Torrey Botanical Society

Is Slow Growth of the Endangered Torreya taxifolia (Arn.) Normal?
Author(s): Mark W. Schwartz and Sharon M. Hermann
Source: *Journal of the Torrey Botanical Society*, Vol. 126, No. 4 (Oct. - Dec., 1999), pp. 307-312
Published by: Torrey Botanical Society
Stable URL: http://www.jstor.org/stable/2997314
Accessed: 09/02/2015 14:10

Journal of the Torrey Botanical Society 126(4), 1999, pp. 307–312

Is slow growth of the endangered *Torreya taxifolia* (Arn.) normal?

Mark W. Schwartz

Department of Environmental Science and Policy, University of California, Davis, CA 95616

Sharon M. Hermann

Tall Timbers Research Station, P.O. Box 678, Route 1, Tallahassee, FL 32312

SCHWARTZ, M. W. (Department of Environmental Science and Policy, University of California, Davis, CA 95616), and S. M. HERMANN (Tall Timbers Research Station, Tallahasee, FL 32312). Is slow growth of the endangered *Torreya taxifolia* (Arn.) normal? J. Torrey Bot. Soc. 126:307–312. 1999.—*Torreya taxifolia* (Arn.), an endangered conifer, is believed to be failing in its environment because of poor growth. Poor growth has been hypothesized to be a result of disease infection, yet a primary disease agent has remained elusive. We compared the growth of *T. taxifolia* to a close congener, *T. californica* (Torrey), to determine if *T. taxifolia* is growing less vigorously in its environment than would be expected under the assumption that the two species should exhibit similar growth patterns. We found that growth patterns do not statistically differ between the two species although *T. taxifolia* shows a slightly higher growth than *T. californica* by most measures. With no reason to believe that *T. californica* is failing in its environment, we cannot reject the hypothesis that the currently observed patterns of growth in *T. taxifolia* are normal for this species. Tree rings were sampled from dead and downed logs that date from the time of the decline. Tree rings show frequent periods of suppression and release consistent with a tree responding to variation in light. In addition, trees planted in high light treatment expanded a terminal bud and grew in height more frequently than those in low light treatments. Our results are consistent with the hypothesis that low light is a primary environmental feature limiting growth in *T. taxifolia.* These observations argue against, but do not reject, the hypothesis that low growth rate is a result of disease stress.

Key words: *Torreya,* conifer, endangered, population, demography, species decline.

Torreya taxifolia (Arn.), a dioecious conifer on the federal endangered species list (USFWS 1986), is endemic to ravine forests along a 35 km stretch of the Apalachicola River in northern Florida and adjacent Georgia (Godfrey 1988). Formerly abundant within this distribution, the current population is estimated to be approximately 1000 individuals (USFWS 1986). The cause of a late-1950's decline that decimated the population remains a mystery (USFWS 1986; Schwartz et al. 1995). Although a fungal disease was implicated in the decline (Godfrey and Kurz 1962; USFWS 1986), and numerous fungal associates have been identified (Alfieri et al. 1994), a primary disease agent remains lacking (Schwartz et al. 1995). Early reports of *T. taxifolia* are unclear regarding the onset of decline; by 1962, mature trees are reported to have all but disappeared (Godfrey and Kurz 1962).

Populations of *T. taxifolia* have failed to recover during the 35 years since the 1960s decline (Schwartz and Hermann 1993). It is unknown if disease continues to limit population recovery, or if recovery is limited by other attributes such as low growth rates in the current low light environments of ravines (Schwartz et al. 1995). Current populations are characterized primarily by small (< 2 m tall) individuals that are failing to achieve reproductive maturity (Schwartz and Hermann 1993). There are no known seed bearing adult females in the wild at the present time. A perceived problem in *T. taxifolia* recovery is that, currently, trees typically extend a terminal bud on main shoots in alternate years. It is not known how frequent terminal bud expansion may have been prior to the decline. The poor growth of *T. taxifolia,* as evidenced by a low frequency of terminal bud expansion, has been hypothesized to be symptomatic of disease (Schwartz 1990). Alternatively, current low growth rates may be a symptom of changing forest management practices. Cessation of selective harvest within ravine forests, combined with fire suppression since the 1950's, has allowed a dense young forest canopy to dominate over *T. taxifolia* juveniles (Schwartz et al. 1995). Both ambient light levels and the frequency of gap formation are likely to be lower at the present time than they were prior to the decline. Thus, growth suppression may be limiting the recovery of this endangered species.

