Seedlings Versus Tissue-Cultured *Kalmia latifolia*: The Case of the Missing Burl

Peter Del Tredici
Arnold Arboretum, 125 Arborway, Jamaica Plain, Massachusetts 02130

Basal burls, also known as lignotubers, are defined as aggregates of developmentally suppressed shoot buds which form at the base of the primary stem of seedlings as part of their normal ontogeny. Basal burls are commonly found in plants native to Mediterranean-type climates where fire is an important part of the local ecology. Following traumatic injury to the main stem, basal burls will sprout out vigorously to produce new shoots. In *Kalmia latifolia* (mountain laurel), the tendency to form basal burls seems to be greater in seedlings than in tissue-cultured plants, an observation that has important implications for the field of plant propagation.

INTRODUCTION AND DEFINITIONS

The subject of burl development in woody plants has never received the attention it deserves in either the horticultural or the botanical literature. The intent of this paper is to remedy the situation by: (1) providing a general overview of what is known about burl development; (2) examining the details of burl development in *Kalmia latifolia*, the mountain laurel (Ericaceae); and (3) exploring the implications of burl development for the field of plant propagation.

The existence of swollen, underground "root crowns" has been documented in a variety of ericaceous genera, including *Arctostaphylos* and *Arbutus* in the chaparral zone in California and *Erica* in the western Mediterranean region (Mesléard and Lepart, 1989). In both of these groups, burls, which are covered with "adventitious" buds, form at the base of plants. These buds remain dormant until some traumatic disturbance—particularly fire—damages or kills the trunk, at which point they sprout to produce new shoots. Garland and Marion define an ericaceous burl as:

> ". . . an aggregation of short branchlets fused into a complex, patterned mass of wood. At its surface the branchlets are terminated by dormant buds, which are capable of sprouting when the main trunk is destroyed or the plant undergoes fire or other injury."

One key concept that should be added to this definition is that burl formation is part of the normal ontogeny of the plant and not simply "induced" by environmental factors. Indeed, the presence or absence of a burl has been used as a valid taxonomic trait for distinguishing species in the genus *Arctostaphylos* in California (Jepson, 1916; Weislander and Schreiber, 1939; Wells, 1969).

While burls typically form at or below the soil surface, they can also develop on above ground portions of the trunk, particularly on older plants. I suggest the term <u>basal burl</u> for those structures that occur underground (Fig. 1), and <u>aerial burl</u> for those that occur on the trunk above ground. Woody plants which are capable of vegetative reproduction from basal burls, or lignotubers as they are also called, are most commonly found in Mediterranean-type climates where fire is an important part of the ecology. Besides being formed on ericaceous plants, burls have also been reported in a variety of non-ericaceous genera including, *Eucalyptus* (Myrtaceae) in Australia (Carr et al., 1984), *Leucospermum* (Proteaceae) in South Africa, and *Ceanothus* (Rhamnaceae), and *Adenostoma* (Rosaceae) in California (James, 1984). Several gymnosperms are also known to form both basal and aerial burls, including *Ginkgo biloba* (Ginkgoaceae) (Del Tredici, 1992) and *Sequoia sempervirens* (Taxodiaceae) (Olson et al., 1990), both of which are considered fire-adapted species.

The earliest stages of basal burl development have been carefully studied in only *Eucalyptus* (Carr et al., 1984) and *Ginkgo* (Del Tredici, 1992). In both cases, burl formation starts with the proliferation of buds located in the axils of the cotyledons of young seedlings. In *Ginkgo* burl development is generally restricted to the cotyledonary node, while in *Eucalyptus*, nodes immediately above the cotyledons also become involved in burl development.

The view that basal burl formation is part of the normal ontogeny of those species in which they occur has not been widely accepted. Typically burls, both basal and aerial, are considered to be a "pathological" condition induced by some unknown vector (Haller, 1986). This misconception has arisen because of the failure to distinguish those burls that are induced by pathogenic agents (such as crown gall) from those that are associated with "normal" developmental processes. The situation is further complicated by the fact that many of the species that form basal burls also form aerial burls in response to severe crown or root damage (Del Tredici, 1992). At the physiological level, the distinction between basal and aerial burls is one of degree rather than substance, the former being triggered by endogenous developmental processes, the latter by exogenous environmental events.

