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Basal area and hillslope position impacts to hydraulic redistribution in a coast redwood forest

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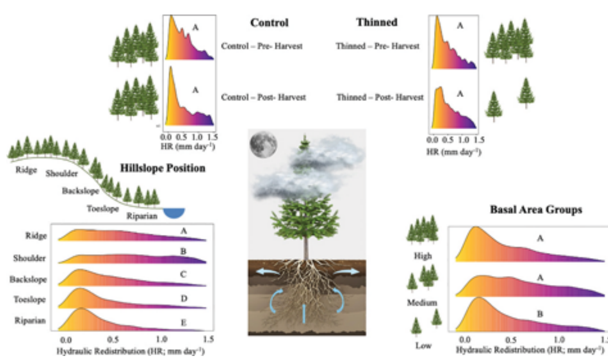
HIGHLIGHTS

- Hydraulic redistribution can be a significant water source, but we do not fully understand the effects of thinning on it.
- To study thinning effects on hydraulic redistribution, we used soil moisture data from pe- and post-harvest years.
- Basal area and hillslope position affected the ecohydrological dynamics at the site.
- A complex interplay of factors may impact soil moisture and hydraulic redistribution dynamics.

GRAPHICAL ABSTRACT



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ABSTRACT

In forest ecosystems, the interplay among plant-driven processes and anthropogenic activities profoundly influences water balance dynamics. Hydraulic redistribution is one plant-driven process that can provide a large proportion of a plant's daily water. However, critical gaps exist in our knowledge of hydraulic redistribution including how forest management processes, like thinning, and site-specific factors like basal area and hillslope position, may affect it. To address these gaps, we used hourly volumetric water content measurements from 2016 to 2021 from four sub-watersheds in a coast redwood forest, three of which were harvested at different basal area reductions in 2018. This dataset enabled us to investigate the effects of thinning, variations in basal area, and hillslope position on hydraulic redistribution magnitude and additional days of soil moisture provided by hydraulic redistribution. We found that thinning had no significant effect on hydraulic redistribution magnitude or on the days of additional stored water provided. However, there were significant differences in soil moisture and hydraulic redistribution magnitude among the different basal area groups — low basal area had the highest magnitude of hydraulic redistribution. Similarly, soil moisture and hydraulic redistribution varied among

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hillslope positions and positions higher on the hillslope had higher magnitudes of hydraulic redistribution. Our findings suggest that a combination of climatic factors and site-specific characteristics may play a crucial role in determining soil moisture and hydraulic redistribution dynamics in coast redwood forests.

1. Introduction

Plants are a key driver of the terrestrial hydrologic cycle and can alter a forest's water balance through a variety of processes. One such process is hydraulic redistribution, or the passive transfer of water from wet to dry soil via the conduits of roots (Caldwell et al., 1998). Hydraulically redistributed water can make up a large proportion of a plant's transpiration and this water may be used by the individual conducting hydraulic redistribution, seedlings, understory plants, and other trees (David et al., 2007, 2013; Quijano et al., 2012; Quijano and Kumar, 2015). As large drought and heat-induced forest mortality events have been seen globally (Allen et al., 2010; Hartmann et al., 2018), it is important to understand what management activities and site-specific factors may affect hydraulic redistribution and how hydraulic redistribution may benefit plants during periods of seasonal or multi-year drought.

Coast redwoods (*Sequoia sempervirens* (D. Don) Endl.) grow in a narrow belt along the Pacific Coast from central California to southern Oregon. Increased summer evapotranspiration demand and decreasing fog frequency (Johnstone and Dawson, 2010; Noss, 2000) heighten the water stress experienced by this species. This means that potentially more soil water is needed to sustain growth and vigor because fog, or fog deposition specifically, is decreasing in the region (Simonin et al., 2009).

In the coast redwood region, where most plant water use is sourced from seasonally-variable precipitation inputs, hydraulic redistribution may be one mechanism that has allowed coast redwood trees to adapt to this seasonally-dry ecosystem (Hahm et al., 2019). A greenhouse study on coast redwood seedlings found evidence of hydraulic redistribution (Weisgrau, 2020), but it is still unclear whether mature coast redwood trees conduct hydraulic redistribution. One requirement for hydraulic redistribution is the presence of a soil water potential gradient along the extent of rooting depth (Neumann and Cardon, 2012). This threshold has been found to range between −0.4 and −0.8 MPa (Domec et al., 2004; Ishikawa and Bledsoe, 2000; Meinzer et al., 2004). However, coast redwood roots are relatively short compared to stem length (Lorimer et al., 2009), limiting access to the deeper soil water and, consequently, may limit hydraulic redistribution in the form of hydraulic lift (i.e., uplifting water from deep to shallow soil).

Coast redwood forests experience frequent fog events, especially during the dry summer months, and have been shown to exhibit foliar uptake of fog water (Burgess and Dawson, 2004; Limm et al., 2012), which is another form of hydraulic redistribution. Previous studies suggest that hydraulic redistribution occurs in coast redwood forests either due to hydraulic lift or foliar uptake, which can occur when transpiration is negligible (Limm et al., 2012; Weisgrau, 2020). It is crucial to identify and understand the processes affecting plant water availability, like hydraulic redistribution, to gauge the resilience and sustainability of coast redwood ecosystems in the face of escalating water stress brought on by the changing climate.

Forest thinning (harvest) is a widely employed practice that influences hydrologic processes and soil moisture dynamics. Soil moisture and both tree and stand-level water use have been shown to increase after thinning across a variety of ecosystems(Callegari et al., 2003; del Campo et al., 2022; Goeking and Tarboton, 2020; Tague et al., 2019; Vose et al., 2016). However, research investigating the direct influence of thinning on hydraulic redistribution is lacking. In one relevant study, an un-thinned 39-year-old Eastern white pine stand (*Pinus strobus* L.) experienced greater hydraulic redistribution than a 74-year-old stand subjected to a 13 % basal area reduction (Skubel et al., 2017). Age-related differences could explain some of the observed variance in hydraulic redistribution among the stands complicating interpretation of this result. Moreover, examination of a single level of basal area reduction may not explain possible variations in hydraulic redistribution across different thinning intensities. This uncertainty is particularly important given that a 50 % basal area reduction is the approximate threshold at which hydrological processes are significantly impacted (del Campo et al., 2022). Given that hydraulic redistribution can constitute an important water source for the redistributing plant and its neighbors (Bleby et al., 2010; Dawson, 1993), a more comprehensive investigation of how thinning practices affect this process is needed.

Basal area, as modified by forest thinning, influences ecohydrological processes including rainfall partitioning, evapotranspiration, and soil moisture (del Campo et al., 2022), but remains understudied in its potential effects on hydraulic redistribution. Intuitively, stands with higher basal area might be expected to have greater magnitudes of hydraulic redistribution due to higher root densities and drier soil in the root zone, however prior research has found lower magnitudes of hydraulic redistribution with higher stand density across temperate ponderosa pine (*Pinus ponderosa* Dougl. Ex P. Laws & C. Laws) or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, and a Brazilian savanna (Meinzer et al., 2004). Stands with lower basal areas, especially those that have been thinned, may have higher throughfall rates and lower transpiration allowing for potentially higher soil infiltration and recharge deeper into the soil column (Molina and del Campo, 2012; Stogsdill et al., 1989; Zhu et al., 2017). Thinned stands may also experience higher rates of evaporation from the soil surface due to increased solar radiation reaching the forest floor enhancing the drying of shallow soil layers (Brooks and Mitchell, 2011; Lagergren et al., 2008). Because lower basal areas may increase deep soil moisture and dry out the shallow soil, it may lead to the development of the necessary soil moisture gradient (−0.4 to −0.8 MPa) between the shallow and deep soil earlier.

