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REGISTRATION

Cultivar

Registration of 'USDA-Basin' and 'USDA-Wasatch' bluebunch wheatgrass, originating from and adapted to the Central Great Basin of the western USA

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Abstract

The USDA-ARS and Utah Division of Wildlife Resources announce the release of bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh.) A. Löve.] cultivars 'USDA-Basin' (Reg. no. CV-35, PI 708099) and 'USDA-Wasatch' (Reg. no. CV-36, PI 708100) (experimental designations: Basin/Basin-STZ4 and Wasatch/Basin-STZ3a, respectively) for their seedling drought tolerance and establishment, and as the first bluebunch wheatgrass cultivars that geographically and genetically originate from the Great Basin region of the United States. Though regionally sourced materials are desired, most bluebunch wheatgrass used for re-seeding this region originate in the Columbia Plateau and Blue Mountains of eastern Washington state. Therefore, bluebunch wheatgrass was collected from the Great Basin and evaluated for relative fitness. Four collections from within each of two phylogeographic groups were selected and crossed to form USDA-Basin and USDA-Wasatch. Genotyping and morphological measurements demonstrated that USDA-Basin and USDA-Wasatch are significantly ($P < 0.05$) different from each other and four check cultivars. In response to drought, seedling root growth for both was greater ($P < 0.05$) than 'Columbia' and 'P-7', but similar to ($P > 0.05$) 'Anatone', whereas they had lesser ($P < 0.05$) specific leaf area than checks, indicative of enhanced seedling drought tolerance. USDA-Basin and USDA-Wasatch were similar ($P > 0.05$) to each other and Anatone for stand establishment (mean of 38%), and both had greater ($P < 0.05$) establishment at two of three sites than Columbia and 'Goldar'. USDA-Basin and USDA-Wasatch originate from two seed transfer zones that compose 65% of reseeding efforts within the Central Great Basin and thus contribute important regional components to restoration projects in this region.

Abbreviations: GBS, genotype-by-sequencing; PC, principal components; RCB, randomized complete block; SNP, single nucleotide polymorphisms; WAS, Wasatch; WGBS, Western Great Basin South.

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Plain Language Summary

Invasive grasses and repeated wildfires result in frequent re-seeding in the Great Basin region of the United States. Bluebunch wheatgrass is one of the keystone species for restoration of the Great Basin. However, even though there is a demand for "local" plant materials, up until now commercial sources of bluebunch wheatgrass have all originated in the Columbia Plateau and Blue Mountains of eastern Washington state. USDA-Basin and USDA-Wasatch are being released for their proven seedling drought tolerance and establishment, and as the first bluebunch wheatgrass cultivars that geographically and genetically originate from the Central Great Basin ecoregion of the western United States. USDA-Basin and USDA-Wasatch both exhibited enhanced drought adaptation, good seedling vigor, and good seedling establishment comparable to Anatone. Thus, these releases will contribute important components to region-specific wildfire and other restoration projects in the Central Great Basin.

1 | INTRODUCTION

Throughout the rangelands of the intermountain Western United States, exotic annual grasses including cheatgrass (*Bromus tectorum* L.) are associated with an increased risk of wildfire, resulting in the loss of the big sagebrush (*Artemisia* Nutt. *spp*.)-biome and greatly diminished ecosystem services (Balch et al., 2013; Crist et al., 2023; Davies et al., 2011; Young & Longland, 1996). Due to the scale of this invasive annual grass–wildfire cycle problem, restoration re-seeding in the intermountain Western United States is greater than anywhere else in the world (Jones, 2019). Therefore, improved seed supplies and successful stand establishment of regionally sourced native grasses is considered a national priority for rangeland restoration. In order to conserve the genetic variation within species, regionally-sourced native plants that are locally adapted are often desired for these restoration efforts (Johnson et al., 2010). Researchers have determined that local adaptation is a response to environmental gradients (Hereford, 2009; Johnson et al., 2010). Thus, delineations by geographic proximity, including ecoregions, seed transfer zones, and phylogeographic relationships have been suggested (Johnson et al., 2010; Larson et al., 2004; St. Clair et al., 2013). Ecoregions encompass a group of multiple similar ecosystems (Bailey, 1995; Omernik & Griffith, 2014) and are defined by such criteria as geological features, soils, hydrology, vegetation, wildlife, and climatic patterns. Seed-transfer zones, widely applied for timber species in the Pacific Northwest, have been developed for restoration species used in the intermountain Western United states, including bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Á. Löve] (St. Clair et al., 2013). Phylogeographic maps, derived from molecular genetic structure and reflecting the history of a species' populations and their movement across geographic space, have also been developed for bluebunch wheatgrass (Larson et al., 2004; Massatti et al., 2018). Bluebunch wheatgrass is a keystone species for restoration and revegetation efforts in the Great Basin. However, even though there is a demand for regionally sourced plant materials, up until now, commercial sources of bluebunch wheatgrass seed used in the Central Basin and Range Level III ecoregion of Nevada and eastern Utah (Omernik & Griffith, 2014) have originated in the Columbia Plateau and Blue Mountains Level III ecoregions of eastern Washington state (Ogle et al., 2010). Research indicates that these commonly used cultivars, including 'Anatone' (PI 635993; Monsen et al., 2003), have high fitness relative to Great Basin populations and therefore, could eventually threaten the genetic base of Great Basin bluebunch wheatgrass (Waldron et al., unpublished data). Thus, there is a need for proven, regionally-specific bluebunch wheatgrass plant material for restoration of the Central Great Basin. This work describes the development of 'USDA-Basin' (Reg. no. CV-35, PI 708099) and 'USDA-Wasatch' (Reg. no. CV-36, PI 708100) that are being released for their proven seedling establishment and drought tolerance. They are the first bluebunch wheatgrass cultivars that geographically and genetically originate from the Central Great Basin of the western USA.

2 | METHODS

2.1 | Breeding history

USDA-Basin and USDA-Wasatch each originated from multi-origin polycrosses of four wildland collections from the Central Basin and Range ecoregion (Omernik & Griffith, 2014) chosen for having high fitness at two Great Basin locations in

comparison to other populations of similar origin. In brief, a total of 78 wildland collections were made in 2004 and 2005 across the central Great Basin by the USDA and Utah Division of Wildlife Resources. These, along with 130 USDA-National Plant Germplasm System accessions, 9 experimental populations, and 4 cultivars, were evaluated for 2 years for biomass, seed production, seedling vigor (i.e., deep-seeding emergence), and for 5- and 10-year persistence at two Central Basin and Range locations: Nephi, UT, and Wells, NV. For the wildland collections, passport data were recorded, including GPS coordinates, and seeds were collected from 30–150 individuals distributed across 0.2–2 ha (0.5–5 acres). Seeds were pooled by sampling locality, cleaned to remove chaff, and stored until used to start plants in the greenhouse for eventual transplanting to a field nursery. The geographic origin of each bluebunch wheatgrass population was determined by plotting collection-location GPS coordinates from the passport data in ArcGIS (https://www.esri.com/), overlaying the appropriate layers/shapefiles and identifying the associated Level III ecoregions (Omernik & Griffith, 2014) and bluebunch wheatgrass seed transfer zones (St. Clair et al., 2013). Genome and ploidy level of each bluebunch wheatgrass population were examined using flow cytometry following the general methods of Arumuganathan and Earle (1991). In addition, DNA was extracted from five plants of each population and phylogeographic genetic structure was modeled by Bayesian clustering of single-nucleotide polymorphism (SNP) genotypes in which Massatti et al. (2018) identified five phylogeographic genetic groups corresponding to the Palouse/Wallowa, Western Great Basin North (WGBN), Western Great Basin South (WGBS), Eastern Great Basin (EGB), and Wasatch (WAS).

