Effects of the Light Environment and Stand History on Beargrass (*Xerophyllum tenax*) Morphology and Demography

Author(s): David H. Peter, Timothy B. Harrington and Mark Thompson
Source: Northwest Science, 91(4):367-382.
Published By: Northwest Scientific Association
https://doi.org/10.3955/046.091.0406
URL: http://www.bioone.org/doi/full/10.3955/046.091.0406

David H. Peter[1], **Timothy B. Harrington**, US Forest Service, Olympia Forestry Sciences Laboratory, 3625 93rd Ave., Olympia, Washington 98512

Mark Thompson[2], School of Environmental and Forest Sciences, University of Washington, Seattle, Washington 98195

Effects of the Light Environment and Stand History on Beargrass (*Xerophyllum tenax*) Morphology and Demography

Abstract

Beargrass (*Xerophyllum tenax* [Pursh] Nutt.) is an herbaceous, evergreen perennial found in higher elevations of the northern Rocky, Sierra Nevada, Klamath, Siskiyou, Cascade and Olympic Mountains and in coastal areas from Washington to northern California. It is used by Native Americans for basketry and is an important floral green, but the conditions needed for reproduction and commercially valuable characteristics are not well known. We studied how the light environment affects size, morphology, color, and reproduction of a lowland, southeastern Olympic Peninsula beargrass population. We examined beargrass crown size distribution in relation to current and past overstory structure and found that beargrass plants had longer, greener leaves, lower crown density, smaller basal diameter, and fewer vegetative offshoots in shaded areas compared to more open areas. Flowering was less and there were fewer seedlings in shaded areas. Beargrass did not reproduce sexually in areas with < 0.3 of full photosynthetically active radiation (equivalent to at least 50% tree cover in our stand). Beargrass abundance matched the locations of anthropogenically maintained woodland openings that have since become forested preventing beargrass reproduction, suggesting that many plants have survived in the shade for more than 60 years. Overstory removal and prescribed burning in a portion of the stand stimulated sexual and asexual reproduction. We concluded that plants in shaded areas, although of somewhat higher commercial quality, are likely to recover more slowly from foliar harvest, and are less likely to be replaced after mortality. Population sustainability requires periodically or permanently open stand conditions.

Keywords: beargrass demography, *Xerophyllum tenax*, anthropogenic burning, floral greens, ecology

Introduction

Beargrass (*Xerophyllum tenax* [Pursh] Nutt.) is an herbaceous, evergreen perennial of forests and openings in the northern Rocky, Sierra Nevada, Klamath, Siskiyou, Cascade and Olympic Mountains and in coastal areas from Washington to northern California. Most beargrass literature focuses on the more common higher elevation communities (Maule 1959, Higgins et al. 2004, Vance et al. 2004, Hummel and Lake 2015), but lower elevation beargrass communities have also been described (Henderson et al. 1989, Kunze 1994, Atzet et al. 1996, Kulzer et al. 2001). The species grows in many forested plant associations that are generally of low timber productivity (Daubenmire and Daubenmire 1968, Pfister et al. 1977, Steele et al. 1981, Hemstrom et al. 1982, Halverson et al. 1986, Logan et al. 1987, Henderson et al. 1989, Williams et al. 1990, Cooper et al. 1991, Henderson et al. 1992, Atzet, et al. 1996, White et al. 1996, Diaz et al. 1997).

Beargrass has been used for basketry by native peoples from California to British Columbia (Gunther 1973, Turner 1979, Anderson 2005) and continues to be culturally and economically important (Schlosser et al. 1992, Shebitz 2005). Important basketry characteristics include leaf length, width, flexibility, tensile strength and the ability to lay flat (Rentz 2003). It has been suggested that the best plants with these characteristics occur in recently burned higher elevation forest understories (Heffner 1984, Lee 2000, Rentz 2003). Rentz (2003) found a reduction in leaf sclerification in the new foliage of recently burned plants resulting in increased flexibility and elasticity of the leaves.

[1]Author to whom correspondence should be addressed. Email: dpeter@fs.fed.us
[2] Deceased

Beargrass gained commercial importance in the 1980s (Weigland 2002, Lynch and McLain 2003) and is now one of the most widely harvested floral greens in the Pacific Northwest (Schlosser et al. 1992, Schlosser and Blatner 1997). Commercially valuable leaves are long, wide, firm, dark green, and free of blemishes or yellow tips growing from the center of large shade grown plants (Schlosser et al. 1992, Thomas and Schumann 1993, Schlosser and Blatner 1997, Higgins et al. 2004, Shebitz 2005).

Mature beargrass plants produce tight clusters of 1–2 cm thick, short, semi-woody rhizomes. Large plants consist of multiple crowded rhizomes with upturned offshoots that produce tufts of long (50–100 cm), narrow (5–10 mm) basal leaves collectively forming a tussock (Maule 1959, Hitchcock and Cronquist 1973). Seedlings consist of two to several fine, involute, glaucous, grass-like leaves with only one shoot (i.e., no rhizomes). Leaves on slightly older pre-rhizomatous plants have serrated edges, similar to mature plants, but are much narrower and shorter. Seedlings and pre-rhizomatous juveniles hold their leaves more or less vertically resulting in very narrow crowns.

Flowering occurs from May through September in different areas (Maule 1959) and has been reported to be cyclical (5–7 years) (Crane 1990, Vance et al. 2004) or annual (Maule 1959). Flowering is reported to be greatest in open areas and to increase after fire (Maule 1959, Kruckeberg 1982, 1991). In any year a tussock may produce none to several flowering stalks. Each offshoot produces a single stalked inflorescence, and then dies following seed production (Kruckeberg 1982).

Beargrass plants commonly grow in cold, seasonally dry, nutrient poor soils. The evergreen leaves can live for at least three years and have characteristics adapted to freezing temperatures, drought and low nutrition including a thickened cuticle, abaxial stomata and extra vein sclerification for support during periods of wilting (Rentz 2003).

On the Olympic Peninsula in the state of Washington, beargrass grows from low to subalpine elevations except in the northeastern rain shadow (Jones 1936, Buckingham et al. 1995). Peter and Shebitz (2006) suggest that once extensive lowland southeastern Olympic Peninsula beargrass savannas had been maintained by native burning that ended around the mid-1800s, and that afforestation of these communities was a consequence of American settlers preventing this management. Shebitz et al. (2008) found a small, but significant 1% loss of beargrass canopy cover from a sample of 11 southeastern Olympic Peninsula sites over the 17 years since they had last been measured by Henderson et al. (1989). Although the cause of the reduction is not clear, overstory and understory canopy cover had significantly increased (6% and 3% respectively) during this time, as had beargrass harvesting for the floral industry.

Beargrass habitat is generally considered to be more or less open (Hitchcock et al. 1969, Schlosser et al. 1992), yet plants of higher commercial value often grow under a forest canopy (Schlosser and Blatner 1997, Higgins et al. 2004). Our purpose was to better understand beargrass reproduction, morphology, and foliar properties in relation to the light environment, stand conditions, and stand history to provide a stronger basis for management decisions. The impetus for the study was the decision by the Olympic National Forest to restore an area of beargrass woodland beginning with an overstory thinning and prescribed burn in 2003. Questions arose as to the appropriate target stand structure to provide for beargrass reproduction as well as foliar qualities associated with commerce and traditional basketry. We compared beargrass reproduction, plant size, and leaf properties in the presence versus absence of overstory coast Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*). Further, we examined demography and stand history to understand the current population distribution in relation to overstory structure.