Other factors may contribute to spatial variability in hydraulic redistribution. For instance, hillslope position may contribute to differences in water availability due to slope, aspect, and soil depth (e.g Famiglietti et al., 1999; Fan et al., 2019; Tromp-van Meerveld and McDonnell, 2006, and others) allowing for variations in the magnitude and onset of hydraulic redistribution along a topographic gradient. The variations in soil moisture along a hillslope may result in some slope positions drying out earlier and reaching the soil water potential threshold sooner, and thereby induce an earlier onset of hydraulic redistribution. Foliar uptake may also be affected by topographic position. Locations more exposed to fog may experience more foliar uptake, resulting in reversal of the water potential deficit between the atmosphere and tree, and reverse sap flow in the trees (Burgess and Dawson, 2004; Gotsch et al., 2010; Petreshen et al., n.d.; Ritter et al., 2009). Integrating topography into hydraulic redistribution analyses may offer valuable insights into how site differences affect hydraulic redistribution.

Despite significant advancements in our understanding of hydraulic redistribution, uncertainties remain regarding the effects of forest thinning and site topography on the magnitude of hydraulic redistribution. This study aims to address these uncertainties by examining site and management factors that may influence hydraulic redistribution. Our five objectives are to: (1) examine differences in soil moisture between basal area groups and hillslope positions, (2) determine if hydraulic redistribution occurs in a coast redwood-dominated forest, (3) investigate the effects of forest thinning on hydraulic redistribution magnitude and additional days of stored water, (4) explore how basal area influences hydraulic redistribution and additional days of stored water, and (5) study how hillslope position impacts hydraulic redistribution and additional days of stored water. This expanded understanding is vital to informing management strategies aimed at sustaining drought vulnerable forested landscapes.

2. Methods

2.1. Study site

We conducted our study in four sub-watersheds of the South Fork of Caspar Creek, located in Jackson Demonstration State Forest, a northern California coast redwood-dominated forest (Fig. 1; 39°21′N, 123°44′W). After the clear-cut of the old-growth coast redwood forest in the late nineteenth century, the South Fork underwent second-entry selection harvest from 1971 to 1973 removing 67 % of the stand and third-entry selection harvest from 2017 to 2019 removing an average of 32 % of pre-harvest basal area across the watershed via a range of harvest intensities across the sub-watersheds (Dymond et al., 2021a). South Fork vegetation is thus primarily third-growth forest with a minor component of residual second-growth and young fourth-growth. Tree species include coast redwood, Douglas-fir, grand fir (*Abies grandies* (Doug ex. D. Don), Lindl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and tanoak (*Lithocarpus densiflorus* (Fook. and Arn. (Rohn.). Soils are predominantly well-drained clay-loam Alfisols and Ultisols derived from Franciscan sandstones and shales with depths of 100 to 300 cm (Rittiman and Thorson, 2006).

The Caspar Creek watershed experiences a Mediterranean climate (Köppen-Geiger Csbn) with cool, dry summers with frequent coastal fog events, and mild, moist winters with rare snowfall events. From 2016 to 2021, water year precipitation averaged 1035 mm with 93 % occurring October through April, with minimal precipitation during the June through September growing seasons (Table S1). However, precipitation varied among water years ranging from 565 mm (2021) to 1637 mm (2017). The 2021 drought was one of the most severe drought events in the 60-year Caspar Creek record (Keppeler et al., 2024). Rainfall is generally routed to stream channels via the subsurface matrix and preferential flow paths in the soil and saprolite. The South Fork has a 30-year mean monthly temperature of 10.6 °C that ranges from 6.8 °C in December to 14.5 °C in August (Dymond et al., 2021a).

2.2. Experimental design

Our experiment uses four sub-watersheds in the South Fork (WIL, TRE, UQL, and ZIE) with elevations ranging from 89 to 329 m and slopes averaging 43 to 51 % (Fig. 1, Table 1). Within each of these four sub-watersheds, we instrumented north-facing hillslope transects selected based on similarities in slope, aspect, and elevations. Each transect contained five hillslope study plots: riparian, toeslope, backslope, shoulder, and ridge (Miller and Schaetzl, 2015; Ruhe and Walker, 1968).

The sub-watersheds studied herein were harvested in 2018 (Dymond et al., 2021a; Table 1). Vegetation was removed via cable-yarding on steep slopes and tracked skidding equipment on less steep ground. The harvest resulted in sub-watershed average basal area reductions of 0 % (WIL), 31.5 % (TRE), 49 % (UQL), and 64 % (ZIE). Harvest reductions in individual 1/20th ha circular study plots generally varied minimally from sub-watershed average rates in the upper three slope positions, however harvest rates were lower in the riparian and toeslope positions due to management constraints (Table 1). We evaluated pre-harvest data from 2016 to 2017 and post-harvest data from 2019 to 2021.

2.3. Soil water status

Beginning in September 2015, METER EC5 soil moisture sensors (METER Group, Inc.; WA, USA; resolutions: 0.001 $m^3\ m^{-3}$; accuracy ± 0.03 $m^3\ m^{-3}$) were installed at each of the transect plots. Soil water content measurements during the pre-harvest period were available for WIL, TRE, and ZIE commencing October 2015, and for UQL commencing December 2017. Sensors were placed vertically into the soil at the 15 cm, 30 cm, and 100 cm depths, connected to EM60 data loggers (Onset Computer Corp; MA, USA) and volumetric water content (VWC, θ) measurements were recorded every 10 min. Because of sensor errors, we only included the 15 cm analysis due to large chunks of incomplete data in the deeper depths. The UQL riparian site data were omitted due to excessive gaps leaving 19 sites for analysis. In 2020, because of sensor

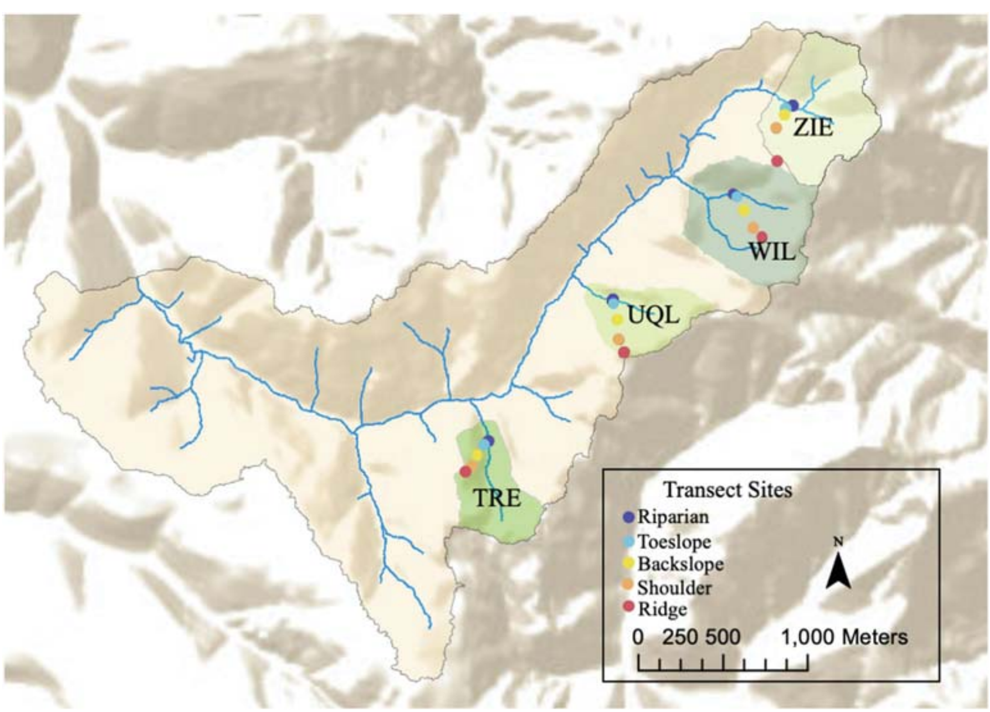

Fig. 1. South Fork Caspar Creek and the four experimental sub-watersheds.

