Douglas-Fir Sapwood Starch In Relation to Log Attack By The Ambrosia Beetle, Trypodendron

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Abstract. Starch in the sapwood of living *Pseudotsuga menziesii* (Mirb.) Franco varies considerably in amount during the year, with maximum and minimum quantities in early spring, and late summer, respectively. In cut logs, it slowly decreases in quantity over a period of many weeks. Logs with relatively much starch are not attacked by *Trypodendron lineatum* (Oliv.). Logs selected by the beetles have little or no starch, but many unattacked logs also contain little or no starch; there does not, therefore, appear to be a direct relationship between starch and log attractiveness.

AMBROSIA BEETLES (Coleoptera: Scolytidae and Platypodidae) generally attack wood of felled or dying trees and bore tunnels, in which they lay eggs and introduce the symbiotic fungi on which they feed (Fisher, Thompson and Webb 1953). Each species of beetle has its own preferences for tree species and tree or log condition.

The attack habits of the common temperate zone species, *Trypodendron lineatum* (Oliv.), may be summarized as follows: it attacks the sapwood of most conifers in western Canada, including Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Prebble and Graham 1957), and a variety of other conifers elsewhere (Hadorn 1933, Novak 1960); during its principal attack flight in spring, it prefers logs felled the preceding autumn or winter (freshly felled logs are not attacked); often there is considerable difference in density of attack on similar logs cut at the same time and place. The long-standing assumption that the beetles are attracted by odors to the logs has recently been confirmed (Chapman 1962).

It is logical to raise the question of the nature of the chemicals which guide *Trypodendron* to logs. Person's theory (1931) of bark beetle attraction assumed end products of a fermentation process to be involved, and Ohnesorge (1953) found several such chemicals to be attractive to one species. There are reports of ambrosia beetles or other scolytids seeking fermenting mixtures (Schneider-Orelli 1913, Frost and Dietrich 1929, Cleare 1938, Binion, 1962, see also, Chapman *l.c.*), and injection of alcohol into trees is known to cause attraction of some ambrosia beetles (Browne

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1952). Bletchley (1961) mentions that creosote, creosote type preparations, and fuel oil have been known to cause increased attacks by ambrosia beetles, possibly because of secondary effects. At present there seem to be no other clues regarding the chemical attraction of *Trypodendron.*

Many questions concerning the chemistry of living trees or cut logs cannot be answered now due to the poor state of present knowledge of tree physiology, and it appears that the search for specific chemicals responsible for log attraction of *Trypodendron* may be difficult. Meanwhile, however, there is much to be learned about the gross changes occurring in cut logs, in relation to beetle attack.

Starch, a basic plant food reserve, can be detected and roughly estimated very simply by the iodine test. This test has proved adequate for revealing major features of seasonal changes of stored food in a number of tree species, and for studying other important physiological features of tree life (e.g., Büsgen 1929, Ishibe 1935, Ruhland 1958). After preliminary tests showed that Douglas-fir starch is readily revealed in this way, a study of this substance in relation to *Trypodendron* attack was undertaken. It was believed that although starch might not be directly related to chemical attraction of this beetle, it must be an important indicator of physiological events in trees and cut logs and might be correlated in some way with log attractiveness. Numbers of attacked and non-attacked logs were tested for starch soon after heavy attack flights had revealed beetle preferences, and changes of starch content in cut logs with time were followed. It was necessary, also, since we could not find the information in the literature, to determine the main pattern of seasonal sapwood starch changes in Douglas-fir.

