

FLOWERING BRANCHES CAUSE INJURIES TO SECOND-YEAR MAIN STEMS OF *ARTEMISIA TRIDENTATA* NUTT. SUBSPECIES *TRIDENTATA*

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ABSTRACT.—Eccentricity of stems of *Artemisia tridentata* Nutt. (big sagebrush) has been reported previously. Analysis of samples observed over 2 years documented that each stem terminal produces about 8–10 branches each year, and during second-year growth, 3–8 of these develop into short, flowering, determinate branches. Each flowering branch produces hundreds of seeds and then dies at the end of the season, while the other vegetative branches persist. However, growth of the determinate flowering branches causes the death of vascular cambium surrounding their attachment points on the main stem. This death then results in the observed eccentric growth of the stem. In a separate experiment, when presumptive flowering branches were removed prior to elongation, the vascular cambium of the stem was not destroyed, and no eccentric growth occurred. Since the vascular cambium is responsible for continued wood production, the effect of these areas of cambial death is amplified during subsequent years and leads to weak stem segments and possibly to limitations on overall growth. Nevertheless, in spite of these negative side effects, flowering stem growth provides for ample seed production year after year. This peculiar eccentric growth phenomenon, coupled with the anomalous interxylary cork that has also been reported for *Artemisia tridentata*, supports the idea that this and related species are descended from an herbaceous ancestry and have therefore evolved their rather imperfect woodiness secondarily.

RESUMEN.—Anteriormente se ha reportado la rareza de los tallos de *Artemisia tridentata* Nutt. (arbusto Artemisa). El análisis de las muestras realizadas durante dos años documentó que cada extremidad del tallo produce aproximadamente de ocho a diez ramas cada año, y durante el segundo año de crecimiento, de tres a ocho de estas ramas se desarrollan en ramas cortas, florecientes y definidas. Cada una produce cientos de semillas y luego mueren al final de la estación, mientras que las otras ramas vegetativas persisten. Sin embargo, el crecimiento de las ramas florecientes y definidas provoca la muerte del cambium vascular que rodea sus puntos de fijación en el tallo principal. Esta muerte luego resulta en el extraño crecimiento que se ha observado en los tallos. En un experimento aparte, cuando se removieron las ramas presumiblemente florecientes antes de la elongación, no se destruyó el cambium vascular de la rama y no se produjo ningún crecimiento extraño. Debido a que el cambium vascular es el responsable de la producción continua de madera, el efecto de estas áreas de muerte cambial aumenta durante los años siguientes y conduce al debilitamiento de los segmentos del tallo y posiblemente a limitaciones del crecimiento general. Sin embargo, a pesar de estos efectos secundarios negativos, el crecimiento de la rama floreciente proporciona una vasta producción de semillas año tras año. Este fenómeno peculiar de crecimiento extraño, junto con un corcho interno del xilema anómalo que también se ha reportado para *Artemisia tridentata*, respalda la idea de que ésta y otras especies relacionadas descienden de un ancestro herbáceo, y por lo tanto su capacidad imperfecta para producir madera evolucionó de manera secundaria.

The Great Basin Desert is the largest desert in the United States (McMahon 1985) and one of the largest shrubland-dominant ecosystems in the world (West 1999). Prior to settlement of Anglo-Americans in the Great Basin Desert region of North America, populations of *Artemisia tridentata* Nutt. occupied large areas in the states of Montana, Wyoming, Idaho, Utah, Nevada, and Colorado. Basin big sagebrush (*A. tridentata* Nutt. ssp. *tridentata*) occupies most nonsaline portions of the Great Basin Desert (Daubenmire 1970, Welch 2005).

Sagebrush plants produce two types of branches (Welch 2005). Vegetative indeterminate branches are produced and may live for

many years; these shoots provide the excurrent growth form for plants. In contrast, determinate, flowering branches arise continuously during the second-year growth of individual stems. Inflorescences are produced only from these determinate branches. Determinate branches are defined as inflorescences in which the terminal flower blooms first, halting further elongation of the main axis (Harris and Harris 2009). These determinate shoots produce small leaves and numerous flowers and seeds. Determinate shoots die during their first winter (on second-year main stems) and are usually shed by the following spring (Miller and Shultz 1987, Billbrough and Richards 1991).