Table 1
Sub-watershed, ID code, topographic position, soil depth, slope, aspect, elevation, pre-harvest basal area (BA), post-harvest BA, and plot-level BA reduction.*

ID	Sub-watershed name	Topographic position	Soil depth (cm)	Slope (%)	Aspect (°)	Elevation (m)	BA_{pre} (m^2 ha^{-1})	BA_{post} (m^2 ha^{-1})	BA reduction (%)	BA_{pre} group	BA_{post} group
WIL	Williams	1 – Riparian	221	46	300	166	264	266	-1	High	High
		2 - Toeslope	193	50	320	173	68	72	−6	Medium	Medium
		3 - Backslope	107	80	350	204	68	79	−16	Medium	Medium
		4 – Shoulder	152	55	357	252	141	154	−10	High	High
		5 – Ridge	155	25	288	274	94	105	−11	Medium	Medium
TRE	Treat	1 – Riparian	111	60	86	89	147	152	−3	High	High
		2 - Toeslope	282	55	77	101	136	122	11	High	Medium
		3 - Backslope	222	45	38	130	48	35	27	Low	Low
		4 – Shoulder	145	70	105	149	48	36	25	Low	Low
		5 – Ridge	254	36	91	165	123	45	63	High	Low
UQL	Uqlidisi	1 – Riparian	205	19	305	135	203	204	0	NA	NA
		2 - Toeslope	242	53	355	142	19	19	−2	NA	Low
		3 - Backslope	170	57	357	180	52	28	47	NA	Low
		4 – Shoulder	387	32	21	217	84	43	49	NA	Low
		5 – Ridge	110	8	3	233	115	56	51	NA	Medium
ZIE	Ziemer	1 – Riparian	107	15	10	196	436	441	−1	High	High
		2 - Toeslope	234	55	0	202	18	24	−32	Low	Low
		3 - Backslope	184	85	18	224	147	57	61	High	Medium
		4 – Shoulder	136	28	351	248	58	22	62	Medium	Low
		5 – Ridge	196	19	294	270	108	32	69	Medium	Low

* Negative BA reductions reflect growth between 2017 and 2019 measurements.

errors the riparian position in ZIE and the shoulder position in TRE had no volumetric water content measurements. Similarly, in 2021 the backslope position in TRE did not have any volumetric water content measurements. Thus, these sites were not included in analyses and plots for those years. Because soil moisture measurements did not begin in sub-watershed UQL in some hillslope positions until December 2017, no UQL sites were included in the pre-basal area groups or in any analyses on thinning effects.

To determine if hydraulic redistribution occurs in a coast-redwood dominated forest (Objective 2), we averaged the 10-min data into hourly VWC for each site. We then used mean hourly VWC to calculate hydraulic redistribution following the equation from Warren et al. (2005) (HR; mm day^{-1}; Eq. 1).

We expected hydraulic redistribution to occur mainly at night when transpiration rates are lowest, and thus defined the period of maximum VWC as either night (17:00 to 06:00 Pacific standard time) or day (06:10 to 16:50 Pacific standard time). If the maximum VWC value used in the hydraulic redistribution equation (Eq. 1), occurred during the day, we considered hydraulic redistribution to be "offset" meaning when the maximum VWC used in the hydraulic redistribution calculation occurred during the day instead of the night.

We estimated the additional days of stored water hydraulic redistribution provided before a given soil water content was reached (Objectives 3 and 4). In our study, we used field capacity as the given soil water content (0.13 cm^3 cm^{-3} at Caspar; Dymond et al., 2021a). We calculated the number of days required to reach that water content without the occurrence of hydraulic redistribution using the mean total daily water use, which does not include hydraulic redistribution, and subtracted this from the estimated number of days required to reach field capacity using net daily water use, which includes hydraulic redistribution (Eq. 2; Brooks et al., 2002).

$$HR\ (mm\ day^{-1}) = \left(Maximum\ \theta_{day\ x+1} - Minimum\ \theta_{day\ x}\right) \times Soil\ depth\ (mm) \times Soil\ Porosity \quad (1)$$

where x is the reference day, soil depth is 150 mm, and soil porosity is 0.453 at our sites (Maidment, 1993).

When precipitation occurred during the growing season (01 June to 30 September), we omitted hydraulic redistribution estimates for the day of and one day after precipitation events (precipitation threshold of 0.0004 in.) following the methodology used in Domec et al., 2010. In analyzing hydraulic redistribution data, we omitted values of 0 or less where hydraulic redistribution was not occurring (13.67 % of daily records). We removed any outliers that may have been caused by soil moisture sensor errors by removing values over the 90th percentile, which resulted in the removal of 5.5 % of all hydraulic redistribution measurements, all of which were above 1.4 mm day^{-1}, the typical maximum range of hydraulic redistribution values (Neumann and Cardon, 2012).

$$Additional\ days = \frac{(\theta_{daily} - \theta_{fc})}{Net\ Daily\ Water\ Use} - \frac{(\theta_{daily} - \theta_{fc})}{Total\ Daily\ Water\ Use} \quad (2)$$

where θ_{daily} is the average daily VWC value; θ_{fc} is the VWC at field capacity (0.13 cm^3 cm^{-3}; Dymond et al., 2021b); Net Daily Water Use is the difference between one diel maximum to the next diel maximum in soil water content (Brooks et al., 2002; Eq. 3); and Total Daily Water Use is the maximum minus the minimum soil water content measured within a day (Brooks et al., 2002; Eq. 4).

$$Net\ daily\ water\ use\ (mm\ day^{-1}) = \left(Maximum\ \theta_{day\ x} - Maximum\ \theta_{day\ x+1}\right) \times Depth\ (mm) \times Soil\ Porosity \quad (3)$$

$$Total\ daily\ water\ use\ (mm\ day^{-1}) = (Maximum\ \theta_{day\ x} - Minimum\ \theta_{day\ x}) \times Depth\ (mm) \times Soil\ Porosity \quad (4)$$

2.4. Analyses

To simplify visualization and post-hoc testing, in a separate analysis we grouped VWC data by plot basal area using three categories of comparable sample sizes for both pre- (n_{pre}) and post-harvest (n_{post}) data: Low (18–48 m^2 ha^{-1}; $n_{pre} = 3$, $n_{post} = 9$), Medium (48.1–122 m^2 ha^{-1}; $n_{pre} = 5$, $n_{post} = 6$), and High (122.1–441 m^2 ha^{-1}; $n_{pre} = 7$, $n_{post} = 4$). Due to the non-parametric nature of the data, we used Kruskal-Wallis and Dunn's test for post-hoc analyses (Dunn, 1964; Kruskal and Wallis, 1952) to determine if daily VWC differed among the three basal area groups and five hillslope positions (Objective 1).

Chi-squared tests were used to determine if hydraulic redistribution occurred during the day or night (i.e., if it was offset), and to detect differences among basal area groups and hillslope positions. To examine among-group differences in hydraulic redistribution magnitude and hours of soil water storage (Objective 4), we used a Kruskal-Wallis and Dunn's test due to non-normal data. We calculated Spearman's correlations (Spearman, 1904) to determine the strength of the relationship between hydraulic redistribution and basal area or elevation (a proxy for hillslope position). We ran a Welch's *t*-test to determine if there was a difference in soil water storage between periods with and without the presence of hydraulic redistribution (Welch, 1947).

