RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Downed woody debris microsite facilitation for planted black huckleberry seedling regeneration

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Black huckleberry (*Vaccinium membranaceum*)—an economically, ecologically, and culturally important shrub across the Pacific and Inland Northwest—is experiencing widespread declines in suitable habitat because of fire suppression and climate change. We tested the role of experimentally placed downed woody debris (DWD) in mitigating unsuitable habitat conditions through creating favorable abiotic microsites and promoting black huckleberry seedling survival. We planted 1-year-old black huckleberry seedlings at four distances (0, 0.25, 0.5, and 1.5 m) from DWD, on the north and south aspects of east-to-west-oriented DWD, at three study sites in Northern Idaho, United States. Over one growing season (May to September), we measured seedling survival, chlorophyll fluorescence (Fv/fm), soil surface temperature (SST), and soil volumetric water content (VWC) monthly. Only 21% of seedlings survived the entire season, but survival on the north DWD aspect (28.3%) was twice that of the south (14.2%). Additionally, survival at the nearest distances (0 and 0.25 m; 29%) was double that of farther distances (0.5 and 1.5 m; 13.6%) for both DWD aspects. The north aspect and nearest distances were also associated with the highest Fv/fm, lowest SST, and highest VWC, confirming expected abiotic characteristics of the DWD-associated microsite. The distinct spatial and directional effects highlight a facet of DWD microsites, which can improve best practices for microsites during restoration. We demonstrate that DWD-facilitated microsites can be a pivotal restoration tool to ameliorate climate extremes and enhance shrub recruitment into more durable life stages.

Key words: **abiotic amelioration, black huckleberry, climate change, first food, habitat restoration, seedling establishment, *Vaccinium membranaceum***

Implications for Practice

- Downed woody debris-associated microsites can mitigate physical stressors in unsuitable habitats, thereby helping prevent demographic bottleneck in planted or regenerated woody plants.
- Microsite amelioration of abiotic growing conditions may become more important to support seedling establishment and survival in a changing world or at the current range margins of species.
- Consideration of spatial and directional patterns of microsites is important to optimize the benefit to regenerating seedlings.

Introduction

Shrubs and other non-tree vascular plants are ecologically important components of forest-capable ecosystems, frequently occurring in greatest abundance following stand-replacing disturbances and tree cutting to promote regeneration of commercial tree species (Swanson et al. 2011, 2014). Shrubs increase structural complexity (McElhinny et al. 2005; Su et al. 2019) and trophic diversity of ecosystems throughout the forest sere (Swanson et al. 2014). Like trees, shrubs often experience a demographic bottleneck during the seedling life stage. Many regeneration studies have focused on tree seedling recruitment into older and more resilient life stages (Devine & Harrington 2007; Hill & Ex 2020; Wooten et al. 2022), but far less attention has been given to restoration strategies that promote shrub seedling recruitment and survival.

In the Pacific and Inland Northwest, black huckleberry (*Vaccinium membranaceum* Dougl. ex Torr.) is recognized for

Author contributions: MIM, MES, ASN, HDA designed the experiment; MIM, MES, JR, NB selected field sites; MIM, MES performed the experiment and collected all data; MIM analyzed all collected data; MIM, LM, MES wrote and edited the manuscript; all authors contributed to the article and approved the submitted version.

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doi: 10.1111/rec.14277
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14277/suppinfo

its significant economic, ecological, and cultural importance as a keystone species (Minore 1972; Trusler & Johnson 2008; Turner et al. 2011). Black huckleberries support commercial and cottage industries, drive regional recreation through berry picking, and provide income to federal agencies through commercial harvest permitting programs (Carroll et al. 2003; Arnett & Crawford 2007; Hobby & Keefer 2010). Black bears (*Ursus americanus*) and Grizzly bears (*Ursus arctos horribilis*) rely on huckleberries as a critical summer food source (Robbins et al. 2007; Holden et al. 2012), and large ungulates also preferentially forage on huckleberry foliage (Stewart et al. 2011). Additionally, black huckleberry is an important subsistence food source for both Indigenous and non-native peoples of the Pacific and Inland Northwest (Bowen 1988). Historically, Indigenous peoples actively managed huckleberries to maintain continually productive patches (Anzinger 2002; Mack & McClure 2002; Turner & Peacock 2005), particularly through intentional setting of fire to reduce tree encroachment and enhance shrub productivity (Turner 1999; Trusler 2002; Steen-Adams et al. 2019).

Climate change, fire suppression, and altered forest landscapes have resulted in widespread declines in suitable black huckleberry habitat across the northwestern United States (Minore 1972; Forney 2016; Prevéy et al. 2020). Warmer summer temperatures and sustained drought have rendered many normal black huckleberry habitats unsuitable, prompting black huckleberry to shift to higher elevations and latitudes where growing conditions have become more favorable (Prevéy et al. 2020). Optimal black huckleberry growth and survival typically occur under 40% or less canopy cover or in full sunlight on cooler, northern aspects (Stark & Baker 1992; Martin et al. 2008; Forney 2016). Without fire to prevent dense overtopping of huckleberry patches, these overstory conditions are difficult to maintain. Extensive habitat manipulation using irrigation, fertilizers, or artificial cover (e.g. shade cloth) to protect black huckleberry from environmental extremes has been implemented to improve unsuitable huckleberry habitats (Barney 1999). However, considering the spatial extent of huckleberry declines, intensive interventions are generally not feasible, and silvicultural attempts to restore black huckleberry have thus far been limited. A proven restoration strategy that can be operationally implemented across large spatial extents with little additional intervention is needed.

For decades, downed woody debris (hereafter DWD) has been recognized as a natural climate solution that promotes tree regeneration through amelioration of extreme environmental conditions. (Maser et al. 1979; Harmon et al. 1986; Harmon & Franklin 1989). DWD holds high amounts of water, particularly in advanced decay states, which effectively increases plant-available water in upper soil horizons (Heinemann & Kitzberger 2006). This added water enhances seedling survival, especially in xeric environments (Heinemann & Kitzberger 2006). Additionally, the process of DWD decomposition actively filters and redistributes critical macronutrients (e.g. N and P; Marra & Edmonds 1994; Hagan & Grove 1999; Chećko et al. 2015). These abiotic benefits constitute a “log microsite” that is more favorable for seedling recruitment and survival compared to other locations on the forest floor (Valenzuela et al. 2016; Hill & Ex 2020; Marangon et al. 2022). For example, Hill and Ex (2020) observed a 357% increase in conifer seedling survival when planted next to DWD versus those growing on the exposed forest floor. Similarly, both Reely and Nelson (2021) and Swanson et al. (2023) found higher seedling survival for trees planted closer to DWD, and this advantage was especially apparent on hotter and drier south-facing topographic aspects. In another recent study, Marangon et al. (2022) observed 17% and 38% higher mortality among control tree seedlings compared to those planted on the south and north DWD microsites (i.e. seedlings planted south of DWD and north of DWD), respectively. This directional component of DWD highlights an anisotropic microsite effect, whereby the microsite benefit is typically stronger on the north side of DWD (Marzano et al. 2013; Marangon et al. 2022).