The literature documenting burl formation in *Kalmia latifolia* consists of a single article by Barrett (1941) describing how burls were collected from wild plants for the purpose of manufacturing smoking pipe bowls, a use to which the burls of other Ericaceous plants, including *Erica arborea* (the true source of briar pipes) have traditionally been put (Fairchild, 1938; Garland and Marion, 1960). Unfortunately Barrett does not document the developmental morphology of burls in young plants or the ecological factors that determine why some plants have large burls and others do not. In the authoritative work on cultivated *Kalmia* (Jaynes, 1988) there is no specific mention of burls, although Figure 2-10 of the book shows a wild plant in Georgia with a large, exposed basal burl. In an unpublished PhD thesis on the ecology of mountain laurel by Kurmes (1961), basal burls are documented as the source of new stems following fire, logging, and hurricane damage.

Kalmia burls are still of economic importance in the mountains of North Carolina, where the plant is collected from the wild for horticultural purposes. The collecting process involves cutting back old plants to near ground level in the fall or winter, thereby inducing them to sprout out from basal burls the following spring. Collectors return the next year to dig up these laurel "plates," as they are called, which are then lined out in a nursery before being sold.

MATERIALS AND METHODS

In order to examine the early stages of burl development in mountain laurel, 50 seedlings of *K. latifolia* of various ages were collected from the wild in Connecticut (along Interstate Highway 84) and at the Harvard Forest in Petersham, Massachusetts. Preliminary observations on the early stages of burl development were made on these plants using a 40× Wild dissecting microscope.

Based on the general observation that burl development seems to originate at the cotyledonary node, a preliminary study was undertaken to examine the question: Do *Kalmia* plants propagated vegetatively from rooted cuttings or tissue culture—and hence lacking the cotyledonary node—show the same tendency to form burls as seedlings do? To test this hypothesis, 4-year-old seedlings and 7-year-old tissue-cultured *Kalmia* plants (an unnamed cultivar) that had been raised under nursery conditions in Hamden, Connecticut, were compared with one another in terms of the extent of basal burl development. This was done by removing the fleshy, outer cortex from the base of the stem. Once the cortex was peeled away, it was relatively easy to count the numbers of clusters of xylem bud traces on the basal portion of the stem using a dissecting microscope.

RESULTS

Preliminary observations on wild-collected seedlings indicate that the first stages of burl development in *Kalmia* become clearly visible with the aid of a dissecting microscope only after the plants are at least two years old. At this stage, all of the axillary buds that are located on the stem segment produced during the first year of growth undergo proliferation to form discrete swellings that protrude out from the stem by the end of their second season of growth. Typically this process involves not only the cotyledonary nodes, but also anywhere from 3 to 8 nodes above the cotyledons. On most of the seedlings, which ranged in age from 1 to 6 years old, the swollen axillary bud clusters remained distinct from one another; on a few of the older plants, however, the basal bud clusters coalesced to form a distinct burl. On seedlings that had experienced severe trauma and were difficult to age, burl development was extensive, and axillary buds produced during the second or third year of growth were involved in burl formation (Fig. 2).

Table 1. Basal burl development in seedlings versus tissue cultured plants of *Kalmia latifolia* raised in a common nursery.

Plant type	Plants number	Mean diameter of basal burls ± s.d. (cm)	Mean bud clusters on basal burls ± s.d.
7-year-old tissue-cultured	7	2.36 ± 0.65	6.6 ± 3.9
4-year-old seedlings	8	1.30 ± 0.23	19.1 ± 3.2

The measurements comparing the nursery-raised seedlings and tissue cultured plants are summarized in Table 1 and illustrated in Figure 3. The most striking finding is that there were nearly three times as many proliferating bud clusters on

Figure 1. A large basal burl on *Kalmia latifolia* growing at the Highstead Arboretum in Redding, Connecticut. Note that in addition to the young sprouts, the burl is covered with numerous suppressed buds.

