O-X-214

THE DETERIORATION OF BALSAM FIR TREES KILLED BY GIRDLING IN EASTERN CANADA

J. T. BASHAM
D. E. ETHERIDGE
J. HUDAK
D. LACHANCE
L. P. MAGASI
M. A. STILLWELL

DECEMBER, 1974

CANADIAN FORESTRY SERVICE

DEPARTMENT OF THE ENVIRONMENT

THE DETERIORATION OF BALSAM FIR TREES KILLED BY GIRDLING IN EASTERN CANADA

J. T. BASHAM[1], D. E. ETHERIDGE[2], J. HUDAK[3],
D. LACHANCE[4], L. P. MAGASI[5],
AND M. A. STILLWELL[5]

[1] Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario

[2] Pacific Forest Research Centre, Victoria, British Columbia

[3] Newfoundland Forest Research Centre, St. John's, Newfoundland

[4] Laurentian Forest Research Centre, Ste. Foy, Quebec

[5] Maritimes Forest Research Centre, Fredericton, New Brunswick

INFORMATION REPORT O-X-214

CANADIAN FORESTRY SERVICE

DEPARTMENT OF THE ENVIRONMENT

DECEMBER 1974

Copies of this report may be obtained from

Director,
Great Lakes Forest Research Centre,
Canadian Forestry Service
Department of the Environment
Box 490, Sault Ste. Marie, Ontario.
P6A 5M7

ABSTRACT

Twenty-two trees on a representative plot in each of five regions of eastern Canada were killed by girdling to compare rates of deterioration and associated microflora in killed balsam fir (*Abies balsamea* [L.] Mill.) stems. Distinct differences among regions were observed. Trees in eastern and western Ontario deteriorated most rapidly, owing to the early development of *Polyporus abietinus* sap rot; deterioration from this cause was slowest in trees in Newfoundland and Quebec. Trees in Newfoundland, New Brunswick and Quebec yielded far more isolates of *Stereum chailletii* (the fungus associated with much of the sap stain encountered) than did those in Ontario. Appreciable differences in climate from region to region, and their effect on populations of insects which attack dying and dead balsam fir stems, are thought to be the principal causes of these observed differences.

RÉSUMÉ

Dans cinq régions de l'est du Canada, on a comparé la vitesse de détérioration, ainsi que la microflore impliquée, de sapins baumiers (*Abies balsamea* [L.] Mill.) morts récemment. Pour ce faire, 22 arbres situés dans une placette typique pour chacune des régions, furent tués par annelage. Des différences sensibles entre les régions sont apparues rapidement. Les sapins des régions de l'Ontario se sont détériorés le plus rapidement, à cause du développement hâtif de *Polyporus abietinus* dans l'aubier; ceux situés à Terre-Neuve et au Québec furent le moins affectés par ce champignon. On a isolé *Stereum chailletii*, champignon associé à la majorité des colorations de l'aubier rencontrées, beaucoup plus souvent sur les sapins de Terre-Neuve, du Nouveau-Brunswick et du Québec que sur ceux de l'Ontario. Les différences appréciables de climat, observées entre les cinq régions étudiées, et leur influence sur les populations d'insectes attaquant les sapins baumiers mourants ou morts récemment, sont considérées comme les causes principales des différences observées dans la vitesse de détérioration du sapin mort.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
STUDY APPROACH	2
DESCRIPTION OF STUDY AREAS, STANDS AND PLOTS	3
RESULTS	6
Climatic comparisons	6
Comparison of tree characteristics	13
Moisture content	15
Insect activity	19
Progress of sap stain and sap rot penetration	24
Microorganisms associated with stem deterioration	24
Occurrence of major fungi and stem position	27
Occurrence of major fungi and period since tree death	27
Occurrence of major fungi and distance within cambium	32
DISCUSSION	40
CONCLUSIONS	44
LITERATURE CITED	47
APPENDIX	

INTRODUCTION

An intensive investigation of the deterioration of balsam fir (*Abies balsamea* [L.] Mill.) killed following spruce budworm defoliation in northwestern Ontario indicated that dead trees deteriorated quite rapidly with much of the sapwood becoming soft and rotted during the second year following death (Basham 1951, 1959). *Stereum chailletii* Pers. (now often called *Amylostereum chailletii* [Fr.] and *Nectria fuckeliana* Booth (formerly called Fungus F [Basham 1959]) were the fungi isolated most frequently from the stained sapwood of trees dead less than one year. *Polyporus abietinus* [Dicks. ex Fr.] Donk) was the only fungus consistently associated with the rotted sapwood of trees dead for more than one year. A few years later a similar investigation was carried out in northwestern New Brunswick (Stillwell and Kelly 1964). A striking difference in the rate of sap rot development between the two regions was apparent: the average depth of radial penetration of advanced deterioration (rot) in trees dead from 2 to 3 years was 0.6 in. (15.6 mm) in northwestern Ontario but only 0.1 in. (2.5 mm) in New Brunswick. Furthermore, the fungus isolated with the greatest frequency from deteriorated sapwood in New Brunswick, *Stereum sanguinolentum* (Alb. & Schw. ex Fr.) (now often called *Haematostereum sanguinolentum* [Fr.] Pouzar), was never isolated in the northwestern Ontario study, and *P. abietinus* was seldom isolated in New Brunswick from trees dead less than 4 years.

An informal workshop meeting of Canadian forest pathologists who were, or had been, involved in research on balsam fir stem decays was held in 1965 at Fredericton, New Brunswick. At that meeting it was suggested that these differences be further investigated by means of killing and periodically examining 20 balsam fir trees in each of five regions, namely, Newfoundland, New Brunswick, Quebec, eastern Ontario and northwestern Ontario. It was agreed that relatively few man-weeks of work annually would provide interesting results, both from a practical and a scientific point of view. For three of the five areas this measure would provide the first indications of the rate of deterioration of killed balsam fir. This information would assist those responsible for determining the economic feasibility of salvage operations following widespread mortality of balsam fir in the wake of outbreaks of spruce budworm (*Choristoneura fumiferana* [Clem.]) or other defoliating insects, such as the eastern hemlock looper (*Lambdina fiscellaria fiscellaria* [(Guen.]). It was hoped that this approach would also help to explain the pronounced differences in the rate of deterioration of killed balsam fir and in the relative importance of the fungi associated with the deterioration of the dead trees in different regions of eastern Canada. Monospore interfertility tests have shown that *P. abietinus* from Ontario and New Brunswick are the same species (Magasi 1972), and laboratory decay tests indicated that there were no significant differences between them. However, it was felt that, even if no regional pathogen variations occur, differences in climate, tree characteristics, insect populations and activity, and other factors could influence the rate of deterioration in the five study areas.

Objectives of the study were 1) to compare rate of deterioration, and the identity and patterns of successions of invading fungi, in standing, artificially killed balsam fir in five areas of eastern Canada, and 2) to elucidate the factors responsible for any observed differences in the rate of balsam fir stem deterioration in those areas.

STUDY APPROACH

In Newfoundland, New Brunswick, Quebec, eastern Ontario and western Ontario, often referred to in tables in this report as study areas 1-5, respectively, sample plots were established in merchantable stands consisting of at least 70% balsam fir stems. Within each plot 24 dominant or codominant balsam fir trees were selected for testing. They were at least 6.0 in. (15 cm) in diameter at breast height and not older than 100 years. During May and June, 1966 approximately 3 weeks after the start of white birch (*Betula papyrifera* Marsh.) "flushing" in each area, 22 of these trees were girdled 1 ft (30 cm) from the ground by removing a 2-in. (5-cm) band of bark and making a 1/2-in. (12.7-mm) incision into the xylem with a chain saw of 1/4-5/16 in. (6.3-8.0 mm) kerf. Loose material was removed from the incisions, and the exposed xylem was surface sterilized and packed and sealed with wound-dressing compound. The girdled trees were examined once a month thereafter during the growing season (May to October) and descriptions of their foliage, bark and twigs were recorded until they died. Trees were considered dead when the removal of two 30-mm-sq patches of bark on opposite sides of the trunk about 2 m above the ground revealed completely brown, dry cambium.

Two annual periods of tree sampling were selected, 3 weeks after the start of white birch flushing in the spring and in the fall at the "peak" of white birch leaf fall. In each study area, at the first of these periods when at least two of the girdled trees had died, two of the dead, girdled trees were selected at random to be felled and processed. The two balsam fir trees that had not been girdled (both of them living) were also felled and processed at that time. Thereafter two girdled, dead trees were sampled at each sampling period until a total of 20 girdled trees in each study area had been processed.

The dbh, total height, and age of each tree were determined at the time of sampling. At three points in the stem, 5 ft (1.5 m) above the ground, at a point 3 in. (7.5 cm) in diameter, and midway between these two points, discs approximately 2 in. (5 cm) thick were cut. From each disc two samples about 2.5 cm square and 5 cm long were immediately obtained from the sapwood and the heartwood along the north radius. These samples were sealed in polyethylene bags as soon as they were cut, and at the laboratory the moisture content of each sample (based on oven-dry weight) was determined. At the same three locations in the stem, 1-ft (30.5-cm) bolts were cut, and were surface sterilized and sealed in paper bags. These were taken to the laboratory where a disc approximately 2 in.

(5 cm) thick was cut from the center of each bolt, and 15 isolation attempts were made, four along each of the cardinal radii, at predetermined depths beneath the cambium. The average depth of sap stain (discolored but firm wood) and sap rot (discolored, softened wood) in these discs was recorded. A second 1-ft (30.5-cm) bolt was cut at each of these three locations. These were used to determine the surface density of bark beetle nuptial chambers, woodborer entrance and exit holes, and woodwasp oviposition and adult exit holes. At each of the three stem locations, the widths of successive five-ring zones from the cambium along the north radius to a depth of 2 in. (5 cm) were measured and recorded.

The general characteristics of each of the sample plots, including the principal forest and groundcover species, drainage, slope, and stand history, were recorded. Temperature, precipitation, and duration of sunshine records were either obtained within the plots, or from existing weather stations within 6 miles (10 km) of the plots.

DESCRIPTION OF STUDY AREAS, STANDS AND PLOTS

The five study areas were distributed from near Lake Nipigon in northwestern Ontario, central Canada, to Corner Brook, Newfoundland near the Atlantic Ocean, a distance of roughly 2,250 km (1,400 miles) (Fig. 1). The southernmost plot was that in eastern Ontario at 45°8' latitude; the northernmost was in western Ontario at 49°15' with Newfoundland almost as far north at 48°52'. The Quebec plot was at the highest elevation, 640 m (2,100 ft), the western Ontario plot was 275 m (900 ft) and the Newfoundland plot was 230 m (750 ft) (Table 1).

All plots were located in mature stands of balsam fir. Balsam fir accounted for from 77% (western Ontario) to 90% (Newfoundland) of the stand compositions; white spruce was the only other species common to all of the stands sampled. Two of the sample plots, Quebec and New Brunswick, appear to have been established in the *Dryopteris-Oxalis* forest type (Linteau 1955); both had fairly good drainage. The eastern Ontario plot resembled Linteau's *Calliergon-Oxalis* forest type, and had moderate drainage. The remaining two plots, those in Newfoundland and western Ontario, were both established in stands closely resembling Linteau's *Hylocomium-Cornus* forest type. The western Ontario plot was wet with rather poor drainage; that in Newfoundland was moderately well drained. Only one of the sample plots, that in Quebec, had a slope of more than 5%. (It was estimated at 12-15%.) The western Ontario plot had a slope of approximately 5%, whereas the slopes of the remaining three plots were between 1 and 5%.

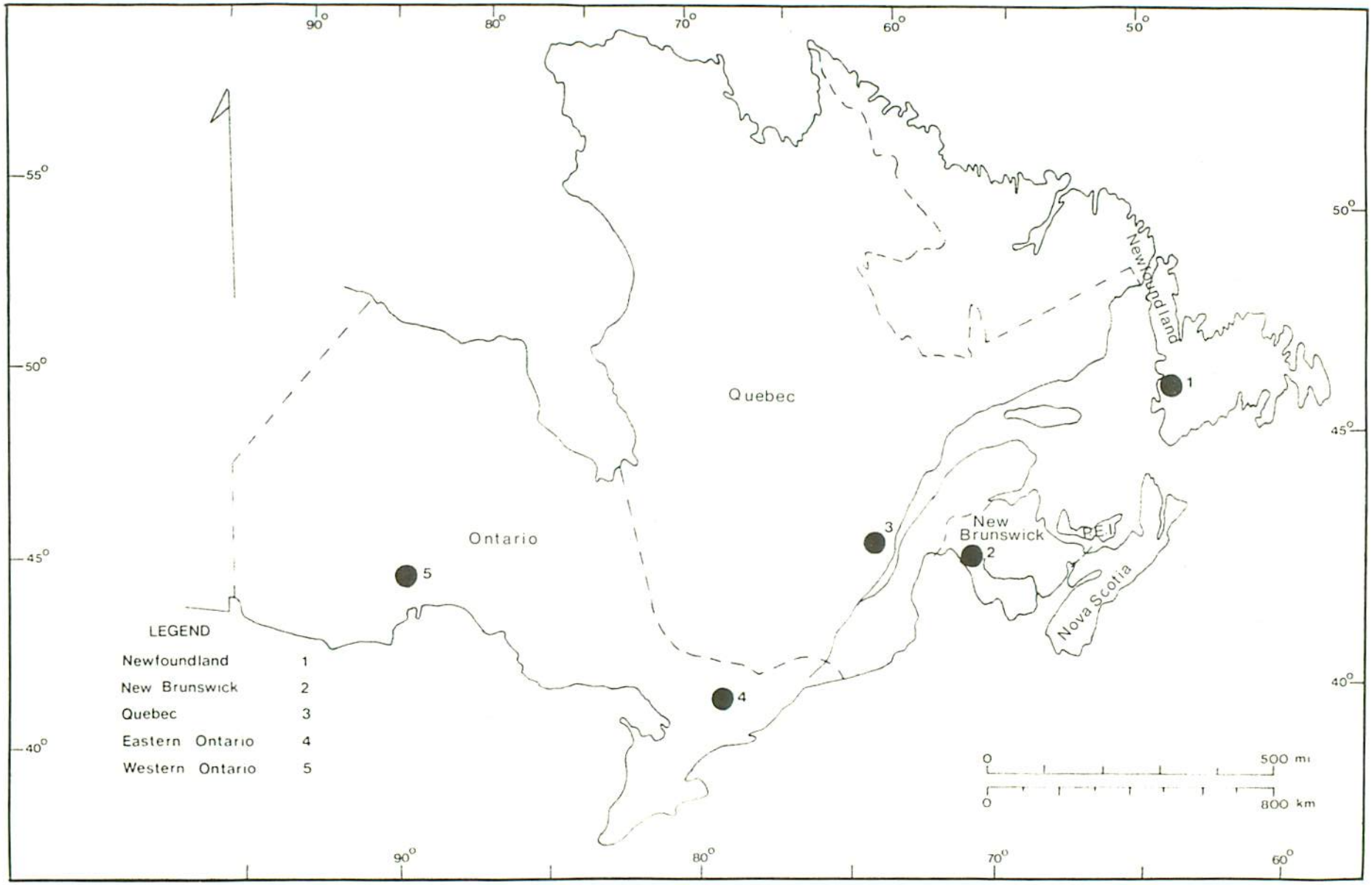

Figure 1. Location of study areas .....●

Table 1. Characteristics of study areas and of sampled balsam fir trees

		Study area				
		1	2	3	4	5
		Newfoundland	New Brunswick	Quebec	Eastern Ontario	Western Ontario
Latitude		48°52'	47°47'	47°10'	45°08'	49°15'
Longitude		57°53'	68°20'	71°15'	78°54'	88°53'
Elevation (m)		230	460	640	365	275
Average period of white birch "flushing"		June 11-19	June 4-12	June 1-9	May 8-16	May 25-June 2
Average peak period of white birch leaf fall		Oct. 4-12	Oct. 2-10	Oct. 1-9	Sept. 29-Oct. 7	Sept. 23-Oct. 1
Dbh of trees (cm)	- average	21.3	17.0	17.8	17.8	19.1
	- range	16.5-24.9	15.5-19.1	15.2-21.8	15.2-20.8	15.2-22.1
Age of trees	- average	64	47	54	71	80
	- range	41-81	43-52	50-65	40-99	69-90
Height of trees (m)	- average	14.3	14.0	17.4	14.3	15.9
	- range	11.9-16.2	12.5-15.6	15.3-18.9	12.5-17.4	13.1-17.7
Site index, height/age		0.73	0.98	1.06	0.66	0.64
Width of 15 most recent growth rings along the north radius (mm)	TOP: average	32	40	33	33	30
	range	25-38	22->50	16-45	24-50	17->50
	MID: average	36	31	26	30	24
	range	19-51	23-39	13-34	10-44	9-36
	BASE: average	30	27	21	26	22
	range	13-47	18-35	7-42	12-44	11-35

The Quebec study plot was established in an undisturbed stand that had resulted from a clear-cut operation in 1910. The Newfoundland plot was in a natural stand that had been subjected to very light selective cutting. The western Ontario plot was established in a virgin stand that had been subjected to severe windthrow about 1925. The eastern Ontario plot had been "high-graded" for white pine and yellow birch in the mid-1920s. The New Brunswick plot was in a coniferous stand originating from severe gales that occurred over a century ago; it is presently disintegrating because of windthrow. Only two of the five sample plots showed any evidence of earlier spruce budworm activity. The western Ontario plot was severely defoliated from 1947 to 1952; however, this resulted in very little mortality. There was very light defoliation caused by the spruce budworm in 1960 and 1961 in the Newfoundland sample plot.

RESULTS

Climatic comparisons

Figures 2 and 3 and Table A1[1] indicate that the three eastern plots generally received more rainfall than the Ontario plots during the four critical months. This was particularly true during the month of August, when the eastern plots averaged 15 1/2 days of measurable rainfall compared with 10 1/2 days in Ontario (Fig. 2). Quebec had the highest average total rainfall for each of the four critical months (Fig. 3), and western Ontario had the least rainfall during this period.

Figures 4 and 5 and Table A1 show clearly that for the study years 1966-1972, during the critical months of June, July, August and September the trees in the two Ontario plots were exposed to more sunlight and warmer temperatures than the three plots to the east. The Ontario plots averaged roughly one extra hour of sunlight per day; the eastern Ontario plot was roughly 7°F (4°C) and the western Ontario plot 3.5°F (2°C) warmer than the plots in Quebec, New Brunswick and Newfoundland.

Figures 6 and 7 compare mean daily maximum and minimum temperatures in the five study areas. Maximum temperatures were again significantly higher in eastern and western Ontario than in the three eastern areas. However, minimum temperatures were relatively high in New Brunswick and the two Ontario areas in comparison with those in Newfoundland and Quebec. Quebec had by far the lowest mean daily minimum temperatures.

---

[1] Tables A1-A15 are found in the Appendix.

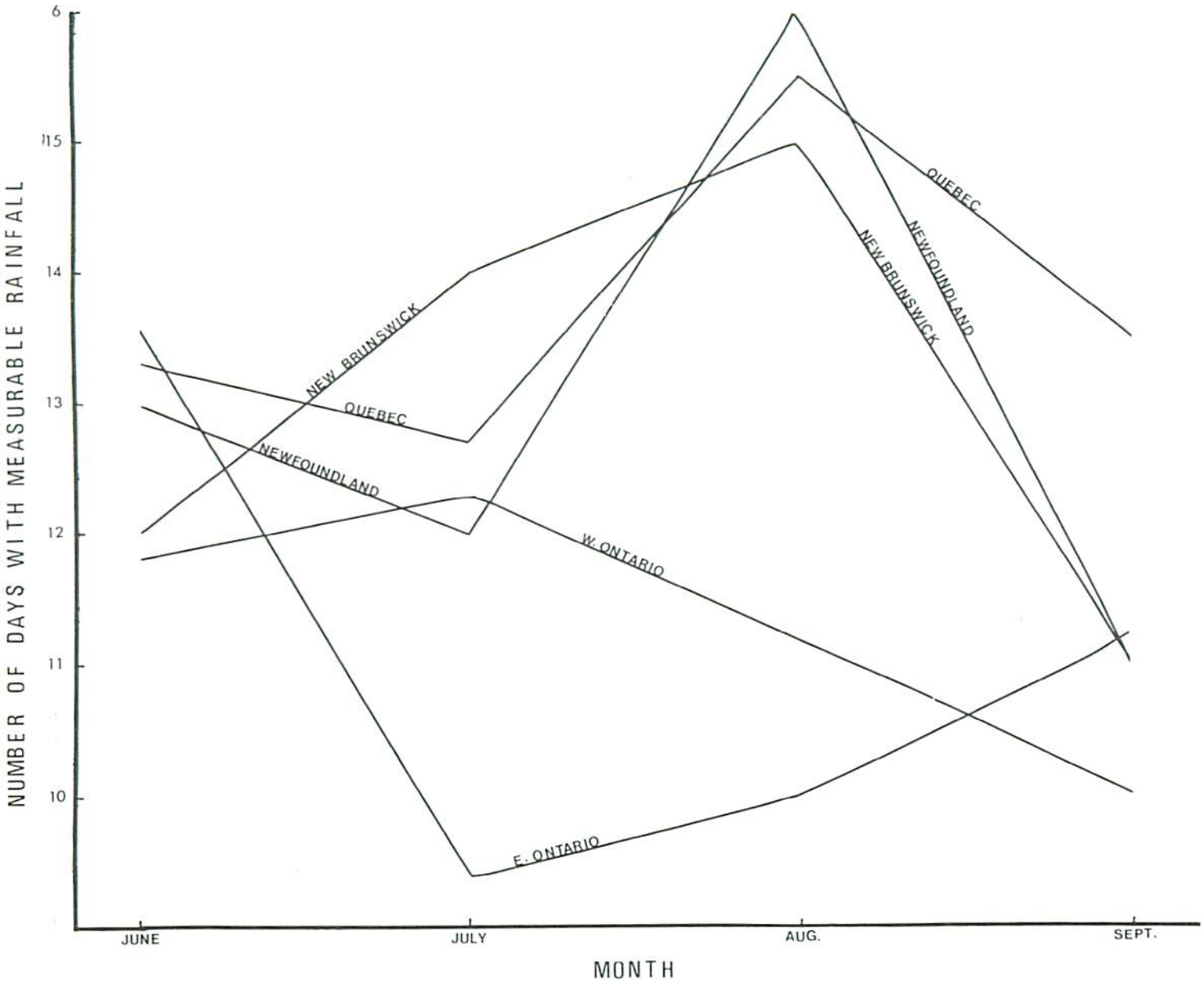

Figure 2. Average number of days per month with measurable rainfall during sampling years in the five study areas.