Understanding the seedling log microsite effect relies on quantifying the abiotic variables that create ideal habitat conditions. Known abiotic variables that support seedling regeneration are higher overall soil moisture or soil volumetric water content (VWC), lower soil surface temperatures (SST) that reduce soil surface evaporation rates, and less direct sunlight (Helgerson 1989; Marangon et al. 2022; Rank et al. 2022). Temperature and moisture conditions may vary depending on DWD aspect and distance from DWD, but the spatial and directional patterns of DWD microsites have yet to be fully explored.

Most studies on DWD microsites have also been observational and unable to account for important DWD factors: DWD size and decay state, soil and substrate conditions, and competing vegetation. Moreover, the few experimental studies of DWD microsites were limited in their scope by number of sites, by species, or by spatial extent of the microsite pattern tested.

In this study, we tested the DWD microsite benefit on black huckleberry seedlings experimentally, seeking to quantify the full spatial and directional influence of DWD microsites. We also explored the combination of fire and microsite effects by implementing prescribed burns on a subsample of DWD microsites. We evaluated how microsite conditions affect huckleberry seedling survival and chlorophyll fluorescence (Fv/fm), or physiological stress, and important abiotic factors—soil moisture and surface temperature—at four distances and two DWD aspects. We addressed the following hypotheses:

(1) Black huckleberries closer to DWD exhibit greater survival and lower physiological stress.
(2) Black huckleberries planted on the north side of DWD exhibit greater survival and lower physiological stress relative to the south side.
(3) SSTs are lower and VWC higher closer to DWD and on the north side of DWD segments.
(4) The strength of the DWD microsite effect differs between burned and unburned DWD planting locations due to differences in abiotic conditions.

Methods

Site Description

We conducted our experiment at three study sites in northern Idaho, United States (Fig. 1). We selected sites with unsuitable

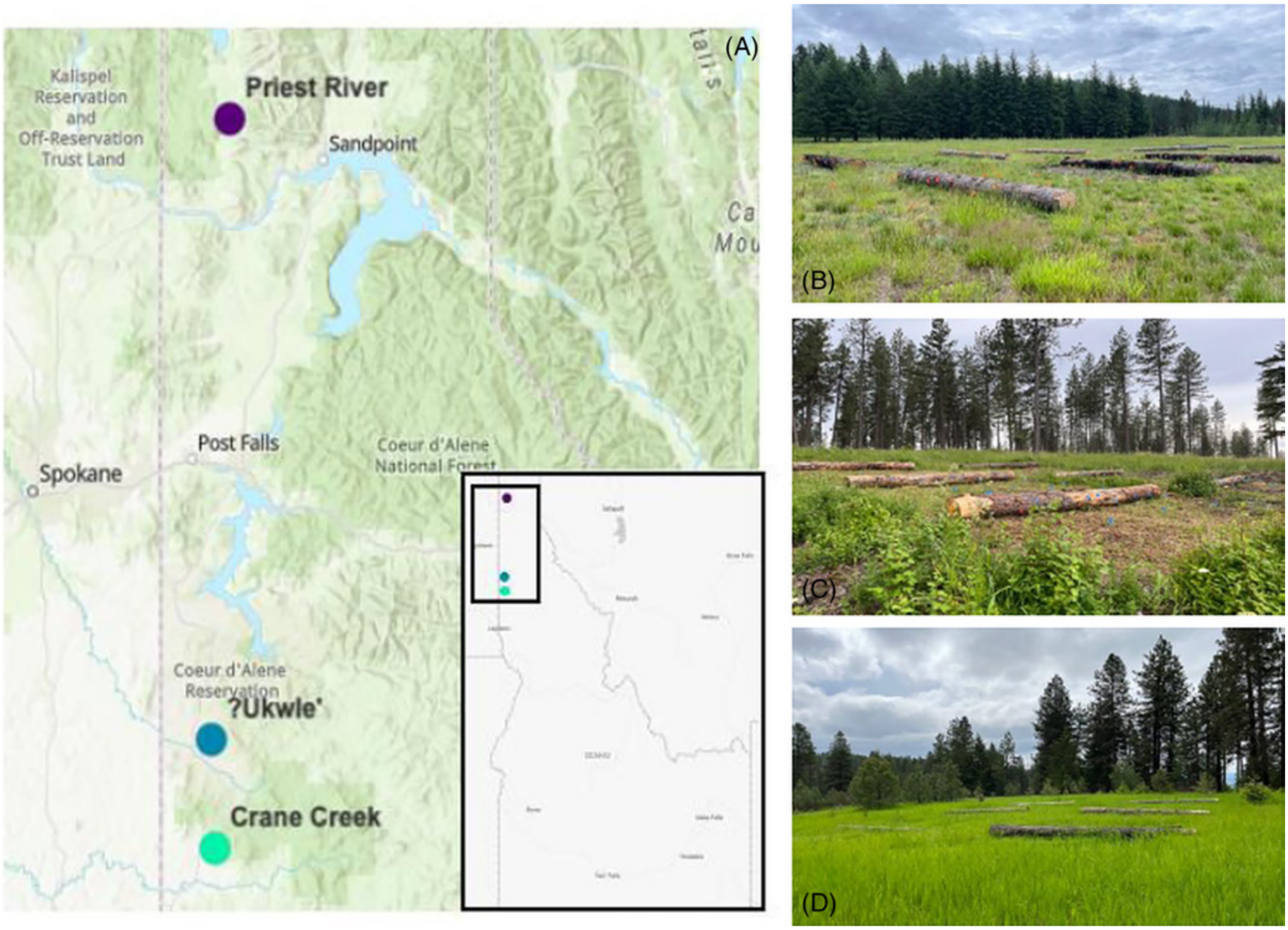

Figure 1. (A) Map of study locations in northern Idaho, United States; purple—Priest River (48.353333°, −116.841389°), blue—?Ukwle' Mountain (47.19194°, −116.8892°), green—Crane creek (46.9875°, −116.88°). (B) Study site at Priest River Experimental Forest. (C) Study site at ?Ukwle' Mountain. (D) Study site at Crane Creek.

conditions for natural huckleberry establishment—no canopy cover, hot and dry soils, and below 900 m.a.s.l. These settings provided an environment in which microsite effects could be clearly attributed to DWD and, furthermore, represent temperature and moisture deficits that are expected to become more widespread with climate change. Under these conditions, survival of black huckleberry seedlings without intervention was unlikely (Barney 1999; Anzinger 2002), making any seedling survival attributable to our designed treatments.