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Eccentric growth is caused by uneven growth of xylem (wood) rings (Diettert 1938). The vegetative stems of *A. tridentata* ssp. *tridentata* are conspicuously eccentric (Ferguson and Humphrey 1959). Eccentricity has been attributed to (1) death of inflorescences on shoots, (2) the destruction of the vascular cambium, and (3) the removal of natural bark tissues (Ferguson and Humphrey 1959), but Ferguson and Humphrey (1959) did not test any hypotheses. Our study focused on growth of determinate and indeterminate branches during the second-year of main stem growth and on the relationship between development of determinate, flowering branches with death of the vascular cambium and lack of production of xylem in second-year main stems. We hypothesized that plants with flowering branches removed would have no damage to their vascular cambium and no eccentric growth, while normal plants that retained their flowering branches (control plants) would exhibit death of the vascular cambium and have eccentric growth similar to control stems.

METHODS

Plants

Plants of *Artemisia tridentata* Nutt. ssp. *tridentata* for this study were located near milepost 312 on U.S. Hwy. 89 in Spanish Fork Canyon (approximate UTM coordinates [NAD 28] are Zone 12, 0458867 E, 4427248 N; 39° N, 111° W; 1560 m elevation) near Thistle, Utah. Most measured plants were 2 m or more in height and were typical for this species in the region. During 2009, 12 terminal stem samples (20–40 cm long) were harvested twice monthly from 25 May to mid-October. During 2010, 2 groups of plants were analyzed. One group had their flowering branches removed in mid-April (prior to flowering branch growth), while the second group had no branches removed from second-year stems. No indeterminate branches were removed from either group. Twelve stems of each group were harvested in late September 2010.

Histological Preparations

All stems were cut and immediately placed in 70% ethanol and shipped via overnight delivery to Manhattan College. Upon receipt, plants were fixed in FAA for 24 h and stored in 70% ethanol until they were processed for his-

tology. Terminals (main stems) up to 5 mm in diameter were used in this study. A sketch and photograph was made for each stem terminal for archival purposes. For each terminal, internode distances, the length of each branch, and the diameter of the main stem at each node were measured. Each branch on the main stem was recorded as vegetative or flowering. At each node of the main stem, diameters of main stems were recorded using a digital caliper (Fisher model #14-648-17, Fisher Scientific Inc., Pittsburgh, PA) accurate to 0.01 mm. Mean stem diameters were determined from 3 measurements at each node. The caliper was calibrated with steel rods of known diameters.

For histological analysis, segments of main stems (processed as described above) were removed and dehydrated through a tertiary butanol series to paraffin. After 2 changes of new paraffin, tissues embedded in paraffin were cut in cross or transverse sections with a microtome at 35 μ m. Tissue sections were placed on microscope slides and stained with safranin and fast green (Sass 1958).

Eccentric Measurements (Death of the Vascular Cambium)

Eccentric measurements were used to quantify the results of death of the vascular cambium (the area of first-year and area of second-year xylem) in stem segments. Measurements of cross-sectional tissues were made using an ocular scale with a microscope, and ocular measurements were converted to micrometers by use of a stage micrometer (AO catalog number 1400, American Optical, Southbridge, MA). In each stem cross-section, measurements of lengths of 8 radii were made at every 45° angle from the center of each stem sample. The radius length from the center of the stem to the vascular cambium (which is outside the second-year xylem) was subdivided into the radius of the (1) pith, (2) first-year xylem, and (3) second-year xylem. From these radius values, we used Microsoft Excel® (Windows XP, Microsoft Corp.) to first calculate the area of the pith, then the area of the first-year xylem, and finally the area of the second-year xylem. These files provided an area estimate for each radius length. The 8 area estimates for the pith, first-year xylem, and second-year xylem were used to calculate a mean area with a standard deviation for each tissue. A tissue was considered to be eccentric if the standard

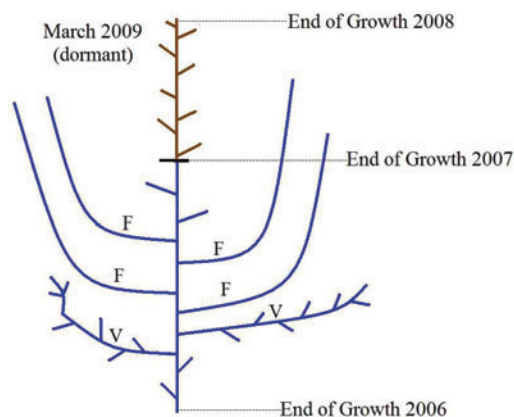


Fig. 1. Diagram of the proposed model of terminal stem growth of *Artemisia tridentata* ssp. *tridentata* for the end of the growing season for 2006, 2007, and 2008. During the growing season of 2008 (brown portion), the shoot terminal had produced 8 short branches. During the second growing season (blue portion), these 8 short branches produced 2 or 3 indeterminate, vegetative branches (V) and 4 or 5 determinate, flowering branches (F). These flowering branches die by the end of the second year.

deviation was 25% or more of the mean value for the 8 areas of a tissue.

