INFLUENCE OF PIT ASPIRATION ON EARLYWOOD PERMEABILITY OF DOUGLAS-FIR

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ABSTRACT

Sapwood earlywood longitudinal gas permeability is a sensitive barometer of the effect of seasoning conditions on pit aspiration. The proportion of aspirated pit pairs was quantitatively linked with longitudinal gas permeability and can be used to explain the earlywood permeability of a given sample. If comparable levels of pit aspiration are found in two samples differing in permeability, however, it may be necessary to examine other anatomical aspects of the wood being permeated. Permeability is a function of the number of open pits per tracheid, which, coupled with tracheid length, determines the probability of occurrence of a continuous flow path through the wood specimen being permeated. Percentage pit aspiration operates in conjunction with number of pits per tracheid to determine the number of open pits per tracheid. While the proportion of aspirated pits can be measured and related to permeability, it is suggested that tracheid length, total number of pits per tracheid, and number of tracheids per square millimeter also be evaluated in order to assess properly the effect of pit aspiration on permeability.

INTRODUCTION

Softwood permeability has often been shown to be decreased by bordered-pit aspiration, but the relation between permeability and pit aspiration has not been demonstrated on a quantitative basis. This report demonstrates the nature of the relation between permeability and pit aspiration and, in the process, points out other anatomical features that have an important relation to longitudinal permeability. Primary emphasis has been placed on sapwood permeability because heartwood permeability is inherently low because of the extensive pit aspiration that occurs during heartwood formation. The proportion of aspirated pits in never-dried wood was determined to provide a base line for comparing various drying techniques.

LITERATURE REVIEW

Aspiration of bordered pits has been widely studied and a definitive literature exists on the subject. Only limited, but pertinent, references will be made here.

Pit aspiration has been shown to occur not only when wood is seasoned, but also in a standing tree as the sapwood moisture content decreases during the course of heart-wood formation in Douglas-fir (*Pseudotsuga menziesii*) (Phillips 1933) and *Pinus radiata* (Harris 1954). Griffin (1919, 1924) studied pit aspiration in relation to the comparative ease with which coastal vs. interior Douglas-fir could be treated with creosote, but dealt mostly with latewood because deepest creosote penetration had occurred there. All or nearly all of the earlywood pit membranes were found to be aspirated in the air-dried material she examined. Griffin found that there was some correlation between creosote penetration and pit aspiration, but her sample size was very small.

Prevention of pit aspiration during drying has been studied extensively and has led to techniques for relating permeability to pit aspiration. Phillips (1933) and Griffin (1919) noted the general effect of alcohol seasoning in preventing pit aspiration. Liese (1951) was able to treat seasoned spruce wood only after preventing pit aspiration by drying green wood from alcohol or acetone. Erickson and Crawford (1959) found that the water permeability of Douglas-fir and western hemlock (*Tsuga heterophylla*) seasoned from several organic liquids was greater than that seasoned from water. They observed that pit aspiration was reduced by

the solvent seasoning technique, although no measurements were given as to the actual amount of aspiration that took place. Wardrop and Davies (1961) noted a sevenfold decrease in air flow through samples seasoned from water rather than from alcohol, a difference they ascribed to pit aspiration.

The apparent reduction in pit aspiration by solvent seasoning noted in the foregoing reports was clarified by Liese and Bauch (1967a). They studied the amount of pit aspiration that occurred when wood was dried from acetone solutions in which surface tension was adjusted by varying water concentration. They found that the critical surface tension for *Pinus sylvestris*, *Abies alba*, and *Picea excelsa* was about 26 dynes/cm, below which earlywood pits were unaspirated after drying. Liese and Bauch also found that water permeability of wood decreased markedly when it was dried from aqueous acetone solutions rather than from absolute acetone. No flow occurred in wood that had been dried from acetone solutions with a surface tension in excess of 26 dynes/cm. Thomas and Nicholas (1966) utilized the low surface tension property of pentane (14 dynes/cm) to prevent pit aspiration when seasoning *Pinus taeda*. Comstock and Côté (1968) reported that factors other than surface tension, such as swelling ability, were also important, and were able to dry wood without pit aspiration from liquids with as much as 44 dynes/cm surface tension.