The first research site was located on the Crane Creek Forest, hereafter "Crane Creek," a private research forest, in Latah County, Idaho (lat 46.9875°N, long 116.88°W). Mean elevation at Crane Creek is 856 m.a.s.l. with a moderate (<5%) slope and SE aspect. Mean annual precipitation at Crane Creek is 579 mm, and mean annual temperature is 7.6°C (NOWData 2023). The Crane Creek study site is a former pasture site with little to no forest overstory nor tree regeneration, and a forb and graminoid layer dominated by Smooth brome (*Bromus inermis*), and also Bird's-foot trefoil (*Lotus corniculatus*), Foxtail grass (*Alopecurus alpinus*), and Maiden blue-eyed Mary (*Collinsia parviflora*). Soils are of the Arson—Carlinton complex—an ashy silt loam derived from loess, volcanic ash, and residuum from metasedimentary rocks of the upper Missoula group (Soil Survey Staff et al. 2019).

Site 2, hereafter "?Ukwle'," was located on ?Ukwle' Mountain in Benewah County, Idaho (lat 47.1919°N, long 116.8892°W). ?Ukwle' Mountain is located on lands of the Coeur d' Alene (Schitsu'umsh) People and is managed by the Coeur d'Alene Tribe Natural Resources Department. ?Ukwle', at 880.9 m.a.s.l., is relatively flat with a moderate (approximately 10%) slope and north facing aspect. Mean annual precipitation at ?Ukwle' is 783 mm and mean annual temperature is 8.6°C (NOWData 2023). The dominant plant association at ?Ukwle' is Douglas fir/Mallow ninebark (*Pseudotsuga menziesii*/*Physocarpus malvaceus*; Cooper et al. 1991). The site is open with an understory layer dominated by Blue wildrye (*Elymus glaucus*), Kentucky bluegrass (*Poa pratensis*), Brome (*Bromus* sp.), Low-lying birchleaf spirea (*Spiraea betulifolia*) and Oceanspray (*Holodiscus discolor*). Soils are of the Ardenvoir/Lotus point complex—an ashy silt loam derived from loess, volcanic ash, and residuum and colluvium of metasedimentary bedrock (Soil Survey Staff et al. 2019).

Site 3, hereafter "PREF," was located on the Priest River Experimental Forest in Bonner County, Idaho (lat 48.3533°N, long 116.8414°W). PREF is a long-term research forest managed by the U.S. Forest Service. The PREF site, at 731.5 m.a.s.l., is flat and open with less than 2% slope and no overstory trees within the study area. Mean annual precipitation is 830 mm and mean annual temperature is 7.2°C (NOWData 2023). The PREF site is in a graminoid-dominated open plantation, primarily populated by Idaho fescue (*Festuca idahoensis*) and Sandberg bluegrass (*Poa secunda*). Soils are of the Mission silt loam complex—an ashy silt loam derived from loess, volcanic ash, and glaciolacustrine sediments (Soil Survey Staff et al. 2019). The site was created from a post-fire stand in the early twentieth century for the purpose of experimental provenance plantings and forest tree nursery operations.

Experimental Design

We placed six DWD segments at each site to test the DWD microsite effect. We collected Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*P. menziesii*) segments that were either harvested timber or slash from blowdowns. Based on standardized decay class criteria (sensu Spies & Cline 1988), all woody pieces were in decay class 1—intact bark layer with little to no decomposition. All segments were a minimum of 5 m in length, a minimum of 24 cm in diameter at the small end and ranged from 35 to 55.7 cm in diameter at the large end. We placed DWD segments in a two three-grid arrangement, where each segment was oriented with long axis east–west to emphasize north and south DWD aspects.

Six of the 18 DWD segments were selected to receive a low-intensity prescribed burn in a 4-m area surrounding each segment and running the 5-m length of each segment; three at Crane Creek, three at PREF and zero at ?Ukwle' due to limitations involving burn window and prescribed fire protocols. We added a 5 cm layer of Ponderosa pine litter to the four 5 m burn area to supplement the fuel bed and standardize fire behavior and severity. We used a drip torch as an ignition device. Flame lengths were in the 30–50 cm range, resulting in near total consumption of all fuels within the planting area. We mechanically treated the remaining 12 DWD segments using a motor-powered string trimmer to crop all standing vegetation to approximately 5 cm height.

After burning and mechanical treatments, we planted black huckleberry seedlings in three transects on both the north and south aspects of each DWD segment. Transects were established at right angles to DWD segments, at 1, 2.5, and 4 m distances along the length of the segment from west to east. Each transect consisted of four seedlings planted at four distances: adjacent to DWD (0 m), 0.25 m from DWD, 0.5 m from DWD, and 1.5 m from DWD. At ?Ukwle' and PREF seedling stock was limited, so seedlings at 0.25 and 0.5 m on the center transects of each segment were omitted. This corresponded to 120 seedlings each at ?Ukwle' and PREF and 144 seedlings at Crane Creek, a total of 384 seedlings. Seedling stock consisted of seedlings grown from seed in 340 mL Styroblock 615A containers (Beaver Plastics, Acheson, AB, Canada) at the University of Idaho Franklin H. Pitkin Nursery and 170 mL plugs, grown in pro-mix high porosity (HP) soil, supplied by Plants of the Wild in Tekoa, Washington. All seedlings were healthy upon planting. Altogether, this experimental framework constituted a split-plot design with burn treatment as the split-plot factor and all DWD segments within the whole plot exploring the four-distance spatial pattern and N-S directional pattern.

