

## Quantification of eccentricity in stems of *Artemisia tridentata* Nutt.

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**ABSTRACT.**—Previous research has shown that stems of *Artemisia tridentata* species exhibit extensive lobe formation. Twenty-two stem samples of *Artemisia tridentata* Nutt. ssp. *wyomingensis* (ARTRW) and 24 samples of *A. t. ssp. tridentata* (ARTRT) were investigated to quantify lobe formation characteristics. For samples of both subspecies, lobe formation values were constant for 8.3-cm-diameter stems. For the above samples, ARTRW had 14 xylem rings, while ARTRT had only 5 rings. Three stem samples (33 to 50 cm long) of ARTRW were cut into a series of 8-mm segments. For the 3 stems, the smallest ends had 8 xylem rings (10 mm<sup>2</sup> area), while the largest ends had 38 xylem rings (700-mm<sup>2</sup> area). Lobes were present in all samples with more than 10 xylem rings. Each stem segment was subdivided into 10 sectors. A difference of more than 10 rings was observed in 13% of all sectors from segment to segment, suggesting that eccentric growth and lobe formation was localized along stems. This is the first publication to quantify lobe formation characteristics in successive stem segments of *A. tridentata*.

**RESUMEN.**—Las investigaciones previas han demostrado que los tallos de las especies de *Artemisia tridentata* exhiben una extensa formación de lóbulos. Para cuantificar las características de la formación de lóbulos, se analizaron 22 muestras de tallos de *A. tridentata* Nutt. ssp. *wyomingensis* (ARTRW) y 24 muestras de *A. t. ssp. tridentata* (ARTRT). En las muestras de ambas subspecies la cantidad de formación de lóbulos fue constante en tallos de 8.3 cm de diámetro. De los cuales, ARTRW presentó 14 anillos, mientras que ARTRT tuvo sólo 5 anillos. Tres muestras de tallos (de 33 a 50 cm de largo) de ARTRW se cortaron en una serie de segmentos de 8 mm. En los 3 tallos, los extremos más pequeños contaron con 8 anillos xilares (área de 10 mm<sup>2</sup>), mientras que los extremos más grandes contaron con 38 anillos xilares (área de 700 mm<sup>2</sup>). Los lóbulos estuvieron presentes en todas las muestras con más de 10 anillos de xilema. Cada segmento del tallo se subdividió en 10 secciones. Se observó una diferencia de más de 10 anillos en el 13% de todas las secciones de segmento a segmento, sugiriendo que el crecimiento excéntrico y la formación de lóbulos se dio en todos los tallos. El presente trabajo es la primera publicación que cuantifica las características de formación de los lóbulos en segmentos sucesivos de tallos de *A. tridentata*.

Desert plants have adapted to live in climates with limited water availability (MacMahon 1985). Woody desert plants must transport water when it is available but also must resist embolisms under water deficits (Schenk et al. 2008). Therefore, these plants may develop unusual hydraulic systems that may include hydraulic redundancy. These plants may also produce stem segments in preparation for embolisms that may destroy some xylem cells and some stem segments (Schenk et al. 2008). In woody plants, vascular cambium produces secondary xylem and phloem (Mauseth 1998). For many species, secondary xylem (wood) appears as visually distinguishable xylem growth rings that collectively provide structural support for vertical growth

and branching architecture. The morphological and mechanical properties of this woody plant scaffolding shape the spatial attributes of diverse aboveground plant communities.

Growth, structure, and composition of secondary xylem may be uneven within and among stems in response to environmental cues (e.g., compression and tension woods), morphological peculiarities, or physiological peculiarities of the species (Schweingruber et al. 2006). When patterns of uneven growth persist through time, stems become increasingly asymmetrical around the central axis or lobe formation in cross-section. The presence of lobes can affect stem mechanical and physiological properties and thus drive the development of aboveground morphology (Billbrough and Richards 1991).

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The mostly herbaceous genus *Artemisia* L. originated in Eurasia during the mid-Tertiary period in response to global expansion of drier and cooler habitats (Raven and Axelrod 1974, Beetle 1979). Global expansion brought the genus to North America toward the end of this period, when the geographic complexity and variable climate of the Quaternary facilitated evolutionary diversification (McArthur and Plummer 1978, Beetle 1979). The *Artemisia* subgenus *Tridentatae* includes about 20 woody members endemic to North America (Beetle 1960, McArthur 1979).

*Tridentatae* species are distinguished from other *Artemisia* species by a combination of traits including woody habit, stem anatomy, floral morphology, plant chemistry, and chromosomal karyotype (McArthur 1979), and are collectively referred to by the common name *sagebrush*. One widely adapted species, *Artemisia tridentata* (big sagebrush), has been called the “most widespread and common shrub of western North America” (MacMahon 1985, McArthur and Stevens 2004).

The sagebrush shrubland desert vegetation of the Great Basin Desert occurs in desert areas with an annual precipitation above 175 mm (Cronquist et al. 1972). Sagebrush vegetation once covered approximately 60 million ha, and it is dominant in nonforested communities at elevations above 1370 m in northern and 1700 m in southern locations of the Great Basin Desert (MacMahon 1985). This community occupied more area than any other community type in the region (Hironaka and Tisdale 1963, Daubenmire 1970, Doescher et al. 1990, Billbrough and Richards 1991, West 1999, Welch 2005, Soulard 2012). The Great Basin Desert is distinct among deserts of North America because it occurs at high elevations, has cold winters, and obtains most of its yearly precipitation through winter snow (Fowler and Koch 1982, MacMahon 1985).

Reconstructions of paleovegetation suggest that big sagebrush and sagebrush-dominated vegetation were widespread in western North America during both glacial and interglacial phases of the Quaternary period (Kitchen and McArthur 2007). Today, such vegetation is found in areas defined by semiarid, typically continental climates, from southern Canada to Baja, California (McArthur and Plummer 1978, McArthur 1979). Beetle (1960) estimated the area of big sagebrush-dominated

vegetation to be 586,306 km<sup>2</sup> at the time of Euro-American settlement. Although some suggest that Beetle’s area value was an overestimate (McArthur and Stevens 2004), big sagebrush-dominated vegetation remains largely accepted as the most widespread nonforested community type of the western United States (Daubenmire 1970, Welch 2005, Soulard 2012). The cumulative impact of intentional sagebrush eradication for the purpose of land-use conversion has resulted in the introduction of weeds and increased wildfires, elevating concerns for the conservation of the sagebrush ecosystem.