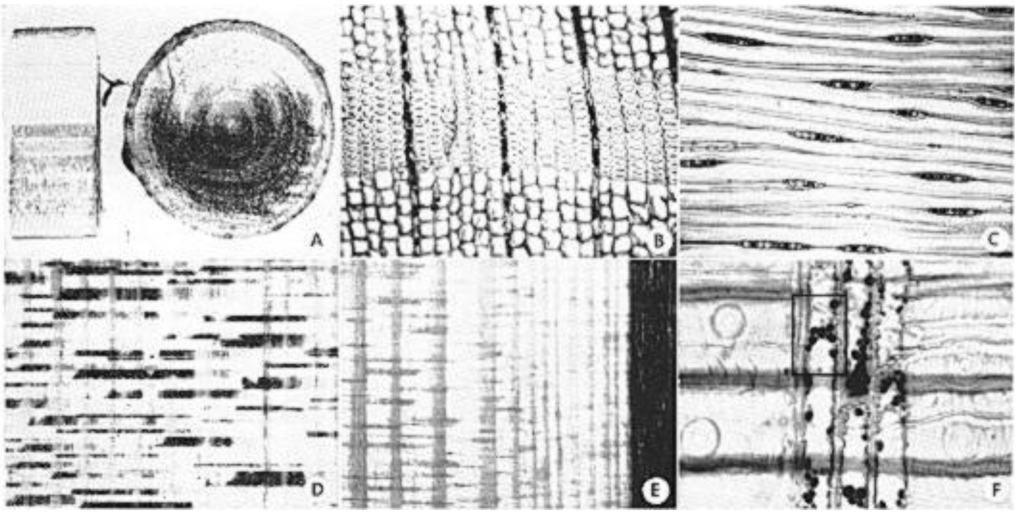


FIGURE 1. *Douglas-fir sapwood after iodine solution added; ratings indicate relative amounts of starch, 5 being maximum. A. Transverse and radial surfaces from young tree, at 1-inch diameter level. Iodine added to half of each piece (rating 5). B. Transverse section with medium starch rating (3)—× 100. C. Tangential section with medium starch rating (3)—× 100. D. Radial surface showing medullary ray parenchyma cells well packed with starch granules (rating 5)—×10. E. Radial surface showing non-uniform distribution of starch, which is depleted near bark (trace) but is appreciable in deeper layers (rating 3)—× 7.5. F. Individual granules in radial section showing arbitrary sampling unit for number of starch granules—the intersection of a wood fiber and medullary ray parenchyma cell (× 470).*

Methods and Results

General. A relative comparison of amounts of starch in different sapwood samples is most easily made by adding the iodine solution (0.3 g I, 1.5 g KI per 100 ml water) to radial surfaces (Compare Fig. 1 – A to E). We used a subjective numerical rating for starch abundance; *0*, trace, *1*, *2*, *3*, *4*, and *5* (maximum). Such a system of arbitrary ratings has been used by many investigators (e.g., Phillips 1938, Roberts 1961) and, although only rough comparisons of different samples can be made, the difference in time required for this as compared with a more accurate chemical analysis is very considerable.

Starch was usually found to be uniformly distributed in the sapwood of a given sample, even in portions with different growth rates. At certain times of the year, however, the amount varied with sapwood depth (Fig. 1-E). The starch grains are quite uniform in size and appearance, and changes in quantity of starch appear to be reflected in numbers of grains rather than their individual size or response to staining (see also, Phillips 1938).

We investigated the possibility of a more objective rating, made by counting individual starch grains in arbitrarily defined sample units in thin wood sections. These units were the rectangular areas formed by intersection of spring wood fibers and ray parenchyma cells (Fig. 1–F). Sections (40 μ) were prepared from blocks of wood with ratings of *1*, *3* and *5*, and numbers of grains were counted in 100 sample units selected by chance in a given section. The results verified the subjective rating differences but this method does not improve upon such ratings and takes far more time (Fig. 3).

Starch in attacked and non-attacked logs. Logging in the West Coast Region is done in large patches (settings) covering many acres. Generally, all trees in a setting are felled and cut into logs within a two or three week period and then lie in place until removal. At times, logs from autumn or winter fellings are still on the ground during the spring attack flights of *Trypodendron.* Even if usable logs have been removed, however, numerous large branches and broken pieces remain.

Settings representing different felling periods were visited several days after heavy attack flights of *Trypodendron,* and logs or large remaining pieces were examined for beetle attack and tested for starch. Because sapwood taken from different positions on the same log usually showed the same starch rating, one sample, taken some distance from an end, bruise or crack, was considered sufficient for each log. Examinations for starch in relation to beetle attack were made over a three year period. During times of heavy flight, beetles are to be found over wide areas. It is assumed, therefore, that all logs tested had been exposed to beetles and that those not attacked