A species effect was noted when Liese and Bauch (1967b) tested the consequence of seasoning from aqueous acetone solutions on sapwood pit aspiration of several gymnosperms. *Pinus sylvestris* earlywood pits became aspirated and impermeable to water flow, when dried from solutions of more than 26 dynes/cm surface tension, while *Sequoiadendron giganteum* earlywood pits became aspirated when surface tension exceeded 32 dynes/cm. Morphological differences were found among earlywood pits of *Cryptomeria japonica* such that a few pits still remained unaspirated when the wood was dried from water. These results

indicate that the limiting surface tension required for pit aspiration differs, depending on the wood species involved. The *C. japonica* results illustrate the importance of individual pit membrane structure in relation to the relative ease with which pit aspiration takes place. In general, seasoning from water causes earlywood pit aspiration in Pinaceae and in other woods that possess a distinct torus. Solvent seasoning prevents pit aspiration, provided that the surface tension and swelling ability of the solvent are sufficiently low for that particular species.

Freeze-drying has been used by Thomas (1969), Comstock and Côté (1968), and Erickson and Schmidt (1969) to reduce pit aspiration. Erickson and Schmidt reported an average of 70% pit aspiration in *Picea sitchensis* and 43% in *Abies amabilis* freeze-dried sapwood, in contrast to 98% pit aspiration in air-dried Sitka spruce sapwood. Erickson and Schmidt also found that acetone-seasoned Sitka spruce sapwood contained very few aspirated pits. Bramhall and Wilson (1971) used several seasoning methods on Douglas-fir wood obtained from the coastal and interior regions of British Columbia and related the observed variations in longitudinal gas permeability to a presumed difference in pit aspiration.

EXPERIMENTAL

The Douglas-fir tangential microtome sections used by Bramhall and Wilson (1971) to determine the effect of drying conditions on longitudinal gas permeability were used here to determine the quantitative relationship between pit aspiration and observed permeability. The samples had been obtained from one coastal (University of British Columbia Research Forest, Haney, B.C.) and one interior (Prince George, B.C.) Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) log and as such were felt to represent the permeable and impermeable wood typically grown in British Columbia. Outer sapwood (3–4 rings from cambium) and outer heartwood (5–6 rings from sapwood-heartwood boundary) had

been taken from vigorous (ca. 10 rings per inch) trees of 16-inch (coast) and 20-inch (interior) diameter. The permeability test specimens had been cut with a sliding microtome in the form of serial tangential sections varying in thickness from about 150 to 200 μm. These sections, approximately 8 mm wide and 25 mm long along the grain, were dried by five different methods: air, oven (70 C), freeze, solvent exchange with 1:2 ethanol:benzene, and boiling in xylene under vacuum. The coast heartwood and sapwood specimens that were air- and oven-dried were used in other permeability studies and, consequently, were lost for microscopic examination.

There were not as many latewood as earlywood specimens available for study from the Bramhall and Wilson material, and the lesser number of latewood pits prevented adequate sampling of latewood for torus position. Observations on latewood pit aspiration, therefore, were limited and are not summarized in detail. Those latewood pits that were observed generally proved to be more resistant to aspiration than adjacent earlywood pits. For example, the pits listed in Table 1 were found on a typical, single permeability specimen containing both earlywood and latewood and therefore were exposed to similar drying conditions. Since the more resistant, smaller diameter latewood pits did not become aspirated as frequently as did the more sensitive, larger diameter earlywood pits, the aspiration of earlywood pit membranes was studied more extensively and is described herein.

Specimens 3-mm square were cut from the permeability sections and were Epon-epoxy embedded via acetone and propylene oxide. Luft's (1961) Epon formulation was used, with equal proportions of mixtures A and B, and the resin polymerized at 60 C. The specimens were shorter than one tracheid length, so the plastic presumably penetrated cells without forming a pressure gradient across pit membranes. Severe distortion of tori as shown by Erickson and Schmidt (1969) was not observed.