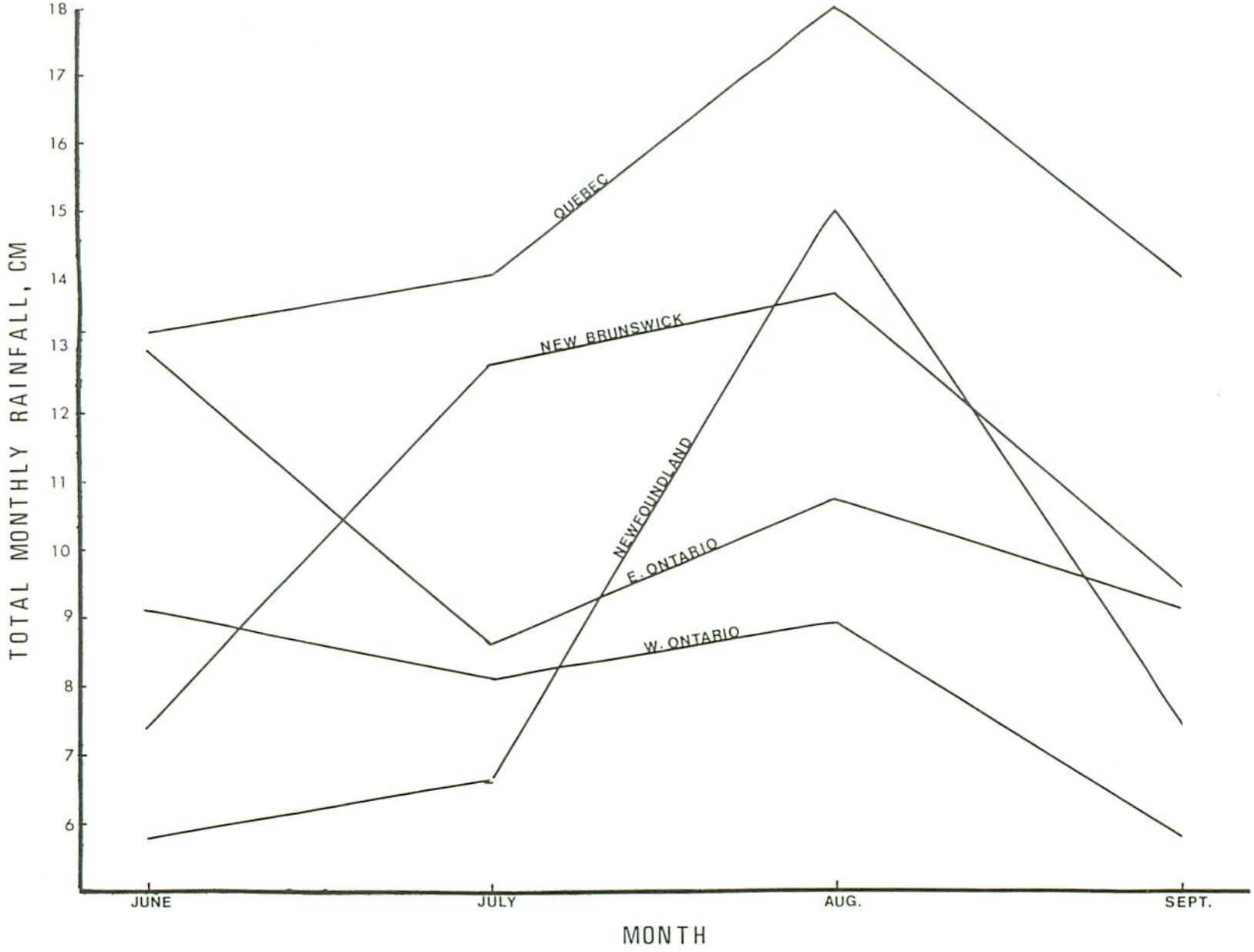

Figure 3. Average total monthly rainfall during sampling years in the five study areas.

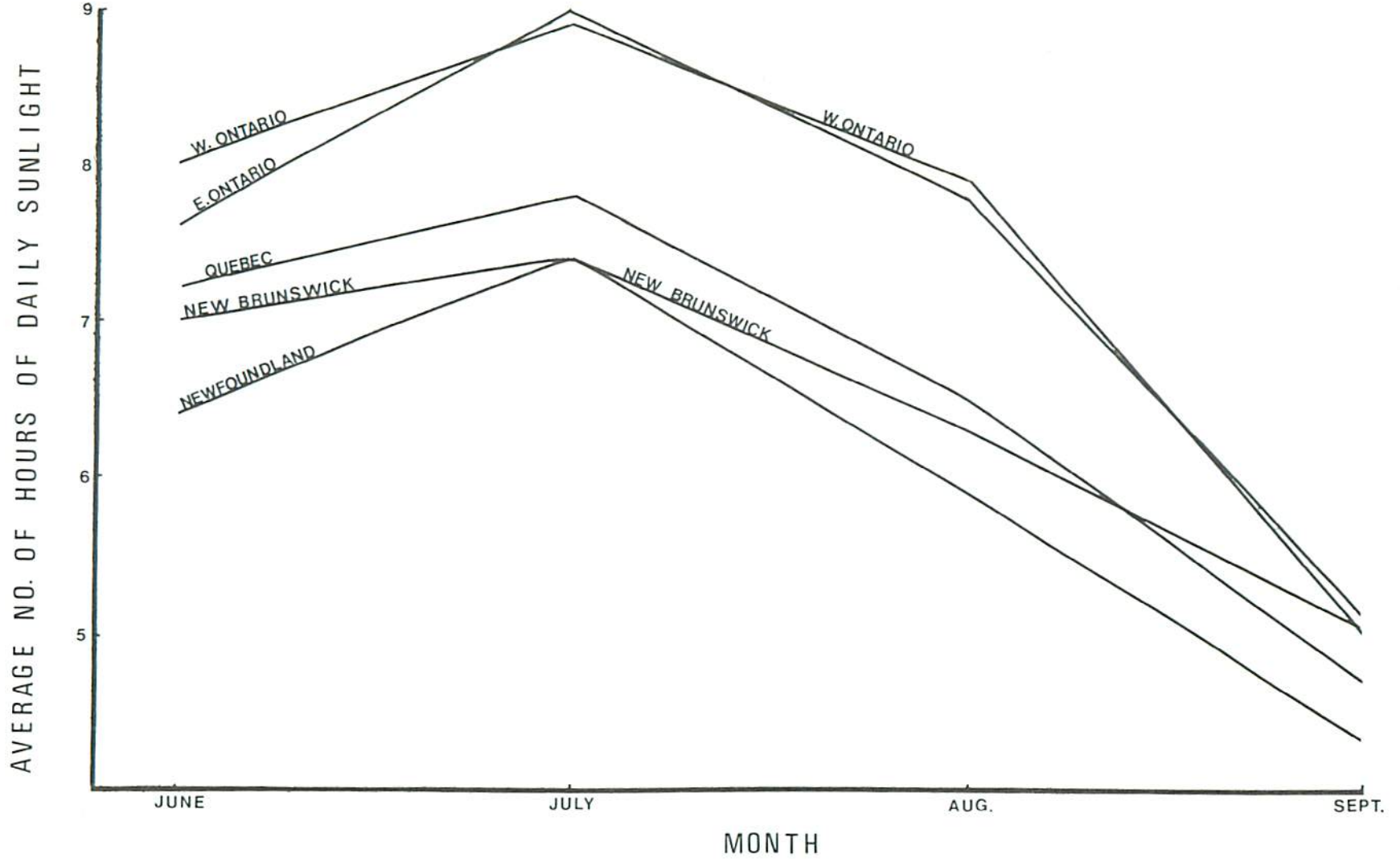

Figure 4. Average daily hours of sunlight in the five study areas.

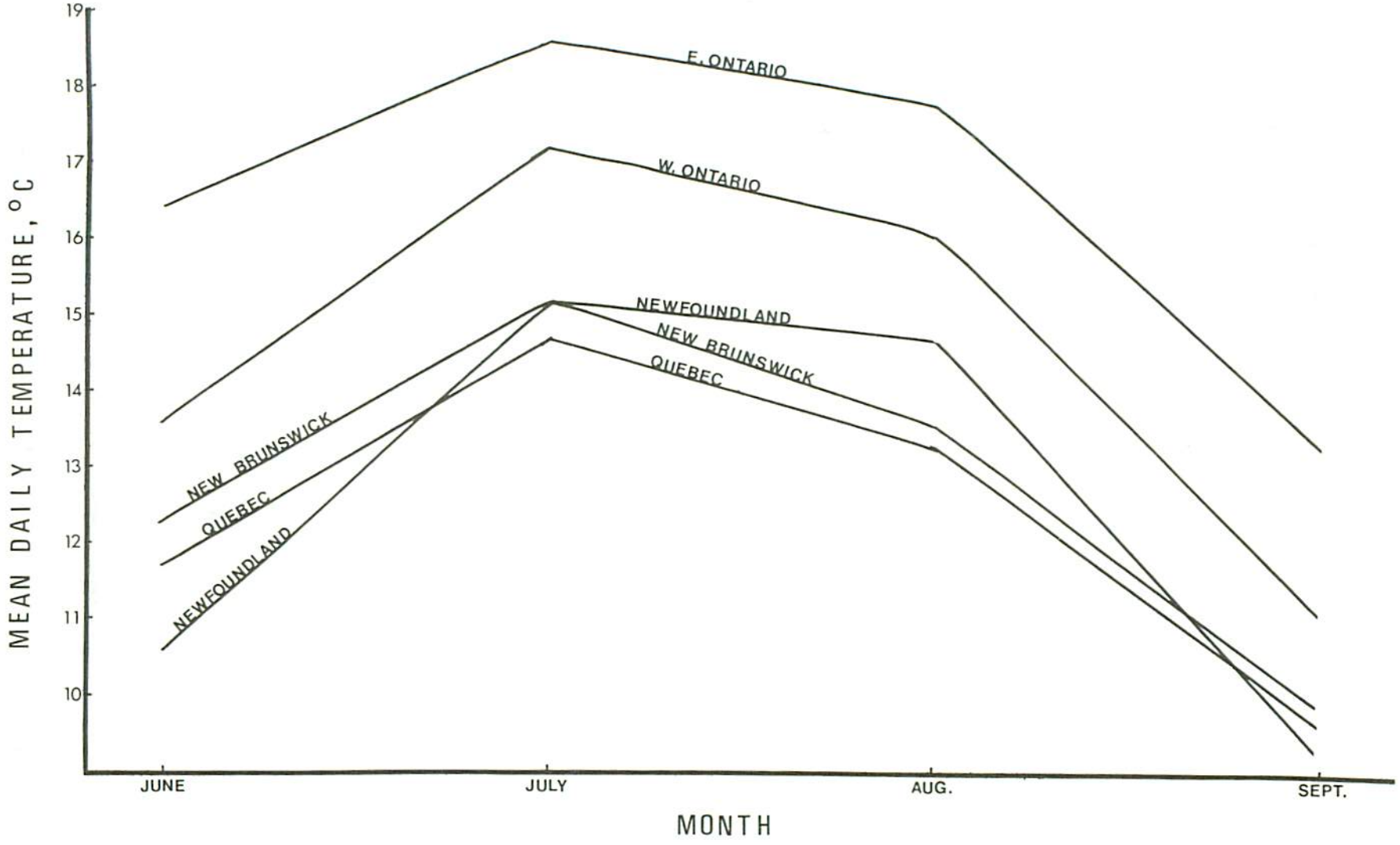

Figure 5. Average mean daily temperature during sampling years in the five study areas.

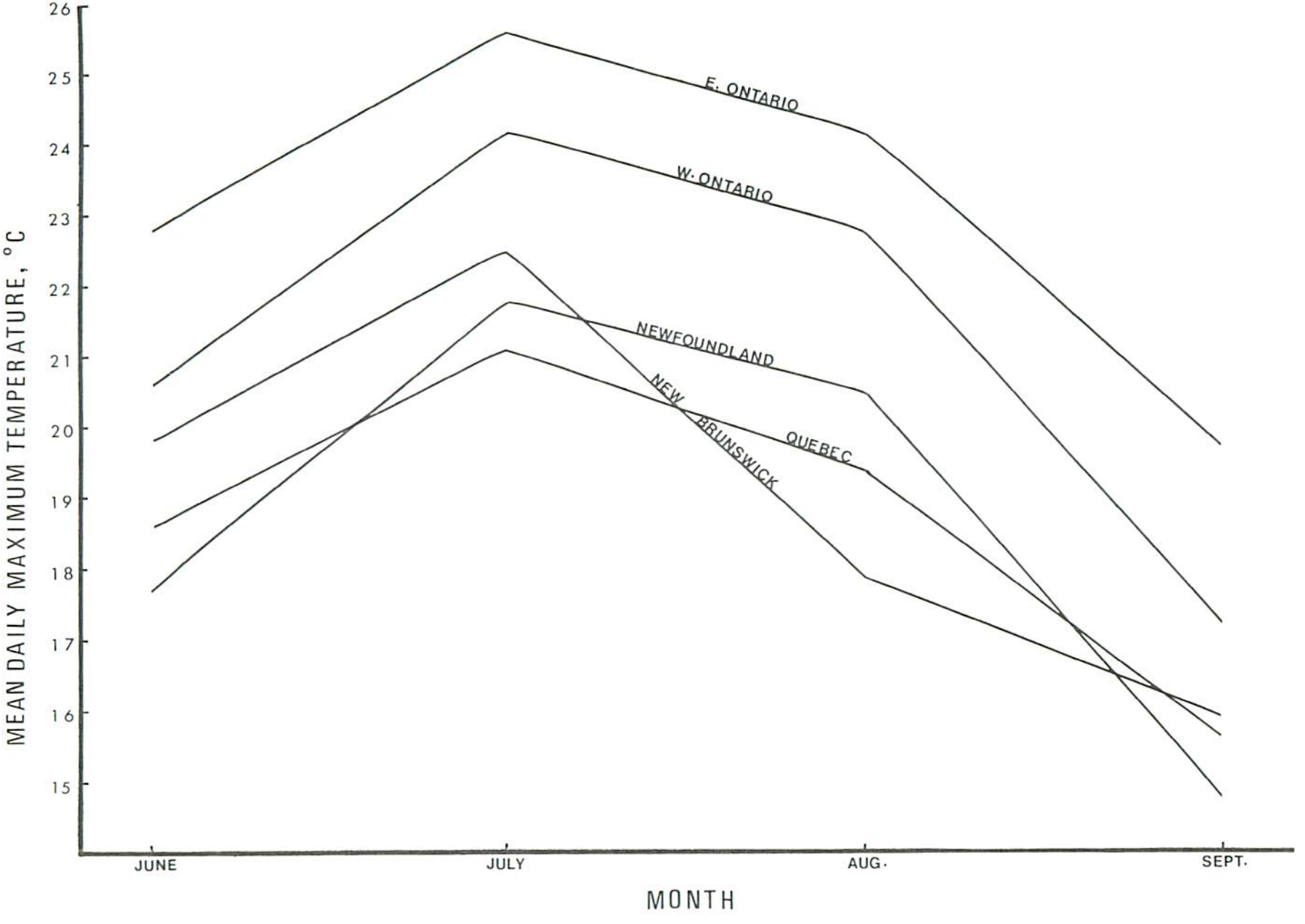

Figure 6. Average mean daily maximum temperatures during sampling years in the five study areas.

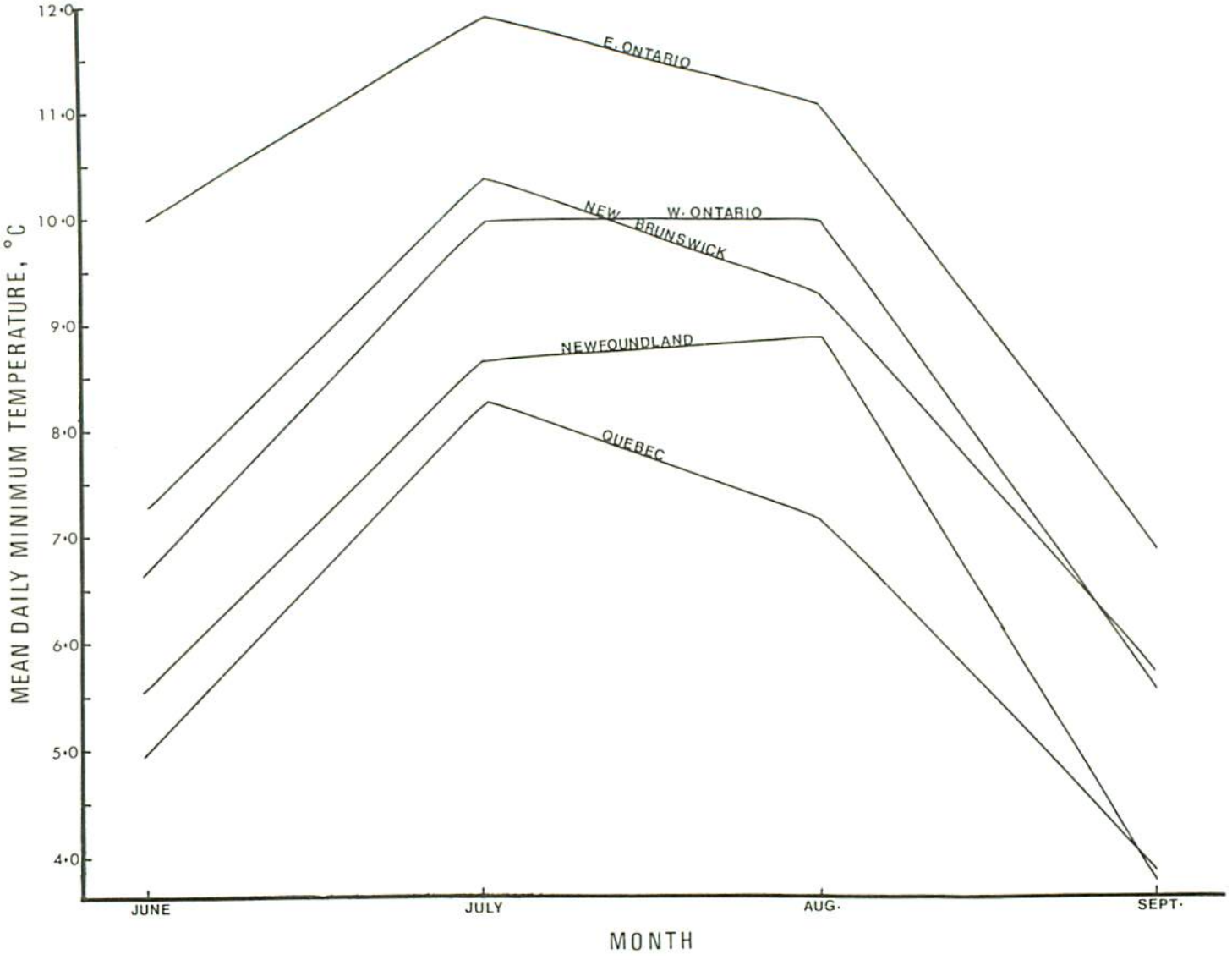

Figure 7. Average mean daily minimum temperatures during sampling years in the five study areas.

In summary, the climate during the study years was appreciably warmer, sunnier, and drier in eastern and western Ontario than in the three eastern areas. New Brunswick differed from Newfoundland and Quebec in that its mean daily minimum temperature was as high as that of western Ontario. Quebec had by far the highest precipitation and the lowest mean daily temperatures of all study areas.

Comparison of tree characteristics

The growing season indicated by white birch phenology did not coincide in the five study areas. Whereas the period of white birch flushing was always in early or mid-June in the three eastern plots, it occurred in mid-May in the eastern Ontario area and from late May to early June in western Ontario. Again, the peak period of white birch leaf fall, admittedly difficult to determine, was recorded between October 1 and October 12 in all three eastern plots, but was a week to 10 days earlier in western Ontario and a few days earlier in eastern Ontario (Table 1).

The average age of the sampled balsam fir ranged from 47 years in New Brunswick to 80 years in western Ontario. Individual tree ages ranged from 49 to 99 years, both extremes occurring in the eastern Ontario plot. New Brunswick had the smallest sample trees, with averages of 17.0 cm (6.7 in.) in dbh and 14 m (46 ft) in height. The greatest average diameter of sample trees occurred in Newfoundland, 21.3 cm (8.4 in.); however, the greatest average tree height was 17.4 m (57 ft) in Quebec (Table 1).

Height:age ratios of all sample trees revealed that the fastest height growth took place in Quebec, with a site index of 1.06, and was closely followed by New Brunswick with 0.98. Western and eastern Ontario sample trees had the slowest average height growth, with site indices of 0.64 and 0.66, respectively (Table 1).

The width of the 15 most recent annual growth rings of the girdled trees at the basal, middle and top sampling locations is presented in Table 1 and in Figure 8. The trees from all five study areas show progressively faster recent growth from the basal to top portions of the stem, with the exception of the Newfoundland trees which peaked at the midpoint. In general, the trees sampled in the Atlantic Provinces of New Brunswick and Newfoundland had the fastest recent growth rate, whereas the narrowest rings, denoting the slowest recent growth, were found in the sample trees from Quebec and western Ontario, particularly the latter.