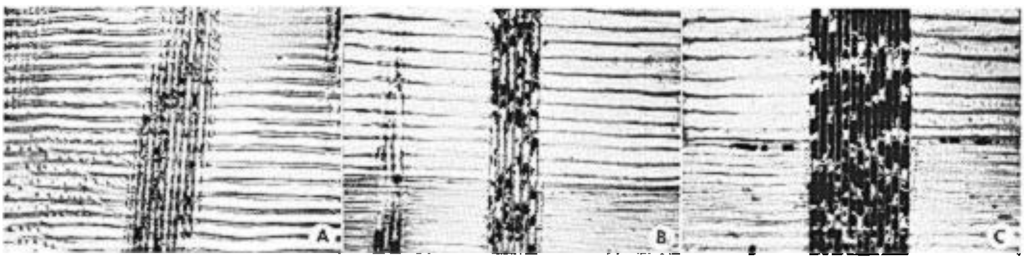


FIGURE 2. *Douglas-fir sapwood after iodine solution added; ratings indicate relative amounts of starch,* 5 *being maximum. A. Radial section with small amount of starch (rating* 1)—× *100. B. Radial section with medium amount of starch (rating* 3)—× *100. C. Radial section with large amount of starch (rating* 5)—× *100.*

were unattractive at the time of flight. Some data on western hemlock were also secured.

In 1958, all logs were classed as unattacked or with light, medium or heavy attacks. Data based on these categories, however, did not differ essentially from those in which logs were considered simply as attacked or unattacked. Moreover, attack density is related to both log attractiveness and numbers of attacking beetles in an area, and comparisons of densities in different logs are only valid and useful for those in the same location. The main feature of the 1958 data is that logs with the higher starch ratings were seldom attacked (Table 1–A).

The following year near Parksville, similar data were obtained. Whenever sapwood starch was not uniformly distributed in depth, both maximum and minimum ratings for a given sample were recorded, and both results are given (Table 1–B). It is apparent that most attacked logs had starch ratings of *0* to *2*. There is considerable overlap, however, in ratings of attacked and non-attacked logs, many of the latter also having only small amounts of starch.

In 1960, data were again taken in the Cowichan Lake area, and included results from an autumn- and a May-felled setting at the same altitude, less than a mile apart. Table 1–C shows that there was a clear difference between these settings in both starch content and beetle attacks, which were confined to the autumn-felled logs.

The May-felled logs displayed a steep starch gradient next to the cut ends. Samples taken within an inch of an end often rated considerably lower than those a foot or so away, examples being *1-3, 1-3, 0-3, 2-3, 1-2, 2-4* for various logs. This sort of difference occurred in all 30 logs examined in this way. These logs had intact bark and were quite moist, with no signs of drying at the ends. Apparently certain physiological changes occurred more rapidly next to the exposed ends; or qualitatively different changes were involved. Possibly such differences are related to oxygen tension, as Henderson (1943) found starch depletion to be related to oxygen supply in ash sapwood. It has been often noted in the field that a scattering of attacks occurs next to a cut end in an otherwise unattacked log. Moreover, short

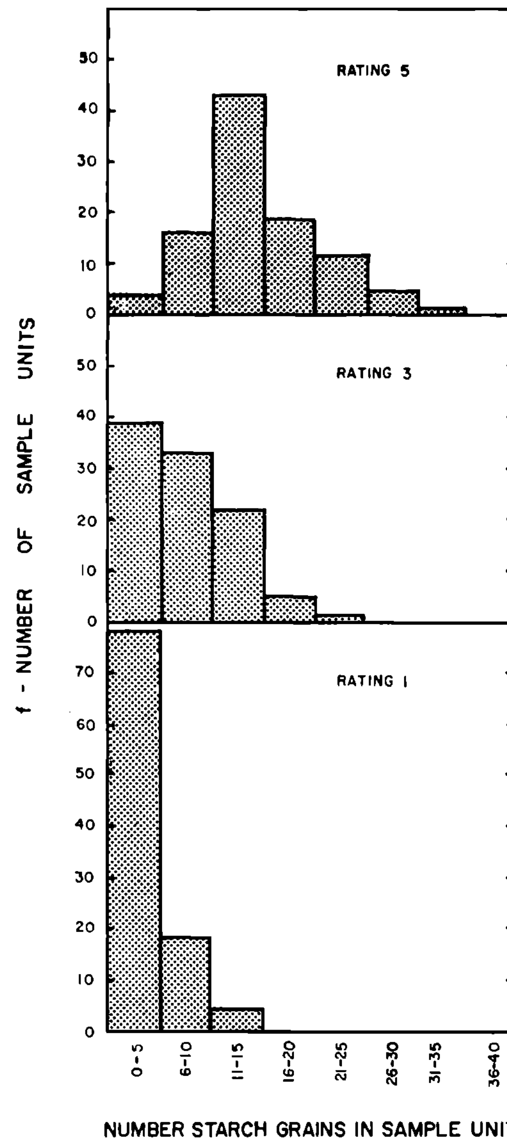


FIGURE 3. *Frequency distribution of numbers of starch granules in 100 sample units selected by chance in 40 micron sections from wood with different starch ratings (see Fig 1-F).*