The four parental wildland collections for each cultivar were chosen for having greater-than-average relative fitness at the Nephi and Wells locations compared to other populations from the same ecoregion, seed transfer zone, and phylogeographic genetic group. In as much as the goal was to develop regionally sourced cultivars with minimal genetic erosion (Rogers, 2004), the minimal additional selection was conducted as described herein. The USDA-Basin parental collections originated from four Nevada sites within the Central Basin and Range ecoregion and seed transfer zone 4, and all were within the WGBS phylogeographic genetic group (Table 1). The USDA-Wasatch parental collections originated from four Utah sites in the Central Basin and Range ecoregion, seed transfer zone 3a, and the WAS phylogeographic genetic group (Table 1). We dug five vigorous plants from each of the four parental sources of USDA-Basin and the four parental sources of USDA-Wasatch at the Wells evaluation nursery in December 2016 and the two populations were polycrossed in isolation in the greenhouse during January 2017 with harvested seed designated Basin-cycle-1A and Wasatch-cycle-1A. Seed set was low from the greenhouse crosses and many of the selected plants died so an additional five plants of the four parental sources were dug from the Wells nursery in August 2017, transplanted to isolated crossing blocks at a location near Logan, UT, and allowed to polycross. Seed was then harvested by plant in 2018, bulked, and the two new populations designated as Basin-cycle-1B and Wasatch-cycle-1B. Both years of polycrosses (cycle-1A and cycle-1B) resulted in low seed set, so this was followed by a cycle of random mating of 90 plants for Basin-cycle-1 and 20 plants for Wasatch-cycle-1 (approximately equally from cycle-1A and cycle-1B seed) to increase linkage equilibrium and genetic stability; and the seed was harvested in 2019 and the two new populations designated as Basin-cycle-2 and Wasatch-cycle-2. Following the cycle of random mating, 200 seedlings of Basin-cycle-2 and 140 seedlings of Wasatch-cycle-2 that emerged when sown at a depth of 4 cm were planted into two separate, isolated crossing blocks in 2020 at the Utah State University (USU) Blue Creek Dryland Research farm, near Howell, UT. Beginning in 2021, and within the Basin-cycle-2 and Wasatch-cycle-2 crossing blocks, seed was harvested, bulked, and declared as breeder seed for USDA-Basin and USDA-Wasatch, respectively. All subsequent comparative evaluations used breeder seed.

2.2 | Molecular characterization

Approximately 30 mg of fresh leaf sample was harvested from at least 24 individual plants from USDA-Basin and USDA-Wasatch and the checks, Anatone, 'Columbia' (Jones & Mott, 2016), 'Goldar' (Gibbs et al., 1991), 'P-7' (PI 619629; Jones et al., 2002), and 'Whitmar' (PI 421022); and five individual plants from each of the four parent populations (i.e., the original collections) of both USDA-Basin (BK-23, BK-35-1, BK-35-2, and U38-04) and USDA-Wasatch (B131-01, B34-03, U35-03, and U49-03). Leaf samples were lyophilized and milled using a MM300 mixer mill (Retsch Inc.) for DNA extraction using the MagMAX Plant DNA Isolation Kit (ThermoFisher Scientific) in a 96-well plate format on a KingFisher Flex (ThermoFisher Scientific). Multi-locus plant genotypes were determined using a two-enzyme genotype-by-sequencing (GBS) approach (Elshire et al., 2011; Poland et al., 2012) using 1 × 75 bp cycle sequencing kits on an Illumina NextSeq at Utah State University. SNPs were called using the TASSEL-GBSv2 pipeline (Glaubitz et al., 2014) and a draft genome assembly for bluebunch wheatgrass. A perl script was used to read the resulting .vcf file, from the TASSEL-GBSv2 pipeline, and convert homozygous calls with less than five reads to missing data. Then, vcftools was used to filter for markers with only two alleles, remove indels, a minimum allele frequency of 0.5, a minimum read depth of five reads, and a maximum of 70% missing genotypes. A *k*-nearest neighbor genotype imputation (LD-kNNi) method was used to infer genotypes from missing data using the LinkImpute

TABLE 1 Parent collections used in the development of USDA-Basin and USDA-Wasatch bluebunch wheatgrass.

	Collection Location								
Parent collection	Site, county, state	Lat. (N)	Long. (W)	Elevation (m)	Mean temp. (°C); and ppt. (mm)	STZ	Nearest STZ	Genetic Group	Ploidy
USDA-Basin									
BK_23	Tuscarora, Elko, NV	41.20113	−116.3863	1788	7.0; 313	4	3a	WGBS	2x
BK_35-1	Water Canyon, Humboldt, NV	40.92103	−117.6505	1824	8.2; 416	4	3a	WGBS	2x
BK_35-2	Water Canyon, Humboldt, NV	40.92103	−117.6505	1824	8.2; 416	4	3a	WGBS	2x
DWR_U38-04	Elko, Elko, NV	40.86694	−115.8691	1829	7.5; 332	4	2a	WGBS	2x
USDA-Wasatch									
DWR_B34-03	Levan, Juab, UT	39.59142	−111.82328	1768	9.0; 414	3a	5	WAS	2x
DWR_B131-01	Paul Bunyan, Juab, UT	39.76511	−112.11444	2073	8.6; 418	3a	4	WAS	2x
DWR_U35-03	Chris Creek, Juab, UT	39.47039	−111.88813	1626	9.1; 404	3a	5	WAS	2x
DWR_U49-03	West Tintic drainage, Juab, UT	39.83320	−112.24623	1762	9.0; 358	3a	5	WAS	2x

Abbreviations: ppt., precipitation; WAS, Wasatch phylogeographic genetic group; WGBS, Western Great Basin South phylogeographic genetic group.

version 1.1.4 software package (Money et al., 2015). The .vcf file from LinkImpute was converted to the hapmap format using TASSEL. The hapmap file was converted to a GenAlEx format using a custom R (https://www.r-project.org/) script, and then converted to a pairwise Euclidean distance matrix using the "bitwise.dist" function of the "poppr" R package (Kamvar et al., 2015, 2014). Analysis of molecular variance (AMOVA) (Excoffier et al., 1992) was used to evaluate the significance of pairwise population differentiation (PhiPT) using GenAlEx 6.5 (Peakall & Smouse, 2006, 2012). A principal coordinates analysis (PCoA) was developed based on the linearized PhiPT using GenAlEx 6.5.

