

## Does bristlecone pine senesce?

R.M. Lanner<sup>a,\*</sup>, K.F. Connor<sup>b</sup>

<sup>a</sup>*Institute of Forest Genetics, USDA Forest Service, Placerville, CA 95667, USA*

<sup>b</sup>*Southern Forest Experiment Station, USDA Forest Service, Starkville, MS 39759, USA*

---

### Abstract

We evaluated hypotheses of senescence in old trees by comparing putative biomarkers of aging in Great Basin bristlecone pine (*Pinus longaeva*) ranging in age from 23 to 4713 years. To test a hypothesis that water and nutrient conduction is impaired in old trees we examined cambial products in the xylem and phloem. We found no statistically significant age-related changes in tracheid diameter, or in several other parameters of xylem and phloem related to cambial function. The hypothesis of continuously declining annual shoot growth increments was tested by comparing trees of varying ages in regard to stem unit production and elongation. No statistically significant age-related differences were found. The hypothesis that aging results from an accumulation of deleterious mutations was addressed by comparing pollen viability, seed weight, seed germinability, seedling biomass accumulation, and frequency of putative mutations, in trees of varying ages. None of these parameters had a statistically significant relationship to tree age. Thus, we found no evidence of mutational aging. It appears that the great longevity attained by some Great Basin bristlecone pines is unaccompanied by deterioration of meristem function in embryos, seedlings, or mature trees, an intuitively necessary manifestation of senescence. We conclude that the concept of senescence does not apply to these trees. © 2001 Elsevier Science Inc. All rights reserved.

*Keywords:* Bristlecone pine; Senescence; Longevity; Physiological aging; Aging; *Pinus longaeva*

---

### 1. Introduction

As Peter Medawar put it, a physiologist wishing to study the problem of aging from scratch “would first of all try to piece together a full empirical description of the phenomenon...as it is reflected in structural changes of tissues and cells and...the type and intensity of tissue and cellular metabolism. Only scraps of such information are now available: he would have to collect more” (Medawar, 1957: 40).

A great mass of data has since accumulated on what happens to animals as they age — especially to *Homo sapiens*. But surprisingly, little beyond conjecture has been written on the effects of aging on the longest-lived of organisms — trees. This is probably due to the

---

\* Corresponding author. Tel.: +1-530-344-0255.

practical nature of most tree research, which aims at producing more and better timber. A notable exception is the study by Baas et al. (1986) of tracheid length in Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey). They found steady increases in this parameter for as much as 2200 years, and dubbed the species a ‘record-breaker’ in wood anatomy. An age-related subject that has received more attention in tree research has been that of phase change (Brink, 1962), the passage from a juvenile stage to maturity. Phase change is also termed ‘ontogenetical aging’. Lyr et al. (1967) distinguished juvenility, maturity, and senility phases; the latter was characterized by growth slowdown and scantiness of fruiting, and very old trees were said to prolong their lives by extending the phase of senility. Phase change in trees is of concern in forestry because it affects such phenomena as age of flowering and success of vegetative propagation (Greenwood, 1984). Also of importance in forestry is the concept of ‘physiological aging’, which is seen as the cause of such morphological changes as the ‘flattening’ of conifer crowns, increased susceptibility to diseases, and reduced annual ring growth. It is apparently synonymous with senescence, but clear definitions of the term are elusive. Foresters view the poor development of young trees on depauperate sites as a manifestation of physiological aging, regardless of the chronological age of the tree. Dendrochronologists commonly invoke physiological aging as a factor in the reduction of growth rings in old trees that must be corrected for when interpreting tree-ring chronologies (Fritts, 1976).