Each spring, plants produce many terminal vegetative “daughter” stems on older “mother” stems that overwintered from previous years. These daughter terminals elongate, and in late summer many become determinant seed-bearing stems. These determinant daughter stems die in autumn. The death of these determinate daughter terminals is associated with the death of the vascular cambium at nodes on their mother stems (Evans et al. 2012). In contrast, daughter terminals that remain vegetative do not produce death of the vascular cambium at nodes on mother stems.

The death of the vascular cambium at nodes on mother stems is asymmetric; thus, death of vascular cambium is very localized at the base of daughter terminals only. In turn, the vascular cambium of the remainder of mother stems is unaffected and produces normal xylem (wood). The production of normal wood adjacent to areas of dead vascular cambium produces lobes in stem cross-sections (Fig. 1) (Diettert 1938, Moss 1940, Ferguson and Humphrey 1959, Ferguson 1964, Evans et al. 2012, Scarinci et al. 2017). “Eccentric growth” is defined as an uneven or asymmetrical growth of tissues in localized areas caused by death of the vascular cambium.

Overall, the purpose of this research was to develop a method to quantify the spatial arrangement of lobes. This quantification will provide a method of understanding the frequency and locations of lobes. Three hypotheses were tested:

- (1) Percentages of eccentric growth will be the same in samples of 2 subspecies of *Artemisia tridentata*.
- (2) Numbers of xylem rings will be constant in individual segments and among segments of *A. tridentata* ssp. *wyomingensis*.

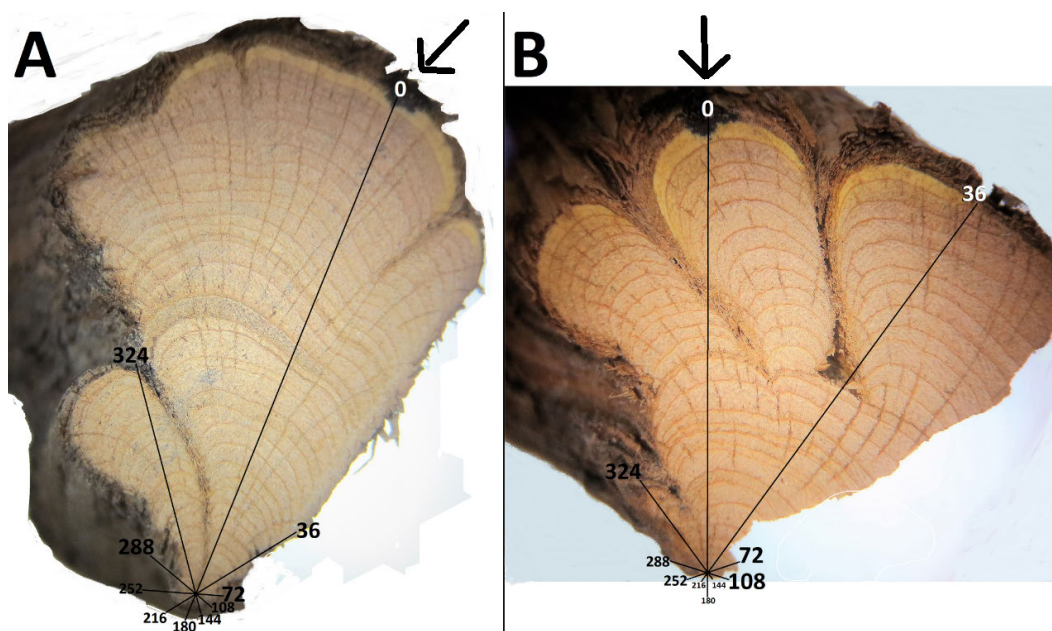


Fig. 1. Images of 2 stem segments of *Artemisia tridentata* spp. *wyomingensis* (ARTRW) showing differences in numbers of xylem rings in 10 sectors. Note the black arrow at the 0° location. Image A shows segment 18 from stem 2. Note the wide wood areas from 324° to 0° and from 0° to 36°. Image B shows segment 17 from stem 2. Note the differences from 324° to 0° and from 0° to 36° compared with segment 18 in image A. Segment 17 shows much more of a lobed configuration. Death of the vascular cambium gave rise to lobe formation in segment 17 that was not present in segment 18. Cross-section surfaces were 8 mm apart.

- (3) Depths of xylem rings will be constant in individual segments and among segments of *A. tridentata* ssp. *wyomingensis*.

## METHODS

### Stem Sampling

One stem sample (about 10 cm in length) was obtained from each of 22 plants in a stand of *A. tridentata* spp. *wyomingensis* (Beetle & Young) (ARTRW) near Milford, Utah (38.4204° N, 113.0937° W; 1515 m elevation). One stem sample was obtained from each of the 24 plants in a stand of *A. tridentata* ssp. *tridentata* (ARTRT) located near Thistle, Utah (40.0° N, 111.5° W; 1800 m elevation). Samples were taken from terminal stems with diameters between 7.0 mm and 10.0 mm. Terminal stems were selected because they are most likely to show death of the vascular cambium from nodes with flowering branches (see above). All samples were obtained during March 2017. Plants and stems were typical for the region. Stems were shipped to Manhattan College, where

for each of the 22 stems of ARTRW and 24 stems of ARTRT, a single wood sample of 8.3 mm in diameter was analyzed (Table 1).