Statistical Analyses

To compare eccentric growth among harvests, data from samples of pith, first-year xylem tissues, and second-year xylem tissues from late May until late September 2009 were examined by analysis of variance followed by a multiple range test (Zar 1974). For the 2010 comparisons between stems having normal determinate flowering branches and stems having the determinate branches removed prior to spring growth, data were analyzed with a Student's *t* test (Windows XP, Microsoft Corp.). Mean and standard deviations were calculated with Microsoft Excel® (Windows XP, Microsoft Corp.).

RESULTS

Morphology of Terminal Stems

Figure 1 shows the terminal stem with 2 years of growth, ending with a dormant vegetative stem at the end of 2008. Growth in 2008 produced 50–75 mm of terminal (first-year) growth with 6–9 new, short branches. The diameter at the base of this 2008 growth was about 1.50 mm (at “End of Growth 2007” location). Thus, first-year growth of a stem should

always resemble that between the labels “End of Growth 2007” and “End of Growth 2008” (see Fig. 1). During the growing year of 2008, short branches produced during the 2007 growing season produced several vegetative (indeterminate) branches and 3–8 flowering (determinate) branches. Some of the short branches produced in 2007 remained as vegetative branches that did not elongate significantly (upper portion of 2007 growth).

Figure 2 shows typical growth during the 2009 growing season. Fig. 2A shows that the stem terminal produced 2 or 3 new branches by June 2009, and 5 new branches were present during July 2009. By the beginning of July 2009, 4 or 5 flowering branches (F) produced during the 2008 growing season had started to elongate, while the first 2 branches of 2008 produced 2 vegetative branches (V). By August 2009, the flowering branches (F) were almost fully elongated (Table 1), but 2 vegetative branches (V) above the flowering branches of 2008 had elongated only slightly. About 5–8 branches were present above the first flowering branch. By November 2009, when growth for 2009 was completed, a total of 10 new branches had been produced. The 5 flowering branches produced in 2008 held hundreds to thousands of developed seeds, and the total length of stems in Fig. 2 was about 150–170 mm in November 2009. This process is reiterative in the sense that the first-year growth produces 5–10 new branches that remain short in their first year. Second-year branches elongate to make several indeterminate vegetative branches and 3–8 flowering (determinate) branches.

Association of Flowering Branches and Death of the Vascular Cambium

Figure 3 shows a stem cross-section with first-year xylem only. This tissue section was 1.6 mm in diameter and had an eccentric percentage of 17.8%, a value indicating moderate eccentric growth. The segment in Fig. 4 was 22 mm below the segment in Fig. 3. The sample in Fig. 4 had a diameter of 2.0 mm and had 2 years of xylem. This section had eccentric percentages of 19% and 34% for first-year and second-year xylem, respectively. The vascular cambium is absent, and there is little second-year xylem at the location of the insertion of the branch near the constriction “C.” The value of 34% for second-year xylem was typical of

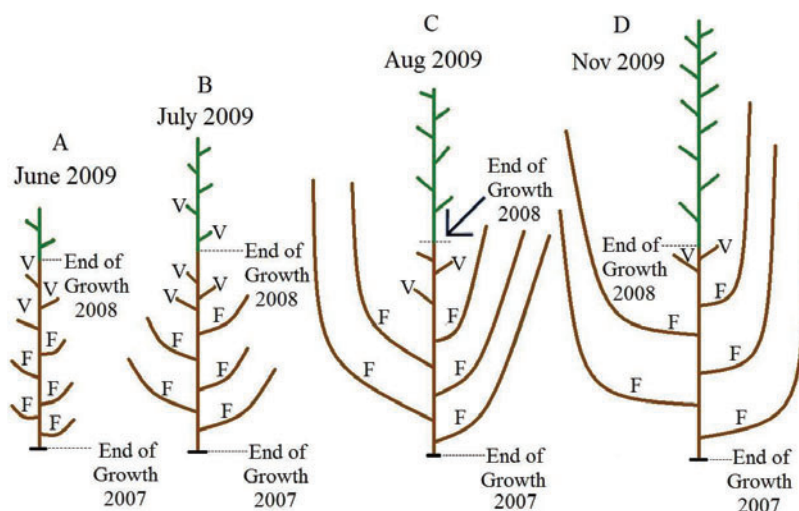


Fig. 2. Diagram of the proposed model of terminal stem growth of *Artemisia tridentata* ssp. *tridentata* for the 2009 growing season. The growth shown in Fig. 1 (brown portion) is shown here. The new terminal growth is shown in green. (Panel A) By June 2009, 2 new terminal branches have been produced. (Panel B) By July 2009, 4 branches have been produced for 2009. There has been elongation of 5 flowering branches (F). Note the presence of vegetative branches (V) that have not elongated much. (Panel C) By August 2009, a few more terminal branches have been produced. Flowering branches (F) have continued to grow longer. (Panel D) By November 2009, growth of the 5 flowering branches (F) has completed. The 10 small terminal branches are present. The dormant shoot for November 2009 should be similar to the shoot shown in Fig. 1, although year-to-year variations in numbers of new branches should occur.