Plant and Abiotic Measurements

Over the course of two growing seasons (May to September 2022 and May to September 2023), we made monthly observations and measurements on each seedling, including seedling survival, chlorophyll fluorescence (Fv/fm), SST, and VWC. Each of these measures was an indicator of seedling health or abiotic conditions and a response variable in our statistical models.

As a metric of physiological stress, we measured dark-adapted chlorophyll fluorescence (Fv/fm) of each seedling using an OS-30p + chlorophyll fluorometer (Opti-Sciences, Hudson, NH, U.S.A.). Specifically, we measured Fv/fm, the ratio of variable to maximum fluorescence in a dark-adapted leaf, which characterizes the maximum quantum efficiency of photosystem II (Kitajima & Butler 1975). Measurements were taken 1 hour after sunset or after 30 minutes of dark adaptation using leaf clips to ensure no influence of actinic light on the photosystem. Upon full dark adaptation, we applied a red, 50% saturated light pulse for 1 second to a randomly selected leaf or clump of leaves. The corresponding Fv/fm value indicated the overall photosynthetic capacity of the seedling, with values falling between 0 and 1 and those between 0.790 and 0.840 typically indicating a healthy seedling with a high photosynthetic capacity (Cavender-Bares & Bazzaz 2004). Values falling below this range indicated a plant under some stress, and values under 0.250 indicated a severely stressed plant with likely imminent mortality (Guadagno et al. 2017).

We recorded SST 5 cm west of each planting spot to the nearest 0.1°C with a hand-held infrared (IR) thermometer 1,080 (Etekcity, Vesync Company, Anaheim, CA, U.S.A.), aimed at litter/duff on the soil surface. SST was measured between 1400 and 1600 Pacific Standard Time (PST) to capture maximum daily temperatures. We measured VWC to the nearest 0.1% using a hand-held HydroSense2 moisture meter with 20 cm rods (Campbell Scientific, Logan, UT, U.S.A.). The moisture meter was inserted along the full 20 cm length of the prongs to capture soil moisture conditions at the rooting depth of the seedlings. Both SST and VWC were measured at all distances, even when a seedling was not present due to seedling shortages at ?Ukwle' and PREF.

Data Analysis

We used the R programming environment, version 4.2.2 (R Core Team 2023) to fit statistical models. For each model, we included DWD aspect (north vs. south), distance from DWD (0, 0.25, 0.5, and 1.5 m), treatment (burned vs. unburned), and the interaction between DWD aspect and distance as main treatment effects. We included the interaction of DWD aspect and distance from DWD in all models, even when this term was not significant, because the interaction of these two variables allowed us to explore the spatial and directional patterns of the microsite.

We analyzed seedling survival using a generalized linear mixed model (GLMM) with a binomial error distribution and logit link function (Bolker et al. 2009). We modeled survival as a Bernoulli random variable (1 = live, 0 = died) assuming a linear combination of model covariates (DWD aspect, distance, time since planting, burned treatment, and aspect distance interaction). We included random intercepts for the study site and DWD segment nested within the study site to account for common localized conditions that would affect the assumption of independence in model residuals. We analyzed chlorophyll fluorescence using a linear mixed effect model assuming a Gaussian error distribution. We took the natural log of all Fv/fm values in order to normalize the right-skewed distribution due to an abundance of 0 values from dead seedlings. We included a random intercept for individual DWD segment. To examine the influence of DWD on SST and VWC, we used linear mixed effects models assuming Gaussian error distributions. We used the same random effects structure as the survival GLMM described above. For all models, we included time since planting (days) as a model covariate because we expected all response variables (survival, Fv/fm, SST, and VWC) to change predictably throughout the summer (e.g. probability of survival would decline with time since planting, and SST would be higher later in the summer). Figure S1 shows mean monthly temperature and precipitation (values are averages across three study sites).

Results

Seedling Survival

Across the three study sites, 81 of 384 (21%) black huckleberry seedlings survived the entire growing season. Seedling survival probability was lower on the south (14.2%) DWD aspect than the north (28.3%; Fig. 2). Survival probability was highest at the 0 m distance (31.1%) and decreased at planting distances of 0.25 m (27.4%), 0.5 m (17.9%), and 1.5 m (9.3%; Fig. 2). The interactions between DWD aspect and all distances were positive, indicating the influence of distance on survival was less negative on the south side compared to the north. The interaction of distance and DWD aspect mattered least at the furthest, control distance (1.5 m), where there was no difference in survival between the north and south aspects (Fig. 2). Each increase in distance on the south side reduced survival probability to a lesser extent than the same increase in distance on the north side. For example, on the north DWD aspect, seedling survival percentage was 43.6% at 0 m, and decreased to 35.7% at 0.25 m, 23.8% at 0.5 m, and 11.1% at 1.5 m, or 32.5% decrease in absolute survival probability between 0 and 1.5 m (74.5% decrease in relative survival). On the south DWD aspect, survival percentage was 18.5% at 0 m, 19.0% at 0.25 m, 11.8% at 0.5 m, and 7.4% at 1.5 m, or 11.1% decrease in absolute seedling survival probability between 0 and 1.5 m (60% decrease in relative survival; Fig. 2). Seedling survival probability was not significantly different between burned and unburned treatment areas, and the probability of a seedling surviving decreased over the course of the growing season.

Physiological Stress-Chlorophyll Fluorescence (Fv/fm)

Fv/fm values were higher on the north DWD aspect compared to the south DWD aspect (Fig. 3). Additionally, Fv/fm values were greatest at 0 m and decreased with distance from DWD. Interactions between DWD aspect and all distances were positive, indicating Fv/fm values decreased less with increasing distance on the south DWD aspect compared to the north (Fig. 3). On the south DWD aspect, average Fv/fm varied little with distance, with 0.255 at 0 m, 0.276 at 0.25 m, 0.275 at 0.5 m, and 0.245 at 1.5 m. However, on the north DWD aspect, distance appeared to have a stronger influence, with an average Fv/fm of 0.435 at 0 m, 0.305 at 0.25 m, 0.287 at 0.5 m, and 0.261 at 1.5 m (Fig. 3). Fv/fm values did not vary significantly between burned and unburned treatment areas and decreased over the growing season.

