A Method for Age Determination of Active Red-cockaded Woodpecker Cavities

- Erik D. Doerr, The Fisheries and Wildlife Program, Department of Forestry, North Carolina State University, Box 8002, Raleigh, NC 27695
- **Richard A. Lancia,** The Fisheries and Wildlife Program, Departments of Forestry and Zoology, North Carolina State University, Box 8002, Raleigh, NC 27695

Phillip D. Doerr, The Fisheries and Wildlife Program, Departments of Zoology and Forestry, North Carolina State University, Box 7617, Raleigh, NC 27695

Abstract: A method for determining the ages of active red-cockaded woodpecker (RCW) (*Picoides borealis*) cavities was developed based on data from 22 RCW cavity trees downed in the Francis Marion National Forest by Hurricane Hugo. Cavity age was measured in growing seasons of the tree from the date of cavity initiation. Age determination was based macroscopic and microscopic wound responses in wood removed from the side of the cavity entrances. The method was tested on 8 active cavities of known age located in the Sandhills Gamelands, North Carolina. All of the cavity age estimates were within 2 years of the known ages. In the year following the test no adverse effects on the birds have been reported. A method for rougher estimation of cavity ages is also presented as are suggestions for improvement, further testing, and application of both cavity aging methods.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 46:230-240

The RCW is an endangered species whose range is limited to mature pine forests in the southeastern United States (U.S. Fish and Wildl. Serv. 1985). The bird is unique among woodpeckers in that it builds its cavities exclusively in the wood of living southern yellow pines, preferably longleaf pine (*Pinus palustris*) or loblolly pine (*P. taeda*). These trees are usually mature, averaging 95 years old for longleaf and 75 years old for loblolly pine (Jackson et al. 1979). Because the availability of potential cavity trees is a primary factor limiting RCW populations, a better understanding of the dynamics of cavity tree creation and loss would likely facilitate management of these populations.

In creating a cavity, a RCW actually inflicts a fairly serious injury on the tree it inhabits, and the tree responds to this injury in a number of ways. These responses, some macroscopic and some microscopic, serve to create barriers between injured wood, which is very susceptible to invasion by decay-causing microorganisms, and the surrounding, uninjured wood, especially that which is created after the injury (Shigo and Marx 1977, Shigo 1979).

The most common large-scale response to a serious physical injury is the formation of a callus, where the tree attempts to grow over the injury (Panshin and DeZeeuw 1980, Shigo 1986). Other macroscopic wound responses common to pines include the creation of false rings and increased production of vertical resin canals (McGinnes et al. 1977, Tippett and Shigo 1980, 1981).

Many microscopic wound responses can also be associated with physical injuries to pines, including disordered tracheid growth, abnormal amounts of ray parenchyma cells, and the formation of tangential bands of marginal parenchyma and vertical resin canals (Tippett and Shigo 1980, 1981; Kuroda and Shimaji 1984; Kuroda 1986).

Previous studies have examined wound responses in trees to date the activities of the animals that caused the injuries. Lawrence (1952) examined cross-sections and increment cores from a number of tree species to determine the ages of beaver (*Castor canadensis*) feeding scars. Spencer (1964) studied cross-sections and cores and Payette (1987) cross-sections alone to date porcupine (*Erethizon dorsatum*) feeding scars to trace the historical expansion and fluctuation in porcupine populations. Unfortunately, none of these studies could confidently assess the accuracy of their techniques. Means (1989), however, demonstrated that single bole scars in Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) could be dated accurately by counting rings in increment cores.

We were presented with a unique opportunity to closely examine 22 cavities obtained from trees blown down in the Francis Marion National Forest by Hurricane Hugo in September 1989. Our objective was to use these trees to devise a method to age active cavities excavated by RCWs. By cavity age we mean the time, measured in growing seasons of the tree, from the initiation of the cavity to the present or to the death of the tree. To accomplish this goal we wanted to: 1) determine the wound responses that commonly occurred in response to cavity initiation and the location and extent of these responses relative to the cavity entrance, 2) devise a method that would allow us to sample wood containing these wound responses in a way that did not interfere with a bird's long-term use of the cavity, and 3) test our cavity aging method on known-age, active RCW cavities.