### Within-Stem Sequential Eccentricity for ARTRW

Stem samples of ARTRW were obtained from 3 plants near Milford, Utah (38.4204° N, 113.0937° W) in June 2014. The stems and plants were typical for the region. The stems were cut and shipped to Manhattan College, where samples were trimmed so that the diameters at the largest and smallest ends were 27 mm and 4 mm, respectively. Stem sample length varied from 334 mm to 550 mm (Table 2). We removed loose bark from these sample stems to expose the outer wood surface, and then drew a straight line (about 1 mm wide) along one side of each stem with a permanent marker. Although the stems twist, the line facilitated accurate alignment of the segments after cutting. The stems were cut into short segments (between 7 mm and 11 mm) using a Dewalt DWHT20541 pull-saw. Individual segment thicknesses were

TABLE 1. Characteristics of stems segments of *Artemisia tridentata* spp. *wyomingensis* (ARTRW) and *A. t.* spp. *tridentata* (ARTRT) to determine lobe formation in stems of constant diameters. Standard deviations are in parentheses. Eccentricity values are given as percentages.

Subspecies	Number of segment samples	Mean diameter (mm)	Mean number of rings	Eccentricity value (EV)		
				Mean	Largest	Smallest
<i>Artemisia tridentata</i> spp. <i>wyomingensis</i>	22	8.35 (2.4)	13.9 (4.0)	111 (50.8)	184	16.8
<i>Artemisia tridentata</i> spp. <i>tridentata</i>	24	8.29 (0.73)	5.1 (2.4)*	50.7 (28.6)*	131	14.5

\*Comparison of values between subspecies is statistically significant at 0.01 probability as determined with a Student's *t* test. For the other variables there were no statistically significant differences.

TABLE 2. Comparisons of stem area, largest number of xylem rings for tip-most and base-most segments, and total branch length among the 3 branch samples of *Artemisia tridentata* spp. *wyomingensis* (ARTRW) examined in this study. For each stem sample, the tip-most and base-most stem segments had stem diameters of approximately 4 mm and 27 mm, respectively.

	Stem sample number		
	1	2	3
BRANCH DETAILS			
Total branch length (mm)	550	334	520
Number of stem segments	62	37	44
Mean thickness of stem segments (mm)	8.9	9.0	11.8
SAMPLE DETAILS			
Tip-most sample			
Stem area (mm <sup>2</sup> )	9.6	13.4	6.4
Number of rings	8	8	6
Base-most sample			
Stem area (mm <sup>2</sup> )	760	603	727
Number of rings	35	38	38

measured with a digital caliper (Fisher model #14-648-17, Fisher Scientific Inc., Pittsburgh, PA) accurate to 0.01 mm.

#### Quantification of Eccentricity in All Stem Segments

After sawing, each segment was given a light sanding and washed with water to improve xylem ring visibility. We secured images of one cut surface of each stem segment using a Canon PowerShot ELPH100HS camera through a Leica EZ4 microscope at 5× magnification (www.leica-microsystems.com). A millimeter ruler was included in each photograph to ensure accurate distance measurements. All measurements of images were obtained using imageJ (imagej.nih.gov/ij). For each image, the black mark (line drawn prior to segment separation) was assigned to zero degrees. Thereafter, lines were drawn

on images using Microsoft Paint from the stem center (pith) to the outer edge of the sample at 36-degree intervals (0°, 36°, 72°, 108°, 144°, 180°, 216°, 252°, 288°, and 324°) in order to create 10 wedge-shaped sectors of equal radial proportion around the center (Figs. 1, 2). The sectors were subsequently numbered from 1 to 10 in the same sequence. We then marked xylem ring boundary locations in Microsoft Paint to determine ring counts (Fig. 2). The total stem area and the area of each sector were mapped and calculated for each stem sample using imageJ (imagej.nih.gov/ij).

#### Statistical Analyses

Eccentricity is a measure of variability among samples, expressed as standard deviations divided by their means and multiplied by 100 (Snedecor and Cochran 1967) so that eccentricity values (EVs) are represented as percentages. This establishes a standard method of variability, creating eccentricity values. An arbitrary threshold greater than 0.25, or 25%, was selected to define eccentricity (Love et al. 2009, Evans et al. 2012).

Additional analyses were performed to determine changes in the number of rings for a sector among 3 successive segments. For this procedure, segments 38, 39, and 40 were chosen at random, and from these 3 segments, sector 3 was randomly selected for analyses. Comparisons were made between the 2 subspecies of *A. tridentata* with a student's *t* distribution (Snedecor and Cochran 1967).

## RESULTS

### Hypothesis 1

With constant stem diameters, the ring number-based EVs for 22 ARTRW plants ranged from 16.8% to 184%, with a mean of



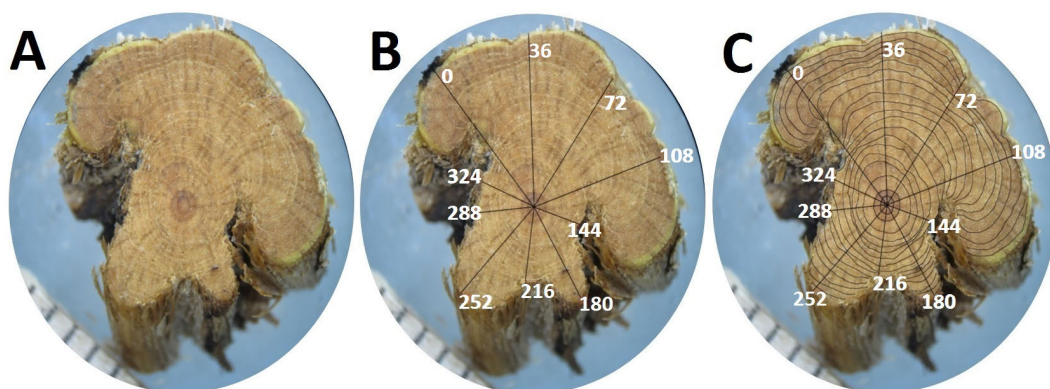


Fig. 2. Three images of segment 34 from stem 1 of *Artemisia tridentata* spp. *wyomingensis* (ARTRW) of this study. Image A shows the segment immediately after saw cutting (i.e., without alterations). Note the black mark on the barked surface in the upper left-hand portion of the segment image. Image B shows lines demarcating the 10 sectors for the segment. The zero-degree ( $0^\circ$ ) location is at the black mark, while the other lines are drawn at 36-degree intervals clockwise from the  $0^\circ$  line. Image C is the same as B except each xylem ring is highlighted. Distance between scale lines is 1.6 mm.

