



Longevity of Nonsprouting *Ceanothus*

Jon E. Keeley

American Midland Naturalist, Volume 93, Issue 2 (Apr., 1975), 504-507.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Midland Naturalist is published by University of Notre Dame. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/notredame.html>.

American Midland Naturalist
©1975 University of Notre Dame

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

Longevity of Nonsprouting *Ceanothus*

ABSTRACT: Evidence is presented indicating species of *Ceanothus* in the subgenus *Cerastes* are generally longer-lived than species in the subgenus *Euceanothus*. It is proposed that this is due, at least in part, to the unique stem morphology of the former. The stems of these plants have a ribbed appearance which arises when branches die. This longitudinal channeling results in less nonphotosynthetic tissue to support and an overall greater efficiency in competing for light and moisture in the chaparral.

A common assumption concerning the California chaparral has been that nonsprouting shrubs, *Ceanothus* species in particular, are short-lived and eliminated from the chaparral by the 3rd or 4th decade following fire (e.g., Lewis, 1961; Hadley, 1961; Patric and Hanes, 1964; Hanes and Jones, 1967; Hanes, 1971). Recently, evidence has been presented showing that the nonsprouting *Ceanothus greggii* var. *perplexans* can be an important part of the southern California chaparral even after 90 years (Keeley, 1973). Keeley pointed out that nonsprouting shrubs typically produce large numbers of seedlings and that as the shrub cover increases there is intense intra- and interspecific competition for light and moisture, so that heavy mortality reflects merely a thinning out of the population rather than a short life span. It is the purpose of this article to examine and discuss the adaptive significance of longevity of *Ceanothus* species.

In addition to the above instance of longevity in *Ceanothus*, there are a number of other cases. Hanes (1971) showed that in southern California the nonsprouting *C. crassifolius* as well as *C. greggii* var. *vestitus* increased in percent cover from the 22-40 year age class to the 41-96 year age class. Hedrick (1951) found *C. cuneatus* to be an important part of the chaparral after 100 years in northern California, and Delting (1961) considered this species to be the climax shrub on xeric slopes of southern Oregon. Personal observations have also shown the nonsprouting *C. verrucosus* to be frequent in climax chaparral. However, there are also data to suggest that some *Ceanothus* species are short-lived. For example, the nonsprouting *C. oliganthus* (Hanes and Jones, 1967) and *C. tomentosus* var. *olivaceus* (P. H. Zedler, California State University, San Diego, pers. comm.) seem to be eliminated within 2-4 decades following fire. In addition, Hanes (1971) shows the sprouting *C. leucodermis* is all but eliminated from the chaparral after 40 years, as is the sprouting *C. velutinus* (Zavitkovski and Newton, 1968) and *C. integerrimus* (Cronemiller, 1959). Thus, it seems that although some nonsprouting species may be long-lived, other nonsprouting as well as sprouting species may be quite short-lived (for further discussion, see Keeley, 1973).

A pattern seemingly exists in that these apparently short-lived *Ceanothus* are all in the subgenus *Euceanothus*, and the species for which there is any evidence of longevity are in the subgenus *Cerastes*. I suggest that those *Ceanothus* species in the entirely nonsprouting subgenus *Cerastes* are generally better adapted to competing in mature chaparral and, unlike many in the other section, are seldom entirely eliminated from older chaparral. In addition, I propose that the ability of these species to compete in mature chaparral is related to their unique and peculiar stem morphology.

The stems of these species have a ribbed appearance which arises when branches die (Fig. 1). That is, when a branch dies it exerts a depressant influence on the adjoining xylem tissues of the main stem both above and below the base of the branch and extending vertically up and down the trunk. In older and denser stands of chaparral this becomes so pronounced that stems often are nearly flat, with only a single strip of live tissue. This "longitudinal

fissioning" of the stem was first described by Jepson (1928) for *C. cuneatus*; he did not speculate as to its adaptive significance, although later (Jepson, 1939) he stated it was "doubtless caused by some pathogenic organism." I have found this stem morphology in *C. cuneatus*, *C. greggii*, *C. verrucosus*, *C. insularis*, *C. crassifolius* and *C. megacarpus* and expect it to occur in the rest of the species in the *Cerastes* section. This widespread occurrence, coupled with the tendency for stem channeling to be more extreme in denser and older stands of chaparral, as well as the fact that no pathogenic organism has ever been found, suggests there is some selective advantage to it.

The advantage to the plant would be a competitive edge on two of the most limited resources in the chaparral: light and moisture. In very dense chaparral, leaves and, consequently, branches of *Ceanothus* in less illuminated parts of the canopy are aborted (Jepson, 1939; McPherson and Muller, 1967). This results in reducing transpirational losses by less productive leaves, so that the plant is



Fig. 1.—Twenty-year-old *Ceanothus greggii* var. *perplexans* showing longitudinal channeling of stem

able to take advantage of small openings in the canopy of the chaparral without having to support branches in less favorable locations. The dead sections of these plants may in part account for the notion of some authors that these shrubs are dying out.

The adaptive role of the unique stem morphology is that when a branch dies the entire vertical section of the main stem dies, reducing the amount of photosynthetic products needed to maintain the shrub. Very old shrubs often will have only a single live branch connected by a single strip of living tissue. This sort of growth pattern does not result in an ever-increasing volume of nonphotosynthetic tissues to maintain—as is the case with symmetrical stemmed shrubs—so that older plants can maintain a somewhat constant ratio of photosynthetic to nonphotosynthetic tissues. A functionally similar phenomenon has been described for *Pinus aristata* (Wright and Mooney, 1965) and for several nonsprouting *Arctostaphylos* species (Davis, 1973). In both of these instances this process was considered to be the primary factor responsible for longevity in these species.