TABLE 1. Subjective ratings of sapwood starch quantity (5 represents maximum) for attacked and non-attacked logs at Cowichan Lake and Parksville, examined after heavy attack flights of Trypodendron *had revealed beetle preference. Numbers of logs in each category are given.*

Species	Starch rating 0	trace	1	2	3	4	5
	Number of logs						
	A—COWICHAN LAKE 1958						
Douglas-fir							
Attacked	14	2	4	1	2	0	0
Non-attacked	4	1	1	0	7	11	0
Western hemlock							
Attacked	37	6	3	5	0	0	0
Non-attacked	25	6	6	8	12	13	0
	B—PARKSVILLE 1959 (LOWEST VALUES)[1]						
Douglas-fir							
Attacked	30	12	6	12	0	0	0
Non-attacked	15	25	12	30	17	1	0
Western hemlock							
Attacked	4	4	2	3	0	0	0
Non-attacked	3	3	4	11	5	2	0
	PARKSVILLE (HIGHEST VALUES)[2]						
Douglas-fir							
Attacked	27	10	7	15	1	0	0
Non-attacked	12	21	9	35	19	2	2
Western hemlock							
Attacked	3	4	1	4	1	0	0
Non-attacked	1	3	3	10	6	4	1
	C—COWICHAN LAKE 1960						
Douglas-fir (autumn-felled)							
Attacked	15	11	3	1	2	1	0
Non-attacked	1	0	0	1	0	0	0
Douglas-fir (May-felled)							
Attacked	0	0	0	0	0	0	0
Non-attacked	0	1	2	5	24	18	1
	D—ALL DOUGLAS-FIR[3]						
Douglas-fir							
Attacked	56	23	14	17	5	1	0
Non-attacked	17	23	12	41	50	31	3

[1]Where rating varied within a sample, lowest value used.
[2]Where rating varied within a sample, highest value used.
[3]Highest values of Parksville ratings used.

blocks cut from a log may become attractive sooner than the rest of the log (Kinghorn 1957).

Results for all Douglas-fir logs examined after heavy beetle flights are given in Table 1–D. It is clear that although those with much starch are seldom attacked, the ratings of unattacked and attacked logs overlap to quite an extent. From this it appears that starch content is not related directly to log attractiveness.

Seasonal changes in Douglas-fir sapwood starch. Information on starch changes of Douglas-fir sapwood, with season and after cutting, is important in considering both log age and time of cutting in relation to beetle attack. To determine seasonal changes of starch, several types of samples were taken, mostly near Cowichan Lake, starting in 1958, at approximately monthly intervals for over a year. They are described as follows:

1. Young saplings, 8 to 9 feet high, cut and tested at the 6-inch, and 3-, 5-, and 7-foot levels. Starch ratings were found to be essentially the same along the tree axis (Fig. 4–A).

2. A small cube of wood cut, with hammer and chisel, from one or two living trees about 55 years old (Fig. 4–B).

3. Increment borer samples from six living mature trees (Fig. 4–C).

4. Lower living branches (about 1 inch in diameter) from 10 young trees 18-25 feet high (Fig. 4–D). Average values are given for each sample period, a trace rating being counted numerically as 0.5. Different types of wood, as stem and branch sapwood, are not easy to compare for starch content, but within any one type, relative ratings can readily be made.

5. Samples from the base of trees recently felled during logging operations. The number of samples with each rating are indicated, together with average values for a given date determined with trace ratings counting as 0.5 (Fig. 4–E). Precise times of felling of given logs were not generally known but checks with logging company records assured that most logs were sampled within one or two weeks of felling. Sampling was carried out at various locations and altitudes and included the Parksville area for two dates. Gaps occurred in the collection sequence due to cessation of felling during mid-winter or summer periods of high fire hazard. Some data for western hemlock were also secured (Fig. 4–F).

Several of the April to August 1958, samples from freshly felled trees showed less starch close to the cambium than in deeper portions of the sapwood. In many of the October 1958, through February 1959, samples the reverse was true, with highest values occurring next to the cambium. It is assumed from this that both summer depletion and autumn and winter regeneration of starch proceed from the cambium.