2.3 | Morphological characterization

To detect morphological distinctness, two spaced-plant trials were established at the Utah State University (USU) Blue Creek and Evans farms in May 2022 (see Field evaluations Trial 1 for site details). At each location, plots were arranged as a randomized complete block (RCB) design with eight replicate blocks and plots of five plants with 0.5 m between plants and 1.0 m between rows. Nineteen morphological characters (Table 1) were evaluated in 2023 using two reproductive culms of at least 30 plants at each location of USDA-Basin, USDA-Wasatch, Anatone, Columbia, P-7, and Goldar. Morphological traits were plant height (cm), flag leaf height (cm), flag leaf length (cm), flag leaf width (mm), leaf abaxial surface pubescence (present or not), leaf adaxial surface pubescence (present or not), spike length (cm), spike width (mm), lower internode length (mm), upper internode length (mm), spikelet length (mm), spikelet width (mm), lemma length (mm), lemma width (mm), lemma awn length (mm), lemma pubescence (1 = pubescent, 2 = partial [on the nerves], or 3 = glabrous), glume length (mm), glume width (mm), and glume awn length (mm). In addition, relative maturity (i.e., days to 50% anthesis) and biomass plant^{-1} were measured in 2023.

2.4 | Seedling growth and vigor evaluations

2.4.1 | Seedling growth traits

An experiment was conducted in a greenhouse at the USDA-ARS, Forage and Range Research Laboratory in Logan, UT, in winter/spring of 2023 to evaluate seedling growth traits using an RCB design with five replicate blocks. Temperature of the greenhouse was maintained at 23 C ± 5 C with radiant heaters, fans, and an evaporative cooling system. Each block consisted of a 98-capacity cone-tainer cell tray (Ray Leach Cone-tainer RL98 tray and SC10 Super Cells [21-cm deep, 3.8-cm diam., 164-cm^3 vol.], Stuewe and Sons) with populations planted in two 7-plant rows (i.e., 14 plants per population) that were randomized within a rack with an empty row between each population. Cone-tainer cells were filled with a 3:1 w/w soil mix consisting of Preston Fine Sand (Mixed, mesic Typic Xeropsamment) collected in Cache County, UT, which had been pre-sieved (1 mm) and peat moss. We compared five bluebunch wheatgrass cultivars: USDA-Basin, USDA-Wasatch, Anatone, Columbia, and P-7. Seeds were sown into cone-tainer cells at a depth of 7 mm with the rachilla pointing down. After sowing, the soil surface was wetted with

deionized water as needed to maintain gravimetric soil water content at 20% (SWC% = g $H^2$0/g dry soil × 100). To promote growth, individual cones were fertilized with 20 mL (20–20–20, N:P:K) solution at 30, 60, and 90 days after emergence.

Seedlings were grown for 90 days before they were uniformly cut to a stubble height of 7 cm, exposed to a 10-day period without any additional water (drought conditions), then cut again to measure regrowth height above 7-cm and regrowth biomass. Regrowth biomass was dried for 48 h at 60°C, weighed, and expressed on a dry-mass basis. Daily watering was then resumed for 14 days, after which half of the seedlings of each population were harvested and carefully extracted from cones (keeping roots and shoots intact) by submerged cones in water-filled trays. Roots were excised below the meristematic crown, dried at 60°C for 48 h, and weighed to determine dry mass. Individual shoots were floated in transparent plexiglass trays filled with water and placed on a flatbed scanner (Epson Expression, 12000 XL). Digital images of shoots were acquired at 200 dpi that were analyzed for leaf (shoot) area using computer software (WinRHIZO Pro 2021, Regent Instruments Inc., Quebec, Canada). Root mass ratio (root mass/total seedling mass) and specific leaf area (shoot area/shoot mass) were calculated to assess growth investment into roots and photosynthetic surface area.

2.4.2 | Seedling vigor

Seedling vigor was evaluated as the percentage and rate of seedling emergence from a planting depth of 4 cm (Waldron et al., 2006). This evaluation occurred during the winter of 2022 in a greenhouse at the USDA-ARS Forage and Range Research Laboratory in Logan. Temperature of the greenhouse was maintained at 23°C ± 5°C with radiant heaters, fans, and an evaporative cooling system. The experiment was arranged as an RCB design with three replicate blocks and repeated in time with two runs. Each block was arranged on separate greenhouse benches and consisted of three, 98-capacity cone-tainer cell trays (Ray Leach Cone-tainer RL98 tray and SC10 Super Cells [21-cm deep, 3.8-cm diam.], Stuewe and Sons) with each bluebunch wheatgrass population planted in one-half of the tray (i.e., in seven 7-plant rows) with populations randomized among the trays. Cone-tainer cells were filled with pre-sieved (1 mm) Preston Fine Sand (Mixed, mesic Typic Xeropsamment) collected in Cache County. One pure live seed was placed at the bottom of a pre-made divot in each cell and then covered to a uniform depth of 4 cm. The cone-tainers were gently watered daily to approach the soil's field capacity. Number of seedlings emerged were counted daily from 5 to 18 days after planting. Seedling emergence rate was measured using the method of Maguire (1962) and total percentage of seedlings emerged was determined. The first run was initiated on January 24, 2022, and the second on February 7, 2022. Seed harvested in 2021 was used for the study and six bluebunch wheatgrass cultivars were compared: USDA-Basin, USDA-Wasatch, Anatone, Columbia, P-7, and Goldar.

2.5 | Field evaluation of establishment and plant growth

Between 2021 and 2024, multiple field trials were conducted to compare establishment, plant growth, and vigor of USDA-Basin and USDA-Wasatch against 3 to 6 (dependent upon trial) of the predominant check bluebunch wheatgrass cultivars. All trials were arranged as RCB designs with three to four blocks (i.e., replications). Biomass was estimated as dry weight (g) above stubble height of 5 cm. Establishment in Trial 1 was by counting seedlings. Establishment was measured in Trial 3 as seedling frequency using the grid system by Vogel and Masters (2001) using 24, 12.5 × 12.5-cm quadrats, the percentage of quadrats containing at least one seedling was recorded and repeated three times per plot (72 quadrats). Then the frequency was converted to a conservative estimate of plants m^{-2} by multiplying frequency by 0.33 as per the equation in Vogel and Masters (2001). Field-trial site description, ecoregion (Level III and IV ecoregions; Omernik & Griffith, 2014), establishment year, seeding rate or type of planting and plot size, phenotypic evaluation, and plant materials are as follows:

1. *Trial 1 – Location 1*: USU Blue Creek Dryland Research Farm, near Howell, UT: Latitude 41.93335, Longitude −112.4376; elevation 1569 m asl; 47 cm annual precipitation; Soil: Parley's silt loam (fine-silty, mixed, mesic, Calcic Argixeroll); Level III, 13 Central Basin and Range, and Level IV, 13c Sagebrush Basins and Slopes; dormant seeded November 8, 2021, with a Wintersteiger single row walk-behind cone-seeder, seeding rate of 1.2 seeds/cm in a single row 1-m in length. Number of seedlings that were established was measured on May 22, 2022. Plant materials in this trial were USDA-Basin, USDA-Wasatch, Anatone, Columbia, and Goldar bluebunch wheatgrass cultivars.
2. *Trial 1 – Location 2*: USU Evans Research Farm, near Millville, UT: Latitude 41.695047, Longitude −111.831396; elevation 1,394 m asl; 46 cm annual precipitation; Soil: Lewiston fine sandy loam (coarse-loamy, mixed, superactive, mesic Calcic Haploxeroll); Level III, 13 Central Basin and Range, and Level IV, 13i Malad and Cache Valleys; dormant seeded November 22, 2021, as described in Location 1. Number of seedlings established were measured on May 26, 2022.

