A-

Morphology of *Torreya taxifolia* Arn.

Lee Barnes

HOS 6112

December 1983

Introduction

Torreya taxifolia Arn.(Taxaceae)(Stinking Cedar, Polecat wood, Gopherwood, Savin, Tumion) is a medium sized, pungent-smelling evergreen tree which is now endemic to the bluffs and ravines along a 20 mile section of the Apalachicola River in the Florida panhandle. *Torreya* spp. were much more common and widely distributed in earlier geological times (Cretaceous through Pliocene) with fossil evidence indicating circumpolar distribution throughout the northern hemisphere.(Boeshore & Gray 1936). Major climatic changes during the last 25 million years (Daubenmire 1978) has resulted in the withdrawal, isolation and speciation of *Torreya* spp.(Boeshore & Gray 1936) Presently six species are known from widely disjunct populations. (*T. taxifolia*-Florida; *T. californica*-California; *T. nucifera*-Japan; *T. grandis*, *T. fargesii*, and *T. jackii*-China)(Burke 1975)

The Florida *Torreya* has persisted in its present location for perhaps five to ten million years (Daubenmire 1978) and has long been the object of botanical curiousity and pilgramage. The present natural population is threatened with extinction due to a fungal needle and twig blight which nearly destroyed the native stands in the late 1950's.(Godfrey & Kurz 1962, Alfieri et al 1967) Presently only diseased juvenile seedlings and basal sprouts (less than three meters) from dead trunks remain with a surveyed population of approximately 1200 individuals. These shoots grow irregularly for an estimated 10-20 years, but as they begin to mature they die completely back. No seed production in the wild has been observed for a number of years although a few plants in cultivation have yielded several hundred seeds during the last two years.

Apparently healthy extant specimums of Torreya taxifolia occur in private ornamental plantings outside of Florida. These trees are highly prized for their ornamental characteristics and could conceivably be saved from extinction by being more widely introduced into the horticultural trade. Their limited horticultural use appears to be due to insufficient understanding of their cultural requirements, propagation techniques and disease control. The purpose of this report is to clarify the botany and morphological development of Torreya and to relate morphology to horticultural manipulation.

Botany

Torreya taxifolia is a slow growing, medium sized evergreen tree with healthy individuals growing to 60 feet in height, with a trunk diameter of one to two (occationally three) feet in diameter. The tree generally develops a conical crown with rhythmic flushes of growth which results in tiers of whorls of distichous, slightly pendulous branches. (Sargent 1896) Its general archetecture appears to fit Massart's model for Auracaria spp. (Hallé et al 1979) The genus is generally considered to be dioecious, however, occationally producing both male and female inflorescences upon different branches of the same individual. (Rowan & Chellman 1980) Personal observation of a limited number of plants suggest that the male trees form a more columnar form. Frequently basal orthotropic sprouts are observed to develop at the base of the trunk and in lower branch axes, however, these generally remain small (less than three feet) and quiescent unless the main trunk is damaged. Numerous authors compare this tendency to produce basal sprouts with that of Sequoia sempervirens, with which Torreya has been found in association in the fossil records. (Arnott 1838, Chapman 1885, Gray 1875, Boeshore & Gray 1936)

Generally, a single orthotropic axis develops producing whorls of plagiotrophic, distichous branches (commonly five or six branches per whorl) which further subdivide forming second and third order horizonal branchlets. Winter buds are 1/8" to 1/2" long, and are covered with loosely imbricated scales. (Sargent 1896) The individual needles are acicular (Sargent discribes 'slightly falcate") with a slightly raised, decurrent leafbase, with each needle an inch and a half long and 1/8" across, narrowing abruptly to a rigid point. When bruised or broken, the leaves and stems emit a resinous smell, identified as "foetid"(Sargent 1896), "terebinthine" (Chapman 1885) or locally as "Stinking Cedar" or "Polecat Wood". Leaves are dark green, lustrous above, paler below with two narrow and shallow stomatal bands. Leaves emerge from the bud in a spiral pattern but soon become distichous due to a twisting of the short petiole. The branchlets are slender, remain bright green for two or three years, and then darken to a dull orange-red brown. The bark of the trunk may be upto 1/2" in thickness, brown or faintly tinged with orange and is irregularly divided into broad, shallow horizonal fissures which are covered by thin, closely appressed scales. (Sargent 1896)

Arnott (1838) discribes the sap as "blood-red turpentine, of a pasty consistance, (and) flows sparingly from the bark."

