Environmental determinants of vegetation in the drawdown zones of a Columbia River Treaty reservoir: a template for ecosystem enhancement

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Abstract

Water storage reservoirs alternately inundate and expose the drawdown zones, limiting riparian vegetation that provides wildlife habitats and contributes to the aquatic food-web. To characterize plant distributions and hydrogeomorphic associations, we inventoried quadrats in transects extending from the full-pool (FP) margin, downwards 12 m through the drawdown zones at sites around the Duncan Reservoir in British Columbia, Canada. Among the 69 plant species, black cottonwoods (*Populus trichocarpa*), willows (primarily *Salix sitchensis*) and other trees and shrubs occurred sparsely, rarely extending below 2 m below FP. Perennial herbaceous plants, especially horsetail (*Equisetum arvense*) and sedges (primarily *Carex utriculata*), were most common, extending down ~5 m below FP, and ruderal annual plants occurred sparsely at greater depths. Vegetation Cover and Species Richness were correlated with environmental factors, with (1) *Elevation* being highly influential, reflecting inundation duration and depth. (2) *Position*, longitudinal location, reflected greater vegetation diversity downstream of the reservoir. (3) Finer *Substrate* texture was favorable to retain moisture, but coarse sediments would resist erosion. (4) Shallow *Slope* was favorable to reduce drainage and included finer sediments. (5) *Distance* from the FP shoreline could reflect seed source proximity. Stepwise linear modeling with combined environmental factors accounted for ~30% of the variation in Vegetation Cover and Richness, and Canonical Correspondence Analysis revealed plant groupings relative to the environmental influences. At this and other storage reservoirs, regimes that reduce the frequency and duration of inundation could promote vegetation in locations with suitable environmental conditions in the upper drawdown zones, thus providing ecosystem enhancement.

Keywords Columbia River Treaty · *Equisetum* · Hydrogeomorphic associations · Riparian vegetation · Substrate · Willows

Introduction

Most of the world's major rivers have been dammed, largely to provide storage reservoirs that display seasonal filling and drawdown to satisfy the objectives of flood control, hydropower generation, and water management for agricultural irrigation and other human uses (Graf 1999; Nilsson et al. 2005). The annual alternations in reservoir level impose lethal combinations of inundation and exposure, and the drawdown zones are consequently relatively barren of riparian or waterside vegetation (Wilcox and Meeker 1991; Nilsson et al. 1997; Luken and Thieret 2001; Riis and Hawes 2002). This reduces ecological benefits including wildlife habitats and contributions to the reservoirs' aquatic food-webs (Tabacchi et al. 1998; Richter and Richter 2000).

Despite the global extent and ecological importance, there have been relatively few analyses of the environmental factors that determine vegetation distributions in reservoir drawdown zones. Baker et al. (2000) and Chapin and Paige (2013) provide integrative reviews, indicating that lethal inundation excludes vegetation, and perennial vegetation is generally limited to the upper few m below the full pool margin. Predictive models have been developed (Nilsson and Keddy 1988; Hill et al. 1998; Rains et al. 2004)

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and there have been suggestions that modest changes in the inundation regime might promote vegetation in the upper drawdown zones (Nishiro and Washitani 2009; Campbell et al. 2016; Meeker et al. 2018). These applications would benefit from a better understanding of the ecophysiological characteristics of the reservoir vegetation, including tolerances to inundation or submergence, and the interacting physical site conditions within the drawdown zones (Wilcox and Meeker 1991; Amlin and Rood 2001; Auble et al. 2005; Howard and Wells 2009).

To contribute to this knowledge foundation, this study investigated a dammed tributary of the Columbia River, which provides the greatest Western Hemisphere flow to the Pacific Ocean. The Columbia River system provides one of the world's most extensively dammed watersheds, with 60 major dams and reservoirs on the mainstem river and its larger tributaries (BC Hydro 2020). Of these, the first, second and fourth largest reservoirs were created by dams that followed the 1964 Columbia River Treaty (CRT) between Canada and the United States. This international agreement sought to coordinate further development of the Columbia River system for two primary objectives, flood control and hydropower generation (Cosens 2016). Approaching the completion of the initial CRT interval in 2024, negotiations to modernize the CRT propose the addition of a third major objective, ecological function (Osborn 2012). The promotion of riparian vegetation within the upper drawdown zones of the CRT reservoirs could contribute towards this objective.

Prior approaches to enhance vegetation around CRT and other reservoirs have generally involved vegetation plantings (Fowler and Hammer 1976; Jackson et al. 1995; Miller et al. 2018b). These are costly, generally involve limited areas, and may fail since conditions that are lethal for natural colonization can be lethal for transplants. An alternative strategy would seek *systemic restoration*, through changes in the reservoir regime. As a systems approach, this would alter the underlying hydrological pattern and could have benefit at locations around the full reservoir. A systemic restoration strategy would extend from the functional environmental flow strategy to restore riverine riparian ecosystems (Stromberg 1993; Richter and Richter 2000; Merritt et al. 2010). That approach involves deliberate dam operations that satisfy the hydrogeomorphic conditions for vegetation colonization and ecosystem development (Rood et al. 2005; Bagstad et al. 2006; Auble et al. 2007; Yarnell et al. 2015).

A parallel, systemic approach for reservoir enhancement requires knowledge of the prevalent plants and their hydrogeomorphic requirements, the combinations of water and other physical conditions for plant colonization and maturation (Hupp and Osterkamp 1996; Dixon et al. 2002; Bagstad et al. 2006; Egger et al. 2015). This approach

recognizes the importance of the patterns of the bank inundation and exposure, along with other environmental factors that determine site suitability. To contribute this information, we inventoried the distributions of vegetation and physical conditions in the drawdown zones of the Duncan Reservoir, in the headwater region of the Columbia River Basin. This CRT reservoir is situated in between the other CRT reservoirs and the findings should thus be applicable those and other storage reservoirs in the North American Pacific Northwest and elsewhere, particularly in mountain drainages with temperate climates (Baker et al. 2000; Miller et al. 2018a).

With this study, we expected that (1) elevation in the drawdown zone would provide the predominant environmental influence on vegetation since this determines the pattern of inundation and submergence, versus exposure (Nilsson and Keddy 1988; Wilcox and Meeker 1991; Hill et al. 1998; Rains et al. 2004; Chapin and Paige 2013). We anticipated elevational bands or strata with different plant species and communities, largely reflecting differing inundation tolerances. We further expected that (2) additional physical environmental factors would influence site suitability and contribute to the hydrogeomorphic conditions that enabled the different plant species and communities (Hupp and Osterdamp 1996; Bagstad et al. 2006; Hough-Snee et al. 2015). Finally, we anticipated that (3) the vegetation composition and distributions and hydrogeomorphic associations would correspond to patterns of riparian vegetation along regional rivers (Polzin and Rood 2006; Egger et al. 2015).

Materials and methods

The Duncan Reservoir

The Duncan Reservoir was created in 1967 by the Duncan Dam on the Duncan River in southeastern British Columbia, Canada (Fig. 1). This 40 m high earthen dam has no hydroelectric turbine and is operated for water storage and release within the Kootenay and Columbia River systems (BC Hydro 2007). The 45 km-long reservoir inundated the natural Duncan Lake and the extensive riparian wetland complexes upstream and downstream (Utzig and Schmidt 2011). Further aspects of this reservoir system and study are described in our technical reports that provide additional analyses and data appendices (Polzin et al. 2010; Rood et al. 2019; Polzin and Rood 2022).

Hydrology

To analyze inundation patterns, historical reservoir levels were obtained from the Water Survey of Canada HYDAT
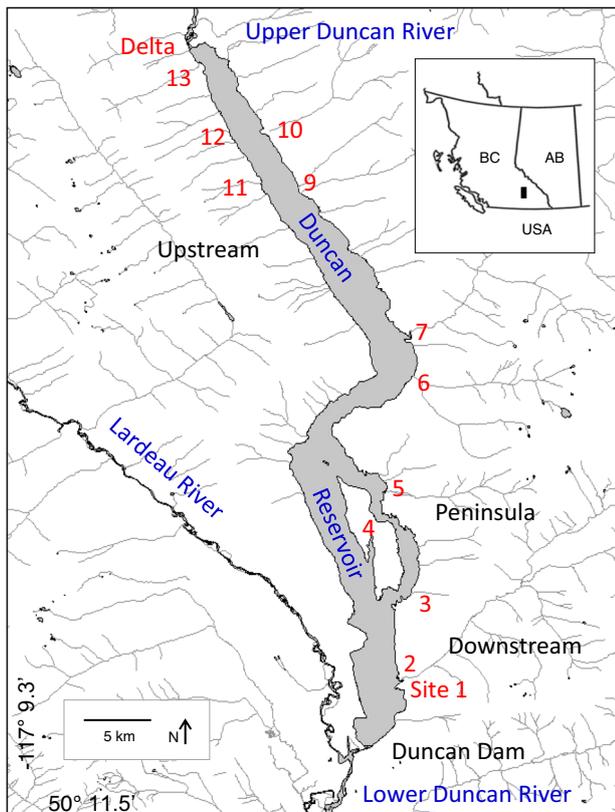
Fig. 1 Map of the study area showing the study sites along the Duncan Reservoir in southeastern British Columbia, Canada

archive https://wateroffice.ec.gc.ca/search/historical_e.html. For the interval following damming, daily levels were at Station #08NH127, 'Duncan Reservoir at Duncan Dam', from 1967 through 2022. To consider the reservoir regime, daily averages were determined for the interval from 2003 through 2007, and daily values were assessed for 2008, prior to our vegetation inventory in 2009. The reservoir regime was revised in 2009 to enhance downstream conditions, and the 2009 hydrograph is provided for comparison. To provide a reference comparison (Wilcox and Meeker 1991), daily levels were obtained for Station #07SB012, 'Duncan Lake near Howser', and averaged for 1957 to 1967, prior to that natural lake being flooded with the Duncan Reservoir.