TABLE 3. Comparisons of eccentricity values (EVs) of stem segments with the xylem ring numbers for the 3 branch samples of *Artemisia tridentata* spp. *wyomingensis* (ARTRW) of this study.

Stem segment ring number	Stem sample number			Mean EV	SD
	1	2	3		
8	27	30	35	30.7	3.3
10	28	57	45	43.3	12.3
14	68	65	103	78.7	17.2
19	64	96	84	81.3	13.2
22	98	70	102	90.0	14.2
25	145	93	94	110	24.2
27	51	113	98	87.3	26.4
34	96	116	174	128	33.5

111%. For ARTRW, the mean number of xylem rings per sector was 13.9 (Table 1). For the 24 plants of ARTRT, EVs ranged from 14.5% to 131%, with a mean of 50.7%. For ARTRT, the mean number of xylem rings per sector was 5.1%? (Table 1). Forty of the 46 samples had lobe formations based upon one or both metrics (ring count or segment area), although the number of xylem rings per sector was statistically different ( $P = 0.01$ ) between the 2 subspecies.

#### Hypothesis 2

Three stems between 0.3 m and 0.5 m in length were used for this analysis. For each of the 3 stems, the smallest segments (4-mm diameter) had 6 or 8 xylem rings, while the largest segments (27-mm diameter) had between 35 and 38 xylem rings (Table 2). The numbers of xylem rings in all sectors for the 3 stems

are shown in Appendixes 1, 2, and 3. Overall, data for the 3 stem samples were similar (Table 3). For stem 1, all segments were eccentric (with  $EV > 25\%$ ). For stems 2 and 3, all segments were eccentric.

As stated above, segments 34, 35, and 36 of stem 1 were selected to illustrate the diversity of xylem ring numbers among sequential segments (Fig. 3A–C). For example, in sector 7 (Fig. 3A–C, red arrows) of segments 36 (Fig. 3A), 35 (Fig. 3B), and 34 (Fig. 3C) (oldest to youngest), 20, 9, and 16 rings were present, respectively. Similarly, there were 10, 16, and 9 rings in sector 9 (Fig. 3A–C, green arrows) for segments 36 (Fig. 3A), 35 (Fig. 3B), and 34 (Fig. 3C), respectively. Similar comparisons can be made for segments 58, 57, and 56 (Fig. 3D–F). For sector 3 (Fig. 3D–F, orange arrows), the number of rings were 30 (Fig. 3D), 7 (Fig. 3E), and 28 (Fig. 3F) for segments