Flowers open in March to April, with numerous solitary staminate flowers developing in the leaf axes. Staminate buds are 1/4" in length, appearing beneath the branch with pale yellow anthers. Female flowers are in pairs, are smaller to 1/8" long and a inconspicuous at the base of young shoots. (Sargent 1896) Fertilization is delayed until August (Coulter & Land 1905) with maturation the next summer. The immature fruit remains small over winter, but becomes light-green and plum sized (obovate to 1 1/4" long x 3/4" wide) by mid-summer with a thin, leathery covering (1/8" thick) the light-brown seed. Upon ripening, the leathery "arillus" becomes dark purple-green and commonly splits before fruit drop.(Sargent 1896)

Penhallow (1907) reports on the internal morphology of the wood:

> Transverse. Growth rings variable, 1.5-3 mm thick. Summer wood of 2-4 or more tracheids, usually very thin, often double and passing gradually into the spring wood: spring tracheids squarish and in regular rows, rather uniform. Structure of the growth ring open throughout. Medullary rays somewhat prominent, 1 cell wide, distant 2-9, rarely 16, rows of tracheids.
>
> Radial. Ray cells straight; the upper and lower walls thick, conspicuously pitted, uniform; the terminal walls thin and entire, sometimes curved; the lateral walls with small, round, but variable pits with a distinct border, the orifice very narrow, 2-5 per tracheid. Bordered pits in 1 or 2 rows. Pits on the tangential walls of the summer tracheids obscure. Spirals of the tracheids in 2 series, distant 5-30 u, very flat, the angle 70.4°, compact and finally vestigial in the summer wood.
>
> Tangential. Rays medium, the cells rather small, oval, or oblong, thick walled.

Additionally, he reports on the wood's relative specific gravity

(0.5145), approximate fuel value (51.08), coefficient of elasticity in kilograms on millimeters (821), as well as other measurements which show that _T. taxifolia_ is stronger and more resistant to crushing and indentation than _T. californica_. He also remarks that the wood is very durable in the soil.

Sargent (1896) estimates radial trunk growth as approximately 0.14" per year based on a single specimum 14" in diameter with 99 rings of annual growth.

Published discriptions of root growth are unknown for _T. taxifolia_, however, rooted cuttings produce only thick, brittle roots, typically 2-3 mm in diameter, infrequently branching with occational adventitious roots emerging through the epidermis. Microscopic examination reveals the presence of simple, minute stubby root hairs (more like bumpy projections of epidermal cells.) Rate of radial increase is unknown. Chick (1903) discribes the root system of _T. myristica_ (now _T. californica_) seedlings as having a strong tap root which bears many laterals, with diarch vascular bundles, large fibers in the secondary phloem, and a many layered pericycle with much secondary wood even in sixteen months old seedlings. Personal observation of a limited number of dead, fallen trunks of _T. taxifolia_ reveal little evidence of a prominate tap root, with only the remains of shallow, horizonal roots which fan out from the base of the trunk.

Morphological Features

General vegetative characteristics are covered in the preceeding section on botany. _T. taxifolia_ has no obvious, distinctive juvenile characteristics other than the occurance of axillary orthotropic shoots along the trunk base or in the lower branch axes. Observation of native trees indicate orthotropic shoots from axes upto 3 feet from the ground. It is not known if these shoots are produced in upper branch axes.

Vegetative Shoot Apex Morphology

The apex of *T. taxifolia* has not been discribed. However, Kemp (1913) discribes the vegetative growth of *T. californica* and concludes that the shoot apex of this genus has a definate cycle of seasonal activity, with three distinct phases: 1) resting period, 2) period of bud expansion and 3) the period of development of a new terminal bud. She also discusses changes in the size of the apex where the apex greatly widens and leaf primordia for the next flush are initiated on the widen flanks. She also discribes the differentiation of the apical meristem into four zones: 1) apical initial group, 2)subapical group, 3) peripheral tissue zone and 4) central tissue zone. She concludes that the apex bears little resemblence to that of *Ginkgo*, *Ephedra* or certain genera of Cycadales, and that the apex of *T. californica* has its closest resemblance to those of *Taxus*, *Abies* and *Cunninghamia*.