Application of our aging method could vastly improve the present understanding of the dynamics of cavity creation and loss. Specifically, the method could be used to verify reports of RCW colony expansion and to determine minimum tree ages for cavity excavation. These applications could have significant implications for the management of the RCW. It is therefore urgent that the method be tested further to better assess its accuracy and to detect any possible adverse effects of the field techniques involved. We thank the U.S. Fish and Wildlife Service and the U.S. Forest Service for funding and the following groups and individuals for their advice and technical assistance which made this research possible: C. A. LaPasha and E. A. Wheeler of the NCSU Wood Anatomy Lab; J. H. Carter, D. K. Woodward, and D. E. Davenport of the NCSU Department of Zoology; W. L. Hafley of the NCSU Department of Forestry; W. S. Bryan and R. C. Gilmore of the NCSU Wood Products Lab; C. Watson and R. G. Hooper of the U.S. Forest Service (Witherbee, S.C.); J. P. Abbott of the NCSU Natural Resources Library; the NCSU Cooperative Fisheries and Wildlife Research Unit; the NCSU Forest Biology Research Center, and the NCSU Departments of Forestry and Zoology.

Description of Cavities

Methods

The RCW cavities we studied were collected by U.S. Forest Service personnel from trees downed by hurricane Hugo in September 1989 on the Francis Marion National Forest in South Carolina. The Forest supports second-growth stands of longleaf and loblolly pine described by Hooper and Lennartz (1981), while the dramatic impacts of the storm were documented by Hooper et al. (1990).

Twenty-two RCW cavities were collected in short bolts 0.5-1.0 m in length. Cavities were bisected longitudinally through the cavity entrance with a radial bolting saw, except the 6 largest bolts (diameter) which had to be split with a chainsaw. Half of each cavity was cross-sectioned using a bandsaw. A first cut was made through the middle of the entrance followed by a cut 5 cm above and another 5 cm below this first cut. At least 1 transverse surface from each cavity was sanded to facilitate close examination of annual rings.

Macroscopic Examination.—All wood surfaces, especially those that had been close to the cavity entrance, were examined carefully for evidence of callus growth or other macroscopic wound responses. A dissecting scope was used to aid examination of some surfaces, especially those containing possible false rings. The age of each cavity was estimated based on the number of growth rings associated with these macroscopic wound responses.

Microscopic Examination.—Small blocks of wood were cut from the side of each cavity entrance, and 40–50 μ m thick transverse sections were cut for examination. For some of the cavities, additional sections were taken farther to the side, above, or above and far to the side of the entrance. Sections were stained with 5% safranin before being mounted onto slides with Polysciences plastic mounting media. Slides were examined for evidence of microscopic responses to injury and provided the basis for revision of our initial cavity age estimates based on macroscopic examination alone.

Results

Macroscopic Responses.—Examination of macroscopic wound responses allowed age estimation for all 22 cavities. These estimates indicated an average cavity age of 12.0 years. In all cases a single annual ring contained the earliest wound responses to injury by a RCW. Wood before this ring appeared to exhibit normal, unaffected growth, while that laid down subsequently showed a variety of responses associated with injury.

A common response (12 of 22) was the formation of an obvious callus, where the tree attempted to close over the wound, namely the cavity entrance. To either side of the entrance the affected growth rings were much wider, often double or triple the width of other rings, and they curved inward near the cavity entrance. The lateral extent of the response was generally limited to 4–6 cm from the entrance. Presumably, only the continued activity of the birds prevented these calli from covering over the cavity entrance. False rings were more common within the thickened rings of a callus than elsewhere and extended only as far as the rings remained abnormally wide. An increased number of vertical resin canals seemed always to accompany callus growth and these were detectable with the unaided eye.