Methods

Study Area

The study area was near the South Fork Skokomish River in the southeastern Olympic Peninsula of Washington State within traditional lands of the Skokomish Tribe (Twana) (Olympic Peninsula Intertribal Cultural Advisory Commission 2002) (Figure 1). The study area was divided into four units based on stand management history and current stand structure (Figure 1):

1. a 13 ha restoration unit that was heavily thinned in 2002 and prescribed burned September 30, 2003 (the restoration unit);
2. a 4 ha forested unit that was thinned in 2002 to 220 trees ha^{-1} (the thinned unit);
3. a 5 ha former woodland that is now a dense forest with scattered legacy woodland tree dominants (the uncut woodland unit);
4. a 6 ha area similar to the uncut woodland in which most of the original woodland trees were cut during the railroad logging era in the first half of the 1900s (the cut woodland unit).

The elevation in the study area varies from 180 m to 210 m. The study area is underlain by relatively infertile (Peter and Shebitz 2006) gravelly Vashon glacial till and outwash (Thorson 1980, Soil Survey Staff 2011). The restoration and thinned units are in the Bogachiel-Ishmael Complex soil series (Ishmael—medial-skeletal, ferrihydritic, or Bogachiel—isotic mesic Typic Udivitrands) and slope gently to the southwest. The soils in the flatter portions of the woodland units are very gravelly loams in the Duskpoint Series (sandy-skeletal, isotic, mesic Typic Hapludands). However, about 25% of the soils in the northern part of the cut woodland unit slope gently to the south and are in the Bogachiel-Ishmael Complex Series. Both soils are somewhat excessively drained. Annual precipitation is about 226 cm (USDA NRCS and OSU 2009).

The sample area is within a former anthropogenically maintained beargrass savanna (Peter and Shebitz 2006) visible in 1929 aerial photographs (1:7500) (Figure 2). These photos, which were taken 60 to 100 years after cessation of anthropogenic burning, show areas with woodland to savanna tree densities in a matrix of closed-crowned forests. Cooper (1859) suggests that Native prescribed burning stopped in some parts of western Washington as early as the 1830s. These savannas and woodlands later grew into closed-crowned forests. In 2010, the densities of trees larger than 10 cm dbh were 785 ha^{-1}, and 798 ha^{-1} for the uncut and cut woodland units respectively. Data from two USFS Ecology

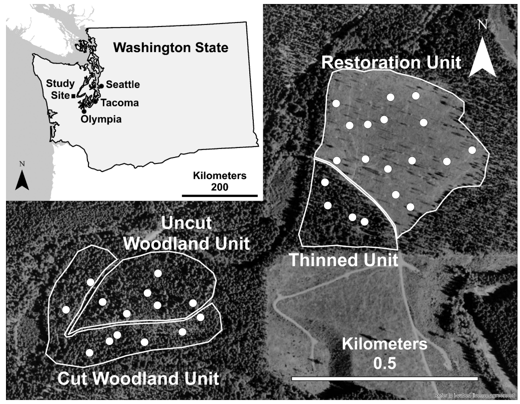

Figure 1. Study location in Washington State (inset) and unit and plot locations.

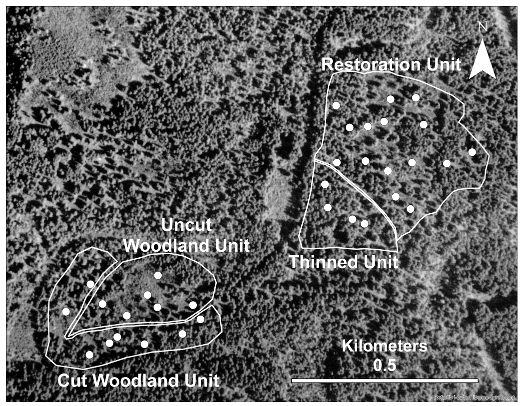

Figure 2. Sample areas as they were in 1929. Note the open canopy and the diversity of crown sizes including some very large crowns.

Program plots from 1998 in the restoration unit show that the mean density of trees larger than 10 cm dbh was 1408 trees ha^{-1}. We do not know the thinned unit density prior to thinning, however the prescription specified thinning to 272 trees ha^{-1} and our four plots in this unit averaged 220 trees ha^{-1} in 2010. The predominant plant association is the western hemlock/salal/beargrass (*Tsuga heterophylla / Gaultheria shallon /Xerophyllum tenax*) association (Henderson et al. 1989).

During 2002–2003, the restoration unit was thinned to 15 trees ha^{-1} to approximate the former woodland structure and then prescribed burned. However, the prescribed burn was hotter than expected and killed most of the leave trees, resulting in a residual density of 1–2 trees ha^{-1}.

TABLE 1. Sampling intensity and general characteristics of beargrass populations by management unit.

Unit	Plots	Unit Area (ha)	Beargrass-Plants	Density* (plants/ha)	Total Cover (%)**	Mean PAR***
Thinned	4	4	4	32	168	0.13
Restoration	15	13	292	659	95	0.63
Cut Woodland	8	6	286	12 313	156	0.17
Uncut Woodland	6	5	333	22 818	183	0.15

*The average of the individually calculated plot densities.
**The sum of all individual species covers on the circular plot in 2010.
***Mean proportion of full sun for all measurements of photosynthetically active radiation.

Sample Design

Each of the sample units was sampled with approximately one randomly located permanent 0.05 ha circular plots ha^{-1} (Table 1). In addition, we re-measured five circular Area 1 USFS Ecology Program plots (Henderson et al. 1989) that fortuitously fell within the sample area: two (0.04 ha) in the restoration unit, one (0.04 ha) in the uncut woodland and two (0.08 ha) in the cut woodland unit. The Ecology Program plots were originally installed in the 1980s and 1990s to support a different study. We installed our random plots and remeasured the Ecology Program plots in 2010 at which time tree size, age and plant community data were collected. Thus, data for this study comes from a total of 33 plots.

Plant Measurements

Beargrass plant measurements were made in 2014. We defined a single mature plant as a clump of offshoots with no offshoot more than 10 cm from its nearest neighbor on the assumption that beargrass rhizomes travel no more than 10 cm between offshoots. We based this assumption on our observation that offshoots in the tussocks that we examined were always less than 10 cm from their nearest neighbor.

We measured a minimum of 10 beargrass plants, provided we could find that many, in each of two series of four 1-by-10 m belt transects: one series of four transects inside and one series of four transects outside of each circular plot (Figure 3). Measurements taken in both series of transects were the same, except that foliage harvesting for above ground biomass was restricted to the outside series to protect beargrass plants growing within each plot. All plants in the inner and outer NE transects were measured, so our minimum sample area was 10 m^2. When fewer than 10 plants were found on either of the NE transects, we added sample area in 1/3 transect increments (3.3 m^2) in a clockwise direction (thus moving to the SE transect and so forth) until at least 10 plants had been sampled on both the inner and outer transect series. In many cases our sample was larger than 10 plants as all plants in the NE transect, and each additional transect segment (when necessary) were measured. If 10 plants were not found after searching the inner or outer transect series (Figure 3) we also searched the entire NE quadrant (to supplement the inner transect series), or an equivalent sized arc just outside the NE quadrant (to supplement the outer transect series), and accepted the sample size for the summed area that had been searched. With this method we found and measured beargrass plants on 28 of the 33 plots. Beargrass plants were not found on three of the thinned unit plots and two of the restoration unit plots.

