

## **Layering and rejuvenation in *Tsuga canadensis* (Pinaceae) on Wachusett Mountain, Massachusetts**

Author(s): Peter Del Tredici David A. Orwig

Source: Rhodora, 119(977):16-32.

Published By: The New England Botanical Club, Inc.

<https://doi.org/10.3119/16-12>

URL: <http://www.bioone.org/doi/full/10.3119/16-12>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

LAYERING AND REJUVENATION  
IN *TSUGA CANADENSIS* (PINACEAE)  
ON WACHUSETT MOUNTAIN, MASSACHUSETTS

PETER DEL TREDICI

Arnold Arboretum of Harvard University, 1300 Centre Street,  
Boston, MA 02131-1013  
email: ptredici@oeb.harvard.edu

DAVID A. ORWIG

Harvard University, Harvard Forest, 324 North Main Street,  
Petersham, MA 01366

**ABSTRACT.** The phenomenon of layering in trees involves the production of adventitious roots by low-growing lateral branches and their subsequent reorientation from horizontal to vertical. This study provides the first documentation of layering in any natural populations of eastern hemlock, *Tsuga canadensis*. Twelve layered hemlock clumps, consisting of 5 to 20 layered branch stems originating from a parent tree, were observed on the upper slopes of Wachusett Mountain in central Massachusetts. Layered hemlocks ranged from 7 to 17 m tall, and several layered branches produced second-generation layers. Harsh growing conditions, slow hemlock growth, and the open habitat associated with small-statured hardwood species and exposed bedrock allowed the hemlocks to retain their lower branches for extended periods of time. Fallen limbs and debris associated with past disturbances pinned these branches to the ground and likely set the stage for layering. The production of physiologically rejuvenated hemlock ramets through the layering process serves to extend the life-span of hemlock genets, expand their spatial dominance of the area, and promote their persistence under stressful growing conditions.

**Key Words:** branch layering, clonal growth, eastern hemlock, physiological rejuvenation, *Tsuga canadensis*, Wachusett Mountain

Research on the phenomenon of clonal growth in trees—defined here as the production of secondary trunks—has traditionally been driven by casual observations in high elevation and/or high latitude sites (cf. Arno and Hammerly 1984; Cooper 1911; Légère and Payette 1981; Payette et al. 1994; Potzger 1937) as well as practical considerations in the fields of forestry and horticulture. It was not until the 1990s that people began looking more deeply at the ecological and evolutionary implications of clonal growth in trees—namely, how extending the lifespan of an individual organism can impact ecosystem structure as well as the genetic diversity and reproductive biology of a given species

(Bellingham and Sparrow 2000; Bond and Midgely 2001; De Witte and Stöcklin 2010).

The modern groundwork for the study of clonal regeneration in plants was laid by Harper (1977) who introduced the concepts of genet and ramet. The former refers to a genetically uniform individual (or clone) that is the product of sexual reproduction, and the latter to the separate, genetically identical modular units that expand the size of the clone over time. The complex developmental and morphological issues associated with clonal growth were reviewed by Groff and Kaplan (1988) who proposed four basic classes of plants based on the ability of their shoot systems to produce roots and *vice versa*. Jenik (1994) produced a review of clonal growth in both temperate and tropical woody plants focusing on morphological and ecological issues; and Del Tredici (2001) described four basic sprout morphologies in temperate trees and distinguished those that are genetically “programmed” from those that are environmentally induced or “opportunistic.” De Witte and Stöcklin (2010) reviewed all documented examples of long-lived clonal plants—including trees, shrubs and herbaceous species—and evaluated the various techniques used for estimating their age; they also discussed the ecological and evolutionary implications of increased genet longevity that results from clonal growth.