Vegetation inventory and characteristics

From 2009 through 2020, we observed the whole reservoir multiple times, including when the levels were near full pool in July and August, and during the drawdown conditions in April into June (Fig. 2). The vegetation inventory was in June 2009, during the 2009 filling. The vegetation distribution would reflect the reservoir regime especially in the prior growing season of 2008, and through spring 2009.

During the development of the Water Use Plan for Duncan Dam (BC Hydro 2007), prospective areas for vegetation establishment were identified in the drawdown zones of Duncan Reservoir. Twelve sites were recognized, which occurred along the full longitudinal extent of the reservoir and included different geomorphic landforms, including alluvial fans at creek inflows, and a peninsula near the middle of the reservoir (Fig. 1).

In June 2009, true-color digital aerial photographs with 10 cm surface resolution were acquired and orthorectified for each study site (Terrasaurus Aerial Photography, Vancouver, Canada). The apparent plant cover types within each site were delineated into polygons based on common appearance (Polzin et al. 2010). Transect locations were randomly selected along the shorelines of each site and extended perpendicular from the full pool (FP, 576.7 m ASL) shoreline and down for 12 m elevation (depth) into the reservoir drawdown zone. Transects were selected until the full range of cover types for that site was represented, resulting in one transect for sites 3, 5 and 6; two transects for sites 1, 4, 11 and 12; three for 2, 7, and 10; and four for sites 9 and 13; providing 28 total transects at the 12 study sites. Initial site 8 was mis-targeted with the aerial photography, but the original numbering was retained because it was included in another study. Since the bank profiles varied, lengths and quadrat numbers varied across the transects.

Following the approach of Stromberg et al. (1996) and Braatne et al. (2007), vegetation sampling was intended to include the range of vegetation types and enable efficient resampling over subsequent years (Polzin and Rood 2022). For each transect, a tape-line was positioned and 1 m x 1 m quadrats commenced below the FP margin and were positioned at locations with changes in vegetation type, and for larger homogeneous patches or barren bands, quadrats were positioned at 10 m intervals along shallow-sloped sites, and 5 m intervals with steeper slopes (>~10%). Elevations were surveyed with a Nikon automatic level (AC-2, Nikon-Trimble Co., CA, USA) at 2 m distance intervals and at other points of substantial change (>25 cm).

For each quadrat, vascular plant species were identified in accordance with Hitchcock and Cronquist (1976) and Parish et al. (1996), with taxonomic treatments reconsidered relative to the United States Department of Agriculture, Plants Database (https://plants.usda.gov/home). That source also provided the basis for native/non-native and wetland status. The percent shoot cover of each species was estimated with a 7-point, modified Daubenmire (1959) scale (0–1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%); the cover class mid-point was used for statistical analysis.

From the vegetation inventory, two community measures were emphasized. *Vegetation Cover* indicated the

Fig. 2 Photographs displaying Duncan Reservoir near full-pool (**A**, Aug. 30, 2020), versus drawn-down (**B**, May 7, 2019). These are facing southward from near Howser Creek, crossing the barren floodplain in the middle of the photo, toward the natural Duncan Lake in the distance. **C** The shoreline north of Glacier Creek displaying woody debris and some cottonwoods. **D** The exposed floodplain near the north end with substantial cover especially by horsetail (*Equisetum*, May 7, 2019)
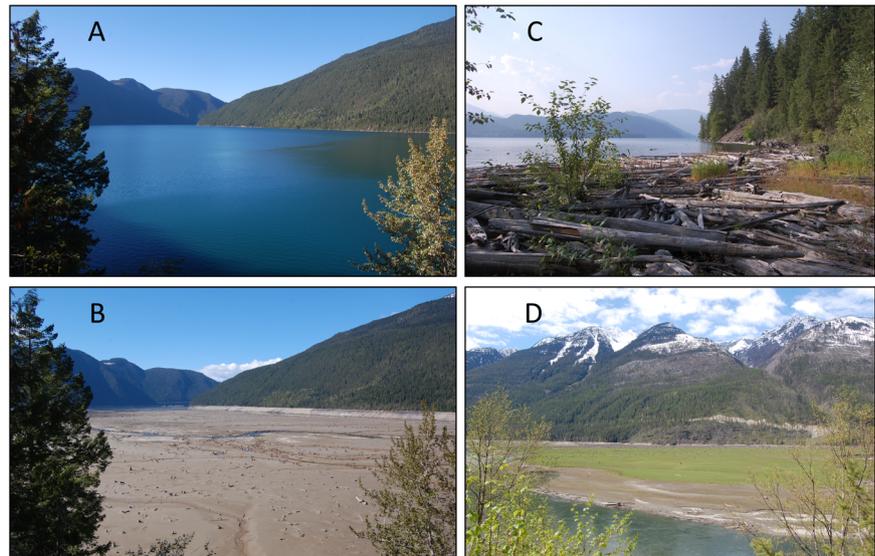
total shoot cover for all species, and since there was ground cover, and the shrub and tree canopy layers, the combined Vegetation Cover could exceed 100%. *Richness* indicated the number of different plant species within each quadrat. We considered different transformations for the vegetation characteristics, and the square root (√) of Richness and log of Vegetation Cover increased some Pearson Product correlations and were adopted. In addition to the community characteristic of combined Vegetation Cover, we also assessed Cover of each plant group: trees, shrubs, herbaceous perennials, and herbaceous annuals, and for the predominant plant species of each group.

Environmental factors and predicted patterns

Seven environmental factors were initially investigated, and five were included in most analyses. These commenced with *Position*, or longitudinal location of the site, measured as the distance along the reservoir midline upstream from Duncan Dam. A square root conversion could account for the three-dimensional seed dispersal and increased correlations with vegetation characteristics and was adopted. As well as reflecting conditions in the respective drawdown zone, site locations and Position would be influenced by the adjacent landscape, including the valley width and nearby land use influences from settlement and agriculture that would influence seed sources. With Position, we anticipated some similarity between nearby sites, and longitudinal patterns, downstream to upstream (south to north).

Distance in m was perpendicular from the reservoir FP shoreline and we anticipated that trees, shrubs and perennials with lower inundation tolerances, would be limited to short distances, near the reservoir margin. We anticipated

that annuals would occur more fully along the transects but that there still might be progressive decrease in abundance, due to increasing distance from seed sources, and longer inundation durations at lower zones.

We anticipated that *Elevation* would provide a predominant physical environmental factor since this represents the plant position relative to the reservoir regime. Elevation is the inverse of reservoir depth and we anticipated decreasing vegetation abundance with lowering Elevation due to increased frequency, duration, and depth of inundation. We expected that Elevation and Distance would be strongly negatively correlated due to the progressive bank slopes.

Characterizing the elevational change over distance, *Slope* was assessed as the percentage fall or rise versus run. We anticipated that shallow slopes would provide more favorable conditions for vegetation since water run-off, flooding, and drainage would be more gradual. We expected steeper slopes to be less favorable since these would be drier and prone to erosive slumping, especially with fine sediments.

Two other spatial factors were considered, but insufficiently represented with our study design. For *Aspect*, the down-slope transect direction was considered relative to an eight-point solar-drying index with 45° intervals. However, the reservoir alignment is fairly consistent and the perpendicular transects provided slight variation. *Reservoir Side* was another candidate factor (1 west, 2 east), but the west side of the valley is generally steep and inaccessible, and includes bedrock exposures. Only three west-side sites were included, and were near the north end. Aspect and Reservoir Side were recorded for each quadrat but with limited variation and contribution, these were not included our final analyses.