Following is a list of field measurements taken on all plants.

1. Basal diameter (mean of longest and perpendicular diameters of the basal rhizomatous clump measured at the soil surface in cm).
2. Number of rhizomatous offshoots in the basal rhizomatous clump.
3. Crown width (mean of longest and perpendicular foliar crown widths in cm).
4. Crown height (to the crest of the foliar crown in cm).

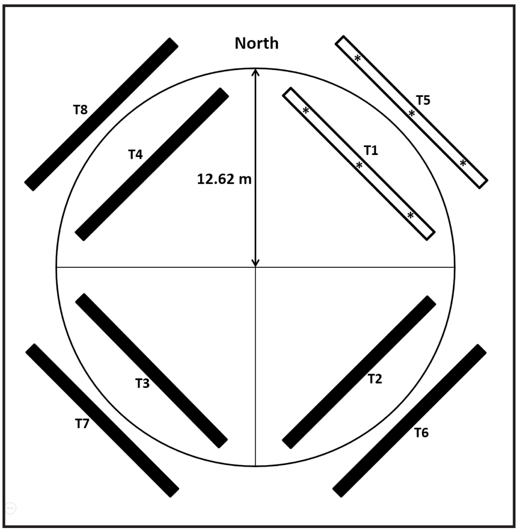

Figure 3. Plot and 1 x 10 m transect layout. The plot radius of 12.62 m is for 0.05 ha plots, but layout for the USFS Ecology Program plots was proportionately similar (but transect size was the same throughout). Asterisks indicate the relative locations of the PAR measurements within the transects.

5. Maximum leaf width (widest of three randomly selected leaves in mm taken at the mid-length of the leaf).
6. Maximum leaf length (longest of three randomly selected leaves in cm).
7. Flower stalks (sum of old and new attached flowering stalks).
8. Basal flower stalk diameter in mm.

We calculated beargrass crown volume as a half sphere with a radius equal to the average of the two crown widths/2 and the height. We individually clipped and bagged all of the green foliage from each of the first 10 plants on the outer transect series and dried it in a 60 °C oven to a stable weight to obtain aboveground biomass (g). The plant biomass divided by the crown volume provided an estimate of foliar crown density (g/m^3).

Ten leaves were randomly selected from the first biomass plant on each outer transect for a laboratory determination of leaf area and Munsell color parameters. Prior to measuring leaf area, we randomly selected two of the ten leaves from each leaf area sample and determined hue, value and chroma at the leaf midpoint with a Munsell Plant Tissue Color Book (Munsell Color 2012). In the Munsell color system, hue indicates a color category including red, yellow, green, blue, and purple, as well as intermediate midpoints (e.g. "gy" is midway between green and yellow). Value indicates lightness on a 1–10 scale (black = 0, white = 10). Chroma is color purity or saturation as a departure from a neutral gray (0 = neutral gray; the upper end is open).

We placed the 10 leaves on a Licor LI-3100 area meter platen and recorded their total leaf area. Then we dried and weighed the 10 leaves and divided their leaf area by this weight to obtain an estimate of the specific leaf area (cm^2 g^{-1}). We then added the weights of these 10 leaves back into the appropriate biomass sample. Specific leaf area was multiplied by plant aboveground biomass to estimate total leaf area per plant.

We measured photosynthetically active radiation (PAR) (400–700 nm spectral band) 0.5 m above ground at three points (1.67 m, 5 m, 8.33 m) on each transect with a Decagon AccuPAR in June or July within two hours of solar noon on cloudless days. The instrument was held level, centered on the transect midline, and pointed south with the observer standing north. Thus, each measurement represented a 1/3 segment of the 10 m transect. A separate PAR sensor was installed on a tripod within the restoration unit where it logged readings of full-sun PAR every minute while AccuPAR measurements were being taken. Proportion of full PAR was obtained by merging the two datasets via their timestamp and dividing the sample location PAR by the full sun PAR. Reported values for PAR are plot means of those measurements closest to where the sample beargrass plants occurred (Figure 4).

Stand Structure

Detailed stand structure measurements were made on all plots in 2010. However, the USFS Ecology Program plots had also been measured previously. Two plots in the cut woodland unit were first measured in 1985. Two plots in the restoration unit and one plot in the uncut woodland unit were first measured in 1998. Measurements included stem diameter at breast height (1.3 m) for all trees

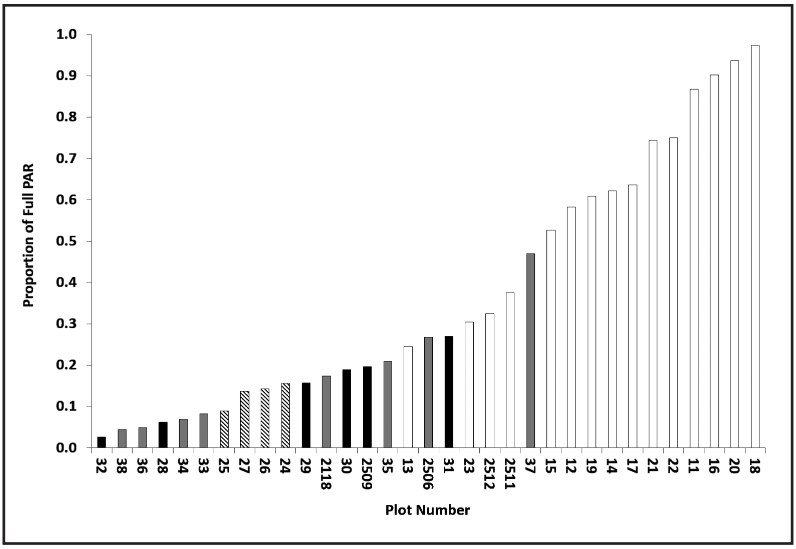

Figure 4. Mean values of photosynthetically active radiation (PAR) by plot showing the gradient of PAR over which beargrass measurements were taken. Black bars represent the uncut woodland unit, gray bars the cut woodland unit, hatched bars the thinned unit and white bars the restoration unit. While a gradient exists, PAR was greater than 0.3 for most of the restoration unit and it was less than 0.3 for most of the woodland and thinned units.

taller than 1.3 m. Tree age was estimated from increment cores collected from a 1/3 subsample of trees over the range of diameters. Trees smaller than 1.3 m in height were sampled in an embedded 12.6 m^2 subplot. Ages for these smaller trees were obtained by cutting basal stem cross-sections from trees of comparable size located off the main plot. The tree rings were counted in the laboratory with the aid of a microscope. In most cases the pith was seen, but when the increment core missed the pith, an estimate of missing rings was made from the inner ring widths and ring curvature (Villalba and Veblen 1997). For cores that failed to reach the tree center, total age was estimated by adding to the counted rings an estimate based on inner ring width and the difference between the tree radius and the core length. To the breast height age, we added six years for coast Douglas-fir, four years for lodgepole pine (*Pinus contorta* Douglas ex Loudon) and seven for western hemlock to estimate each tree's year of origin. These numbers were calculated for each tree species from the linear relation between tree height and age taken from young, natural, open grown trees in the restoration unit plots.

We reconstructed tree recruitment at the stand level with the date of origin for 229 trees from our plots (171 Douglas-fir, 37 lodgepole pine, 21western hemlock). These tree ages came from 20 plots scattered across the four management units. We present these data as a graph of the percentage of the sample originating from each decade for the four units combined, as they were in close proximity to each other.