Greenhouse experiments suggested that the low light typical of understory habitats limits growth in *T. taxifolia* (Schwartz et al. 1995). Physiological studies of the light response of T.

Received for publication February 26, 1999 and in revised form July 8, 1999.

taxifolia indicates that it may well tolerate higher light conditions than those characterizing the current habitat (Koehn and Doudrick 1999). Lacking a specific disease agent, we proposed that low light may be the principle feature currently limiting growth of *T. taxifolia* (Schwartz et al. 1995).

In this paper we use: 1) growth patterns of a closely related congener, *T. californica*; 2) growth from a experimental planting of *T. taxifolia*; and 3) tree ring data from dead *T. taxifolia* to assess the hypothesis that light, and not disease, may be functionally limiting growth of this endangered species.

Methods. *Torreya californica,* the only North American congener of *T. taxifolia,* grows patchily on moderately mesic, mid-elevation, slopes of the Sierra Nevada and Coast Ranges in California (Hickman 1993). Growth patterns of *T. californica* may provide clues regarding the normal growth patterns of *T. taxifolia.* We have collected growth information for over 100 *T. taxifolia* individuals during our population censuses conducted from 1989 to 1998. To compare growth patterns we surveyed 65 *T. californica* in coast range (R.L. Stephenson State Park, Napa County) and Sierran populations (Feather Falls National Recreational Trail, Butte County). We do not know whether these trees are from seed or if they are resprouts. Neither species exhibits obvious signs that an individual is a stem sprout or a first generation stem from seed. Morphologically, the *T. californica* we surveyed were very similar to the *T. taxifolia* in terms of total height, number of stems and number of side branches. Surveys of *T. californica* were conducted shortly after bud break (18–19 May 1998) so that new growth on terminal buds was readily identifiable. Repeat surveys of tagged individuals provided a measure of the frequency of terminal bud expansion in *T. taxifolia.* To estimate long-term bud expansion frequency we measured the ratio of lateral internodes from branch points along the main stem to terminal internodes above that point. Under the assumption that lateral branches expand a bud each year, this ratio estimates the frequency of terminal growth. We have observed that lateral branches of *T. taxifolia* expand lateral internodes more frequently than terminal internodes, although we do not know if they expand internodes in every year. If lateral branch buds do not expand every year, then our estimate of the frequency of terminal bud expansion is an overestimate of growth frequency along the main stem.

To estimate long-term primary stem growth rates we measured: 1) internode lengths of the amount of terminal growth for the previous three to five years worth of growth; 2) total tree height; 3) basal diameter of the principle stem; and 4) the apparent age, as evidenced by the number of internodes present on the main stem. We compared height and basal diameter to estimated age to derive a lifetime growth rate function. We estimated the age of trees by dividing the apparent age of the main stem by the mean frequency of terminal bud expansion. Thus, age estimates reflect the indeterminant nature of bud expansion.

In the late winter of 1996 an experiment was initiated to examine the role of light in growth of *T. taxifolia.* Three replicated blocks were planted with 10 trees in high light environments and 10 trees in nearby low light environments. The high light treatment was created by cutting canopy gaps above plots. Plant material was grown from cuttings in the greenhouse. Plants ranged from 15 to 50 cm tall and most had established apical dominance. Unfortunately, the planting was followed by a very dry spring and the mortality rate of trees in the experiment was high. By June 1997 only 6 trees in high light environments and 11 trees in low light environments in just two of the locations remained of the 60 trees originally planted. Nonetheless, we surveyed growth of these 17 trees for 1997 and report the results here.

Tree rings provide a historical record of growth with which to assess the role of periodic intervals of high light on the maturation of trees. Despite the fact that sampling of live *T. taxifolia* is not possible because there are no trees in the wild large enough to core without danger of stem damage, there are samples available from dead and downed logs from which to reconstruct growth patterns. The wood of *T. taxifolia* decays slowly and some downed and dead wood remains intact from the decline in the 1950s. Cross-cut sections from five logs, along with increment cores from an additional 13 logs were analyzed. All sampled logs were between 10 and 20 cm diameter at their base. Samples were collected from downed and dead trees that likely date from the time of the decline. Tree samples were collected from across the entire 35 km span of the species distribution (Fig. 1).