The most famous case of sprouting by a temperate tree is the ‘Pando’ clone of *Populus tremuloides* Michx. (Salicaceae) in south-central Utah that covers 43 ha and is thought to be between 10,000 and 80,000 y old (Kempferman and Barnes 1976; Mitton and Grant 1996). Within the past 15 y, a number of articles have been published describing woody plants reaching extreme ages based on their capacity for clonal growth, including root suckers of *Ulmus procera* Salisb. (Ulmaceae): 2000-y-old (Gil et al. 2004); lignotubers in *Olea europea* subsp. *laperrinei* (Batt. & Trab.) Cif. (Oleaceae): 3000-y-old (Baali-Cherif and Besnard 2005); collar or crown sprouts in *Quercus palmeri* Engelm. (Fagaceae): 13,000-y-old (May et al. 2009); rhizomes in *Serenoa repens* (W.Bartram) Small (Arecaceae): 1227 to 5215-y-old (Takahasi et al. 2011); branch layering in *Picea abies* (L.) H.Karst. (Pinaceae): 9550-y-old (Öberg and Kullman 2011); and basal sprouting in *Adansonia digitata* L. (Malvaceae): 1400 ± 50-y-old (Patrut et al. 2015). These last two examples are particularly significant because the authors were able to accurately determine the age of clones using radiocarbon dating, in contrast to the other studies in which growth rates formed the basis of age estimates.

The phenomenon of “layering” is the focus of this study and involves the production of adventitious roots by low-growing lateral branches

and their subsequent reorientation from plagiotropic (horizontal) to orthotropic (vertical). The proximal end of the layered branch usually retains its original thickness, whereas the distal end—beyond the point of adventitious root production—thickens in proportion to the vigor of the reoriented branch (Figure 1). Over time the original connection to the mother trunk will often rot away, leaving a free-standing, functionally independent trunk. Such trunks will always show a strong curvature at their base—away from the mother trunk—as well as a distinct taper at their proximal end (Figure 2). Conceptually, plants that display the layering behavior fit Groff and Kaplan's "Class 2" category in which the genet consists of a single shoot system with multiple root systems.

The layering of lateral branches as a method of horticultural propagation for crop trees goes back to the dawn of horticulture—having been described by various ancient Greek and Roman authors including Theophrastus, Cato, Columella and Pliny—and was inspired by the observation of wild-growing plants. When cultivated as open-grown specimens, most trees have the capacity to produce branch layers when low-hanging branches come in contact with soil (Del Tredici 2001; Koop 1987; Rackham 1986). The lead author has personally documented branch layering in a wide variety of cultivated gymnosperms and angiosperms in botanical gardens and parks where the wide spacing of specimen trees promotes the retention of lower branches longer than they would under forested conditions, including: *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. (Cupressaceae) and *C. pisifera* (Siebold & Zucc.) Endl., *Picea abies*, *Taxus cuspidata* Siebold & Zucc. (Taxaceae), *Thuja occidentalis* L. (Cupressaceae) and *T. plicata* Donn. ex D. Don, *Fagus sylvatica* L. (Fagaceae), *Franklinia alatamaha* Marshall (Theaceae), *Ginkgo biloba* L. (Ginkgoaceae), *Heptacodium miconioides* Rehder (Caprifoliaceae), *Magnolia grandiflora* L. (Magnoliaceae) and *M. kobus* DC., *Platanus ×acerifolia* (Aiton) Willd. (Platanaceae), *Quercus virginiana* Mill. (Fagaceae) and *Salix ×fragilis* L. (Salicaceae).

Layering is less readily observed on trees in the wild, but nevertheless it is fairly common, especially among conifers in the Pinaceae and Cupressaceae families, as documented in early work by Cooper (1911, 1931), Fuller (1913), Potzger (1937), Griggs (1938), Curtis (1946) and thoroughly reviewed by Timell (1986, pp. 902–911). The ecological impacts of layering are especially noteworthy among conifers growing on exposed, high elevation and high latitude sites where harsh, sunny conditions promote the retention of lower branches and the formation of a "krummholz" growth habit (Arno and Hammerly 1984), as



Figure 1. Left: recently formed adventitious roots in a layered hemlock branch. The buried portion of the stem is brown, the aerial portion whitish. Right: a well-rooted hemlock branch. Note the greater branch thickness at the distal end of the branch.

documented for *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae) and *Picea engelmannii* Parry ex Engelm. (Pinaceae; Griggs 1938; Marr 1977); *Pinus mugo* Turra (Pinaceae; Jenik 1994); *Pinus pumila* (Pall.) Regal (Pinaceae; Kajimoto 1992); *Picea mariana* Britton, Sterns & Poggenb. (Pinaceae; Légère and Payette 1981; Payette et al. 1994); and *Picea abies* and *Pinus sylvestris* L. (Pinaceae; Öberg and Kullman 2011; Senfeldr and Madera 2011).