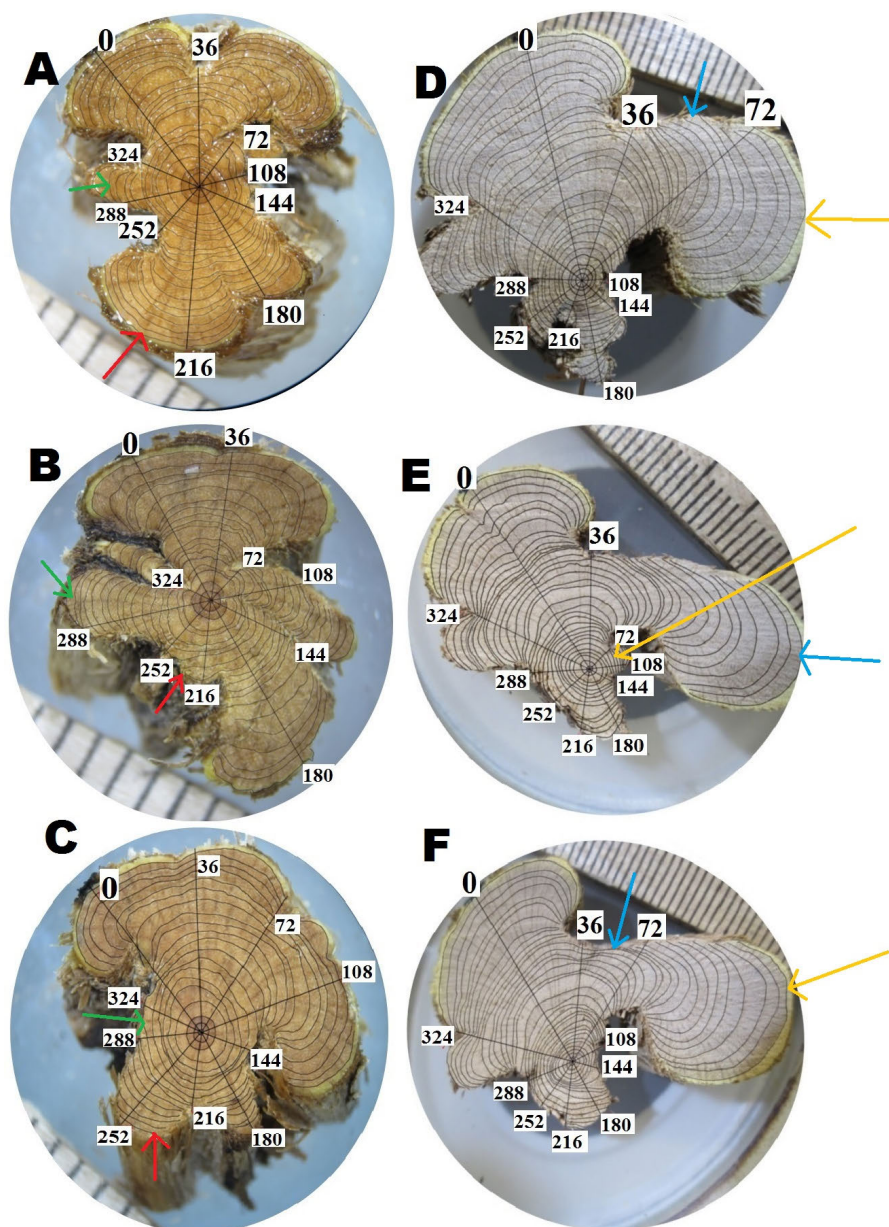


Fig. 3. Examples of lobe formation among stem segments from stem 1 of *Artemisia tridentata* spp. *wyomingensis* (ARTRW) of this study. For each image, the black mark ( $0^\circ$ ) is rotated to the upper left-hand area so the orientation among segments is maintained. All successive segments are aligned using the locations of the biological center and the sector lines every 36 degrees. For simplicity, sectors  $0^\circ$  to  $36^\circ$ ,  $36^\circ$  to  $72^\circ$ ,  $72^\circ$  to  $108^\circ$ ,  $108^\circ$  to  $144^\circ$ ,  $144^\circ$  to  $180^\circ$ ,  $180^\circ$  to  $216^\circ$ ,  $216^\circ$  to  $252^\circ$ ,  $252^\circ$  to  $288^\circ$ ,  $288^\circ$  to  $324^\circ$ , and  $324^\circ$  to  $360^\circ$  are referred to in the text as sectors 1 through 10, respectively. Thus, with these points of reference, each image was rotated and aligned as necessary to compare changes among successive segments. Images A through C are segments 36, 35, and 34, respectively. Comparisons made in the text refer to sectors 7 and 9. Red arrows show comparisons for sector 7, while green arrows show comparisons for sector 9. The distance between scale lines in images A through C is 1.6 mm. Images D through F are segments 58, 57, and 56, respectively. For sector 3 (orange arrows, D through F), the numbers of xylem rings are 30 (D), 7 (E), and 28 (F), respectively. Lateral expansion of rings in sectors occurred. For example, expansion of sector 2 (blue arrows) occurs between segments 58 and 57. The distance between scale lines in images D through F is 1 mm. The distance between consecutive segments is 7.8 mm.

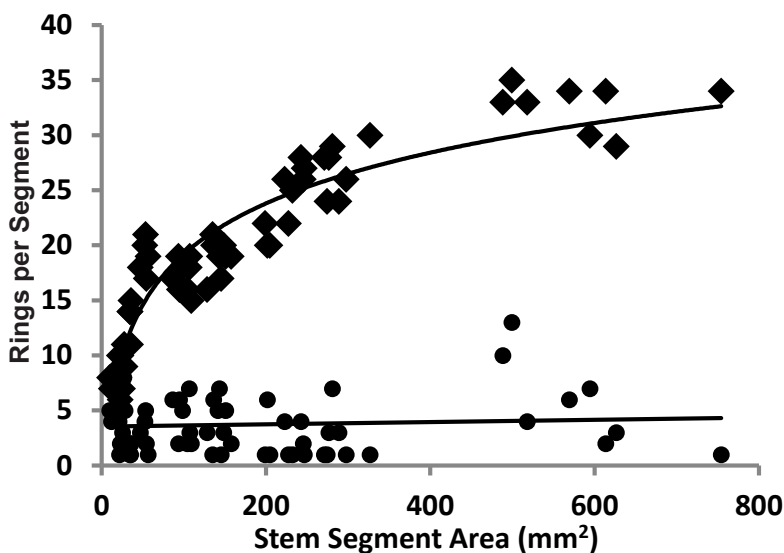


Fig. 4. Maximum (diamonds) and minimum (circles) numbers of xylem rings for stem segments of stem 1 of *Artemisia tridentata* spp. *wyomingensis* (ARTRW). The equation of the line for the largest number of rings was  $y = 3.08x^{0.37}$  ( $r^2 = 0.87$ ), while the equation of the line for the smallest number of rings was  $y = 0.0005x + 3.41$  ( $r^2 = 0.014$ ).

58, 57, and 56, respectively. Lateral expansion of rings in sectors occurred. For example, expansion of sector 2 (Fig. 3, blue arrows) occurred between segments 58 and 57. These results demonstrate that the number of rings varied markedly from segment to segment in stems.

Data from stem 1 were analyzed to determine the minimum and maximum numbers of xylem rings as a function of the stem area (Fig. 4). For all the stem segments, at least one sector had  $<5$  rings (minimum). In contrast, in at least one sector per segment, the maximum number of rings increased markedly with the stem segment area.

### Hypothesis 3

Xylem ring depths were measured as ring areas for this study. To determine differences in xylem characteristics of sectors among sequential stem segments, areas of sector 3 for 3 segments of stem 1 were determined. There were no statistically significant differences between segments 38 (Fig. 5, diamonds) and 39 (Fig. 5, squares). Areas of segment 40 (Fig. 5, circles), specifically rings 12 to 20, were larger than areas of segments 39 and 38.

Areas also differed among sectors within single segments. There were no statistically

significant differences between sectors 5 (Fig. 6, diamonds) and 4 (Fig. 6, squares) for segment 40. However, data for rings 6 to 17 of sector 3 (Fig. 6, circles) were statistically different from sectors 4 and 5. Thus, in addition to variations in numbers of rings, there was a nonuniform pattern in ring areas among segments and among adjacent sectors within segments.

### DISCUSSION

Lobe formation is ubiquitous in stems of many species of *Artemisia* and subspecies of *A. tridentata* (Diettert 1938, Moss 1940, Ferguson and Humphrey 1959, Ferguson 1964). More recently, these same characteristics of lobe formation were documented for ARTRW and ARTRT, for *A. nova*, for *A. filifolia*, for *A. bigelovii*, and for *A. tripartita* (Evans et al. 2012). Although lobe formation occurs in many species of *Artemisia* as well as subspecies ARTRW and ARTRT, lobe formation characteristics cannot be directly compared among these species because the species occur in various areas and grow under a variety of conditions.