Surface *Substrate* was assessed for each quadrat during the vegetation inventory. The cover proportions were estimated for five particle size classes: 1, silt (and clay, < 0.1 mm); 2, sand (0.1–2 mm); 3, gravel (2–6 mm); 4, cobble (6–25 cm); and 5, boulders (>25 cm, or bedrock). The composite Substrate Texture Index was calculated based on the number of the sediment class x the estimated proportional area and ranged from 1 (very fine) to 5 (very coarse). We anticipated that finer substrates would be beneficial for vegetation, since these would retain moisture and increase capillarity, moisture rise above the phreatic zone. While coarser substrates could be less favorable for seedling colonization, these would be more resistant to erosion from wave action and floating woody debris, which was common around the reservoir. Also reflecting erosion patterns, we expected interactions between slope and substrate, with sands and finer gravels being sparse on steeper slopes since these would be depleted with slumping and with erosion from water and even wind.

Statistical analyses—correspondences within and between environmental factors and vegetation characteristics

The statistical analyses with SPSS 27 (SPSS IBM, NY) commenced with descriptive statistics for the different environmental factors and vegetation characteristics. We then undertook bivariate correlations with the quadrat data, with the Pearson Product r, and rank-order Kendall τ and Spearman ρ tests. The two non-parametric tests provided very similar outcomes, and we present the Spearman ρ correlations that are closer to the Pearson Product r. For plotting clarity, we grouped the quadrat data into categories for each environmental factor and undertook linear or quadratic regressions.

Modeling and ordination

To assess multiple environmental factors, forward-stepwise linear modeling was undertaken, with the SPSS terminology for the output measures (SPSS: Regression, Automatic Linear Modeling, Objective: Standard Model). Richness and Vegetation Cover were the separate target variables, with the five environmental factors as predictors: Position, Distance, Elevation, Slope and Substrate. In addition to the modeling with all five factors, factor subsets were included to assess models with one, two or three factors, and the outcomes with higher accuracies are presented.

Relationships and groupings of different plant species relative to the environmental factors were assessed with Canonical Correspondence Analysis (CCA) using PC-ORD

(v. 5.31 MjM Software, Oregon; McCune and Grace 2002; McGarigle et al. 2000). The 15 prevalent (occurrence x cover) species were analyzed, and we present the ordination with the environmental variables that might be commonly applicable across draw down reservoirs: Elevation, Substrate, and Slope. For this, the variables were relativized by dividing the quadrat value by the maximum observed, providing values up to 1. For CCA scaling, axis scores were centered and standardized to unit variance, axes were scaled to optimize species representation, and scores for graphing quadrats were linear combinations of environmental variables (McCune and Grace 2002).

Results

The Duncan reservoir

When full, Duncan Reservoir resembles a mountain lake (Fig. 2A) as the flooding raised and expanded the natural Duncan Lake that existed prior to damming (Fig. 3B). With drawdown, the exposed floodplain zones were largely barren of vegetation, with exposed stumps from the forest that was cleared prior to flooding (Fig. 2B). At locations with more gradual slopes and primarily on the alluvial fans of the tributary creeks, the drawdown zone slopes are shallower, and the creeks also contribute surface and groundwater. These tributary fans were the primary sites that were inventoried in this study and included some vegetation and sparse black cottonwood trees (Fig. 2C). Floating logs and other woody debris were common around the reservoir, and these often accumulated in the shallower drawdown zones (Fig. 2C). With wave action, these would increase scour of the surfaces and vegetation. The floodplain zone at the upstream end is shallower and consequently has less inundation and more exposure. This allowed more extensive vegetation, and especially the abundant horsetail (*Equisetum arvense*) (Fig. 2D).

Hydrology

The Duncan Reservoir undergoes an annual cycle of drawdown and refilling (Fig. 3A; and Polzin and Rood 2022 for additional years). Winter drawdown releases water that passes downstream through six hydropower facilities on the Kootenay River, and then eleven downstream along the Columbia River. The drawdown also provides storage capacity to contribute to downstream flood flow attenuation (Cosens 2016).

With the winter drawdown, the reservoir progressively declined almost 30 m from September through April, with steeper recession through the winter interval from January through March (Fig. 3A). Reservoir filling followed from

Fig. 3 A Annual fluctuation of Duncan Reservoir: average of the 1967 to 2007, 2008, which preceded the field study; and a new operating regime implemented in 2009. The cottonwood seed dispersal interval is from Herbison et al. (2015). **B** Average annual fluctuation of the natural Duncan Lake, which preceded the reservoir—note the different y-axis scale (0 corresponds to 545.6 m ASL). Thirty-day intervals are designated, with letters for months
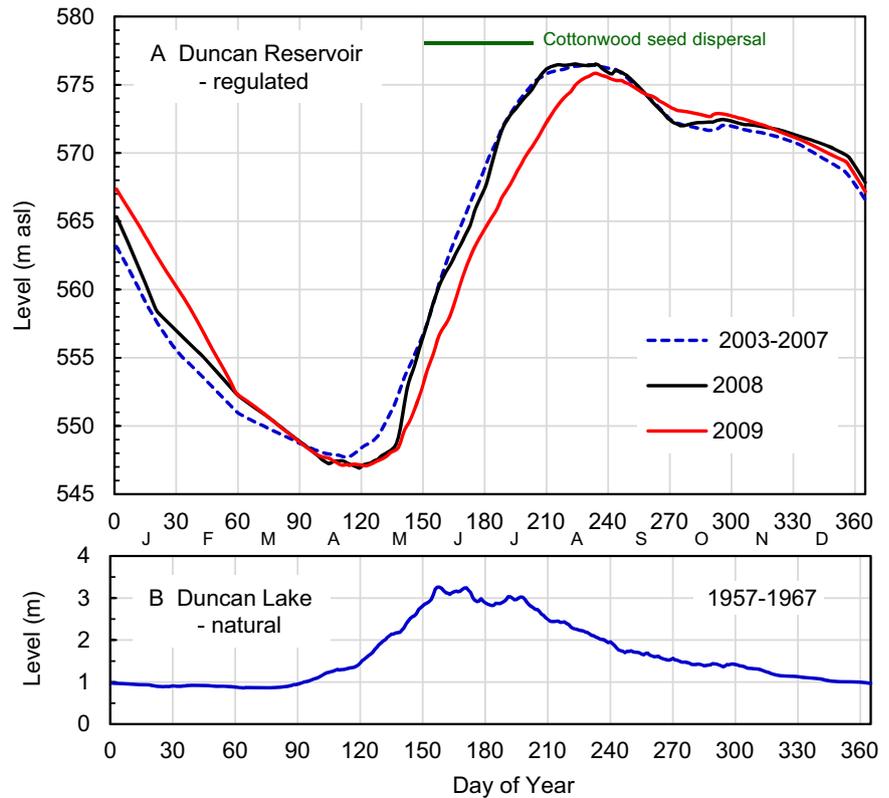
May to approach the full-pool (FP) level in July, and it remained relatively full through August (Fig. 3A). A new operational regime commenced in 2009 (Fig. 3A), but our vegetation inventory was in the early summer of 2009, prior to the operational change.

This regulated, reservoir regime provided a water level pattern that was somewhat inverted from the natural, regional river stage regime, or the pattern of the natural Duncan Lake that was flooded by the reservoir (Fig. 3B). The natural nival pattern would provide the highest river stage or lake level in early June, following the major interval of snowmelt, and the common late spring and early summer rains. With the natural pattern, gradual recession would follow (Fig. 3B), and seed release of cottonwoods and other native riparian plants would often coincide with the recession (Fig. 3A; Herbison et al. 2015). This would provide ideal timing since the seeds would land on or float to the newly exposed, saturated banks that are ideal for seedling establishment (Polzin and Rood 2006). In contrast, the artificial reservoir regime provided rising water during cottonwood seed release, which could submerge or uprooted newly established seedlings. The reservoir exposure regime would allow colonization by plants with year-round seed availability, including introduced and weedy plants, and thus the seeding phenology would strongly influence the reservoir colonization, as has been observed for other reservoirs (Akazami et al. 2013).

Table 1 Characteristics of the 69 plant species observed in the Duncan Reservoir drawdown zone (as defined in the Methods)

Growth form		Status		Wetland classification	
Tree	6	Native	53	Obligate Upland	8
Shrub	15	Weedy	9	Facultative Upland	22
Perennial Forb	31	Non-Native	16	Facultative	23
Perennial Grass-type	7	Weedy	11	Facultative Wetland	11
Annual Forb	8			Obligate Wetland	5
Annual Grass-type	2				

Vegetation inventory

There were 563 assessed quadrats along the 28 transects at the 12 study sites. We observed 69 plant species, with 6 trees, 15 shrubs, 38 herbaceous perennials, and 10 annuals (Table 1). For both the perennials and annuals, about 4/5 were forbs, with graminoids (grass-like) being less common. About 77% of the plants were native, reflecting the relatively remote location of this reservoir. While 29% were designated as weedy, this categorization reflects influence in agricultural systems, and about one-half of these were native species.