Cross sections were cut 1 μm thick with

TABLE 1. *Pit membrane position in a coast sapwood freeze-dried sample*

	Aspirated %	Un-aspirated %	Partially aspirated %
Earlywood			
Pits on radial walls (264 pits)	53	39	7
Latewood			
Pits on radial walls (50 pits)	4	82	14
Pits on tangential walls (58 pits)	2	95	3
Pits between last latewood and first earlywood tracheid (59 pits)	12	88	0

a diamond knife in an ultramicrotome. The sections were stained with methylene blue for light-optical microscopy. The embedding resin was left in place so that the position of the tori at the time of embedding could be determined. It was impossible for the knife to dislodge the tori without also moving the embedding resin, so that torus position at the time of embedding could be determined with certainty. Such sectioning artefacts as occurred were in the form of gross distortions of sections, with cell walls and the embedding resin each wrinkled or torn. Nearly all sections were flat and wrinkle free, so that the pit membranes to be counted were distinct.

Each pit-aspiration value for the dried material in Table 2 is based on 183 to 1,474 pit-membrane-position observations. These were obtained from 50 to 200 sections per specimen, depending on the number of useful sections obtained. The number of pit membranes observed per section varied, depending on whether or not the section passed through the heavily pitted tracheid-overlap areas of a specimen. Bramhall and Wilson dried each section they obtained, but determined only the permeability of representative sections from the rings under study. Since extra sections had been prepared in parallel with specimens used for permeability determinations, the extra sec-

TABLE 2. *Effect of method of drying microsections on aspiration of earlywood intertracheid bordered-pit pairs*

Method of drying	Coast sapwood			Coast heartwood			Interior sapwood			Interior heartwood		
	% aspirated	% unaspirated	% partially aspirated	% aspirated	% unaspirated	% partially aspirated	% aspirated	% unaspirated	% partially aspirated	% aspirated	% unaspirated	% partially aspirated
Never-dried controls	2	98	–	100	0	–	32	68	–	–	–	–
Air	(samples not available)						93	6	1	95	3	2
Oven	(samples not available)						98	0	2	92	2	6
Solvent (1:2-ethanol: benzene)	34	38	28	89	6	5	55	29	17	91	5	4
Freeze	48	38	13	91	4	5	88	12	0	91	2	7
Boil under vacuum	43	32	25	84	10	6	92	4	5	97	2	1

tions were used for determination of pit aspiration to increase the number of observations.

Never-dried samples of all but interior heartwood were available that had been stored since their collection in a refrigerated thymol solution. The number of aspirated pits in never-dried wood was found for the same rings tested for permeability. Cross sections used for determining never-dried pit aspiration were cut from specimens embedded after either acetone dehydration or freeze drying in an experimental freeze-drying unit prior to vacuum embedding, using temporary microtome sections to monitor the dehydration and embedding processes.

RESULTS AND DISCUSSION

Most earlywood pits in never-dried outer sapwood were unaspirated. However, a difference was observed in the actual percentage of unaspirated pits between coast and interior wood samples. Two per cent of the coast and 32% of the interior sapwood pit pairs were aspirated (Table 2). All observed coast heartwood pit pairs were aspirated in never-dried samples. The actual percentage of aspirated pit membranes

is not as significant as the general observation that, for these particular never-dried samples, the tendency was for nearly all pits in the outer sapwood of coastal Douglas-fir to be unaspirated; whereas in the outer sapwood of interior Douglas-fir a substantial number of pits were aspirated.