Layering is also common on conifers growing in sunny, moist habitats at lower elevations where the soil conditions facilitate the development of adventitious roots as documented for *Picea sitchensis* (Bong.) Carrière (Pinaceae), *Tsuga heterophylla* Sarg. (Pinaceae) and *T. mertensiana* (Bong.) Carrière (Cooper 1931); *Thuja occidentalis* (Curtis 1946; Larson et al. 1993); *Picea mariana* (Fuller 1913; Stanek 1968); and *Sequoia sempervirens* Endl. (Cupressaceae; Del Tredici 1998, 1999). In *Silvics of North America* (Burns and Honkala 1990), layering is reported as occurring in the native habitats of the following North American conifers: *Abies lasiocarpa*, *Chamaecyparis lawsoniana*



Figure 2. Photo from 2006 of the entirety of layered hemlock clump JF 1 on Wachusett Mountain. The mother trunk is surrounded by “windswept” layered branches. Figure 3 shows the same plant from the same orientation and provides details on the size and age of the ramets.

(*A. Murray bis*) Parl. (Cupressaceae) and *C. nootkatensis* (D. Don) Spach, *Larix laricina* (Du Roi) K. Koch (Pinaceae), *Picea engelmannii*, *P. glauca* (Moench) Voss (Pinaceae), *P. mariana* and *P. sitchensis*, *Taxus brevifolia* Nutt. (Taxaceae), *Thuja occidentalis*, *T. plicata* and *Tsuga mertensiana*. Interestingly, *Pinus rigida* Mill. (Pinaceae), which grows on mountain tops and sandy soils in eastern North America, has never been documented to form rooted, reoriented branch layers despite the fact that it often produces prostrate lower branches in direct contact with the soil surface (Abrams and Orwig 1995; Motzkin et al. 2002).

#### MATERIALS AND METHODS

Wachusett Mountain in central Massachusetts was initially identified as containing old-growth forests in 1996. As determined by Orwig et al. (2001), these forests were concentrated in four distinct areas, and contained three species of trees: *Betula lenta* L. (Betulaceae), *B. alleghaniensis* Britton and *Quercus rubra* L. (Fagaceae) that had reached ages very near or exceeding their maximum known longevity (300–385

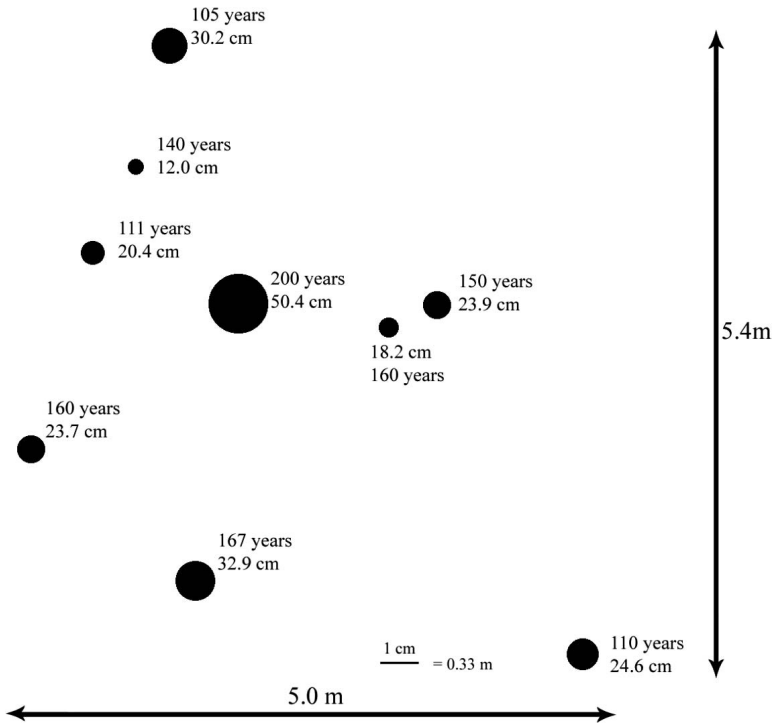


Figure 3. A schematic map of clump JF 1 (see Figure 2) on the periphery of the hemlock forest on Wachusett Mountain in 1999. Numbers represent diameter (in cm) at breast height (1.37 m) and age in years determined from core samples.

y). Most of the old-growth forest was restricted to steep, upper slopes with extensive rock outcrops. Trees were relatively short in stature, with considerable crown damage from frequent winter storms.