Unfortunately, most of the empirical comparisons of young vs. old trees that one can find in the literature are based on trees that did not contrast greatly in age, because there was more concern with the tree’s commercial development than its biological lifespan. For example, Forward and Nolan (1964) looked for aging effects on red pines (*Pinus resinosa* Ait.) whose maximum age was 50 years, only about a sixth of the species’ lifespan (Altman and Dittmer, 1962). A highly influential paper by Möller et al. (1954) dealt with the photosynthesis/respiration ratio of European beeches (*Fagus sylvatica* L.) aged a maximum of 85 years compared to a lifespan that occasionally exceeds 900 years (Büsgen and Münch, 1929). Greenwood (1984) compared shoot development in loblolly pine (*Pinus taeda* L.) scions taken from ortets ranging from one to 12 years of age. And in another influential paper in which conclusions were drawn on the aging of Scots pine (*Pinus sylvestris* L.), Wareing (1958) reported on a single 5-year-old branch taken from a tree aged 13 years! In several studies of age-related changes in the cambial growth of various pines, the outer limits of age were 30, 130, 140, and 600 years (Scholtes, 1953; Fritts, 1969, 1976; Mikola, 1950). In recent years, tree physiologists have shown renewed awareness of age-related changes in trees, as they try to better understand ‘old-growth’ forests and the loss of productivity with age (Kaufmann and Watkins, 1990; Yoder et al., 1994; Kaufmann, 1996; Hubbard et al., 1999). Most of these efforts have focused on photosynthesis and water transport. The first scientific conference devoted to the issues of development and aging in forest trees took place in Italy in September 2000, contemporaneously with the conference at which this paper was presented.

## 2. Our studies and objectives

Though there has never been a ‘full empirical description’ of the effects of aging in

trees, many investigators have assumed such effects exist, and have tried to rationalize them. Some of their explanations are vague, but a few are testable. Using the world's oldest known tree species, Great Basin bristlecone pine (*P. longaeva*), as our test organism, we have subjected these testable proposals to observation or experiment, in a search for biomarkers of aging (Boddé, 1981). This reflects our assumption that 4000 years or so should provide ample opportunity for aging biomarkers to appear. The proposals we found testable, which we regard as hypotheses, are listed below with our reasons for testing them.

### 2.1. *The vascular system*

As a tree gets older, larger, and more complex, water transport problems create increased water stress. This results in diminished growth and hormone production, and finally, death (Went, 1942; Jankiewicz and Stecki, 1976; Westing, 1964. See also Hubbard et al., 1999; Ryan and Yoder, 1997).

Water transport in trees takes place in the sapwood, the more recently laid down annual increments of wood formed by the lateral meristem (cambium) that clothes the trunk, branches, and roots beneath the bark. The cells responsible for this transport in conifers are the tracheids, spindle-shaped cells that are oriented longitudinally. They die and develop empty lumens shortly after forming, and they are interconnected by openings known as pits. Water taken up in the roots passes through the vascular system entirely within tracheids until it enters the leaves. Centrifugal to the wood, or xylem, is the phloem layer which is formed on the outside of the cambium while tracheids form on its inside. Phloem cells transport mainly carbohydrate solutions made in the foliage, the product of photosynthesis. Unlike tracheids, which must be dead to function as pipes, phloem cells must be alive. They are short-lived and form only a very narrow sheath between the cambium and dead bark tissues. So to add weight to our tracheid studies, we also observed some parameters of phloem.

We chose to study the diameters of the tracheids, to see if they become constricted over the life of a very old tree. If so, water movement could be impeded. We also sampled living trees to detect, by color changes, how thick the sapwood is in trees of differing age, and how many years of living ray cells there are in trees of differing age. Ray cells form radial ribbons within the wood and phloem. They are alive in the sapwood, dead in the heartwood. We also compared phloem thickness in trees of differing age. Age-related changes in any of these parameters could indicate a cambium malfunctioning due to aging, perhaps as a result of 'replicative senescence' (Campisi, 2001).

### 2.2. *Photosynthetic balance*

As a tree ages, the proportion of photosynthetic to non-photosynthetic tissue causes an unfavorable photosynthesis/respiration balance, resulting in gradual decline and subsequent death. This has been suggested in several versions by Jacobs (1955), Möller et al. (1954), Molisch (1929), Woolhouse (1972), Wright and Mooney (1965) and Gerrish (1990). The concept has been made most explicit by Wareing (1958, 1959) and Moorby and Wareing (1963), who operationally defined aging in woody plants as, among other traits, the loss of vigor associated with declining annual increments of shoot growth, and therefore declining photosynthetic tissue, over the years.