During observations of dried material, it was common to find partially aspirated as well as completely aspirated pit membranes. Partially aspirated pit membranes were defined as those that were deflected to one side, so that a major portion of the margo was in contact with the pit chamber surface. The torus of the partially aspirated pit membrane shown in Fig. 1 does not actually touch the pit chamber wall over its entire circumference, so that limited quantities of permeating fluids could still pass through the remaining elevated portions of the margo. Partial pit aspiration, also referred to as incomplete pit aspiration, has been noted in the past (Stone 1939; Kishima and Hayashi 1962; Comstock and Côté 1968; Thomas and Nicholas 1966). Since the magnitude of fluid flow through partially aspirated pit pairs in comparison with unaspirated pit pairs has not been deter-
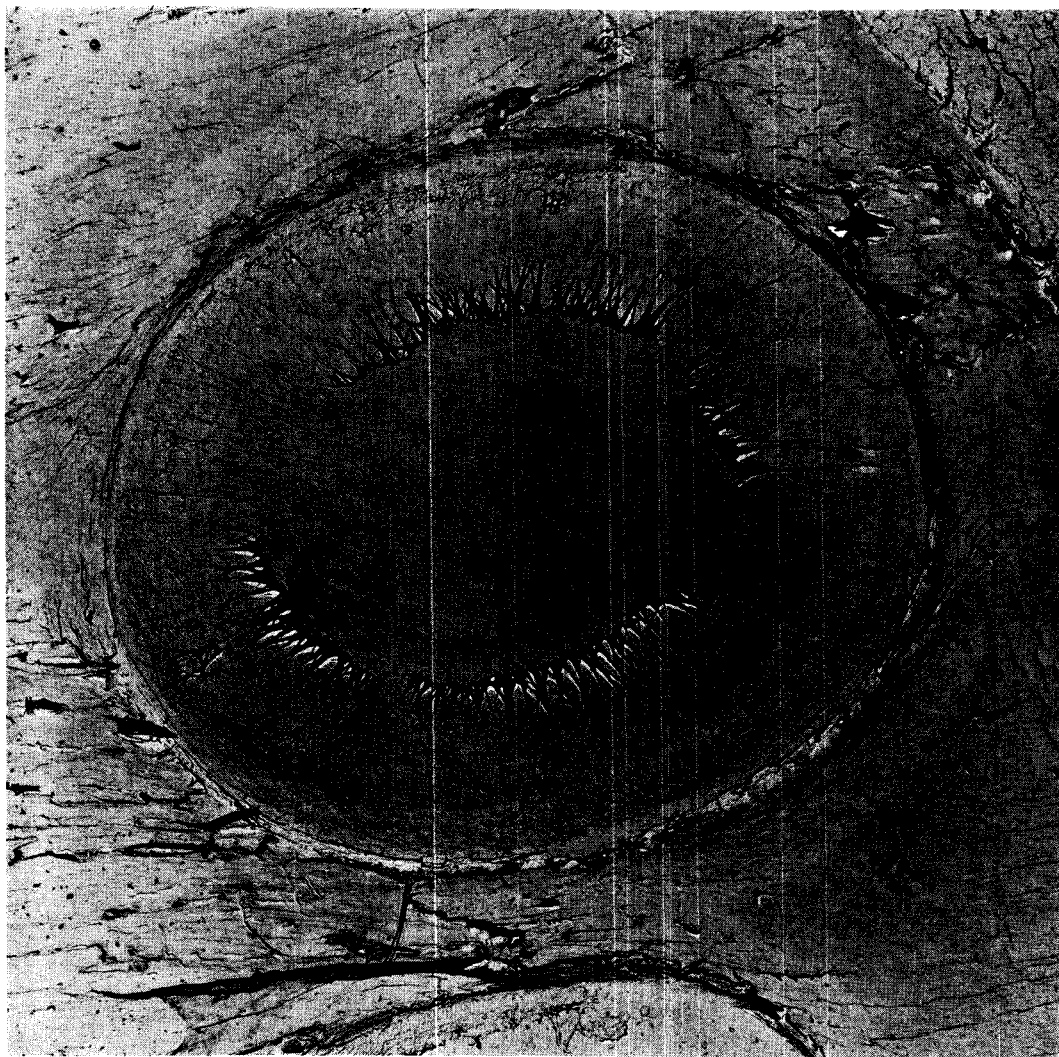
Fig. 1. Partially aspirated pit membrane. Shadows surrounding most of the torus indicate where it is not appressed to the pit chamber surface, although most of the margo is in contact with the pit chamber surface.

mined, any deductive use of this phenomenon is precluded.

The effect of method of drying on aspiration of earlywood pits is summarized in Table 2. Method of drying had a notable effect on the percentage of aspirated pits found in seasoned material.