eccentric growth of all samples. The sample in Fig. 5 was taken 41 mm below the section in Fig. 4. The segment in Fig. 5, with 3 years of growth, had a diameter of 2.6 mm and eccentric percentages of 16%, 30%, and 35%, respectively, for the 3 years of xylem. Note the lack of second-year and third-year xylem at the base of the flowering branch “B.” The eccentric growth caused by the death of the vascular cambium present in the second-year xylem is perpetuated in the third-year xylem. Death of the cambium is permanent, and the lack of xylem production will be exaggerated as the stems enlarge. Data associated with Figs. 4 and 5 show strong associations between death of the vascular cambium and dead flowering branches. No interxylary cork (layers of cork [bark] occurring between annual rings) was present in any of our samples. Presumably, it would be present in older tissues that were not used for this study (Moss 1940, Carlquist 1980).

Growth of second-year xylem was highly correlated with stem diameter growth. Data in Fig. 6 were taken randomly from 9 individual stems that ranged from 1.6 to 4.3 mm in diameter. Areas of second-year xylem were highly

TABLE 1. Characteristics of stems of *Artemisia tridentata* ssp. *tridentata* during the growing season of 2009. Within each column, values followed by different letters are significantly different by an analysis of variance followed by a multiple range test. Conversely, differences between values followed by the same letter are not statistically significant.

Day of year	Mean stem diameter (mm)	Length of first flowering branch (mm)
145	2.1 b	5.8 d
159	1.8 c	9.6 c
173	2.5 a	10.8 b, c
187	2.5 a	14.0 b
201	2.1 b	14.4 b
215	2.3 a, b	16.3 a
228	2.1 b	17.6 a
259	2.7 a	17.4 a

Fig. 3. Photomicrograph of a stem segment of *Artemisia tridentata* ssp. *tridentata* that shows pith (P), first-year xylem (X), and phloem-bark (B). The section does not show any eccentric behavior for first-year xylem. The section shows some microtome knife damage. Scale bar = 500 μ m.

Fig. 4. Photomicrograph of a stem segment of *Artemisia tridentata* ssp. *tridentata* that shows pith, noneccentric first-year xylem, eccentric second-year xylem, and phloem-bark. Note the constricted area (C) of the second-year xylem that is associated with a dead flowering branch, and the nonconstricted area (N) of the second-year xylem. Scale bar = 500 μ m.