3. *Trial 2*: USU Nephi Farm, near Nephi, UT: Latitude 39.645458, Longitude −111.870497; elevation 1594 m asl; 33 cm annual precipitation; Soil: Nephi silt loam (fine-silty, mixed, mesic Calcic Argixeroll); Level III, 13 Central Basin and Range; Level IV, 13c Sagebrush Basins and Slopes; dormant seeded November 2022; dormant seeded at 1 PLS/linear cm, plots were 1.5 × 6.0 m with four rows spaced 25 cm apart. Seedling establishment (frequency and number of plants) was measured. Plant materials were 18 bluebunch wheatgrass cultivars and breeding populations that included USDA-Basin, USDA-Wasatch, Anatone, Columbia, P-7, Goldar, Whitmar, Wahluke, and Atomic.
4. *Trial 3*: USU Richmond Farm, near Richmond, UT: Latitude 41.894363, Longitude −111.823353; 1379 m asl; 46 cm annual precipitation; Soil: Parleys silt loam (Fine-silty, mixed, superactive, mesic Calcic Argixeroll); Level III, 13 Central Basin and Range, and Level IV, 13i Malad and Cache Valleys; Spaced-transplants established spring 2022, 7-plant plots on 0.5-m centers. Biomass plant^{-1} measured on September 20, 2022. Plant materials were 14 bluebunch wheatgrass cultivars and breeding populations that included USDA-Basin, USDA-Wasatch, Anatone, Columbia, P-7, Goldar, Whitmar, Wahluke, Atomic, and Twin.

2.6 | Statistical analysis

All phenotypic and morphological measurements were analyzed across and within locations (and/or years, and/or runs as appropriate) using the MIXED procedure of SAS (SAS Institute Inc., Version 9.3). Bluebunch wheatgrass cultivars and breeding populations and locations were treated as fixed effects and years and/or runs and blocks (e.g., replications) within locations were considered random. For morphological data analysis, plant was considered nested within variety and block. LSmeans were computed and mean comparisons made using Fisher's protected least significant difference (LSD) test at the $P = 0.05$ level of probability. Variety × location (or × year, or × run, as appropriate for the study) interactions were examined and when appropriate the pooled mean is presented. Morphological data also were subjected to multivariate analyses as performed by R v4.3.1 (https://www.r-project.org/) and the R packages GGPLOT2 (Wickham, 2016), MASS (Venables & Ripley, 2002), and FACTOEXTRA (Kassambara & Mundt, 2020). A principal component (PC) analysis was performed using the correlation matrix (e.g., to account for different units of measure) and PC biplots of individuals and variables were created to examine morphological relationships among cultivars and breeding populations (i.e., concentration ellipses for variety were added at $P = 0.90$ using the habillage option). The loadings from PC analysis were examined to determine which morphological traits were the most influential in describing the variation.

3 | CHARACTERISTICS

3.1 | Molecular characterization

A total of 7224 different SNP loci were identified by GBS. The average number of SNPs between individual plants within populations ranged from 729 in B34-03 to 2387 in P-7, indicating that P-7 is the most diverse population (Table 2). The average number of SNPs between populations ranged from 1181 to 3803 (Table 2). All PhiPT values were significant except for the comparison of BK35-1 and BK-35-2 (Table 3), with only 3.9% difference between these two source populations. Although smaller PhiPT were observed, the significance of the PhiPT values is determined in part by the number of individuals sampled from each population. Approximately 29% of the overall genetic variation was apportioned among populations and 71% within populations. The principal coordinates analysis of the PhiPT values captured 57.4% of the variation in the first coordinate and 14.4% of the variation in the second coordinate (Figure 1). It shows three major groups including Basin and its four source populations, Wasatch and its four source populations, and a group comprised of the five reference cultivars (Anatone, Columbia, Goldar, P-7 and Whitmar). However, Wasatch appears to be somewhat intermediate between its four source populations and Basin.

3.2 | Morphology

Significant differences among cultivars were observed for all morphological traits except leaf adaxial surface pubescence, lemma width, and lemma pubescence (Table 1). Of the significant traits, location × variety interactions were observed for all except flag leaf height, spike length, internode lower length, and lemma length. However, the interaction was primarily due to magnitude differences between Evans and Blue Creek farms, with measurements at Evans being 20% to 50% greater than Blue Creek due to a mid-summer drought at Blue Creek. However, rank was primarily the same between the locations. Thus, morphological data are presented as the means over the two locations. Morphological characters were able to distinguish both USDA-Basin and USDA-Wasatch from the other released cultivars and from each other (Table 4; Figure 2). The first four PC had eigenvalues greater than "1" and cumulatively explained 68.9% of the variation among bluebunch wheatgrass cultivars (Figure 2). Traits of primary importance in describing the variation were: for PC 1, spikelet length, glume length, spike length, lower internode length,

TABLE 2 Molecular genetic characterization using genotype-by-sequencing data for USDA-Basin and USDA-Wasatch bluebunch wheatgrass, parent populations, and checks. The average number of single nucleotide polymorphisms (SNPs) within populations (diagonal) and between populations (above diagonal).

	Anatone	Basin	BK-23	BK-35-1	BK-35-2	Columbia	B131-01	B34-03	U35-03	U38-04	U49-03	Goldar	P-7	Wasatch	Whitmar
Anatone	**2186**	3023	3069	3150	3123	2942	3544	3617	3578	3078	3457	2792	2908	3014	3060
Basin		**1749**	2094	2160	2076	3069	3162	3261	3208	1947	3120	2976	3031	3087	3204
BK-23			**1299**	2477	2451	3144	3009	3087	3046	2115	2980	3032	3099	2996	3281
BK-35-1				**1184**	1785	3129	3294	3392	3338	2451	3230	3090	3104	3219	3265
BK-35-2					**1103**	3141	3283	3369	3312	2383	3226	3048	3114	3189	3276
Columbia						**2162**	3603	3692	3639	3173	3497	2904	2652	3278	2678
B131-01							**837**	1303	1315	3194	1477	3507	3551	2349	3718
B34-03								**729**	1181	3292	1489	3580	3633	2346	3803
U35-03									**766**	3251	1485	3539	3587	2343	3764
U38-04										**1035**	3165	3031	3121	3134	3293
U49-03											**850**	3412	3431	2378	3605
Goldar												**2032**	2867	3109	3091
P-7													**2387**	3237	2663
Wasatch														**2153**	3408
Whitmar															**2252**

Abbreviations: USDA-Basin (Basin); USDA-Wasatch (Wasatch).

TABLE 3 Molecular genetic characterization using genotype-by-sequencing data for USDA-Basin and USDA-Wasatch bluebunch wheatgrass, parent populations, and checks. Pairwise population differentiation (PhiPT), lower diagonal, and corresponding probability values (*p*), upper diagonal, based on 999 permutations.