The effectiveness of solvent seasoning in preventing or reducing pit aspiration has been well demonstrated elsewhere. The surface tension of the ethanol-benzene mix-

ture used to solvent season this wood was not determined by Bramhall and Wilson, but was probably about 27 dynes/cm, just greater than the critical 26 dynes/cm value found by Liese and Bauch (1967a) for three Pinaceae species. It is probable that the number of aspirated pits found in ethanol-benzene dried Douglas-fir was due to a surface tension near the threshold level for these pits, causing the more sensitive pits to become aspirated.
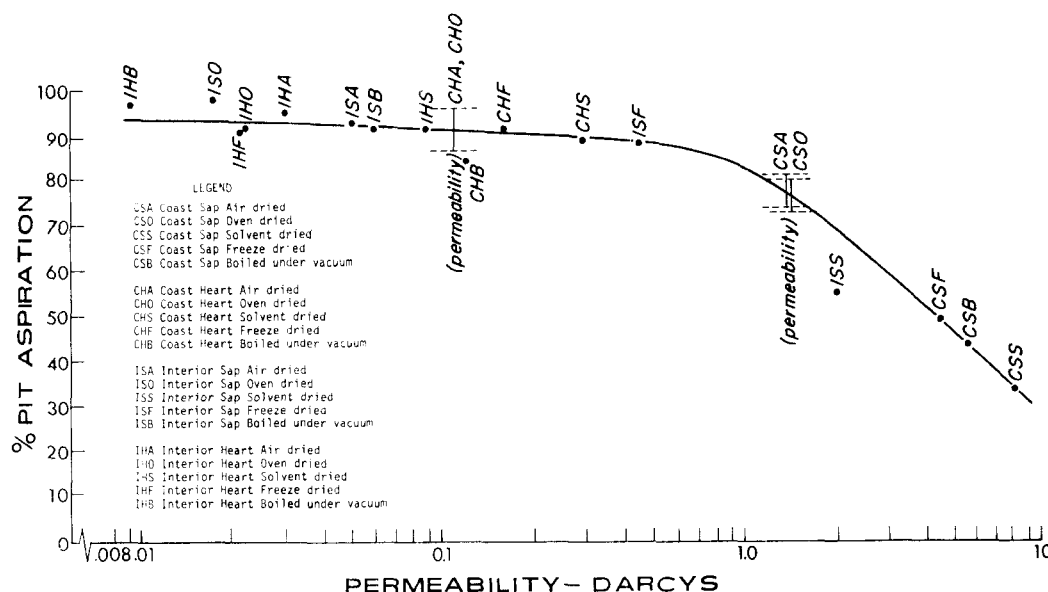
FIG. 2. Relation between pit aspiration and longitudinal earlywood gas permeability. Since coast heartwood and sapwood, both air- and oven-dried, were unavailable for microscopic examination, their permeabilities were added for comparison.

The freeze-drying technique prevented many pit membranes from aspirating during drying, but it definitely was not as effective as solvent seasoning. Results presented here correlate roughly with results given by Erickson and Schmidt (1969) for *Picea sitchensis* and *Abies amabilis*, and suggest that freeze-drying of wood may not always prevent pit aspiration. Actual drying conditions and sample size are critical. Pit aspiration was nearly completely prevented when some of the coast sapwood never-dried samples listed in Table 2 were freeze-dried under carefully controlled freeze-drying conditions, using temperatures approaching -70 C and pressure just less than 1 mm Hg to embed them for examination. These samples were dried in a small, experimental freeze-drier rather than the commercial freeze-drier used by Bramhall and Wilson.

The proportion of aspirated pits in wood seasoned by boiling under vacuum did not bear a constant relationship to other seasoning techniques used on wood of the same growth origin and wood zone. Boiling under vacuum is, therefore, of uncertain value in preventing pit aspiration, and the lack of literature relating pit aspiration to this seasoning technique prevents any further conclusions.

Both air- and oven-drying cause aspiration of nearly all earlywood bordered pits. These results were expected for interior Douglas-fir and serve as control figures for comparison of the other drying techniques.

Method of drying had little effect on aspiration of heartwood bordered pits. The level of pit aspiration was high, and was approached only by those interior sapwood specimens dried directly from water—by air, oven, freeze, and boil under vacuum drying.