The results of the various types of sampling for starch during a season show a basic consistency. Considering that the difference in amount of starch between ratings of *1* and *5*, for example, is much greater than implied by the arithmetic values of these numbers (cf. Figs. 2 and 4), it is apparent that there is a marked seasonal change in Douglas-fir sapwood starch, with maximum amounts in late winter and early spring and minimums during the August-November period.

Unfortunately, information on recent and current cone production of the trees represented by the samples could not readily be taken, so our data do not reveal anything about the possible relationship between starch and cone crop. It should be noted, however, that 1959 was an unusually good seed year for Douglas-fir in this region. (B.C. Forest Service 1960).

Starch depletion in spring-felled logs. Aside from the need to know how rapidly starch changes occur in felled material in order to interpret samples taken after some delay, it is of interest to know what sort of log aging period is necessary for starch depletion. This question was studied by felling trees and sampling them over a period of time. In all instances starch ratings decreased markedly within a few months. For example, a tree felled March 10 showed the following ratings: March 10—*5*, April 29—*4*, July 4—*1*, July 31—*1*, September 2—trace.

The most complete data came from a series of seven trees felled May 14, 1959 (Table 2). The several samples taken each date from each tree indicated that variability in starch around the circumference or along the axis of a tree is usually small. It is apparent that May-felled trees gradually lost their starch so that by September of that year the ratings were of the same low levels—*0*, trace, *1*, occasionally *2*, which seem to be associated with *Trypodendron* attacks in autumn- or winter-felled logs. Logs felled in August or September would usually have these low values at the time of cutting.

Discussion

The possible importance of tree condition at the time of felling in relation to later insect or fungus attack was clearly realized long ago by Mer (1903), who investigated sapwood starch and methods of reducing it. Many years later, interest in starch in

TABLE 2. Changes in sapwood starch with time in trees felled May 14, 1959. Samples consisted of outer inch of wood taken each date at basal, mid and upper portions of each tree. At each position, top, north and south sides of log were sampled. Sample holes were painted with pine tar to prevent abnormal drying of logs.

Tree No.	May 22	June 30	Aug. 3	Sept. 17	Nov. 13
			DOUGLAS-FIR		
1	4.1[1]	1.9	0.95	0.05	0.16
2	4.0	2.4	1.3	0.22	0.16
3	4.6	2.5	2.0	1.5	0.94
4	3.6	2.6	1.8	0.16	0.11
5	3.6	1.9	1.3	1.11	0.72
			WESTERN HEMLOCK		
6	2.6	1.8	0.22	0.22	0.05
7	4.3	2.9	0.88	0.44	0.16