For wetland classification that reflects inundation tolerance, most species were assessed as facultative plants

(Table 1). Facultative and obligate upland plants were more common than facultative or obligate wetland plants, indicating that along with inundation tolerance, drought tolerance was also influential. Most of the observed plant species (Table 2) are commonly found in the regional riparian zones, such as along the lower Duncan River, or the regional Kootenay or Elk Rivers (Egger et al. 2015; Polzin and Rood 2006). Trees included black cottonwood (*Populus trichocarpa*), the predominant riparian tree throughout the Pacific Northwest. Trembling aspen (*P. tremuloides*) was sparse, and generally in higher and drier positions, while western redcedar (*Thuja plicata*) is commonly a late successional tree in regional riparian forests (Egger et al. 2015).

The observed shrubs were also typical for regional riverine riparian zones, with willows (*Salix* spp., especially S. sitchensis) being most common (Table 2). Sitka alder (*Alnus crispa*) was common and in regional riparian zones, often occurs away from the dynamic stream channels, where willows are more abundant. Dogwood (*Cornus stolonifera*) was common and is often intermediate in distribution between the willows and alder. Other shrubs were less prevalent (Table 2).

Perennial herbaceous species were the most abundant plants, providing two-thirds of the prevalence of plants in the drawdown zones (67%, Table 2). Horsetail (*Equisetum arvense*) was most abundant, representing about one-half of the perennials (51%). Sedge, especially *Carex utriculata*, was the second most common plant type (20%), and like horsetail, occurred with substantial occurrence at most of the sites (Table 2). In contrast, some other plants such as primrose (*Oenothera villosa*) had more localized distributions. Of the perennials, potential problem plants included the noxious, introduced spotted knapweed (*Centaurea stoebe*), and reed canarygrass (*Phalaris arundinacea*), which is extensive along the nearby Kootenai River and around Arrow Reservoir, another Columbia River Treaty reservoir that is nearby (Merigliano and Lesica 1998; Enns et al. 2010; Miller et al. 2018a).

Annual plants extended to the lower drawdown zones, and these commonly display ruderal strategies, with rapid colonization. Silver hairgrass (*Aira caryophyllea*) and smartweed (*Polygonum lapathifolium*; syn. *Persicaria*) were most common, along with a mix of other native and non-native species (Table 2).

Environmental factors and correspondences with vegetation

Across the study quadrats, there were positive and negative correlations within and between the environmental factors and vegetation characteristics (Table 3). Similar outcomes were derived with the parametric Pearson Product *r* and the non-parametric, rank-order Spearman ρ correlations (Table 3).

Within the environmental factors (Table 3), *Position* (location) was negatively correlated with *Distance* and positively correlated with *Slope*, reflecting the longer, shallower sites especially near the north end delta where the upper Duncan River flows into the reservoir (Fig. 1). As expected, Distance was negatively correlated with Elevation and Slope, since the transects progressively dropped in elevation and longer transects were shallower. *Substrate* was only slightly correlated with Elevation, and more strongly correlated with Slope, reflecting coarser sediments on steeper slopes.

The vegetation community characteristics of *Richness* and *Vegetation Cover* were strongly correlated (Table 3), indicating common favorability for multiple plant species. Both vegetation measures were correlated with the five environmental factors, except for the pairing of Cover and Distance (Table 3). Richness was most strongly correlated with Position ($r = -0.443$), with higher Richness at the sites near the south end of the reservoir (Fig. 4), closer to agricultural and other land use activities, and the diverse delta zone where the Lower Duncan River outflows into Kootenay Lake. Vegetation Cover was slightly correlated with Position and plotting of the vegetation characteristics for the Sites suggests multiple influences (Fig. 4). Near the south end, sites 1, 2 and 3 (Fig. 1) had high Richness, reflecting the proximity to diverse vegetation communities, but low Vegetation Cover. The peninsula sites 4 and 5 displayed high Richness and high Vegetation Cover, indicating favorable environments for diverse vegetation. Towards the north end, sites 6 to 12 were on small alluvial fans from minor creek outflows and displayed low Richness and low Vegetation Cover. Approaching the delta at the north end, site 13 included a larger alluvial fan and the shallow drawdown zone was more favorable, as indicated in the high Vegetation Cover, but its remote location resulted in intermediate Richness (Fig. 4).

As expected, quadrat *Elevation* was positively correlated with the vegetation characteristics (Table 3). Elevation reflected the extent of reservoir flooding, including duration and depth, which determines inundation and submergence. Elevation was correlated with Richness and provided the strongest environmental correlate with Vegetation Cover ($r = 0.406$). Vegetation Cover displayed a linear decline downwards into the drawdown zone (Fig. 5A). The linear trend was interrupted with a consistently dense band above 572 m, coinciding with the reservoir being held within 1 m below this level in the preceding years (Fig. 3). Excluding that offset value raised the linear correspondence (R^2) to 0.84.

The total number of observed plant species was combined for each elevational band, and this was much higher at the reservoir full-pool shoreline (Fig. 5B). This would

Table 2 List of the vascular plant species found in the Duncan Reservoir drawdown zones, including the more abundant (extent of cover) and numerous (number of occurrences) species by growth form

| Scientific Name	Common name	Growth Form	Native Status	Wetland Classification	Quadrats (#)	Sites (#)	Mean % Cover	Prevalence
Trees								
Populus trichocarpa	black cottonwood	T	N	FACW	43	7	20.1	923
Populus tremuloides	trembling aspen	T	N	FAC	5	4	15.5	139
Thuja plicata	western redcedar	T	N	FAC	7	4	8.2	87
Shrubs								
Alnus crispa	Sitka alder	S	N	FACW	15	2	66.7	517
Salix sitchensis	Sitka willow	S	N	FACW	35	2	39.1	463
Cornus stolonifera	red osier dogwood	S	N	FACR	13	4	21	303
Rubus parviflorus	thimbleberry	S	N	FAC	8	4	10.3	117
Salix lucida	Pacific willow	S	N	FACW	7	2	15	79
Lonicera utahensis	Utah honeysuckle	S	N	FAC	8	1	24.7	70
Perennials								
Equisetum arvense	field horsetail	PF	N, W	FAC	754	12	25.6	8,435
Carex utriculata	beaked sedge	PG	N	OBL	387	10	17	3,344
Cinna latifolia	drooping woodreed	PG, R	N	FACW	515	11	7	1,747
Oenothera villosa	evening primrose	PF	N	FAC	41	3	42.1	809
Agrostis gigantea	redtop	PG, R	NN	FAC	331	8	5.2	757
Cerastium fontanum/ nutans	mouse-ear/nodding chickweed	PF/AF, R	N, W	UPL/FACU	386	5	3.7	363
Calamagrostis canadensis	bluejoint	PG, R	N	OBL	68	6	5.3	262
Rumex crispus	curly dock	PF	NN, W	FAC	85	5	3.8	175
Dryas drummondii	yellow mountain avens	PF	N	FACU	8	1	33.8	96
Erysimum inconspicuum	small wallflower	PF	N	UPL	42	1	14.1	91
Leucanthemum vulgare	oxeye daisy	PF, R	NN, W	FACU	11	3	8.2	82
Phalaris arundinacea	reed canarygrass	PG	N, W	FACW	6	3	8.8	65
Centaurea stoebe	spotted knapweed	PF, R	NN, NOX	UPL	9	3	6.7	60
Myosotis asiatica	mountain forget-me-not	PF	N	FACW	90	2	2.5	47
Epilobium angustifolium	fireweed	PF	N, W	FACU	6	4	4.6	45
Taraxacum officinale	dandelion	PF	NN, W	FACU	22	3	2.5	35
Geum macrophyllum	large-leaved avens	PF	N	FAC	6	1	8.8	22
Medicago lupulina	black medick	PF	NN, W	FAC	69	1	2.5	21
Poa pratensis	Kentucky bluegrass	PG	NN	FAC	107	1	1.8	19
Euphorbia esula	leafy spurge	PF	NN, W	FACU	15	1	2.5	10
Annuals								
Aira caryophyllea	silver hairgrass	AG	NN	UPL	462	6	11.2	1,444
Polygonum lapathifolium	smartweed	AF	N, W	FACW	745	11	4.3	1,291
Bromus tectorum	cheatgrass	AG, R	NN, W	UPL	181	8	7.3	786
Chenopodium album	lambs quarters	AF, R	N, W	FAC	475	8	4.2	732
Collomia linearis	narrow-leaved collomia	AF	N	FACU	387	6	3.1	366
Erysimum cheiranthoides	wormseed mustard	AF	N, W	FACU	256	9	2.4	346
Matricaria discoidea	pineapple weed	AF, R	NN, W	FACU	78	4	9	318
Mimulus guttatus	yellow monkey-flower	AF	N	OBL	62	2	5	79
Rorippa palustris	marsh yellow-cress	AF	N	OBL	91	4	2	76
Lappula occidentalis	western stickseed	AF	N, W	UPL	96	1	2.5	24