Nearly all the photosynthesis in our test organism occurs in leaves (needles) that are formed in winter buds, and growth of the tree's crown is determined by the growth of shoots formed by elongation of the buds. We therefore searched for age-related changes in the number of needles formed in the buds and in the amount of new shoot growth emanating from these buds.

### 2.3. *Mutational load*

As a tree ages, especially at high elevations, cosmic ray bombardment eventually causes the accumulation of deleterious mutations that result in malfunctions leading to death (Sax, 1962; Westing, 1964).

In *Pinus* it is relatively easy to screen large samples for evidence of putative mutations, using pollen, seeds, and seedlings. Mutational load decreases pollen viability (Briggs and Knowles, 1967), and inviability can be detected in laboratory tests. Seed from trees of various ages can be subjected to germination tests, the results of which could be affected by mutational load. Seedling growth rates can be affected by mutation, and are easily compared for biomass accumulation. Finally, using seedlings grown from the seed of various-aged trees, one can screen for 'standard' pine seedling mutations (Franklin, 1970, 1977).

## 3. Materials and methods

We sampled Great Basin bristlecone pines from natural stands in the White Mountains of southeastern California (Inyo National Forest: Methuselah Grove, Patriarch Grove, Campito Mountain) and from Mammoth Creek and the Table Cliffs in southern Utah (Dixie National Forest). Elevations ranged from 2835–3505 m in the White Mountains to 2560–2896 m at the Utah sites. To minimize environmental impacts we also used dated bristlecone pine cores taken in previous years from trees in the White Mountains and archived at the Laboratory of Tree-Ring Research at the University of Arizona. Tree ages varied in the several studies, with extremes of 225 and 4713 years. For studies of xylem and phloem we used a stereomicroscope equipped with a drawing tube and a compound microscope equipped with a 35-mm camera; IKI and toluidine blue as stains; glycol methacrylate as an embedding medium; and Classification and Regression Tree (CART) analyses, randomization tests, and linear regression, to analyze data (Connor and Lanner, 1990). Our needle development and shoot growth studies utilized trees aged 14–2052 years from Mammoth Creek and the Methuselah and Patriarch Groves, and utilized CART analysis, randomization tests, and linear regression (Connor and Lanner, 1989). The pollen, seed, and seedling studies utilized trees 700–4713 years old from the Mammoth and Methuselah Grove sites, tetrazolium chloride as a vital stain for pollen, greenhouse culture for the seedlings, and CART and linear regression analyses (Connor and Lanner, 1991a).

## 4. Our findings

### 4.1. A cautionary note

The findings below, represent only a portion of our total results, due to limitations of space. For a complete statement of our results, see Connor and Lanner (1989, 1990, 1991a,b). The conclusions drawn, however, are consistent with all of our results.

### 4.2. Age-related changes in xylem and phloem

At all locations, there was no consistent age-related trend in mean tracheid diameter. At Mammoth Creek, three out of four trees exhibited increases of tracheid diameter (Fig. 1), in tree TRL 80-209 (2047 years old) the upward trend was evident for the past 300 years. At the Methuselah Grove, three out of four trees showed a recent tracheid diameter decrease, the exception being tree TRL 80-140 which at 3162 years was the second oldest (Fig. 2). At Campito Mountain all four trees, ranging in age from 949 to 1283 years, showed recent tracheid diameter increases. In tree TRL 83-176 that trend had lasted 300 years. And at the Patriarch Grove, three out of four trees aged 875–1253 years had clearly increasing tracheid diameters over the last century. All of these recent trends followed a lifetime of periods of tracheid diameter increase and decrease that did not follow a visually apparent general trend. Thus we found no evidence of ‘cambial aging’ among even the oldest of these trees.