All of the trees in this study were girdled at roughly the same time, between May 19 and June 15, 1966, using a rigidly standardized method. However, the trees varied greatly in the length of time they remained alive following girdling. At the period of white birch leaf fall in 1966 only three of the 110 girdled trees were dead, all in the eastern Ontario study plot. For this reason tree sampling in 1966 was

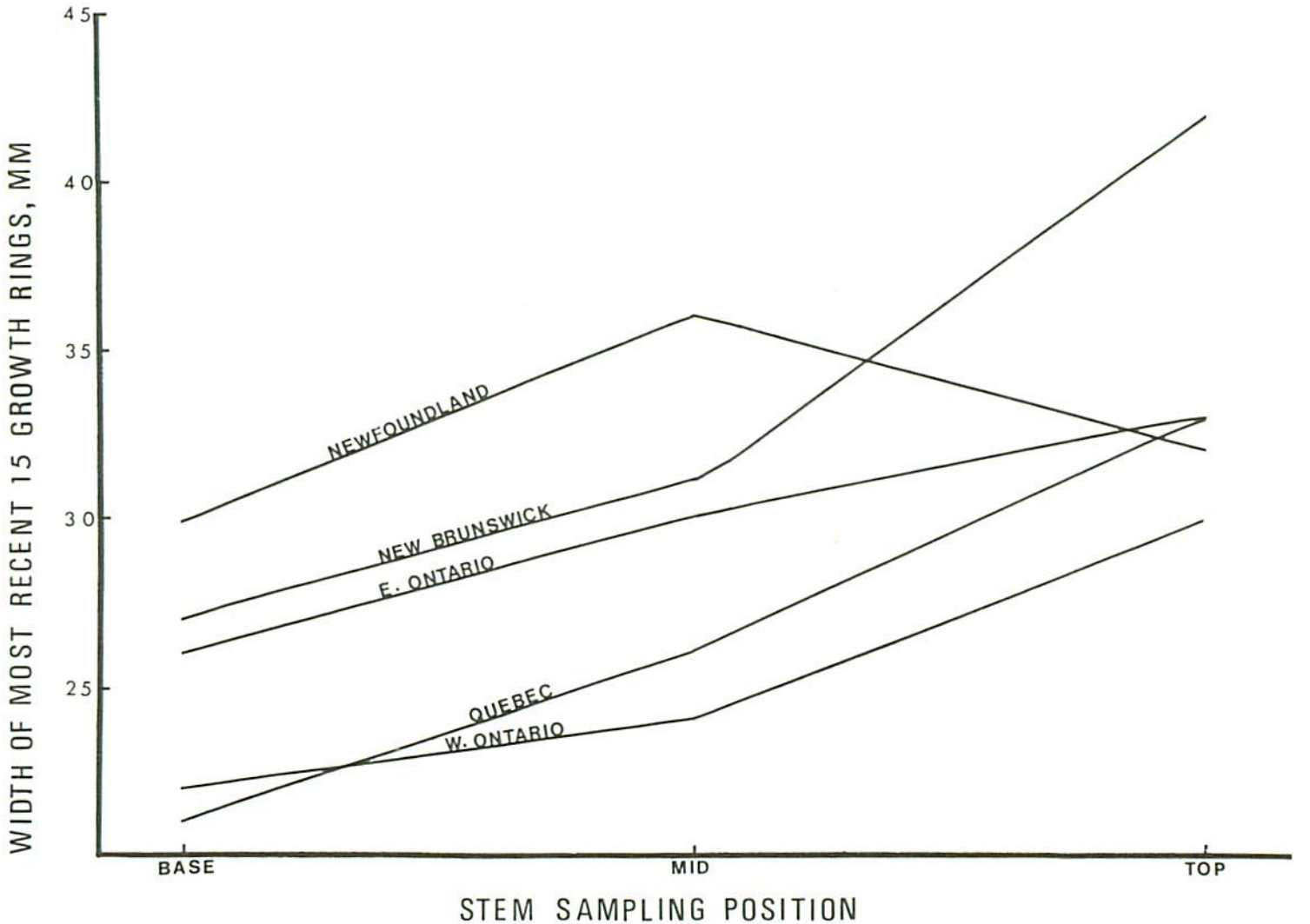

Figure 8. Comparison of recent growth rate at different stem positions in killed, girdled balsam fir in the five study areas.

limited to this plot. This involved two of the three dead trees plus the two living "control" trees. By the time white birch flushing occurred in the spring of 1967, approximately one year after the trees had been girdled, five more of the girdled trees had died in eastern Ontario, eight were dead in New Brunswick, six in Quebec, two in western Ontario, and all of the girdled trees were still alive in Newfoundland. Sampling was therefore initiated in New Brunswick, Quebec and western Ontario, and continued in eastern Ontario. At the time of white birch leaf fall in 1967 many of the girdled trees in the Newfoundland plot had died, so that tree sampling was then carried out on all study plots for the first time. Most of the girdled trees in the other four plots that had survived until the spring of 1967 died during the summer months. However, a few trees lingered on; one of the trees girdled in western Ontario did not die until the winter of 1968-1969, 2 1/2 years after girdling.

The wide variation in the length of time it took for girdled trees to die was ignored because no appreciable changes occurred in the stems prior to tree death, and because comparisons of the rate of deterioration, etc., could be made only by comparing trees that had been dead for approximately the same length of time. However, most of the deteriorating activity, both pathological and entomological, takes place during the growing season (May-October). It is safe to assume that any deterioration that takes place in the stems of dead trees during the period November 1-April 30 when cold temperatures render the fungi (and insects) virtually inactive would have negligible influence on the rate of deterioration. Therefore, as a basis for comparison, all sample trees were grouped according to the number of months of "influential fungal activity" (May-October) between the time of tree death and sampling. Table 2 shows the distribution of the sample trees in each study area on this basis. It is evident that the sample trees from all areas were distributed almost equally among these five arbitrarily chosen time periods.

Moisture content

The average moisture content of the heartwood of the two living balsam fir cut in each plot ranged from an average of 146% in western Ontario to 84% in New Brunswick (Table A2). Figure 9 indicates that following tree death the heartwood dried out relatively slowly so that after 19 or more months' exposure to influential fungal activity (generally 3 or more years) the heartwood moisture content ranged from 95% in western Ontario to 52% in Quebec (Table A2). No noticeable differences were apparent in the rate of heartwood drying in the five study areas (Fig. 9).

The sapwood of the ten living balsam fir had somewhat higher moisture contents than the heartwood, ranging from an average of 171% in eastern Ontario to 121% in Quebec (Table A2). Figure 10 shows the

Table 2. The number of girdled, killed balsam fir trees grouped according to the number of months of influential fungal activity (May-October) since death

	Study area	No. of trees (grouped according to no. of months of influential fungal activity since death)					
		0-3	4-6	7-12	13-18	19+	Total
1	Newfoundland	3	2	5	3	7	20
2	New Brunswick	3	3	4	4	6	20
3	Quebec	4	2	5	4	5	20
4	Eastern Ontario	5	3	5	4	3	20
5	Western Ontario	2	4	6	5	2	19[a]
Total		17	14	25	20	23	99

[a] A complete sample of 20 trees in western Ontario was impossible because three girdled trees suffered windthrow, and only two extra trees had been girdled in each plot.

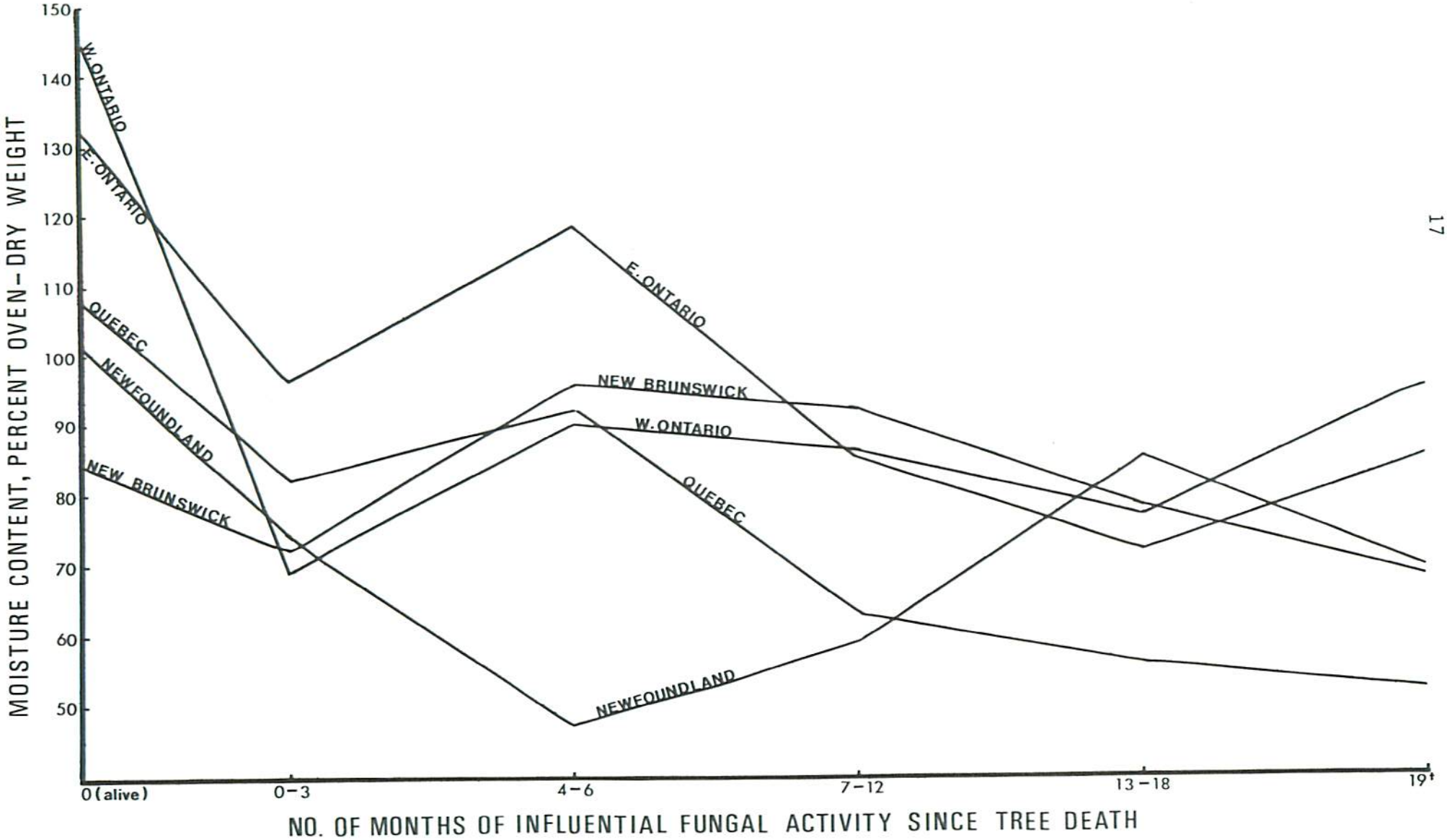

Figure 9. Changes in the moisture content of heartwood following tree death in the five study areas.

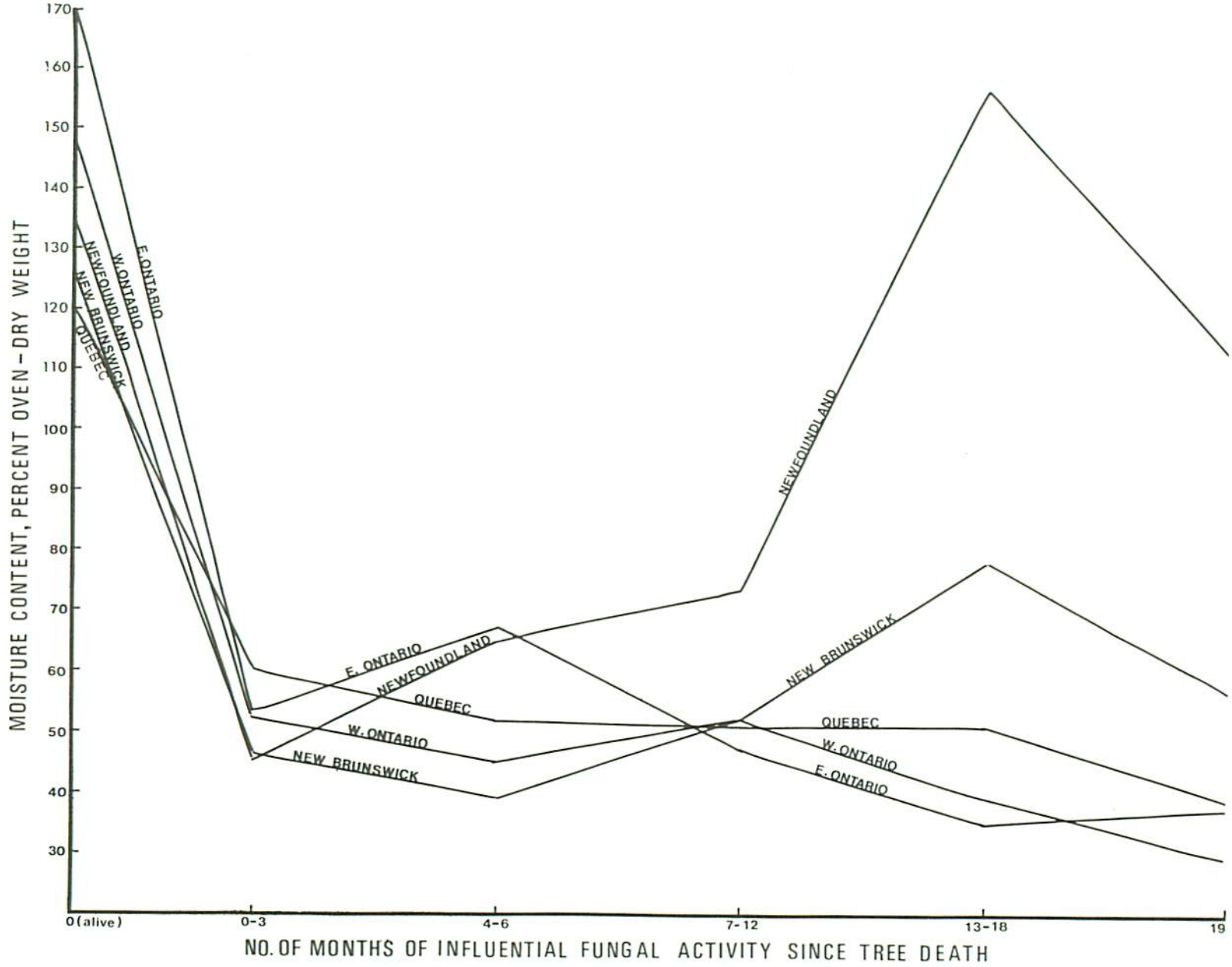

Figure 10. Changes in the moisture content of sapwood following tree death in the five study areas.

pronounced, sudden drop in sapwood moisture content in trees sampled very shortly after death. Sampled trees that had been exposed to less than 3 months of influential fungal activity already showed a reversal in the normal living tree sapwood-heartwood moisture content relationship. The average moisture content of the sapwood of these trees ranged from 60% (Quebec) to 45% (Newfoundland), whereas the average moisture content of heartwood ranged from 96% (eastern Ontario) to 72% (New Brunswick) (Tables A2 and A3).

The sapwood moisture content of the girdled and killed trees remained at approximately 50% through the remainder of the study period. An exception was noted in the Newfoundland trees that were exposed to 13-18 months of influential fungal activity. These (three) trees had an average sapwood content of 157%, which is high even for the sapwood of living balsam fir. These high values were associated with a heavy rainfall of 3 in. (7.5 cm) shortly before the trees were sampled. It is reasonable to expect that the outer sapwood of these dead, standing trees with much or all of the bark sloughed off would absorb considerable moisture during periods of heavy rain. During the years 1966-1972 when the girdled trees were sampled, the Quebec plot had appreciably higher average precipitation levels in all four critical months than did the other plots (Table A1), whereas the Quebec trees had consistently low sapwood moisture contents (Figure 10). This suggests that heavy or prolonged rain can result in a greatly increased sapwood moisture content in dead, standing trees. However, this is of short duration, and with dry weather the sapwood soon resumes its basic, relatively dry condition.

Considering variations in moisture contents at the different sampling positions within the stems of living trees and girdled, dead trees it is evident from Figure 11 and Table A4 that both the sapwood and heartwood of living trees tend to be drier at the base compared with the midstem and top stem sections. Once a tree was dead there were no appreciable differences among stem heights in the moisture content of sapwood or heartwood. However, there was a tendency for heartwood in the top stem sections to be drier than in the midsections or basal sections; indeed, it was very nearly as dry as the sapwood. Consequently, the higher moisture content in the heartwood than in the sapwood of dead trees as noted in Table A2 was almost entirely attributable to the relatively high heartwood moisture content in the basal and midstem sections.

Insect activity

Despite the complete lack of insect data from Quebec, it is evident from Figures 12, 13, and 14 and Tables A5, A6, and A7 that noteworthy differences in the abundance of bark beetles, woodwasps, and *Monochamus* borers exist among the other study areas. Figure 12 shows that bark beetles were far more abundant on the eastern Ontario

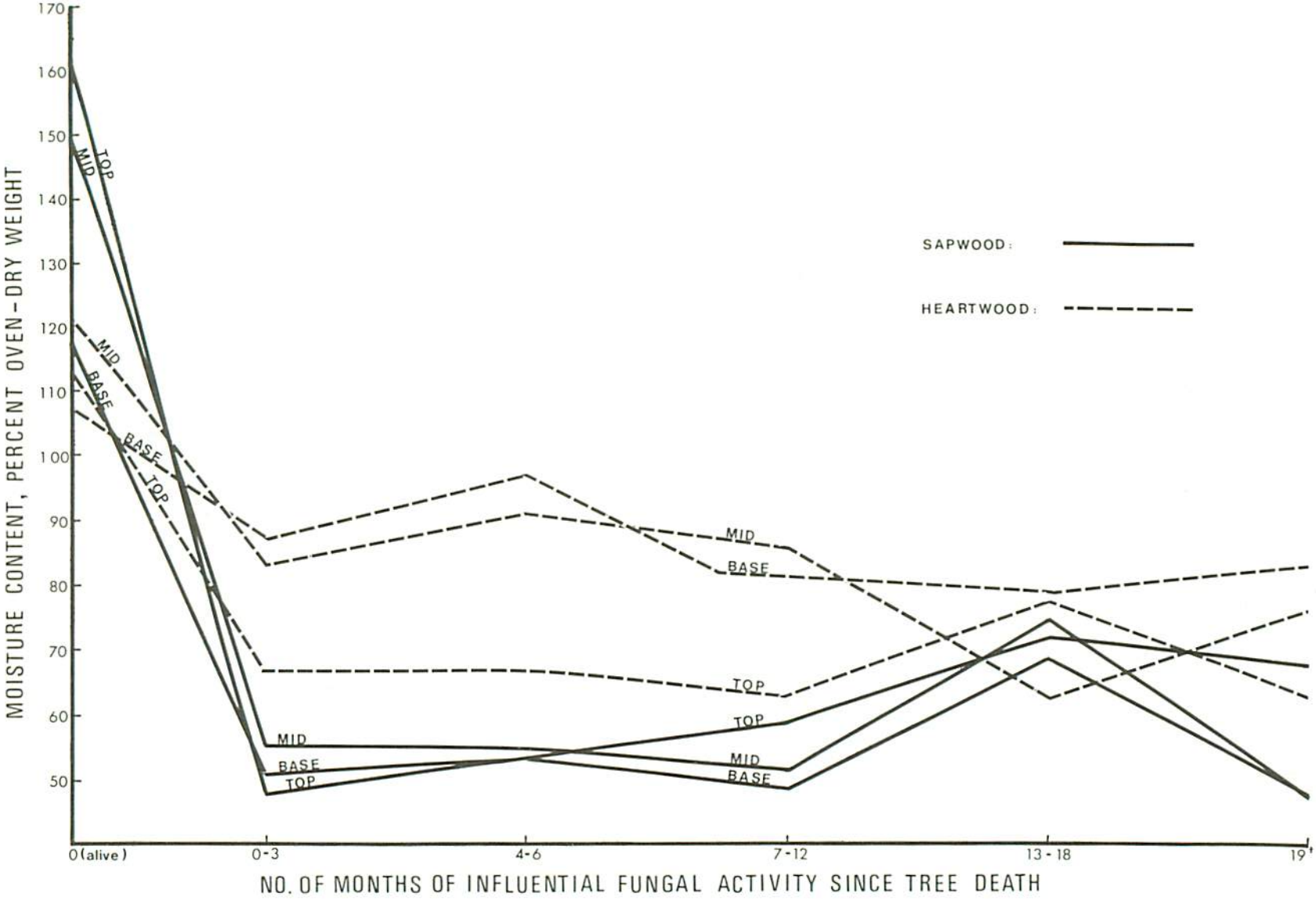

Figure 11. Changes in the moisture content of sapwood and heartwood following tree death at three stem positions in the five study areas.

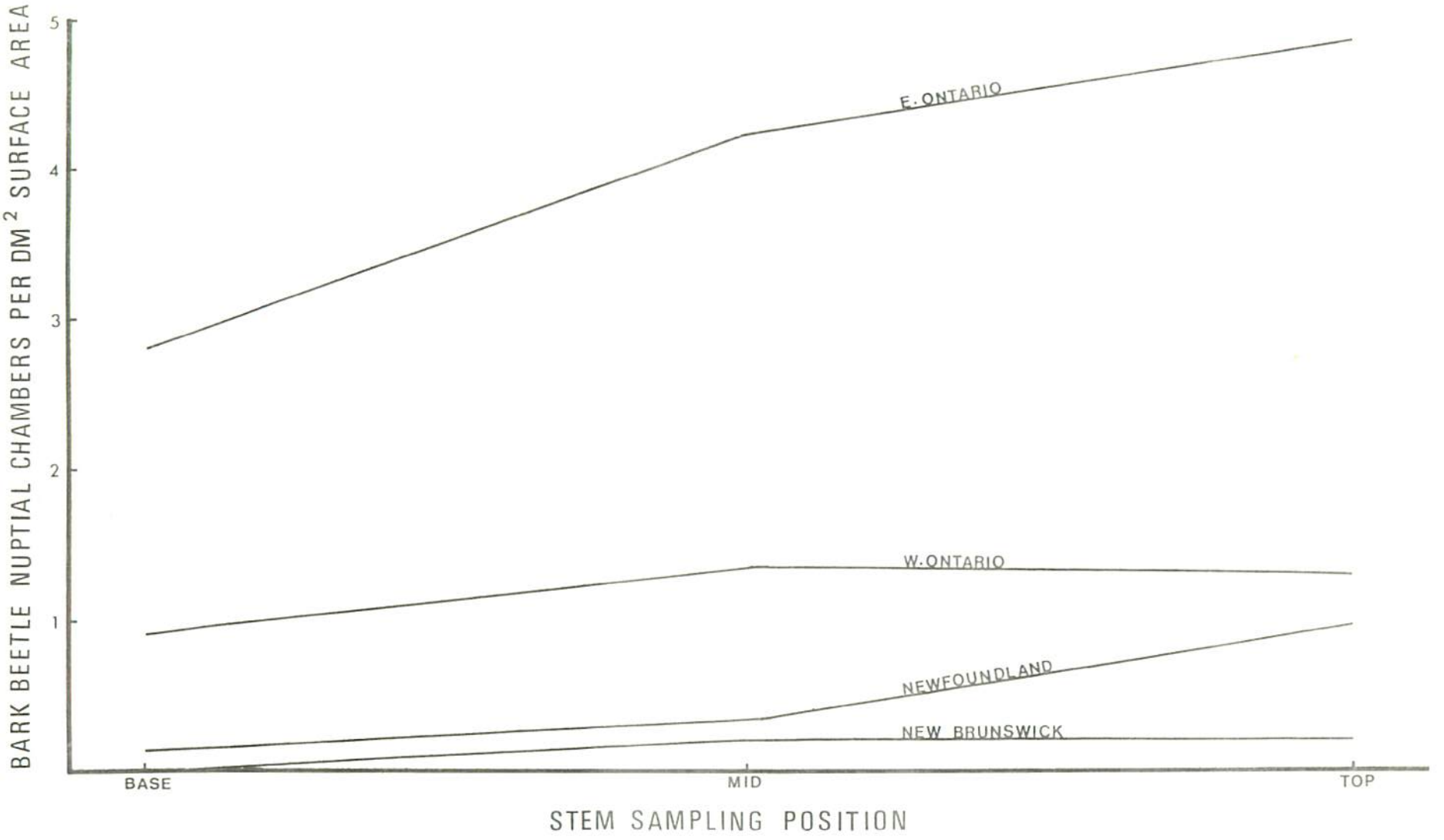

Figure 12. Bark beetle activity in girdled, killed balsam fir at three stem positions in four of the study areas.