	Anatone	Basin	BK-23	BK-35-1	BK-35-2	Columbia	B131-01	B34-03	U35-03	U38-04	U49-03	Goldar	P-7	Wasatch	Whitmar
Anatone	–	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Basin	0.298	–	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
BK-23	0.284	0.083	–	0.010	0.013	0.001	0.006	0.009	0.011	0.012	0.014	0.001	0.001	0.001	0.001
BK-35-1	0.318	0.142	0.248	–	0.136	0.001	0.001	0.003	0.009	0.010	0.014	0.001	0.001	0.001	0.001
BK-35-2	0.324	0.130	0.265	0.039	–	0.001	0.010	0.010	0.008	0.009	0.001	0.001	0.001	0.001	0.001
Columbia	0.206	0.307	0.294	0.309	0.324	–	0.002	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
B131-01	0.430	0.459	0.468	0.540	0.557	0.438	–	0.010	0.007	0.017	0.009	0.001	0.001	0.001	0.001
B34-03	0.452	0.488	0.507	0.577	0.592	0.463	0.099	–	0.006	0.009	0.027	0.001	0.001	0.001	0.001
U35-03	0.443	0.475	0.491	0.562	0.577	0.451	0.086	0.050	–	0.011	0.010	0.001	0.001	0.001	0.001
U38-04	0.325	0.094	0.172	0.321	0.327	0.340	0.560	0.598	0.584	–	0.022	0.001	0.001	0.001	0.001
U49-03	0.399	0.433	0.427	0.500	0.520	0.402	0.099	0.165	0.143	0.529	–	0.001	0.001	0.001	0.001
Goldar	0.198	0.315	0.310	0.340	0.343	0.224	0.455	0.477	0.467	0.349	0.424	–	0.001	0.001	0.001
P-7	0.157	0.258	0.236	0.256	0.271	0.066	0.388	0.412	0.401	0.283	0.346	0.174	–	0.001	0.001
Wasatch	0.227	0.313	0.264	0.331	0.336	0.283	0.175	0.196	0.188	0.335	0.152	0.278	0.238	–	0.001
Whitmar	0.230	0.325	0.314	0.327	0.340	0.113	0.442	0.464	0.455	0.352	0.408	0.264	0.064	0.305	–

Abbreviations: Basin, USDA-Basin; Wasatch, USDA-Wasatch.

TABLE 4 Morphological summary of the traits for USDA-Basin and USDA-Wasatch bluebunch wheatgrass and checks combined over two locations, Blue Creek and Millville, UT.

Morphological trait	Parameter	Anatone	Columbia	Goldar	P-7	USDA-Basin	USDA-Wasatch
Anthesis date, days	mean	156.6 b	155.9 b	158.1 a	155.8 b	156.4 b	156.6 b
	std.dev.	2.4	2.7	2.7	2.5	2.5	1.9
Plant height, cm	mean	61.4 c	64.6 bc	65.2 ab	68.4 a	66.1 ab	61.6 c
	std.dev.	13.6	7.6	14.6	12.9	13.7	12.9
Flag leaf height, cm	mean	26.1 c	31.6 ab	31.5 ab	32.6 a	32.2 ab	29.6 b
	std.dev.	7.0	5.5	8.2	6.4	5.7	5.8
Flag leaf length, cm	mean	9.5 bc	10.4 ab	9.5 bc	10.8 ab	11 a	9 c
	std.dev.	4.0	2.9	4.1	3.3	3.9	3.9
Flag leaf width, mm	mean	2.2 b	1.7 c	2.4 a	1.7 c	2.1 b	2.2 ab
	std.dev.	0.6	0.3	0.7	0.3	0.7	0.7
Leaf abaxial surface, 1 = pubescent; 2 = glabrous	mean	1.8 a	1.4 c	1.8 a	1.4 c	1.6 b	1.8 a
	std.dev.	0.3	0.4	0.3	0.5	0.4	0.3
Leaf adaxial surface, 1 = pubescent; 2 = glabrous	mean	1.8 ab	1.9 a	1.9 a	1.9 ab	1.8 b	1.9 a
	std.dev.	0.3	0.2	0.2	0.3	0.4	0.2
Spike length, cm	mean	12.5 ab	12.3 b	13.3 a	13.4 a	11.7 b	12 b
	std.dev.	3.5	3.0	4.0	3.3	3.4	3.3
Spike width, cm	mean	7.5 c	7.5 c	9.7 ab	8 bc	10.4 a	8.5 bc
	std.dev.	2.9	2.7	5.8	2.8	8.1	3.4
Internode lower length, mm	mean	20.1 ab	21.4 a	22.3 a	22 a	20.1 ab	18.5 b
	std.dev.	7.8	7.1	7.0	7.1	8.1	6.1
Internode upper length, mm	mean	14.5 b	13.8 b	16.1 a	14.1 b	14.7 ab	14.2 b
	std.dev.	3.7	2.4	5.2	2.5	3.9	3.2
Spikelet length, mm	mean	20.3 bc	19.4 cd	21.8 a	20 c	21.5 ab	18.7 d
	std.dev.	4.8	3.2	5.7	3.5	5.7	3.9
Spikelet width, mm	mean	5.3 bc	5 c	6.8 ab	5.5 bc	7.9 a	5.7 bc
	std.dev.	2.4	2.0	4.9	2.4	8.1	2.8
Lemma length, mm	mean	11.3 c	11.4 c	20.9 a	12.1 c	21.4 a	15.3 b
	std.dev.	2.7	5.0	5.7	1.9	5.2	4.6
Lemma width, mm	mean	1.4 a	1.4 a	1.5 a	1.5 a	1.5 a	1.6 a
	std.dev.	0.1	0.2	0.2	0.3	0.2	0.9
Lemma awn length, mm	mean	1.2 d	0.2 d	10.4 b	1.2 d	12.1 a	5.8 c
	std.dev.	2.6	0.4	4.7	1.6	3.8	4.2
Lemma pubesence, 1 to 3; 1 = pubescent; 3 = glabrous	mean	3.0 a	3.0 a	3.0 a	3.0 a	3.0 a	3.0 a
	std.dev.	0.0	0.1	0.0	0.1	0.0	0.0
Glume length, mm	mean	7.4 bc	7.7 b	8.3 a	7.9 ab	7.5 bc	7.0 c
	std.dev.	1.2	1.1	2.1	1.1	1.6	1.3
Glume width, mm	mean	1.2 b	1.2 b	1.3 a	1.2 b	1.2 b	1.2 b
	std.dev.	0.1	0.2	0.1	0.2	0.1	0.1
Glume awn length, mm	mean	0.0 b	0.0 b	0.3 a	0.0 b	0.2 a	0.0 b
	std.dev.	0.1	0.1	0.5	0.1	0.3	0.1

Note: Values within a row with different letters are significantly different at the 0.05 probability level.