Cross-sections and cores were sanded and tree ring growth increments measured using a 40

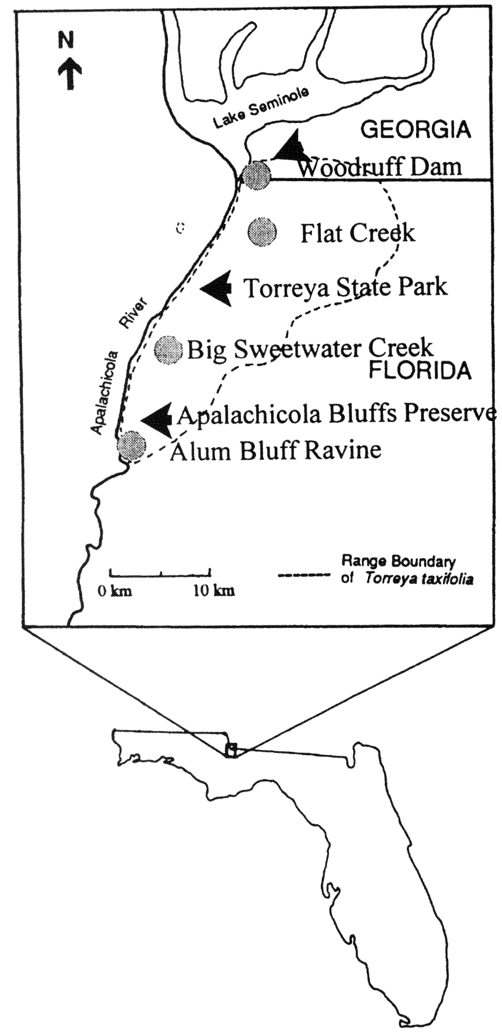

Fig. 1. The approximate distribution of *Torreya taxifolia* showing locations where tree ring samples were collected (circles). Arrows indicate populations of extant trees in reserves.

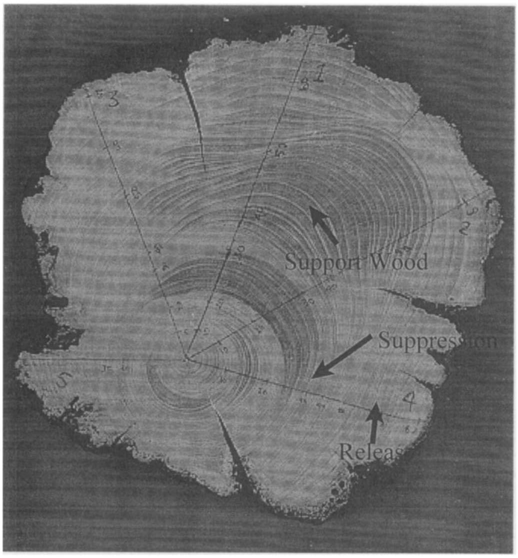

Fig. 2. Scanned image of a *Torreya taxifolia* cross-section. Note that 1) there is substantial variation in ring width patterns for rings of similar ages around the circumference of the tree; 2) there is a the concentration of dark bands between transects 1 and 2; and 3) the center of the tree is not located near the center of the cross-section.

power dissecting microscope and a Henson movable stand (Fred C. Henson Instruments, Mission Viejo, CA). Ring widths on cross-sections were measured on four or five transects from the perimeter to the center of each section. *Torreya taxifolia* trunks are characterized by uneven tree rings around the center of a tree (Fig. 2). The uneven center and heavily colored areas with thickened rings represents allocation toward structural support tissue and is commonly observed in trees growing on steep slopes (Cook and Kairiukstis 1990). Typically, dendrochronologists fit tree ring widths to a curve to extract patterns of decreasing ring width with increase size and age of trees so that standardized tree

Table 1. Summary statistics comparing growth frequency and amount for *Torreya taxifolia* and *T. californica.*