In addition to originating from shaded branches, it is likely this process may be initiated by roots under high water stress. Waisel *et al.* (1972) have shown that many arid land shrubs have a sectorial pattern of water movement such that a single root connects to a single branch. This has also been shown, using radioactive tracers, to be true for some chaparral shrubs (S. C. Keeley, University of Georgia, pers. comm.) and is likely the case in *Ceanothus*. If so, then a root under water stress would abort only one branch. The section of the main stem connected to this aborted branch would also then die leaving the living parts of the plant free to support only their portion of the trunk.

This strategy of aborting branches in less favorable sections of the canopy and those connected to roots in less favorable sections of the soil may be of particular significance to nonsprouting shrubs; for as light and moisture availability decreases, seed production also decreases (Whittaker, 1962; Harvey and Mooney, 1964). Since nonsprouting shrubs are dependent upon seedlings following fire, selection would favor those shrubs which were the more efficient seed-producers. In addition, if values for seed predation in the chaparral are typically as high as 80%, as indicated by data from Keeley (1973), or the longevity of seed viability under field conditions as low as that found by Went (1969), there would be selection for those nonsprouting shrubs capable of sustained seed production. Longitudinal fissioning has likely evolved in these *Ceanothus* species in response to just such selection pressures.

LITERATURE CITED

- CRONEMILLER, F. B. 1959. The life history of deerbrush. A fire type. *J. Range Manage.*, **12**: 21-25.
- DAVIS, C. B. 1973. "Bark striping" in *Arctostaphylos* (*Ericaceae*). *Madrono*, **22**: 145-149.
- DELTING, L. E. 1961. The chaparral formation of southern Oregon with consideration of its post-glacial history. *Ecology*, **42**: 348-357.
- HADLEY, E. B. 1961. Influence of temperature and other factors on *Ceanothus megacarpus* seed germination. *Madrono*, **16**: 132-138.
- HANES, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.*, **41**: 27-52.
- AND H. W. JONES. 1967. Postfire chaparral succession in southern California. *Ecology*, **48**: 259-264.
- HARVEY, R. A. AND H. A. MOONEY. 1964. Extended dormancy of chaparral shrubs during severe drought. *Madrono*, **17**: 161-163.
- HEDRICK, D. W. 1951. Studies on the succession and manipulation of chamise brushlands in California. Ph.D. Thesis, Texas A & M College, College Station. 113 p.

- JEPSON, W. L. 1928. Biological peculiarities of California flowering plants—I. *Madrono*, **1**:190-192.
- . 1939. A flora of California. 3 Vol. Associated Students Stores, University of California.
- KEELEY, J. E. 1973. The adaptive significance of obligate-seeding shrubs in the chaparral. M.S. Thesis, California State University, San Diego. 79 p.
- LEWIS, F. H. 1961. Chaparral lands of southern California, p. 13-17. *In*: A. Macey and J. Gilligan (eds.). Man, fire and chaparral—a conference on southern California wildland research problems. Univ. Calif. Agric. Publ., Berkeley.
- MCPHERSON, J. K. AND C. H. MULLER. 1967. Light competition between *Ceanothus* and *Salvia* shrubs. *Bull. Torrey Bot. Club*, **94**:41-55.
- PATRIC, J. H. AND T. L. HANES. 1964. Chaparral succession in a San Gabriel mountain area of California. *Ecology*, **45**:353-360.
- WASEL, Y., N. LIPSCHITZ AND Z. KULLER. 1972. Patterns of water movement in trees and shrubs. *Ibid.*, **53**:520-523.
- WENT, F. W. 1969. A long term test of seed longevity. II. *Aliso*, **7**:1-13.
- WRIGHT, R. D. AND H. A. MOONEY. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains, California. *Am. Midl. Nat.*, **73**:257-284.
- WHITTAKER, R. H. 1962. Net production relations of shrubs in the Great Smoky Mountains. *Ecology*, **43**:357-377.
- ZAVITKOVSKI, J. AND M. NEWTON. 1968. Ecological importance of snowbrush, *Ceanothus velutinus*, in the Oregon Cascades. *Ibid.*, **49**:1134-1145.
- JON E. KEELEY, Department of Botany, University of Georgia, Athens 30602. Submitted 15 January 1974; accepted 18 March 1974.

A Method for Preparing and Sectioning Mink (*Mustela vison*) Mandibles for Age Determination¹

ABSTRACT: Techniques of preparation and sectioning of mink mandibles for use in age determination are reported. Data from three known-age animals indicate that age in years equals the number of annuli. Ages of 31 wild mink ranged from age class 1 to age class 4.

Klevezal and Kleinenberg (1969) have reviewed aging techniques by use of annual rings in teeth and bone in nine mammalian orders. They found that mink could be aged by using sections of teeth or mandibles. In our study we modified their method for preparing and sectioning mandibles by adapting techniques from successful studies on teeth in other species. To verify the validity of aging by use of annual rings in mandible sections as described by Klevezal and Kleinenberg (1969), and to familiarize ourselves with the application of the modified technique, we checked the number of mandibular annuli in three known-age ranch mink. Then the modified method was applied in aging a sample of wild Iowa mink collected previously for another study.

Klevezal and Kleinenberg (1969) sectioned mandibles by cutting and polishing the bone with grindstones, or by decalcification and sectioning with a freezing microtome. With the equipment at our disposal, we found it easier to get uniformly thin sections by embedding the decalcified bone and sectioning with a rotary microtome. The method we used began with decalcification of the mandibles in a solution of 40% formaldehyde solution:formic acid:water

¹Journal Paper No. J-7635 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 1844. Financial support was provided by Public Health Service Research Grant ES-00205 from the National Institute of Environmental Health Sciences, and North Central Regional Project NC-96.