This considered growth habit and duration (USDA-Plants Database) and included trees (T), shrubs (S), annual and perennial forbs (AF, PF), annual and perennial graminoids (grass-type, AG, PG), and consideration as ruderals (R). Status categories included: native (N) or non-native (NN), based on USDA-Plants, and plants assessed as weedy (W), including noxious (NOX). Wetland classifications were based on the US National Wetland Inventory (Region 9) supplemented with site information from E-Flora BC, and included: upland (UPL), facultative upland (FACU), facultative (FAC), facultative wetland (FACW), and obligate wetland (OBL). The numbers of occurrences in quadrats (out of 2569 total) and sites (12 total), and mean percent covers in occupied quadrats are also presented, along with the composite Within groups, the plants are listed by declining Prevalence = √(# Quadrats) x # Sites x Mean % Cover

Table 3 Bivariate correlations between environmental factors and vegetation characteristics for quadrats in the drawdown zone of the Duncan Reservoir ($n = 563$)

| | Environmental Factors | | | | | Vegetation Characteristics | | |
	Position (√)	Distance	Elevation	Slope	Substrate Texture	Richness (√)	Cover (log)	[Sum]
						Pearson Product (r)		
Position		−0.426**	0.048	0.187**	0.062	−0.443**	−0.209*	0.652
Distance	−0.200**		−0.561**	−0.341**	−0.033	0.137**	−0.003	0.140
Elevation	0.124**	−0.682**		−0.080	−0.090*	0.225**	0.406**	0.631
Slope	0.172**	−0.500**	−0.038		0.322**	−0.190**	−0.208**	0.398
Substrate	−0.025	−0.190**	−0.079	0.343**		−0.235**	−0.303**	0.538
Richness	−0.357**	0.050	0.204**	−0.221**	−0.209**		0.798**	
Cover	−0.0061	−0.092*	0.389**	−0.223**	−0.267**	0.816**		
	Spearman ρ							

The matrix includes the parametric Pearson Product correlation as the upper right triangle, and the non-parametric Spearman ρ as the lower left triangle. Significant correlations are indicated (* = $p < 0.05$; **$p < 0.01$), with positive correlations in red, and negative correlations in blue

Fig. 4 Mean (±SE) vegetation abundance (cumulative % cover) versus mean (±SE) species richness at 12 numbered sites along the drawdown zone of Duncan Reservoir (original site 8 was not sampled in this study). Similar sites are grouped with the dashed ovals, with reservoir zones indicated. For figures, solid lines indicate significant ($p < 0.05$) regressions
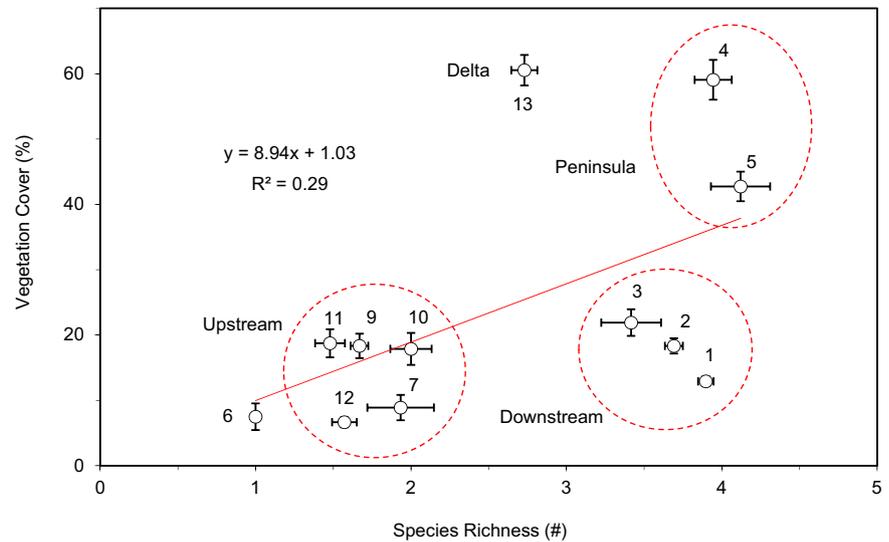
combine plant species from the upland zone and the upper drawdown zone, increasing the vegetation diversity. Below that reservoir margin band, the total species number displayed nearly complete correspondence with Elevation (96%). The decrease would reflect the increasing inundation duration and depth that would progressively exclude different plant species.

The species Richness represented the number of plant species within each quadrat and displayed an inverted-U response versus Elevation (Fig. 5C). This reflected the overlapping occurrences of the perennials and annuals at intermediate elevations (Fig. 6). The perennial plants decreased with declining Elevation, as those longer-lived plants did not survive prolonged inundation and deeper submergence. Conversely, the Cover of annuals increased with decreasing elevation, possibly reflecting reduced competition with the established perennials.

We were particularly interested in the distributions of the trees and shrubs that provide greater contributions to vegetation structure (vertical diversity) that expands habitats for birds and other wildlife. Both groups of woody plants were restricted to the upper drawdown zones, with some occurrence in the top 1 m below full pool and sparse extension downwards into the next elevational band (Fig. 6). These transect results suggest similar distributions for the trees and shrubs (Fig. 6), but with greater abundance on the reservoir delta at the inflow of the upper Duncan River, we observed that the willows extended to lower positions than the cottonwoods (Rood et al. 2019).

Vegetation Cover was significantly associated with *Substrate* texture, with the negative correlation indicating increased vegetation abundance with finer sediments (Table 3). With quadrat grouping into 0.1 sediment texture index classes, there was substantial association between
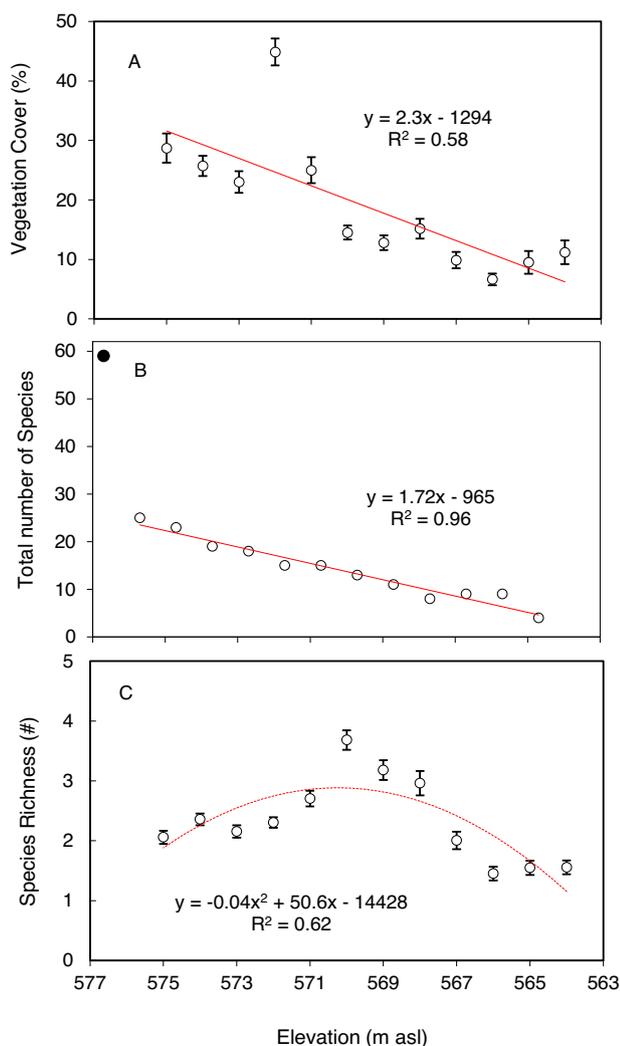
Fig. 5 Mean (±SE) vegetation cover (**A**), total number of plant species in that elevational band (**B**), and species richness, # of species per quadrat (**C**) versus elevation for quadrat data grouped into 1 m elevation intervals, from the drawdown zone of Duncan Reservoir (declining elevation for downward progression). Regressions are provided with the regression for the total number of species (**B**) excluding the high value at the reservoir shoreline (577 m)

Substrate texture and Vegetation Cover (Fig. 7). Conversely, Richness only tended to be favored by finer substrates (Fig. 7).

The substrate specificity varied considerably across the plant species (Fig. 8). Displaying a specialist pattern, the most abundant plant in the drawdown zones, *Equisetum arvense*, was largely restricted to fine substrates. In contrast, the weedy annual, *Polygonum lapathifolium*, occurred over a broad range of surface sediment types. The other abundant species, *Carex rostrata* and *Aira caryophylla*, were intermediate, favoring finer surfaces but with some occurrences on intermediate and even coarser surfaces (Fig. 8, and further species are displayed in Polzin et al. 2010).