For the other cavities there were other, less obvious, clues that dated cavity initiation. These trees often exhibited characteristics of callus growth in the same areas that callus responses were seen in other trees, but without formation of an obvious callus. In most cases there was some widening of annual rings, but not to the same extent as in a callus. The response was often highlighted by the presence of false rings or by especially thick bands of latewood cells.

In 5 cases, further evidence for the dating of initial injury was provided by the presence of a ring shake. A ring shake is a crack or split in the wood either between rings or within a single annual ring (Panshin and DeZeeuw 1980, Shigo 1986). Shakes occurred commonly at locations where various microscopic response to cavity initiation rendered the wood structurally weak (Tippett and Shigo 1980).

Microscopic Responses.—In all cases there was wound tissue that could correspond to what others have referred to as a barrier zone—a wall of special tissue that acts to protect wood formed after an injury against infection by decay organisms in the wounded wood (Shigo and Marx 1977, Shigo 1979). Many characteristics of this wound tissue were consistent for all cavities. However, based on the cavities from which sections were taken from more than 1 location, the spread of the response away from the injury is not consistent. In general the degree of response decreased with distance from the entrance, but the response often seemed to be patchy or intermittent, affecting wood directly to the side of the entrance but not that 1 cm higher or vice versa.

Occasionally wound tissue had the appearance of a false ring, and vertical resin canals were always associated with it. Often several resin canals were lined up in a row almost touching, an occurrence never seen in healthy tissue. The tissue surrounding the resin canals consisted of parenchyma cells and disordered tracheids (Tippett and Shigo 1980, 1981; Kuroda and Shimaji 1984). These tracheids did not at all appear to have been formed in the orderly columns of normal wood and were often completely chaotic in their arrangement. Usually, some of these tracheids appeared to have reticulately thickened walls, giving their interiors a webbed appearance. We do not know the specific nature of these tracheids. Often they appeared earlier in the wood than any other response to the injury. Because the unusual

walls were formed during the wall thickening stage of tracheid development they may have been in response to injury that occurred after the cells were actually formed. These "webbed" tracheids could also have been the result of what Kuroda and Shimaji (1984) described as the invasion of mature tracheids by strongly activated (by injury) ray parenchyma cells which then reticulately thickened and lignified their cell walls. This conclusion may be supported by the fact that in many cavities wood formed after the initial injury contained enlarged ray parenchyma cells, which made the rays much wider in the affected area.

Correlation Between Macroscopic and Microscopic Responses.—Based on our examination of all of the microscopic wound responses described above, the initial cavity age estimates were revised. The correlation between macroscopic and microscopic wound responses was fairly good (Table 1). On average, the revised age estimates differed from the initial estimates by 1.3 years. Fourteen of the 22 macroscopic estimates were within ± 1 year of the microscopic estimates.

We placed more confidence in our microscopic estimates than in our macroscopic estimates for the following reasons. We assumed that microscopic wound responses were more closely correlated to the initiation of the cavity start (when the cambium was first penetrated) than were macroscopic wound responses. Micro-

| | Estimate | e (yrs) | Difference |
|------------|-------------|-------------|-----------------|
| Cavity no. | Macroscopic | Microscopic | (Micro - Macro) |
| 1 | 7 | 8 | + 1 |
| 2 | 10 | 11 | +1 |
| 3 | 6 | 6 | 0 |
| 4 | 8 | 10 | +2 |
| 5 | 10 | 11 | +1 |
| 6 | 8 | 8 | 0 |
| 7 | 18 | 21 | + 3 |
| 8 | 12 | 11 | -1 |
| 9 | 36 | 36 | 0 |
| 10 | 5 | 5 | 0 |
| 11 | 16 | 16 | 0 |
| 12 | 15 | 10 | - 5 |
| 13 | 14 | 16 | + 2 |
| 14 | 8 | 8 | 0 |
| 15 | 16 | 16 | 0 |
| 16 | 6 | 7 | +1 |
| 17 | 13 | 14 | +1 |
| 18 | 5 | 5 | 0 |
| 19 | 11 | 9 | -2 |
| 20 | 14 | 17 | + 3 |
| 21 | 16 | 18 | + 2 |
| 22 | 9 | 13 | +4 |
| Average | 12.0 | 12.5 | ±1.3 |
| SD | 6.7 | 6.9 | 1.9 |