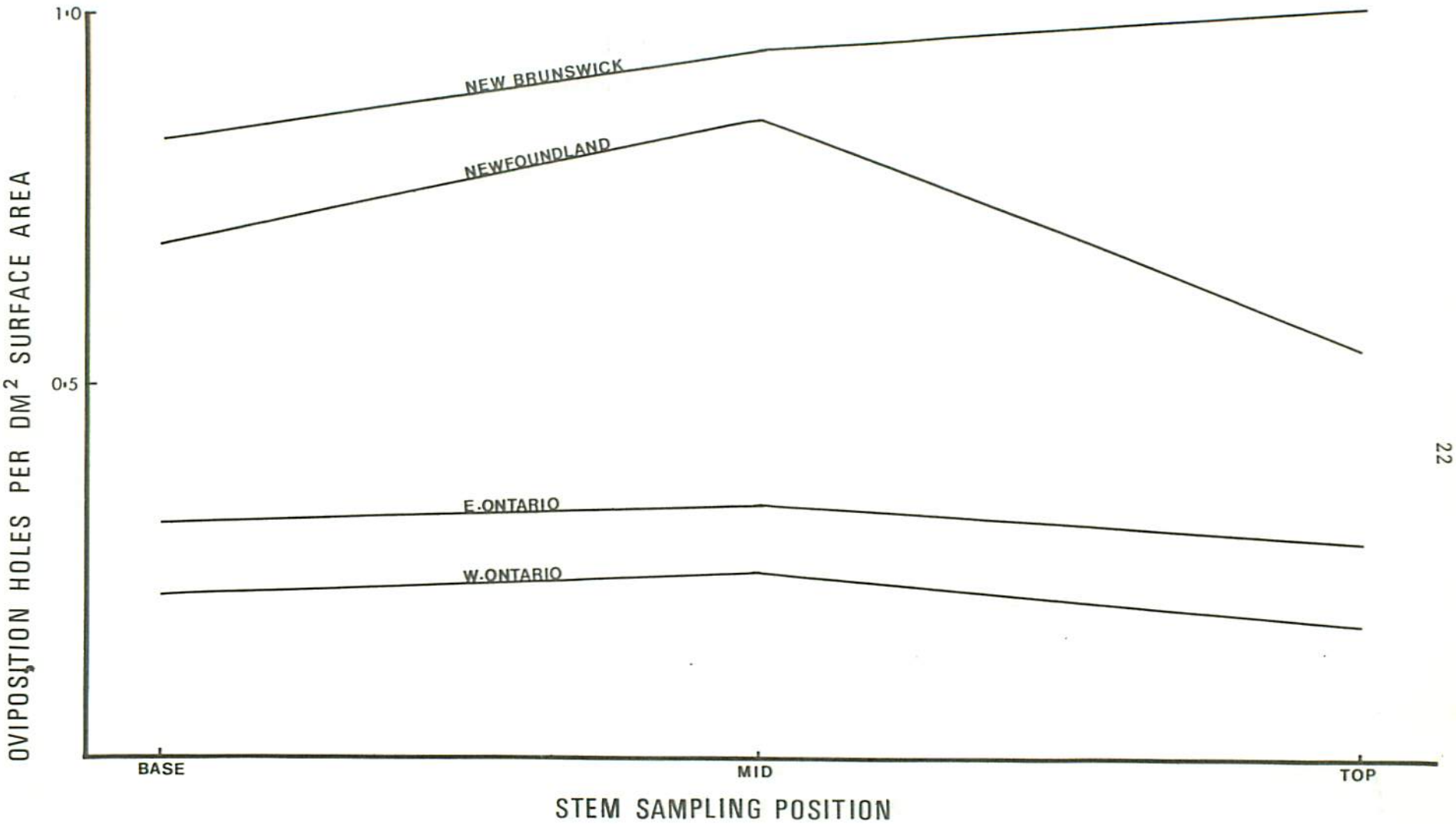

Figure 13. Woodwasp oviposition holes in girdled, killed balsam fir at three stem positions in four of the study areas.

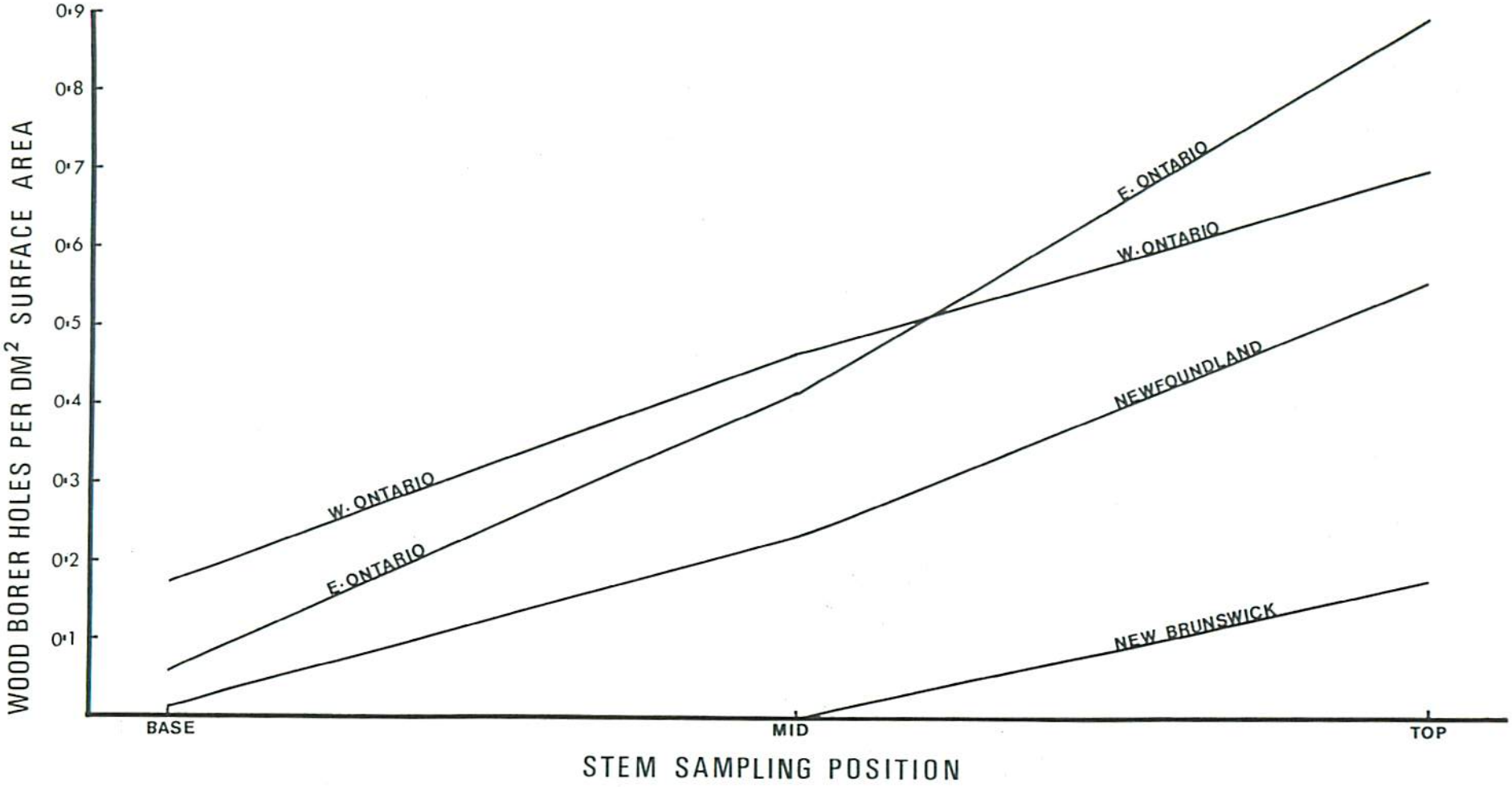

Figure 14. *Monochamus* wood borer activity (entrance and exit holes) in girdled, killed balsam fir at three stem positions in four of the study areas.

girdled balsam than on the trees in the other three areas; they were rarest on the New Brunswick trees. In all regions bark beetle numbers were lightest in the basal stem and generally heaviest in the top. Figure 13 shows that woodwasp oviposition holes were quite plentiful on the Newfoundland and New Brunswick trees, but were much rarer in both Ontario plots. It is of interest to note (Table A6) that in the most recently killed trees woodwasp attacks were very abundant in Newfoundland compared with the other three regions. However, the data also show that exit holes of adult woodwasps were most abundant in New Brunswick and least abundant in Newfoundland. Some of this difference might be attributed to parasites as large numbers of *Rhyssa* spp. and *Ibalia* spp. exit holes were counted in Newfoundland. Figure 14 shows that girdled trees in the two Ontario plots had the highest numbers of *Monochamus* wood borers, and New Brunswick the lowest. Without exception, *Monochamus* populations show a positive relationship to height along the length of the stem. In fact, in New Brunswick borer holes were found only in the top sections of the trees.

Progress of sap stain and sap rot penetration

Unfortunately, no information on depth of sap stain or sap rot was available from Quebec. From Figure 15 and Table A8 it is evident that there were no pronounced differences in the rate of penetration of sap stain in western Ontario, eastern Ontario, or New Brunswick. In Newfoundland, however, sap stain developed very quickly in trees exposed to less than 3 months of influential fungal activity following death. The radial penetration of sap stain in these trees was almost as deep as that in trees exposed to the end of the study period. Figure 16 and Table A8 show that sap rot was insignificant in the four study areas other than Quebec until dead trees had been exposed after death to more than 6 months of influential fungal activity. Following this period the rate of sap rot penetration was very rapid in western Ontario, somewhat less rapid in eastern Ontario, and very rapid after a much slower start in New Brunswick. Sap rot development was by far the slowest in Newfoundland.

Table A8 also shows that, in these four study areas, sap rot, and to a lesser degree sap stain, penetrated the stem much more rapidly in the top stem position than in the midregions or basal regions. There were 21 instances in which groups of trees within a single study area and exposed to fungal activity for the same period of time exhibited the deepest penetration of stain or rot in the top stem section. This is in contrast to seven instances in which the deepest penetration occurred in the midsection, and six in which it occurred in the basal section. Five of the six cases in which the most rapid deterioration occurred in the butt section were in Ontario.

Microorganisms associated with stem deterioration

The overall frequency of occurrence of microorganisms isolated from the stem within 30 mm of the cambium of the 99 killed balsam fir

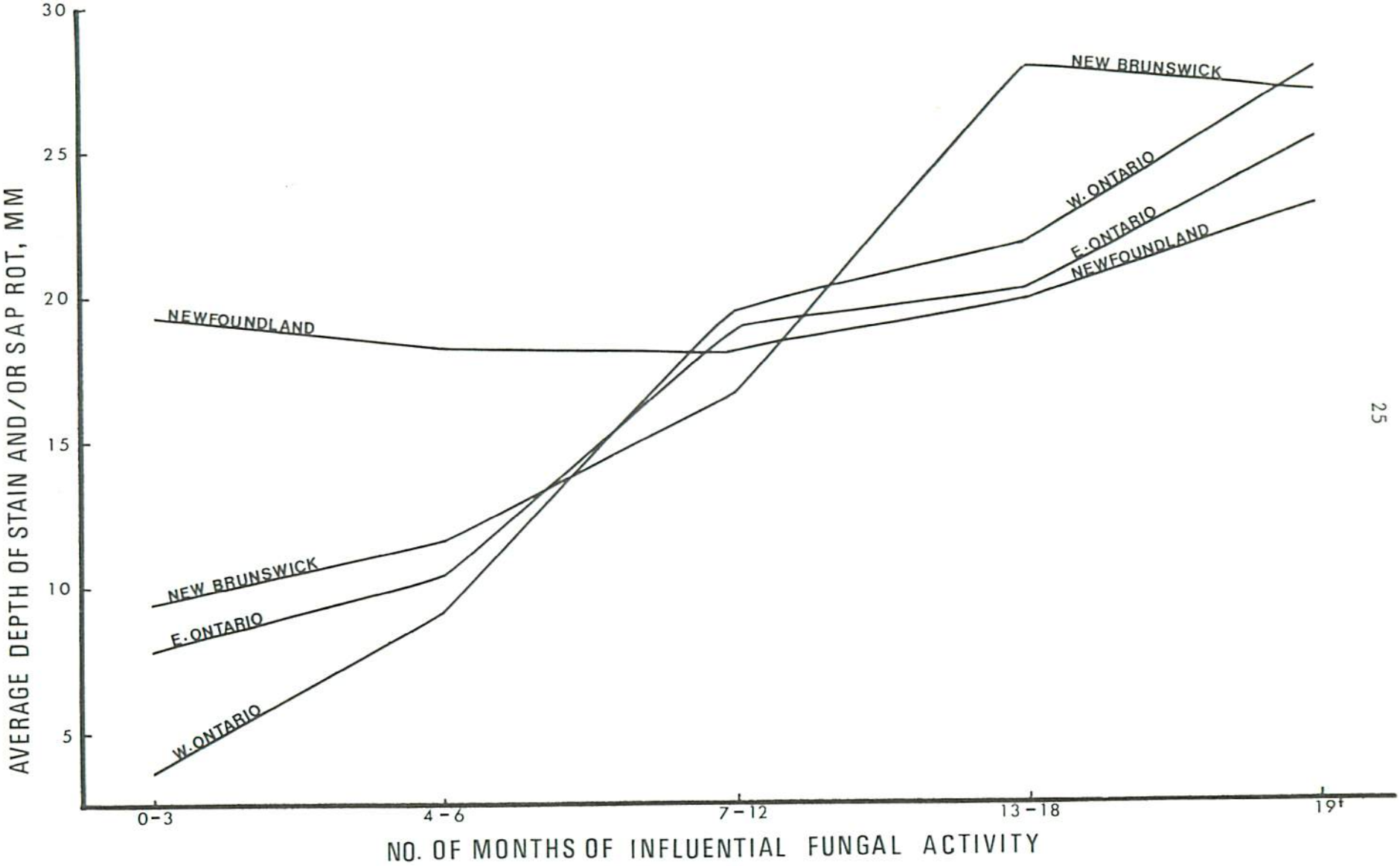

Figure 15. Average rate of penetration of sap stain and/or rot in four of the study areas.

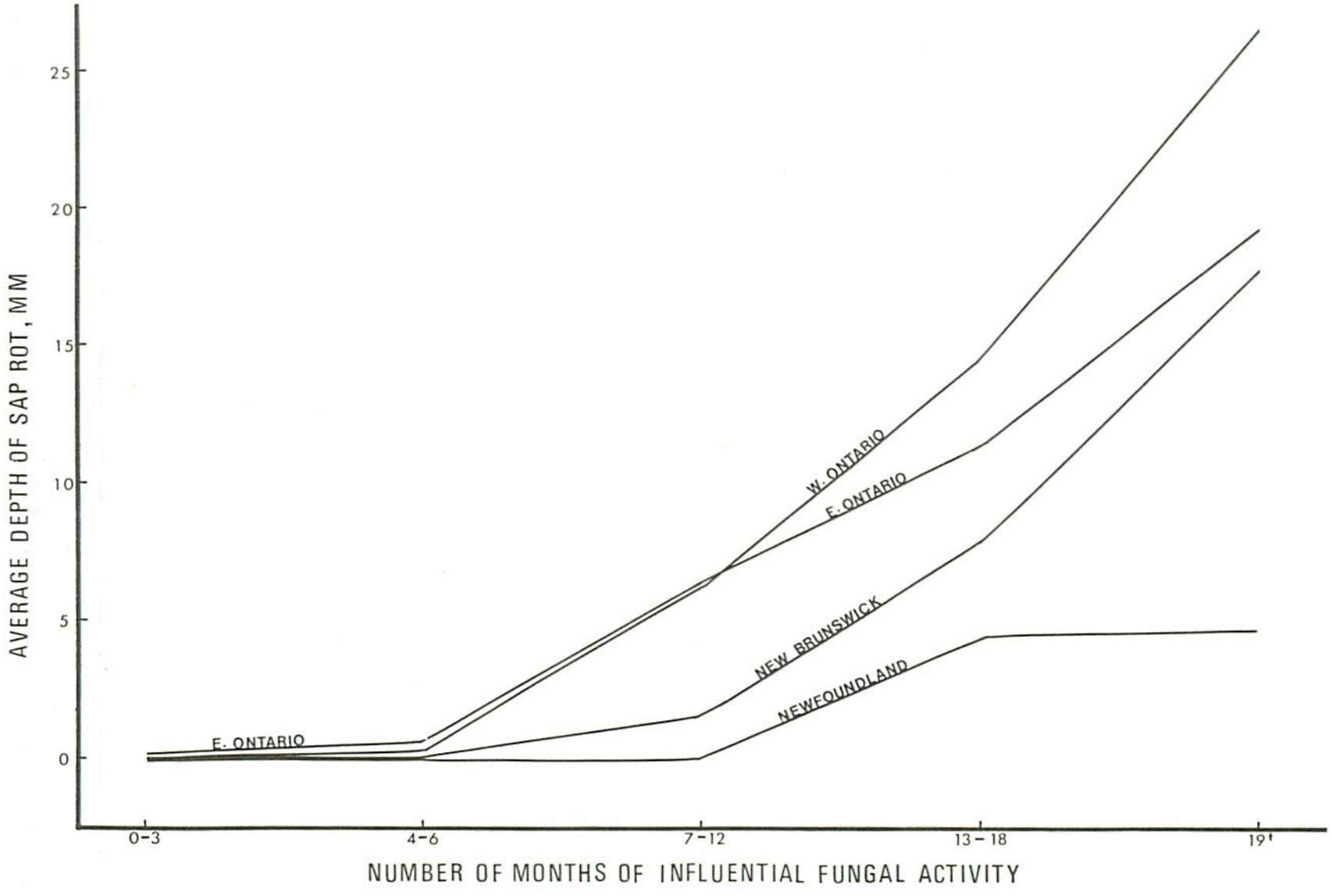

Figure 16. Average rate of penetration of sap rot in four of the study areas.

trees is shown in Table 3. Six species of fungi were obtained more than 100 times from the 4,612 isolation attempts made in these trees. In order of frequency of occurrence these were *Stereum chailletii*, *Polyporus abietinus*, *Trichoderma viride*, *Nectria fuckeliana*, *Rhinocladiella elatior*, and *Stereum sanguinolentum*. Fungi from three other genera, each consisting of two or more unidentified species, were also isolated more than 100 times. These were, in decreasing order of frequency of occurrence, *Ceratocystis*, *Cephalosporium*, and *Penicillium*. It is likely that most, if not all, of the *Penicillium* isolates were contaminants that may or may not have been present in the dead, standing trees. Both bacteria and yeasts were also isolated more than 100 times, but no attempt was made to identify species or genera in these groups. Basidiomycetes in addition to the three common ones listed above, again in decreasing order of frequency of occurrence, were *Trechispora brinkmanni*, *Fomes pinicola*, *Coniophora puteana*, *Corticium laeve*, *Trechispora raduloides*, *Odontia bicolor*, *Basidioradulum radula*, *Peniophora cinerea*, *Schizophyllum commune*, *Stereum murraii*, *Stereum purpureum*, *Peniophora gigantea*, *Polyporus schweinitzii* and *Armillaria mellea*.

The five principal organisms associated with the deterioration of balsam fir in eastern Canada are considered to be the four fungi most frequently isolated in this study, *S. chailletii*, *P. abietinus*, *T. viride*, and *N. fuckeliana*, plus *S. sanguinolentum*. *Stereum sanguinolentum* was added because in an earlier study of balsam fir deterioration in New Brunswick (Stillwell and Kelly 1964) this fungus was isolated more frequently than any other organism from the deteriorated sapwood. It should be pointed out that although *T. viride* in this study was isolated more frequently than all but two other fungi, it is suspected of being limited to a secondary role and not involved in the actual mechanisms of deterioration except perhaps as a competitor.

Occurrence of major fungi and stem position

Table A9 shows that only two of the major fungi, *P. abietinus* and *S. chailletii*, are related to sampling height in the stem. *Polyporus abietinus* was positively related whereas *S. chailletii* was negatively related to height. Figures 17 and 18 show that these relationships exist in all five study areas with one exception: in eastern Ontario the occurrence of *S. chailletii* was neither positively nor negatively related to sampling height. In general, *S. chailletii* was the only Basidiomycete consistently isolated from the basal position.

Occurrence of major fungi and period since tree death

Table A10 shows the frequency of occurrence of the five major fungi associated with deterioration, and of negative isolation attempts, in relation to the period of exposure to influential fungal activity in each of the five study areas.