Abiotic Site Variables-Soil Surface Temperature and Volumetric Water Content

SST was consistently higher on the south DWD aspect compared to the north (Fig. 4). SST was also higher at greater distances from DWD, with temperatures increasing by an average of 7.3°C at 0.25 m, 8.8°C at 0.5 m, and 14°C at 1.5 m compared to temperatures recorded at 0 m (Fig. 4). Negative distance aspect interactions indicated that SST increased less at further distances from DWD on the south aspect compared to the north (Fig. 4). On the north DWD aspect, SST averaged 23.7°C at 0 m, and increased to 26.9°C at 0.25 m, 37.3°C at 0.5 m, and 40.0°C at 1.5 m (Fig. 4). The south DWD aspect exhibited higher temperatures with less variation across the distances: an average of 39.7°C at 0 m, 39.3°C at 0.25 m, 39.9°C at 0.5 m, and 40.1°C at 1.5 m (Fig. 4). SST did not significantly differ between burned and unburned areas and steadily increased over the growing season (Figs 4 & S2).

VWC was an average of 1.28% lower on the south aspect compared to the north (Fig. 4). VWC was highest at the 0 m distance, exhibiting a nonsignificant decline of 0.51% at 0.25 m, 0.98% at 0.5 m, and a significant decline of 1.86% at 1.5 m when compared to average VWC at 0 m from DWD (Fig. 4). The interactions between the DWD aspect and all distances were positive, indicating that VWC decreased less with increasing distance on the south aspect compared to the average VWC for the same distances on the north aspect (Fig. 4). This pattern is associated with consistently low VWC on the south side of DWD compared to near locations on the north side. VWC was not significantly different between burned and unburned areas and declined over the growing season (Fig. S3).

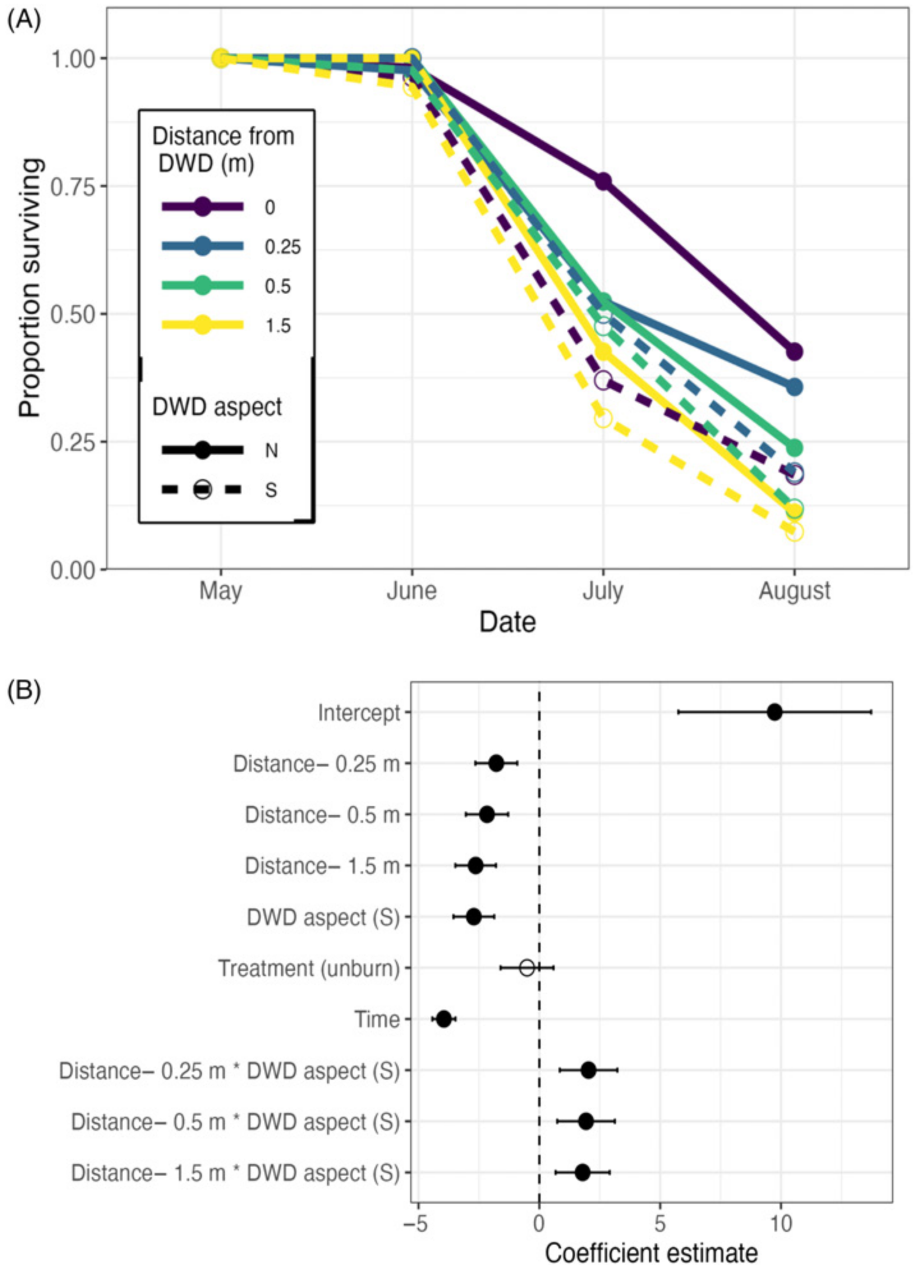

Figure 2. (A) Proportion of seedlings surviving over one growing season ($n = 384$), with each line representing a DWD aspect and distance from DWD. (B) Coefficient plot for a generalized linear mixed model estimating seedling survival probability over one growing season as function of distance from DWD, aspect relative to DWD, and burning treatments. Points greater than zero indicate increased survival, points less than zero indicate decreased survival. Filled circles indicate significant parameter estimates ($p < 0.05$), and open circles represent nonsignificant parameters. Error bars represent 95% CI.