Both vegetation characteristics were negatively correlated with *Slope*, but with lower correspondence sums than Position, Elevation, or Substrate (Table 3). Grouping into 1% slope classes displayed the pattern, with extensive variation up to 20% slope, and limited vegetation on slopes greater than 30% (Fig. 9). With the grouped results there was no correspondence between Slope and Richness, partly due to quadrats along two unusual transects with a few plant species on steeper banks (Fig. 9).

Multifactor modeling and ordination

Forward-stepwise linear modeling for Richness and Vegetation Cover, revealed improvements in predictive accuracy with additional factors (Table 4). For *Richness*, Position was the predominant factor, reflecting the more diverse vegetation near the southern end of the reservoir. Elevation and then Substrate provided the additional influential factors, with Distance slightly improved the 4-factor model that provided about 30% accuracy across the quadrats.

For *Vegetation Cover*, Elevation was the strongest predictor (Table 4). Substrate or Distance similarly improved the model, with about 30% accuracy with both, along with Elevation. There was only marginal improvement in the 4-factor with the further addition of Position. A 4-factor model excluding Elevation explained only 13% of the variation, well below Elevation alone (19%).

For ordination with Canonical Correspondence Analysis (CCA), Elevation, Substrate, and Slope were considered along with the predominant species (Fig. 10). The eigenvalues indicated that Axes 1, 2, and 3 accounted for 11.9%, 1.7%, and 0.9% of the total variance, and the ordination provided a cumulative R^2 of 0.191. Axis 1 was strongly correlated with Elevation (canonical coefficient: $r = 0.977$), Axis 2 with Substrate ($r = 0.977$) and Axis 3 with Slope ($r = 0.995$). The plot in Fig. 10 displays Axes 1 and 2, while Slope is flattened in the 2-dimensional representation.

The CCA revealed four groupings from the 15 prevalent plant species. Group I occurred at lower elevations (left side) and included most of the annual plants. For this group, the vertical spread over Axis 2 reflected differing substrate specificity and there was a mixing of plants relative to wetland classification. Group II included a mix of plants that occurred on coarser substrates at intermediate elevations. Group III included the most abundant plants in the drawdown zones, including the three most common perennials, which occurred in intermediate elevations and on finer substrates. Group IV included the common shrubs, which were restricted to higher elevations near the full pool margin.

Fig. 6 Mean (±SE) percent cover versus elevation for the two most abundant Trees and Shrubs, and all Perennials and Annuals (with regressions) in the drawdown zone of Duncan Reservoir. Note the different Y-axis scales for the upper versus lower pairs of figures
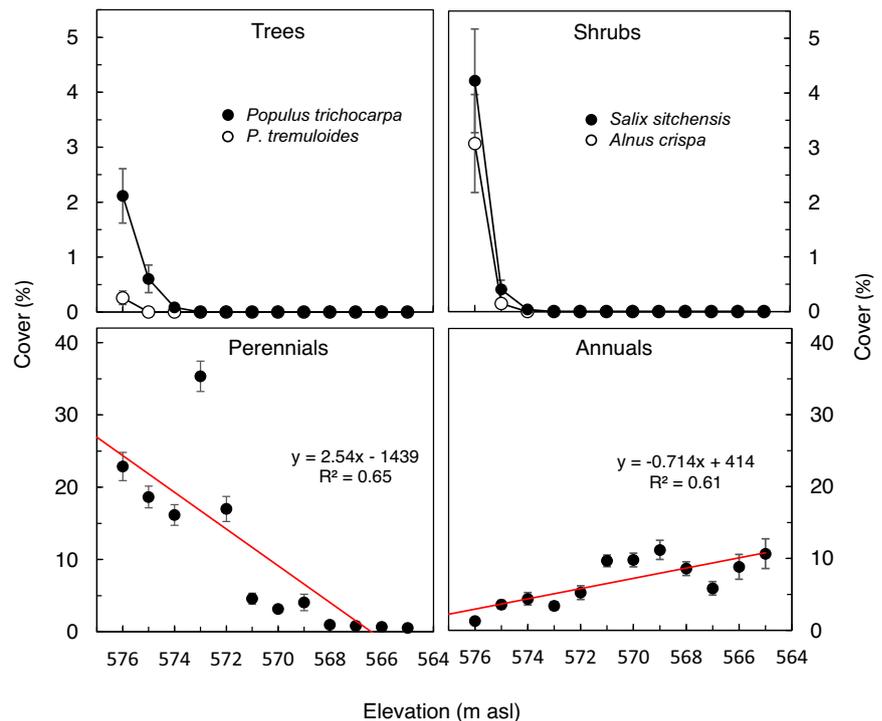
Discussion

Vegetation strata—four elevational bands

Within the drawdown zones of Duncan Reservoir, the vegetation species and communities were loosely stratified to produce four sequential, *Elevation* bands. These probably reflected differences in inundation tolerances (Wilcox and Meeker 1991), and generally similar banding and the vegetation groupings were observed for two other storage reservoirs in the Pacific Northwest, Williston Reservoir in northeastern BC, and Chester Morse, in western WA (Baker et al. 2000; Chapin and Paige 2013). Confirming the causal influence of the frequency and duration of inundation and submergence, at other reservoirs the bands of willows and the perennial herbaceous plants have risen following reservoir raising and fallen with reservoir lowering (Odland and del Moral 2002; Auble et al. 2007; Wilcox and Nichols 2008; Chapin and Paige 2013; Meeker et al. 2018).

For these reservoirs, black cottonwoods characterized the upper band, near the reservoir margin (Fig. 6). Willows provide predominant shrubs characterize the second band, which may extend downwards from 1 to 3 m below the cottonwoods (Baker et al. 2000; Chapin and Paige 2013; Rood et al. 2019). Willows were also common in the drawdown zones of other storage reservoirs around the Northern Hemisphere (Rains et al. 2004; Chapin and Page 2013; Zhang et al. 2013). At the Miharu Reservoir in Japan, eight willow species were observed, with crack willow,

Salix fragilis, extending down as low as 8 m in the drawdown zone (Azami et al. 2013). That unusual extent probably reflected very high inundation tolerance, combined with an extended interval of seed dispersal. That willow can also readily propagate from fallen stem fragments with buds, providing a clonal colonization mechanism.

At regional reservoirs and other reservoirs around the Northern Hemisphere, the perennial herbaceous plants provide the third vegetation band below the full pool shoreline. Horsetails (*Equisetum* spp.) and sedges (*Carex* spp.) often provide abundant plants (Nishihiro and Washitani 2009; Rains et al. 2004; Zhang et al. 2013). These overlap with, and then extend well below the willows, commonly to 5 or more m below full pool (Baker et al. 2000; Chapin and Paige 2013). Similarly, the most abundant plant by far within the Duncan Reservoir drawdown zone was the common or field horsetail (*Equisetum arvense*), which commonly extended down 5 m below full pool (Fig. 6). This primitive, spore-producing fern has high inundation tolerance and the related species, water horsetail (*Equisetum fluviatile*) thrives around freshwater shorelines, commonly as an inundated emergent (Pearce and Cordes 1988). Hybridization and introgression are extensive within *Equisetum* and could further contribute to the ecophysiological adaptation to the drawdown zones.

Also common in the herbaceous perennial band, the second most abundant plant in the Duncan Reservoir drawdown zone was beaked sedge (*Carex utriculata*). This and other sedges also occur in the drawdown zones of other