Table 3. The results of attempts at isolating microorganisms from the outer 30 mm of girdled, killed balsam fir stems

Isolated microorganisms	Overall frequency of occurrence	No. of trees in which microorganisms were isolated or negative attempts occurred[a] (by study area)					% of total isolation attempts in each study area from which microorganisms were isolated[b] (by study area)				
		1	2	3	4	5	1	2	3	4	5
Negative (sterile)	739	8	16	16	18	15	4.4	24.7	16.5	15.8	19.0
Stereum chailletii (Pers. ex Fr.) Fr.	742	20	16	18	9	12	27.1	17.6	19.5	9.6	6.7
Polyporus abietinus Dicks ex Fr.	517	8	11	4	10	12	7.9	12.3	3.9	16.3	14.8
Trichoderma viride Pers. ex Fr.	472	3	12	13	11	11	1.4	12.1	8.5	15.1	14.0
Nectria fuckeliana Booth	423	16	5	13	16	18	8.8	2.3	10.2	10.7	14.3
Bacteria	367	16	6	15	15	19	13.7	3.1	9.9	6.9	6.4
Rhinocladiella elatior Mang.	290	14	11	-	10	10	6.3	16.3	-	4.1	3.8
Ceratocystis spp.	268	8	5	12	15	7	2.7	1.1	6.9	12.6	5.8
Cephalosporium spp.	130	13	3	-	11	10	3.5	0.6	-	5.0	4.6
Yeasts	125	17	-	-	13	9	4.0	-	-	6.2	3.1
Penicillium spp.	114	2	2	4	8	7	0.4	3.8	3.2	3.0	2.1
Stereum sanguinolentum (Alb. & Schw. ex Fr.) Fr.	111	6	2	5	1	8	2.3	0.5	1.3	3.1	4.7
Trechispora brinkmanni (Bres.) Rogers & Jacks	66	5	4	6	2	1	3.6	0.9	3.4	0.2	0.1
Fomes pinicola (Sw. ex Fr.) Cooke	61	4	3	-	-	2	2.6	2.5	-	-	1.3
Phialophora spp.	52	12	-	-	4	6	4.1	-	-	0.4	1.0
Verticillium spp.	50	4	5	-	3	3	0.9	2.7	-	1.3	0.3
Ceractocystis piceae (Münch) Bakshi	46	7	-	2	5	1	2.6	-	1.0	0.8	0.6
Cytospora spp.	44	-	-	5	4	3	-	-	2.2	1.4	1.4
Kirschteiniella thujina (Peck) Pomerleau & Etheridge	40	2	5	5	-	1	0.3	2.7	1.2	-	0.1
Ascocoryne sarcoides (Jacq. ex Gray) Groves & Wilson	35	7	2	1	1	-	2.1	1.3	0.2	0.1	-
Cytospora kunzei Sacc.	25	-	-	7	-	-	-	-	3.1	-	-
Phoma spp.	24	2	-	-	4	9	0.3	-	-	0.5	1.8
Coniophora puteana (Schum ex Fr.) Karst.	23	1	-	-	2	5	0.1	-	-	0.8	1.5
Corticium laeve Pers. ex Fr.	23	1	-	4	-	-	0.5	-	2.2	-	-
Cladosporium sp.	23	2	1	-	4	1	0.2	0.5	-	0.6	0.1
Rhizoctonia sp.	20	-	-	5	-	-	-	-	2.4	-	-

(continued)

Table 3. The results of attempts at isolating microorganisms from the outer 30 mm of girdled, killed balsam fir stems (concluded)

Isolated microorganisms	Overall frequency of occurrence	No. of trees in which microorganisms were isolated or negative attempts occurred[a] (by study area)					% of total isolation attempts in each study area from which microorganisms were isolated[b] (by study area)				
		1	2	3	4	5	1	2	3	4	5
Trechispora raduloides (Karst.) Rogers	14	-	-	-	1	3	-	-	-	0.1	1.4
Peniophora aspera (Pers.) Sacc.	14	-	-	-	2	4	-	-	-	0.3	1.2
Ceratocystis bicolor (Davids. & Wells) Davids.	14	-	-	-	4	-	-	-	-	1.5	-
Aureobasidium pullulans (de Bary) Arnaud	14	-	1	6	-	-	-	0.5	1.1	-	-
Calcarisporium sp.	12	-	-	-	4	3	-	-	-	0.8	0.4
Chloridium sp.	12	6	-	-	-	-	1.3	-	-	-	-
Paecilomyces sp.	8	2	-	-	-	2	0.3	-	-	-	0.6
Actinomycetes	8	-	1	-	3	-	-	0.1	-	0.7	-
Spicaria sp.	8	-	3	-	1	-	-	0.5	-	0.3	-
Oidiodendron sp.	7	4	-	-	-	-	0.7	-	-	-	-
Retinocyclus abietis (Crouan) Groves & Wells	6	1	-	3	-	-	0.1	-	0.6	-	-
Tympanis sp.	6	-	-	4	-	-	-	-	0.7	-	-
Sclerophoma pithyophila (Corda) Höhn.	6	2	1	1	-	-	0.3	0.2	0.1	-	-
Leptographium sp.	5	-	-	-	2	1	-	-	-	0.3	0.2
Odontia bicolor (Alb. & Schw. ex Fr.) Quèl.	5	-	-	-	1	1	-	-	-	0.3	0.2
Verticicladium sp.	5	1	-	1	-	-	0.3	-	0.2	-	-
Chaetopsis sp.	5	-	-	1	-	-	-	-	0.6	-	-
Radulum orbiculare Fr.	5	1	-	-	-	-	0.5	-	-	-	-
Peniophora cinerea (Fr.) Cooke	4	-	-	1	-	-	-	-	0.5	-	-
Schizophyllum commune Fr.	3	-	-	2	-	-	-	-	0.4	-	-
Dasyscyphus agassizii (Berk. & Curt.) Sacc.	3	2	1	-	-	-	0.2	0.1	-	-	-
Fungi isolated only twice[c]	12	2	-	6	2	-	0.2	-	0.8	0.2	-
Fungi isolated only once[d]	13	1	1	4	2	5	0.1	0.1	0.4	0.2	0.5
Misc. ascomycetes and fungi imperfecti	493	20	12	14	17	16	25.0	8.2	6.2	6.9	6.1
Misc. basidiomycetes	89	1	9	1	7	5	0.3	5.4	0.1	2.1	1.4
Misc. phycomycetes	8	1	-	-	4	-	0.2	-	-	0.6	-

[a] Based on 20 trees in each study area except for 19 trees in area 5.

[b] Based on a total of 960 isolation attempts in areas 1, 2 and 4, 912 attempts in area 5, and 820 attempts in area 3. For each area these total more than 100% because of isolation attempts which yielded more than one organism.

[c] Study area in parentheses: *Gliocladium roseum* Bain (4), *Arthrobotrys* sp. (3), *Fusidium* sp. (3), *Phialocephala* sp. (3), *Mucor* sp. (3), *Phialophora heteromorpha* (Nannf.) Wang (1).

[d] Study area in parentheses: *Alternaria* sp. (5), *Fusarium oxysporum* Schlecht. emend Snyd. and Hans (5), *Stereum murrayi* (Berk and Curt.) Burt. (5), *Dactylaria* sp. (5), *Chaetomium* sp. (5), *Stereum purpureum* (Pers. ex Fr.) Fr. (4), *Peniophora gigantea* (Fr.) Massée (4), *Polyporus schweinitzii* Fr. (3), *Armillaria mellea* (Vahl ex Fr.) Kummer (3), *Dermea* sp. (3), *Aspergillus* sp. (3), *Thysanophora penicilloides* (Roum.) Kendrick (2), *Bispora* sp. (1).

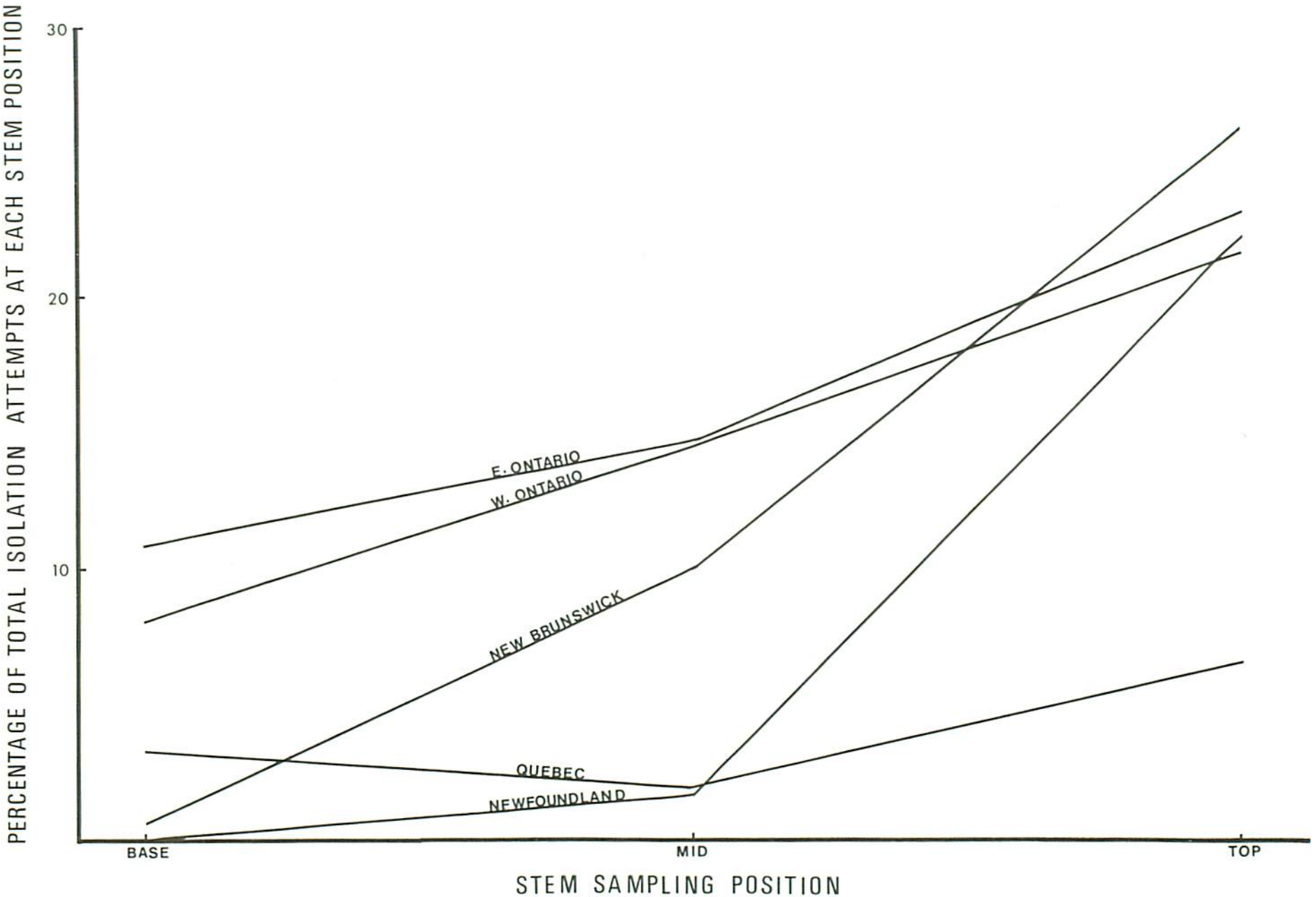

Figure 17. Occurrence of *Polyporus abietinus* at three stem positions in the five study areas.

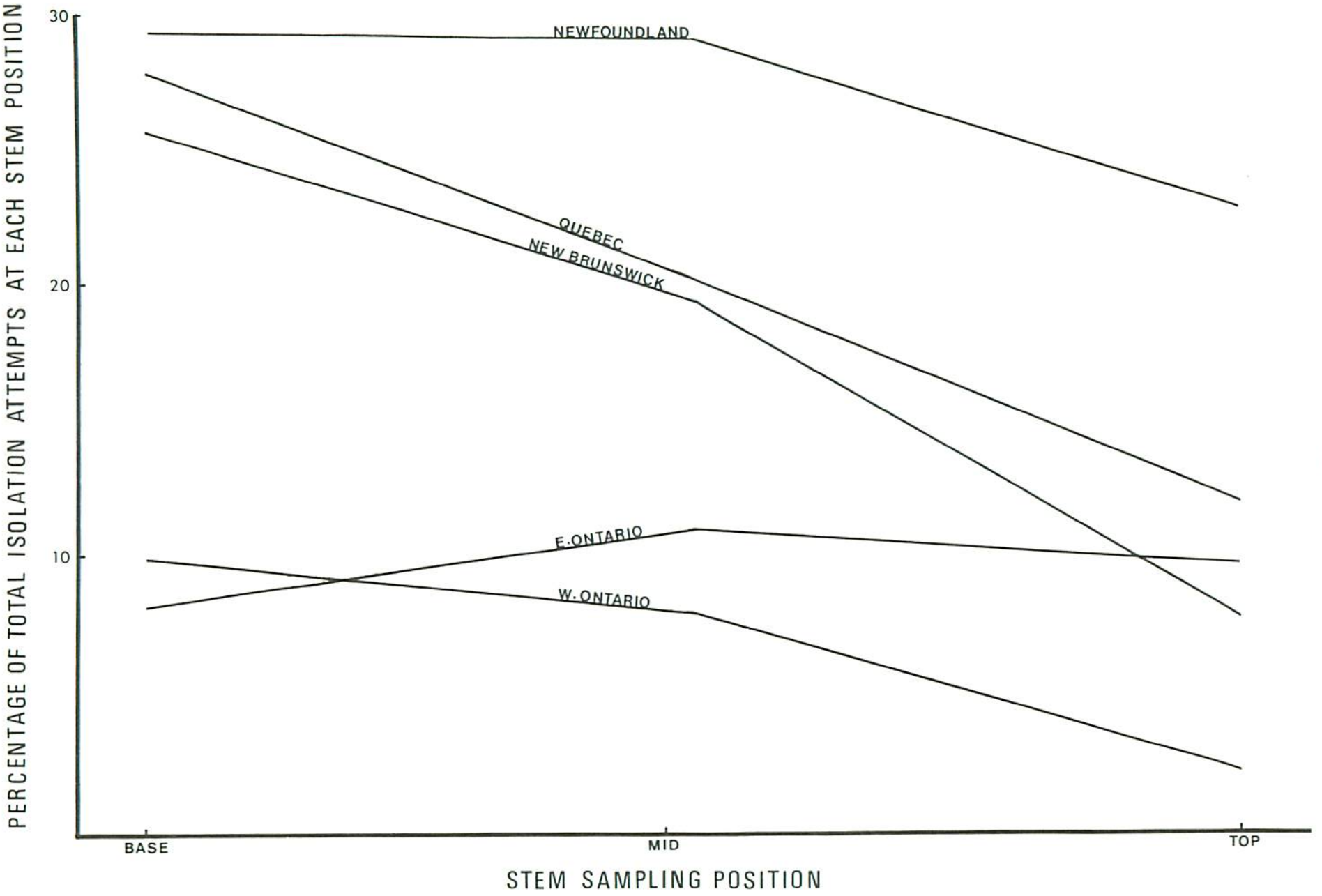

Figure 18. Occurrence of *Sterewm chailletii* at three stem positions in the five study areas.

Negative attempts, as would be expected, decreased markedly with increasing period of exposure. The percentage of negative isolation attempts made in trees in the 0-3 month class ranged from 37.1 in eastern Ontario to 81.3 in New Brunswick (except for Newfoundland, where only 9.7% were negative).

The data also show that *P. abietinus* (Fig. 19) and *T. viride* generally increased with the period of exposure. *Polyporus abietinus* was virtually absent in trees exposed to 6 months or less of influential fungal activity. It then increased appreciably in frequency up to 18 months of exposure, after which it tended to level off. In all of the sample trees exposed to up to 12 months of influential fungal activity, *P. abietinus* was isolated 65 and 55 times from eastern and western Ontario respectively, only seven times from New Brunswick, but never from Quebec and Newfoundland (Table A10)!

Stereum chailletii in all study areas was most abundant in either the 4-6 or the 7-12 month class, although it was relatively rare in western Ontario. Figure 20 shows that after this period it became much less frequent in trees in the 13-18 month exposed class. However, this trend was then reversed and at all positions it increased in abundance in trees exposed for over 19 months to influential fungal activity. No explanation is offered for this unexpected pattern, which was consistent in all study areas except Quebec.

The occurrence of *N. fuckeliana* in the study areas showed no consistent correlation with period since death. *Stereum sanguinolentum* occurred somewhat more frequently following 12 months of exposure to influential fungal activity than it did before. This fungus was by far the least common of the five major fungi in the 99 sample trees. It occurred in less than half of the trees in each study area, in only one tree in eastern Ontario and in two trees in New Brunswick.

Occurrence of major fungi and distance within cambium

Figures 21-25 and Tables A11-A15 show the frequency with which the five major fungi were isolated, at various distances within the cambium, from trees grouped according to period of exposure to influential fungal activity.

Table A11 and Figure 21 reveal that, regardless of period of exposure, *S. chailletii* was isolated more frequently from depths of roughly 13-19 mm than from shallower (less than 7 mm) or deeper (25 mm) positions. It was noticeably the least frequent at the deepest isolation depth of 25 mm.

Table A12 and Figure 22 confirm that the frequency of occurrence of *N. fuckeliana* did not change appreciably in dead trees exposed to different periods of influential fungal activity. They do show that the

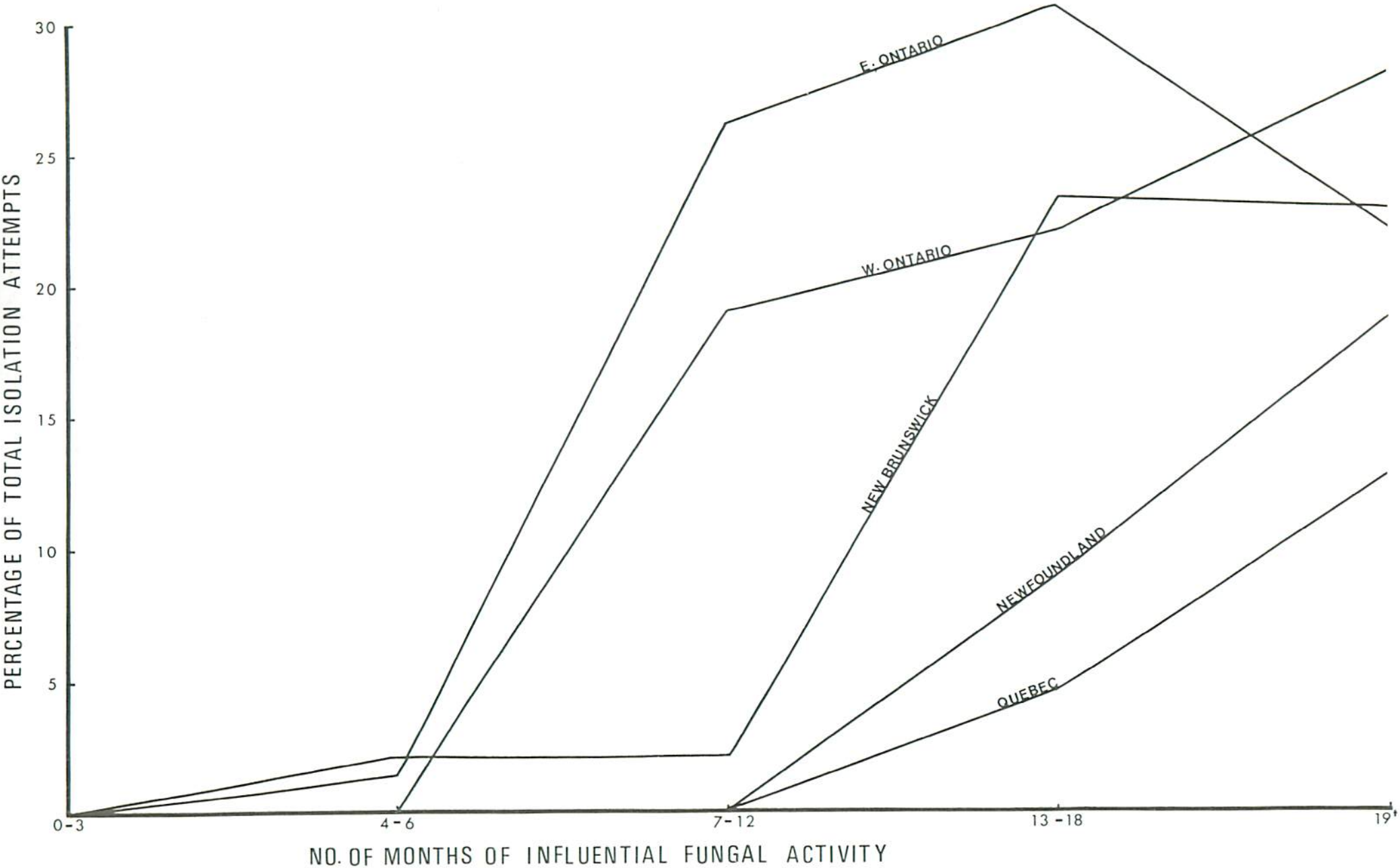

Figure 19. Occurrence of *Polyporus abietinus* in the five study areas at various periods of exposure to influential fungal activity.

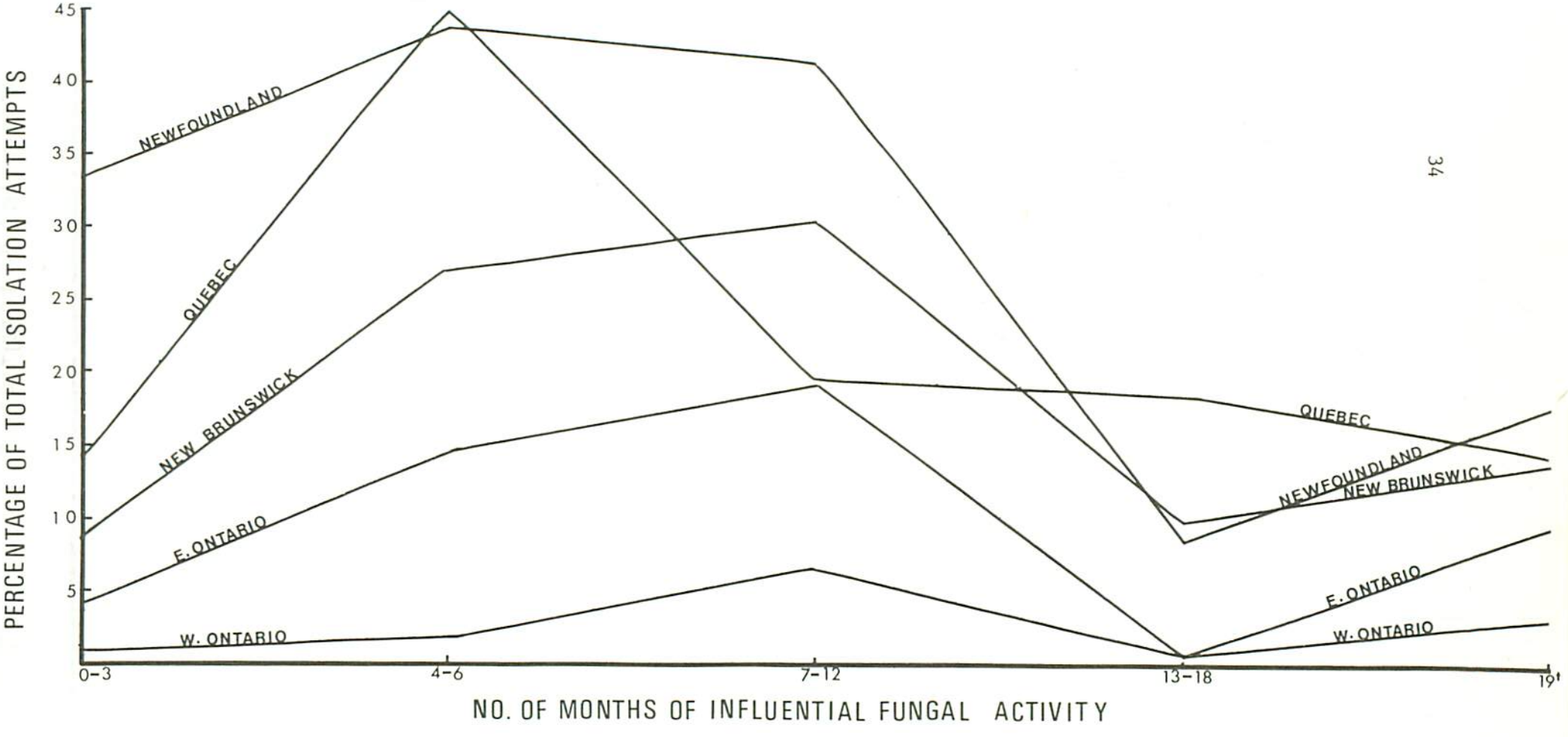

Figure 20. Occurrence of *Stereum chailletii* in the five study areas at various periods of exposure to influential fungal activity.