Discussion

Seedling and Abiotic Response

Overall black huckleberry seedling survival was low (21%) but followed specific patterns within the microsite: highest survival on the north DWD aspect and at the nearer 0 and 0.25 m locations (hereafter N-0 and N-0.25). These planting locations were also associated with higher chlorophyll fluorescence values, and therefore greater photosynthetic efficiency and lower physiological stress, compared to the south side and farther distances. Given the low elevation and entirely open canopy at the study sites, any increase in seedling survival is evidence of DWD benefits (Barney 1999; Anzinger 2002). Our results are consistent with those of Marzano et al. (2013) and Marangon et al. (2022) that demonstrated the anisotropic benefit of the DWD microsite, in favor of the north DWD aspect (for the northern hemisphere). Additionally, as supported by Swanson et al. (2023), our results indicate the microsite benefit weakens

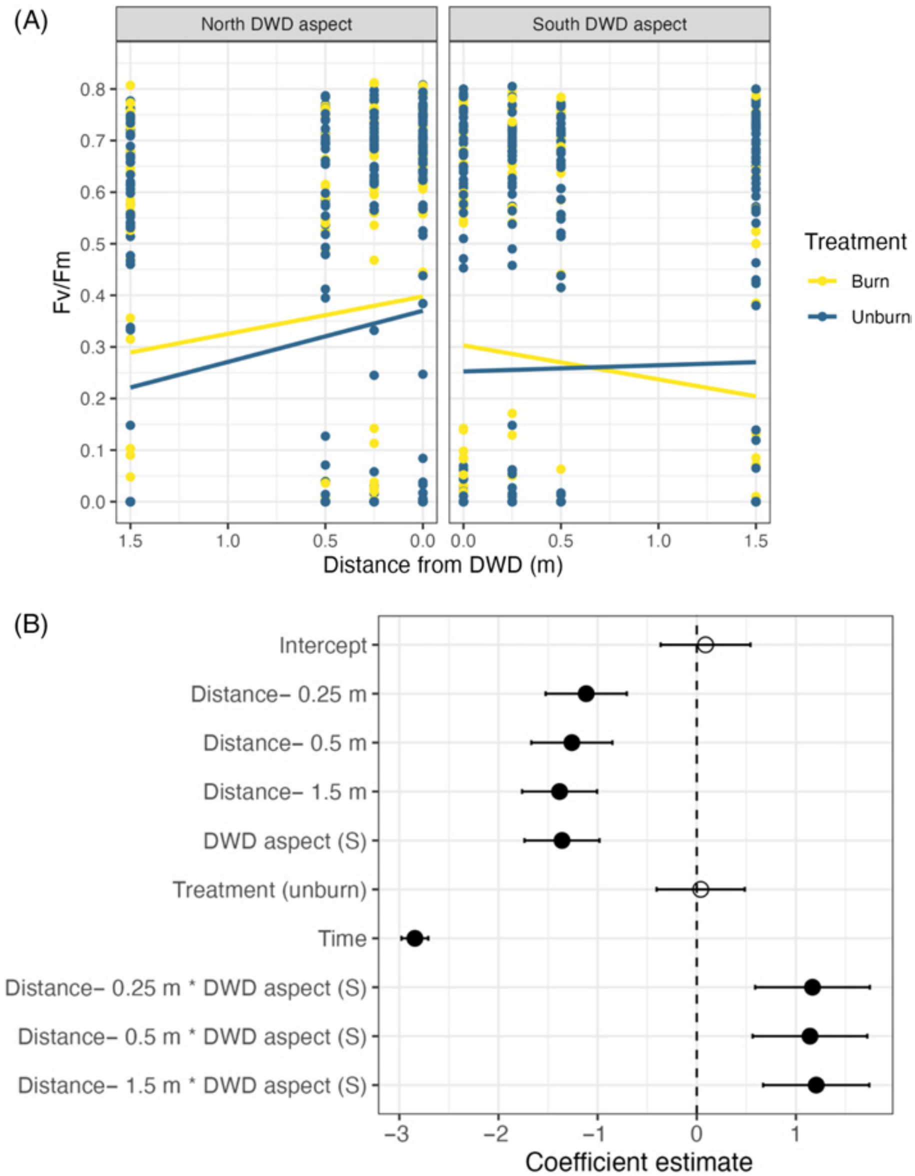

Figure 3. (A) Fv/fm values for all seedlings alive at the end of the growing season, pooled across three study sites. (B) Coefficient plot for a linear mixed model estimating black huckleberry seedling Fv/fm values over one growing season. Points greater than zero indicate higher Fv/fm values, points less than zero indicate lower Fv/fm values. Filled circles indicate significant parameter estimates (<0.05), and open circles represent nonsignificant parameters. Error bars represent 95% CI.

as distance from DWD increases. Compared to the 1.5 m control distances, seedlings planted within the hypothesized zone of microsite influence (0–0.5 m) exhibited higher survival, suggesting a spatially limited role of DWD microsites in seedling establishment and survival. The interaction between DWD aspect and distance suggests the effect of distance differs between north and south. All distances on the south side were less suitable for seedlings than the north and varied little with increasing distance, with only 11.1% higher seedling survival probability at 0 m compared to 1.5 m; however, distance greatly changed the microsite benefit on the north side, with 31.5% higher seedling survival at 0 m compared to 1.5 m.

The spatial and directional pattern of survival can be explained by the timing of amelioration of extreme heat throughout the growing season. On areas with minimal to no slope and therefore no topographic aspect, like our study sites, DWD casts shade to its north when the sun is at its peak (midday in northern hemisphere summers) and temperatures are at daily maxima. Seedlings planted in DWD shade during these midday temperatures experienced lower SSTs, and therefore reduced radiant heat. Midday SST measurements were consistently lower at N-0 and N-0.25 m, providing a seedling refugium when ambient air temperatures were extreme. VWC followed the temperature trends closely as well. We measured the highest soil