Fig. 7 Mean (±SE) vegetation cover (top) and species richness (bottom) versus the substrate texture index (1 = silt (very fine) to 5 = boulder (very coarse)), for quadrats in the drawdown zone of the Duncan Reservoir. Linear regression lines are plots, with the dashed line indicating only a statistical trend ($p < 0.1$)
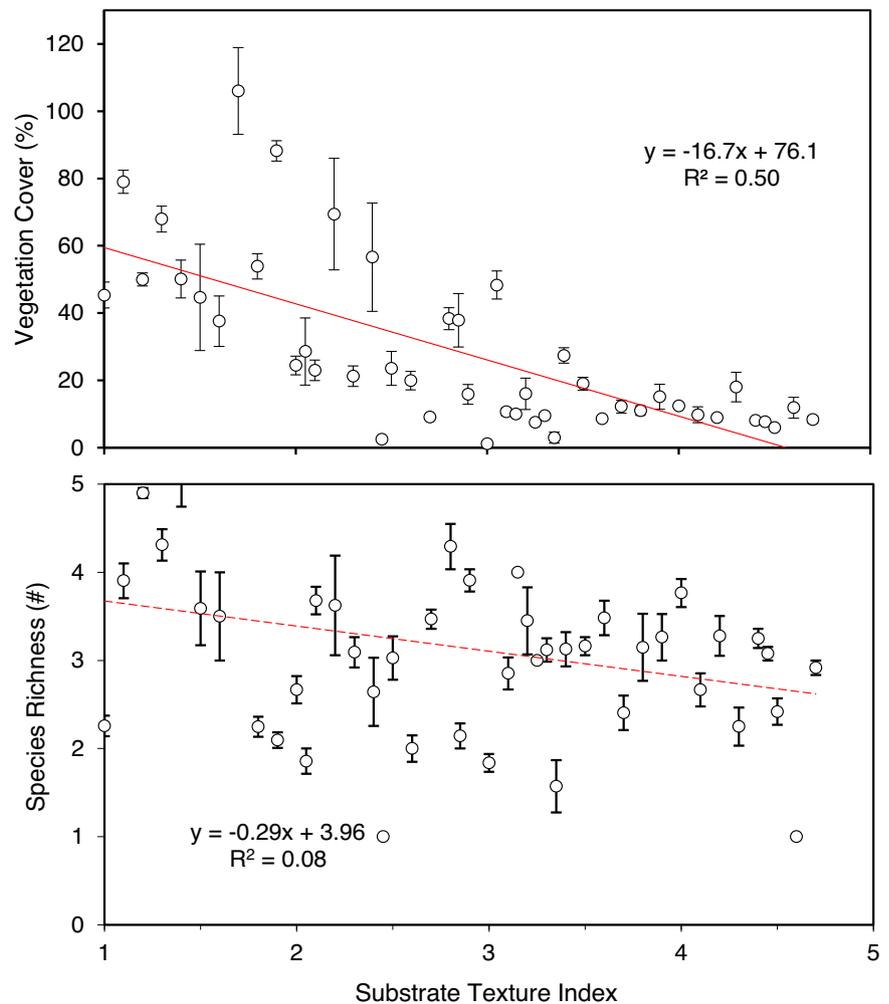
regional reservoirs, including the other Columbia River Treaty reservoirs (Enns et al. 2010; Miller et al. 2018a). The sedges are common wetland plants, and their abundance also suggests some drought adaptation, to tolerate the intervals when the drawdown zones are exposed and drier (Wilcox and Nichols 2008). Conversely, the Duncan Reservoir was relatively full through the warm and dry summer interval when drought stress would increase.

The fourth and lowest vegetation band includes the ruderal annual plants. These plants often display a swift life history, and with extensive seed production and they can quickly establish and even complete their life cycle within the limited interval when the lower drawdown zones are exposed. Their colonization occurs in spring when the reservoir is lowest, and snowmelt and spring rains provide surface moisture for seedling germination. This vegetation group includes plants with varying wetland classification, which largely reflects inundation tolerance, but the lower elevation zone is deeply submerged for extended intervals, exceeding the inundation and submergence tolerances of all plants. Thus, this deeper zone would require recolonization

each spring, for the annuals and the less abundant seedlings of the perennial plant species.

Contributing environmental factors

We anticipated deterministic associations for vegetation in the reservoir drawdown zones, whereby plant species and groupings would display distributions that reflected the predominant physical environmental influences. This was supported as there were strong correspondences between the vegetation community characteristics of Richness or Vegetation Cover with the environmental factors, and ranked by importance, Position, Elevation, Substrate texture, and Slope. There were generally progressive trends, except for the inverted-U pattern for Richness versus Elevation, a composite pattern with increased diversity at intermediate elevations reflecting the overlap of the higher, perennial, and lower, annual species.

While the observed elevational banding emphasizes the importance of the inundation duration and depth, the other physical environmental factors contributed. Finer *Substrate*

Fig. 8 Percent cover versus substrate texture indices for the two most abundant Perennial (top) and Annual (bottom) plant species in the drawdown zone of Duncan Reservoir. Note the variation in the y-axis scale
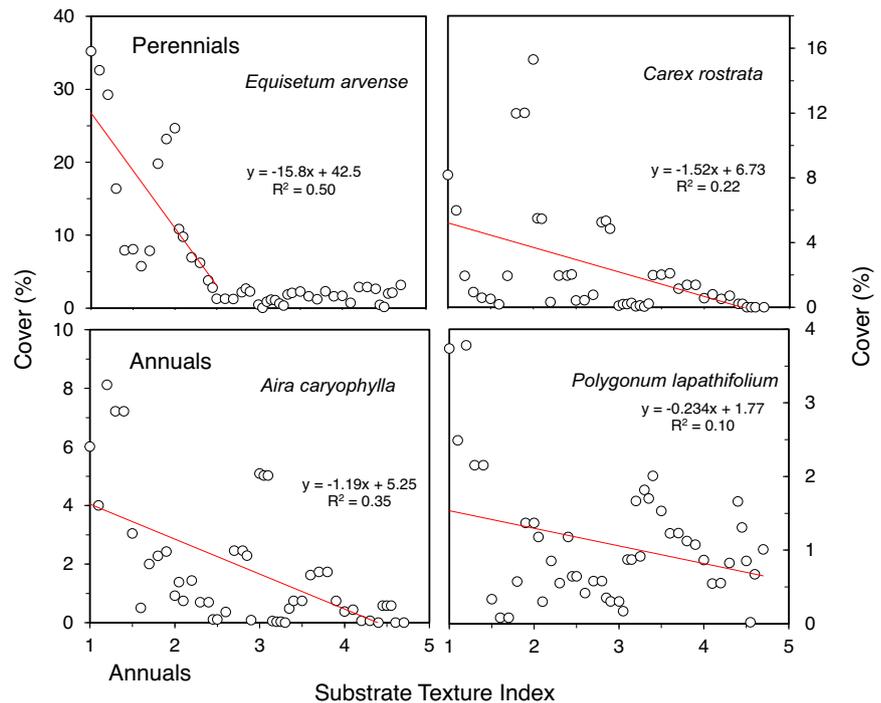
was apparently more favorable, especially for some plants such as *Equisetum*. Finer sediments would increase water retention and capillarity and could increase nutrient fertility (Kwon et al. 2007). This is consistent with findings around the massive Three Gorges Reservoir in China, where vegetation is similarly restricted to the upper drawdown zones, primarily with herbaceous plants and especially *Equisetum* and *Polygonum* (Zhang et al. 2013), similar to the Duncan Reservoir.

At the Duncan Reservoir, shallower *Slope* was also generally more favorable, as expected. This would reduce surface and subsurface drainage, thus increasing water availability during the intervals of exposure. This finding is also consistent with patterns at the Three Gorges Reservoir and elsewhere (Zhang et al. 2013, Cho et al. 2019), with limited vegetation on slopes steeper than 20° (Azami et al. 2013). At the Duncan and other reservoirs, there were interactions between substrate and slope, with flatter surfaces often covered with finer substrates to produce 'mud flats', that were favorable for sedges (*Carex* spp.) and other plants (Luken and Thieret 2001; Cho et al. 2019). There are complexities however, since coarser substrates increase the stability on steeper slopes, favoring vegetation survival in some of those locations.

Finally, the influence of *Position*, or longitudinal location, was substantial, especially for Richness. This would reflect the local seed sources (Cho et al. 2019), and the greater Richness at the downstream sites at the Duncan Reservoir would reflect the increased diversity of riparian

and wetland vegetation along the lower Duncan River and its delta zone into Kootenay Lake.

The observed combination of physical factors enables a hydrogeomorphic characterization of the suitability of the drawdown zones for riparian vegetation. With the predominant influence of Elevation, the frequency, duration, and depth of inundation is important, with reduced inundation being more favorable (Nilsson and Keddy 1988; Rains et al. 2004; Zhang et al. 2013). Favored locations for vegetation would also generally have shallow slopes and finer sediments that would promote colonization by a broader range of plant species. These combinations are naturally provided on the alluvial fans of the tributary creeks, which also provide supplemental surface and groundwater that increase survival and growth through dry intervals.

And reflecting the combined physical influences, a general conclusion is that riparian vegetation would be favored in positions with riparian vegetation prior to reservoir flooding. There would be consistency over time, whereby the physical environmental conditions that supported more abundant and diverse vegetation in one interval would be likely to enable more abundant vegetation in future intervals. Following this conclusion, if vegetation plantings were undertaken, these would probably be more successful in locations with some vegetation, rather than positions that were barren of vegetation. Planting or transplanting would bypass colonization, but environmental conditions that were lethal for natural vegetation could also be lethal for plantings (Miller et al. 2018b).

