N. Pace

White Mountain
Tree Ages.

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Longevity under Adversity in Conifers[1]

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On marginal sites in semiarid regions of the western United States, trees of several coniferous species have been found that far exceed the generally accepted maximum ages for these species. The annual stem growth of such trees is extremely small (*1*); nevertheless, the width of the annual rings in many of these trees is particularly sensitive to the varying rainfall from year to year (*2*). This remarkable combination of longevity and sensitivity makes it possible to derive tree-ring indices of past year-by-year rainfall that are more reliable than indices based on the much younger trees found on less arid sites. Field sampling has been largely limited to conifers because, in the areas studied, they live longer than the hardwoods, are far more extensively distributed, and have rings that are easier to date and interpret than the rings in most hardwood species.

During some 15 field seasons, in each of which an intensive search was made for overage coniferous trees, criteria have been recognized that aid in finding

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the oldest ones. The types of sites that had been found to be favorable for sensitive growth reaction to dry or wet years (*3*), such as steep rocky slopes or ridges, lower forest limits for the species, and open stands, were also found to favor longevity.

Special characteristics of the oldest individual trees seem to be (*a*) low ratio of height growth to diameter; (*b*) sparse foliage; (*c*) relatively smooth and thin bark; (*d*) gnarled or spiral growth in some species; (*e*) centuries-long longitudinal retreat of the cambium-edge from the leaders (here called endogenous dieback, for this spike form of the dead leaders should be distinguished from the characteristic branchlet-covered form that results from the rapid killing by pests); and (*f*) lateral retreat of the cambium-edge in some species, as shown by barkless stem areas or by one or more barkless strips along the branches, down the stem, and along exposed roots.

Although the overage drouth conifers are found on very thin or patchy soils derived from both sedimentary and igneous rocks, the former type, particularly the limestone group, seems to provide a more favorable environment for maximum attainable ages. Whether this is related to specially favorable soil properties or to biotic factors is not known.

The part of the species range in which the tree is located also seems to be closely related to its potential longevity. For each of the extensively sampled species, one or more areas of absolute maximum age have been found; in other areas, the maximum ages tend to be lower with distance from the "high," in a pattern similar to that of the isolines on weather maps.

Numerous living giant trees of many species are said to be at least 3000 yr old (*4*); these ages are based on estimates of growth in the outer stem, growth in neighbors, size alone, or legend. Most, or possibly all, such trees, except a few standing giant sequoias, are perhaps much overestimated, for it is becoming increasingly clear that almost all very large trees are growing in locally favorable environments and have relatively rapid early growth. Instrumental and other problems have not, in general, permitted bark-to-pith coring of these trees, which, when followed by precise ring dating, is essential to the true age determination. Of the thousands of examined stumps of giant sequoias, only four have yielded verifiable ages in excess of 3000 yr (*3, 5*). The oldest of these, felled in 1892, was found to have an inner-ring date of 1307 B.C. on the stump sample, to which may be added about 10 yr of center growth decayed away and some 5 yr of height growth to stump-top.

Far shorter than in *Sequoia* is the normal maximum life span in *Pinus,* which for various American species has for decades been considered to lie approximately within the range of 100 to 600 yr (*6*). Only recently have verifiable maximum ages exceeded this by 2 or 3 centuries (*7*). If we confine the list of maximum ages to those based on actual ring analysis, no pines are known in Scandinavia above 550 yr (*8*) or in central Europe above 750 yr (*4*), as far as the writer is aware.

However, estimates of maximum ages of pine far exceed the limits noted. One, made by Klein in 1899 and fully discussed by Molisch, of about 1100 yr for a Swiss stone pine seems safer than most. In recent years, the high altitude bristlecone pines in the White Mountains of California were recognized by National Forest personnel as likely to reach unusual ages, and a selected stand has recently (November, 1953) become especially protected in a natural area. In the Grand Teton Mountains of Wyoming, Griggs estimated whitebark pine (*P. albicaulis*) to reach 1500 to 2000 yr (*9*), on the basis of maximum diameters and the observed growth rate in smaller trees.