Thin stem segments (between 8.8 mm and 11.2 mm) were required to best determine

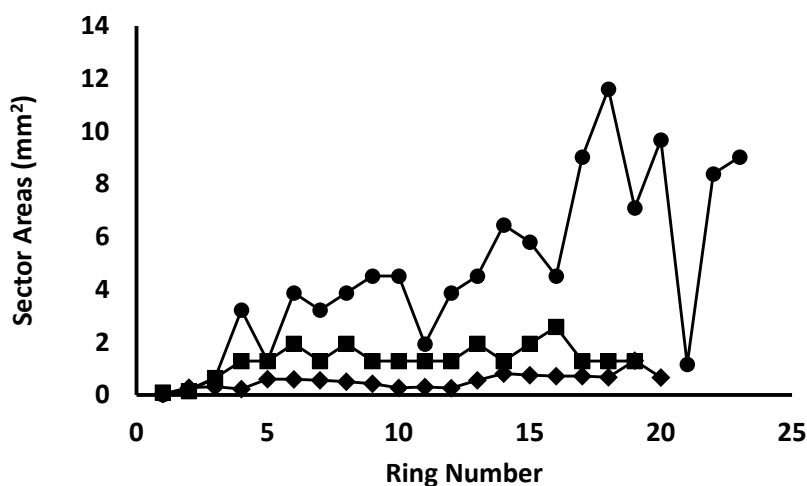


Fig. 5. Comparison of sector areas of xylem rings for sector 3 for stem segments 40 (circles), 39 (squares), and 38 (diamonds) of stem 1 of *Artemisia tridentata* spp. *wyomingensis* (ARTRW). There were no statistically significant differences between segments 38 and 39; however, data for rings 4, 6 through 10, and 12 through 20 for segment 40 were statistically different ( $P = 0.05$ ) from the data for rings of segments 38 and 39.

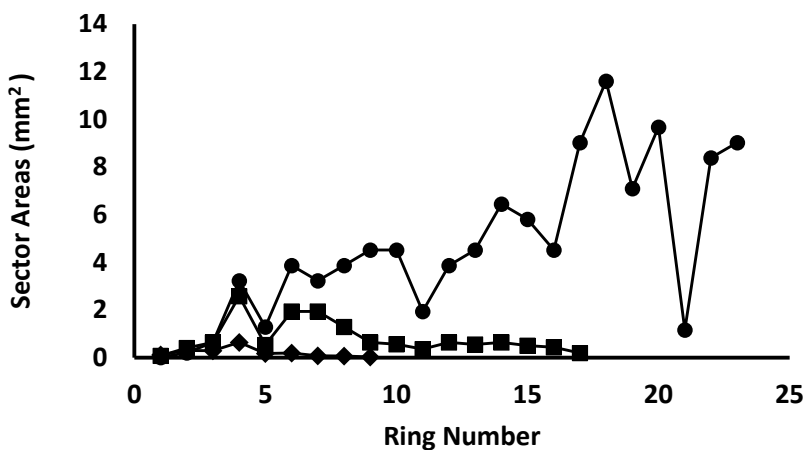


Fig. 6. Comparison of sector areas of xylem rings for sectors 5 (144° to 180°, diamonds), 4 (108° to 144°, squares), and 3 (72° to 108°, circles) for stem segment 40 of stem 1 of *Artemisia tridentata* spp. *wyomingensis* (ARTRW). There were no statistically significant differences between sectors 5 and 4. However, data from sector 3 for rings 6 to 17 were statistically different ( $P = 0.05$ ) from sectors 4 and 5.

differences in xylem/lobe characteristics in sectors from one segment to the next. Analysis of the numbers and areas of xylem layers in individual sectors provided an effective method for overall comparisons. No previous study has documented segment-to-segment differences in sector characteristics of stems of *Artemisia* or any other species that has eccentric characteristics. While the demarcations of sectors by the establishment of the 0°

line was arbitrary, the method of quantifying differences in numbers of xylem rings and areas of xylem rings among sectors within 1 segment or among segments along a stem was accurate.

The 3 entire stem samples from 3 separate plants of ARTRW had similar diameters, lengths, and maximum numbers of xylem rings per unit of stem area, so they were considered replicate stems. Moreover, the 3 stems had



similar lobe-formation characteristics, such as similar numbers of rings among sectors and segments. Although there is a similar pattern for the 3 sample stems, we speculate that no 2 branches of *Artemisia* exhibit the same pattern of lobe formation from segment to segment.

Eccentric growth (i.e., lobe formation) of *Artemisia* differs from that of reaction woods. Reaction woods (i.e., tension and compression woods) do not result from the death of the vascular cambium; rather, they are manifestations of variable depths of xylem rings that accumulate unevenly over time (Mauseth 1998). Lobe formation for *Artemisia* is not like axis splitting in branch axils of smaller shrubs (Ginsburg 1963). Axil splits create 2 stems from 1 in which there is a bifurcation of cells in shoot apical meristems (Jones and Lord 1982). Splitting to produce new stems did not occur in any of the stems of *Artemisia* species in our collections.

Previous research has shown that stems of *A. tridentata* species exhibit extensive lobe formation. The current study has shown that *EV* values were relatively constant when stem diameters remained constant, even though lobes were present in every stem sample. Moreover, all the stems exhibited lobe formation when they had more than 10 xylem rings. From one segment to the next, and from one sector to an adjacent sector on the same stem sample, there can be a decrease of more than 10 xylem rings and up to a 100% difference in sector areas. Thus, lobe formation is localized and appears randomly along stems. This is the first publication to quantify *EV* in stems of *A. tridentata*.

*Artemisia* stems have both interxylary cork and eccentric growth (lobe formation). Wang postulated that North American herbaceous *Artemisia* species may have descended recently from woody ancestors (Wang 2004). The current research shows that eccentric growth (lobe formation) in *A. tridentata* is caused by localized death in vascular cambium. Exposure of xylem rings, caused by eccentric growth, may increase chances of decay and stem twisting, which contributes to reduced mechanical strength and in turn limits growth of individual stems and plant size.