 Table 1.
 Comparison of red-cockaded woodpecker cavity age

 estimates based on macroscopic and microscopic wound responses.

scopic wound responses should thus appear earlier (closer to the injury) than macroscopic responses; and in fact, 11 microscopic estimates gave an older estimate, while only 3 macroscopic estimates provided the older estimate. Other research on conifers has shown that microscopic wound responses occurred soon after injury to the cambium and corresponded to the location of the cambial initials when the injury occurred (Kuroda and Shimaji 1984, Kuroda 1986). Furthermore, macroscopic wound responses must be the result of microscopic processes and responses, whereas the opposite is not true. Logically then, we expect microscopic responses to be noticeable at the same time or earlier in the wood than macroscopic responses, and thus to correspond more closely to the time of injury.

Miscounting rings was also a problem. It is often difficult to differentiate between true annual rings and false rings without examining thin sections under a microscope. Additionally, injured wood tends to have a far greater frequency of false rings than does healthy wood. For 3 of our macroscopic estimates, we judged a false ring to be a true one or vice versa. These errors were only discovered after microscopic examination of the wood.

The lack of better congruence between macroscopic and microscopic wound responses effectively eliminated the possibility of developing a cavity aging method based solely on increment cores. Thin sections required for the examination of microscopic wound responses cannot be made from increment cores. Also, when examining an increment core it can be very difficult to differentiate between actual annual rings and false rings. Unlike the feeding scars of beavers or porcupines or other reported injuries, the injuries associated with cavity initiation, excavation, and maintenance are nearly continuous. Thus, wound responses including false rings occur in most or all annual rings following cavity initiation. For these reasons we devised a cavity aging method based on the removal of a small block of wood from the side of the cavity entrance.

Cavity Aging Method and Validation

Methods

We looked for known-age cavities on the Sandhills Gamelands (SGL) study area described in detail by Walters et al. (1988). SGL comprised nearly 17,000 ha of second-growth lengleaf pine forest with a scrub oak (*Quercus spp.*) midstory and a wiregrass (*Aristeda stricta*) dominated groundcover.

We used the cavity tree data set compiled by NCSU researchers since the early 1970s (J. H. Carter, III, P. D. Doerr, and J. R. Walters, unpubl. data) to identify 8 known-age cavities. We looked for cavities that had been discovered as recent cavity starts, with entrances <7.5 cm deep. Our search was complicated by the fact that RCWs may start a cavity and abandon it for years before turning it into a real entrance or a completed cavity. This makes it impossible to judge the age of an entrance or cavity start simply on the basis of appearance. We also wanted cavities that were discovered as starts in trees that already had ≥ 1 cavities or that were near

trees that did. This increased the likelihood that the start was located soon after its creation.

The first step in the cavity aging method was the removal of a block of wood, 1.5 cm high by 2.5 cm wide, from the side of the cavity entrance. The depth of the block depended on an a priori estimate of the cavity age, which was judged on the basis of its external appearance, particularly on the extent of plate development—the larger the plate the older the suspected age of the cavity. A minimum depth of 3 cm was taken when there was no plate. In cases where a large and well-developed plate indicated an old cavity, up to 5 cm were taken.

To remove the blocks, a cordless drill and a 5/32'' bit were used to perforate the wood around the block. By drilling at different angles across these perforations nearly all of the wood along the edges of the block was removed. Finally, a sharp wood chisel was used to pry the block loose of the surrounding wood.