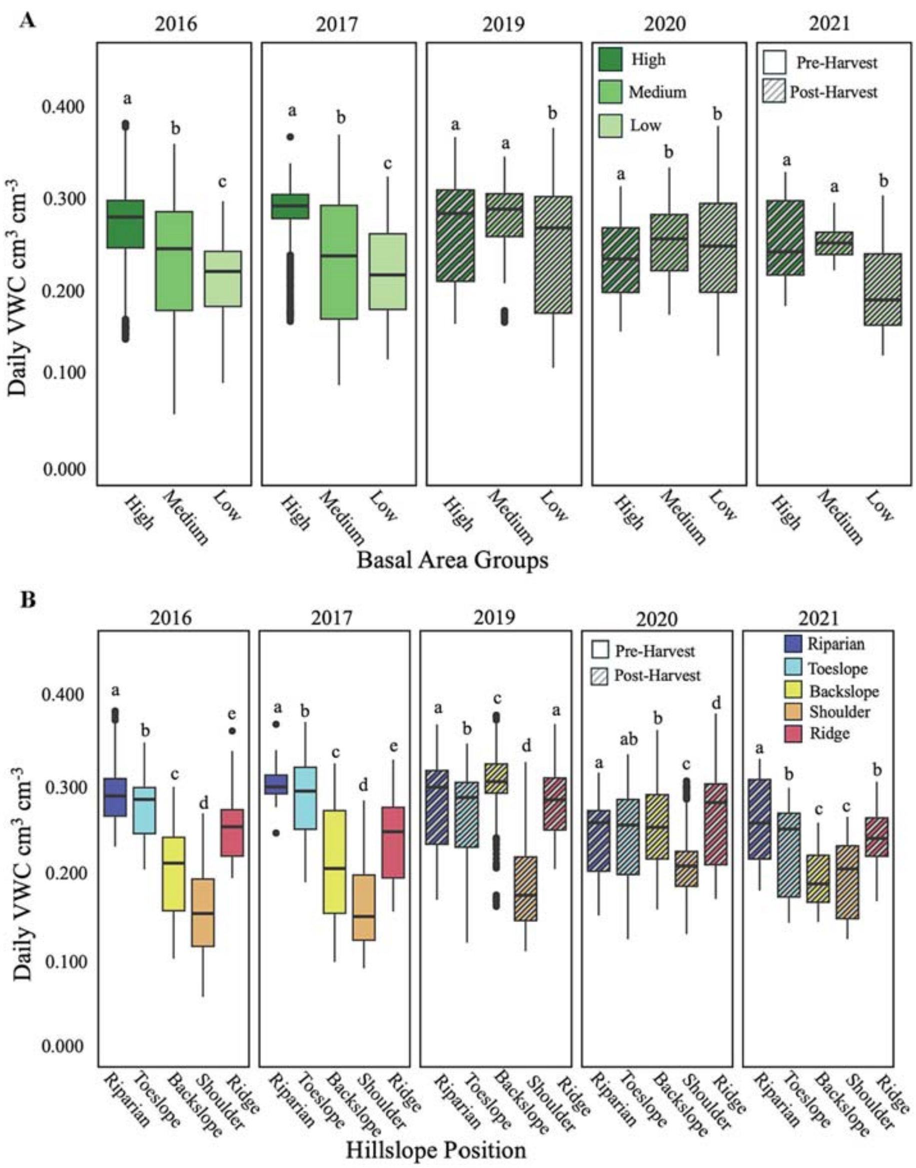

Fig. 2. Boxplots of daily volumetric water content during the growing season (01 June to 30 September) for each basal area group (A); and hillslope position during WY2016 (water year accumulated precipitation = 1358 mm), WY2017 (water year accumulated precipitation = 1637 mm), WY2019 (water year precipitation = 1390 mm), WY2020 (water year accumulated precipitation = 675 mm), and WY2021 (water year accumulated precipitation = 564 mm) growing seasons (B). Hatched bars indicate post-harvest years. Letters (a - e) indicate statistically different hourly VWC values within years using Dunn's test (α < 0.01).

For our analysis of the effects of thinning on hydraulic redistribution magnitude and days of additional stored water (Objective 3), we used a generalized linear mixed model (GLMM) to test for the presence of hypothetically important random effects (e.g., hillslope position, sub-watershed, year) (Bolker et al., 2009). The model determined the proportion of variance in hydraulic redistribution or days of additional stored water explained by the fixed effects of period (pre- or post-harvest), treatment (control or harvested) and their interaction (the treatment effect). Water years (Oct. 01 – Sept. 30) 2016–2017 were defined as pre-harvest and 2019–2021 as post-harvest. We used the Akaike's Information Criterion (AIC) to determine the best fit model (Akaike, 1974). Analyses were performed using the glmmTMB function in the glmmTMB package (Brooks et al., 2024).

For the hydraulic redistribution magnitude model, we used a Gamma distribution and log link function because most hydraulic redistribution values were clustered towards lower values with a long tail extending towards higher values. For the additional days of stored water model, we used a tweedie distribution and log link function because of the combination of excess zeros and continuous data. Both models included sub-watershed, hillslope position, and year as potentially random effects. Additionally, to address observed autocorrelation, we included an autocorrelation function (ar1) in our generalized linear mixed model based on time of observation for each ID. All analyses were performed in R 4.3.2 (R Core Team, 2023).

3. Results

3.1. Soil moisture differences between hillslope positions and basal areas

Daily VWC differed among basal area groups (Fig. 2A). During the pre-harvest years, median daily VWC scaled with basal area (High $\tilde{x}_{pre} = 0.285$, Medium $\tilde{x}_{pre} = 0.239$, Low $\tilde{x}_{pre} = 0.216$ $cm^3\ cm^{-3}$) (Fig. 2). Post-harvest, median daily VWC was highest in the medium basal area group; this was true in both the wet (2019) and dry (2020−2021) years (High $\tilde{x}_{post} = 0.248$, Medium $\tilde{x}_{pre} = 0.261$, Low $\tilde{x}_{pre} = 0.235$ $cm^3\ cm^{-3}$).

Similarly, daily VWC differed among the five hillslope positions (Fig. 2B). During the pre-harvest period, and in 2021, soil moisture generally decreased from riparian to shoulder positions with the ridge-tops having higher VWC values than the backslope or shoulder positions. In 2019 and 2020, this pattern was less evident. The shoulder position exhibited the lowest or near-lowest VWC both pre- and post-harvest. The riparian ($\tilde{x}_{pre} = 0.291$, $\tilde{x}_{post} = 0.262$ $cm^3\ cm^{-3}$) and toeslope positions ($\tilde{x}_{pre} = 0.284$, $\tilde{x}_{post} = 0.260$ $cm^3\ cm^{-3}$) had significantly lower VWC post-harvest compared to pre-harvest ($p < 0.0001$). However, the backslope ($\tilde{x}_{pre} = 0.208$, $\tilde{x}_{post} = 0.260$ $cm^3\ cm^{-3}$), shoulder ($\tilde{x}_{pre} = 0.151$, $\tilde{x}_{post} = 0.189$ $cm^3\ cm^{-3}$), and ridges ($\tilde{x}_{pre} = 0.247$, $\tilde{x}_{post} = 0.272$ $cm^3\ cm^{-3}$) had higher VWC values post-harvest compared to pre-harvest ($p < 0.01$).