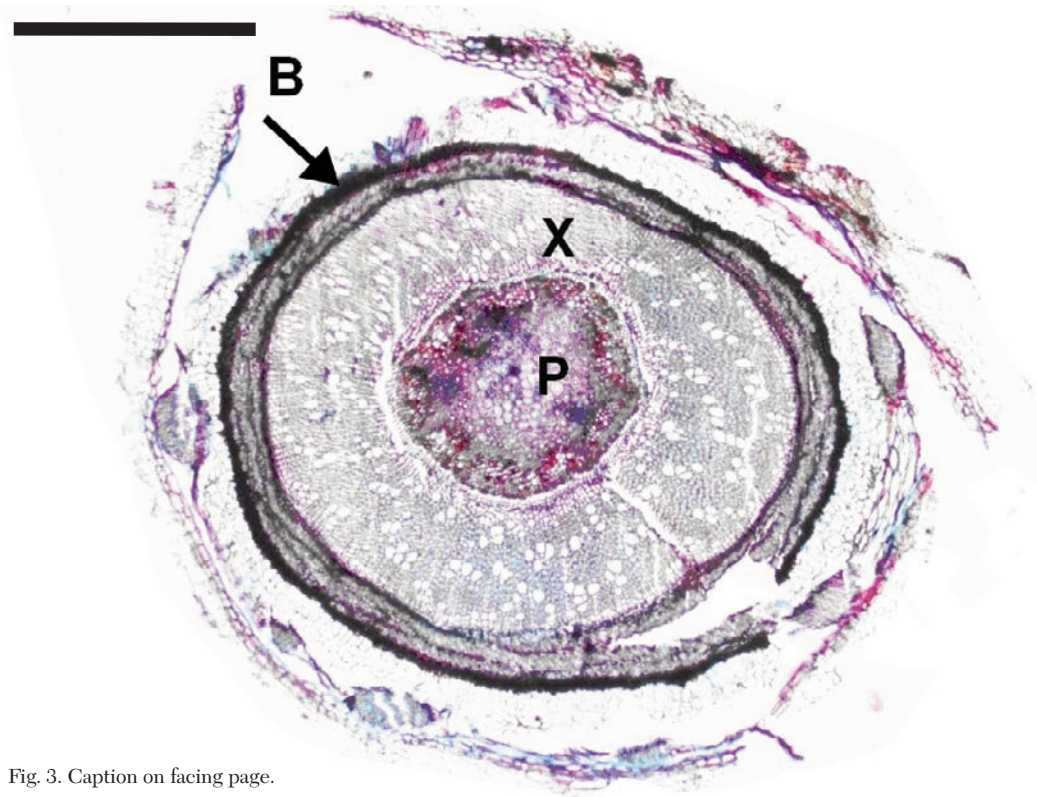


Fig. 3. Caption on facing page.