Floral Bud Formation & Development

Spermatogenesis

Coulter & Land (1905) discribe the gametophytes and embryo of *T. taxifolia*. Staminate strobili are first observed in July or August in the axes of leaves of the current season's growth. In October these buds are small, ovoid and are displayed along the undersurface of the branch due to curving of the short peduncle. The strobilus consists of a series of closely overlapping sterile bracts, in four verticle rows, completely enclosing the tip of the floral axis. The sporophylls are discribed as sterile below and fertile above, with the sporophylls in spiral succession. By early September, sporangia become distinct. Seven sporangia, three adaxial and four abaxial are radially arranged about the central axis. The abaxial sporangia develop normally, while the three adaxial sporangia do not further develop and disintegrate, fuse and become a single adaxial resin cavity. Initially a single hypodermal archesporial cell gives rise to two layers of wall cells and a single primary sporangeous cell, while the mature sporangium has three or four wall layers.

No stages intermediate to this early stage and pollen shedding (late March-April) were examined. The pollen germinates but does not "cut off" a prothallial cell, as is the case with most Coniferales except Podocarpaceae and Abietae. After the first division the generative and tube cells are distinct and seperated by a thin membrame. The tube nucleus is sometimes spherical, but more often amoeboid.

By early April, binucleate pollen grains were observed resting on the nucellus and filling the micropyle by the end of June. Growth of the germ tubes are variable but fertilization occurs about the middle of August. The body cell divides just before fertilization resulting in two unequal male cells due to unequal distribution of the cytoplasm. Therefore, approxfifteen months elapse between first appearance of microsporagiate strobilus and fertilization.

Oogenesis

The ovulate strobili occur in pairs on very short axillary branches at the base of the last flush of growth. Occcationally two pairs are observed, rarely three. This cluster of two (to six) strobili appears at the base of the strobilus-bearing shoot but usually only the lowest pair will further develop and form seeds. The strobilus is simple, composed of four enclosing bracts with a single terminal ovule with two integuments. The female strobili are first seen in late July, but show no differentiation until the following spring, presumably passing the winter in the mother-cell stage, with synapsis of the mother-cell in early April. (Coulter & Land 1905)

The megaspore develops with free nuclear division until sixteen to 32 nuclei in parietal position are observed. Wall formation within the endosperm was not observed before the 1st of July or within the month of July. Wall formation begins when 256 free nuclei are observed which is a common number among conifers. Shortly thereafter a single archegonium initial can be observed. Most of the endosperm seems to develop after fertilization. The archegonium initial occurs slightly off the central axis and divides forming a central cell and a neck cell which then divides anticlinally forming a two-celled neck. The central cell enlarges rapidly with a spherical nucleus. At the time of fertilization the gametophyte contains 400-800 cells with thin walls and little cytoplasm, however, there is abundant accumulation of reserve food in the peripheral cells of the antipodal region.

Fertilization occurs with the apparently forcible discharge of the tube contents into the egg cell. The male nuclei passes through the egg cytoplasm and comes into close contact with the egg nuclei. Male cytoplasm appears to remain closely appressed to the surface of the egg nuclei and stains distinctly differently from the female cytoplasm.

Shortly after fertilization, two divisions of the egg nuclei (zygote) occurs resulting in four large free nuclei which almost fills the egg cell. One nuclei relocates near the base of the egg, while the others form a plane above and wall formation occurs. Two weeks later the egg is completely filled with a proembryo of 12-18 cells.(please note that all observations by Coulter & Land were made from specimums collected every two weeks during the year so that many intermediate stages are not reported) At this stage the cells are arranged in three distinct tiers: those nearest the neck of the archegonium (5 or 6 cells) form a primary suspensor, the middle tier (5 or 6 cells) form a secondary suspensor, while the lowest tier consists of a single cell which eventually contributes to the suspensor-formation and forms the embryo. This proembro remains quiescent over winter. In spring, the suspensor develops further and a distinct embryo is formed along with the development of the testa and rumination of the endosperm. The embryo further develops and two cotyledons become evident. An unusual development occurs this second season where a number of small "embryos" develop from cells of the suspensor region, however, these embryos do not develop further unless the primary embryo is damaged. Thus, the time span from first appearance of the megasporangiate strobilus to maturity of the seed is about thirty months. (Coulter & Land 1905)