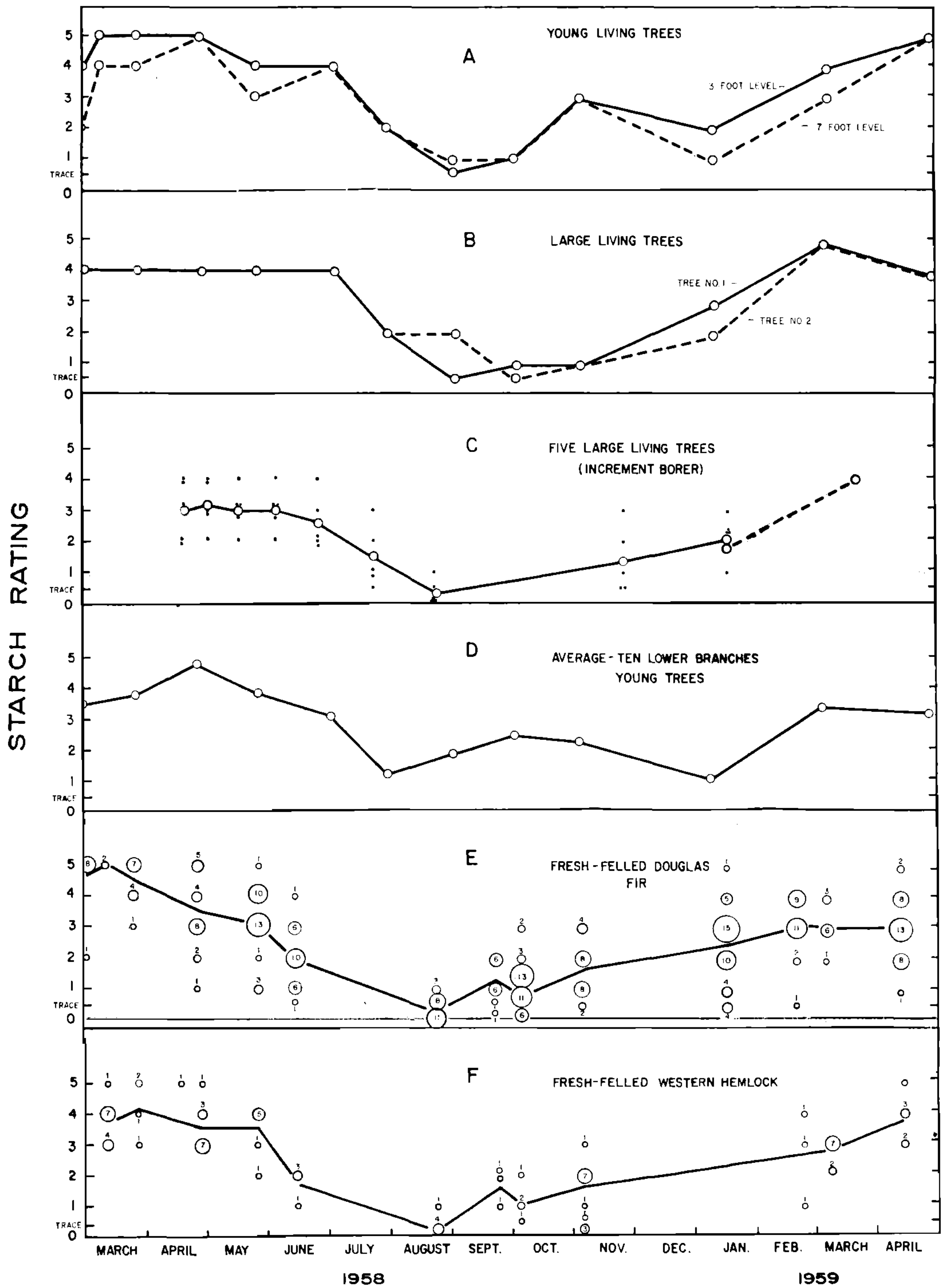
[1]Figures represent average of 9 samples, taken from top, north and south sides of each tree at base, mid-portion and upper bole. Maximum starch rating is 5; trace amount counted as 0.5.

relation to insect attack was renewed. Wilson (1933, 1935) confirmed the use of sapwood starch as food by *Lyctus* powder post beetles. He showed that it gradually disappears when wood is seasoned slowly, but remains unchanged if wood is steamed or dried quickly; further, that respiration continues for several months in freshly cut logs prevented from drying rapidly. Others have extended and confirmed Wilson's findings in regard to powder post beetles (e.g., Henderson 1943, Parkin 1943, Cummins and Wilson 1953, Roberts 1961). There have also been a few studies on the general question of time of felling in relation to other insect or fungus problems (e.g., Hopkins 1907, Björkman 1958).

There has been little attempt, however, to consider starch in relation to ambrosia beetle activity, although Jover (1951) found attacks of one of these beetles to be greater on boiled than on control logs, and suggested that the greater starch content of the former had something to do with this.

A direct relationship between wood starch and ambrosia beetle attack would not be expected, because these insects feed, both as immature forms and adults, primarily on their symbiotic fungus. The fungus, however, utilizes cell contents, not cell wall materials and presumably its growth is influenced by starch, sugars or other nutritional substances in the wood cells. Nevertheless, any assumption that the beetles have evolved a behavior pattern which results in selection of logs most suitable for growth of their fungus cannot be accepted without reservation at present. In regard to starch itself, our data indicate that wood with little or none is preferred. Starch could be a precursor for the actual attractant, or related by various metabolic

FIGURE 4. *Sapwood starch in relation to season, based on subjective ratings of iodine treated radial surfaces from several sources. A. Single small trees (8 to 9 feet high). B. Small cubes of sapwood cut from living trees about 55 years old, near the four foot level. C. Increment borer cores from 5 mature living trees, felled in Jan. 1959. Dotted line indicates extra single tree. D. Average ratings of 10 lower branches, at base, about 1-inch diameter, from separate trees 18 to 25 feet high. E. Individual and average ratings for freshly felled Douglas-fir. Size of circles, and figures within, indicate the numbers of samples having the various ratings. F. Individual and average ratings for freshly felled western hemlock, as in E.*


