)	450YR	PSME	450	2.27	2.98		
	Year 1 (1998)	40YR	PSME	40	1.07	6.30		
	Year 1 (1998)	450YR	PSME	450	1.29	5.23		
Wind River, WA	Year 1	ESN 2006	PSME	10	2.11	0.60	summer; 4 month mean (May to Aug)	Wharton et al., 2009
	Year 2	ESS 2007	PSME	14	2.35	0.35		
	Year 1	OG 2006	PSME	450	1.65	0.66		
	Year 2	OG 2007	PSME	450	1.87	0.43		

PSME: *Pseudotsuga menziessii* (Douglas-fir), PIPO *Pinus ponderosa* (Ponderosa Pine).

Despite initial increases in water availability for tree growth, soil moisture, or annual yield, these responses can be temporary, even in heavy thinning treatments (Gray et al., 2002; D'Amato et al., 2013; Hawthorne et al., 2013; Sohn et al., 2016). Furthermore, in a spatial context, it appears that thinning increases in tree water use are driven by local competitive conditions (e.g., tree removal within 10 m of individual trees), as these increases were evident in the uphill thinned area, but not in the riparian buffers (Ruzicka et al., 2017). In the same context, observations from Dung et al. (2012) suggest that regular spaced thinnings (remaining trees spread throughout the stand) had less impact on the hydrological cycle than more concentrated thinnings.

4. Discussion and conclusions

4.1. Low flow responses: implications for current forest practices

The 25 catchment studies we reviewed documented low flow responses to treatments that represented forest practices at the time studies were initiated. Many of these treatments reflect historic practices when harvest included large clearcuts of old-growth trees without the retention of riparian buffers. Site preparation in the Pacific Northwest in the 1950s -1970s included broadcast burning of remaining logs and slash, often with high intensity fires. Regeneration by reseeding was common, and often required several efforts for seedlings to establish (e.g., Moore et al., 1974). Currently, a wide range of forest practices exist across the landscape because regulations are defined by each state or province, differ by ownership (private, state/province, federal), and are periodically refined. Forest management objectives further contribute to the variety of practices implemented (i.e., typical harvest age, regeneration techniques, thinning).

Despite this variability, common elements across Pacific Northwest states and provinces include smaller sizes of contiguous harvest units, retention of riparian buffers along fish-bearing and some non-fishbearing reaches, burning of slash in piles, replanting by seedlings, competition release herbicide spraying, guidelines for road construction, and limited silvicultural activities near streams. Collectively these practices create a finer-scale mix of forest stand conditions and ages in all catchments (Fig. 4), reduce spatial extent of soil heating and hydrophobic soils, and promote more rapid forest regeneration than in the past (i.e., four seeding efforts occurred at HJ Andrews WS1; Lutz and Halpern, 2006). These changes likely affect the hydrologic budget, and alter low flow hydrological responses for periods 1, 2, and 3, through multiple pathways by reducing changes in ecosystem scale evapotranspiration, increasing soil infiltration and storage, and reducing runoff (Table 4). We generally lack long-term data on the suite of current forest practices that are common on the landscape, as well as future practices, including riparian buffers of varying widths, riparian buffers with varying levels of management activities, pre-commercial and commercial thinning, uneven stand management, monoculture or diverse tree species. Some prior treatments are relevant, and aid in our understanding of long-term low flow responses to current practices.

4.1.1. Riparian buffers

Few studies in our review included riparian buffers in their treatments, but these observations suggest that a range of low flow responses can occur with the retention of riparian buffers. First, hydrological period 2 responses were observed in two catchments and hydrological period 3 responses were observed in three of the five catchments with buffers (Table 2; Gronsdahl et al., 2019; Segura et al., 2020). Second, following recent forest practices with buffers (initiated in 1990s to 2009), the immediate response to harvest included low flow increases (2 catchments; Reid, 2012; Surfleet and Skaugset, 2013), no change (2 catchments; Gronsdahl et al., 2019), or decreases (1 catchment; Segura et al., 2020). No change and decreases in low flow were observed relative to reference catchments with stand ages >100 y. The occurrence of low flow increases in hydrological period 1 was 40% among these buffer studies relative to 84% among all catchments reviewed (Table 2).