The authors first observed the layering of eastern hemlock, *Tsuga canadensis* (L.) Carrière in the fall of 1999 at the top of the Jack Frost Trail, at the northern edge of the Hemlock Forest, near its intersection with the Loop Trail. This was the first time either author had seen this behavior in wild-growing eastern hemlock and they speculated that the area must have been more open in the past than it currently was. The authors returned to the area on December 22 of the same year and measured the dimensions of a particularly large clump of layered stems (clump JF 1) and took core samples at breast height (1.37 m) from each of the individual layers to determine their respective ages relative to the mother trunk (Figures 2, 3).

The authors returned to Wachusett Mountain on April 14, 2009 and October 30, 2015, to search all four of the old-growth forest areas for more examples of hemlock layering. They located 11 additional large clumps of layered hemlocks and plotted their GPS locations on “Google Earth” (Figure 4). The authors documented the dimensions of the 12 layered clones using a tape measure to record 1) the distance around the polygon formed by the individual layered stems surrounding the mother trunk and 2) the DBHs of all the stems making up each clone (Table 1).

#### RESULTS

The twelve layered hemlocks were located in three distinct areas: 1) around the northern and eastern periphery of the Hemlock Forest (4 trees); 2) in the mixed woods along the Harrington Trail north of the Hemlock Forest and just beyond where it connects with the Link Trail (6 trees); and 3) along the Old Indian Trail (2 trees) just northwest of the summit (Figure 4; Orwig et al. 2001). The Hemlock Forest differed from the nearby old-growth hardwood stands in two ways: the dominance of a single species (*T. canadensis* made up roughly 72% of the density) and the fact that nearly 70% of all the trees were recruited within a relatively short 60-y time period, between 1770 and 1830. In addition to the clones that were measured, signs of past layering were evident on many of the hemlocks in the area, including within the hemlock forest proper, but the interconnections between the ramets had long since rotted away, leaving only a small branch stub pointing at a large tree with a slightly curved trunk.

It should be noted that three of the hemlock clumps along the Harrington Trail site (numbers 6, 8 and 11) were growing adjacent to the area where a 10-m-wide swath of trees had been cleared in the early 1900s to make way for a low-voltage power line up to the top of the mountain (Sinclair 1996; Figure 4). Maintaining the clearance for this line over the past 100 y created sunny, open conditions conducive to the layering of adjacent hemlocks. Along the Old Indian Trail, layered hemlocks were located within a mixture of stunted hardwoods growing on thin, barren soil, including *Quercus rubra*, three species of maples [*Acer rubrum* L. (Sapindaceae), *A. saccharum* Marshall and *A. pensylvanicum* L.], *Betula alleghaniensis*, *Fagus grandifolia* Ehrh. (Fagaceae), and *Ostrya virginiana* (Mill.) K.Koch (Betulaceae). There was extensive exposed ledge throughout the area where low-bush blueberry, *Vaccinium angustifolium* Aiton (Ericaceae), formed the dominant groundcover (Figure 5).



Figure 4. “Google Earth” locations of 12 layered hemlock clumps in vicinity of hiking trails and the power line on Wachusett Mountain described in this study. Most of the evergreen trees in the center of this image are hemlocks located in the Hemlock Old Growth area. Imagery from the Office of Geographic Information (MassGIS), Commonwealth of Massachusetts, MassIT.

Table 1. Dimensions of twelve clumps of layered hemlocks on the Jack Frost (JF), Harrington (HT) and Old Indian (OI) trails on Wachusett Mountain.