Nor were there any consistent age-related changes in other characters that are related to

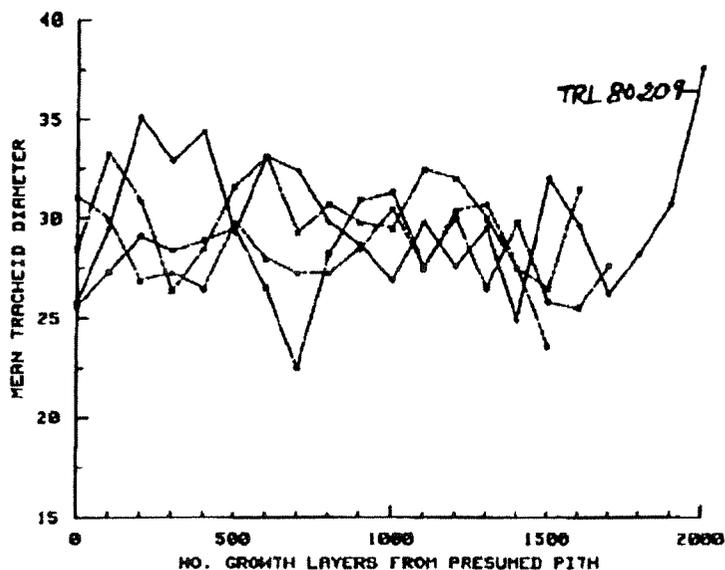


Fig. 1. Mean tracheid diameters from four Great Basin bristlecone pine trees from Mammoth Creek, UT (modified from Connor and Lanner, 1990).

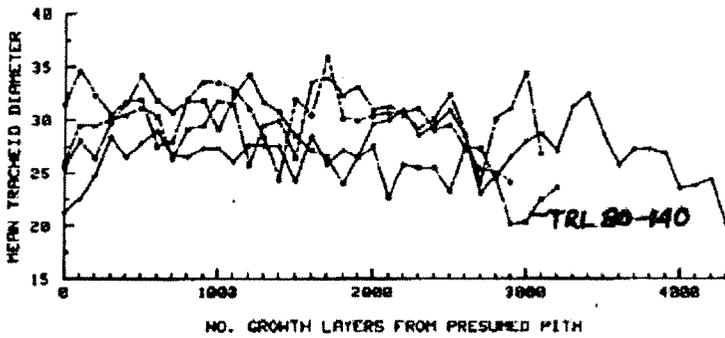


Fig. 2. Mean tracheid diameters from four Great Basin bristlecone pine trees from the Methuselah Grove, CA (modified from Connor and Lanner, 1990).

cambial performance — sapwood thickness, number of growth layers in the sapwood, mean radial (ring) growth, ray cell longevity, number of growth layers in the phloem, phloem thickness, and annual phloem (sieve cell) production (Connor and Lanner, 1990).

#### 4.3. Age-related changes in bud content and shoot elongation

At all the sites where trees were sampled for bud and shoot studies, there was no significant relationship between age and the tree shoot parameters studied: recent annual shoot length, production of stem units within buds, and final stem unit length. In other words, there was no detectable age-related trend in the morphogenesis of stem units within buds (Lanner, 1976), or the elongation potential of those stem units in determining final shoot length (Fig. 3).

At Mammoth the 1984 shoot lengths of the 5 youngest trees averaged 35 mm, the 5 median-aged trees, 22 mm, and the 5 oldest trees, 28 mm. At the Methuselah Grove, the corresponding means were 15, 12, and 16. Other data show similarly inconsistent trends (Connor and Lanner, 1989). The results of this study do not support the contention (Wareing, 1958, 1959) that aging is indicated by a diminishment of annual shoot length, and therefore of leaf production as well.

#### 4.4. Age-related evidence of mutational damage in the reproductive system

Pollen viability was generally poor for all 41 of the trees sampled from Mammoth and the Methuselah Grove. The regression of percent pollen viability on tree age was not significant at either site or when data were combined (Connor and Lanner, 1991a). Mean pollen viability from the 5 youngest trees in the study (mean age 137 years) was 18.3%, from the 5 median-aged trees (mean age 985 years), 6.8% and from the 5 oldest (mean age 2,172 years), 5.9%. The CART analysis, however, did not produce a binary tree with these data.