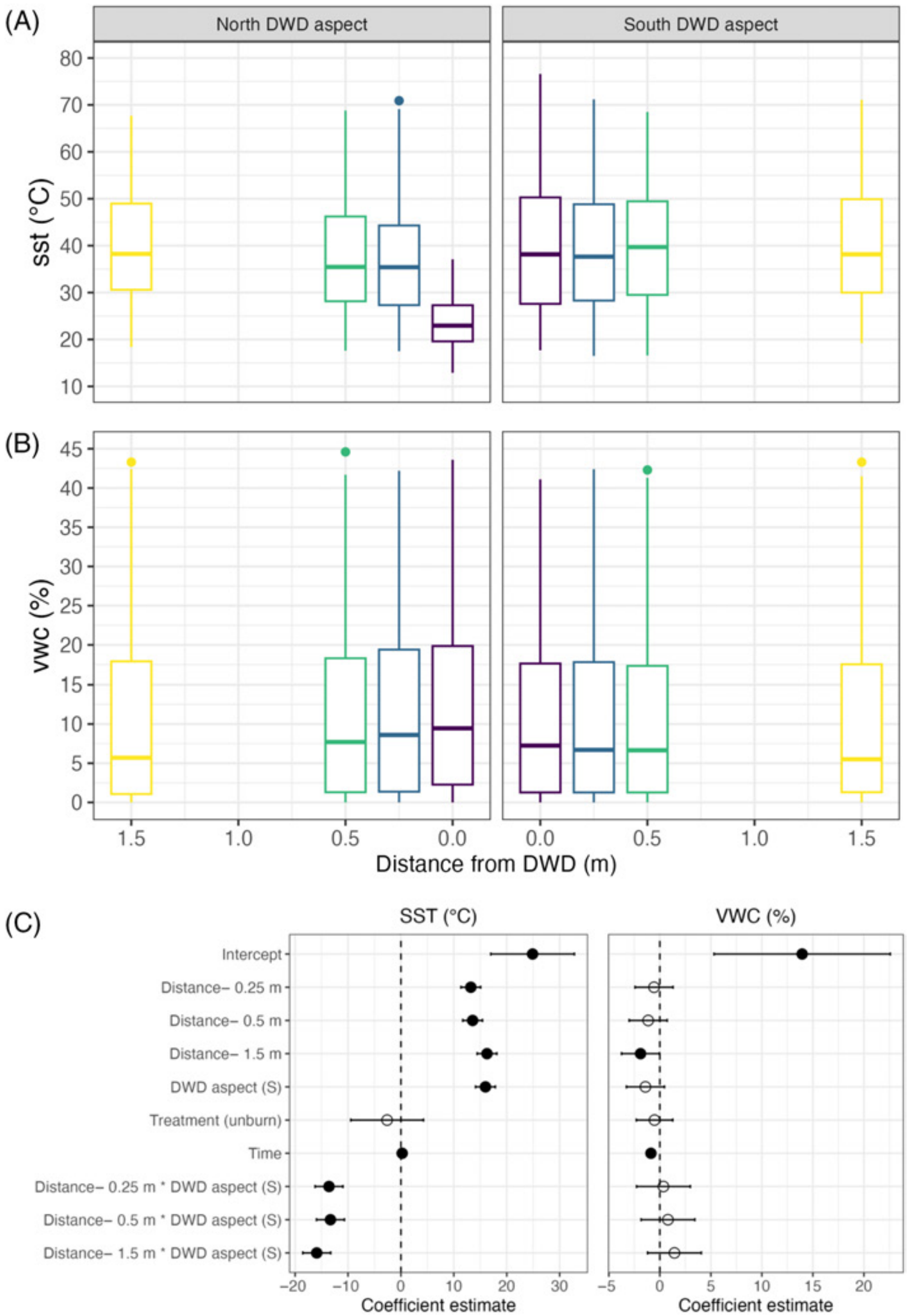

Figure 4. Abiotic variables ameliorated within the DWD microsite. (A) Soil surface temperature (°C) as a function of DWD aspect and distance from DWD (m). (B) Volumetric water content (%) as a function of DWD aspect and distance from DWD (m). (C) Coefficient plots for linear mixed models estimating SST (°C) and VWC (%). Filled circles indicate significant parameter estimates ($p < 0.05$), and open circles represent nonsignificant parameters. Error bars represent 95% confidence of parameter estimates.

moisture at N-0 m during all measurements. The lower temperatures next to DWD directly correlate with higher soil VWC caused by a lower vapor pressure deficit and less evaporative demand required for soil cooling and seedling transpiration (Roberts et al. 2005; Marzano et al. 2013; Marangon et al. 2022). Our finding that DWD facilitates lower SST and higher VWC agrees with previous studies that demonstrated soil moisture and temperature are directly influenced by DWD presence (Marzano et al. 2013; Marangon et al. 2022; Swanson et al. 2023).

Prescribed burn treatment was not important in determining survival and fluorescence of black huckleberry seedlings, nor in determining SST and VWC trends. While fire has historically been a restoration and management tool to maintain suitable black huckleberry habitats, the benefits of prescribed burning, including clearing encroaching conifers and stimulating bud production from underground rhizomes, may be less important during initial seedling establishment (Trusler 2002; Carroll et al. 2003; Steen-Adams et al. 2019). These benefits may also be less important in open sites (like those used in the study), but may become important when fire is implemented in habitats with dense overstory encroachment. Our results suggest the larger role of fire may be in reducing conifer cover and creating a disturbance pulse of microsite-creating DWD at the landscape scale, instead of altering physical or chemical conditions at the scale of the individual seedling. However, both mowing and prescribed fire could have impacted seedling survival by removing competing vegetation, but this benefit would be difficult to quantify given that all DWD received one of these treatments.

Finally, seedling survival and chlorophyll fluorescence declined over time at all locations, although this decline was less at N-0 and N-0.25 m. This may be because natural exposure to heat, herbivory, disease, and desiccation throughout the growing season resulted in reduced productivity and lower leaf fluorescence compared to newly exposed leaves at the start of the season (Percival et al. 2012). Decreased seedling survival over the growing season corresponds well with climatic trends in the Pacific and Inland Northwest in which temperatures rapidly increase and precipitation rapidly decreases over the growing season, and conditions become hot and dry in August. DWD microsites, and specifically nearer locations on the northern aspects, may therefore become more important over time, as hotter, drier conditions become more frequent under global change (Prevéy et al. 2020).

Relevance

Many shrub and tree seedlings, including black huckleberry, experience high mortality during initial establishment and during the seedling life stage (Urza et al. 2019). Barriers to natural regeneration include environmental factors like high ambient air and SSTs and low available soil moisture during these vulnerable establishment periods (Bailey et al. 2012; Forney 2016; Urza et al. 2019). Our study showed that microsite amelioration of these hostile conditions can facilitate higher seedling survival at least during the first year, and thus, an avenue for escaping this demographic bottleneck.

Warmer and dryer climates associated with global change have direct and tangible implications for black huckleberry growth, survival, and long-term productivity (Prevéy et al. 2020). Black huckleberries are flowering and fruiting earlier in the year, leading to phenological mismatch between huckleberries and important pollinators (Prevéy et al. 2020; Weaver & Mallinger 2022). Additionally, habitat deterioration has prompted range shifts to higher latitudes and elevations (Prevéy et al. 2020). Accordingly, range and phenology shifts may directly correspond with more frequent droughts, caused by increased temperatures, higher vpd deficits, and drier soils in the summer months (Watt et al. 2018). Lower SST and higher VWC within the DWD microsite may therefore be directly applicable to ameliorate growing conditions under these new climatic norms.