Because positions higher on the hillslope (i.e, the shoulder and ridge) were generally associated with the low and medium basal area groups, we conducted a generalized linear mixed model to determine whether the interaction between basal area groups and hillslope positions were significant. We found significant interactions between the basal area groups and different hillslope positions ($p < 0.01$). This finding suggests that the impact of hillslope position on VWC varies with basal area group and vice versa (Table S2).

3.2. Hydraulic redistribution: Frequency and timing

Soil moisture at all four sub-watersheds followed the expected pattern of hydraulic redistribution — VWC increased at night and decreased during the day (Fig. 3). All nineteen plots exhibited hydraulic redistribution throughout all six years of data, although magnitude and frequency varied (Table S3).

At some sites, hydraulic redistribution was offset from the expected nocturnal occurrence and VWC increased during the day instead of at night (Fig. 4). Offset hydraulic redistribution was periodically evident during all years, and in all basal area groups and hillslope positions (Table S4). The percentage of days where offset hydraulic redistribution occurred was significantly different among years, with 2017 having the most offsets (47 % of hydraulic redistribution events occurred during the day) and 2021 the least (31.6 % of hydraulic redistribution events occurred during the day) ($\chi^2 = 74.3$, df = 4, $p < 0.0001$). The offset frequency varied by basal area with the lowest basal area group having the most offsets and no differences between the medium and high groups ($\chi^2 = 76.2$, df = 2, $p < 0.0001$). Offset frequency also varied by hillslope position with more frequent occurrences at the shoulder (4; 52.3 % of events occurring during the day) and the fewest at the toeslope (2; 31.2

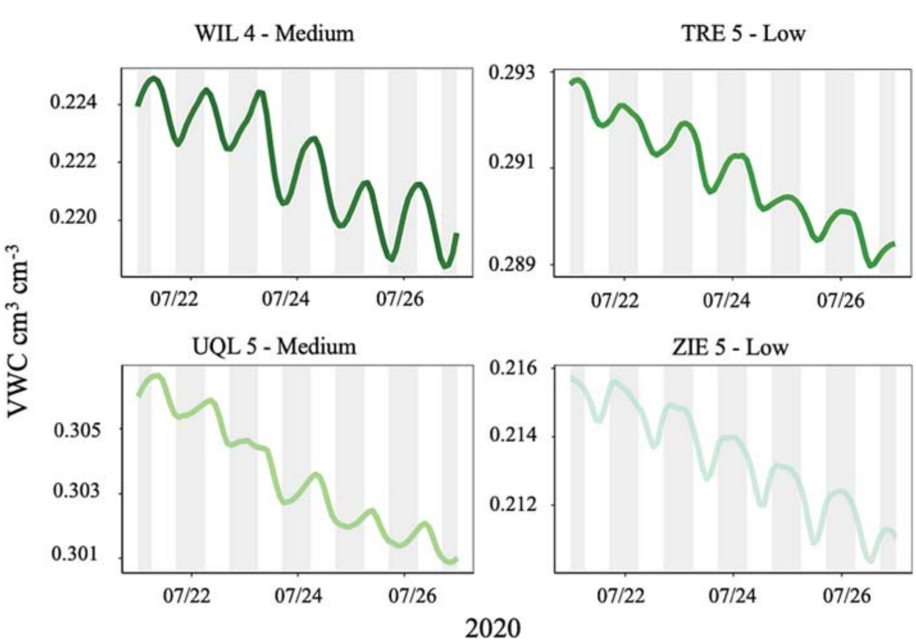

Fig. 3. Examples of diurnal fluctuations in VWC indicative of hydraulic redistribution during July 2020 at shoulder (4) and ridge (5) positions. Gray bars represent night (17:00 to 06:00). Plots are labelled by site, hillslope position, and basal area group.

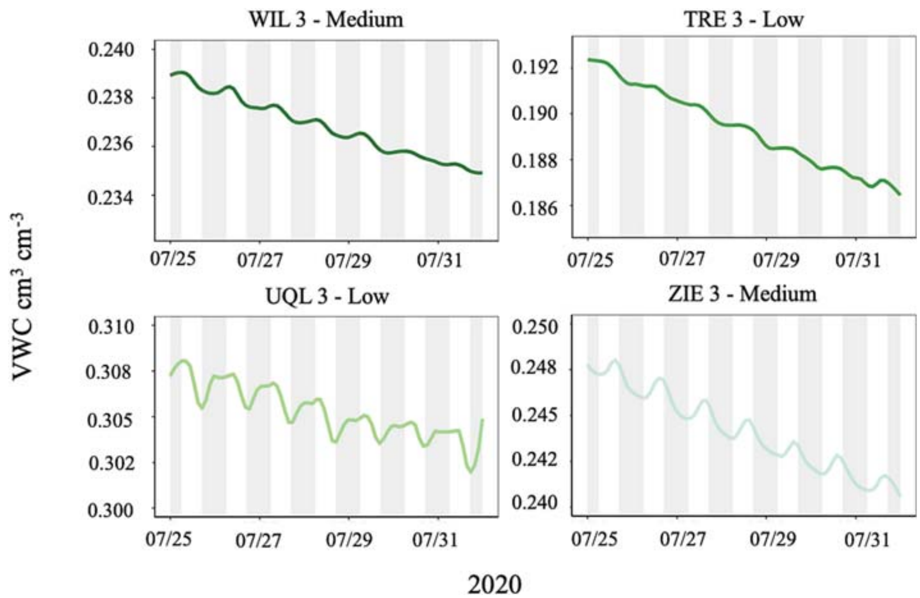

Fig. 4. Examples of diurnal fluctuations in VWC indicative of offset hydraulic redistribution at the backslope position (3) in four sub-watersheds during July 2020. The fluctuations are most evident in ZIE 3. Gray bars represent nighttime (17:00 to 06:00). Plots are labelled by site, hillslope position, and basal area group.

% of events occurring during the day) ($\chi^2 = 154.8$, df = 4, p < 0.0001).

3.3. Magnitude of hydraulic redistribution

Hydraulic redistribution magnitude was significantly correlated with VWC at the 15 cm depth ($r_s = -0.36$, p < 0.0001) and antecedent water year precipitation ($r_s = -0.05$, p < 0.0001). However, neither period, treatment, or the interaction between treatment and period were significant in the model, indicating that thinning did not have a significant effect on hydraulic redistribution magnitude (Table S5; Fig. S1).

Hydraulic redistribution magnitude differed among basal area groups ($p < 0.0001$; Fig. 5A). Typically, the group with the lowest post-harvest basal area had the highest magnitude of hydraulic redistribution and the most even distribution. In 2021, a drought year, the low group showed a distinct bimodal distribution. Hydraulic redistribution was negatively correlated with basal area in all years (Fig. 6A). The strength of the relationship differed between years — 2016 had the strongest correlation ($r_s = -0.27$) and 2020 had the weakest significant correlation ($r = -0.06$).

There were also differences in hydraulic redistribution magnitude across hillslope positions during all years ($p < 0.0001$). In general, the shoulder position had the highest magnitude of hydraulic redistribution across all years, while the ridge often had the second highest (Fig. 5B). Hydraulic redistribution was positively correlated with elevation in all years except 2016 (Fig. 6B). The strongest correlation between hydraulic redistribution and elevation was observed in 2019 ($r_s = 0.43$), the year after the harvest occurred.

Because positions higher on the hillslope (i.e, the shoulder and ridge) were generally associated with the low and medium basal area groups, we conducted a generalized linear mixed model to determine whether the interaction between basal area groups and hillslope positions were significant. We found no significant interactions between the basal area groups and hillslope positions ($p > 0.01$; Table S6), which indicates that the impact of basal area group on hydraulic redistribution does not often vary between hillslope positions and vice versa.