Replacement blocks of slightly varied dimensions but about the size of those to be removed were prepared before going into the field. Many small chips of varying thickness were also cut. After a block was removed from the side of an entrance, a pre-cut pine block closely matching the gap created was selected and shaped to fit. The walls of the gap were coated with carpenter's wood filler, and the replacement block inserted along with small chips to wedge it in tightly. The sharp edge of the chisel was used to carve and shape the replacement block to match the original contours of the entrance. Finally, wood filler was used to fill any remaining gaps and for other final cosmetic touches.

For cavity entrances with plates around them, an increment borer was used to take cores from the tree at the same height as the entrance. The first core was taken 6 cm from the side block and then additional cores every 6 cm until the edge of the plate was passed. The blocks and cores from each cavity were assigned an arbitrary number so that the age estimates would be blinded.

At least 1 transverse surface of each block was sanded. We examined the sanded surfaces and cross-dated annual rings with the cores to formulate macroscopic age estimates for all of the cavities. Cross-dating was necessary because the outermost growth rings were often absent if there was a plate around the entrance. Thin sections from each block were prepared as previously described. Microscopic examination allowed verification or adjustment of the initial age estimates.

Results

Our estimates were within 2 years of the known ages of all 8 cavities (Table 2); 6 of the 8 estimates were within 1 year. The average error relative to the known ages was between ± 0.75 and ± 1.1 years (3 cavities had 2 possible known ages). At least three of our estimates were lower than the known age. The only clear overestimate was for cavity No. 4, which had 1 of the most uncertain "known-ages" as well as the single most uncertain estimate.

Our initial estimates based solely on macroscopic responses were all within 4 years of the known ages, and 7 of 8 were within 2 years. The average error in these estimates was between ± 1.6 and ± 2.0 years.

| Cavity no. | Known age (yrs) | Estimated age (yrs) | Error |
|------------|-----------------|---------------------|---------|
| 1 | 4 | 3 | - 1 |
| 2 | 8 | 7 | -1 |
| 3 | 2-3 | 2 | 0 or -1 |
| 4 | 8 | 10 | +2 |
| 5 | 7 | 7 | 0 |
| 6 | 7–8 | 8 | +1 or 0 |
| 7 | 12 | 10 | -2 |
| 8 | 7–8 | 77 | 0 or -1 |

 Table 2.
 Comparison of known-age cavities located on the

 Sandhills Gamelands, N.C., and estimated from our cavity aging method.

All wound responses observed in the cavities from the Francis Marion National Forest were seen in the wood taken from the known-age cavities. Our age estimates were based on macroscopic wound responses, the most important being callus formation, and on microscopic responses which included disordered or chaotic tracheid growth, "webbed" tracheids, false rings, and the proliferation of vertical resin canals and parenchyma cells. The increment cores taken from the 3 cavity trees with plates allowed accurate cross-dating to account for rings missing near the cavity entrances.

Discussion

Although the age estimates provided by our cavity aging method were all close to the known ages of the tested cavities, we believe that the method is capable of yielding even more accurate information. Much of the error in our estimates may be correctable via minor procedural changes. Additionally, some of the error was likely due to error in the "known-ages" of the cavities, which were actually just estimates based on different data.

Error in "Known-Ages"

Of the 8 "known-age" cavities tested, none of the ages was unequivocally certain, and 3 ages were definitely uncertain. Unfortunately, it was not uncommon for cavity trees to be missed during annual cavity tree updates (in April). Three of our cavities were discovered as apparently new starts in a cavity tree that had not been updated for 2 years; thus we had no way of knowing whether these cavities were initiated 1 or 2 years before discovery. In some cases we used cavities that had been the first start discovered in a tree, meaning that there had been no previous records for the tree. We felt reasonably safe in assuming that, because in these cases other cavity trees were nearby, the start was discovered during the first annual update after the cavity was created. However, there can be no guarantee of this, nor is there any guarantee that a new start discovered in a tree that already had cavities or starts

and was being updated annually was not simply overlooked the previous year. Also, a "known-age" could be off by a year if the cavity was initiated late in the year after the growing season of the pines had ended. Thus, a "known age" could be too low by 1 or 2 years. Finally, 1 of the cavity trees we tested (No. 1) was recorded dead as of April 1990. We assumed that the last growth ring at cavity height was the 1989 ring, but since trees do not die evenly or all at once, we cannot be sure of this fact.