Seed weight also showed no statistically significant or consistent age-related trend, either at Mammoth or the Methuselah Grove (Fig. 4A). The mean weights of sixteen ten-seed lots (each lot from a separate seed tree) from Mammoth were: from the 5 youngest

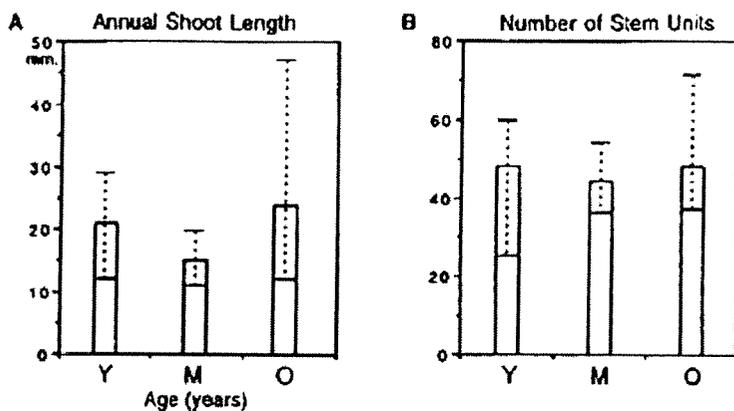


Fig. 3. A, B. Shoot growth characteristics of aging Great Basin bristlecone pine. Five youngest trees (Y) are 883–1219 years old; five median-aged trees (M) are 1564–1944 years old, and five oldest trees (O) are 2863–4256 years old. Bars indicate means and ranges. Data from Methuselah Grove (Connor and Lanner, 1989), graph from Finch, 1999.

trees (mean age 344 years), 0.123 g; the 5 median-aged (mean age 876 years), 0.107 g; and the 5 oldest (mean age 1239 years), 0.104 g. At the Methuselah Grove, the corresponding statistics for seventeen ten-seed lots were 0.069, 0.091, and 0.064 g, with mean ages of 1006, 1732, and 3062 years, respectively.

Seed germinability was also unrelated to tree age (Fig. 4B). The seed lots with the highest germinability, 78 and 85%, respectively, were from the two oldest trees in the study, TRL 80-138 (4257 years) and the Methuselah tree (4713 years). These results are supported by those of Johnson and Johnson (1978), who germinated all 36 seeds taken from a cone of the Methuselah tree. Our results also agree with a little-noticed figure caption in Edmund Schulman's famous report, *Bristlecone Pine, Oldest Known Living Thing*, which appeared in *The National Geographic Magazine* (Schulman, 1958: 365). It reads "Seed from an Old Pine Grows as Vigorously as That from a Youngster. Dr Frits W. Went... holds baby pines he grew from the cones of a 100-year-old and a 1500 year-old tree. By varying growth conditions artificially, Dr Went hopes to learn whether old bristlecones differ basically from young ones." The photograph accompanying this caption shows the eminent botanist Frits Went peering at a container of similar seedlings from each of the two trees. His contemplated further studies seem to have not materialized.

Seedling biomass was determined by obtaining oven-dry weights of greenhouse-grown seedlings after 30, 60, 90, and 120 days. The seedlings were progenies of the trees from Mammoth and the Methuselah Grove used in the work described above. Of the Mammoth-origin seeds, 51% of 2911 seeds germinated. Of the Methuselah Grove-origin seed, 61% of 7986 germinated. There were no statistically significant relationships between a tree's age and the biomass of its offspring (Fig. 4C).