For comparison, we graphed a data set from a wider area of forests in the southeastern Olympic Peninsula consisting of one Douglas-fir tree age from each of 208 southeastern Olympic Peninsula plots collected by the USFS Ecology Program in the 1980s and 1990s (Henderson et al. 1989). We used plots from Townships 21–23 North and Ranges 4–6 West which includes most of the Skokomish River Watershed, and small portions of two adjacent watersheds. These tree ages came from increment cored dominant Douglas-fir trees on the plot, or from recently harvested Douglas-fir tree stumps in clearcuts adjacent to the plots, and represent the stand age where the plot was located since the last fire or harvest.

Analysis

We analyzed beargrass data at the plot level by first averaging the plant measurements for plants > 10 cm crown width. Smaller plants have very different morphology than larger plants, and although numerous in the restoration unit, they were nearly absent in the woodland and thinned units. Scatterplots of the beargrass variables versus

PAR revealed two distinct populations with little overlap: those in the restoration unit and those in the other management units. Therefore, plots were assigned to categories of overstory present (i.e., the woodland and thinned units) or absent (restoration unit). Mean values of PAR, size, morphology, and leaf color of beargrass were subjected to a *t*-test ($\alpha = 0.05$) to determine whether they differed in the presence versus absence of overstory Douglas-fir. For each variable, the equality of variances between the two populations was calculated and the approximation of Cochran and Cox (1950) was used to assess significance when the variances were unequal; otherwise, a pooled sample *t*-test was used.

Most plants growing in low light levels grew under the canopy of the woodland and thinned units while most of the plants growing in higher light levels grew in the restoration unit and had been released from a subcanopy position in 2003. We assumed, from the bimodal distribution of plants in the restoration unit, that plants smaller than 10 cm in crown width represented plants that had grown from seed since the 2003 fire. Many appeared to be seedlings as judged from their small size, involute leaf structure and single shoot. The remainder were small, non-rhizomatous, single shoot plants with mature leaf structure. We also assumed that plants larger than 10 cm crown width ("mature plants") lived most of their lives under a canopy similar to that of the woodland units and had adjusted to the higher light levels in the 11 years since overstory removal.

We used graphical analysis to examine effects of PAR on the crown width frequency distribution of individual beargrass plants. We first divided the beargrass plants into those growing in high (> 0.3 PAR) and low light intensities (< 0.3 PAR). We then grouped the plants in each light category into 1 cm crown width size classes and calculated the number of plants per ha represented by each 1 cm size class to reveal the size structure of the beargrass population relative to these two light regimes. We assumed a positive relation between beargrass plant size and age, but could not quantify that relation with our data. We used regression analysis to characterize the relation between PAR and cover of overstory trees.

Results

Photosynthetically Active Radiation

Based on all measurements, photosynthetically active radiation (PAR) was similar in the thinned and woodland management units (0.13 to 0.17 of full sun), but it was considerably greater in the restoration unit (0.63 of full sun) (Table 1). Likewise, PAR measurements closest to the sampled beargrass plants averaged greater in the absence of overstory trees (0.65 of full sun) than in their presence (0.16 of full sun) (Table 2).

Plant Size and Foliage

Basal diameter of beargrass plants growing in the absence of overstory Douglas-fir (8.5 cm) was almost twice that of plants growing in their presence (4.5 cm); however, plant height, crown width, and crown volume did not differ between overstory levels (Table 2). Leaf length and specific leaf area were higher while leaf area and crown density were lower in the presence versus absence of overstory trees. Variables of reproductive ability (number of offshoots, number of flower stalks, and flower stalk diameter) were greater in the absence versus presence of overstory trees. Foliar browse was not observed on plants in this study and thus did not affect plant size.

Each of the Munsell color parameters (i.e., hue, value, and chroma) differed between the presence and absence of overstory trees (Table 2). Hence, leaves of shade-grown beargrass plants were greener (hue) and darker (value), but they had somewhat lower color intensity or saturation than those of sun-grown plants.

Plants growing in < 0.3 PAR had a bell-shaped crown size distribution with a peak in the range of 40 to 70 cm crown width (Figure 5a) and there were few small plants and no seedlings. The much smaller number of plants growing in > 0.3 PAR had a very high proportion of small, pre-rhizomatous and seedling plants (< 10 cm crown width). By far, the majority of the plants with > 0.3 PAR were in the restoration unit where all of the seedlings and

TABLE 2. Average values (standard deviations in parentheses) and *t*-tests for comparing photosynthetically active radiation (PAR) and size, morphology, and leaf color of beargrass plants > 10 cm crown width in the presence versus absence of overstory Douglas-fir.

	Overstory Present		Overstory Absent		
Variable	Mean (SD)	*n*[1]	Mean (SD)	*n*	Prob. > *T*
PAR (proportion of full sun)	0.16 (0.12)	15	0.65 (0.22)	13	< 0.001
Basal diameter (cm)	4.5 (2.13)	15	8.5 (4)	13	0.013
Height (cm)	28 (3.1)	15	30 (4.51)	13	0.134
Crown width (cm)	57 (8.52)	15	57 (19.11)	13	0.963
Crown volume (m^3)	0.057 (0.02)	15	0.072 (0.04)	13	0.239
Maximum leaf length (cm)	62 (5.42)	15	46 (9.37)	13	< 0.001
Maximum leaf width (mm)	2.5 (0.35)	15	2.6 (0.54)	13	0.542
Live foliar biomass (g)	17.2 (16.65)	15	78.5 (63.39)	12	0.007
Leaf area (cm^2)	996 (883.04)	15	6111 (4101.5)	12	0.001
Specific leaf area (cm^2 g^{-1})	76 (9.3)	15	63 (5.2)	12	< 0.001
Crown density (g m^{-3})	274 (116.19)	15	1033 (311.77)	12	< 0.001
Number of offshoots	2.1 (1.08)	15	8.4 (6.24)	13	0.004
Number of flower stalks	0.1 (0.19)	15	2.7 (2.09)	13	< 0.001
Flower stalk diameter (mm)	6.2 (0.28)	2	7.9 (0.93)	8	0.042
Hue	5.9 (0.66)	15	4.7 (0.52)	12	< 0.001
Value	3.7 (0.39)	15	4.5 (0.45)	12	< 0.001
Chroma	4.4 (0.46)	15	5.6 (0.76)	12	< 0.001

[1]Sample size (number of plots) for each overstory level

most pre-rhizomatous plants smaller than 10 cm in crown width were found. We assume that these seedlings and small plants represent reproduction that occurred since the 2003 thinning and burning. No small plants were found in the nearby thinned unit that was not burned.

The mean crown width for plants with < 0.3 PAR was 52 cm (stdev = 20 cm), while the mean crown width for all plants with > 0.3 PAR was 34 cm (stdev = 32 cm). The large standard deviation of sun-grown plants is due to the skewed and bi-modal distribution that included seedlings and mature plants (Figure 5b). If only plants > 10 cm crown width were included, then the means are 55 cm (stdev = 17 cm) for plants with < 0.3 PAR and 57 cm (stdev = 23 cm) for plants with > 0.3 PAR.

Flowering and Reproduction

Flowering was sparse in the season of our study and nearly all of the flowering parts at the ends of the stalks were browsed off. We therefore report the sum of live and attached dead flowering stalks which provides an index of flowering over the last two or three years. The restoration unit had more flowering plants and more stalks per plant than the woodland units (Table 3). The restoration unit also had many seedling and young plants, but there were few to none of these in the woodland units. Even so, the woodland units had far more mature (> 10 cm) plants than the restoration unit. At our site, 0.3 PAR occurred with 50% tree cover: $\mathrm{sqrt(PAR)} = 0.805 - 0.005 \times \text{tree cover}$ ($R^2 = 0.63$, N = 33, $P < 0.01$). Thus, beargrass reproduction required less than 50% tree cover.