The relationship obtained when the percentages of completely aspirated pit membranes in Table 2 are plotted against the average gas permeabilities for the specimens dried in a like manner is shown in Fig. 2. The permeability values corresponding to the unavailable coast air- and oven-dried specimens have been added for comparison. The relative position of heartwood and

TABLE 3. *Anatomical characteristics of sapwood rings tested for longitudinal gas permeability*

British Columbia wood source	Ring age years	Av tracheid length mm	Max tracheid length mm	Pits/ tracheid	Pits/mm tracheid length	No. tracheids/ sq mm cross section
Coastal	56	4.94	5.64	144	29.2	413
Interior	70	3.49	4.36	65	18.6	533

sapwood and of coastal and interior-grown wood is apparent from the letter codes. Specifically, coast sapwood samples are associated with the most permeable end of the curve and interior heartwood with the least permeable end. Pit aspiration appears to be the controlling factor in determining earlywood gas permeability; seasoning method is important only insofar as it determines the proportion of aspirated pits. The curve is nearly flat for high levels of pit aspiration, with a definite inflection point, suggesting a threshold value of pit aspiration below which permeability increases rapidly. Interior heartwood permeability is generally lower than that of interior sapwood for comparable levels of pit aspiration, perhaps because heartwood pit-membrane encrustation further reduces permeability after the membranes become aspirated.

It is apparent from Fig. 2 that the permeability of solvent-seasoned interior sapwood did not respond to percentage pit aspiration in the same manner as did coast sapwood specimens. Limited sampling of available never-dried material provided the basis for a comparison of several anatomical features, as summarized in Table 3. Tracheid length (45 measurements) and number of pits per tracheid (30 tracheids) were determined on macerated earlywood of the rings indicated in Table 3, corresponding to one of the two sapwood rings for which Bramhall and Wilson determined permeability. Pits on both the front and back walls of tracheids were counted. Numbers of cells per square mm were calculated, using measurements of tangential and radial tracheid diameters on sections taken from 68 different permeability specimens.

When tracheid length alone is considered,

the shorter-tracheid interior wood cannot be as permeable as the longer-tracheid coastal wood because, for permeability samples of equal length, the permeating fluid must pass through more pits per unit length of wood. Stamm, Clary, and Elliot (1968) give the following formula for the number (N) of pits traversed in series through a given length (t) of wood, where the maximum (f_{max}) and average (f_{av}) fiber lengths are known:

$$N = 1 + 4/3 \left[(t - f_{max}) / (f_{av}) \right].$$

When this formula is applied to the 25 mm-long longitudinal permeability samples of Bramhall and Wilson (1970), the number of pits traversed in series in the interior sample is found to be 8.9, while for the coast sample the number is 6.2.

The difference in tracheid length was significant at the 99% level. The shorter tracheids of the interior tree were obtained from an increment of greater age from the pith than the tracheids from the coastal tree. Since tracheid length tends to increase with increasing tree age, the observed difference in tracheid length is not due to cambial age differences. The present results do not allow an extrapolation to coast and interior Douglas-fir in general, because only one tree from each region was sampled, but the difference in tracheid length for these particular samples is certainly reflected in a difference in their permeability. Krahmer (1961) also observed a similar tracheid length phenomenon for Douglas-fir grown in Oregon, the average fiber length of his permeable samples being 5.59 mm and for his refractory samples, 3.68 mm.

The practical effect of greater numbers of pits per tracheid is that, at a given level of pit aspiration, there will be more functioning pits per tracheid. The coast tree

had more pits per tracheid than did the interior tree, the difference being significant at the 95% level.

The number of pits per mm of tracheid length is not equal for coast and interior tracheids. The large difference suggests that the number of pits does not vary directly with tracheid length, but rather that there was an inherent difference between the trees examined. The permeability of the interior-grown samples, therefore, could be less than the coast-grown specimens, not only because tracheids are shorter and the absolute number of pits per tracheid is less, but also because there are fewer pits per unit volume of wood.