STARCH RATING
A
YOUNG LIVING TREES
3 FOOT LEVEL
7 FOOT LEVEL
B
LARGE LIVING TREES
TREE NO. 1
TREE NO 2
C
FIVE LARGE LIVING TREES
(INCREMENT BORER)
D
AVERAGE - TEN LOWER BRANCHES
YOUNG TREES
E
FRESH-FELLED DOUGLAS FIR
F
FRESH-FELLED WESTERN HEMLOCK
5
4
3
2
1
TRACE
0
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MARCH
APRIL
1958
1959

pathways to it. On the other hand, it may play no part in attractant production, but serve as a general indicator of physiological change in a log.

As mentioned earlier, a number of studies have provided information on seasonal changes of starch in both deciduous and coniferous trees. Perhaps because many tree species have been involved and various parts of trees sampled (twigs, main stem, foliage, roots) and various parts of the world represented, an entirely consistent picture of seasonal starch changes in conifers is not revealed. It seems generally agreed, however, that maximum amounts occur in spring, just before growth commences, and our findings are consistent with this. The starch changes in western hemlock appear to parallel those of Douglas-fir, and the two species are probably similar in regard to the question of starch and *Trypodendron* attack.

A consequence of the marked seasonal change in food reserves is that logs cut at different times of the years must differ physiologically. The data in Figure 4–E indicate variability in starch of logs cut at the same time; there is frequently considerable variability in *Trypodendron* attacks on logs cut at the same time. There is, furthermore, little doubt that extensive physiological changes occur in fresh logs. This has been realized since the time of Mer but has been studied by only a few investigators, in a general way (e.g., Yatsenko-Chmélévsky and Konnchevska 1935, Parkin 1943, Henderson 1943).

A question may be raised as to the relative importance, for beetle attacks, of the log aging period and of tree condition at time of felling. Some sort of time interval is apparently required before logs or severely weakened trees become attractive to *Trypodendron* (Trägårdh 1921, Morley 1939, Belyea 1952, see also, Kinghorn and Chapman 1957, Novak 1960). It must be remembered, however, that the heavy beetle attack flights occur in spring and log attractiveness is only clearly revealed then. Until it is definitely ruled out, the possibility must be considered that logs felled in autumn or winter are attractive as soon as they are cut, due to their physiological condition, but are not attacked then because beetles are not active at that time of year. Finally, it is possible that both log aging period and tree condition at time of cutting are important in relation to the production of substances attractive to *Trypodendron.*

Literature Cited

Belyea, R. M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Can. Ent. 84: 325-335.

Binion, W. 1962. Attraction of the ambrosia beetle, *Trypodendron,* by beer dregs. Proc. Ent. Soc. B.C. 59:53.

Björkman, E. 1958. Log blue stain and storage decay in pine and spruce timber with special reference to felling time and treatment during floating. Roy. School Forestry, Stockholm. Bull. No. 30:1-62.

Bletchly, J. D. 1961. A review of factors affecting ambrosia beetle attack in trees and felled logs. The Empire Forestry Review 40:13-18.

British Columbia Forest Service (1959). 1960. Annual report Dept. Lands and Forests. Victoria, B.C.

Browne, F. G. 1952. Suggestions for future research in the control of ambrosia beetles. Malayan Forester 15:197-206.

Büsgen, M. 1929 (3rd Ed. Rev., E. Münch, Trans. T. Thompson). The structure and life of forest trees. Chapman and Hall. London.

Cleare, L. D. 1938. Damage caused to rum puncheons by boring beetles. Agric. J. Brit. Guiana 9:237-245.

Chapman, J. A. 1962. Field studies on attack flight and log selection by the ambrosia beetle *Trypodendron.* Can. Ent. 94:74-92.

Cummins, J. E., and H. B. Wilson. 1935. The starch content of some Australian hardwoods in relation to their susceptibility to attack by the powder post borer, *Lyctus brunneus* Stephens. J. Coun. Sci. Ind. Res. 8:101-110.

Fisher, R. C., G. H. Thompson and W. E. Webb. 1953. Ambrosia beetles in forest and sawmill. Their biology, economic importance and control. Part I. Biology and economic importance. For. Abstr. 14:381-389.

FROST, S. W., and H. DIETRICH. 1929. Coleoptera taken from bait-traps. Ann. Ent. Soc. Amer. 22:427-437.