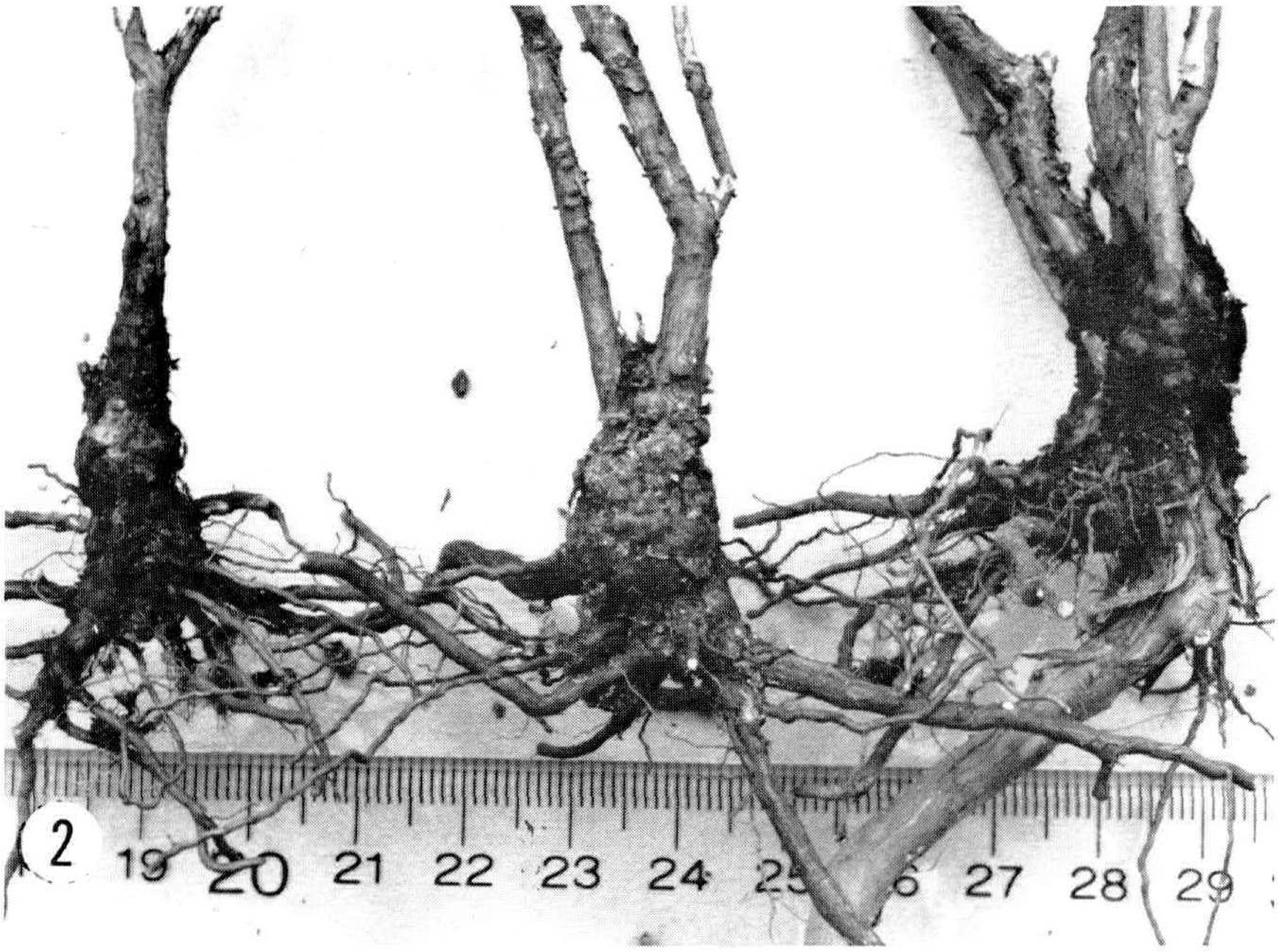

Figure 2. Young plants of *Kalmia latifolia* collected from the wild along Interstate highway 84 in Connecticut. Note the extensive basal burl development. Scale is in centimeters.

the basal portion of the stems of seedlings than on the stems of the tissue-cultured plants, this despite the fact that the seedlings were only slightly more than half as old and half as large as the tissue-cultured plants. This observation, which must be considered strictly preliminary, suggests that the ability to form basal burls is much greater in seedlings than in tissue-cultured plants. Whether this difference is due to the absence of the cotyledonary node has not yet been determined, but, at present, it is the most plausible explanation. A more thorough investigation of role of the cotyledonary node in basal burl formation is currently under investigation by the author.