Stand Structure and History

Prior to 2003 all units had more than 90% tree cover. This was documented with USFS Ecology Program plots: two measured in 1985 in the cut woodland unit, as well as two in the restoration unit and one in the woodland unit in 1998. These high covers correspond to observations from a 1982 aerial photo of the site.

Tree cover was assessed for the four units with a 1929 aerial photo of the site and compared to tree cover determined from our vegetation plot assessments in 2010 (Table 4). This comparison shows that the most open area in 1929 was the

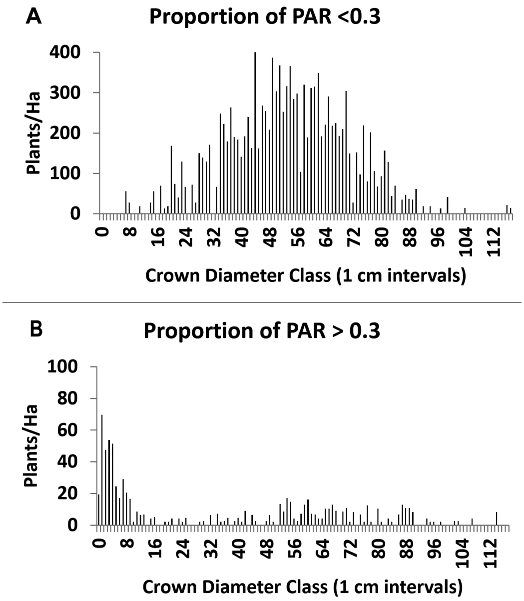

Figure 5. Beargrass population density by crown size and light environment. Less reproduction occurred when PAR was less than 0.3 of full sunlight (A) than when it was more than 0.3 of full sunlight (B). Note the difference in scale of the Y axis in A and B.

uncut woodland and all areas were more open than in 2003 prior to the restoration thin and burn. These activities opened the restoration unit the most, but also the thinned unit to a lesser extent. However, by 2010 the thinned unit already had 68% cover and may not have been below 50% cover even after thinning. Current beargrass plant density was highest in the areas that were the most open in 1929.

Our reconstruction of tree recruitment shows only occasional tree establishment for more than two centruries prior to 1870. The trees recruited during this period were primarily Douglas-fir with only a few lodgepole pine (Figure 6). In contrast, surrounding forested areas of the southeastern Olympic Peninsula show strong pulses of Douglas-fir tree recruitment following various fires in the 1600s, 1700s and 1800s (Henderson et al. 1989). Douglas-fir and lodgepole pine require high light levels to establish and are considered seral species in this region. Tree recruitment rapidly increased at our site beginning around 1870, but in other southeastern Olympic Peninsula forests, not until around 1910 to 1920. Tree recruitment peaked in the southeastern Olympic Peninsula forests more than 10 years before recruitment peaked at our study site.

Discussion

Foliar and Crown Characteristics

Native American basket weavers from the Olympic Peninsula and California indicate that the highest quality beargrass foliage comes from partially shaded areas, and that this condition was maintained by burning (Anderson 2005, Shebitz 2005). Others have found diffused sunlight, and even heavy shade produce better commercial quality foliage than open areas (Schlosser and Blatner 1997, Higgins et al 2004).

We also found that shaded plants had more commercially valuable properties. Leaves tended to be longer in the shade, and specific leaf area was greater in the shade, which we interpret to mean thinner, less sclerified and therefore more pliable leaves. This suggests that shade leaves achieve their length at the expense of heavier structural tissues. Traditional weavers prefer longer, more pliable leaves (60–90 cm length) (Jones 1977, Shebitz 2009b). Greater saturation of yellow tones in higher light suggests greater concentrations of protective xanthoid pigments, although thicker leaves might also contribute to higher color saturation. Our findings suggest that shaded areas more consistently produced commercially desirable leaves; however, our highly variable data do not rule out finding some plants with desirable commercial properties at higher light levels.

Higgins et al. (2004) found a trend toward greater commercial value for shade grown beargrass in the higher elevation silver fir (*Abies amabilis* [Douglas ex Loudon] Douglas ex Forbes) and mountain hemlock (*Tsuga mertensiana* [Bong.] Carrière) zones. They concluded that plants growing in stands with less than 60% overstory cover tended to have leaves with too high of a Munsel color value (> 6) to be of commercial value. In

TABLE 3. Measures of fecundity in the combined woodland units compared to the restoration unit.

Woodland Units	Restoration Unit
density: 17 566 plants ha^{-1}	density: 659 plants ha^{-1}
5% with flowering stalks	28% with flowering stalks
0–8 flowering stalks/plant	0–15 flowering stalks/plant
0.5% plants < 10 cm crown width	53% plants < 10 cm crown width

TABLE 4. Tree cover (%) in 1929 and 2010 based on 1929 aerial photography and 2010 measured plots and associated density of beargrass plants. The thinned and restoration units had > 90% cover before 2003.

Unit	1929 Tree Cover (%)	2010 Tree Cover (%)	Plant Density (plants ha^{-1})
Thinned	84	68	32
Restoration	57	9	659
Cut Woodland	52	90	12 313
Uncut Woodland	26	91	22 818

our study, leaves in open areas tended to have higher Munsel color values, but did not exceed a value of 6.

Higgins et al. (2004) found that plants growing in denser shade tended to be larger than in open areas. Our analysis suggests that young (small) plants are only found in open areas, thus reducing the average open area plant size. When we included only plants with crown widths greater than 10 cm, the average crown widths did not differ significantly indicating that there is no difference in the crown widths of mature plants from open or shaded areas. Maule (1959) observed similar sized plants growing in both full sun and dense shade at Mount Rainier National Park, although measurements were not taken in shaded areas suggesting a possible observational bias in favor of mature plants.

While mature crown width was similar in sun and shade, biomass per unit volume of crown (foliar density) and basal diameter of the rhizomatous crown was less in shade, suggesting a decline in biomass. This observation, together with our findings of fewer flowering plants, fewer flower stalks per plant, fewer vegetative offshoots, and a lack of successful seedlings in shaded areas compared to more open areas, suggests that shaded populations experienced an overall loss of vigor and reproductive effort. Therefore, plants in heavily shaded areas, although of somewhat higher commercial quality, are likely to recover more slowly from foliar harvest, and are less likely to be replaced after mortality. The lack of flowering in shade is a common observation (Maule 1959, Daubenmire and Daubenmire 1968, Shebitz 2005); however, we believe our study is the first quantitative documentation of it.

Stand History and Beargrass Demography

Our study site presented an interesting conundrum that we suspect is common. Greater amounts of flowering, regeneration and foliar density indicated that the open restoration unit was better for beargrass reproduction and vigor than the closed woodland units, yet the densest population was found in the heavily shaded uncut woodland. The explanation lies in the stand histories. We found no beargrass reproduction below 0.3 PAR which occurred with 50% tree cover. An examination of 1929 aerial photos showed that although the uncut woodland unit had only 26% tree cover at that time, all other units had more tree cover. Thus, as far back as 1929 the only unit with less than 50% tree cover was the uncut woodland unit. Therefore, it is likely that reproduction more recent than 1929 largely, or only took place in the uncut woodland until it also surpassed 50% tree cover, or in the restoration unit after it was re-opened in 2003.