Although the uncertainty in estimates such as those cited is widely recognized, it appears from work during the last two field seasons that the verifiable maximum ages in certain species of *Pinus* do, in fact, far exceed the long-established limits. The trees of great longevity that have been found recently are all from environments strongly limited with respect to moisture or temperature or both.

It may be noted in Table 1 that the two oldest pine trees presently known are represented, respectively, by 1658 and 1495 yr of growth on the increment cores. Both trees are sound and would appear to have life-expectancies still measurable in centuries. One may also note that (*a*) the species, limber pine and bristlecone pine, in which the maximum ages have been found have been only spottily sampled, (*b*) the maximum-age distribution patterns for these species are thus particularly ill-defined, and (*c*) other long-lived species of pine remain to be studied. Thus, we may conclude that pine trees of certain types can at least slightly exceed 2000 yr in age.

Of physiological interest is the limit to the slowness of annual stem growth in trees such as those reported in Table 1. Since, in poor growth years, this limit may be zero in a selected area of the cambium, even for uninjured fast-growing trees, the total radial growth of a century is here examined. In the several thousand North American drouth conifers now sampled, a total accretion of less than 15 mm is common, 10 mm is very rare, and 8 mm is the minimum anywhere in the lower stem of these trees. The minimum radial growth observed in a branch, in tree 3966 (Table 1), was about 3 mm/century; the interval A.D. 362 to 1018, when local death of the cambium on the measured radius occurred, showed an over-all mean growth rate for the 657 yr of almost exactly 0.04 mm/yr.

Since the average annual radial growth in the lower stem of a mature drouth conifer is of the order of 0.3 mm and the standard deviation in its ring widths is found to be 20 to 40 percent or more, a high incidence of locally omitted annual rings could well make precise dating of the ring sequence impossible. Omission of a ring in any increment core represents, of course, local quiescence in cambial-cell division during the entire growth season of that year. Such omissions seem to be relatively rare in those overage conifers that grow in the central and northern Rocky Mountains and also at elevations above 8000 ft or so in the

TABLE 1. Some growth characteristics of the oldest known drouth conifers.[1]

Tree No.[2]	Sampling date	Species[3]	Sapwood		Inner ring, A.D.	Outer ring, A.D.	Mean ring width (mm)		Radius (mm)		Age (yr)	
			(mm)	(yr)			Over-all	Min. century	Sample	Total (estm.)	Sample	Tree[4]
3996	7/52	LBP	10	53	458	1952	0.27	0.08	402	500	1495	1700
4020	9/53	ʻʻ			296	1953	0.36	0.18	610	620	1658	1680
3966	7/52[5]	ʻʻ	15	75	333	1953	0.25[5]	0.12[5]	428	428	1621	1650
4025	9/53	ʻʻ	20	84	584	1953	0.33	0.20	448	575	1370	1600
4026	9/53	BCP	26	86	535	1953	0.43	0.16	607	750	1419	1500
4038	9/53	ʻʻ			655 –	1953	0.26	0.11	343	400	1299 +	1500
4057	10/53	ʻʻ	15	70	892	1953	0.36	0.15	384	525	1062	1400
2522	5/48	PNN			975	1947	0.43		416	416	973	980
957	10/41	ʻʻ			1089	1941	0.27		232	240	853	860
4002	7/52	PP	23	130 +	1110 –	1952	0.42	0.14	354	375	843 +	860
3084	6/50	DF	22	79	1080	1950	0.36	0.22	313	340	871	890
3335	9/50	ʻʻ	15	78	1084	1950	0.20	0.09	176	185	867	880
3339	9/50	ʻʻ	27	78	1092	1950	0.24	0.16	206	210	859	875
1456	8/44	BCS	28	125	1385	1944	0.50	0.23	278	325	560	625
2983	1/50	AL	23	175 +	713 –	1949	0.30	0.12	366	750	1237 +[6]	1800
3018	2/50	ʻʻ	12	170 +	652 –	1949	0.25	0.05[7]	320	550	1298 +	1600
3773	7/51	SCJ	12	82 +	928 –	1951	0.38[8]	0.16	385	760	1024 +	1500
3562	6/51	WJ	46	205 +	896 –	1950	0.31	0.20	320	575	1055 +	1300[9]

[1] *Fitzroya cupressoides* (trees 2983 and 3018), a wet-climate species, is an exception, listed here for comparative purposes. The rings in the two alerce and the two junipers at the end of the table were not datable. Data for tree 4038 represent the central stem of "The Patriarch," 37.7 ft in circumference, which was discovered by Ranger Alvin E. Noren.