Finally, only two putative mutations were found among the seedlings grown from

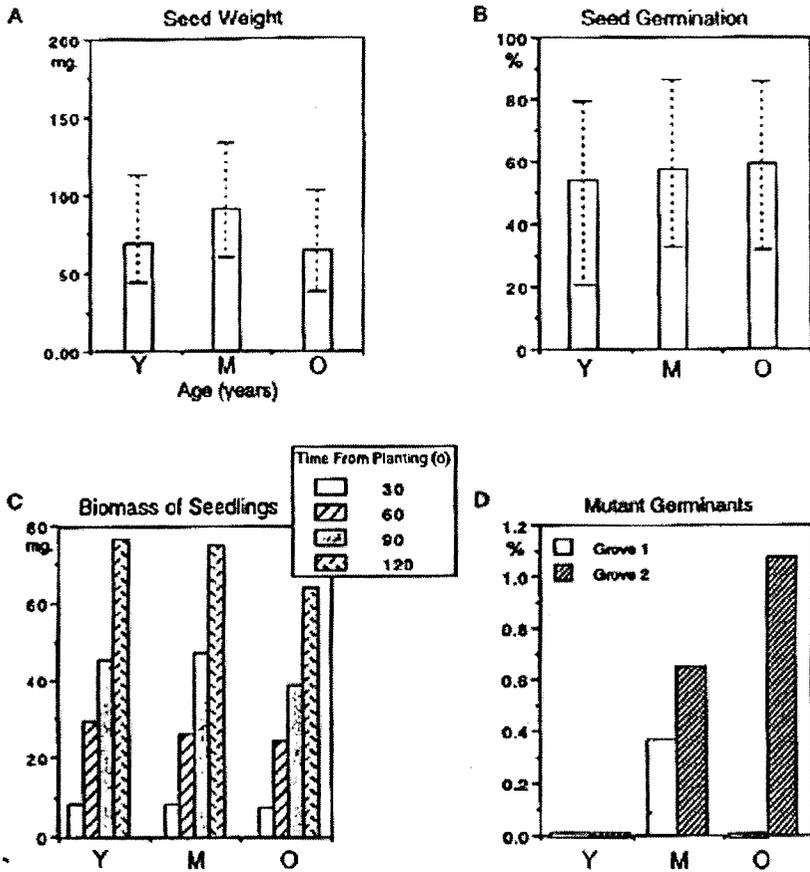


Fig. 4. A–D. Seed and seedling characteristics of aging Great Basin bristlecone pine. Age groups ( $n = 5$ ) are young (Y) 700–1269 years old (mean = 1006), median (M) 1558–1945 years old (mean = 1732 years), and old (O) 1995–4713 years (mean = 3062 years). Bars indicate mean and range in A and B. C shows seedling growth of two individuals from each age group from the Methuselah and Mammoth Groves. D shows frequency of putative mutant seedlings grown from seed from trees of both groves. Data from Connor and Lanner, 1991a; graphs from Finch, 1999.

Mammoth trees. These were plants that had yellow or pale green cotyledons (seed leaves) and a red stem, instead of green. Both were from an 823-year-old tree. Neither survived for 60 days. Twenty-five seedlings of Methuselah Grove origin had aberrant pigmentation or malformed cotyledons. The mother trees varied in age from 1549 to 4713 years, and all these seedlings died prior to the 60-day harvest. Although the number of putative mutants from the three age-classes of trees from the Methuselah Grove suggest an age trend (Fig. 4D), a significant relationship was supported by neither regression nor CART analyses. Therefore, we were unable to find evidence that putative mutation rates were related to tree age in these bristlecone pines of greatly contrasting ages from Mammoth and the Methuselah Grove.

## 5. Discussion

Trees grow by the activity of meristems — tissues that retain totipotent cells for another growth cycle, while most of the cells created in the present growth cycle differentiate to form specialized tissues. In an ideal tree every bit of surface area of root, trunk, limb, and branchlet would be underlain by a continuous sheath of meristem — the vascular cambium — and every shoot and root tip would be terminated by an apical meristem. Injuries sustained over a lifetime, however, partially compromise the integrity of this system of meristems.

The differential growth performance of a tree over time is therefore a direct consequence of the differential performance of its meristems; and any factor that modifies a tree's growth must do so by modifying meristematic behavior.

In the studies summarized here, we found no evidence of an age-related change in the quantitative or qualitative behavior of cambial or apical meristems. Nor did we find persuasive evidence of enhanced rates of spontaneous mutation in the pollen or seed of very old trees. We must therefore conclude that the age-related changes in trees that have been referred to as physiological, meristematic, or mutational aging and subsumed in the term senescence, do not appear to apply to Great Basin bristlecone pine.