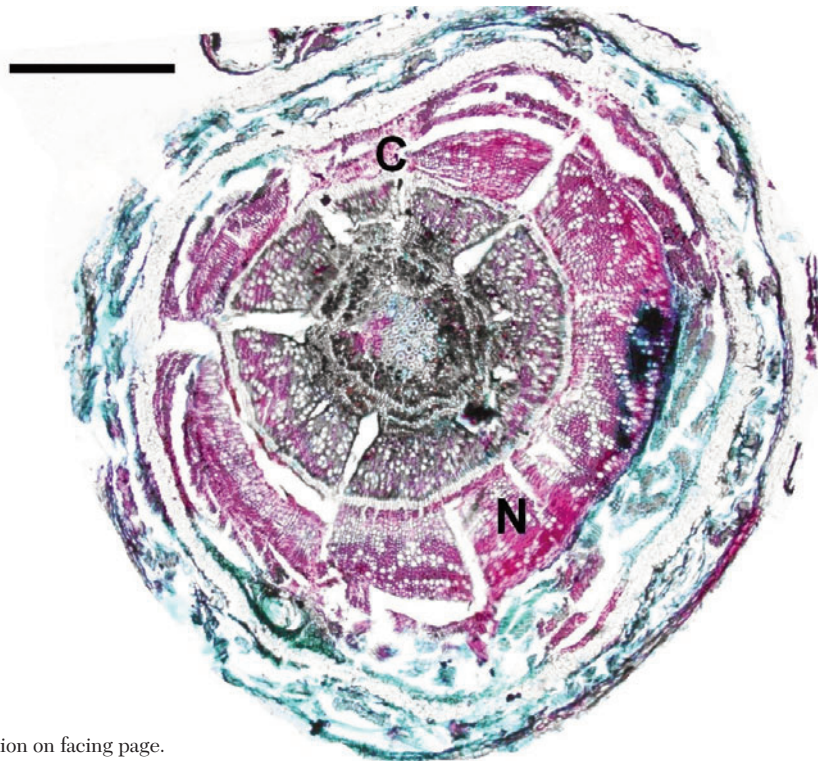


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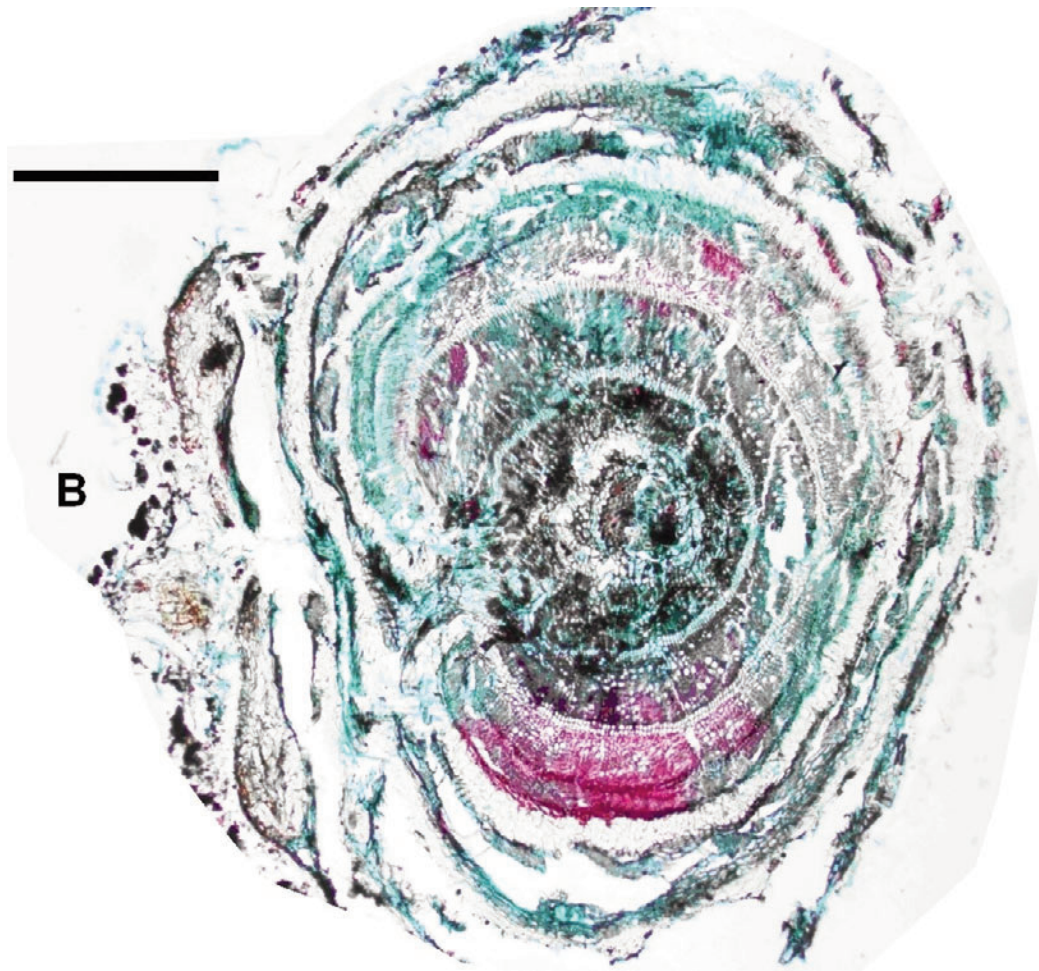


Fig. 5. Photomicrograph of a stem segment of *Artemisia tridentata* ssp. *tridentata*. Besides normal tissues, note the eccentric second-year xylem and eccentric third-year xylem. The constricted portions of xylem are associated with a dead branch (B). Scale bar = 500 μ m.

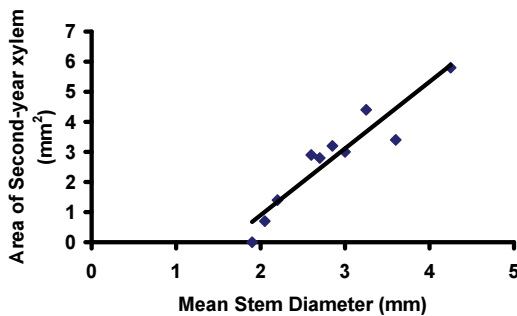


Fig. 6. Relationship between mean area of second-year xylem and mean stem diameter for stems of *Artemisia tridentata* ssp. *tridentata*. Each point is the mean of 12 samples. The equation of the line was $y = 2.12x - 3.28$; $r^2 = 0.90$.

correlated with stem diameter ($y = 2.1x - 3.3$; $r^2 = 0.90$). For these stems, growth of first-year xylem was complete when stems attained a mean diameter of 1.5 mm and when the maximum area of first-year xylem was about 0.70 mm². The second-year xylem started to form when stems attained a diameter of 1.5 mm.

If flowering branches are produced only on 2-year-old stem segments, (1) the main stem at the node of the first flowering branch must have a small amount of second-year xylem and (2) the main stem at the node of the last flowering branch must also have second-year xylem but no third-year xylem. Eight samples from 259 DOY (day of year) showed that (1) main stems (mean diameter = 1.9 mm) at the

TABLE 2. Areas of tissues within stem samples of *Artemisia tridentata* during 2009. Standard deviations are in parentheses. Within each column, values followed by different letters are significantly different by an analysis of variance followed by a multiple range test. Conversely, differences between values followed by the same letter are not statistically significant.

Day of year	Pith (mm ²)	First-year xylem (mm ²)	Second-year xylem (mm ²)	Bark (mm ²)	Total (mm ²)	First-year eccentric xylem (%)	Second-year eccentric xylem (%)
159	0.29 (0.12)	0.81 (0.45)	3.03 (1.03) c	1.77 (1.25) b	5.88 (2.63) c	12.45 (7.90)	13.91 (4.30) c
187	0.24 (0.11)	0.81 (0.29)	6.39 (2.08) b	2.61 (0.86) b	10.06 (2.70) b	11.38 (7.27) b	18.13 (6.17) b, c
201	0.18 (0.06)	0.63 (0.24)	7.87 (7.05) b	2.49 (1.06) b	11.17 (7.87) b	9.00 (5.51)	24.00 (5.16) b
215	0.16 (0.05)	0.37 (0.14)	6.66 (3.16) b	3.17 (3.12) a	10.36 (5.90) b	16.86 (5.01)	38.29 (14.07) a
228	0.30 (0.13)	0.64 (0.35)	8.25 (5.76) a	4.74 (2.22) a	16.2 (7.370) a	11.40 (6.20)	38.60 (14.21) a
ANOVA P values	0.066	0.130	0.002	0.015	0.013	0.068	<0.001