3.4. Hydraulic redistribution and additional days of stored water

Hydraulic redistribution provided a median of 0.42 (± 5.92) additional days of stored water before field capacity (0.13 cm^3 cm^{-3}) at the 15 cm depth was reached. This increase was significant according to a Wilcoxon signed-rank test (V = 648,882,300, $p < 0.0001$). The generalized linear mixed model found no significant effects of treatment, period, or in the interaction of treatment and period (Table S7). The additional days of stored water provided by hydraulic redistribution differed among years ($\chi^2 = 619.2$, df = 4, p < 0.0001), 2017 had the highest median value ($\widetilde{x} = 0.05 \pm 10.76$) while 2021 had the lowest ($\widetilde{x} = 0.00 \pm 7.39$).

In all years, there were significant differences in the additional days of stored water provided by hydraulic redistribution among basal area groups ($\chi^2 = 582.4$, df = 2, $p < 0.01$; Table 2). Pre-harvest the high and low basal area groups generally had more additional days provided whereas post-harvest there was only a significant difference in 2021 with the low group having fewer days.

Hydraulic redistribution also increased the number of additional days of stored water provided before reaching field capacity across hillslope positions (Table 2), and the number of additional days differed across positions ($\chi^2 = 2557.5$, df = 4, p < 0.0001). Pre-harvest, positions lower on the hillslope, and the ridge in 2016, generally had more additional days of stored water whereas post-harvest positions higher on the hillslope often had more additional days.

4. Discussion

4.1. Hydraulic redistribution at Caspar Creek

We found evidence of hydraulic redistribution near coast redwood trees at Caspar Creek with a clear diurnal signal at the 15-cm depth within the range of other hydraulic redistribution studies (Neumann and Cardon, 2012). Observed offsets or delays in the timing of hydraulic redistribution at our site were unexpected. We hypothesize that these offsets may have been due to fog or dew events both of which are not infrequent at Caspar Creek. Coast redwood forests occupy the fog belt of northern California, and studies show that they can uptake water through their leaves and bark (Burgess and Dawson, 2004; Limm et al., 2012; Mason Earles et al., 2016; Weisgrau, 2020). At Caspar Creek, fog season is from May 1st to September 30th and occurred on 57 % and 51 % of the days from 2020 to 2021 (Keppeler, 2007; Petreshen et al., n.d.). Previous work at Caspar Creek reports that fog drip events typically occur at times between 18:00 and 12:00, peaking around 06:00

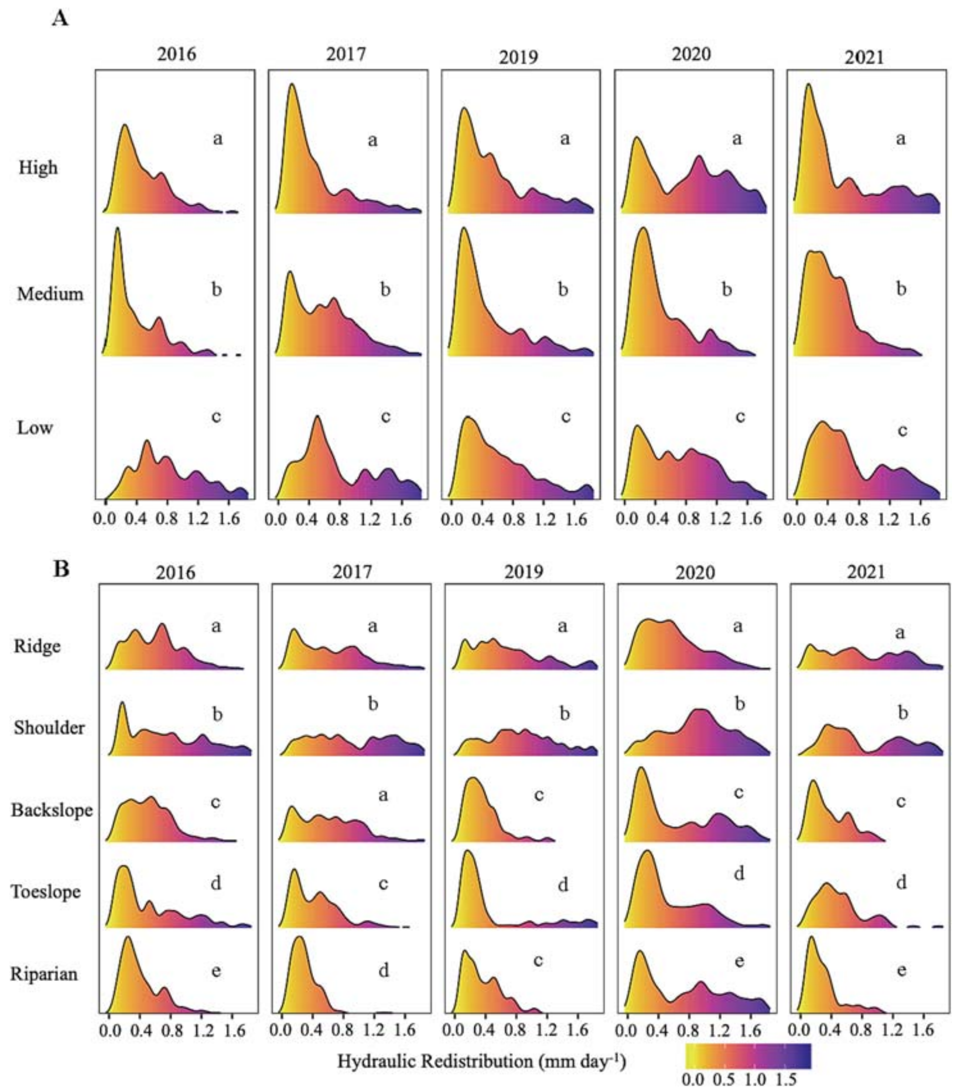

Fig. 5. Hydraulic redistribution at ridgeline plots by basal area group (A) and hillslope position (B). Letters (a-e) indicate statistically significant differences within each year ($p < 0.01$) according to the Dunn's nonparametric post-hoc test.

(Keppeler, 2007) and that there is minor infiltration of fog moisture into the soil column (Petreshen et al., n.d.). Thus, the increase in soil moisture at our sites was likely either from foliar uptake and redistribution or more likely from hydraulic lift occurring during transpiration-suppressed fog events. Though reverse sap flow has been observed at Caspar Creek during fog events, we propose that it is more likely suppressed transpiration that is leading to the offset in hydraulic redistribution as opposed to water moving down through the stem into the soil.

4.2. Forest thinning had minimal effects on hydraulic redistribution magnitude and onset

Hydraulic redistribution magnitude was not affected by period (pre-versus post-harvest), treatment (unharvested versus harvested), or the interaction between the two. Rather, like another study (Warren et al., 2006) we found that soil moisture was negatively correlated with hydraulic redistribution. We propose that the differences in soil moisture between hillslope positions may have dampened the effects of thinning on hydraulic redistribution. The upper hillslope positions (backslope, shoulder, and ridge) were the only hillslope positions that were harvested (except for the toeslope site in TRE), and because of the relationship between hillslope position and soil moisture, the effects of thinning on hydraulic redistribution may have been masked. However, though we found a significant interaction between basal area groups and hillslope positions when looking at soil moisture, we found no significant interactions when looking at hydraulic redistribution. Thus, our results suggest that hydraulic redistribution is more impacted by intrinsic conditions in the sub-watersheds like soil moisture or climatic factors.