Competitive restrictions associated with morphologically imposed limitations to plant height may be counterbalanced by a rela-

tively low energetic investment in wood and neutralized by a physical environment where limited soil moisture is the prevailing factor controlling plant height. Stems of *A. tridentata* also exhibit wood decay, stem rot, and other anomalous injuries that occur in nature. Although these injuries may occur in nature, they do not lead to lobe formation for any of the samples of this study. In fact, we believe that lobes produce sector displacements or shifts. As stated in a previous section, a straight vertical line was drawn along each of the 3 stems, with just a small amount of bark removed. Then, wood segments were sawed. With this description in mind, the 2 segments in Fig. 1 show little wood between the 36° to 72° sector in Fig. 1A, while there was much wood between the 36° to 72° sector in Fig. 1B. In contrast, there was more wood between the 288° to 324° sector in Fig. 1A than for the same sector in Fig. 1B. Relative to the 0° axis, there were marked differences between the 2 segments that were 8 mm apart. The 2 segments have segments displaced or shifted slightly relative to 0°, which is not a true twisting.

Lobes that produce relatively high *EV*s with uneven wood production in sectors may produce internal mechanical stresses that may shift lobes from one sector to another. In any case, the twisting of the stems described above is caused by uneven production of xylem cells by the vascular cambium. Lobe formation and twisted stems are due to eccentric growth. To our knowledge, this is the first publication to quantify eccentric growth characteristics and resultant lobe development in *A. tridentata*. Moreover, to our knowledge, no other studies have quantified lobe characteristics of any plant species.

As shown in this study, the eccentric growth of *Artemisia* stems produces extensive lobe formation. Other woody species, such as blackbrush (*Coleogyne ramosissima*), cliffrose (*Purshia glandulosa*), and juniper (*Juniperus osteosperma*) also develop lobes around the central stem axis. Is lobe formation in these other species caused by eccentric growth? Because all of these species inhabit semiarid continental climates, we can hypothesize a relationship between climate and selection for lobe formation, eccentric stem morphology, and other stem abnormalities (Schenk et al. 2008).

## ACKNOWLEDGMENTS

The authors appreciate the generous financial support of the Catherine and Robert Fenton Endowed Chair to LSE for this research. Jason Durney of the Manhattan College carpentry shop provided expert sawing of stem segments. The authors appreciate the editorial suggestions and revisions of RikkiLynn Shields, Lilliana McHale, and Dr. Heidi Laudien.

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Received 4 October 2018

Revised 22 February 2019

Accepted 29 March 2019

Published online 9 October 2019

APPENDIX 1. Number of xylem rings for the 10 sectors for the 62 segments of stem 1 of *Artemisia tridentata* ssp. *wyomingensis*. Segment 1 was the smallest-diameter segment and segment 62 was the largest-diameter segment sampled. Lobe formation (LF) percentage was calculated as the standard deviation divided by the mean and expressed as a percentage of all sectors in a segment.

Segment	Sectors <sup>a</sup>										LF (%) <sup>b</sup>
	1	2	3	4	5	6	7	8	9	10	
1	8	8	5	5	5	6	8	8	8	8	21
2	7	7	7	4	7	7	5	5	5	7	20
3	2	2	3	6	6	6	6	3	4	4	40
4	7	4	7	5	3	5	7	7	7	7	26
5	8	4	4	4	8	8	8	8	8	8	27
6	4	8	8	8	8	7	8	8	8	8	17
7	9	9	9	9	9	9	8	9	9	9	3
8	7	9	9	9	7	6	7	9	9	9	15
9	9	9	9	9	6	6	5	5	9	9	24
10	10	10	1	10	7	7	7	9	10	10	36
11	9	9	9	10	10	10	9	9	9	9	5
12	10	10	9	11	1	9	10	10	10	10	32
13	11	11	11	11	5	3	1	1	1	2	83
14	14	14	14	13	8	6	3	2	2	5	64
15	3	14	8	1	8	5	4	3	3	3	73
16	3	15	5	3	2	2	2	2	2	2	105
17	15	15	2	2	2	2	2	2	2	3	116
18	21	16	7	6	6	6	5	6	10	21	62
19	18	18	6	3	3	3	3	5	14	19	77
20	17	13	6	2	2	2	2	2	7	17	91
21	19	9	3	4	6	1	1	1	1	1	124
22	16	6	15	10	9	7	6	6	6	10	41
23	18	18	17	10	10	10	10	5	5	18	43
24	16	16	4	2	8	8	8	7	14	16	53
25	10	18	18	13	9	9	7	7	11	17	37
26	18	19	2	17	10	11	8	13	2	5	60
27	20	4	19	15	10	11	7	6	20	20	48
28	16	9	6	7	7	7	16	17	17	10	42
29	20	20	20	15	11	11	8	6	11	6	44
30	17	17	17	14	10	9	1	5	5	17	54
31	16	15	12	8	8	6	5	5	5	3	54
32	13	19	18	2	7	7	7	13	17	17	49
33	7	16	19	19	3	8	13	8	3	5	63
34	11	19	19	17	7	15	16	16	9	8	36
35	18	18	6	14	13	20	9	7	16	3	37
36	20	13	6	6	7	18	20	7	10	7	52
37	8	20	20	8	19	1	11	21	21	17	48
38	20	20	20	20	16	14	11	5	5	20	41
39	8	19	19	14	5	5	11	13	19	14	43
40	7	1	23	17	9	4	6	9	13	19	64
41	20	20	6	1	1	1	1	1	1	2	145
42	8	23	9	1	1	1	1	3	5	24	122
43	20	8	6	5	5	5	5	5	4	26	86
44	26	7	4	2	3	4	4	5	13	26	99

## APPENDIX 1. Continued

Segment	Sectors <sup>a</sup>										LF (%) <sup>b</sup>
	1	2	3	4	5	6	7	8	9	10	
45	22	22	22	1	1	1	1	3	10	22	98
46	26	26	20	1	1	1	1	1	1	14	121
47	25	25	16	1	1	1	1	1	1	1	143
48	28	27	23	22	13	5	1	1	1	17	80
49	28	28	22	21	16	8	4	4	7	15	61
50	28	16	5	3	4	6	16	24	24	28	67
51	24	11	10	6	3	6	13	17	19	24	56
52	7	29	26	24	13	10	7	9	9	10	59
53	30	30	8	16	11	1	1	1	1	7	108
54	9	27	20	8	1	1	1	1	1	3	128
55	30	18	18	11	7	16	10	10	7	10	51
56	35	24	28	7	7	14	17	13	13	35	56
57	33	20	7	13	5	14	13	11	14	29	58
58	27	17	30	4	7	18	9	14	12	21	51
59	33	33	28	13	10	10	15	12	24	33	48
60	35	35	28	15	21	16	13	15	26	24	36
61	34	29	15	10	5	4	3	2	3	34	96
62	34	21	4	1	1	1	8	7	16	12	101

<sup>a</sup>For simplicity, sectors 0° to 36°, 36° to 72°, 72° to 108°, 108° to 144°, 144° to 180°, 180° to 216°, 216° to 252°, 252° to 288°, 288° to 324°, and 324° to 360° are referred to as sectors 1 through 10, respectively.