Seed Maturation

Seed maturation occurs with the outer integument developing into a fleshy arillus with numerous resin cavities. The inner integument differentiates into two distinct layers, similar to the development in cycads and ginkgo. The outer layer forms the stony seed coat after the embryo and endosperm have completed their development. The hardening of the seed coat begins near the apex of the ovule and extends downward. The inner layer of the inner integument comprises of several layers of thin walled cells which are generally termed perisperm or nuclear tissue. (Coulter & Land 1905)

The development of the endosperm is peculiar, resulting in a ruminated endosperm, compared to the endosperm of nutmeg. Apparently the development of the perisperm is irregular and regional and the aggressively developing endosperm irregularly encrouches the perisperm creating irregular edges. (Coulter & Land 1905)

Buchholz (1940) compares the embryogeny of three species of Torreya (T. taxifolia, T. nucifera, T. californica). He presents a similar suite of developmental events as Coulter & Land (1905), however, he notes slightly smaller mean dimentions of the female gametophyte of T. taxifolia (average 173 x 270 µ *vs* 200 x 300 μ by Coulter & Land). He compares the phylogeny of these *Torreya* spp. and concludes that *T. taxifolia* has more advancced features including reduction in the number of archegonia (2-4 for *T. nucifera* and *T. californica*, and only one for *T. taxifolia*); reduction in the size of the female gametaphyte (*T. californica* *T. nucifera* *T. taxifolia*); the pollen tube of *T. taxifolia* reaches the female gametophyte much earlier than with the other species and remains in intimate contact with the archegonium through its development; and that in *T. taxifolia*, the proembryo occupies almost all of the archegonium while the other species occupy only 2/3 of the space.

Seed Germination

Seed germination of *T. taxifolia* is considered the preferred method of propagation since it produces normal upright growing trees. (Chapman 1885) However, seed germination is slow and irregular. Several sources indicate that seed germination usually requires two seasons (Meyers 1982, Schopmeyer 1974) with occational germination the first year but most germination the second year. Both *T. taxifolia* and *T. californica* have immature embryos at fruit drop and that the embryo further increases in size following warm stratification (Schopmeyer 1974, Sesock 1982) or following planting (Buchholz 1940). Schopmeyer expresses some doubt as to the benefit of alternating warm and cold stratification. He reports that maximum germination was reported following 3 months of warm stratification with 92 % germination nine months after sowing. Personal communication with several persons indicate that cracking the hard seed coat before stratification was necessary for rapid germination.

Germination has been discribed as hypogeal with enlargement of the cotyledons which grow into the endosperm and becomes firmly entrenched similarly to the germination of cycads and ginkgo.(Chick 1903)

Horticultural Problems

Torreya taxifolia has the potential to be more widely used as an ornamental if improved means of propagation are determined and if control measures for the needle blight can be determined. Seed propagation is limited by availability and unclarified pretreatment requirements. The morphology of the seed suggests that pretreatments such as are recommended for *Zamia* (Dehgan & Schultzman 1983) whereby seeds are scarified or cracked followed by growth regulator treatment with Gibberellic acid may greatly hasten and improve germination. Propagation by cuttage is easy but limited by the problem of plagiotrophic growth of lateral cuttings. Lateral cuttings can be used to produce an irregular ground cover which will eventually produce seeds. The production of orthotrophic basal shoots allows some propagation by cuttings, however, only a few basal shoots (one upto five or six) are normally available. Horticultural techniques such as hedging, or chemical treatment (i.e. cytokinin sprays) may increase the number of orthotropic shoots. There are however, conflicting reports of slow growth of rooted cuttings (Chapman 1885, Meyers 1982, Rowan & Chellman 1980) while Turner (1983) reports that rooted cuttings grow faster than seedlings. His observation may be due to the fact that seedlings produce extensive root systems before much top growth.(Chick 1903) Also numerous individuals have noted that Torreya spp. grow naturally slow. It has also been observed that many species with thick roots grow slowly unless inoculated with mycorrhizae (ex. Citrus, sweetgum--Johnson 1982) Currently investigations are underway to determine if mycorrhizal inoculation will increase the growth rate of rooted cuttings and micropropagated plants.