Figure 6 suggests that Douglas-fir and lodgepole pine recruitment increased sharply around 1870,

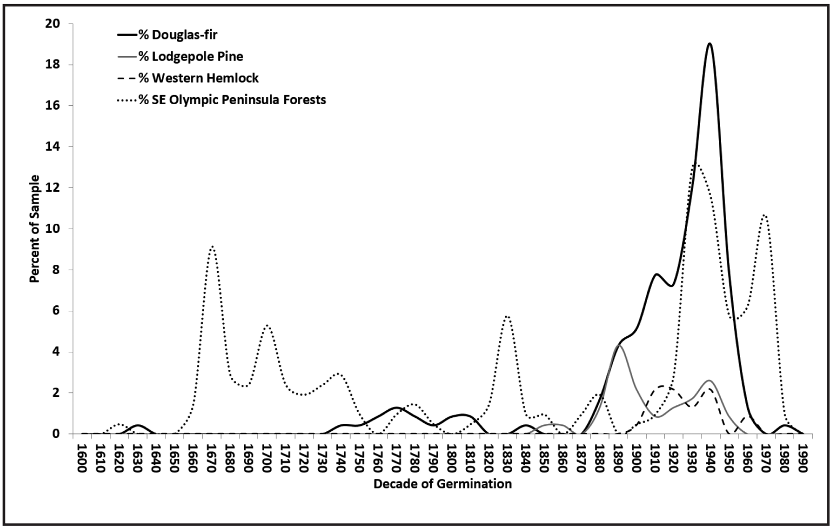

Figure 6. Comparison of tree establishment generally on the southeastern part of the Olympic Peninsula and specifically in the study area. Graph lines for Douglas-fir, lodgepole pine and western hemlock derive from combined plot data for the four units of the study area. The two post-1900 recruitment peaks for the southeastern Olympic Peninsula forests represent earlier railroad and later truck logging in different parts of the watershed.

implying that these stands were even more open in the 1800s. Prior to that, recruitment was sporadic and did not produce a canopy dense enough to prevent occasional recruitment of Douglas-fir—a species with high light requirements—for at least two centuries. We believe that the Twana people prevented canopy closure by burning this area to maintain useful plants and animals that frequent open areas (LaLande and Pullen 1999, Leopold and Boyd 1999, Peter and Shebitz 2006). This contention is supported by Twana oral traditions which describe the burning of beargrass savannas or woodlands in this area about every three years until the late 1800s (Shebitz 2005). The light environment for beargrass reproduction in these savanna or woodland-like areas would have been optimal, but a scattering of trees may have provided conditions for higher quality basketry foliage. Tree recruitment increased steadily after 1870 resulting in > 50% canopy cover in three of the units by 1929 and crown closure sufficient to curtail even western hemlock recruitment in all of the units before 1950.

Similarly maintained open woodlands were once extensive througout the Puget Lowlands (Leopold and Boyd 1999, Peter and Harrington 2014). Cultural burning was practiced by all native groups in the Pacific Northwest and Rocky Mountain states (Lewis 1973). In California, beargrass was burned by Indians annually in late summer or early fall permitting collection of high quality foliage from the burned plants for two to three years (Hunter 1988, Lewis 1973).

The forests around the study site had a different tree establishment pattern (Figure 6). Tree recruitment followed extensive stand replacing fires in the 1600s, 1700s and around 1833 from a smaller fire (Henderson et al. 1989). After each fire, tree recruitment resulted in crown closure, and suppression of Douglas-fir recruitment. We assume that rapid recruitment and crown closure similar to what occurred in these forests was prevented at our study site by anthropogenic burning which ended before 1870.

Although we do not know when the uncut woodland stand surpassed 50% crown cover, we can say that crown closure over all units was complete by 1945 to 1950 (Figure 6), and crown closure has prevailed since then. If beargrass cannot reproduce in dense shade as our analysis suggests, then the plants in the uncut woodland unit are at least 60 years old and probably older, especially in the units that have been closed longer. This suggests considerable longevity and a high degree of shade tolerance for beargrass in the vegetative, but not reproductive sense. Nevertheless, these plants appear to be declining, given their reduced foliar density and biomass.

Laursen (1984) considers beargrass to be long-lived and semi-shade tolerant, but provides no data or references. Nor do we know of any other data to suggest longevity for beargrass, except that it has been suggested that continuous rhizome production indicates a long lifespan (Crane 1990, Vance et al 2004). The only quantitative age data that we found is for *Xerophyllum asphodeloides*, the only other member of this genus. Bourg et al. (2015) showed that *Xerophyllum asphodeloides* averaged 45 years of age in Virginia.

If beargrass requires high light levels for reproduction, then wherever it grows in forests, some kind of periodic disturbance will be required for its maintenance. Fire is an obvious candidate for such disturbance, especially because native people from California to Washington state have oral traditions of burning for maintenance of beargrass collecting localities (Lee 2000, Rentz 2003, Anderson 2005, Peter and Shebitz 2006). This was clearly a high value plant that was widely traded (Gunther 1973, Turner 1979) justifying considerable effort for its maintenance. A recent review of literature found estimates of anthropogenic burn intervals from 2–20 years (Hummel et al. 2012).

Not only can fire maintain higher light levels required for flowering and overall plant vigor, but Shebitz et al. (2009a) found that smoke infused water increased beargrass seed germination, suggesting another reproductive benefit of fire for beargrass. Shebitz et al. (2009b) also showed that beargrass seedling establishment and vegetative reproduction increased within two years after fire in an open area. Both of these studies took place partially at, or used materials from our restoration site. *Xerophyllum asphodeloides* also increased flowering by 60–280% in response to controlled burning experiments (Bourg et al. 2015) and populations in the eastern US were shown to be associated with historical mean fire return intervals of 9–18 years. They consider *Xerophyllum asphodeloides* to be a long-lived fire adapted species (Borg et al. 2015).

Natural fire return intervals in beargrass habitats are reported to range from 27 to > 200 years in northern Idaho (Smith and Fischer 1997) and up to “rarely in 500 years” for the Alaska huckleberry (*Vaccinium alaskaense* Howell)/beargrass associations in the silver fir and mountain hemlock zones of the Olympic Peninsula (Henderson et al. 1989). How a species that is so limited by shade for its reproduction survives in rarely burned habitats is open to question. However, these areas have slow growing, and relatively short trees, slow post-fire reforestation, deep winter snowpacks, steep slopes, thin soils, and exposed bedrock. It seems reasonable that openings might persist for very long periods, even centuries, and may be augmented by blowdown, snow breakage and root rot.

Climate change may also be playing a role in high elevation beargrass populations. During the Little Ice Age (circa 1300 to 1850) (Porter 1986) alpine glaciers expanded in the northern hemisphere, and alpine timberlines moved down (Heuser 1957, Henderson et al. 1989). Vegetation change due to the Little Ice Age has been documented in the Olympic Mountains (Gavin and Brubaker 1999). Thus, much of the mountain hemlock zone may have been more open and park-like as late as the mid-1800s. Slow closure of these high elevation openings and the shade tolerance of beargrass could account for the current presence of beargrass in these rarely burned areas. However, a continuation of this process could render these sites unsuitable to beargrass in the future.