[2] Location:

3996	43° 46′ N	114° 16′ W	6500 ft	Sun Valley Area, Idaho
4020	37 32	118 08	10500	White Mountains, Calif.
3966				See 3996
4025–26				See 4020
4038	37 32	118 11	11300	White Mountains, Calif.
4057	37 25	118 10	10200	White Mountains, Calif.
2522	38 37	110 22	7200	N of Sunnyside, Utah
957	37 35	108 33	7500	N of Dolores, Colo.
4002	37 39	112 05	7000	Bryce Canyon Natl. Park, Utah
3084	39 48	110 20	7200	NE of Price, Utah
3335	39 37	106 51	6700	W of Eagle, Colo.
3339				See 3335
1456	33 43	116 44	4700	S of Idyllwild, Calif.
2983	42 34′ S	71 53	4500 ±	Lago Cisne, Argentina
3018	41 50′ S	72 35	4500	Hornopiren Peninsula, Chile
3773	41 50′ N	111 38	8500	NE of Logan, Utah
3562	37 57	119 13	8300	W of Leevining, Calif.

[3] AL	Alerce, *Fitzroya cupressoides*
BCP	Bristlecone pine, *Pinus aristata*
BCS	Bigcone-spruce, *Pseudotsuga macrocarpa*
DF	Rocky Mountain Douglas-fir, *Pseudotsuga menziesii* var. *glauca*
LBP	Limber pine, *Pinus flexilis*
PNN	Pinyon pine, *Pinus edulis*
PP	Ponderosa pine, *Pinus ponderosa*
SCJ	Rocky Mountain juniper, *Juniperus scopulorum*
WJ	Western juniper, *Juniperus occidentalis*

[4] A minimum number of years were added to those on the sample, on the basis of early growth rate, estimated length of untapped radius, and estimated sapling age at sampling level.

[5] Tree cut Sept 13, 1953; entry represents the 1952 increment core, with inner ring at A.D. 563.

[6] East radius; west radius, 1210 rings in 343 mm; south radius, 1094 rings in 251 mm.

[7] Outer 130 rings in 6.0 mm; outer 800 rings in 99 mm; inner 50 rings in 45 mm.

[8] Inner two centuries on core 0.66 mm; inner 50 yr, 0.90 mm: this is the Old Utah or Jardine Juniper (ref. 4, Fig. 7).

[9] Several weathered western juniper trees north of Tenaya Lake, Yosemite Natl. Park, yielded ring counts on eroded stem surfaces which seem to place them in the 2000-yr class, but no successful boring of these trees has yet been made.

Southwest. This is fortunate, for it is in such areas that the very oldest trees in the sampled species were found. The low frequency of locally omitted rings seems to be characteristic of growth in the upper, as well as the lower, stem and also in the branches and roots of such trees. False, or nonannual, rings are rarely found and, when present, are easily recognized in overage conifers.

Even at 10,000-ft elevation or as far north as lat. 51°, however, it was found that, in a small fraction of the increment cores from overage trees, as many as five or more rings were omitted per century. The recognition of such omissions and, hence, the precise dating of the entire sequence of rings on such a core were possible for certain stands of trees—those in which the amount of ring growth from year to year was found to fluctuate more or less synchronously in the various trees, so that detailed cross comparisons in chronology could be made.