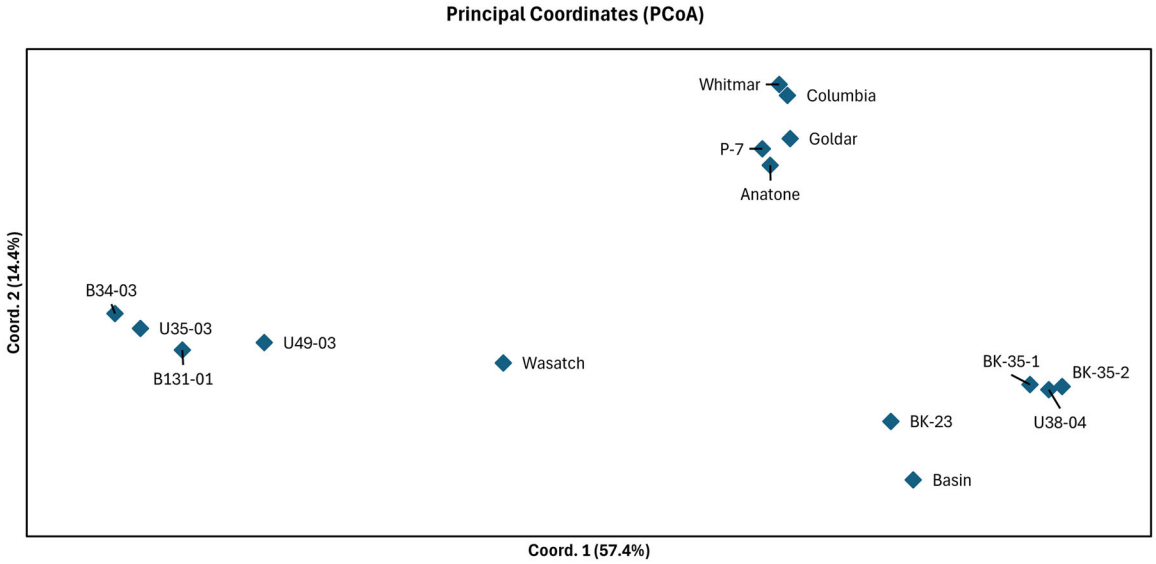


FIGURE 1 Molecular genetic characterization using genotype-by-sequencing data for USDA-Basin and USDA-Wasatch bluebunch wheatgrass, parent populations, and checks. Principal coordinates analysis based on the pairwise population differentiation (PhiPT). USDA-Basin (Basin); USDA-Wasatch (Wasatch).

flag length; for PC 2, lemma awn length, lemma length, glume awn length; for PC 3, spikelet width, spike width, leaf abaxial surface; and for PC 4, flag leaf height. USDA-Basin and Goldar were the most distinct from other cultivars, whereas Anatone, Columbia, and P-7 grouped very closely together (Figure 2). USDA-Wasatch was intermediate between these major groupings, partially overlapping both (Figure 2).

Morphologically, USDA-Basin was most like Goldar (Figure 2) but differed ($P < 0.05$) for many discriminating traits, including being 2 days earlier to anthesis, longer (11.0 vs. 9.5 cm) and narrower (2.1 vs. 2.4 mm) flag leaves, shorter spike inflorescences (11.7 vs. 13.3 cm), longer lemma awns (12.1 vs. 10.4 mm), but shorter (7.5 vs. 8.3 mm) and narrower (1.2 vs. 1.3 mm) glumes (Table 4). USDA-Wasatch was most like Anatone but differed ($P < 0.05$) with flag leaves oriented higher on the culm (29.6 vs. 26.1 cm), shorter spikelet length (18.7 vs. 20.3 mm), and longer lemma (15.3 vs. 11.3 mm) and lemma awn (5.8 vs. 1.2 mm) lengths (Table 4). USDA-Basin and USDA-Wasatch differ ($P < 0.05$) from each other, with USDA-Basin having taller plants (66.1 vs. 61.6 cm), longer flag leaves (11.0 vs. 9.0 cm), longer (21.5 vs. 18.7 mm) and wider (7.9 vs. 5.7 mm) spikelets, longer lemmas (21.4 vs. 15.3 mm), and longer lemma- (12.1 vs. 5.8 mm) and glume-awns (0.2 vs. 0.0 mm) (Table 4). In comparison with the other cultivars, USDA-Basin had significantly ($P < 0.05$) taller plants, flag leaves oriented higher on the culm, longer flag leaves, wider spike inflorescences, wider spikelets, longer lemmas, and longer lemma and glume awns than Anatone; wider flag leaves, wider spike inflorescences, longer and wider spikelets, longer lemmas, and longer lemma and glume awns than Columbia; and wider flag leaves, shorter but wider spike inflorescences, longer and wider spikelets, longer lemmas, and longer lemma and glume awns than P-7 (Table 4). In comparison to the other cultivars, USDA-Wasatch had significantly ($P < 0.05$) shorter but wider flag leaves, shorter upper internodes, and longer lemmas and lemma awns than Columbia; 1 day earlier to anthesis, shorter plants, shorter spike length, shorter upper and lower internodes, shorter spikelets, shorter and narrower glumes, and shorter lemma- and glume-awns than Goldar; and had shorter plants and flag leaves oriented lower on the culm, shorter but wider flag leaves, shorter spike inflorescences and spikelets, shorter lower internodes, and longer lemmas and lemma awns than P-7 (Table 4).

3.3 | Seedling growth and vigor

3.3.1 | Seedling growth

In response to a 10-day drought, regrowth of seedling shoots of USDA-Basin and USDA-Wasatch produced more ($P < 0.05$) biomass than Anatone and Columbia (Figure 3). Following the drought event, seedling root biomass and root mass ratio were similar ($P > 0.05$) to Anatone, but greater ($P < 0.05$) than Columbia and P-7. However, both USDA-Basin and USDA-Wasatch had lesser ($P < 0.05$) specific leaf area than Anatone, Columbia, and P-7, which has been shown to be indicative of enhanced adaptation to drought (Kramp et al., 2022) (Figure 4). In comparison to each other, USDA-Wasatch had greater ($P < 0.05$) seedling shoot biomass and specific leaf area, but lesser ($P < 0.05$) root biomass than

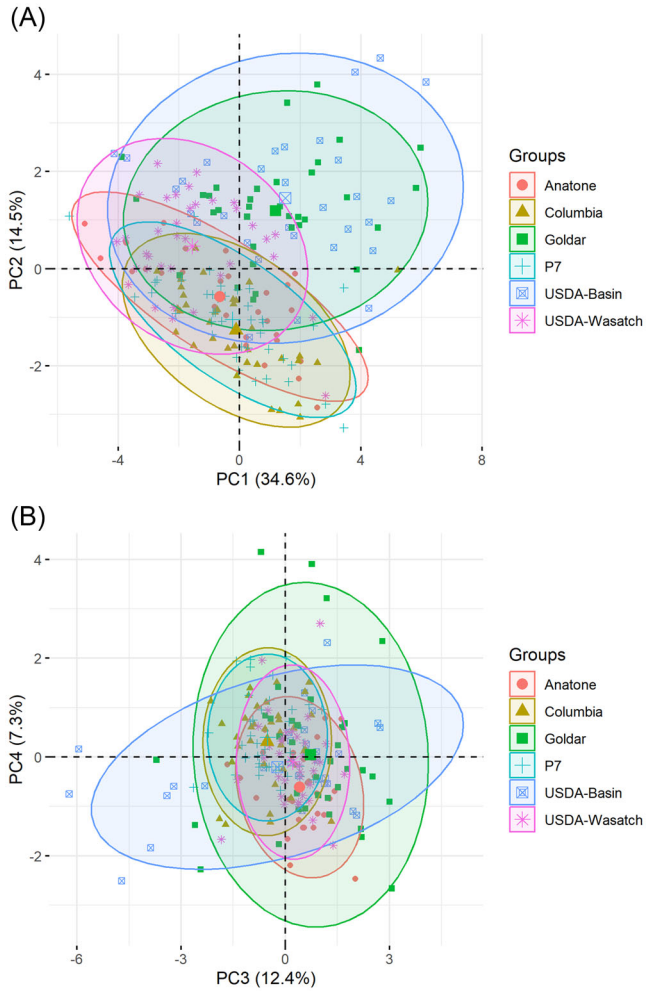


FIGURE 2 Principal component (PC) analysis of morphological characteristics for bluebunch wheatgrass cultivars evaluated at two Great Basin locations, (A) PC 1 vs. PC2, and (B) PC3 vs. PC4. Concentration ellipses for groups added at normal probability of 0.90.