Clump	# of layered branch stems	Core (mother) tree DBH (cm)	Clone circumference (m)	Perimeter stem DBH range (cm)	Perimeter stem DBH total sum (cm)	Clone height (m)
JF 1	9	50.4	18.6	12.0-32.9	185.9	13
JF 2	8	missing	16.8	12.2-23.5	144.6	11
JF 3	9	32.3	17.7	15.0-36.4	214.4	15
HT 4	9	45.9	13.2	4.0-29.2	170.2	13
HT 5	5	41.8	11.5	13.2-27.7	215.7	17
HT 6	6	29.0	13.3	17.3-27.7	114.9	15
HT 7	14	30.5	20.6	5.0-30.4	209.3	13
HT 8	20	28.5	24.0	3.6-28.8	235.7	16
OI 9	12	21.7	13.7	1.5-14.9	81.9	8
OI 10	15	20.5	22.5	3.8-20.7	164.5	7
HT 11	5	28.5	16.0	3.9-24.1	116.6	10
JF 12	7	36.3	12.1	10.8-21.5	113.6	10

Based on the breast-height ring counts of the stems in Jack Frost clump JF 1 (Figures 2, 3), the mother trunk became established in 1799; the first layers from this stem formed between 1842 and 1849; a second set of layers formed between 1859 and 1869; and a third set between 1898 and 1904. The timing of these three layer-forming periods corresponds roughly to reductions in radial growth observed in nearby trees within the Hemlock Forest which occurred during the 1830s and 40s (modest reductions in most trees), the 1860s (abrupt declines in 60% of trees) and the early 1900s (declines in 40% of trees; Orwig et al. 2001). A severe ice storm occurred on the mountain in the early 1900s, leading to downed trees and branches throughout the reservation (WMSRC 1901). During the recent investigations, fallen branches were common in and around the forests studied, and the authors observed lower hemlock branches being pinned to the ground and several of the “first generation” layers possessed lower branches that produced roots and had given rise to “second generation” layers. It is likely that past disturbances produced similar conditions that led to layering at this site.

The data presented in Table 1 show considerable morphological variation among the hemlock clumps. Among the 12 measured clones, the number of layered branches varied from 5 to 20; heights varied from 7 to 17 m, with the shortest clones nearest the summit; clone circumference varied from 11.5 to 24 m; and the summed total DBH of the branch layers varied from 81.9 to 235.7 cm. In all cases except one, the DBH of the mother stem was greater than that of any of the layers. There was no relationship between the mother stem DBH and number of layered branches.

#### DISCUSSION

Although tropical trees produce a wide array of aerial and/or adventitious roots from their trunks and branches—best exemplified by mangroves (*Rhizophora* spp.) or various figs (*Ficus* spp.)—the phenomenon is not nearly so common in temperate trees and is not readily visible. In addition to adventitious roots produced by lateral branches in contact with soil, other types of *in situ* adventitious root production can be categorized by their location on the tree, including: 1) lateral branches high up in the canopy that are covered with moisture-trapping epiphytes (canopy roots; Nadkarni 1981, 1994); 2) swollen collars or lignotubers located at the base of the trunk or from the young stems that emerge from this tissue following traumatic injury (collar roots; Del Tredici 1992, 1998, 1999); 3) the cambium tissue of the trunk where it comes into contact with the moist decaying wood



Figure 5. Top: hemlock clump OI 10 consisting of 15 layered stems with a clone circumference of 22.5 m growing on rocky ledge. Bottom: the interior of hemlock clump OI 10 showing the layered lateral branches; note the atrophy of the lateral branches proximal to the location of adventitious root formation.

inside a damaged trunk (endocaulous roots; Jenik 1994; Liu and Wang 1992); and 4) fallen trunks or trunks that have been partially buried in silt following flooding (trunk roots; Del Tredici 1998; Koop 1987).

The traditional interpretation of adventitious roots, especially among plant physiologists, is that they are a manifestation of “juvenility” in the shoots that produce them, a view that derives mainly from the fact that, under controlled conditions, cuttings or

tissue cultured plants propagated from “juvenile” shoots root more readily than those taken from “mature” shoots (Barlow 1994; Greenwood 1995). The production of adventitious roots by mature trees under natural, forested conditions is a totally different matter and requires a different interpretation. Basic physiological research suggests that layering is a two stage process: 1) auxin—via polar transport—accumulates in stems that come in contact with wet soil and induces the formation of adventitious roots which 2) produce cytokinins that promote the “physiological rejuvenation” (i.e., reorientation) of that portion of the shoot system distal to their point of attachment (Sachs 1991; Thimann 1977). According to Sachs (2002), it is likely that “the apices of the lateral branches revert to vertical, dominant shoot growth in response to hormonal effects of the newly initiated roots at their base.” Indeed, the pronounced swelling of the distal portion of the layered branch—beyond the region of adventitious root formation (see Figures 1, 2 and 5)—can be interpreted as a morphological manifestation of the unidirectional or polar transport of auxin. Not unsurprisingly, a similar morphology has been observed in the ramets of many root-suckering trees (Del Tredici 2001; Kormanik and Brown 1967).