Though the correlation between accumulated precipitation and hydraulic redistribution magnitude was small, it was still significant, which may explain some of the variation between years. The two wettest years in our study (2016 and 2019) had the lowest magnitudes of hydraulic redistribution ($\bar{x} = 0.47$; $\bar{x} = 0.47$ mm day^{-1}). Comparatively, the two driest years in our study (2020 and 2021) had the highest magnitudes of hydraulic redistribution ($\bar{x} = 0.54$- and 0.49-mm day^{-1}, respectively). In 2016 and 2019, the soil may have taken longer to dry out and reach the threshold at which hydraulic redistribution occurs (-0.4 to -0.8 MPa; Domec et al., 2004; Ishikawa and Bledsoe, 2000). One study found that the soil might need to dry out enough to effectively compete for water with the trunk and leaves of the tree (Meinzer et al., 2004). For the drier years, 2020 and 2021, likely the threshold was initiated sooner, and the drier soil may have led to greater amounts of hydraulic redistribution. These findings underscore the fact that while thinning may influence soil moisture dynamics, contextual factors like site conditions and to a lesser extent at our site, climate, appear to be

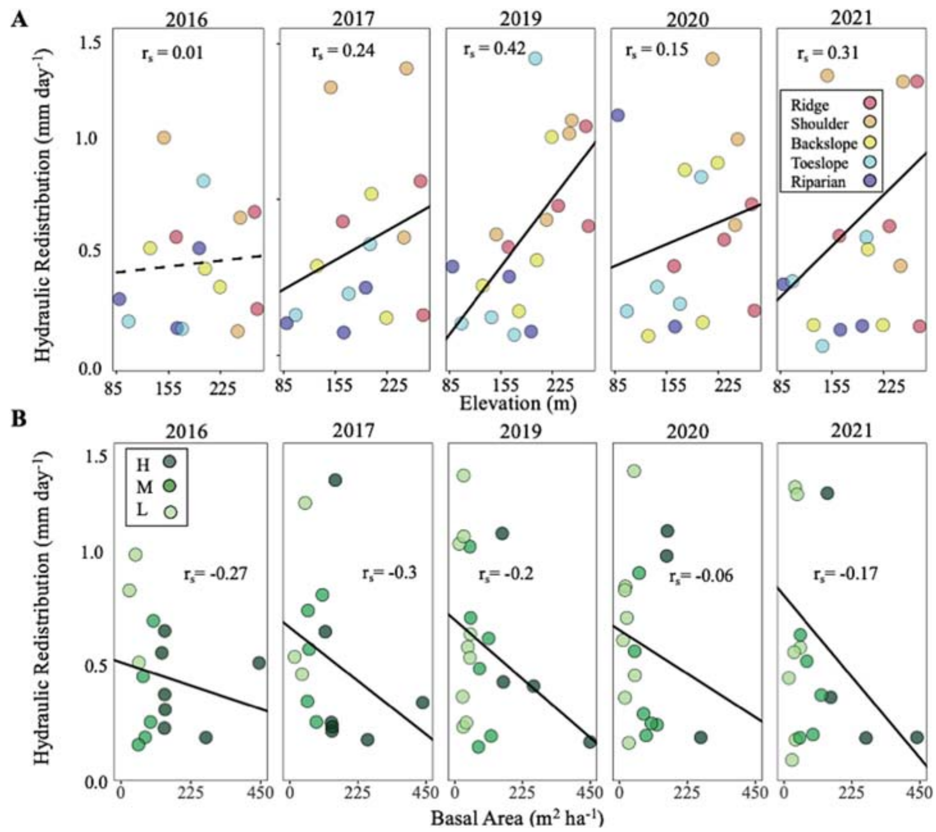

Fig. 6. Spearman's correlation between hydraulic redistribution and basal area (A) and elevation (B). Solid lines indicate significant correlations ($p < 0.01$). The riparian position in ZIE and the shoulder position in TRE had no VWC measurements in 2020. Similarly, the backslope position in TRE did not have any VWC measurements in 2021. No UQL measurements are included in 2016 or 2017.

more important for hydraulic redistribution, emphasizing the multi-faceted nature of watershed management.

4.3. Basal area impacts water relations

The different patterns between VWC and basal area pre- and post-harvest suggest that VWC patterns at Caspar Creek may be more influenced by hillslope position or sub-watershed characteristics rather than stand density as measured by basal area. We observed lower pre-harvest VWC with decreasing basal area, but post-harvest the highest VWC occurred in sites with mid-range basal area (48.1–122 m^2 ha^{-1}). Higher rates of soil evaporation in the upper 15 cm of the soil profile may explain the low VWC observed in our low basal area sites. Soil evaporation may be higher in thinned stands due to increased solar radiation reaching the soil and increased wind speeds (Brooks and Mitchell, 2011; Lagergren et al., 2008). Furthermore, although thinning may reduce transpiration (Kubota et al., 2013; Sun et al., 2017), some studies report higher rates of transpiration in thinned stands during severe droughts (del Campo et al., 2019; Simonin et al., 2007). At Caspar, mean understory evapotranspiration was found to be the highest in the lowest basal area watershed and lowest in the unharvested control watershed (Kassuelke et al., 2022). The difference in understory vegetation abundance and their different root vegetation may contribute to creating the necessary water potential gradient for hydraulic redistribution. This suggests that higher rates of basal area reduction may lead to lower soil VWC where soil evaporation rates may be enhanced, and understory evapotranspiration may be higher.

Elevated magnitudes of hydraulic redistribution have been observed in stands with less sapwood (Meinzer et al., 2004). This phenomenon holds true across diverse forest types, including old-growth ponderosa pine forests, old- or young-growth Douglas-fir forests, and three Brazilian savanna stands (Meinzer et al., 2004). We observed a similar pattern in our coast redwood forest. Stands with lower basal area exhibited the highest hydraulic redistribution magnitudes. Aside from 2021, our low basal area sites exhibited the lowest VWC—a finding consistent with previous research (Skubel et al., 2017). Hydraulic redistribution develops when a water potential gradient of sufficient magnitude is present (−0.4 to −0.8 MPa; Domec et al., 2004; Ishikawa and Bledsoe, 2000; Meinzer et al., 2004), suggesting that this gradient developed less regularly at our sites with high and medium basal areas.

4.4. Hillslope position may impact soil water relations

In the context of topography, our study revealed decreasing VWC from riparian to shoulder sites, but the ridge sites were wetter than mid-slope positions. We propose several potential explanations for this finding. First, pre-harvest, the ridges may have been wetter at the 15 cm depth (see Dymond et al., 2021a, 2021b for deeper depths) than the shoulders and backslopes because of gentler surface slopes (Table 1). The steeper slopes of the shoulders and backslopes may have led to lower infiltration rates and/or more efficient subsurface drainage due to the steeper gradient and greater development of preferential flow paths, which could lead to lower soil moisture compared to the ridges (Chen et al., 2019; Famiglietti et al., 1999).

Post-harvest, we found that the ridge, the shoulder, and the backslope all had significantly higher VWC values than before the harvest. These three positions were more heavily harvested sites than the riparian and toeslope sites (Table 1). Prior research in a century-old North Fork Caspar Creek stand reported rainfall interception and canopy evaporation rates of 22 % – rainfall that was evaporated and never reached the soil (Reid and Lewis, 2009). In addition, forest thinning led to increased throughfall at two South Fork Caspar Creek study plots

Table 2
Additional days of stored water provided hydraulic redistribution across three basal area groups and five years. Table values are median, standard deviation (in parentheses), minimum, and maximum additional hours. Letters (A – D) indicate significant differences among basal area groups or hillslope positions according to Dunn's test ($p < 0.01$).