	Torreya taxifolia		*Torreya californica*		
	Mean (s.d.)	n	Mean (s.d.)	n	Probability (test)
Growth Frequency					
Proportion of trees with expanding terminal buds	0.482	734	0.438	64	0.516 (Fisher's exact)
Terminal internodes/lateral internodes	0.528 (.160)	101	0.456 (.160)	67	0.007 (t-test = 2.761)
Growth Amount					
Main stem internode length (cm)	9.31 (3.85)	132	9.71 (4.56)	63	0.543 (t-test = 0.610)

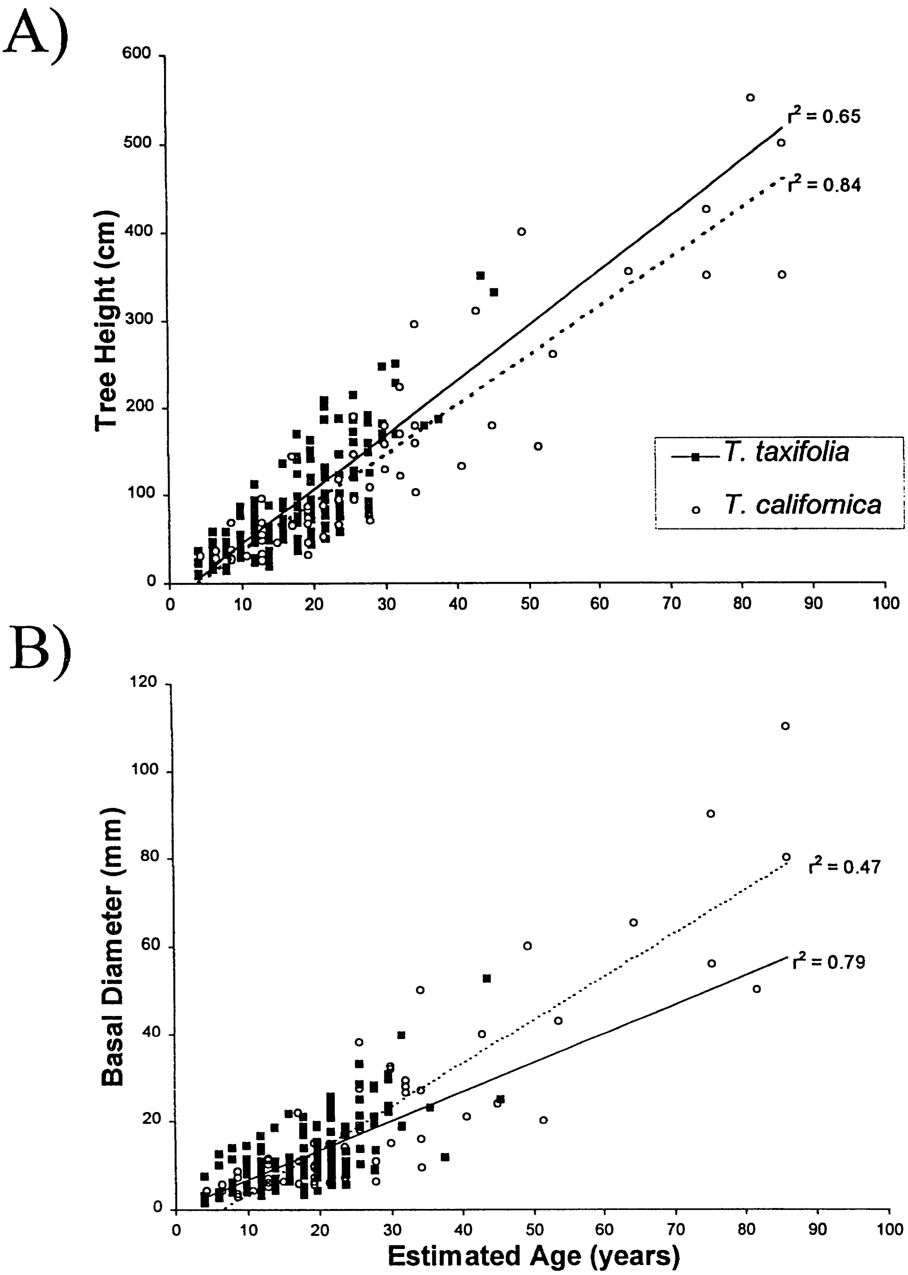

Fig. 3. Scatter plots of estimated tree age versus A) tree height and B) basal diameter for *Torreya taxifolia* and *T. californica*. Fitted lines are least square regression lines for *T. taxifolia* (solid line) and *T. californica* (dashed line).