It is clear that secondary sprouting can greatly increase the life-span of an individual genet, thereby increasing its chances of successful sexual reproduction (Bond and Midgley 2001; DeWitte and Stöcklin 2010). It has also been speculated that basal sprouting can act as a mechanism to preserve genetic diversity by preventing “mutational meltdown” (e.g., genetic drift resulting from sexual reproduction in reduced populations) that would otherwise occur as a result of sexual reproduction within a small population (Baali-Cherif and Besnard 2005). The physiological rejuvenation associated with basal sprouting (or layering) in woody plants promotes both longevity and genetic stability by resetting the “aging clock” to an earlier developmental phase (Bon et al. 1994).

Layering in eastern hemlock is quite rare and the lead author has recently observed the phenomenon in only one other location: on an exposed granite outcrop at mid-elevation (560 m) along the Boulder Loop Trail in North Conway, New Hampshire. The trees were growing in soil-filled crevices where the roots and the lower branches were protected from the wind and the main stems were growing in full sun with little or no shading from adjacent trees. Five stunted 3–5 meter-tall trees were producing one to three layers each, and none of them were more than a meter from the mother trunk. Given that layering eastern hemlock has been observed on two different mountains, it

seems likely that it can be found on other mountain tops in the northeast, including locations disturbed by human activities, as seen along the 10-meter-wide power cut on Wachusett Mountain.

The authors speculate that at least four factors were involved in promoting the development of layered lateral branches: 1) the harsh weather and abundant surface bedrock have resulted in the extremely slow growth of both hemlock and its surrounding vegetation; 2) the sparse, open canopy associated with the surrounding small-statured hardwood species allowed the hemlocks at the edge of the stand to retain their lower branches longer than they would under shadier conditions; 3) over time, these slow-growing lower branches became longer and heavier, eventually coming close to or in contact with the soil surface; and 4) fallen limbs and debris associated with frequent weather disturbances on the mountain pinned these low-hanging branches to the ground, thereby setting the stage for the generation of adventitious roots and their reorientation to vertical. It also seems likely that damage to the main trunk, which is a frequent occurrence on exposed mountain tops, can also act as a stimulus to layering.

From an ecological perspective, layering not only extends the life-span of individual hemlock genets but also allows them to spread, albeit slowly, into adjacent hardwood dominated areas. In short, layering has enhanced the persistence of the hemlock population under the stressful growing conditions found on Wachusett Mountain. Potter et al. (2012) studied genetic variation in eastern hemlock across its range and found, surprisingly, that “populations in formerly glaciated regions are not less diverse than in putative southern refugial regions.” This finding suggests that the layering of *T. canadensis* could have been an important factor allowing the species to persist in northern regions during periods of Quaternary glaciation. As seen with many conifers growing at high elevations today, layering could well have enhanced eastern hemlock’s chances of survival under the exposed, subalpine conditions brought on by past periods of glaciation. Although such conditions have disappeared throughout much of eastern hemlock’s current range, they may still persist—at least on a functional level—on Wachusett Mountain and other exposed, high elevation locations.

ACKNOWLEDGMENTS. We would like to thank the Massachusetts Department of Conservation and Recreation and Wachusett Mountain State Reservation for access to these study sites. David Foster and Neil Pederson provided comments on the draft manuscript and Brian Hall provided assistance with Figures. Thanks also to the two anonymous reviewers who provided extremely helpful suggestions. This research is

a publication of the Harvard Forest Long Term Ecological Research Program, and was supported by NSF grants 0620443 and 1237491.