One factor serving to increase the relative permeability of interior-grown wood over coast-grown wood is that there was a greater number of tracheids per unit cross-sectional area in the interior samples. This was because both tangential and radial tracheid diameters were smaller. Krahmer (1961) observed similar differences for permeable and refractory Douglas-fir grown in Oregon. A greater number of tracheids favors greater permeability because there are then more tracheids available for conduction in parallel. The observed differences in tracheid diameters are themselves expected to have only minor influences on permeability since most resistance to longitudinal flow is in bordered-pit membranes connecting longitudinal tracheids. Because the coast sample was more permeable than the interior sample, the effect of numbers of tracheids per square mm must be overshadowed by other factors, such as tracheid length and the number of pits per tracheid. Tracheid length and number of functioning pits per tracheid were, therefore, used to determine the probability of occurrence of a continuous permeability pathway from the entrance to exit faces of a wood sample.

The permeability curve in Fig. 2 has an inflection point at about 90% pit aspiration. When fewer than this proportion of pits are aspirated, the probability of occurrence of a continuous flow path between the entrance and exit faces of the permeability specimens

increases rapidly. The tracheid lengths and number of pits per tracheid listed in Table 3 were used in conjunction with per cent pit aspiration to determine the probability of finding one or more unaspirated pit pairs between overlapping tracheids of a 25-mm-long series of tracheids corresponding to the permeability specimens used by Bramhall and Wilson. The model (Fig. 3) used for determining the probabilities was a simplistic model of a tracheid similar to one used by Stamm, Clary, and Elliot (1968) and Comstock (1970), in which tracheids overlap one another by one quarter of their length, and the average numbers of pits per tracheid (n) are divided evenly among the four tracheid-tracheid contact faces. No flow will occur from tracheid to tracheid if all pits connecting the two tracheids are aspirated. Each pit is assumed to have the same probability of being aspirated (q), or of being unaspirated (p), where $p + q = 1$. It is possible to determine the probability p that a permeating fluid will penetrate any given distance using the relation $p_{i+1} = p_i(1 - q^{n/4})[2 - p_i(1 - q^{n/4})]$.*

The values for i, n, and q are peculiar for any given piece of wood and may be determined microscopically. Using the values for i (sample length expressed in number of complete tracheids) and n (number of pits per tracheid) obtained from examination of the coastal and interior-grown wood used by Bramhall and Wilson, and using values for q ranging from 0.90 to 0.99 (corresponding to 90 to 99% pit aspiration), Table 4 was constructed.

The tabulated values for p_i are the probabilities that a tracheid in the ith layer of tracheids from the wood surface will become filled with a permeating fluid at the listed per cent pit aspiration. In the layer of tracheids 25 mm from the entrance face of a piece of wood in which 95% of the pits are aspirated, 96% of the tracheids would be fluid filled for a coast specimen, but only 46% would become filled for an interior specimen, suggesting a substantial difference in permeability.

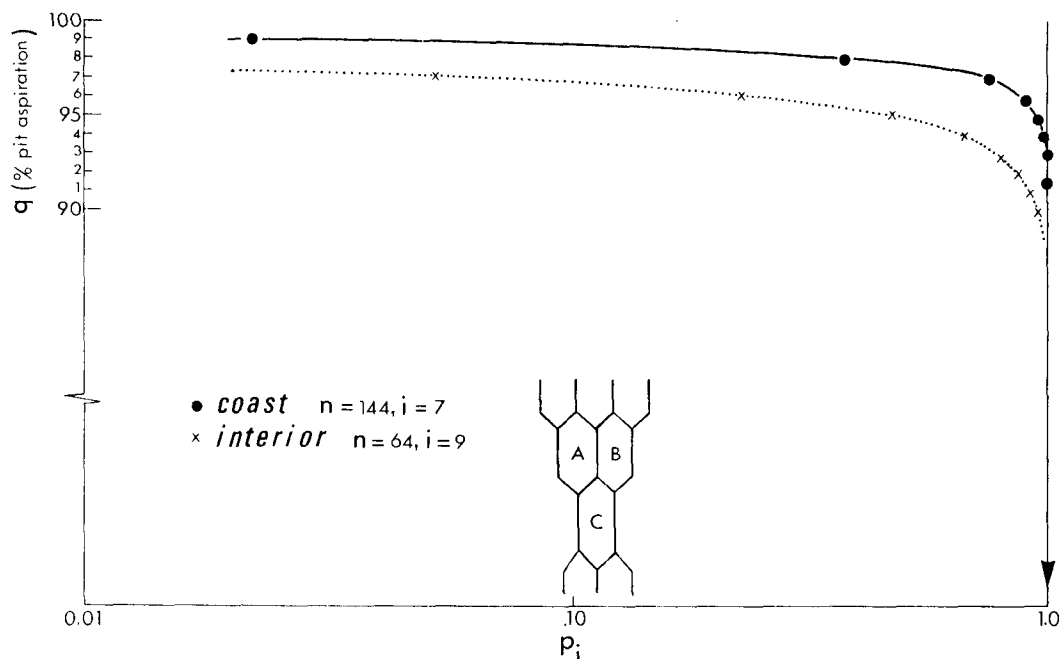* Complete derivation is given in Appendix.