Investigations of disease control have proceeded with difficulty due to the slow growth of cuttings, and limited expression of disease symptoms by juvenile plants and plants which have been grown under nonstressed conditions.(Alfieri et al. 1967, Rowan & Chellman 1980) Additional evidence is accumilating which suggests that there is predisposition of disease severity due to drought stress.(Schoenweiss 1975, Barnes 1982) Disease severity and dieback in the wild appears to be highly correlated with droughts in the 1930's and especially in the mid-1950's.(Barnes 1983) This observation is further supported by the healthy extant trees under cultivation at Biltmore Estate in Asheville, North Carolina which may be due to their avoidance of the drought stress which destroyed the native stands. Another tree in Norlina, N.C. appeared healthy until a few years ago but has now declined following a two year summer drought period.

Fortunately, a handful of enthusiastic individuals incouraged by the Florida Department of Natural Resources are now involved in formulating a recovery plan which includes management of the remaining plants in Torreya State Park and cultivated plants at Maclay Gardens in Tallahassee; distribution of propagules; and scientific investigation of disease control and propagation. Unfortunately, little funding is available to support these investigations although efforts to update grant proposals has been recently renewed at a symposium in Tallahassee (November 1983). These efforts may be the last chance to prevent the total demise of this species.

References

1. Alfieri, S.A., A.P. Martinez, and C. Wehlburg. 1967. Stem and needle blight of Torreya taxifolia Arn. Florida State Horticultural Society 80:428-431.

2. Arnott, G.A.W. 1838. On the genus Torreya. Annals of Natural History. Vol. I. Ser. 1.pp.126-132.

3. Barnes, L.R. 1982. Water deficit predisposition to plant disease: drought and disease induced forest change. (unpubl.)

4. Barnes, L.R. 1983. Current status of research into conventional propagation and micropropagation of endangered Torreya taxifolia Arn. and Taxus floridana.Nutt.(unpubl.)

5. Boeshore, I. and W.D. Gray. 1936. An upper Cretaceous wood: Torreya antiqua. Amer. J. Botany 23:524-528.

6. Buchholz, J.T. 1940. The embryogeny of Torreya, with a note on Austotaxus. Bull. Torreya Bot. Club 67:734-754.

7. Burke, J.G. 1975. Human use of the California nutmeg tree, Torreya californica, and other members of the genus. Economic Botany 29:127-139.

8. Chapman, A.W. 1885. Torreya taxifolia, Arnott.: A reminiscence. Bot. Gazette Vol. X No. 4 April pp.249-254.

9. Chick, E. 1903. The seedling of Torreya myristica. The New Phytologist. Vol. 2 pp. 83-91 and plates VII, VIII.

10. Coulter, J.M. and W.J.G. Land. 1905. Gametophytes and embryo of Torreya taxifolia. Bot. Gazette 39(3):161-178 and plates A, I,II,III.

11. Daubenmire, R. 1978. Evolution of north american vegetation. Plant Geography. Acad. Press pp. 48-65.

12. Dehgan, B. and B. Schultzman. 1983. Effect of H_2SO_4 and GA_3 on seed germination of Zamia furfuracea. HortScience 18(3):371-372.

13. Florida Dept. Natural Resources. 1983. Torreya tree management symposium. November.

14. Godfrey, R.K. and H. Kurz. 1962. The Florida Torreya destined for extinction. Science 136:900-902.

15. Gray, A. 1875. A pilgrimage to Torreya. Amer. Agriculturist Vol. 34(July):266-267.

16. Hallé. F., R.A.A. Oldeman and P.B. Tomlinson. 1978. Tropical trees and forests: An architechtual analysis. Springer-Verlag.

17. Kemp, M. 1913. Morphological and ontogenetic on *Torreya californica* Torr. I. The vegetative apex of the megasporangiate tree. Amer. J. Botany 30:504-517.

18. Johnson, C. 1982. Personal communication.

19. Meyers, G. 1982. Personal communication.

20. Penhallow, D.P. 1907. A manual of the North American Gymnosperms. Grinn & Co. Boston. pp.210-211.

21. Rowan, S.J. and C.W. Chellman. 1980. Research Project Proposal. Regeneration and salvation of the endangered tree species, *Torreya taxifolia* Arn.

22. Sargent, C.S. 1896. *Tumion taxifolia*. Silva of North America. Houghton-Mifflin. pp. 57-60.

23. Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. USDA For. Ser. Agric. Handbook No. 450.

24. Sesock, F.T. 1982. Personal communication.

25. Turnage, B. 1983. Personal communication.