HADORN, C. 1933. Recherches sur la morphologie, les stades évolutifs et l'hivernage du bostryche liseré (*Xyloterus lineatus* Oliv.). Supp. aux org. de la Soc. forestière suisse No. 11. Berne.

HENDERSON, F. Y. 1943. The depletion of starch from sapwood of the ash (*Fraxinus excelsior*) and its relation to attack by powder-post beetles (*Lyctus* spp.). Ann. Appl. Biol. 30:201-208.

HOPKINS, A. D. 1907. Pinhole injury to girdled cypress in the south Atlantic and Gulf states. U. S. Dept. Agric. Bur. Ent. Circ. 82.

ISHIBE, O. 1935. The seasonal changes in starch and fat reserves of some woody plants. Mem. College Sci., Kyoto Imperial Univ. Ser. B. Vol. XI (1).

JOVER, H. 1951. Note préliminaire sur les modalités de l'attaque du bois d'Avodiré (*Turreanthus africana* Welv. Pellegrin) par différents coléoptères xylophages en Basse-Côte-d'Ivoire. Rev. Path. Veg. 30:54-55.

KINGHORN, J. M. 1957. An induced differential bark-beetle attack. Bi-Monthly Progress Report, Can. Dept. Agric., Forest Biology Div. 13(2):3-4.

KINGHORN, J. M., and J. A. CHAPMAN. 1957. The effect of Douglas-fir log age on attack by the ambrosia beetle, *Trypodendron lineatum* (Oliv.). Proc. Ent. Soc. B.C. 54:46-49.

MER, E. 1903. De divers moyens propres à préserver de l'attaque des insectes les écorces et les bois par résorption de leur réserve amylacée. Mém. Soc. Nat. Agric. France 140:233-247. Paris.

MORLEY, P. M. 1939. Time of cut as a factor influencing infestation of coniferous logs. Can. Ent. 71:243-248.

NOVAK, V. 1960. (The striped wood-boring beetle (ambrosia beetle) and the fight against it.) Statni Zemedëlske Nakladatelstvi. Prague.

OHNESORGE, B. 1953. Der Einfluss von Gerucks- und Gesmacksstoffen auf die Wahl der Frasspflanzen beim grossen brauners Rüsselkäfer. Beitr. z. Ent. 3:437-468.

PARKIN, E. A. 1943. The depletion of starch from timber in relation to attack by *Lyctus* beetles. V. The effect upon starch content of storing timber in the log. Forestry 17: 61-66.

PERSON, H. L. 1931. Theory in explanation of the selection of certain trees by the western pine beetle. J. For. 29:696-699.

PHILLIPS, E. W. J. 1938. The depletion of starch from timber in relation to attack by *Lyctus* beetles. I. Starch, with special reference to its occurrence in timber. Forestry 12:15-37.

PREBBLE, M. L., and K. GRAHAM. 1957. Studies of attack by ambrosia beetles in softwood logs on Vancouver Island, British Columbia. For. Sci. 3:90-112.

ROBERTS, H. 1961. Seasonal variation in the starch content of the sapwood of *Triplochiton scleroxylon* K. Schum Sterculiaceae (Trade Name—Wawa Obeche) in Ghana, West Africa. Empire Forestry Review 40: 61-65.

RUHLAND, W., ED. 1958. Encyclopedia of Plant Physiology. Vol. VI. Formation-storage-mobilization and transformation of carbohydrates. Springer, Berlin.

SCHNEIDER-ORELLI, O. 1913. Untersuchungen über den pilzzüchtenden Obstbaumborkenkäfer *Xyleborus* (*Anisandrus*) *dispar* und seine Nährpilz. Centralb. f. Bak. Parasit. u. Infektionskrank. 38:25-110.

TRÄGARDH, I. 1921. Untersuchungen über den grossen Waldgärtner (*Myelophilus piniperda*). Reports Swedish Inst. Exper. Forestry No. 18, Stockholm.

WILSON, S. E. 1933. Changes in the cell contents of wood (xylem parenchyma) and their relationships to the respiration of wood and its resistance to *Lyctus* attack and to fungal invasion. Ann. Appl. Biol. 20:661-690.

————. 1935. The fate of reserve materials in the felled tree. Forestry 9:96-105.

YATSENKO-CHMÉLÉVSKY, A. A., and H. L. KONNCHEVSKA. 1935. La transformation de l'amidon dans le bois des Hêtres abattus. Rev. Gen. Bot. 47:552-563.