What then might account for the obvious morphological changes that make old trees so different in appearance from young trees, aside from the 'slings and arrows' of life itself? Surely, if this question is addressed by other investigators, many possible answers may be suggested. We wish to make just one suggestion, however, what appear to be age-caused changes in tree habit could be due to nutrient deficits caused by the 'mining out' of the soil from which the tree derives its mineral resources. Especially in rocky terrain inhabited by the roots of other trees, a time will come when the soil available for a tree's prospecting will have lost more nutrients than is being replenished from recycling on the surface or mineralization of the bedrock. From this point on, the tree will be operating in an environment of reduced nutrition, and may appear to be a senescing organism, even if it is not.

What then of death? Is there no limit to the life of a non-senescing pine? Must it not die someday, and if so, of what? Schulman (1943) was the first to point out the correlation between long life and rigorous habitat. Like him, we believe that the rigors of dry, high-elevation sites reduce the likelihood and intensity of attack by insect, fungal, and vertebrate pests. Even more influential may be the low frequency of fire on sites with scant vegetative cover. One of us has suggested that if a tree avoids its pests long enough, it will eventually succumb to soil erosion, as its roots are deprived of their anchorage (Lanner, 1984, 1999). Thus it would be premature to postulate immortality even for bristlecone pines.

## Acknowledgements

This paper is dedicated to Dr Edmund Schulman, who first determined the existence of

4000 year-plus trees in his studies of Great Basin bristlecone pine in the White Mountains; and who expressed the hope that “when research has been carried far enough in these Methuselah pines, perhaps their misshapen and battered stems will give us answers of great beauty (Schulman, 1958, p. 368).”

## References

- Altman, P.L., Dittmer, D.S., 1962. Growth, Including Reproduction and Morphological Development. Federation of American Societies for Experimental Biology, Washington.
- Baas, P., Schmid, R., van Heuven, B.J., 1986. Wood anatomy of *P. longaeva* (bristlecone pine) and the sustained length-on-age increase of its tracheids. *IAWA Bull. New Ser.* 7, 221–228.
- Boddé, T., 1981. Biomarkers of aging: key to a younger life?. *Bioscience* 31, 566–567.
- Briggs, F.N., Knowles, P.F., 1967. Introduction to Plant Breeding. Reinhold, New York.
- Brink, R.A., 1962. Phase change in higher plants and somatic cell heredity. *Q. Rev. Biol.* 37, 1–22.
- Büsgen, M., Münch, E., 1929. The Structure and Life of Forest Trees. Chapman & Hall, London.
- Campisi, J., 2001. From cells to organisms: can we learn about aging from cells in culture?. *Exp. Gerontol.* 36 607–618.
- Connor, K.F., Lanner, R.M., 1989. Age-related changes in shoot growth components of Great Basin bristlecone pine. *Can. J. For. Res.* 19, 933–935.
- Connor, K.F., Lanner, R.M., 1990. Effects of tree age on secondary xylem and phloem anatomy in stems of Great Basin bristlecone pine (*Pinus longaeva*). *Am. J. Bot.* 77, 1070–1077.
- Connor, K.F., Lanner, R.M., 1991. Effects of tree age on pollen, seed, and seedling characteristics in Great Basin bristlecone pine. *Bot. Gaz.* 152, 107–113.
- Connor, K.F., Lanner, R.M., 1991. Cuticle thickness and chlorophyll content in bristlecone pine needles of various ages. *Bull. Torrey Bot. Club* 118, 184–187.
- Finch, C.E., 1999. Longevity without senescence: possible examples. In: Robine, J.-M., Vaupel, J., Jeune, B., Allard, M. (Eds.). *Paradoxes of Longevity*. Springer, Heidelberg.
- Forward, D.F., Nolan, N.J., 1964. Growth and morphogenesis in the Canadian forest species. VII. Progress and control of longitudinal growth of branches in *Pinus resinosa* Ait. *Can. J. Bot.* 42, 932–950.
- Franklin, E.C., 1970. Survey of mutant forms and inbreeding depression in species of the family Pinaceae. USDA Forest Service Research Paper SE-61, pp. 1–21.
- Franklin, E.C., 1977. Use of mutants in forest genetics research. Proceedings of the 14th Southern Tree Improvement Conference, Gainesville.
- Fritts, H.C., 1969. Bristlecone pine in the White Mountains of California: growth and ring-width characteristics. . Pap Lab Tree-Ring Res 4. University of Arizona Press, Tucson.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, New York.
- Gerrish, G., 1990. Relating carbon allocation patterns to tree senescence in *Metrosideros* forests. *Ecology* 71, 1176–1184.
- Greenwood, M.S., 1984. Phase change in loblolly pine: shoot development as a function of age. *Physiol. Plant.* 61, 518–522.
- Hubbard, R.M., Bond, B.J., Ryan, M.G., 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol.* 19, 165–172.
- Jacobs, M.R., 1955. *Growth Habits of the Eucalyptus*. Australian Forestry and Timber Bureau, Canberra.
- Jankiewicz, L.S., Stecki, Z.J., 1976. Some mechanisms responsible for differences in tree form. In: Cannell, M.G.R., Last, F.T. (Eds.). *Tree Physiology and Yield Improvement*. Academic Press, New York.
- Johnson, L.C., Johnson, J., 1978. Methuselah: fertile senior citizen. *Am. For.* 84, 29–31 (see also p. 43).
- Kaufmann, M.R., Watkins, R.K., 1990. Characteristics of high- and low-vigor lodgepole pine trees in old-growth stands. *Tree Physiol.* 7, 239–246.
- Kaufmann, M.R., 1996. To live fast or not: growth, vigor, and longevity of old-growth ponderosa pine and lodgepole pine trees. *Tree Physiol.* 16, 139–144.
- Lanner, R., 1976. Patterns of shoot development in *Pinus* and their relationship to growth potential. In: Cannell,