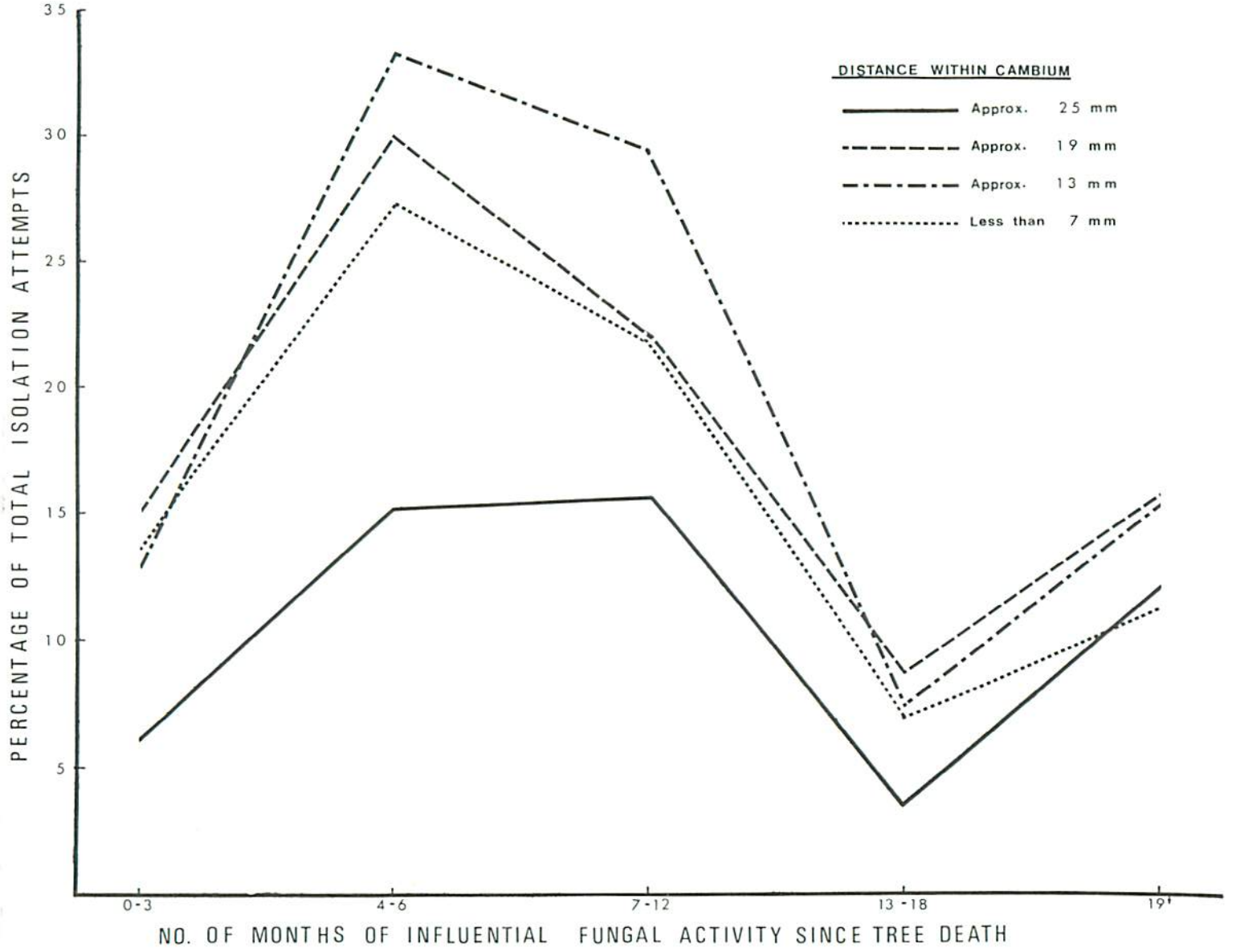

Figure 21. Occurrence of *Stereum chailletii* in girdled, killed balsam fir at different distances within the cambium at various periods of exposure to influential fungal activity.

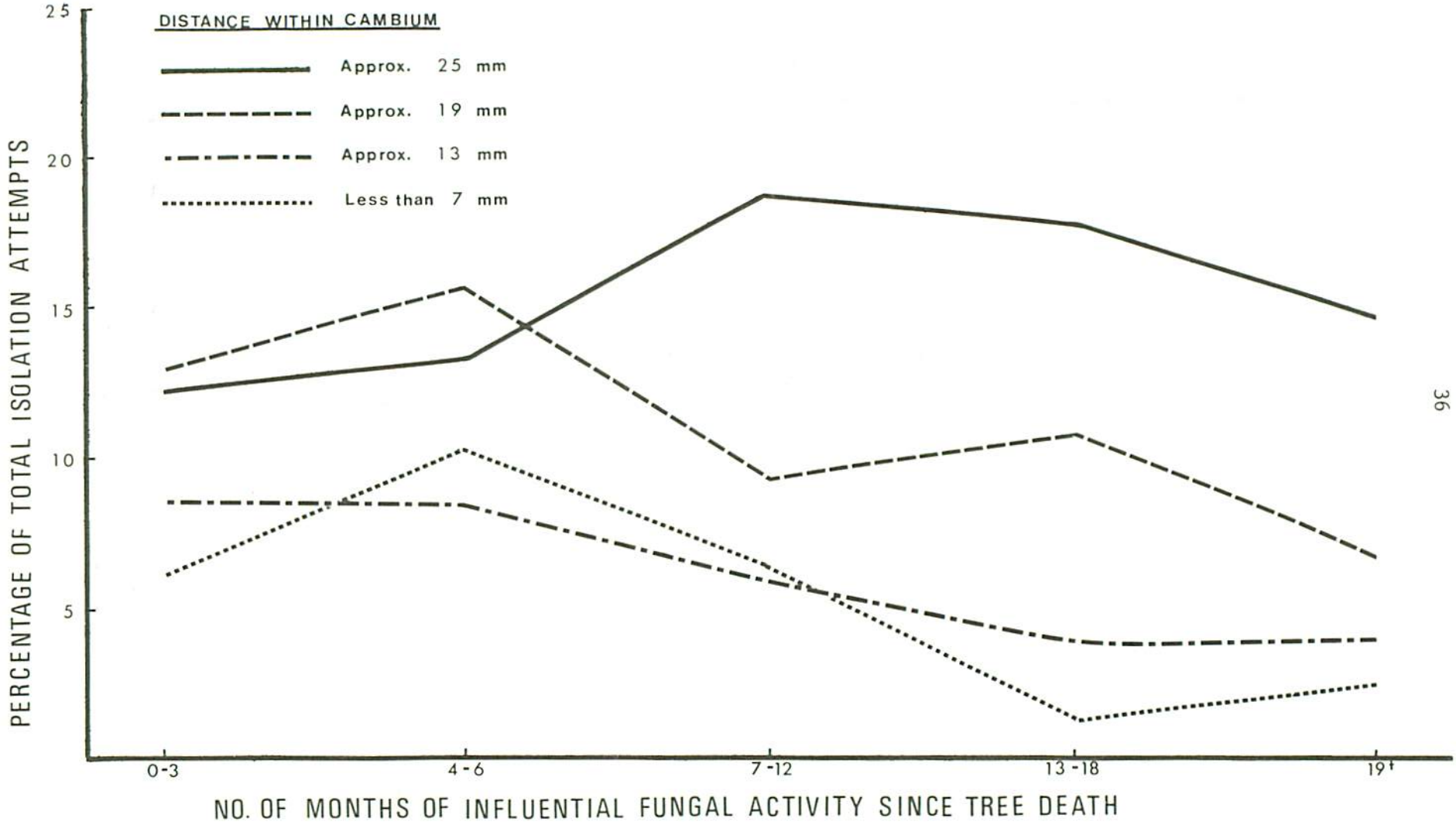

Figure 22. Occurrence of *Nectria fuckeliana* in the girdled, killed balsam fir at different distances within the cambium at various periods of exposure to influential fungal activity.

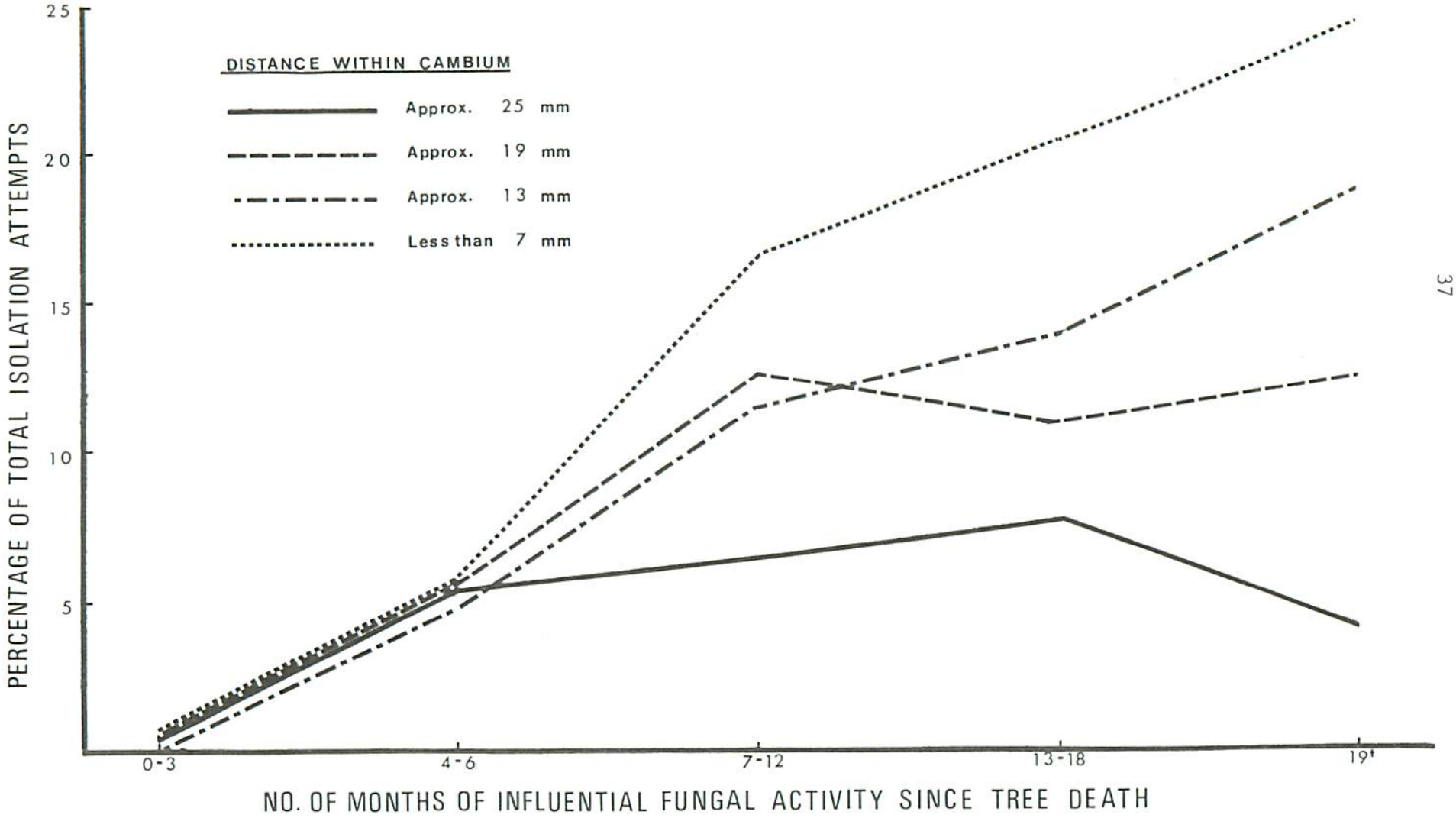

Figure 23. Occurrence of *Polyporus abietinus* in girdled, killed balsam fir at different distances within the cambium at various periods of exposure to influential fungal activity.

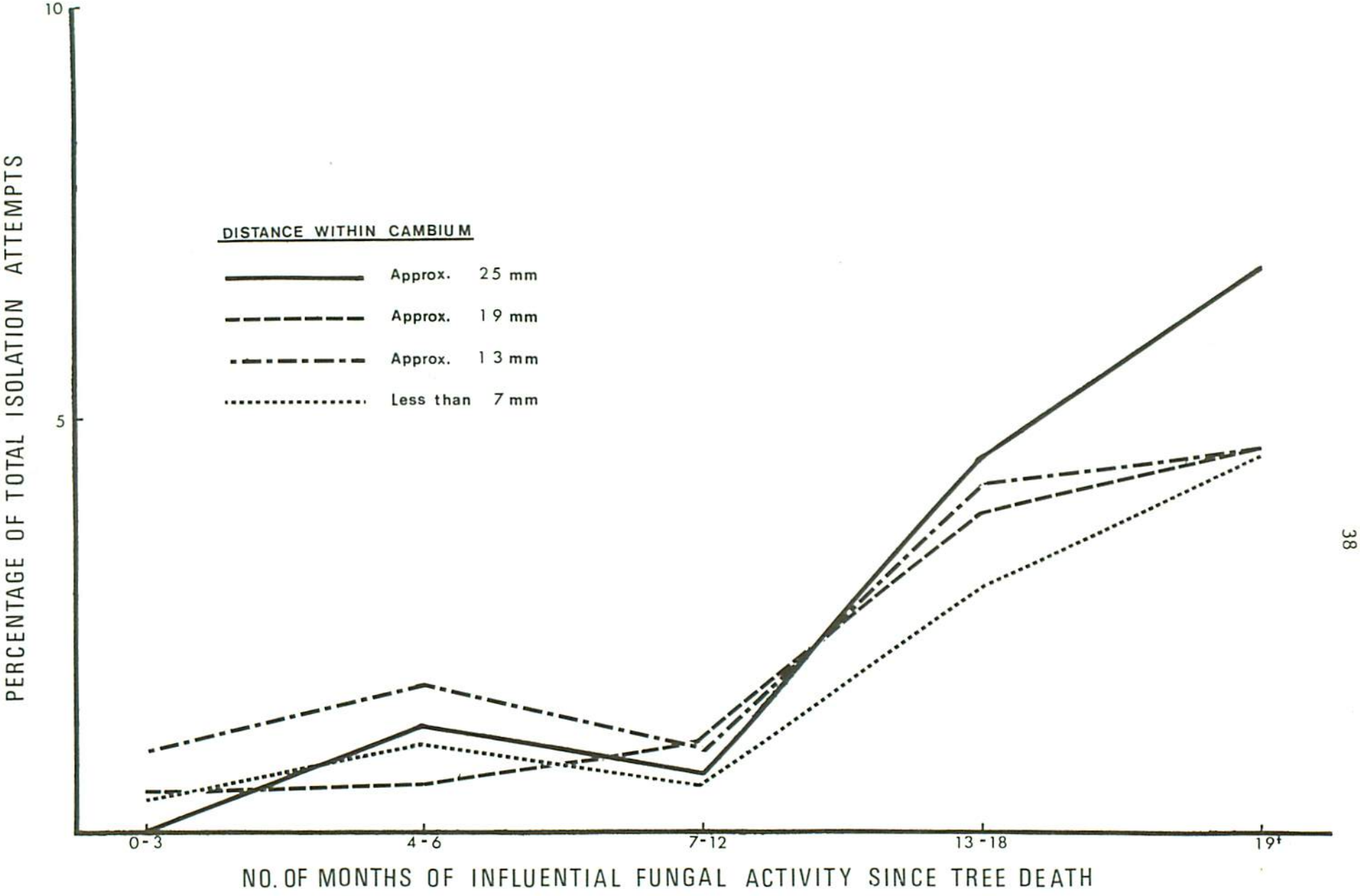

Figure 24. Occurrence of *Stereum sanguinolentum* in girdled, killed balsam fir at different distances within the cambium at various periods of exposure to influential activity.

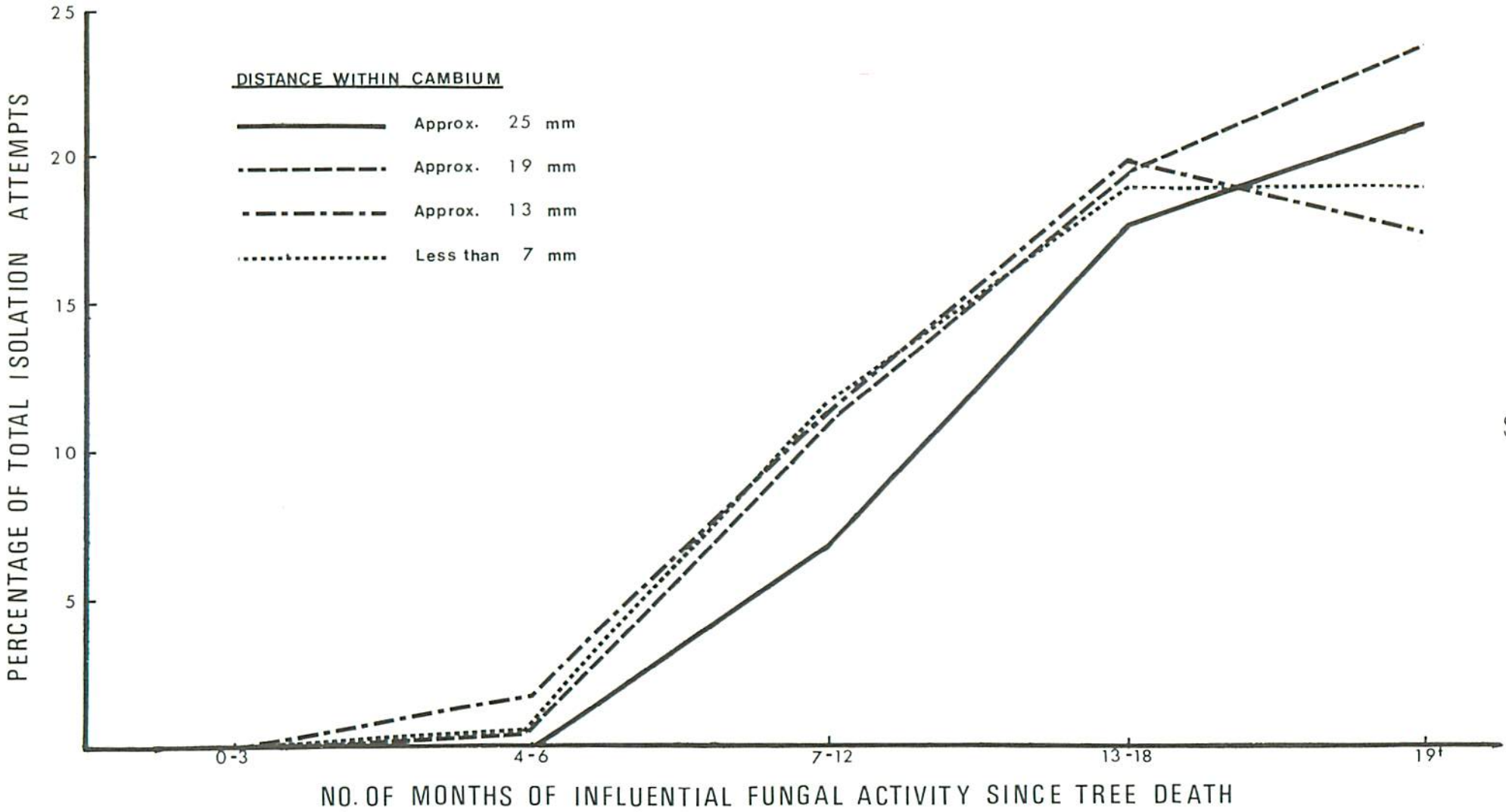

Figure 25. Occurrence of *Trichoderma viride* in girdled, killed balsam fir at different distances within the cambium at various periods of exposure to influential fungal activity.

occurrence of this fungus increased with increasing distance within the cambium.

Table A13 and Figure 23 show that *P. abietinus* was obtained with about equal frequency at all distances within the cambium with the exception of the deepest, 25 mm, where it was consistently less frequent in trees exposed to less than 19 months of influential fungal activity.

Stereum sanguinolentum occurred with approximately the same frequency at all depths beneath the cambium (Table A14 and Figure 24). Figure 24 confirms the observations noted earlier that *S. sanguinolentum* was relatively rare in the sample trees, particularly in trees with less than 12 months of exposure to influential fungal activity.

Table A15 and Figure 25 show that, in trees exposed to more than 6 months of influential fungal activity, the frequency with which *Trichoderma viride* was isolated decreased appreciably with increasing distance from the cambium. This supports the postulation made earlier that *T. viride* is probably a secondary organism, invading stem tissue previously colonized and deteriorated by other fungi.

DISCUSSION

During the planning stage of this study considerable time was spent deciding upon the method to be used to stimulate spruce budworm defoliation of balsam fir in the five widely separated study areas. Manual defoliation of 22 mature trees in each area was quickly rejected because of the difficulties and excessive man-days involved. Killing the foliage rapidly using some form of fire was considered but was felt to be too risky, particularly if the spring of 1966 proved to be excessively dry and hot in one or more of the study areas. The standardized girdling technique was adopted as the safest, simplest, and most easily duplicable method of obtaining recently dead balsam fir within a reasonable length of time. The wide variation in the time required for trees to die following girdling, particularly the absence of any mortality in the Newfoundland plot one full year later, was not anticipated. Of course, rigid adherence to a standardized girdling procedure is not sufficient to ensure that all treated trees will take the same period of time to die. There are numerous possible reasons for this, including climate, soil moisture, nutrient conditions, crown size, etc. All sample plots were in stands composed mainly of balsam fir so that considerable root grafting would be expected; hence, neighboring untreated trees could sustain girdled trees for months or perhaps even years. Noel (1970) attributed tree survival following girdling to an initial abundance of carbohydrates and the maintenance of transpiration, with a gradual degeneration until general metabolic failure triggers off an irreversible and rapid fatal breakdown. It is not surprising, then, that the first mortality occurred in the eastern Ontario plot since it was 2°-4° latitude south of all other plots, resulting in appreciably longer, hotter days (Fig. 4 and 5) and a longer growing (metabolically active) season.

Newfoundland and western Ontario were the two northernmost plots (Table 1); the fact that girdled trees survived longest in the former area was probably due to a combination of more favorable climatic conditions for survival in Newfoundland, including less sunlight per day, cooler temperatures, and more rainfall during the growing season (Fig. 3, 4, and 5), than in western Ontario. Climate, then, is the one factor studied which appears to explain, at least in part, observed differences among study areas in the average period between girdling and tree death.