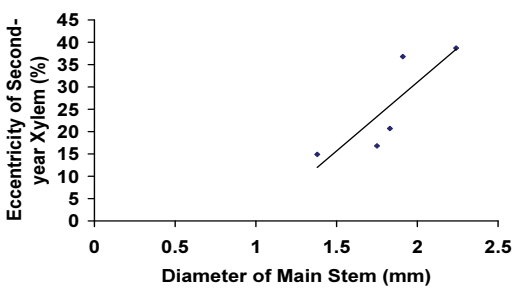


Fig. 7. Relationship between percentage of eccentric second-year xylem and diameter of main stem for stems of *Artemisia tridentata* ssp. *tridentata* during the 2009 growing season. Each point is the mean of 12 samples. The equation of the line was $y = 32.1x - 31.0$; $r^2 = 0.57$.

node of the uppermost flowering branch had an area of 3.2 mm² of second-year xylem while (2) main stems (mean diameter = 2.8 mm) at the node of the lowest flowering branch had an area of 7.2 mm² of second-year xylem and no third-year xylem. Thus, the determinate stems only produce flowers and then die. The main stems are indeterminate and continue to grow from year to year.

Analyses of stem tissue samples are shown in Table 2. Areas of the pith and first-year xylem did not change significantly over the period from 159 to 228 DOY. In contrast, the areas of second-year xylem and bark increased 350% and 269%, respectively, 159 to 228 DOY. Percentages showed that eccentric growth of second-year xylem is concomitant with development of flowering branches. Eccentric percentages of first-year xylem ranged from 9.0% to 16.9%, values not considered eccentric. In contrast, eccentric percentages of second-year xylem increased from 13.9% to 38.6% over the period. These data show that second-year xylem of samples from 215 (03 August) and 228 (16 August) DOY were eccentric, and the 24% value of 201 (20 July) DOY suggests that such stems are already nearly eccentric. Overall, eccentric growth of second-year xylem occurs as flowers and seeds develop in flowering branches. From 159 to 228 DOY, the percentage of second-year xylem was correlated with diameter of the main stem (Fig. 7; $y = 32.1x - 31.0$; $r^2 = 0.57$). Moreover, the results demonstrate that eccentricity was initiated during active growth of stems and not as flowering branches died near the end of the second-year growing season.

TABLE 3. Eccentric behavior in second-year stem tissues of *Artemisia tridentata*. Stems were harvested in September 2010.

Treatment	Eccentricity of second-year xylem (%)	
	Mean	SD
Flowering branches removed 05 April 2010	8.4	2.3
Flowering branches not removed	28.9	3.8
T-test <i>P</i> value	<0.01	

Removal of Flowering Branches

The presence of determinant flowering branches on main stems caused the death of the vascular cambium of second-year main stems (Table 3). For stems with only flowering branches removed prior to branch elongation, eccentric values were 8.4%. In contrast, when no branches were removed from stems (control samples), eccentric values were 36.9%. A *t* test showed that these treatments were different statistically ($P < 0.01$). These data also confirm that death of the vascular cambium is the cause of eccentric growth in second-year stems.

DISCUSSION

Past reports have shown that stems of *Artemisia tridentata* ssp. *tridentata* exhibited eccentric growth. The present study measures this eccentric growth as a method to quantify loss of the vascular cambium, since the cambium produces xylem tissues. Previous research by Ferguson and Humphrey (1959) showed that vegetative stems of *Artemisia* were eccentric, but their research did not attribute eccentric behavior to any causal agent. Older stem tissues exhibited in publications by Moss (1940) and by Ferguson and Humphrey (1959) showed eccentric growth with large amounts of interxylary cork in older stems.

The current research was centered on first-year and second-year stem tissues only. Second-year stems exhibited eccentric growth as a result of the death of the vascular cambium at the base of determinate, flowering branches. These second-year stems were usually <2.5 mm in diameter. This eccentric growth in second-year stems was localized at flowering stems only. In most cases, main stem tissues 5 mm above and below the branch node (inser-

tion of the branch) had no eccentric xylem. Thus, the effect of the death of determinate, flowering branches was localized in main stems. Moreover, no first-year or second-year stems of this study exhibited interxylary cork. Thus, eccentric growth is not associated with interxylary cork. The vascular cambium in these nodes is permanently lost, so the eccentric growth of second-year main stems is perpetuated in older stems (Diettert 1938, Ferguson and Humphrey 1959, Ferguson 1964).