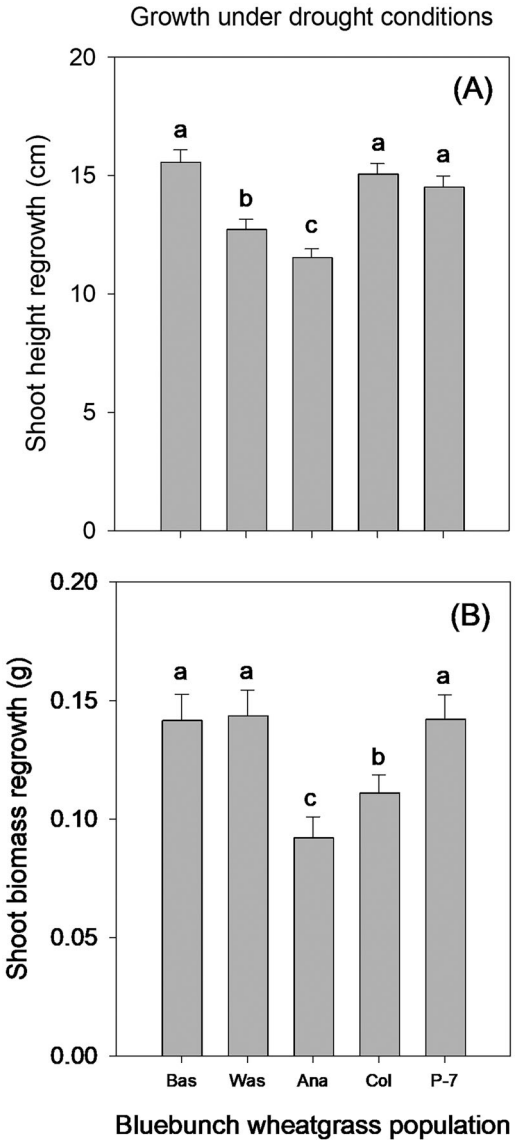


FIGURE 3 Regrowth of shoot height (A) and shoot biomass (B) for five bluebunch wheatgrass populations (Bas = USDA-Basin, Was = USDA-Wasatch, Ana = Anatone, Col = Columbia, and P-7) grown in a greenhouse for 90 days, clipped to a height of 7 cm, and exposed to a 10-day drought (water-stressed conditions). Bars represent the mean (± 1 SE) of five replicated blocks that contained 14 plants of each grass variety. Within a response variable, bars with different lowercase letters denote significant differences based upon Fisher's corrected least significant difference ($P < 0.05$).

USDA-Basin following drought (Figure 4), possibly reflecting the drier home environment of the USDA-Basin parents (Table 1).

3.3.2 | Seedling vigor

Seedling emergence from a deep depth has been correlated with field-based seedling vigor as reviewed by Waldron et al. (2006). Deep-seeding emergence was one of the traits comprising relative fitness of the bluebunch wheatgrass collections evaluated as parents (Waldron et al., unpublished data). As such, USDA-Basin and USDA-Wasatch had greater ($P < 0.05$) deep-seeding emergence (84% and 85%, respectively) than Columbia and Goldar (71% and 64%, respectively) (Table 5). Nevertheless, there was little variation in either percentage of seedlings emerged or emergence rate observed among the bluebunch wheatgrass cultivars tested (Table 5).

3.4 | Establishment and plant growth

Seedling establishment is a critical trait for restoration reseeding following disturbances such as wildfires. As such, Anatone has been widely used, in part, because of its

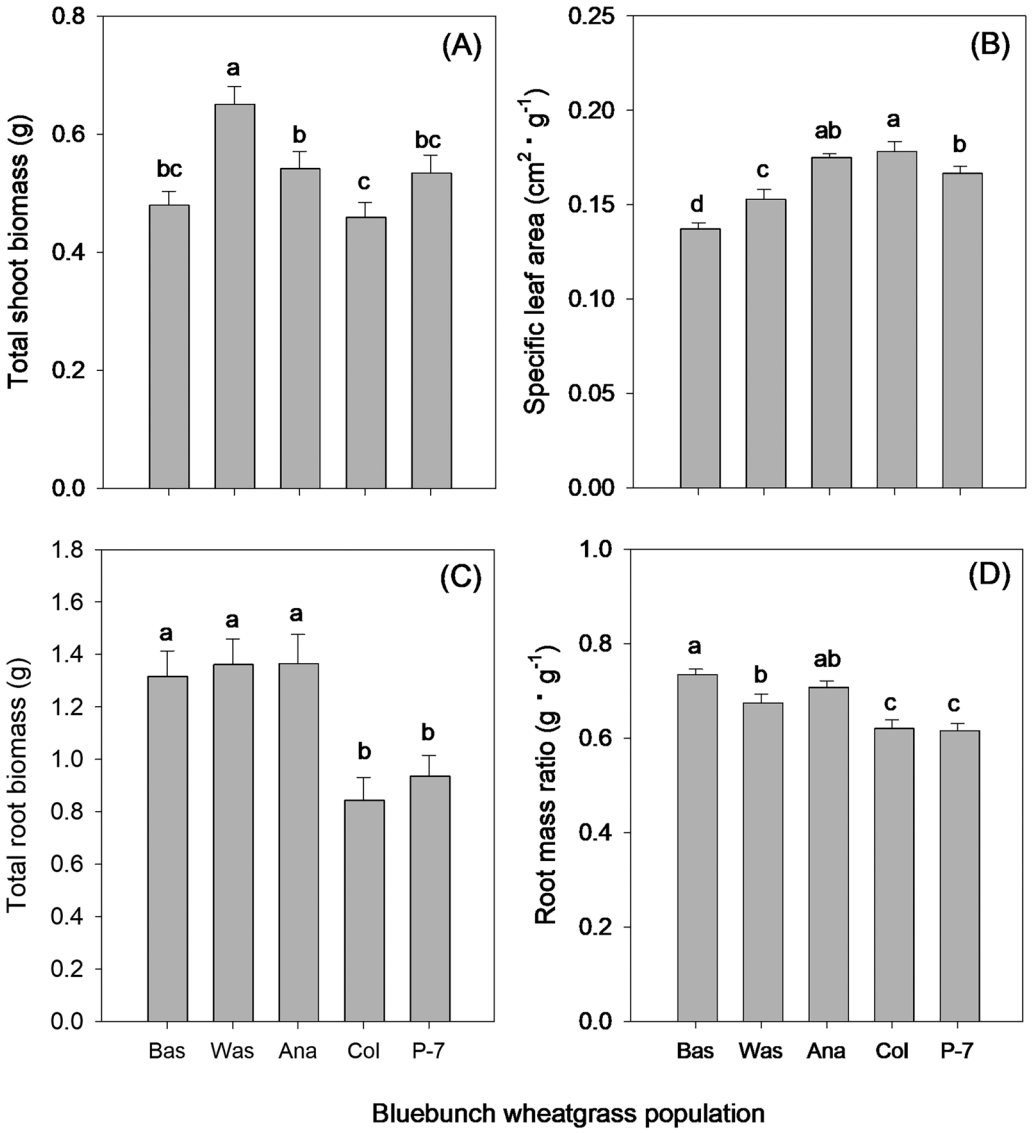


FIGURE 4 Total root dry mass (A), root mass ratio (B), total shoot dry mass (C), and specific leaf area (D) for five bluebunch wheatgrass populations (Bas = USDA-Basin, Was = USDA-Wasatch, Ana = Anatone, Col = Columbia, and P-7) grown in a greenhouse for 90 days, clipped to a height of 7 cm, and exposed to a 10-d drought. Plants were then grown for an additional 14 d with daily watering (non-stressed conditions) before harvesting plants. Bars represent the mean (± 1 SE) of five replicated blocks that contained 7 plants of each grass variety. Within a response variable, bars with different lowercase letters denote significant differences based upon Fisher's corrected least significant difference ($P < 0.05$).