The very rapid development of stain in the sapwood of trees girdled and killed in Newfoundland did not occur in balsam fir recently killed following balsam woolly aphid (*Adelges piceae* [Ratzeburg]) attack and hemlock looper defoliation (Hudak 1959, Hudak et al. 1960). This suggests that killing balsam fir by girdling results in a different rate of deterioration than death due to attacks by these insects. On the other hand, there was a definite similarity in the rate at which sap rot developed in insect-killed and girdled balsam fir in Ontario and New Brunswick. In balsam fir dead for approximately 2 years following spruce budworm defoliation, western Ontario trees had about 25% of their gross merchantable volume in a state of advanced decay, compared with only 0.5% in New Brunswick trees (Basham and Belyea 1960, Stillwell and Kelly 1964). Approximately 5 years after death these percentages had risen to 42 and 27, respectively. Although data were collected and analyzed somewhat differently for the girdled trees, Figure 15 and Table A8 do show that sap rot began earlier in the two Ontario plots than in New Brunswick, penetrating over four times as deep in trees exposed to 7-12 months of influential fungal activity. After that period the rate at which sap rot depth increased was quite similar in both provinces.

The microflora inhabiting the outer stemwood of killed balsam fir give the strongest indication that death by girdling results in somewhat different substrate conditions than death by other causes. Practically all of the sap rot encountered in trees killed by girdling in both Newfoundland and New Brunswick was associated with *Polyporus abietinus*, whereas in balsam fir killed by blowdown in Newfoundland, *Lenzites saepiaria* was the chief cause of advanced decay (Stillwell 1959). In balsam fir killed in New Brunswick following spruce budworm defoliation, *P. abietinus* was associated with less than half of the advanced decay and was very rare in trees dead for less than 4 years (Stillwell and Kelly 1964). *Stereum sanguinolentum* was never isolated in western Ontario, but was the fungus most frequently isolated in New Brunswick from the outer stemwood of balsam fir killed following spruce budworm defoliation (Basham and Belyea 1960, Stillwell and Kelly 1964). However, in the girdled balsam fir, *S. sanguinolentum* was isolated most frequently in western Ontario and least frequently in New Brunswick.

Other microfloral differences that cannot be attributed to different causes of tree death were encountered among the study areas. The two principal differences were as follows: 1) *Stereum chailletii* in the outer stemwood of girdled trees exposed to only a few months of influential fungal activity after death was far more abundant in the three eastern provinces than in Ontario; and 2) *P. abietinus*, the "climax" species that caused advanced sap rot in all of the study areas, became established in girdled, dead balsam fir much sooner and more extensively following tree death in eastern and western Ontario than in the three eastern provinces.

From this study and previous studies on the rate of deterioration of killed balsam fir in eastern Canada there emerges a consistent, rather striking difference in the pattern of deterioration between Ontario and the three other provinces. In Quebec, New Brunswick, and Newfoundland sap stain caused mainly by *S. chailletii* developed rather rapidly, and was followed 2 or 3 years later by the appearance of sap rot caused mostly, if not entirely, by *P. abietinus*. In Ontario there was far less sap stain development in the early months following tree death, but a much more rapid and extensive development of sap rot caused by *P. abietinus*. Fruiting of *P. abietinus* on dead balsam fir stems was far more abundant in Ontario than in eastern Canada. However, Magasi (1972) has concluded that "...differences in strains of *P. abietinus* in Ontario and New Brunswick do not account for the differences in decay rates in the two provinces", and that "balsam fir wood from the two provinces also failed to show differences in decay resistance". Two factors examined in this study, recent tree growth rate and outer stemwood moisture content, can quickly be eliminated as explanations for these differences. The slowest recent tree growth rates occurred in western Ontario and Quebec trees. The moisture content of heartwood and sapwood of both living and killed balsam fir showed no marked differences between study areas that could not be explained by variations in rainfall just prior to sampling. The results indicate that the moisture content seldom drops below 45%, so that it is unlikely to restrict fungal activity. It was pointed out that the moisture content of the outer stemwood in the upper trunk was the same as or slightly higher than that in the midtrunk and lower trunk, and that the most rapid rate of deterioration of the girdled trees occurred at this location. Two other studies of the deterioration of conifers following mortality caused by insect defoliation have reported contrary results, namely that the upper trunks of dead trees deteriorated relatively slowly. However, in both cases it was shown that, soon after tree death, the moisture content in these regions fell below the limits required for decay (Thomas and Craig 1958, Hinds et al. 1965).

There is a pronounced difference in the climate of the two Ontario study areas and the three study areas in the other provinces. Conceivably the warmer climate of Ontario, particularly in the eastern Ontario study area, could account for the greater activity of *P. abietinus*

and *T. viride* in girdled, killed balsam fir here than in the three cooler eastern provinces. Magasi (unpublished data) and others have shown that the optimum growth of *P. abietinus in vitro* takes place at a relatively high temperature. *Polyporus abietinus* was somewhat more active in girdled, killed trees in New Brunswick than in Newfoundland and Quebec; this could be explained by the fact that the mean daily minimum temperatures in New Brunswick were similar to those in western Ontario and significantly higher than those in Newfoundland and Quebec. The greater activity of *T. viride* at higher temperatures in balsam fir has been recorded (Etheridge 1969). The occurrence of *S. chailletii*, on the other hand, was consistently negatively related to mean daily minimum temperatures in the five study areas.

There were pronounced differences in the extent to which various insects attacked the stems of balsam fir killed by girdling in the five study areas. Bark beetle numbers were highest in trees in eastern Ontario, followed by western Ontario and Newfoundland, and were relatively rare in New Brunswick. There is a strong positive relationship between the occurrence of bark beetles and temperature, particularly mean daily maximum temperature. The data show no evidence of a relationship between the abundance of bark beetles and the occurrence of any of the five major fungi. Evidence has been presented that bark beetles act as vectors for yeasts and *Ceratocystis bicolor* from dead to dying or recently killed balsam fir (Basham and Belyea 1960). In this study, *C. bicolor* occurred only in eastern Ontario, and yeasts and *Ceratocystis* spp. were more common here than in any of the other study areas. Yeasts were also frequently isolated from the Newfoundland trees. Girdled New Brunswick trees, on the other hand, yielded no isolates of yeasts or of *C. bicolor*, and relatively few of *Ceratocystis* spp.

Woodwasp oviposition holes were approximately three times as numerous in the stems of killed, girdled balsam fir in New Brunswick and Newfoundland than in the stems of trees killed in both eastern and western Ontario. The killed balsam fir in New Brunswick and Newfoundland developed far more sap stain caused by *S. chailletii* than did those in eastern and western Ontario. Woodwasp oviposition holes and sap stain caused by *S. chailletii* were both exceptionally abundant in trees exposed to less than 3 months of influential fungal activity since death in Newfoundland. This is not surprising, as woodwasps are known to act as vectors for *S. chailletii* (Stillwell 1966). The Newfoundland trees died very slowly following girdling, and undoubtedly bore many oviposition holes which served as *S. chailletii* infection centers before tree death. The reason for the relatively low woodwasp population in the two Ontario study areas is not known, since they are reported to prefer higher temperatures (Stillwell 1966). Differences in the winter climate may be the answer. Another possible explanation is that little if any balsam fir mortality or felling operations occurred within 20-25 miles of both Ontario study areas, precluding any population buildup; this was not the case as far as the New Brunswick and Newfoundland study areas

are concerned. Of course it is possible that the numbers of woodwasps in Ontario were as high as those in the eastern provinces, but the relative rapidity with which the Ontario trees died following girdling resulted in the lower densities of oviposition holes in dead trees.

Monochamus wood borers were most active in the stems of the girdled, killed balsam fir in both of the Ontario study areas, and least active in New Brunswick. Although they were not recorded in Quebec, investigators there recall that they were quite rare. This corresponds fairly closely with the relative rates with which sap rot caused by *P. abietinus* developed in the five study areas. Furthermore, both the density of *Monochamus* borer holes and the extent of *P. abietinus* sap rot were greatest in the top of the stems and least in the basal regions. A similar positive correlation between intensity of *Monochamus* activity and extent of *P. abietinus* sap rot in dead balsam fir stems has been noted earlier (Basham and Belyea 1960). In the same earlier study the occurrence of *Nectria fuckeliana* was also positively correlated with *Monochamus* activity. In girdled, killed balsam fir the occurrence of *N. fuckeliana* and of *Monochamus* were both consistently greatest in the top stem sections. Furthermore, the New Brunswick trees yielded far fewer isolates of *N. fuckeliana* than did trees from any other study area. Considering only those trees exposed to 3 months or less of significant fungal activity following death, New Brunswick with the lowest recorded *Monochamus* activity and Quebec where *Monochamus* activity was thought to be very low were the only areas reporting no occurrences of *N. fuckeliana*.

CONCLUSIONS

In the five study areas across eastern Canada, the differences in the rate of deterioration of girdled, killed balsam fir stems, and in the frequency of occurrence of the various fungi associated with deterioration, were related to some degree to pronounced differences in the number and kinds of insects that attack dying and dead stems. These variations in insect populations, and some of the microfloral differences, are very likely associated with the distinct climatic differences between study areas. These two factors, insects and climate, are the only ones among all of those studied that would appear to have a major influence on the deterioration process as far as regional differences are concerned. The cooler, cloudier, and wetter climate of the three eastern provinces resulted generally in trees dying more slowly than in Ontario. This was particularly true in Newfoundland. Trees that were weakened but believed to be technically still alive were therefore attacked by woodwasps over a longer period, and *S. chailletii* was very likely introduced during the process of oviposition by these insects. Consequently, sap stain associated with *S. chailletii* was well established in many of these trees before death. In Ontario, on the other hand, which is warmer, sunnier, and drier, balsam fir died more quickly and were far more heavily attacked by bark beetles and *Monochamus*

wood borers. This resulted in less *S. chailletii* sap stain in the early stages of deterioration but a much earlier and more extensive invasion by *P. abietinus*, the cause of sap rot in these stems. Although *P. abietinus* did not appear in dead stems in New Brunswick as early as in Ontario, once established it developed at almost the same rate, that is, much faster than in Quebec or Newfoundland. It is postulated that this may be because the mean daily minimum temperature during the growing season in New Brunswick is almost as high as that in Ontario, and *P. abietinus* grows fastest at relatively high temperatures (Magasi, unpublished data).

Polyporus abietinus was the most important fungus involved in the deterioration of the girdled, killed balsam fir stems, being responsible for practically all of the unfirm, advanced sap rot. Its occurrence was strongly positively related to the sampling height within tree stems, to the number of months since tree death, and to *Monochamus* borer activity. *Stereum chailletii* was the fungus most frequently isolated from sap stain. It was obtained more frequently from a depth of 10-20 mm beneath the cambium than from shallower or deeper isolation attempts, and its occurrence was strongly correlated with woodwasp activity. *Nectria fuckeliana* occurred more frequently at positions deep within the cambium, was positively related to *Monochamus* borer activity, and in Ontario was isolated from clear, sound wood or firm but stained wood. *Stereum sanguinolentum*, a common wound parasite of living balsam fir (Etheridge 1969), was isolated from the outer stemwood of only 22 of the 99 girdled trees, and was not a major cause of deterioration. In Ontario it was isolated mostly from advanced or incipient sap rot; however, there was evidence that several of the isolates were a result of heart rot infections moving outward rather than saprophytic invasions from the cambium region. *Trichoderma viride* isolations showed a strong negative relationship to the distance beneath the cambium, and a positive relationship to the period of time since tree death. This, plus the fact that they occurred mainly in advanced sap rot, supports other evidence that this fungus is a secondary organism that invades only tissues already colonized and deteriorated by other organisms. *Rhinocladiella elatior*, though not included in the tables as a "principal fungus", was nevertheless isolated quite frequently in all study areas except Quebec. In the two Ontario study areas it was isolated mainly from advanced sap rot.

The spruce budworm is currently defoliating and killing balsam fir over vast regions in New Brunswick, Quebec, Ontario, and in some stands previously defoliated by the hemlock looper in Newfoundland. The rates of deterioration of the girdled, killed balsam fir in this study, supported by the rates recorded in earlier studies of trees killed following spruce budworm defoliation, indicate that under average stand conditions, to avoid substantial amounts of undesirable sap rot, salvage operations must be carried out within 1-1½ years in Ontario and within 3 years in New Brunswick. The absence of any large-scale studies in Newfoundland or Quebec dealing with the rate of deterioration of balsam fir killed following spruce budworm defoliation makes it far more difficult

to designate such periods in those regions. However, the results of the present study, though admittedly based on only 20 trees in one stand for each region, do provide some evidence that the rate of deterioration in those two provinces may correspond more closely to the slower New Brunswick rate than to the faster Ontario rate. The balsam fir girdled and killed in Newfoundland had an even slower rate of development of sap rot than those in New Brunswick. The rate of deterioration of the girdled, killed balsam fir in Quebec was not recorded. However, the economically important form of deterioration, advanced sap rot, was consistently associated with isolations of *P. abietinus* in Ontario, New Brunswick, and Newfoundland. The trees sampled in Quebec yielded by far the fewest isolations of *P. abietinus*; indeed, it was obtained from only four of the 20 sample trees compared with 8-12 trees in the four other regions. It is therefore safe to assume that the girdled, killed balsam fir sampled in Quebec had the slowest rate of development of sap rot among the five study areas.

It must be remembered, however, that as a rule tree mortality following insect attack occurs over several years. Furthermore, the different rates of deterioration of dead trees observed among study areas were attributed largely to differences in the intensity of insect attack and in climate, particularly growing season temperatures. These factors are by no means uniform throughout a region or province, and local variations in these and other factors must be considered when estimating the period during which salvage of killed balsam fir will be economically feasible.

LITERATURE CITED

Basham, J.T. 1951. The pathological deterioration of balsam fir (*Abies balsamea* [L.] Mill.) killed by the spruce budworm (*Choristoneura fumiferana* Clem.). Pulp Pap. Mag. Can. 52(8):120-134.

Basham, J.T. 1959. Studies in forest pathology. XX Investigations of the pathological deterioration in killed balsam fir. Can. J. Bot. 37:291-326.

Basham, J.T. and Belyea, R.M. 1960. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part III. The deterioration of dead trees. For. Sci. 6(1):78-96.

Etheridge, D.E. 1969. Factors affecting infection of balsam fir (*Abies balsamea*) by *Stereum sanguinolentum* in Quebec. Can. J. Bot. 47(3):457-479.

Hinds, T.E., Hawksworth, F.G. and Davidson, R.E. 1965. Beetle-killed Engelmann spruce. Its deterioration in Colorado. J. For. 63(7):536-542.

Hudak, J. 1969. Pathological condition of balsam woolly aphid infested fir in Newfoundland. Can. Dep. Fish. For., For. Res. Lab., St. John's, Nfld. Int. Rep. N-17.

Hudak, J., Meades, J.P. and Sutton, W.J. 1970. Rate of deterioration of balsam fir stands damaged by the eastern hemlock looper in Newfoundland. Can. Dep. Fish. For., For. Res. Lab., St. John's, Nfld. Int. Rep. N-29.

Linteau, A. 1955. Forest site classification of the northeastern section boreal forest region, Quebec. Can. Dep. North. Aff. Nat. Resour., For. Branch Bull. 118, 85 p.

Magasi, L.P. 1972. A comparative study of *Polyporus abietinus* in Ontario and New Brunswick. Can. For. Serv., Fredericton, N.B. Int. Rep. M-73.

Noel, A.R.A. 1970. The girdled tree. Bot. Rev. 36(2):162-195.

Stillwell, M.A. 1959. Further studies of the pathological deterioration in wind-thrown balsam fir in Newfoundland. For. Chron. 35(3): 212-218.

Stillwell, M.A. 1966. Woodwasps (Siricidae) in conifers and the associated fungus, *Stereum chailletii*, in eastern Canada. For. Sci. 12(1):121-128.

Stillwell, M.A. and Kelly, D.J. 1964. Fungus deterioration of balsam fir killed by spruce budworm in northwestern New Brunswick. For. Chron. 40(4):482-487.

Thomas, G.P. and Craig, H.M. 1958. Deterioration by fungi of killed Douglas-fir in interior British Columbia. Can. Dep. Agric., For. Biol. Lab., Victoria, B.C. Reg. Rep. 1958-3.

APPENDIX

Table A1. Comparison of climatic features during the 4 months of greatest fungal activity in the five study areas during the period 1966-1972

		Study area				
	Month	1	2	3	4	5
Distance between study plot and weather instrument station (km)		0.0	3.2	4.5	1.6	5.6
Mean daily temperature (°C)	June	11.6	12.3	11.7	15.4	13.5
	July	15.2	15.2	14.7	18.6	17.2
	Aug	14.7	13.6	13.3	17.8	16.1
	Sept	9.3	9.9	9.7	13.3	11.1
	Mean	12.7	12.8	12.3	16.5	14.5
Mean maximum temperature (°C)	June	17.7	19.8	18.6	22.8	20.6
	July	21.8	22.5	21.1	25.6	24.2
	Aug	20.5	17.9	19.4	24.2	22.8
	Sept	14.8	15.9	15.6	19.7	17.2
	Mean	18.7	19.0	18.7	23.1	21.2
Mean minimum temperature (°C)	June	5.6	7.3	5.0	10.0	6.7
	July	8.7	10.4	8.3	11.9	10.0
	Aug	8.9	9.3	7.2	11.1	10.0
	Sept	3.8	5.7	3.9	6.9	5.6
	Mean	5.7	8.2	6.1	10.0	8.1
Avg total precipitation (cm)	June	5.8	7.4	13.2	12.9	9.1
	July	6.6	12.7	14.0	8.6	8.1
	Aug	15.0	13.7	18.0	10.7	8.9
	Sept	7.4	9.4	14.0	9.1	5.8
	Mean	8.7	10.8	14.8	10.3	8.0
Avg no. of days with measurable precipitation	June	13.0	12.0	13.3	13.6	11.8
	July	9.0	14.0	12.7	9.4	12.3
	Aug	16.0	15.0	15.5	10.0	11.2
	Sept	11.0	11.0	13.5	11.2	10.0
	Mean	12.2	13.0	13.7	11.0	11.3
Avg hours of sunlight per day	June	6.4	7.0	7.2	7.6	8.0
	July	7.4	7.4	7.8	9.0	8.9
	Aug	5.9	6.3	6.5	7.8	7.9
	Sept	4.3	5.0	4.7	5.1	5.0
	Mean	6.0	6.4	6.5	7.4	7.4

Table A2. Average moisture content of sapwood and heartwood of control trees and of killed balsam fir in the five study areas

Tissue	Study area	Moisture content expressed as % of oven-dry weight						
		Control trees	Killed trees, grouped according to no. of months of influential fungal activity since death					
			All	0-3	4-6	7-12	13-18	19+
Sapwood	1	136	85	45	65	73	157	113
	2	126	54	46	39	52	78	56
	3	121	51	60	52	51	51	39
	4	171	48	53	67	47	35	37
	5	149	43	52	45	51	39	29
Heartwood	1	101	68	74	47	59	85	69
	2	84	81	72	96	92	78	68
	3	108	69	82	92	63	56	52
	4	132	91	96	118	85	72	85
	5	146	83	69	90	86	77	95

Table A3. Average moisture content of heartwood at different stem positions in control trees and in killed balsam fir at various periods of exposure to influential fungal activity in the five study areas

Sampling position in stem	Study area	Moisture content of heartwood expressed as % of oven-dry weight						
		Control trees	Killed trees, grouped according to no. of months of influential fungal activity since death					
			All	0-3	4-6	7-12	13-18	19+
Top	1	142	89	61	53	76	162	100
	2	98	74	67	66	78	75	82
	3	98	66	68	77	69	73	41
	4	111	55	81	96	40	33	23
	5	115	53	56	43	50	46	68
Mid	1	109	62	81	48	51	54	59
	2	82	81	66	102	100	62	77
	3	124	67	71	87	69	50	56
	4	145	108	119	117	114	99	90
	5	144	85	76	101	98	51	98
Base	1	52	54	80	40	50	37	47
	2	71	89	83	119	98	96	48
	3	92	75	108	112	50	45	58
	4	141	111	88	140	100	84	143
	5	179	112	74	125	110	133	119
Top	All	113	67	67	67	63	78	63
Mid	All	121	81	83	91	86	63	76
Base	All	107	88	87	107	82	79	83

Table A4. Average moisture content of sapwood at different stem positions in control trees and in killed balsam fir at various periods of exposure to influential fungal activity in the five study areas

Sampling position in stem	Study area	Moisture content of sapwood expressed as % of oven-dry weight						
		Control trees	Killed trees, grouped according to no. of months of influential fungal activity since death					
			All	0-3	4-6	7-12	13-18	19+
Top	1	189	95	54	72	89	152	148
	2	159	54	39	39	40	63	88
	3	161	54	60	48	49	70	41
	4	171	43	50	55	51	29	31
	5	129	48	39	50	68	48	33
Mid	1	118	85	45	49	71	189	76
	2	130	52	50	42	35	88	47
	3	134	53	61	73	50	34	48
	4	187	51	56	71	53	35	41
	5	181	41	61	39	51	28	27
Base	1	102	75	37	74	59	130	115
	2	88	57	49	37	82	83	32
	3	108	41	59	35	35	50	28
	4	156	49	52	74	36	41	40
	5	138	40	56	45	34	41	26
Top	All	162	55	48	53	59	72	68
Mid	All	150	56	55	55	52	75	48
Base	All	118	52	51	53	49	69	48

Table A5. Bark beetle activity as indicated by density of nuptial chambers in girdled balsam fir in four of the study areas

No. of months of influential fungal activity since tree death	Sampling position in stem	No. of bark beetle nuptial chambers per dm^2 surface area			
		Study area[a]			
		1	2	4	5
0-3	Base	.00	.00	1.60	.23
	Mid	.00	.00	3.21	.69
	Top	.15	.19	3.60	.73
4-6	Base	.56	.00	2.39	1.46
	Mid	1.41	.21	3.99	1.65
	Top	1.37	.22	5.53	1.44
7-12	Base	.11	.00	2.68	.22
	Mid	.22	.03	3.85	1.00
	Top	1.33	.12	4.21	.15
13-18	Base	.70	.03	4.73	1.80
	Mid	.22	.68	6.06	1.98
	Top	.32	.50	4.57	2.57
19+	Base	.70	.00	2.57	.23
	Mid	.74	.00	4.23	.81
	Top	1.48	.08	7.25	1.40
All	Base	.14	.01	2.82	.93
	Mid	.33	.21	4.24	1.33
	Top	.98	.22	4.87	1.31

[a] Data not available from Quebec (Study area 3).