Retention of riparian buffers, along with other current harvest practices, may limit low flow increases (hydrological period 1) but one study suggests buffers may not relieve low flow declines (hydrological period 3) that are already occurring following earlier harvest (Segura et al., 2020). In the Alsea watershed of Oregon, low flow responses to original harvesting of 110 year old stands resulted in low flow declines up to 50% lower in 40 to 53 year old regenerating Douglas-fir stands than reference (>110 y) stands. Recent harvesting of the regenerating 40 to 53 year old Douglas-fir stands, where a ~ 15 m riparian buffer was retained on fish-bearing reaches, did not alleviate low flow declines.

Table 4
Anticipated effects of contemporary practices on forest hydrology.

Examples of contemporary practices	Anticipated effect on forest hydrology (relative to historic practices)	Hydrological period affected
Minimize compacted area and impacted area-stream connectivity: fewer roads, reduced landing size, placement of new roads away from stream, decommissioning of legacy roads, restrict tractor logging and implement equipment exclusion zones, less soil compaction during harvest/yarding operations, limit skid trails, limit broadcast burning reduces water repellent soils	Increase infiltration, potentially increase groundwater recharge, reduce runoff	I, II, III
Appropriately sized culverts or bridges that prevent blockage and allow for passage of water, sediment, wood, and biota	Improved streamflow through culvert, reduced road erosion at crossings	I, II, III
Reduced size of harvest units, reduced clearcut (cutblock size), adjacency limitations Reforestation requirements within a limited time frame (e.g. 4 years); planting of seedlings rather than seeding, use of herbicides to control competing vegetation, and genetically-selected seedlings lead to more rapid recovery of overstory vegetation and increased ET Riparian buffers on fish-bearing streams (buffers on non-fish bearing streams vary regionally and by ownership): passive restoration of buffers over time will eventually allow mature buffers to develop as old-growth As a result of these practices (limited size, 'green-up', and buffer retention multiple stand ages present in the catchment, particularly at larger scales, which may have important implications for ecosystem-scale ET that may vary with successional forest stage	Ecosystem-scale ET (reduced duration of low rates; onset and duration of high rates)	I (most pronounced), II or III if groundwater recharge is affected
Reduced size of harvest units: less reduction in canopy interception at catchment scale Reforestation requirements, planting of seedlings rather than seeding, use of herbicides to control competing vegetation, and genetically-selected seedlings lead to more rapid recovery of overstory vegetation and reduced duration with less canopy interception	Reduced loss of canopy interception	I (most pronounced), II or III if groundwater recharge is affected

When compared with reference stands aged 40 to 53 y, low flow increased. These results suggest stand age of the reference catchment may influence the directionality of low flow responses. Low flow declines (relative to >110 y stands) returned two years after harvesting, indicating similarly high evapotranspiration in the catchment among pre-harvest (40 to 53 y Douglas-fir) and post harvest (≤ 8 y planted Douglas-fir and 40 to 53 year old Douglas-fir and red alder in the riparian buffer) stands. The relative contributions of the riparian buffer versus young planted trees are not well understood (Segura et al., 2020). In an earlier experiment within this watershed, removal of only trees in the riparian buffer (5 m wide) while retaining all other trees in the catchment suggested trees closer to the stream did not control diel variation in streamflow (Hale, 2011), in contrast to the proposed near-stream zone of influence hypothesis (Bond et al., 2002).

As riparian buffers continue to age, eventually reaching late-seral then old-growth conditions, those stands may contribute to age-related reductions in ET rates during the low flow season. Therefore, if dense, young stands within riparian buffers are currently contributing to reductions in low flow via elevated ET rates (i.e., Segura et al., 2020), on longer timescales these responses may not persist. With such limited information on low flow responses in buffered catchments, it is difficult to understand or make clear predictions of future responses. Riparian buffers serve many important aquatic functions by providing shade, limiting alterations in stream temperature, and reducing erosion and solute delivery to streams (Cristan et al., 2016). Forest management must balance these multiple objectives, while also considering their immediate and long-term effects on annual and seasonal scales.