## LITERATURE CITED

- ABRAMS, M. D. AND D. A. ORWIG. 1995. Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. *Oecologia* 101: 353–360.
- ARNO, S. F. AND R. P. HAMMERLY. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers, Seattle, WA.
- BAALI-CHERIF, D. AND G. BESNARD. 2005. High genetic diversity and clonal growth in relict populations of *Olea europaea* subsp. *laperrinei* (Oleaceae) from Hoggar, Algeria. *Ann. Bot.* 96: 823–830.
- BARLOW, P. W. 1994. The origin, diversity and biology of shoot-borne roots, pp. 1–23. *In*: T. D. Davis and B. E. Haissig, eds., *Biology of Adventitious Root Formation*. Plenum Press, New York, NY.
- BELLINGHAM, P. J. AND A. D. SPARROW. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409–416.
- BON, M. -C., F. RICCARDI, AND O. MONTEUUIS. 1994. Influence of phase change within a 90-year-old *Sequoia sempervirens* on its *in vitro* organogenic capacity and protein patterns. *Trees* (Berlin) 8: 283–287.
- BOND, W. J. AND J. J. MIDGLEY. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16: 45–51.
- BURNS, R. M. AND B. H. HONKALA, eds. 1990. *Silvics of North America*. 2 vols. U.S. Forest Service, Agriculture Handbook 654. U.S.D.A., Washington, DC.
- COOPER, W. S. 1911. Reproduction by layering among conifers. *Bot. Gaz.* 52: 369–379.
- . 1931. The layering habit in Sitka spruce and the two western hemlocks. *Bot. Gaz.* 91: 441–451.
- CURTIS, J. D. 1946. Preliminary observations on northern white cedar in Maine. *Ecology* 27: 23–36.
- DEL TREDICI, P. 1992. Natural regeneration of *Ginkgo biloba* from downward growing cotyledonary buds (basal chichi). *Amer. J. Bot.* 79: 522–530.
- . 1998. Lignotubers in *Sequoia sempervirens*: Development and ecological significance. *Madroño* 45: 255–260.
- . 1999. Redwood burls: Immortality underground. *Arnoldia* 59, No. 3: 14–22.
- . 2001. Sprouting in temperate trees: A morphological and ecological review. *Bot. Rev.* 67: 121–140.
- DE WITTE, L. C. AND J. STÖCKLIN. 2010. Longevity of clonal plants: why it matters and how to measure it. *Ann. Bot.* 106: 859–870.

- FULLER, G. D. 1913. Reproduction by layering in the black spruce. *Bot. Gaz.* 55: 452–457.
- GIL, L., P. FUENTES-UTRILLA, A. SOTO, M. T. CERVERA, AND C. COLLADA. 2004. Phylogeography: English elm is a 2000-year-old Roman clone. *Nature* 431: 1053.
- GREENWOOD, M. S. 1995. Juvenility and maturation in conifers: current concepts. *Tree Physiol.* 15: 433–438.
- GRIGGS, R. F. 1938. Timberlines in the northern Rocky Mountains. *Ecology* 19: 548–564.
- GROFF, P. A. AND D. R. KAPLAN. 1988. The relation of root systems to shoot systems in vascular plants. *Bot. Rev.* 54: 387–422.
- HARPER, J. L. 1977. *Population Biology of Plants*. Academic Press, New York, NY.
- JENIK, J. 1994. Clonal growth in woody plants: A review. *Folia Geobot. Phytotax. (Praha)* 29: 291–306.
- KAJIMOTO, T. 1992. Dynamics and dry matter production of belowground woody organs of *Pinus pumila* trees growing on the Kiso mountain range in central Japan. *Ecol. Res.* 7: 333–339.
- KEMPFERMAN, J. A. AND B. V. BARNES. 1976. Clone size in American aspens. *Canad. J. Bot.* 54: 2603–2607.
- KOOP, H. 1987. Vegetative reproduction of trees in some European natural forests. *Vegetatio* 72: 103–110.
- KORMANIK, P. P. AND C. L. BROWN. 1967. Root buds and the development of root suckers in sweetgum. *Forest Sci.* 13: 338–345.
- LARSON, D. W., U. MATTHES-SEARS, AND P. E. KELLEY. 1993. Cambial dieback and partial shoot mortality in cliff-face *Thuja occidentalis*. Evidence for sectorial radial architecture. *Int. J. Pl. Sci.* 154: 496–505.
- LÉGÈRE, A. AND S. PAYETTE. 1981. Ecology of a black spruce (*Picea mariana*) clonal population in the hemiarctic zone, northern Quebec: Population dynamics and spatial development. *Arctic Alpine Res.* 13: 261–276.
- LIU, Q. AND Z. WANG. 1992. Root system inside heart-rot stem of *Betula ermanii*. *Res. Forest Ecosyst.* 6: 68–71.
- MARR, J. W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* 58: 1159–1164.
- MAY, M. R., M. C. PROVANCE, A. C. SANDERS, N. C. ELLSTRAND, AND J. ROSS-IBARRA. 2009. A Pleistocene clone of Palmer's oak persisting in southern California. *PLoS-ONE* 12: 1–5.
- MITTON, J. B. AND M. C. GRANT. 1996. Genetic variation and the natural history of quaking aspen. *BioScience* 46: 25–31.
- MOTZKIN, G., D. A. ORWIG, AND D. R. FOSTER. 2002. Vegetation and