For this study, we considered a stem to be eccentric if the standard deviation (SD) per mean percentage of radial xylem measurements was $\geq 25\%$. A comparable measurement of eccentricity was used by Love et al. (2009). Of course, horizontal branches of plants have reaction (compression and tension) wood (Mauseth 1998). The eccentric xylem of *A. tridentata* ssp. *tridentata* is not reaction wood since stems of *A. tridentata* are predominately vertical (Ferguson 1964). Overall, our criterion for eccentricity is reasonable, reproducible, and easy to measure.

Many other plant species show eccentric growth of some type (Fisher and Marler 2006). Horizontal branches of the cycad, *Cycas micro-nesica*, produce eccentric wood in the place of compression wood (reaction wood). Possibly other species do likewise. Eccentric growth in plants may result from reaction wood, loss of bark, death of the cambium, and possibly other causes.

Samples of this species and other *Artemisia* species that were obtained from other locations showed eccentric xylem occurring in second-year growth for (1) *Artemisia tridentata* ssp. *tridentata* from both Oreana, Idaho, and Ventucopia, California; (2) *Artemisia nova* from Eureka, Nevada; (3) *Artemisia filifolia* from Mexican Hat, Utah; (4) *Artemisia bigelovii* from the San Rafael Swell, Emery Co., Utah; and (5) *Artemisia tripartita* from Los Gatos Creek, Coalinga, California. However, the amounts of eccentric growth in the species/locations above were much lower than for *Artemisia tridentata* ssp. *tridentata* from the main site of this study. Eccentric growth was not found in the second-year xylem of stems of (1) *Artemisia spinescens* from Oreana, Idaho, or (2) *Artemisia tridentata* ssp. *parishii* from Rosamond, California. Eccentric xylem production appears to be a normal process for *A. tridentata* ssp. *tridentata* and, as mentioned above, is not a reaction wood

response (response to gravity). Overall, eccentric growth is a widespread phenomenon in young stems of many species of *Artemisia*, and, for all these species, the death of the vascular cambium was the cause of eccentricity.

To our knowledge, this study is the first to show the growth pattern of terminal stems of *Artemisia*. Overall, (1) terminal stems produce 8–11 small branches during the first year of growth, (2) 3–8 of the above branches develop as determinate, flowering branches during the second year of growth, (3) development of these determinate branches during the second year causes death of the vascular cambium at nodes of main stems, (4) death of the vascular cambium is the cause of the eccentric growth pattern in second-year stems, (5) death of the vascular cambium never occurred at the bases of indeterminate, vegetative branches, and (6) eccentricity caused by flowering branches occurs naturally in young stems of *A. tridentata* ssp. *tridentata*. Loss of cambium associated with the presence of flowering branches occurs annually in second-year stem segments in every branch of the flowering (upper) part of the plant. Thus, all major stems of the plant show eccentricity throughout their length. The overall effects of this extensive eccentricity must be very significant to growth and longevity. Some of the photographs of Diettert (1938) show a loss of 30% and 70% of xylem in older stems. Undoubtedly, this loss of wood leads to a reduced ability to transport water and nutrients, as well as a negative effect against mechanical stresses due to wind and snow loading. However, the small size of a shrub in comparison with that of a tree apparently makes these costs bearable under natural selection.

Woodiness appears to be primitive among flowering plants (Kim et al. 2004), and, as a result of the lengthy evolution of this lineage (Labandeira et al. 1994), the structure and physiology of woody plants shows much sophistication. However, these adaptations, being no longer necessary, have a tendency to be lost in taxa that become herbaceous, and, once the genetic basis for an adaptation has been lost, it might be a very long time before it can be regained, if ever. Thus, abnormalities of woody structure are expected in plants that have evolved woodiness secondarily, after having been herbs (Stebbins 1972, 1977, Bergh and Verbloem 2011). Although the Asteraceae prob-

ably came from ancestors that were shrubby (Lundberg 2009), much of the family is herbaceous, and *Artemisia* may have thus descended from ancestors that were not woody (Wang 2004). The anomalies of interxylary cork, as mentioned above, and eccentric xylem, apparently caused by a fragile vascular cambium, which is the subject of this paper, provide evidence that this scenario has been the case.

ACKNOWLEDGEMENT

We are grateful for the Catherine and Robert Fenton Endowed Chair to LSE for financial support for the research.

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Received 16 February 2012
Accepted 10 September 2012