ring measurements may be compared within and among trees independent of specific growth rates (Cook and Kairiukstis 1990). In the case of *T. taxifolia,* we did not fit ring width series to size curves because there was no evidence that ring widths systematically decrease with tree size. In fact, ring widths fit a pattern of declining ring width with tree size in just two of the 18 samples collected for this work. Thus, ring widths were standardized within increment bores and cross-sections by dividing each ring width by the mean for that series. We defined a "release" as any three consecutive years of growth that exceeded the mean. Periods of release terminated

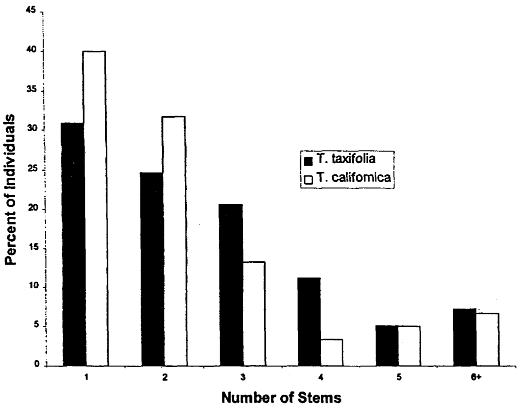

Fig. 4. A histogram of the number of stems per individual for *Torreya taxifolia* (dark bars) versus *T. californica* (open bars). Both species have similar profiles with respect to the number of stems per individual tree.

when two or more consecutive growth rings did not fall above the mean.

Results and Discussion. Most measures of growth collected for comparison indicate that *T. taxifolia* grows similarly to *T. californica.* Out of 64 *T. californica* surveyed, 28 (43.8%) expanded a terminal bud in 1998, a frequency of growth that is comparable to *T. taxifolia* for the period of 1989 to 1996 (48.2%, Table 1). A comparison of the number of terminal internodes above the oldest living lateral branch, and the number of lateral internodes on that lateral branch closely approximates the growth frequencies estimated above. In this case, however, the estimated frequency of terminal bud expansion is significantly higher in *T. taxifolia* than *T. californica* (Table 1). Comparing the amount of terminal growth over the past five episodes of terminal growth likewise indicates little difference between the species (Table 1).

Our assessment of total plant performance demonstrates only slightly different growth patterns between species. A regression of tree height or basal diameter by estimated age for these species shows that both species exhibit a good fit between size and age variables. *Torreya taxifolia* has a slightly, although not significantly ($p = 0.18$), higher rate of height growth by age (Fig. 3a). In contrast, *T. californica* has a significantly higher rate of basal diameter growth with age than *T. taxifolia* (Fig. 3b, $p < 0.001$). Differences in slope were tested using the General Linear Model of SYSTAT 7.0 testing for effects of age, species, and an age by species interaction for both height and diameter.

A final observation collected for comparison was the number of stems per individual. Owing to the fact that stem sprouts appear to remain suppressed by the main stem and never become independent ramets, basal sprouts in *T. taxifolia*

Table 2. The number of identified growth release periods, average duration, interval between releases, age of first release, and average radial ring width for 18 *Torreya taxifolia* tree ring samples.