Table A6. Woodwasp activity as indicated by density of oviposition holes and of adult exit holes in girdled balsam fir in four of the study areas[a]

No. of months of influential fungal activity since tree death	Sampling position in stem	No. of woodwasp holes per dm^2 surface area							
		Oviposition holes[b]				Adult exit holes			
		Study area				Study area			
		1	2	4	5	1	2	4	5
0-3	Base	2.31	0.66	0.14	0.23	0.27	0.00	0.00	0.00
	Mid	3.91	0.68	0.20	0.38	0.14	0.03	0.00	0.00
	Top	2.38	0.51	0.33	0.16	0.00	0.19	0.00	0.00
4-6	Base	1.22	1.03	0.00	0.14	0.14	0.12	0.05	0.20
	Mid	1.38	0.78	0.40	0.00	0.00	0.07	0.03	0.06
	Top	0.82	1.94	0.26	0.10	0.00	0.32	0.00	0.03
7-12	Base	0.40	1.15	0.33	0.14	0.00	0.05	0.10	0.20
	Mid	0.91	1.20	0.56	0.52	0.00	0.21	0.16	0.22
	Top	0.47	1.24	0.61	0.32	0.00	0.52	0.56	0.27
13-18	Base	0.24	0.24	0.00	0.31	0.00	0.02	0.18	0.11
	Mid	0.64	0.25	0.44	0.17	0.00	0.00	0.07	0.12
	Top	0.48	0.00	0.14	0.11	0.00	0.04	0.00	0.00
19+	Base	0.66	1.11	0.58	0.27	0.00	0.54	0.59	0.17
	Mid	0.32	2.01	0.10	0.20	0.00	0.54	0.32	0.16
	Top	0.25	1.39	0.13	0.29	0.02	0.08	0.05	0.07
All	Base	0.69	0.83	0.32	0.22	0.00	0.16	0.16	0.14
	Mid	0.86	0.95	0.34	0.25	0.08	0.20	0.11	0.12
	Top	0.55	1.01	0.29	0.18	0.04	0.24	0.02	0.08

[a] Data not available from Quebec (Study area 3).

[b] Based on all 20 sample trees in area 1, but on only 10 randomly selected sample trees in the other three areas.

Table A7. Wood borer (*Monochamus*) activity as indicated by density of larval entrance and adult exit holes in girdled balsam fir in four of the study areas

No. of months of influential fungal activity since tree death	Sampling position in stem	No. of *Monochamus* entrance and exit holes per dm^2 surface area											
		Study area[a]											
		1			2			4			5		
		Ent.	Exit	Total	Ent.	Exit	Total	Ent.	Exit	Total	Ent.	Exit	Total
0-3	Base	.00	.00	.00	.00	.00	.00	.06	.00	.06	.02	.00	.02
	Mid	.00	.00	.00	.00	.00	.00	.38	.00	.38	.29	.03	.32
	Top	.48	.00	.48	.05	.00	.05	1.72	.15	1.88	.87	.00	.87
4-6	Base	.00	.00	.00	.00	.00	.00	.16	.00	.16	.11	.03	.14
	Mid	.00	.00	.00	.00	.00	.00	.55	.06	.61	.17	.04	.20
	Top	.14	.00	.14	.22	.00	.22	.67	.21	.87	.15	.00	.15
7-12	Base	.01	.00	.01	.00	.00	.00	.00	.00	.00	.11	.07	.18
	Mid	.12	.02	.14	.00	.00	.00	.15	.07	.21	.57	.38	.95
	Top	.48	.03	.51	.15	.12	.27	.22	.17	.39	.18	.18	.37
13-18	Base	.03	.00	.03	.00	.00	.00	.08	.02	.10	.20	.10	.30
	Mid	.42	.10	.52	.00	.00	.00	.55	.09	.64	.30	.13	.43
	Top	.98	.11	1.09	.12	.04	.16	.77	.22	.99	.35	.18	.53
19 +	Base	.01	.00	.01	.00	.00	.00	.02	.00	.02	.09	.06	.14
	Mid	.18	.07	.25	.00	.00	.00	.24	.05	.29	.16	.13	.28
	Top	.38	.10	.48	.08	.08	.17	.41	.00	.41	.38	.17	.55
All	Base	.01	.00	.01	.00	.00	.00	.06	.01	.06	.12	.06	.17
	Mid	.18	.05	.23	.00	.00	.00	.36	.05	.41	.31	.15	.46
	Top	.49	.06	.56	.12	.06	.18	.73	.15	.89	.35	.11	.47

[a] Data not available from Quebec (Study area 3).

Table A8. Average radial penetration of sap stain and sap rot at different stem positions in girdled, dead balsam fir in four of the study areas[a]

No. of months of influential fungal activity since tree death	Sampling position in stem	Average distance of stain and rot beneath the cambium (mm)							
		Area 1		Area 2		Area 4		Area 5	
		Stain & rot	Rot only	Stain & rot	Rot only	Stain & rot	Rot only	Stain & rot	Rot only
0-3	Top	18.7	0.0	8.0	0.0	7.2	0.0	5.0[b]	0.0
	Mid	20.5[b]	0.0	10.0	0.0	8.8[b]	0.0	4.0	0.0
	Base	18.7	0.0	10.3[b]	0.0	7.4	0.2[b]	2.0	0.0
4-6	Top	20.0[b]	0.0	13.3[b]	0.0	12.0[b]	1.3[b]	7.3	0.8[b]
	Mid	18.2	0.0	10.7	0.0	9.7	0.3	11.5[b]	0.0
	Base	16.4	0.0	12.7	0.0	9.3	0.0	8.5	0.0
7-12	Top	14.3	0.0	19.0[b]	5.0[b]	18.8	10.8[b]	14.7	8.8[b]
	Mid	20.2[b]	0.0	15.3	0.0	23.2[b]	7.8	21.2	3.7
	Base	19.5	0.0	14.8	0.0	14.6	0.4	22.7[b]	6.2
13-18	Top	21.8	13.2[b]	32.0[b]	15.5[b]	18.8	12.3[b]	19.8	15.2
	Mid	25.1[b]	0.0	24.0	6.5	22.3[b]	11.0	19.6	12.0[b]
	Base	12.3	0.0	27.5	1.0	19.3	10.8	25.6[b]	16.2[b]
19+	Top	25.6[b]	12.7[b]	28.7[b]	21.7[b]	27.7[b]	14.7	34.0[b]	33.0[b]
	Mid	22.0	1.0	25.2	18.0	22.3	19.3	25.0	25.0
	Base	21.6	0.0	27.0	13.0	26.0	23.7[b]	24.5	21.5
0-3	All	19.3	0.0	9.4	0.0	7.8	0.1	3.7	0.0
4-6	All	18.2	0.0	11.5	0.0	10.3	0.6	9.1	0.2
7-12	All	18.0	0.0	16.5	1.5	18.9	6.3	19.5	6.2
13-18	All	19.7	4.4	27.8	7.7	20.1	11.3	21.7	14.5
19+	All	23.1	4.6	26.9	17.7	25.3	19.2	27.8	26.5

[a] No data available from Quebec (Study area 3).

[b] Stem position with the greatest average radial penetration of stain plus rot, or of rot only, within each of the study areas and "months fungal activity" groups.

Table A9. The occurrence of the major fungi associated with deterioration of girdled balsam fir at different stem positions

Fungus	Sampling position in stem[a]	Study area 1: Total no. of isolations	1: % of all isolations by positions	1: % of all isolation attempts at each position	Study area 2: Total no. of isolations	2: % of all isolations by positions	2: % of all isolation attempts at each position	Study area 3: Total no. of isolations	3: % of all isolations by positions	3: % of all isolation attempts at each position	Study area 4: Total no. of isolations	4: % of all isolations by positions	4: % of all isolation attempts at each position	Study area 5: Total no. of isolations	5: % of all isolations by positions	5: % of all isolation attempts at each position
Polyporus abietinus	Top	71	93.4	22.2	84	71.2	26.3	19	59.4	6.5	74	47.4	23.1	66	48.9	21.7
	Mid	5	6.6	1.6	32	27.1	10.0	5	15.6	1.7	47	30.1	14.7	44	32.6	14.5
	Base	0	0.0	0.0	2	1.7	0.6	8	25.0	3.3	35	22.4	10.9	25	18.5	8.2
Sterewn chailletii	Top	73	28.1	22.8	25	14.8	7.8	35	21.9	12.0	31	33.7	9.7	77	11.5	2.3
	Mid	93	35.8	29.1	62	36.7	19.4	58	36.3	20.1	35	38.0	10.9	24	39.3	7.9
	Base	94	36.1	29.4	82	48.5	25.6	67	41.8	27.9	26	28.3	8.1	30	49.2	9.9
Sterewn sanguinolentum	Top	1	4.5	0.3	0	0.0	0.0	5	45.5	1.7	7	23.3	2.2	7	16.3	2.3
	Mid	15	68.2	4.7	0	0.0	0.0	0	0.0	0.0	15	50.0	4.7	35	81.4	11.5
	Base	6	27.3	1.9	5	100.0	1.6	6	54.5	2.5	8	26.7	2.5	1	2.3	3.3
Nectria fuckeliana	Top	33	39.3	10.3	14	63.6	4.4	42	50.0	14.4	30	29.1	9.4	44	33.9	14.5
	Mid	33	39.3	10.3	6	27.3	1.9	41	48.8	14.2	48	46.6	15.0	38	29.2	12.5
	Base	18	21.4	5.6	2	9.1	0.6	1	1.2	0.4	25	24.3	7.8	48	36.9	15.8
Trichoderma viride	Top	0	0.0	0.0	36	31.0	11.3	22	31.4	7.5	27	18.6	8.4	45	35.1	14.8
	Mid	7	53.8	2.2	45	38.8	14.1	17	24.3	5.9	62	42.8	19.4	44	34.4	14.5
	Base	6	46.2	1.9	35	30.2	10.9	31	44.3	12.9	56	38.6	17.5	39	30.5	12.8

[a] Top: 3-in. diameter.

Mid: midpoint between top and base.

Base: 5 ft above ground.

Table A10. The occurrence of (a) major fungi associated with deterioration and (b) negative isolation attempts in girdled balsam fir at various periods of exposure to influential fungal activity

Results of isolation attempts	No. of months of influential fungal activity since tree death	Study area 1		2		3		4		5	
		Frequency of isolation	% of all isolation attempts	Frequency of isolation	% of all isolation attempts	Frequency of isolation	% of all isolation attempts	Frequency of isolation	% of all isolation attempts	Frequency of isolation	% of all isolation attempts
Polyporus abietinus	0-3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
	4-6	0	0.0	3	2.1	0	0.0	2	1.4	0	0.0
	7-12	0	0.0	4	2.1	0	0.0	63	26.2	55	19.1
	13-18	13	9.0	45	23.4	8	4.7	59	30.7	53	22.1
	19+	63	18.8	66	22.9	24	12.7	32	22.2	27	28.1
Stereum chailletii	0-3	48	33.3	13	9.0	23	14.0	10	4.2	1	1.0
	4-6	42	43.8	39	27.1	36	45.0	21	14.6	37	1.9
	7-12	99	41.3	58	30.2	43	19.5	46	19.2	19	6.6
	13-18	12	8.3	19	9.9	31	18.4	1	0.5	1	0.4
	19+	59	17.6	40	13.9	27	14.3	14	9.7	3	3.1
Stereum sanguinolentum	0-3	4	2.8	0	0.0	0	0.0	0	0.0	0	0.0
	4-6	1	1.0	0	0.0	0	0.0	0	0.0	7	3.6
	7-12	0	0.0	0	0.0	3	1.3	0	0.0	7	2.1
	13-18	0	0.0	5	2.6	3	1.7	0	0.0	28	1.2
	19+	17	5.1	0	0.0	5	2.6	30	20.8	1	1.0
Nectria fuckeliana	0-3	36	25.0	0	0.0	0	0.0	31	12.9	9	9.4
	4-6	12	12.5	0	0.0	5	6.2	27	18.8	33	17.2
	7-12	23	9.6	5	2.6	27	12.2	20	8.3	50	17.4
	13-18	2	1.4	1	0.5	21	12.5	20	10.4	32	13.3
	19+	11	3.3	16	5.6	31	16.4	5	3.5	6	6.3
Trichoderma viride	0-3	0	0.0	0	0.0	3	1.8	0	0.0	0	0.0
	4-6	0	0.0	32	22.2	0	0.0	1	0.7	2	1.0
	7-12	0	0.0	0	0.0	1.0	4.5	59	24.6	71	24.6
	13-18	0	0.0	33	17.2	35	20.8	40	20.8	17	7.1
	19+	13	3.9	51	17.7	22	11.7	45	31.2	38	39.6
Negative (sterile)	0-3	14	9.7	17	81.3	94	57.3	89	37.1	76	79.2
	4-6	4	4.2	29	20.1	17	21.3	35	24.3	34	17.7
	7-12	13	5.4	46	23.4	12	5.5	8	4.2	12	6.3
	13-18	11	7.6	22	11.5	6	3.6	10	6.9	51	21.3
	19+	0	0.0	23	8.0	6	3.2	10	6.9	0	0.0

Table A11. The occurrence of *Stereum chailletii* at different distances within the cambium in balsam fir killed by girdling in the five study areas

Study area	No. of months of influential fungal activity since tree death	Total no. of trees sampled	Percentage of isolation attempts that yielded *Stereum chailletii* — Approximate distance within cambium			
			<7 mm	13 mm	19 mm	25 mm
1 Newfoundland	0-3	3	30.4	38.8	38.8	24.8
	4-6	2	16.8	50.0	66.8	41.6
	7-12	5	40.0	53.2	38.4	33.2
	13-18	3	5.6	2.8	14.0	11.2
	19+	7	16.8	19.2	16.8	18.0
2 New Brunswick	0-3	3	19.4	8.3	5.6	2.8
	4-6	3	36.1	33.3	33.3	5.6
	7-12	4	33.3	31.3	27.1	29.2
	13-18	4	10.4	10.4	12.5	6.3
	19+	6	8.3	13.9	18.1	15.3
3 Quebec	0-3	4	15.3	13.6	25.0	0.0
	4-6	2	87.2	45.8	12.5	0.0
	7-12	5	21.1	33.3	6.3	2.5
	13-18	4	18.8	22.9	22.7	3.6
	19+	5	11.8	18.8	25.0	0.0
4 Eastern Ontario	0-3	5	3.3	5.0	6.7	1.7
	4-6	3	13.9	22.2	13.9	8.3
	7-12	5	18.3	23.2	23.2	11.7
	13-18	4	2.1	0.0	0.0	0.0
	19+	3	11.1	8.3	11.1	8.3
5 Western Ontario	0-3	2	0.0	0.0	4.2	0.0
	4-6	4	6.2	27.0	27.0	16.7
	7-12	6	2.8	9.7	11.1	2.8
	13-18	5	0.0	1.7	0.0	0.0
	19+	2	0.0	8.3	4.2	0.0
All study areas	0-3	17	13.6	13.0	15.0	6.1
	4-6	14	27.3	33.3	30.0	15.1
	7-12	25	21.8	29.5	22.1	15.7
	13-18	20	7.1	7.5	8.9	3.6
	19+	23	11.3	15.4	15.8	12.1

Table A12. The occurrence of *Nectria fuckeliana* at different distances within the cambium in balsam fir killed by girdling in the five study areas

	Study area	No. of months of influential fungal activity since tree death	Total no. of trees sampled	Percentage of isolation attempts that yielded *Nectria fuckeliana*			
				Approximate distance within cambium			
				<7 mm	13 mm	19 mm	25 mm
1	Newfoundland	0-3	3	11.2	22.4	36.0	22.4
		4-6	2	8.4	12.4	12.4	16.8
		7-12	5	8.4	8.4	8.4	13.2
		13-18	3	0.0	0.0	2.8	2.8
		19+	7	1.2	2.4	2.4	7.2
2	New Brunswick	0-3	3	0.0	0.0	0.0	0.0
		4-6	3	0.0	0.0	0.0	0.0
		7-12	4	6.3	2.1	2.1	0.0
		13-18	4	0.0	0.0	2.1	0.0
		19+	6	4.2	2.8	6.9	8.3
3	Quebec	0-3	4	0.0	0.0	0.0	0.0
		4-6	2	3.1	12.5	6.3	0.0
		7-12	5	9.2	6.9	21.9	20.0
		13-18	4	6.3	10.4	6.8	35.7
		19+	5	3.9	10.9	25.0	62.5
4	Eastern Ontario	0-3	5	11.7	13.3	11.7	15.0
		4-6	3	19.4	5.6	25.0	25.0
		7-12	5	0.0	5.0	8.3	20.0
		13-18	4	0.0	4.2	16.7	20.8
		19+	3	0.0	0.0	2.8	11.1
5	Western Ontario	0-3	2	12.5	4.2	12.5	8.3
		4-6	4	16.7	12.5	25.0	14.6
		7-12	6	6.9	5.6	9.7	47.2
		13-18	5	0.0	3.3	20.0	30.0
		19+	2	0.0	0.0	8.3	16.7
	All study areas	0-3	17	6.1	8.5	12.8	12.2
		4-6	14	10.2	8.3	15.6	13.2
		7-12	25	6.3	5.8	9.2	18.6
		13-18	20	1.3	3.8	10.6	17.7
		19+	23	2.4	3.9	6.7	14.6

Table A13. The occurrence of *Polyporus abietinus* at different distances within the cambium in balsam fir killed by girdling in the five study areas

	Study area	No. of months of influential fungal activity since tree death	Total no. of trees sampled	Percentage of isolation attempts that yielded *Polyporus abietinus*			
				Approximate distance within cambium			
				<7 mm	13 mm	19 mm	25 mm
1	Newfoundland	0-3	3	0.0	0.0	0.0	0.0
		4-6	2	0.0	0.0	0.0	0.0
		7-12	5	0.0	0.0	0.0	0.0
		13-18	3	11.2	8.4	8.4	8.4
		19+	7	19.2	18.0	19.2	19.2
2	New Brunswick	0-3	3	0.0	0.0	0.0	0.0
		4-6	3	2.8	5.6	0.0	0.0
		7-12	4	0.0	4.2	0.0	4.2
		13-18	4	27.1	20.8	22.9	22.9
		19+	6	23.6	23.6	23.6	20.8
3	Quebec	0-3	4	0.0	0.0	0.0	0.0
		4-6	2	0.0	0.0	0.0	0.0
		7-12	5	0.0	0.0	0.0	0.0
		13-18	4	6.3	6.3	2.3	3.6
		19+	5	14.5	7.8	16.7	16.7
4	Eastern Ontario	0-3	5	0.0	0.0	0.0	0.0
		4-6	3	0.0	2.8	2.8	0.0
		7-12	5	31.7	30.0	23.3	20.0
		13-18	4	27.1	35.4	31.3	29.2
		19+	3	22.2	25.0	27.8	13.9
5	Western Ontario	0-3	2	0.0	0.0	0.0	0.0
		4-6	4	0.0	0.0	0.0	0.0
		7-12	6	25.0	22.2	22.2	6.9
		13-18	5	20.0	25.0	26.7	16.7
		19+	2	12.5	12.5	41.7	45.8
	All study areas	0-3	17	0.0	0.0	0.0	0.0
		4-6	14	0.6	1.8	0.6	0.0
		7-12	25	11.7	11.5	11.0	6.8
		13-18	20	18.8	20.0	19.5	17.7
		19+	23	18.8	17.5	23.8	21.2

Table A14. The occurrence of *Stereum sanguinolentum* at different distances within the cambium in balsam fir killed by girdling in the five study areas

Study area	No. of months of influential fungal activity since tree death	Total no. of trees sampled	Percentage of isolation attempts that yielded *Stereum sanguinolentum*			
			Approximate distance within cambium			
			<7 mm	13 mm	19 mm	25 mm
1 Newfoundland	0-3	3	2.8	5.6	2.8	0.0
	4-6	2	4.0	0.0	0.0	0.0
	7-12	5	0.0	0.0	0.0	0.0
	13-18	3	0.0	0.0	0.0	0.0
	19+	7	4.8	4.8	4.8	6.0
2 New Brunswick	0-3	3	0.0	0.0	0.0	0.0
	4-6	3	0.0	0.0	0.0	0.0
	7-12	4	0.0	0.0	0.0	0.0
	13-18	4	2.1	2.1	2.1	4.2
	19+	6	0.0	0.0	0.0	0.0
3 Quebec	0-3	4	0.0	0.0	0.0	0.0
	4-6	2	0.0	0.0	0.0	0.0
	7-12	5	1.3	1.4	3.1	0.0
	13-18	4	2.1	2.1	2.3	0.0
	19+	5	3.9	3.1	0.0	0.0
4 Eastern Ontario	0-3	5	0.0	0.0	0.0	0.0
	4-6	3	0.0	0.0	0.0	0.0
	7-12	5	0.0	0.0	0.0	0.0
	13-18	4	0.0	0.0	0.0	0.0
	19+	3	16.7	19.4	19.4	27.8
5 Western Ontario	0-3	2	0.0	0.0	0.0	0.0
	4-6	4	2.1	6.3	2.1	4.2
	7-12	6	1.4	2.8	2.8	2.8
	13-18	5	8.3	13.3	11.7	13.3
	19+	2	0.0	0.0	0.0	4.2
All study areas	0-3	17	0.4	1.0	0.5	0.0
	4-6	14	1.1	1.8	0.6	1.3
	7-12	25	0.6	1.0	1.1	0.7
	13-18	20	2.9	4.2	3.8	4.5
	19+	23	4.5	4.6	4.6	6.7

Table A15. The occurrence of *Trichoderma viride* at different distances within the cambium in balsam fir killed by girdling in the five study areas

Study area	No. of months of influential fungal activity since tree death	Total no. of trees sampled	Percentage of isolation attempts that yielded *Trichoderma viride*			
			Approximate distance within cambium			
			<7 mm	13 mm	19 mm	25 mm
1 Newfoundland	0-3	3	0.0	0.0	0.0	0.0
	4-6	2	0.0	0.0	0.0	0.0
	7-12	5	0.0	0.0	0.0	0.0
	13-18	3	0.0	0.0	0.0	0.0
	19+	7	7.2	6.0	1.2	1.2
2 New Brunswick	0-3	3	0.0	0.0	0.0	0.0
	4-6	3	19.4	22.2	25.0	22.2
	7-12	4	0.0	0.0	0.0	0.0
	13-18	4	27.1	14.6	10.4	16.7
	19+	6	20.8	22.2	16.7	11.1
3 Quebec	0-3	4	1.4	0.0	4.2	4.2
	4-6	2	0.0	0.0	0.0	0.0
	7-12	5	9.2	4.2	0.0	0.0
	13-18	4	27.1	18.8	25.0	7.1
	19+	5	19.7	6.3	12.5	0.0
4 Eastern Ontario	0-3	5	0.0	0.0	0.0	0.0
	4-6	3	2.8	0.0	0.0	0.0
	7-12	5	43.3	20.0	21.7	13.3
	13-18	4	27.1	29.2	16.7	10.4
	19+	3	44.4	36.1	27.8	16.7
5 Western Ontario	0-3	2	0.0	0.0	0.0	0.0
	4-6	4	4.2	0.0	0.0	0.0
	7-12	6	26.4	29.2	29.2	13.9
	13-18	5	16.7	5.0	33.3	3.3
	19+	2	79.2	58.3	16.7	4.2
All study areas	0-3	17	0.4	0.0	0.5	0.5
	4-6	14	5.7	4.8	5.6	5.3
	7-12	25	16.5	11.5	12.5	6.4
	13-18	20	20.4	13.8	11.0	7.7
	19+	23	24.3	18.6	12.5	4.2