The low productivity typical of beargrass habitat can be due to a variety of conditions, but always increases the time the stand remains open after disturbance. Periodic disturbance is also typical in many areas (Crane 1990), and the balance of these two characteristics may determine beargrass habitat. Thus, a positive relation is implied between productivity and disturbance frequency. On harsh sites, natural disturbance frequencies may suffice even if infrequent, but on more productive sites augmentation with anthropogenic disturbance is probably required.

At higher elevations beargrass mostly occupies steep, dry, upperslope positions with southerly aspects and so has a very short growing season both due to the long winter and to droughty summer soils (Pfister et al. 1977, Hemstrom et al. 1982, Halverson et al. 1986, Logan et al. 1987, Henderson et al. 1989, Williams 1990, Cooper et al. 1991, Atzet et al. 1996, White et al. 1996, Diaz et al. 1997). These plants also contend with low soil fertility and cold growing season soil temperatures. Beargrass is also often found in frost pockets, to which it is more tolerant than many other species (Hemstrom et al. 1982, Halverson et al. 1986). At lower elevations, coarse, droughty, nutrient poor, or sometimes ultramafic soils are implicated (Henderson et al. 1989, Atzet et al. 1996). Beargrass may also grow in lowland sphagnum bogs with nutrient poor soil, and poor root zone aeration (Henderson et al. 1989, Kunze 1994). In all of these cases, forest succession is slow, and openings are long lasting. Where forest succession is fast and time between disturbances long, beargrass is not found. Thus, beargrass is a fire tolerant species of wide ecological amplitude, but is usually limited by its reproductive needs to open areas or periodically disturbed forests.

Conclusions

Knowledge of the longevity of beargrass plants, especially in shaded conditions, is important for its management. It is also critical to know how well beargrass tolerates foliar harvesting when growing in different light envirionments. Beargrass growing under heavy forest competition may not tolerate harvest as well as beargrass growing with more light. Thomas and Schumann (1993) suggest that three years are required for a plant to fully recover when only the center leaves are removed, but did not specify the level of shade under which this might occur.

Although our study is a case history, we believe that the fundamental physiological nature of our findings apply more broadly. Our results support Higgins et al. (2004) finding that commercial value is enhanced by shade. We have also called into question whether beargrass in shaded sites, even those with high beargrass cover, is sustainable. Stand histories of such sites need careful evaluation, and we believe a consistent need for periodic disturbance will emerge.

Our finding that beargrass did not reproduce, and may be declining in heavy shade has strong management implications because beargrass can be found in old forests, and commercial harvesters prefer beargrass grown under forest canopies. If preserving a forested beargrass population is a management priority, the use of thinning to provide >30% PAR, and prescribed burning to control a vigorous understory response might be considered. More research is needed to determine the target thinned density, thinning rotation length, prescribed burn interval and burn intensity, all of which vary by habitat. Also, more research may reveal an intermediate level of light that supports both commercial qualities and adequate reproduction. Although beargrass has considerable longevity in shade, vigor slowly declines under these conditions, and the evidence points to greater health and reproduction in areas with more light.

Acknowledgments

We wish to thank our field crew for their excellent work including James Dollins and Lorea Fadgen. We thank the Olympic National Forest for logistical support, especially Susan Piper and Robin Shoal. We appreciate the suggestions of the reviewers of this manuscript that contributed measureably to its readability and accuracy. We also wish to remember our co-author Mark Thompson with whom we spent many fine hours in the field collecting data and sharing ideas. Mark was a bright and thoughtful graduate student from the University of Washington, who contributed importantly to this work. He was a truly fine person, and we will not forget him. Thank you Mark.

Literature Cited

Anderson, M. K. 2005. Tending the Wild: Native American Knowledge and the Management of California's Natural Resources. University of California Press, Berkeley.

Atzet, T., D. E. White, L. A. Macrimmon, P. A. Martinez, P. R. Fong, and V. D. Randall. 1996. Field guide to the forested plant associations of southwestern Oregon. R6-NR-ECOL-TP-17-96, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Bourg, N. A., D. E. Gill, and W. J. McShea. 2015. Fire and canopy removal effects on demography and reproduction in turkeybeard (*Xerophyllum asphodeloides*), a fire-dependent temperate forest herb. Journal of Sustainable Forestry 34:71-104.

Buckingham, N. M., E. G. Schreiner, T. N. Kaye, J. E. Burger, and E. L. Tisch. 1995. Flora of the Olympic Peninsula. Northwest Interpretive Association, Seattle, WA.

Cochran, W. G. and G. M. Cox. 1950. Experimental Designs. John Wiley and Sons, New York.

Cooper, J. G. 1859. Report upon the botany of the route. *In* A. R. Anderson (editor), Plant Life of Washington Territory, a Douglasia Occasional Papers, 1994, Vol. 5. Washington Native Plant Society, Bellingham, WA. Pp. 2-37.

Cooper, S. V., K. E. Neiman, and D. W. Roberts. 1991. Forest habitat types of northern Idaho: a second approximation. Gen. Tech. Report INT-236, USDA Forest Service, Intermountain Research Station, Ogden, UT.

Crane, M. F. 1990. *Xerophyllum tenax*, Fire Effects Information System. Fire Sciences Laboratory, USDA Forest Service, Rocky Mountain Research Station, Missoula, MT. Available online at https://www.fs.fed.us/database/feis/plants/forb/xerten/all.html (accessed 17 October 2017).

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Technical Bulletin 60. Washington Agricultural Experiment Station, Pullman.

Diaz, N. M., C. T. High, T. K. Mellen, D. E. Smith, and C. Topik. 1997. Plant association and management guide for the mountain hemlock zone, Gifford Pinchot and Mt. Hood National Forests. R6-MTH-GP-TP-08-95, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Gavin, D. G., and L. B. Brubaker. 1999. A 6000-year soil pollen record of subalpine meadow vegetation in the Olympic Mountains, Washington, USA. The Journal of Ecology 87:106-122.

Gunther, E. 1973. Ethnobotany of Western Washington. The Knowledge and Use of Indigenous Plants by Native Americans. University of Washington Press, Seattle.

Halverson, N. M., C. Topik, and R. V. Vickle. 1986. Plant association and management guide for the western hemlock zone, Mt. Hood National Forest. R6-ECOL-232A-1986, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Heffner, K. 1984. Following the smoke: contemporary plant procurement by the Indians of Northern California. Unpublished report on file at the USDA Forest Service, Six Rivers National Forest, 1330 Bayshore Way, Eureka, CA.

Hemstrom, M. A., W. H. Emmingham, N. M. Halverson, S. E. Logan, and C. Topik. 1982. Plant association and management guide for the Pacific silver fir zone, Mt. Hood and Willamette National Forests. R6-ECOL-100-1982a, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Henderson, J. A., R. D. Lesher, D. H. Peter, and D. C. Shaw. 1992. Field guide to the forested plant associations of the Mt. Baker-Snoqualmie National Forest. Technical Paper R6 ECOL TP 028-91, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Henderson, J. A., D. H. Peter, R. D. Lesher, and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. R6-ECOL-TP 001-88, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Higgins, S., K. Blatner, B. K. Kerns, and A. Worthington. 2004. Relationship between *Xerophyllum tenax* and canopy density in the southern Cascades of Washington. Western Journal of Applied Forestry 19:82-87.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson, editors. 1969. Vascular Plants of the Pacific Northwest. University of Washington Press, Seattle.