Year	Metric	Median(SD)	Min	Max
	Basal Area Groups			
2016	High^{A}	0.42 (13.19)	0.00	36.97
	Medium^{B}	0.14 (4.45)	0.00	36.83
	Low^{A}	0.73 (7.86)	0.00	94.60
2017	High^{A}	0.61 (8.97)	0.00	111.23
	Medium^{B}	0.11 (2.93)	0.00	36.80
	Low^{A}	0.41 (4.94)	0.00	66.49
2019	High^{A}	0.36 (4.93)	0.00	49.47
	Medium^{A}	0.60 (8.72)	0.00	113.73
	Low^{A}	0.30 (3.55)	0.00	43.80
2020	High^{A}	0.45 (6.25)	0.00	71.55
	Medium^{A}	0.63 (4.18)	0.00	50.88
	Low^{A}	0.35 (4.22)	0.00	34.18
2021	High^{A}	0.42 (6.84)	0.00	67.62
	Medium^{A}	0.53 (4.25)	0.00	34.21
	Low^{B}	0.27 (3.50)	0.00	48.36
	Hillslope Position			
2016	Riparian^{A}	0.62 (3.71)	0.00	36.97
	Toeslope^{A}	0.91 (5.00)	0.00	36.96
	Backslope^{BC}	0.16 (7.57)	0.00	94.60
	Shoulder^{C}	0.15 (0.65)	0.00	4.39
	Ridge^{A}	0.87 (4.01)	0.00	24.51
2017	Riparian^{A}	1.18 (5.71)	0.00	41.47
	Toeslope^{B}	0.52 (8.98)	0.00	111.23
	Backslope^{C}	0.15 (1.25)	0.00	9.11
	Shoulder^{C}	0.15 (2.08)	0.00	18.85
	Ridge^{B}	0.31 (8.64)	0.00	111.08
2019	Riparian^{A}	0.43 (5.71)	0.00	49.47
	Toeslope^{B}	0.22 (7.29)	0.00	113.73
	Backslope^{C}	0.94 (6.19)	0.00	64.00
	Shoulder^{B}	0.15 (1.01)	0.00	12.41
	Ridge^{AC}	0.71 (5.74)	0.00	47.50
2020	Riparian	0.41 (7.30)	0.00	71.55
	Toeslope^{A}	0.29 (3.33)	0.00	27.14
	Backslope^{A}	0.67 (4.92)	0.00	50.88
	Shoulder^{A}	0.31 (3.22)	0.00	23.24
	Ridge^{A}	0.57 (4.16)	0.00	43.80
2021	Riparian^{AC}	0.24 (4.29)	0.00	23.60
	Toeslope^{A}	0.29 (2.60)	0.00	24.39
	Backslope^{B}	0.06 (3.91)	0.00	34.21
	Shoulder^{AC}	0.38 (5.82)	0.00	67.62
	Ridge^{C}	0.53 (5.60)	0.00	48.36

where 2018 harvest reduced basal area by 27 and 56 % (unpublished data). Thus, enhanced infiltration and soil moisture at the ridges, shoulders, and backslopes likely resulted from thinning (del Campo et al., 2022; Stogsdili et al., 1992). Thinning at Caspar Creek also reduced transpiration in upslope positions relative to the riparian locations that were undisturbed (Dymond et al., in prep.). These findings underscore the importance of considering multiple factors when planning forest harvesting or thinning.

As hypothesized, there was a relationship between hillslope position and hydraulic redistribution. Positions higher on the hillslope, specifically the shoulder, had the highest magnitudes of hydraulic redistribution. Topographic position has been shown to affect hydraulic redistribution in low-relief watersheds, with a higher magnitude of hydraulic redistribution in quaking aspen (*Populus tremuloides* Michx.) in uplands versus lower peatlands in the Boreal Plains of Alberta (Depante et al., 2019). Although a relationship between elevation and hydraulic redistribution was observed in our data, it was not particularly strong in part because of lower hydraulic redistribution at the ridge sites in comparison to the shoulder and backslope.

At our sites, the high magnitudes of hydraulic redistribution observed at the shoulders, in contrast to the other positions, were probably related to lower soil moistures as shown by the negative correlation between hydraulic redistribution and VWC. First, the lower soil moisture at the shoulders may be due to steep slopes, potentially leading to increased interflow and more rapid drainage (Mirus, 2015). Lower soil moisture at the shoulder may have led to more frequent development of the required soil water potential gradient necessary for hydraulic redistribution to occur than at other hillslope positions. Second, fog deposition was higher at the shoulder sites than ridge sites at both the logged ZIE site and the WIL control (Petreshen et al., n.d.). During foggy periods, transpiration may have been suppressed and sap flow reversed (Petreshen et al., n.d.) because of reduced transpiration and/or foliar uptake of fog water. Other studies on coast redwoods and other species have found sustained periods of reverse flow during fog periods, and this fog water may be redistributed to the soil (Burgess and Dawson, 2004; Nadezhdina et al., 2010). To summarize, it appears that the higher hydraulic redistribution magnitudes at our shoulder sites may have been due to influences of both antecedent soil moisture conditions and fog.

We remain uncertain as to why the ridges often had relatively higher magnitudes of hydraulic redistribution despite their high soil moisture. Our ridge sites have relatively deep soil (Table 1) and higher groundwater levels (McKeever et al., in prep) making the potential for a soil moisture gradient more likely as roots could extend deeper in this region because of deeper soil. Coast redwoods are stump sprouters and roots continue to function and nourish rapid regrowth even after the main stem has been removed (Fritz, 1959). Redwood sprouts from living stumps have been shown to have greater growth rates than seed sprouted and planted seedlings — this may be a consequence of continuing hydraulic redistribution by pre-existing root systems providing more water to seedlings (Fritz, 1959; Leffler et al., 2005). The remaining stumps and roots left after harvest at the ridges may have continued transporting and conducting hydraulic redistribution.

4.5. Hydraulic redistribution impacts soil water storage

Hydraulic redistribution increased soil water storage at Caspar Creek sites. There were a significant number of additional days of soil water storage in the top 15 cm due to hydraulic redistribution (Table 2). It is likely that this increased soil water storage benefited not only those plants conducting hydraulic redistribution, but also neighboring herbaceous plants and trees that have been shown to obtain a significant proportion of their water from hydraulic redistribution by other plants (Caldwell and Richards, 1989; Dawson, 1993; Domec et al., 2010; Emerman and Dawson, 1996).

5. Conclusion

Our study sheds light on the complex interplay between forest management practices and site factors influencing hydraulic redistribution dynamics in a coast redwood forest. We did not measure any effect of forest thinning (harvest) on hydraulic redistribution or additional days of stored water within the upper soil profile. Meanwhile, variations in annual precipitation and consequential variations in soil moisture were shown to be influential on the magnitude of hydraulic redistribution. Low basal area resulted in the highest magnitude of hydraulic redistribution. Positions higher on the hillslope had higher magnitudes of hydraulic redistribution, underscoring the need to discuss topographic characteristics in watershed management strategies. These results contribute to our understanding of how trees affect the movement of water through soils as well as how forest thinning can affect that movement. Specifically, climate and site factors appear to have more control over hydraulic redistribution than forest thinning.

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CRediT authorship contribution statement

E.W. McKeever: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Data curation, Conceptualization. **S.F. Dymond:** Writing – review & editing, Methodology, Data curation, Conceptualization. **E.T. Keppeler:** Writing – review & editing, Methodology, Funding acquisition, Data curation, Conceptualization. **J.W. Wagenbrenner:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Elise McKeever reports financial support was provided by National Science Foundation. Salli Dymond reports financial support was provided by National Science Foundation. Elise McKeever reports a relationship with American Geophysical Union that includes: travel reimbursement. If there are other authors, they 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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Data availability

Data will be made available on request.

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