Previous science demonstrated how DWD microsites support seedlings in unsuitable habitats resulting from landscape disturbances and climate change. Bailey et al. (2012) observed DWD microsites supporting eucalypts in agricultural lands that receive low rainfall. Marcolin et al. (2019) and Marangon et al. (2022) documented beneficial DWD microsites in windthrown and fire-disturbed habitats. Additionally, Swanson et al. (2023) highlighted beneficial microsites during an extreme heat wave event. This study builds off these previous works, demonstrating how beneficial microsites can facilitate seedling survival for vulnerable species in unsuitable habitat conditions.

DWD in Management and Restoration

Use of naturally occurring DWD may be the least invasive and least expensive way to utilize DWD microsites for restoration. DWD naturally occurs in forested environments and varies in abundance during different stages of forest succession (Harmon et al. 1986; Spies & Cline 1988; Stevens 1997). DWD retention after timber harvesting will increase microsite abundance. While many managers tend to remove most large woody debris resulting from disturbance or logging to limit perceived fire risks or maximize profits (Spies & Cline 1988), our results indicate that at least some DWD retention may be important if attempting to ameliorate harsh conditions for planted seedlings. In environments where naturally occurring DWD is less frequent and retention of DWD after logging is not feasible, intentional placement of DWD, or directional felling of dead trees should be considered as a restoration strategy. Intentional DWD placement or felling allows for control of DWD direction, prioritizing *E*-W or NW-SE orientation to capitalize on the anisotropic shading benefit. It also allows for control of DWD species, decay class, and size, all factors, which may impact the DWD microsite.

Whichever method is used to obtain DWD, its location and direction relative to establishing seedlings are important. To maximize the microsite benefit, seedlings should be planted on the north or northeast side of DWD and within 0.25 m, taking advantage of those locations with the most favorable abiotic growing conditions. It should be noted that the extent of the ameliorated microsite may be greater for larger DWD, and future research should address the relation between the diameter of the sheltering DWD and the spatial extent of the microsite.

Other forms of microsite-creating objects have been widely studied to support regeneration and restoration efforts, including nurse shrubs, stumps, and shade cards (Childs & Flint 1987; Devine & Harrington 2007; Marsh et al. 2023). While all these shelters offer benefits like DWD, each has limitations compared to DWD. Rather than facilitating seedling establishment, nurse shrubs can easily shift from a benefactor to a competitor for limited resources like soil water and nutrients (Plamboeck et al. 2008). Stump microsites are spatially limited, only having room for one to a few seedlings to establish, particularly on the north side. Shade cards may be less desirable as they are more expensive and only affect conditions at the surface and not deeper into the soil (Childs & Flint 1987). DWD does not compete with seedlings for resources, provides a large microsite area for seedling establishment, naturally occurs in forests, and persists a long time in temperate and boreal environments.

Future Research

Our chosen field sites were consistent in their low elevations and completely open overstories—habitat qualities that made them unsuitable for natural black huckleberry establishment. Future work should test the microsite benefit in sites with varying habitat qualities. Variation in seedling survival across study sites indicates other habitat conditions (e.g. soil type, land use histories) not tested in this study also affect huckleberry seedling survival. By testing a variety of conditions, future research could identify the optimum habitat and microsite combination that will lead to maximum seedling survival.

Future studies should also test the microsite effect using DWD of varying species, sizes, and decay classes, which may lead to different microsite conditions (Harmon et al. 1986; Lee & Sturgess 2001). For example, larger diameter DWD may lead to a larger microsite effect, reaching out to 0.5 m or farther, where our chosen DWD size only demonstrated microsite benefits out to 0.25 m. Different decay classes and different species may have different moisture and nutrient retention that would change the strength and quality of the DWD microsite (Stevens 1997; Laiho & Prescott 2004; Kumar et al. 2018). By testing DWD of various characteristics, we can identify DWD qualities that facilitate the strongest microsite and therefore should be utilized in huckleberry restoration. Additionally, previous work has suggested highly decayed DWD or DWD partially buried in the soil substrate may provide additional benefits to establishing seedlings (Barney 1999) by increasing soil moisture and nutrient availability. Subsurface or highly decayed DWD can more directly affect soil moisture conditions at the seedling root zone, which will be important under current and predicted drought conditions.

Finally, we chose to study the microsite effect on black huckleberry shrubs due to the cultural, economic, and ecological importance of this species, climate- and successional-related threats, its abundance, and its ideal abiotic conditions that correlate well with those that are facilitated by the DWD microsite. By expanding the microsite effect from tree seedling to black huckleberry seedlings, we demonstrated how the benefit of microsites can variably affect different species and different growth habits. In order to establish the ubiquity of DWD as a restoration tool, further studies should expand on these works, testing the microsite for different species and different age classes, and demonstrate how DWD microsites and their associated patterns can restore growing conditions for different vegetative forms that face declines in a changing world.

Acknowledgments

We acknowledge the assistance of H. L. Osborne, M. Osborne, J. Link, and H. Basham in experiment installation and data collection. Experimental sites were provided by N. Boothe and the Coeur d’ Alene Tribe Natural Resources Department, Priest River Experimental Forest, and H. L. Osborne. Black huckleberry seedlings were provided by Franklin H. Pitkin Nursery, Moscow, Idaho and Plants of the Wild, Tekoa, Washington. Invaluable statistical advice was kindly provided by R. J. Smith, D. Gannon, T. L. DeJong, and D. P. Rice. M.I.M. was supported by the Emerging Research Issues in Agriculture program, Grant #PG00019576, College of Agricultural, Human, and Natural Resource Sciences at Washington State University. M.E.S. and H.A.D. were supported by the USDA NIFA McIntire-Stennis program (project 1019284).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Average temperature (°C) and precipitation (cm) from 2000 to 2023 averaged across all three sites.
Figure S2. Average soil surface temperature (°C) over the growing season by distance from DWD (m) and DWD aspect.
Figure S3. Average soil volumetric water content (%) over the growing season by distance from DWD (m) and DWD aspect.

Coordinating Editor: Markus Wagner

Received: 2 May, 2024; First decision: 16 July, 2024; Revised: 23 August, 2024; Accepted: 23 August, 2024