DISCUSSION

As a working hypothesis, I would like to propose that the physiological processes that result in burl formation in *K. latifolia* are initiated at the cotyledonary node. Lacking the cotyledonary node as an organizing center, vegetatively propagated plants ought to show a diminished tendency to form burls. Other nodes located at the base of the stem of vegetatively propagated plants will form discrete clusters of embedded buds, but I suggest that these will not coalesce into the distinct basal burl which is typical of plants raised from seed. The implications of this are that in comparison to seedlings, vegetatively propagated plants (either tissue-cultured or rooted cuttings) ought to show a reduced ability to sprout following traumatic injury. The confirmation of this theory awaits further experimentation.

There can be no doubt that burls play an important role in the life cycles of those species in which they occur, and that a knowledge of the ecology, morphology, and

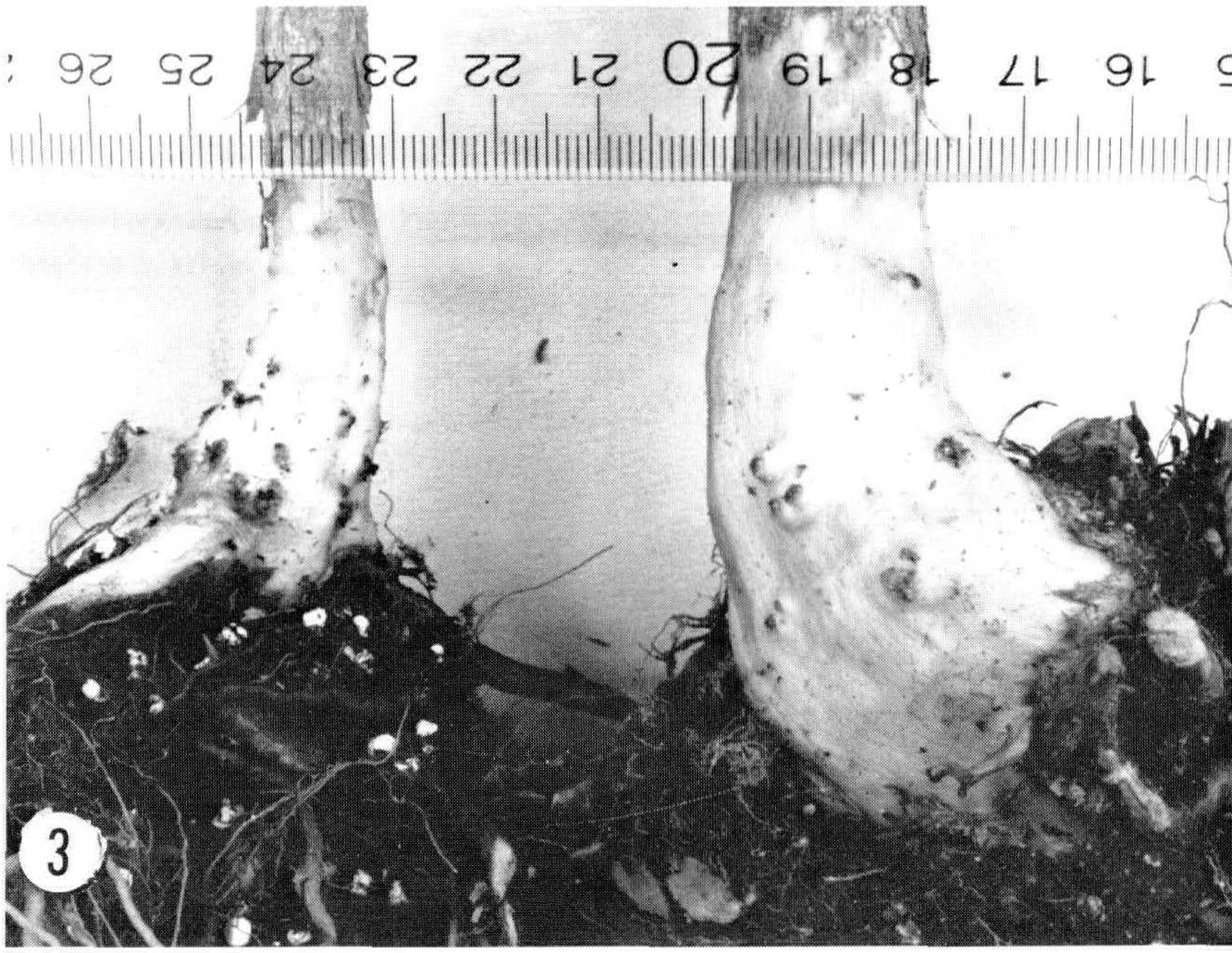

Figure 3. On the left is 4-year-old *Kalmia latifolia* seedling that has been decorticated to show the extent of basal burl development; on the right a 7-year-old tissue cultured plant. The seedling has 19 suppressed bud clusters in its basal region while the tissue cultured plant has only 9 suppressed bud clusters. Scale is in centimeters.