<sup>b</sup>If LF ≥ 25, the segment is considered eccentric. If LF < 25, the segment is considered not eccentric.

APPENDIX 2. Number of xylem rings for the 10 sectors for the 37 segments of stem 2 of *Artemisia tridentata* ssp. *wyomingensis*. Segment 1 is the smallest-diameter segment and segment 37 is the largest-diameter segment sampled. Lobe formation (LF) percentage was calculated as the standard deviation divided by the mean and expressed as a percentage of all sectors in each segment.

Segment	Sectors <sup>a</sup>										LF (%) <sup>b</sup>
	1	2	3	4	5	6	7	8	9	10	
1	8	6	4	3	4	5	5	8	8	8	30
2	9	9	8	8	8	5	4	4	4	8	30
3	13	13	7	3	2	2	3	6	3	3	58
4	10	11	7	2	1	1	1	1	1	8	57
5	11	12	7	3	1	1	1	1	1	9	61
6	13	12	11	9	2	2	2	2	2	8	63
7	13	13	2	2	2	2	2	2	4	12	67
8	14	13	1	1	1	2	2	4	4	7	65
9	13	5	2	2	2	2	3	4	8	8	58
10	14	4	2	2	2	2	2	2	8	13	62
11	16	8	5	4	3	3	3	4	8	16	65
12	20	9	9	4	2	1	1	1	8	14	81
13	21	21	3	2	2	2	3	3	10	15	101
14	19	20	5	4	2	3	4	4	4	19	96
15	19	14	1	1	1	1	1	1	1	19	102
16	17	18	7	3	3	3	3	4	8	16	80
17	4	19	9	3	2	2	2	2	3	7	68
18	16	15	14	4	1	1	1	1	1	11	83
19	24	22	1	1	1	1	1	1	1	6	114
20	25	7	1	1	1	1	1	1	1	7	93
21	12	26	1	1	1	1	1	1	1	5	98
22	3	25	23	1	1	1	1	1	1	1	113
23	26	23	1	1	1	1	1	1	1	7	113
24	23	11	3	1	1	1	1	1	1	20	98
25	24	22	5	1	1	1	1	1	1	21	113
26	25	26	7	3	1	1	2	2	4	26	123
27	25	1	1	1	1	1	1	5	11	1	8730
28	2	3	4	12	12	8	14	19	34	1	107



## APPENDIX 2. Continued

Segment	Sectors <sup>a</sup>										LF (%) <sup>b</sup>
	1	2	3	4	5	6	7	8	9	10	
29	27	4	11	2	2	2	2	2	17	31	123
30	34	4	1	1	1	1	1	1	1	2	116
31	34	22	2	1	1	1	1	1	1	11	142
32	9	21	2	2	2	4	5	6	11	12	63
33	37	24	11	3	1	1	1	2	11	32	142
34	38	29	9	4	1	1	1	1	1	5	63
35	38	27	12	2	3	3	4	4	2	2	142
36	36	23	9	10	7	1	1	1	1	1	140
37	1	7	20	30	2	1	1	1	3	4	140

<sup>a</sup>For simplicity, sectors 0° to 36°, 36° to 72°, 72° to 108°, 108° to 144°, 144° to 180°, 180° to 216°, 216° to 252°, 252° to 288°, 288° to 324°, and 324° to 360° are referred to as sectors 1 through 10, respectively.

<sup>b</sup>If  $LF \geq 25$ , the segment is considered eccentric. If  $LF < 25$ , the segment is considered not eccentric.

APPENDIX 3. Number of xylem rings for the 10 sectors for segments of stem 3 of *Artemisia tridentata* ssp. *wyomingensis*. Segment 1 was the smallest-diameter segment sampled and segment 44 was the largest-diameter segment sampled. Not all segments are shown. Lobe formation (LF) percentage was calculated as the standard deviation divided by the mean and expressed as a percentage of all sectors in a segment.

Segment	Sectors <sup>a</sup>										LF (%) <sup>b</sup>
	1	2	3	4	5	6	7	8	9	10	
1	6	6	6	6	6	3	6	6	6	6	15.8
5	5	6	6	6	6	6	6	5	5	5	8.7
9	2	2	2	2	3	4	4	2	16	17	103
13	5	18	15	6	4	4	4	2	2	3	83.7
17	16	20	5	2	2	3	3	3	8	8	85
21	21	21	2	2	2	6	2	2	3	12	102
25	22	22	13	9	6	6	6	8	8	22	55
29	1	37	30	6	5	1	1	1	1	1	152
33	25	17	16	1	1	1	1	1	21	25	94.1
37	28	30	2	3	3	3	3	6	10	28	98.2
41	34	1	1	1	1	1	1	1	1	21	174
44	38	4	4	5	1	1	1	25	38	38	104

<sup>a</sup>For simplicity, sectors 0° to 36°, 36° to 72°, 72° to 108°, 108° to 144°, 144° to 180°, 180° to 216°, 216° to 252°, 252° to 288°, 288° to 324°, and 324° to 360° are referred to as sectors 1 through 10, respectively.

<sup>b</sup>If  $LF \geq 25$ , the segment is considered eccentric. If  $LF < 25$ , the segment is considered not eccentric.