- disturbance history of a rare dwarf pitch pine community on Mount Everett, Massachusetts. *J. Biogeogr.* 29: 1455–1467.
- NADKARNI, N. M. 1981. Canopy roots: Convergent evolution in rainforest nutrient cycles. *Science* 214: 1023–1024.
- . 1994. Factors affecting the initiation and growth of above ground adventitious roots in a tropical cloud forest tree: An experimental approach. *Oecologia* 100: 94–97.
- ÖBERG, L. AND L. KULLMAN. 2011. Ancient subalpine clonal spruces (*Picea abies*): Sources of postglacial vegetation history in the Swedish Scandes. *Arctic* 62: 183–196.
- ORWIG, D. A., C. V. COGBILL, D. R. FOSTER, AND J. F. O'KEEFE. 2001. Variations in old-growth structure and definitions: Forest dynamics on Wachusett Mountain, Massachusetts. *Ecol. Apps.* 11: 437–452.
- PATRUT A., S. WOODBORNE, K. F. VON REDEN, G. HALL, M. HOFMEYR, D. A. LOWY, AND R. T. PATRUT. 2015. African baobabs with false inner cavities: the radiocarbon investigation of the Lebombo EcoTrail baobab. *PLoS ONE* 10: e0117193. doi:10.1371/journal.
- PAYETTE, S., A. DELWAIDE, C. MORNEAU, AND C. LAVOIE. 1994. Stem analysis of a long-lived black spruce clone at treeline. *Arctic Alpine Res.* 26: 56–59.
- POTTER, K. M., R. M. JETTON, W. S. DVORAK, V. D. HIPKINS, R. RHEA, AND W. A. WHITTIER. 2012. Widespread inbreeding and unexpected geographic patterns of genetic variation in eastern hemlock (*Tsuga canadensis*), an imperiled North American conifer. *Conservation Genet.* 13: 475–498.
- POTZGER, J. E. 1937. Vegetative reproduction in conifers. *Amer. Midl. Naturalist* 18: 1001–1004.
- RACKHAM, O. 1986. *The History of the Countryside*. J. M. Dent, London, U.K.
- SACHS, T. 1991. *Pattern Formation in Plant Tissues*. Cambridge University Press, Cambridge, U.K.
- . 2002. Developmental processes and the evolution of plant clonality. *Evol. Ecol.* 15: 485–500.
- SENFELDR, M. AND P. MADERA. 2011. Population structure and reproductive strategy of Norway spruce (*Picea abies* L. Karst) above the former pastoral timberline in the Hrubý Jeseník Mountains, Czech Republic. *Mountain Res. Developm.* 31: 131–143.
- SINCLAIR, W. M. 1996. *Wachusett: Wajuset Gatherings from Then and When*. Higginson Book, Salem, MA.
- STANEK, W. 1968. Development of black spruce layers in Quebec and Ontario. *Forest. Chron.* 44: 25–28.
- TAKAHASHI, M. K., L. M. HORNER, T. KUBOTA, N. A. KELLER, AND W. G. ABRAHAMSON. 2011. Extensive clonal spread and extreme longevity in saw palmetto, a foundation clonal plant. *Molec. Ecol.* 20: 3730–3742.

- THIMANN, K. V. 1977. *Hormone Action in the Whole Life of Plants*. University of Massachusetts, Amherst, MA.
- TIMELL, T. E. 1986. Compression Wood in Gymnosperms. Springer-Verlag, Berlin, Germany. [pp. 902–911]
- WACHUSETT MOUNTAIN STATE RESERVATION COMMISSION (WMSRC). 1901. *First Annual Report of the Wachusett Mountain Commission*. Wright and Potter Printing, Boston, MA.