physiology of burl development might help explain the behavior of these species under cultivation. For example, the shoots produced by burls are considered physiologically "juvenile" in comparison to those produced by "mature" branches, and, consequently, they are usually much easier to root. In fact, many of the tree species that are successfully propagated by the traditional technique of "stooling" are burl formers in their native habitat. Another example of a situation where the process of burl formation may be relevant to propagation is in the phenomenon of "tissue proliferation," that has been reported to be a serious problem in tissue-cultured *Rhododendron* (LaMondia et al., 1992). It has been suggested that this unusual pattern of development is either (1) an artifact of the tissue-culture process itself; or (2) caused by an external pathogen. It seems to this author, however, that tissue proliferation could simply be a case of uncontrolled burl development that has been stimulated by the hormonal conditions that prevailed during the process of tissue culture propagation. Be that as it may, it seems likely that a clear understanding of the process of burl development as it occurs in nature might shed light on the behavior of *Rhododendron* microcuttings in tissue culture.

Acknowledgments. The author would like to thank Richard Jaynes of Broken Arrow Nursery in Hamden, Connecticut, for donating seedlings and tissue-cultured plants used in this study, which was partially funded by a grant from the Highstead Foundation in Redding Connecticut.

LITERATURE CITED

Barrett, L.I. 1941. War revives an old industry. American Forests 47:503-506, 543.

Carr, D.J., R. Jahnke, and **S.G.M. Carr**. 1984. Initiation, development and anatomy of lignotubers in some species of *Eucalyptus*. Aust. J. Bot. 32:415-437.

Del Tredici, P. 1992. Natural regeneration of *Ginkgo biloba* from downward growing cotyledonary buds (basal chichi). Amer. J. Bot. 79:522-530.

Fairchild, D. 1938. The world was my garden. Scribner's Sons, New York.

Garland, H. and **L. Marion.** 1960. California manzanita for smoking pipes. U.S.D.A. For. Serv. PSW Misc. Paper 53. Pacific Southwest Forest and Range Expt. Stn., Berkeley, Calif.

Haller, J.M. 1986. Tree care. Macmillan Publ. Co., New York.

James, S. 1984. Lignotubers and burls—their structure, function and ecological significance in Mediterranean ecosystems. Botanical Review 50:225-266.

Jaynes, R.A. 1988. *Kalmia*: The laurel book II. Timber Press, Portland, Oregon.

Jepson W.L. 1916. Regeneration in manzanita. Madrono 1:3-11.

Kurmes, E.A. 1961. The ecology of mountain laurel in southern New England. Ph.D. dissertation, Yale Univ., New Haven, Conn.

LaMondia, J.A., T.M. Rathier, V. L. Smith, T.M. Likens, and **M.H. Brand.** 1992. Tissue proliferation/crown gall in *Rhododendron*. Yankee Nursery Quarterly 2(2):1-3.

Mesléard, F. and **J. Lepart.** 1989. Continuous basal sprouting from a lignotuber: *Arbutus unedo* L. and *Erica arborea* L., as woody Mediterranian examples. Oecologia 80:127-131.

Olson, D.F., D.R. Roy, and **G.A. Walters.** 1990. *Sequoia sempervirens*. In: Silvics of North America, R. M. Burns and B. H. Honkala, (eds.). Agriculture Handbook 654, USDA.

Sinclair, W.A., H.H. Lyon, and **W.T. Johnson.** 1987. Diseases of trees and shrubs. Cornell Univ. Press, Ithaca, N. Y.

Wells, P.V. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264-267.

Wieslander, A.E. and **B.O. Schreiber**. 1939. Notes on the genus *Arctostaphylos*. Madroño 5:38-47.