4.1.2. Downstream low flow responses and a mosaic of stand age

With increasing catchment size, a diverse mix of forest stand ages can occur (Fig. 4), and the relative proportion of newly harvested areas is reduced. Hydrological modeling at Mica Creek, Idaho, suggested that extending the rotation age, and thereby reducing the proportion of harvest units in discrete age classes, avoided hydrological period 3 declines altogether and dampened the magnitude of low flow increases (Case study 3). Furthermore, by measuring low flow responses to current practices at 7 nested gaging stations, the Mica Creek dataset that calibrated the model simulations was uniquely suited to evaluate the downstream persistence of low flow responses in successively larger catchments. The results indicate the magnitude of low flow responses attenuated at downstream points as catchment size increased (Case study 3; Fig. 3). Similarly, our review of large-scale catchments found increases in low flows occurred when a greater percentage of the catchment was disturbed, and low flow declines were not observed at these scales (Supplemental Table 1). Across large scale catchments, the three catchments with an increase in low flows generally had greater percentages of forest disturbance of 25, 37, and 62% compared with 5, 19, 25, and 29% disturbance in the catchments with no change in low flow. These findings are in line with prior conclusions that forest disturbance must exceed 25% of the catchment before a low flow response will be observed (Johnson, 1998). Several studies have reported on the potential for forestry and climate change to off-set effects given that they often exhibit opposite trends at large catchment scales (Jones et al., 2012; Zhang and Wei, 2012). In the Upper Similkameen River Watershed in BC, climate variability decreased seasonal low flows by 17.9 mm (−70.8%) from 1986 to 2013, while forestry increased low flows by 7.4 mm (29.2%) (Li et al., 2018). Zhang and Wei (2012) suggested that with increased forest disturbance in a catchment, the contribution of forest disturbance to flow variability can increase relative to the contribution of climate.

Natural disturbance can elicit similar hydrological responses to harvest of overstory vegetation, and at larger catchment scales hydrological responses to forest harvest are often confounded with natural disturbance. For example, low flow and annual runoff increased following a mountain pine beetle epidemic (Potts, 1984) and following forest fires (Niemeyer et al., 2019). Seasonal and annual responses can also differ following disturbance. Following a wildfire that affected 45% of the Boise River catchment in Idaho, water yield increased annually and in most months, but declines were observed in June and July (Luce et al., 2012). Annual runoff, but not low flows, increased with proportion of Swiss needle cast in the catchment in the Oregon Coast Range (Bladon et al., 2019). Low flows on the eastern slope of the Washington Cascades were elevated for the first 7 years following wildfire across all three catchments examined, but post-fire only the two catchments that were salvage logged and seeded with barley had returned to baseline 35 to 41 years post-fire (Niemeyer et al., 2019). Low flow in the burned reference, which was unmanaged post-fire, remained elevated 35 to 41 years post-fire, presumably due to delayed vegetation recovery (Niemeyer et al., 2019).

4.2. Aquatic biota responses to seasonal low flow and low flow declines

Native aquatic taxa in the Pacific Northwest are adapted to seasonal low flow conditions when resources become concentrated for weeks to months. Generally, seasonal low flow presents stressors for biota. During seasonal low flow, aquatic invertebrates emerge from dry streambeds (Banks et al., 2007), invertebrate drift declines (Danehy et al., 2016), amphibian larvae metamorphose, and basal food resources can control food webs (Power et al., 2008). When low water levels reduce the availability of cover, fish survival is low (Berger and Gresswell, 2009), vulnerability to predators is especially high (Harvey and Nakamoto, 2013; Penaluna et al., 2016) and the consumption of prey is reduced (Li et al., 2016). Reduced consumption likely occurs because suitable locations to feed are reduced (Fausch, 1984; Hayes et al., 2007) leading fish to have minimal growth or weight loss (Penaluna et al., 2016; Jensen, 2017). Consecutive years of extremely low seasonal flows associated with drought have been shown to have long-lasting consequences for aquatic food webs (Power et al., 2008; Matthews and Marsh-Matthews, 2017).

Isolating the response of biota to harvest-related changes in flow relative to other parameters can be difficult because harvest also affects other key parameters (i.e., temperature, light availability, and sediment; Gregory et al., 1987, Leach et al., 2012; Reiter et al., 2019; Bywater-Reyes et al., 2017) that can contribute to changes in basal food resources, prey availability, and aquatic biota in higher trophic levels. A wide variety of biotic responses to forest harvest have been reported, and these are both idiosyncratic and context-dependent (Murphy and Hall, 1981; Bisson et al., 2008; Banks et al., 2007; Penaluna et al., 2015). Some fish populations can increase in density and/or biomass immediately following current harvest practices, potentially due to increased low flows in hydrological period 1 (Mellina and Hinch, 2009; Bateman et al., 2016; Bateman et al., 2018) which can benefit fish by creating more available habitat (Penaluna et al., 2015; Harvey and White, 2017).