Most of these factors contributing to uncertainty of the "known-ages" would cause a known age to be too low, whereas more of our estimates actually underestimated the known ages. The only plausible way that a known age could have been too old was if the bird initiated the cavity between the end of a growing season and the following cavity update in April. The records would indicate that initiation took place the year before the update, but wound responses would appear in the ring laid down during the growing season following the update.

Error in Our Age Estimates

There were a number of factors that led to varying degrees of uncertainty in the age estimates provided by our cavity aging method. One of the cavities in particular demonstrated the mistake of not taking cores from all cavity trees tested. The cores we took were invaluable in estimating the number of rings lost due to plate formation in 3 of the trees, but cavity No. 4 did not have a plate, and therefore no cores were taken. The cavity did, however, have an extensive zone of extremely chaotic growth. This zone extended laterally across the entire block and radially over an indeterminate number of rings, making accurate age estimation extremely difficult. We were also somewhat uncertain about 2 other estimates (cavities No. 2 and No. 5). In both cases there was 1 ring that contained obvious microscopic wound responses, while the preceding ring contained slight or ambiguous wound responses. For different reasons we chose the more recent ring for cavity No. 2 and the older one for No. 5. However, in both cases, the cavity tree records indicated that the older ring was the correct one. Perhaps, as a general rule, the older ring should be chosen when there is uncertainty as to which of 2 annual rings is the first containing responses to cavity initiation.

Finally, there was a slight, but possibly very important, difference between the time period estimated by the known-ages and by our age estimates. The known-ages were the best estimates, based upon cavity tree records and current knowledge of RCW behavior, of the time between cavity initiation (cambial penetration) and block removal. Our age estimates, based on wound responses in wood from the side of the cavity entrance, could not actually reveal the time of initial cambial penetration because the microscopic wound responses that occur in response to cambial injury do not generally spread more than a centimeter from the actual injury. Therefore, wood affected by the initial injury is eventually removed as the start is expanded to the full width of a cavity entrance. The responses that we examined in our wood blocks actually corresponded to the time when the start reached entrance width (about 5 cm). Usually, one would expect the time between the initiation of a start

and its widening to entrance size to be fairly short. However, it is conceivable that this period could be long enough to place the responses to the 2 events in different growth rings. If this is a common occurrence, estimates based on injury responses would often be low, and in fact at least 3 of our 8 estimates were lower than the known-age.

Two Levels of Accuracy

We developed our cavity aging method to provide the highest accuracy possible without significantly affecting the RCWs' use of the cavities. Some field applications may not require this degree of accuracy. In these cases a shorter version of our method based exclusively on macroscopic wound responses could be employed. The procedure for this short version would be identical to that used to provide the initial estimate for the long version. The laboratory-based procedures for sectioning and verification through microscopic examination would be eliminated. This short version of the cavity aging method would sacrifice much of the accuracy of the long version, but would be quicker, less costly, and generally less complicated. Alternate methods for microscopic examination, such as hand sectioning and mounting in karo syrup or glycerin, could also be explored.

The Future of the Cavity Aging Method

The cavity aging method worked well under field conditions and yielded estimates within 2 years of the known age. Rough estimates based solely on macroscopic responses were within 4 years. In the year following the test the birds using the cavities did not seem to have been affected by our activities. The field test also indicated that accuracy of at least 1 of the estimates could have been improved if ≥ 1 core had been taken from all cavities, even those lacking plates.