Although this discussion is primarily concerned with trees in arid or arid-alpine areas, certain features in the growth of *Fitzroya cupressoides* (alerce), a South American wet-climate tree, are of relevance here and data are included in Table 1. The ring numbers in these trees represent counts only, since no consistent chronology was present in the succession of ring widths in the older trees that would permit cross check with neighboring trees. Thus, omission of rings, which in the very crowded and highly variable ring sequences in these trees may amount to several percent, cannot be recognized. However, the annual nature of the ring has been verified. Although, in many properties, trees of this species bear some astonishing resemblances to *Sequoia,* they appear able to reach much lower growth rates. The record low accretion of some 4.6 mm in radial stem growth per century, measured in the outer 130 + rings of tree 3018 (Table 1), is the more remarkable in that it was laid down as normal growth in a tree of good crown and entire bark, at about 4500-ft elevation in a cold-climate mountain jungle enjoying a mean rainfall of approximately 200 in./yr. However, the maximum stem diameter in *Fitzroya* does not approach that in *Sequoia*; the largest alerce observed, the "Silla del Presidente" (*10*), near Puerto Montt in southern Chile, had a diameter of 120 in. inside the bark and above the basal flares. Growth on the stump, a characteristic shell only, suggests an age of the order of 2000 yr. On the basis of only a minor sample of the small existing range, the two trees listed in Table 1 were the oldest standing ones found in Argentina and Chile, respectively; all the old sampled trees of this species showed center rot, usually advanced.

To what may we ascribe the great longevity under adversity of trees such as those here reported? Observed in the field were the well-recognized causes for the death of trees: (*a*) gross destruction by man, fire, insects, wind, erosion and imbalance, lightning, flooding, and the like; and (*b*) more subtle destruction in parasitic attack, especially that causing rot, and insufferable climatic years with resulting starvation or fatally weakened resistance to disease. Do trees become senile, with death as the end stage? This is a possibility many plant physiologists reject, according to Molisch (*4*); he presents some evidence in its favor. Is the increased resistance to water transport with growth in size (*11*) a factor of reduced importance in the characteristically stunted trees here reported? The following observations would seem to be relevant to these questions.

1. The areas of maximum ages for each species have maximum numbers of hardy, overage trees.
2. Extremely slow-growing overage trees of some coniferous species tend, in general, to be relatively free of center rot at ages that are associated with much rottenness in fast-growing, favorably situated trees of the same species. (Is center rot a form of dieback?)
3. Open stands, rocky sites, stunted size, and sparse vegetation seem to inhibit the direct agents of destruction.
4. Some individual resinous conifers, having suffered severe mechanical injury, were stimulated to excess resin production and, thus, perhaps fought off the agents of decay.
5. In *Pseudotsuga menziesii* and in the extensively sampled species of *Pinus,* longitudinal retreat of the cambium-edge has been observed in an essentially complete range, the endogenous dieback in 400 to 500-yr trees at tips only culminating (in trees centuries older) in but one or two remaining living branchlets. In some localities numerous dead snags testify to the end-result.
6. Laterally retreating cambium-edge has been observed, in some species, to reach the stage in the oldest trees of a single vertical or spiraling thin strip of bark-covered living tissue, the trees still showing little or no sign of center rot. In the analyzed species, lateral retreat seems to be possible only in the presence of longitudinal retreat; however, the latter may exist with no visible sign of the former, as in *Sequoia gigantea.*

Perhaps the most intriguing of the unanswered questions regarding longevity in conifers has to do with *Sequoia gigantea* trees, which, some believe, may enjoy perpetual life in the absence of gross destruction, since they appear immune to pest attack. However, if we may reason by analogy in this case, the endogenous dieback of the main stem, which is observable in all old trees of this species, and the relentless progress of this phenomenon with advancing age in other species do not support this belief. Pertinent also is the well-known fact that standing snags of this species, other than those resulting from factors of gross destruction, are unknown. Does this mean that shortly preceding 3275 yr ago (or 4000 yr ago, if John Muir's [*12*] somewhat doubtful count was correct) *all* the then living giant sequoias were wiped out by some catastrophe? Does the probability of any individual *Sequoia* surviving all the forces of gross destruction for much more than 3000 yr become vanishingly small?

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