Fig. 9 Mean (±SE, with multiple occurrences) vegetation abundances (cumulative % cover across species) (top) and species richness (bottom) grouped by slope (%, fall/run), for the Duncan Reservoir drawdown zone. Linear and logarithmic regressions are plotted for the relationship between cover and slope. There was no significant relationship between richness and slope
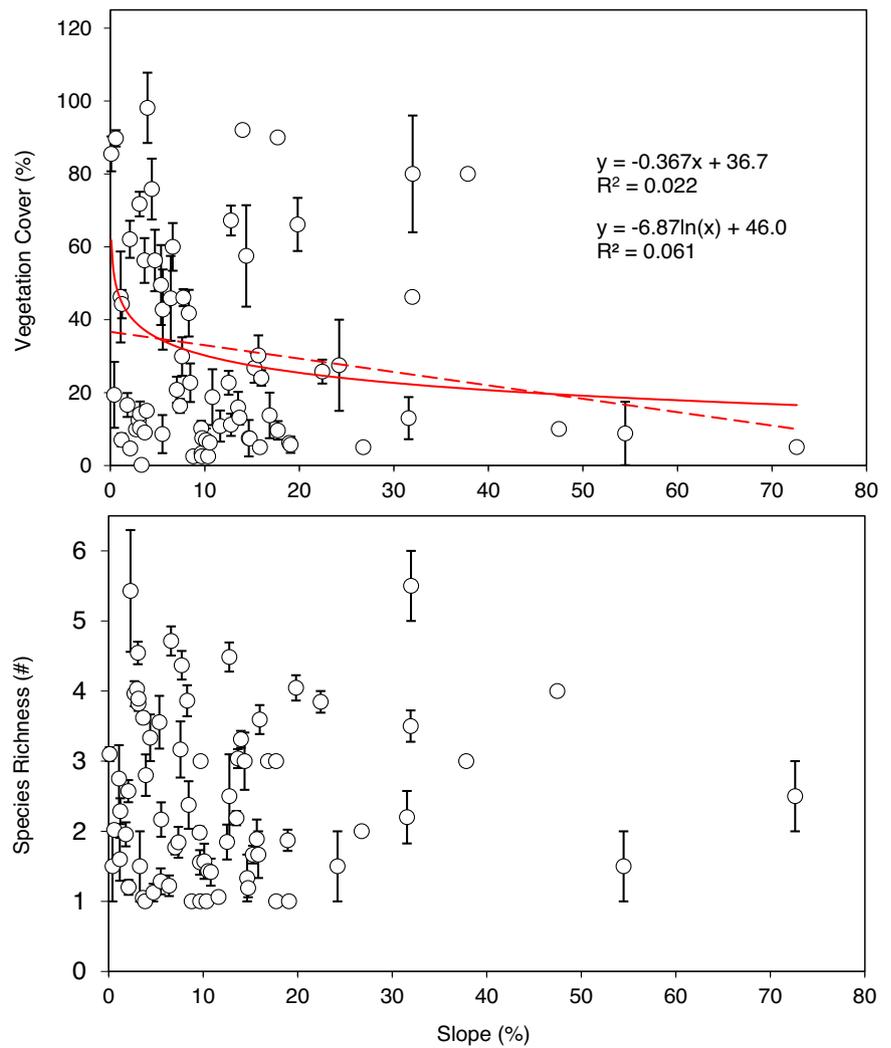

$$y = -0.367x + 36.7$$
$$R^2 = 0.022$$

$$y = -6.87\ln(x) + 46.0$$
$$R^2 = 0.061$$

Table 4 Results from forward-stepwise linear modeling, with the best 1-, 2- and 3-Factor models, the optimal All Factor model, and the model excluding the best predictor for each vegetation characteristic. The favored models are in red

|	Predictive factor—Importance					
	Position	Distance	Elevation	Slope	Substrate	Accuracy
Richness (√)						
1 Factor	1.0					19.5%
2 Factor	0.75		0.25			25.9%
2 Factor	0.81				0.19	23.6%
3 Factor	0.68		0.20		0.12	29.1%
All Factors	0.56	0.04	0.28		0.13	29.9%
Exclude Position		0.36	0.51		0.12	17.6%
Cover (log)						
1 Factor			1.0			18.9%
2 Factor			0.72		0.28	25.3%
2 Factor		0.21	0.79			25.5%
3 Factor		0.16	0.69		0.15	30.1%
All Factors	0.05	0.09	0.69		0.17	31.4%
Exclude Elevation	0.12	0.20		0.24	0.44	13.2%
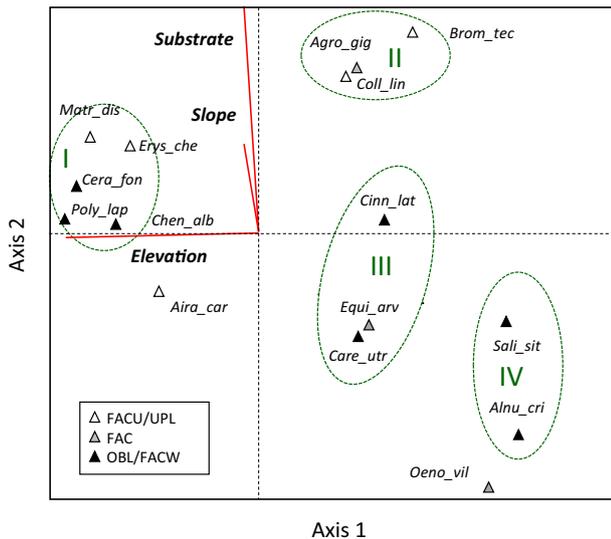
Fig. 10 Ordination with Canonical Correspondence Analysis (CCA) of the 15 prevalent plant species in the drawdown zone of Duncan Reservoir. Abbreviations are by genus (4 letters) and species (3 letters), with complete names in Table 1. Affiliated species groups are interpreted in dashed line ovals

Other environmental factors

Our study emphasized some primary physical environmental factors and there are also other influences. We anticipated influences from aspect, which would influence insolation and wind that would affect colonization and vegetation community development. The reservoir side or position would relate to aspect and to other physical influences. In particular, wave action provides a powerful erosive force, which can be amplified with floating woody debris that crash into the shoreline zone. Wave erosion and woody debris retarded vegetation colonization and community development at some exposed locations around the Duncan Reservoir, as is the case elsewhere (Rains et al. 2004).

And human influences provide further impacts. Recreational use is favored on the gradually sloped alluvial fans and can include motorized vehicles that destroy vegetation and contribute to bank and floodplain compaction and erosion. Livestock grazing is absent around the Duncan Reservoir but provides a major disturbance around other reservoirs, including Koocanusa Reservoir, another Columbia River Treaty reservoir.

The multiple factors also occur across different spatial scales. Our study emphasized the site factors and localized geomorphic influences, and broader landscape and watershed scale influences such as climate are also influential (Hough-Snee et al. 2015). These larger scale influences and particularly climate variation, such as with the Pacific Decadal Oscillation and progressive climate change provide overarching influences (Rood et al. 2008; Capon et al. 2013), which further interact with the localized environmental factors.

Reservoir management for ecosystem enhancement

Systemic restoration might provide an alternative to costly and localized plantings. This phrase relates to two aspects: (1) this restoration approach seeks to manage the underlying system, the water regime, and (2) the consequences affect the drawdown zones around the full reservoir, the whole system. For this approach, reservoir regulation could provide hydrologic regimes to enable natural seedling colonization and subsequent vegetation community development (Meeker et al. 2018). With a similar strategy for the restoration of riparian vegetation along regulated rivers, systemic restoration is becoming a favored and cost-effective approach (Rood et al. 2005; Merritt et al. 2010). This restoration or enhancement approach involves deliberate dam operations to provide environmental flow regimes that satisfy the life history requirements for riparian plants, enabling recruitment and subsequent community development. The environmental river flows mimic components of the natural flow regime, including seasonal and interannual variation (Richter and Richter 2000). The systemic restoration applications have benefited broader riverine ecosystems with the riparian revegetation followed by increases in birds and other wildlife, and flow normalization has also improved conditions for fish and the aquatic ecosystems (Rood et al. 2005).

A similar ecosystem enhancement strategy could be applicable for the CRT reservoirs (Wilcox and Meeker 1991; Thomson et al. 2018). Deliberate reservoir regulation could deliver hydrologic regimes that would allow seedling colonization and subsequent vegetation community development in the upper drawdown zones (Meeker et al. 2018). To contribute to this ecosystem approach, this study characterized some of the hydrology-vegetation relationships that underlie the vegetation community distributions around this and the other CRT reservoirs. The characterization of these environmental influences should be applicable for ecosystem enhancement at other storage reservoirs in temperate ecoregions and mountain areas, and in other regions, worldwide.

Data availability

Two cited technical reports are available through permanent, open-access web-links (Polzin et al. 2010; Polzin and Rood 2022). As indicated in the manuscript, these include further analyses and appendices with the vegetation results and additional environmental data.

primarily by MLP and SBR, with ordination by KMT. The text and figures were largely developed by SBR and MLP, with revisions by KMT and BH.

Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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