Hummel, S., S. Fotz-Jordan, and S. Polasky. 2012. Natural and cultural history of beargrass (*Xerophyllum tenax*). Gen. Tech. Rep. PNW-GTR-864, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Hummel, S., and F. K. Lake. 2015. Forest site classification for cultural plant harvest by tribal weavers can inform management. Journal of Forestry 113:30-39.

Hunter, J. E. 1988. Prescribed burning for cultural resources. Fire Management Notes 49:2.

Jones, G. N. 1936. A Botanical Survey of the Olympic Peninsula, Washington. University of Washington, Seattle.

Kruckeberg, A. R. 1982. Gardening with Native Plants of the Pacific Northwest. University of Washington Press, Seattle.

Kruckeberg, A. R. 1991. The Natural History of Puget Sound Country. University of Washington Press, Seattle.

Kulzer, L., S. Luchessa, S. Cooke, R. Errington, and F. Weinmann. 2001. Characteristics of the low-elevation sphagnum-dominated peatlands of western Washington: A community profile. US Environmental Protection Agency, Seattle, WA.

Kunze, L. M. 1994. Preliminary classification of native, low elevation, freshwater wetland vegetation in western Washington. Washington State Department of Natural Resources, Natural Heritage Program, Olympia, WA.

Lalande, J., and R. Pullen. 1999. Burning for a "fine and beautiful open country": native uses of fire in southwestern Oregon. *In* R. Boyd, (editor), Indians, Fire and the Land in the Pacific Northwest. Oregon State University Press, Corvallis. Pp. 255-276.

Laursen, S. B. 1984. Predicting shrub community composition and structure following management disturbance in forest ecosystems of the intermountain west. Ph.D. Dissertation, University of Idaho, Moscow.

Lee, J. T. 2000. Emphasis on the regeneration of the bear grass (*Xerophyllum tenax*) within the Wolf Creek timber sale. Technical Fire Management TFM14, USDA Forest Service, Region 5, Plumas National Forest, Mount Hough Ranger District, Quincy, CA.

Leopold, E. B., and R. Boyd. 1999. An ecological history of old prairie areas in southwestern Washington. *In* R. Boyd, (editor), Indians, Fire and the Land in the Pacific Northwest. Oregon State University Press, Corvallis. Pp. 139-163.

Lewis, H. 1973. Patterns of Indian burning in California: Ecology and ethnohistory. *In* T. C. Blackburn and K. Anderson (editors), Before the Wilderness. Ballena Press, Menlo Park, CA.

Logan, S. E., M. A. Hemstrom, and W. Pavlat. 1987. Plant association and management guide, Willamette National Forest. Pocket field guide R6-ECOL-257-A-86, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Lynch, K. A., and R. J. McLain. 2003. Access, labor, and wild floral greens management in western Washington's forests. General Technical Report PNW-GTR-585. USDA, Forest Service, Pacific Northwest Research Station, Portland, OR.

Maule, S. M. 1959. *Xerophyllum tenax*, squawgrass, its geographic distribution and its behavior on Mount Rainier, Washington. Madroño 15:39-48.

Munsell Color. 2012. Munsell Plant Tissue Color Book. Munsell Color, Grand Rapids, Michigan.

Olympic Peninsula Intertribal Cultural Committee. 2002. Native Peoples of the Olympic Peninsula. University of Oklahoma Press, Norman.

Peter, D. H., and T. B. Harrington. 2014. Historical colonization of south Puget Sound prairies by Douglas-fir at Joint Base Lewis-McChord, Washington. Northwest Science 88:186-205.

Peter, D., and D. Shebitz. 2006. Historic anthropogenically maintained beargrass savannas of the southeastern Olympic Peninsula. Restoration Ecology 14:605-616.

Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. GTR-INT-34. USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, UT.

Porter, S. C. 1986. Pattern and forcing of Northern Hemisphere glacier variations during the last millennium. Quaternary Research 26:27-48.

Rentz, E. D. 2003. Effects of fire on plant anatomical structure in native Californian basketry materials. M.S. Thesis. San Francisco State University, San Francisco.

Schlosser, W. E., and K. Blatner. 1997. Special forest products: an east-side perspective. General Technical Report PNW-GTR-380, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Schlosser, W. E., K. A. Blatner, and B. Zamora. 1992. Pacific northwest forest lands potential for floral greenery production. Northwest Science 66:44-55.

Shebitz, D. 2005. Weaving traditional ecological knowledge into the restoration of basketry plants. Journal of Ecological Anthropology 9:51-68.

Shebitz, D. J., S. H. Reichard, and W. Woubneh. 2008. Beargrass (*Xerophyllum tenax*) on the Olympic Peninsula, Washington: autecology and population status. Northwest Science 82:128-140.

Shebitz, D. J., K. Ewing, and J. Gutierrez. 2009a. Preliminary observations of using smoke-water to increase low-elevation Beargrass *Xerophyllum tenax* germination. Native Plants Journal 10:13-20.

Shebitz, D. J., S. H. Reichard, and P. W. Dunwiddie. 2009b. Ecological and cultural significance of burning beargrass habitat on the Olympic Peninsula, Washington. Ecological Restoration 27:306-319.

Smith, J. K., and W. C. Fischer. 1997. Fire ecology of the forest habitat types of northern Idaho. General Technical Report INR-GTR-363, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT.

Soil Survey Staff. 2011. Official soil series descriptions. USDA Natural Resources Conservation Service. Available online at https://soilseries.sc.egov.usda.gov/osdname.aspx. (accessed December 10 2014).

Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1981. Forest habitat types of central Idaho. General Technical Report INT-GTR-114, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT

Thomas, M. G., and D. R. Schumann. 1993. Income opportunities in special forest products. Self-help suggestions for rural entrepreneurs. Agriculture Information Bulletin 666, USDA, Forest Service, Washington DC.

Thorson, R. M. 1980. Ice-sheet glaciation of the Puget Lowland, Washington, during the Vashon Stade (late Pleistocene). Quaternary Research 13:303-321.

Turner, D. R. 1979. Plants in British Columbia Indian Technology, Handbook No. 38. Royal British Columbia Museum, Victoria.

USDA NRCS (Natural Resources Conservation Service National Water and Climate Center) and OSU (Oregon State University Spatial Climate Analysis Service. 2009. Parameter-elevation regressions on independent slopes model (PRISM), Available online at http://prism.oregonstate.edu/normals/ (accessed January 20, 2015).

Vance, N. C., P. Bernhardt, and R. M. Edens. 2004. Pollination and seed production in *Xerophyllum tenax* (Melanthiaceae) in the Cascade Range of central Oregon. American Journal of Botany 91:2060-2068.

Received 10 April 2017
Accepted 18 September 2017

Villalba, R., and T. T. Veblem. 1997. Improving estimates of total tree ages based on increment core samples. Ecoscience 4:534-542.

Williams, C. K., T. R. Lillybridge, and B. G. Smith. 1990. Forested plant associations of the Colville National Forest. Pocket field guide, USDA Forest Service, Colville National Forest, Colville, WA.

Weigland, J. 2002. Overview of cultural traditions, economic trends, and key species in nontimber forest products of the Pacific Northwest. *In* E. T. Jones, R. J. McLain, and J. Weigland, (editors), Nontimber Forest Products in the United States. University of Kansas Press, Lawrence. Pp.57-64.

White, J. D., J. C. Haglund, and T. K. Mellen. 1996. Early seral plant communities, Pacific silver fir zone, Mt. Hood National Forest. R6-NR-TP-16-96, USDA Forest Service, Pacific Northwest Region, Portland, OR.