Obviously, such a limited sample does not allow definitive assessment of the accuracy of our methods. Moreover, there was considerable uncertainty associated with the "known ages" of the test cavities. Ideally, we should test both versions of the aging method on a larger sample of RCW cavities for which the dates of initiation are known with a high degree of certainty. Because such a sample might not be available, an alternative would be to test artificially drilled cavities. Many such cavities already exist, and some have been in place for several years (Copeyon 1990). Wound responses in these cavities may be quite similar to those found in cavities constructed by the birds themselves, and the exact dates of initiation would be known.

The additional tests suggested above would simply provide further evaluation of the accuracy of our cavity aging methods. However, we already have considerable confidence in the methods as developed. We believe that the estimates provided by the short version of the method will be within 2 years of the actual cavity ages about 75% of the time and within 4 years at least 90% of the time. Estimates provided by the complete method will be accurate within 1 year 75% of the time and within 2 years more than 90% of the time.

Literature Cited

- Copeyon, C. K. 1990. A technique for constructing cavities for the red-cockaded woodpecker. Wildl. Soc. Bul. 18:303–311.
- Hooper, R. G. and M. L. Lennartz. 1981. Foraging behavior of the red-cockaded woodpecker in South Carolina. Auk 98:321–334.
- —, J. C. Watson, and R. E. F. Escano. 1990. Hurricane Hugo's initial effects on redcockaded woodpeckers in the Francis Marion National Forest. North Am. Wildl. and Nat. Resour. Conf. 55:220–224.
- Jackson, J. A., M. R. Lennartz, and R. G. Hooper. 1979. Tree age and cavity initiation by red-cockaded woodpeckers. J. For. 77:102–103.
- Kuroda, K. 1986. Wound effects on cytodifferentiation in the secondary xylem of woody plants. Wood Res. 72:67-118.
 - and K. Shimaji. 1984. Wound effect on xylem cell differentiation in a conifer. Internatl. Assoc. Wood Anatomists Bul. 5:295–305.
- Lawrence, W. H. 1952. Evidence of the age of beaver ponds. J. Wildl. Manage. 16:69-79.
- Means, J. E. 1989. Estimating the date of a single bole scar by counting tree rings in increment cores. Can. J. For. Res. 19:1491-1496.
- McGinnes, E. A., J. E. Phelps, P. S. Szopa, and A. L. Shigo. 1977. Wood anatomy after injury: a pictorial study. Res. Bul. Mo. Agric. Exp. Sta. No. 1025. 35pp.
- Panshin, A. J. and C. DeZeeuw. 1980. Textbook of wood technology: structure, identification, properties, and uses of the commercial woods of the United States and Canada, 4th ed. McGraw-Hill Book Co., New York, N.Y. 722pp.
- Payette, S. 1987. Recent porcupine expansion at tree line: a dendroecological analysis. Can. J. Zool. 65:551-557.
- Shigo, A. L. 1979. Tree decay: an expanded concept. U.S. Dep. Agric., Agric. Inf. Bul. No. 419. 73pp.
- ------. 1986. A new tree biology dictionary: terms, topics, and treatments for trees and their problems and proper care. Shigo and Trees, Assoc., Durham, N.H. 132pp.
- and H. G. Marx. 1977. Compartmentalization of decay in trees. U.S. Dep. Agric., Agric. Inf. Bul. No. 405. 73pp.
- Spencer, D. A. 1964. Porcupine population fluctuation in past centuries revealed by dendrochronology. J. Appl. Ecol. 1:127–149.
- Tippett, J. T. and A. L. Shigo. 1980. Barrier zone anatomy in red pine roots invaded by *Heterobasidion annosum*. Can. J. For. Res. 10:224-232.
- and ———. 1981. Barriers to decay in conifer roots. European J. For. Pathol. 11:51– 59.
- U.S. Fish and Wildlife Service. 1985. Red-cockaded woodpecker recovery plan. U.S. Dep. Int. Fish and Wildl. Serv., Atlanta, Ga. 88pp.
- Walters, J. R., P. D. Doerr, and J. H. Carter III. 1988. The cooperative breeding system of the red-cockaded woodpecker. Ethology 78:275–305.