establishment success. USDA-Basin and USDA-Wasatch did not differ ($P > 0.05$) from each other in establishment in the four field evaluations (Table 5). Furthermore, they were equal to Anatone for establishment in three trials and had greater ($P < 0.05$) establishment than Anatone at Blue Creek (Table 5).

Plant growth (e.g., biomass) was not emphasized during the development of USDA-Basin and USDA-Wasatch, but it was measured in the field the year following establishment at three sites. Great Basin bluebunch wheatgrass ecotypes are known to display relatively low vegetative growth. This was true for USDA-Basin and USDA-Wasatch, which had comparable ($P > 0.05$) plant biomass, but less ($P < 0.05$) than Anatone, Columbia, P-7, and Goldar at Millville and Richmond sites, which had greater annual precipitation than the Blue Creek site (Table 6). At the Blue Creek site, USDA-Wasatch had less ($P < 0.05$) biomass than P-7, similar ($P > 0.05$) biomass as Columbia and Goldar, and greater ($P < 0.05$) biomass than Anatone and USDA-Basin (Table 6).

4 | CONCLUSIONS

USDA-Basin and USDA-Wasatch have been released for their proven seedling drought tolerance and establishment, and as the first bluebunch wheatgrass cultivars that

TABLE 5 Seedling vigor and establishment (number of seedlings and stand frequency [freq.]) for USDA-Basin and USDA-Wasatch bluebunch wheatgrass compared to commercial cultivars.

	Seedling vigor[a]		Establishment[b]			
Genotype	Emerged	Rate	Blue Creek, UT	Millville, UT	Nephi, UT[c] (2023)	Nephi, UT (2024)
	%	seedlings day^{-1}	Seedlings (freq., %)	Seedlings (freq., %)	Seedlings (freq., %)	Plants (freq., %)
USDA-Basin	84 a	5.0 ab	21 (18) a	33 (28) a	23 (70) abc	16 (48) de
USDA-Wasatch	85 a	4.9 abc	26 (22) a	31 (26) a	24 (73) abc	17 (52) cde
Anatone	78 ab	4.9 abc	12 (10) b	23 (19) abc	27 (82) ab	20 (61) bcd
Columbia	71 bc	4.5 bc	12 (10) b	20 (17) bc	25 (76) abc	18 (55) bcd
Goldar	64 c	4.1 c	11 (09) b	17 (14) c	29 (88) a	22 (67) abc
P-7	86 a	5.5 a	.	.	28 (85) a	24 (73) ab
Wahluke	.	.	.	.	22 (67) bc	12 (36) e
Whitmar	.	.	.	.	26 (79) ab	17 (52) cde

Note: Values within column with different letters are significantly different at the 0.05 probability level.

[a]Seedling vigor estimated from emergence from a depth of 4 cm.

[b]Establishment: maximum possible seedlings/plants (for calculating frequency) were for Blue Creek and Millville, 120, and Nephi (2023) and (2024), 33.

[c]Nephi, UT, trial consisted of 12 bluebunch wheatgrass cultivars and breeding populations. All commercial cultivars that were included are shown.

TABLE 6 Vegetative growth (biomass, g plant^{-1}) the year following establishment, comparing USDA-Basin and USDA-Wasatch bluebunch wheatgrass to commercial cultivars at three locations.

Cultivar	Blue Creek, UT	Millville, UT	Richmond, UT[a]
USDA-Basin	2.5 e	14.8 d	2.4 g
USDA-Wasatch	5.7 bc	15.4 d	6.1 def
Anatone	3.8 d	26.0 c	7.8 cd
Columbia	6.3 ab	31.2 b	8.9 bc
Goldar	5.0 c	47.2 a	6.8 cde
P-7	7.2 a	44.2 a	9.0 bc
Wahluke	.	.	4.0 fg
Whitmar	.	.	12.3 a

Note: Values within a column with different letter are significantly different at the 0.05 probability level.

[a]Richmond, UT, trial consisted of 14 bluebunch wheatgrass cultivars and breeding populations. All commercial cultivars that were included are shown. The mean of the trial was 6.3 g plant^{-1}.

geographically and genetically originate from the Central Great Basin ecoregion of the Western United States. Due to the invasive annual grass–wildfire cycles, restoration seedings in the intermountain Western United States are more extensive than anywhere else in the world. Therefore, enhanced seed supplies, successful stand establishment, and development of regionally sourced native grasses is considered a national priority for rangeland restoration. The predominantly used cultivar, Anatone, and other cultivars originating in Washington have high relative fitness, which poses a possible threat to the future genetic base of Great Basin bluebunch wheatgrass populations. USDA-Basin and USDA-Wasatch geographically and genetically originate from the Central Basin and Range Level III ecoregion, including two seed transfer zones that comprise over 65% of reseeding efforts and the two major phylogeographic genetic groups found within this ecoregion. USDA-Basin and USDA-Wasatch both exhibited enhanced seedling drought adaptation, good seedling vigor, and seedling establishment comparable to Anatone. Thus, these releases will contribute to regionally specific wildfire and other restoration projects in the Central Great Basin.

5 | AVAILABILITY

To maintain their unique genetic and geographic integrity, US Plant Variety Protection (PVP) is pending for USDA-Basin (PVP no. 202500367) and USDA-Wasatch (PVP no. 202500366). Breeder, foundation, registered, and certified seed classes will be recognized. Foundation and registered fields may be established from breeder seed. Breeder seed will be maintained by the USDA-ARS Forage and Range Research Laboratory at Logan, UT. Information on licensing these cultivars is available from the USDA-ARS, Office of Technology Transfer, Licensing Section, 5601 Sunnyside Avenue, Room 4-1159, Beltsville, MD 20705–5131 (e-mail: license@ars.usda.gov). Seed of USDA-Basin and USDA-Wasatch have also been deposited into USDA-ARS National Laboratory for Genetic Resources, where they will be available 20 years from the date of PVP issuance.

AUTHOR CONTRIBUTIONS

Blair L. Waldron: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; writing—original draft; writing—review and editing. **Steven R. Larson**: Formal analysis; investigation; writing—original draft. **Jason L. Vernon**: Funding

acquisition; investigation; resources. **Daniel D. Summers**: Funding acquisition; investigation; resources; writing—review and editing. **Thomas A. Monaco**: Investigation; writing—review and editing. **Thomas A. Jones**: Investigation; writing—review and editing. **Kevin B. Jensen**: Investigation; methodology; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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