- M.G.R., Last, F.T. (Eds.). *Tree Physiology and Yield Improvement*. Academic Press, New York, pp. 223–243.
- Lanner, R., 1984. *Trees of the Great Basin*. University of Nevada Press, Reno.
- Lanner, R., 1999. *Conifers of California*. Cachuma Press, Los Olivos.
- Lyr, H., Polster, H., Fiedler, H.J., 1967. *Gehölzphysiologie*. G. Fischer, Jena.
- Medawar, P.B., 1957. *The Uniqueness of the Individual*. Basic Books, New York.
- Mikola, P., 1950. Puiden kasvun vaihteluista ja niiden merkityksestä kasvutukimuksissa. *Commun. Inst. For. Fenn.* 385, 1–131.
- Molisch, H., 1929. *Lebensdauer der Pflanze*. G. Fischer, Jena.
- Möller, C., Müller, D., Neilsen, J., 1954. Graphic presentation of dry matter production of European beech. *Forstl. Forsogsvaes Dan* 21, 327–335.
- Moorby, J., Wareing, P.F., 1963. Ageing in woody plants. *Ann. Bot.* 27, 291–308.
- Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. *Bioscience* 47, 235–242.
- Sax, K., 1962. Aspects of aging in plants. *Annu. Rev. Plant Physiol.* 13, 489–506.
- Scholtes, W.H., 1953. The concentration of forest tree roots in the surface zone of some piedmont soils. *Proc. Iowa Acad. Sci.* 60, 243–259.
- Schulman, E., 1943. Over-age drought conifers of the Rocky Mountains. *J. For.* 41, 422–427.
- Schulman, E., 1958. Bristlecone pine, oldest known living thing. *Natl. Geogr. Mag.* 111, 355–372.
- Wareing, P.F., 1958. Reproductive development in *Pinus sylvestris*. In: Thimann, K.V. (Ed.). *The Physiology of Forest Trees*. Ronald Press, New York.
- Wareing, P.F., 1959. Problems of juvenility and flowering in trees. *J. Linn. Soc. (London)* 56, 282–289.
- Went, F.W., 1942. Some physiological factors in the aging of a tree. *Proc. Natl. Shade Tree Conf.* 9, pp. 330–333.
- Westing, A.H., 1964. The longevity and aging of trees. *The Gerontologist* 4, 10–15.
- Woolhouse, H.W., 1972. *Ageing Processes in Higher Plants*. Oxford Biol. Readers. Oxford University Press, Oxford.
- Wright, R.D., Mooney, H.A., 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. *Am. Midl. Nat.* 73, 257–284.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40, 513–527.