Tree sample	Number of releases	Average duration	Interval between releases	Age of first release	Mean ring width (mm)
Cross sections					
Big Sweetwater #1	2	10.5	29.0	14	0.72
Big Sweetwater #2	3	7.3	20.7	26	0.92
Alum Bluff ravine #1	1	18.0	—	1	1.28
Alum Bluff ravine #2	2	7.0	22.0	29	0.87
Alum Bluff ravine #3	1	12.0	—	17	1.06
Tree cores					
Woodruff dam rav. #1	0	—	—	—	5.10
Woodruff dam rav. #2	2	6.0	29.0	1	1.24
Woodruff dam rav. #3	1	17.0	—	21	1.55
Woodruff dam rav. #4	2	7.0	19.5	26	1.80
Woodruff dam rav. #5	1	4.0	—	31	1.08
Flat Creek ravine #1	2	4.0	9.5	4	1.75
Flat Creek ravine #2	1	6.0	—	1	1.76
Big Sweetwater #1	2	7.5	15.5	19	3.60
Big Sweetwater #2	3	7.3	13.7	4	2.70
Big Sweetwater #3	1	3.0	—	1	1.36
Alum Bluff ravine #1	1	1	—	1	1.07
Alum Bluff ravine #2	2	10.5	11.5	5	1.55
Alum Bluff ravine #3	2	10.5	45.0	21	0.93
Average	1.6	7.8	21.5	11.7	1.69

may be a stress response. We compared the stem number profiles of our sample for *T. californica* to our census population of *T. taxifolia* and find, again, that the two species are quite similar (Fig. 4). *Torreya taxifolia* has fewer single and two stemmed trees (Kolmogorov-Smirnov two sample test, maximum difference = 0.207; p = 0.071).

Our results of the high/low light planting experiment showed significantly (p = 0.035, Fisher's exact test) higher growth frequencies in high light treatments. All six trees in high light treatments expanded a terminal bud in 1997, compared to just 4 of 11 (36.4%) trees in the low light treatment. Despite the fact that these results are very preliminary, they support the contention that increasing incident light levels increases growth rates.

Among the eighteen tree ring samples, all but one showed evidence of suppression and growth release (Table 2). The single tree that did not had the highest mean growth rate of all trees (Table 2). Most trees demonstrated between 1 and 3 periods of release, where periods of release averaged 7.8 years (Table 2).

In aggregate, the results of this work suggest that the observed low growth rates of *T. taxifolia* might not be indicative of disease-induced stress. The similarity between *T. taxifolia* and *T. californica* growth rates and patterns is consistent with the hypothesis that *T. taxifolia* is growing normally within its environment. The infrequent expansion of terminal buds may simply be the way that these trees naturally grow in low light environments. Evidence of suppression and release growth pattern in tree rings, along with a preliminary observation that trees in high light environments grow more frequently than those in low light, support the hypothesis that growth in *T. taxifolia* is light limited. Given the continued lack of an identified primary disease agent, we recommend pursuing further tests of the light limitation hypothesis, and management to increase light levels above extant trees in the wild.

Literature Cited

ALFIERI, S. A. JR., K. R. LANGDON, J. W. KIMBROUGH, N. E. EL-GHOLL AND C. WEHLBURG. 1994. Diseases and Disorders of Plants in Florida. Bulletin #14, Florida Dept. of Asgriculture and Consumer Services, Gainesville, FL.

COOK, E. R. AND L. A. KAIRIUKSTIS. 1990. Methods of Dendrochronology: Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht, Netherlands.

GODFREY, R. K. 1988. Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia and Alabama. Univ. of Georgia Press, Athens.

GODFREY, R. K. AND H. KURZ. 1962. The Florida torreya destined for extinction. Science 136: 900–902. HICKMAN, J. C. 1003. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley.

HICKMAN, J. C. 1003. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley.

KOEHN, A. C. AND R. L. DOUDRICK. 1999. Diurnal patterns of chlorophyll fluorescence and CO2 fixation in orchard grown Torreya taxifolia (Arn.). J. Torrey Bot. Soc. 126: 93–98.

SCHWARTZ, M. W. AND S. HERMANN. 1993. The continuing population decline of *Torreya taxifolia* Arn. Bulletin of the Torrey Botanical Club 120: 275–286.

SCHWARTZ, M. W., S. M. HERMANN AND C. S. VOGEL. 1995. The catastrophic loss of Torreya taxifolia: assessing environmental induction of disease hypotheses. Ecological Applications 5(2): 501–516.

SYSTAT 7.0. SPSS Inc. Chicago, IL.

U. S. FISH AND WILDLIFE SERVICE. 1986. Florida torreya, *Torreya taxifolia* recovery plan, Atlanta, GA, United States Fish and Wildlife Service.