Forest harvest may also have delayed effects on aquatic biota. In the only study that has simultaneously documented long-term fish responses and low flow declines, salmonid fish biomass recovered to original pre-harvest levels despite 50% reductions in summer low flow (Bateman et al., 2018; Segura et al., 2020). With similar 50% reduction in late summer flow in hydrological period 3 at the Andrews Forest, the previously harvested headwater streams had similar macroinvertebrate densities and diversity as old-growth reference streams (Frady et al., 2007). In Carnation Creek, B.C., growth and survival of Coho salmon *Oncorhynchus kisutch* initially increased by 65% for three decades followed by declines in production and survival below pre-harvest levels; these declines were likely due to delayed habitat degradation from landslides decades earlier (Tschaplinski and Pike, 2017), and it is unclear whether low flow responses may have also contributed to these fish responses (Hetherington, 1987). In Upper Penticton, B.C., where low flow declines were observed after harvest in two catchments, declines in modeled fish habitat were found in one of the two catchments (Gronsdahl et al., 2019). Overall, the relationship between long-term forestry-related changes in low flow and biotic populations is not well understood; the available but limited data suggests that reductions in low flow associated with hydrological period 3 did not negatively impact stream macroinvertebrates (Frady et al., 2007) or salmonid biomass (Bateman et al., 2018; Segura et al., 2020).

Experimental manipulations of seasonal low flow regimes suggest only extreme flow reductions affected invertebrate and fish populations, and these experiments can aid in understanding how forestry-related low flow declines (hydrological period 3) may affect biota by isolating the manipulation of flow from other physical variables. When experimental reductions of low flow in small streams were limited to 50 to 75% little or no changes were observed for invertebrates and fish, but abundance and production declined when reductions exceeded 75% (Kraft, 1972; Rimmer, 1985; Nuhfer and Baker, 2004; Harvey et al., 2006; Wills et al., 2006; Dewson et al., 2007; Walters and Post, 2008). For example, when low flow was reduced by 75 to 80% in northern California invertebrate prey drift and growth of rainbow trout declined, but fish survival was not affected (Harvey et al., 2006). Similarly, reductions of low flow by 40 to 80% led to reduced fish length in a Connecticut stream (Walters and Post, 2008). More observational and experimental research in locations where forestry-related low flow declines have been observed is warranted to understand species interactions to the effects of seasonal low flow, contemporary forest harvest, and climate change.

5. Summary and next steps, remaining questions

Ultimately, any forest management that seeks to limit low flow increases (hydrological period 1) or mitigate long-term declines (hydrological period 3) must be informed by a mechanistic understanding of the underlying processes. Yet, basic mechanistic questions such as how water uptake by trees affects subsurface water storage and streamflow or how distribution of trees in the catchment (riparian versus upland) affect water use remain active topics of research. Stand age and associated ET rates have been identified as important mechanisms to explain seasonal low flow declines (Perry and Jones, 2017), but additional information is needed to identify how ecosystem level ET rates differ across the mosaic of stand ages, densities, and species compositions that occur on the contemporary forest landscape. In snow-dominated catchments alterations to the accumulation and timing of snowmelt following harvest may contribute to low flow declines (Gronsdahl et al., 2019), hence an improved understanding of how different forest structures and climate conditions affect snow dynamics across the region is needed. Hydrological modeling efforts can aid in generating hypotheses to assess these predictions, but ultimately these models must be informed by extensive spatial and temporal data that incorporate the entire water budget and reflect current management practices. Specifically, hydrologic data is needed that documents effects of current and potential future practices including: riparian buffer retention, commercial thinning, and uneven stand management across private and public land. Management efforts should also consider hydrological effects across longer timescales, and not focus solely on the immediate response.

Compiling simultaneous evaluations of flow and biotic changes (i.e., macroinvertebrate, amphibian, or fish) in locations where low flow declines have been observed is essential to understanding the potential implications of changes in flow for stream ecosystems.

Specifically, studies should consider evaluating low flow responses during hydrological period 3 in fish-bearing, and more specifically salmonid-rearing, streams to understand low flow responses and how downstream effects on biota and species interactions accumulate across large catchments. Future studies will entail scaling up to larger catchments and multi-phased harvesting of units that comprise smaller relative proportions of the landscape over extended periods of successive harvesting (e.g., Keppeler, 1998; Gronsdahl et al., 2019; Case study 3). At large scales, different statistical approaches will be necessary to separate low flow responses to forest disturbance from climate impacts; these could include quasi-paired catchment studies, hydrological modeling, time series modeling, and graphical methods (flow duration curves; Zhang et al., 2017). To facilitate comparisons of responses across small paired catchment studies and larger catchment-scale studies using multiple methods, future low flow publications should report sufficiently detailed information on low flow responses, such as absolute change by month and year.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.138926.

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