FIG. 3. Probability of occurrence of fluid-filled tracheids 25 mm from wood surface, obtained using anatomical parameters for coast and interior Douglas-fir sapwood. The anatomical model is explained in Appendix.

Wood permeability is expressed as the flow of a certain volume of fluid in a given time interval. Since the probabilities obtained for the coast and interior wood samples do not take into account the relative fluid-carrying capacities of the pits involved, the tabulated probabilities do not strictly indicate the relative permeabilities of wood involved. Furthermore, the probabilities indicate only that tracheids in question can be reached by permeating fluid. For example, in developing the tabulated probability, a tracheid-tracheid contact face with four or five open pits is assumed to give the same contribution as a contact face with only one open pit. The amount of fluid that could flow between these two tracheids in a given time would obviously be very different. The tabulated probabilities lend themselves to a description of the relative depth of penetration of the two wood types, however. Because the ultrastructural characteristics of bordered pits of the two wood types are believed to be quite similar, the

probabilities also may well indicate their relative permeability if comparable numbers of pits are open in each tracheid. On this basis, the relative permeabilities at the same level of pit aspiration of the two wood types are quite different, based solely on tracheid length and number of pits per tracheid.

Since at the 95% level of pit aspiration less than half of the interior-grown tracheids will possibly become fluid filled, while 96% of coast tracheids could become filled, the relative permeabilities of the two wood types are probably quite different. The actual permeability data indicate that this is the case.

Data from Table 4 corresponding to permeability specimens 25 mm long are plotted in Fig. 3. The general shape of the curves is similar for both permeability vs. pit aspiration (Fig. 2) and probability vs. pit aspiration (Fig. 3), suggesting that pit aspiration can be reasonably assumed to explain the observed differences in earlywood perme-

TABLE 4. *Probability of occurrence of fluid-filled tracheids*

	Coast ($n = 144$)			Interior ($n = 64$)*		
$i \backslash q$	0.90	0.95	0.99	0.90	0.95	0.99
1	0.9995	0.9751	0.5150	0.9657	0.8063	0.2750
2	0.9995	0.9680	0.2883	0.9545	0.6991	0.0800
3	0.9995	0.9659	0.1674	0.9506	0.6296	0.0236
4	0.9995	0.9652	0.0990	0.9491	0.5807	0.0070
5	0.9995	0.9650	0.0592	0.9486	0.5446	0.0021
6	0.9995	0.9649	0.0356	0.9484	0.5168	0.0006
7	0.9995	0.9649	0.0215	0.9483	0.4950	0.0002
8	—	—	—	0.9483	0.4774	0.000055
9	—	—	—	0.9483	0.4632	0.000016

n = number of pits per tracheid
i = sample length, expressed as number of tracheid lengths
q = probability of a given pit being aspirated (or per cent pits aspirated)
* = for purposes of calculation, 64 pits were assumed to occur in interior tracheids although 65 pits per tracheid are re-
ported in Table 3.

ability, provided differences in tracheid length and numbers of pits per tracheid are accounted for. Furthermore, the different probability curves for coast and interior Douglas-fir suggest that, for the samples used here, at comparable levels of pit aspiration, interior-type Douglas-fir is not as permeable as coast-type Douglas-fir because of differences in tracheid length and number of pits per tracheid.

CONCLUSIONS

Longitudinal gas permeability of thin earlywood sections of Douglas-fir is dependent on the degree of aspiration of the intertracheid bordered-pit pairs. Gas flow is most pronounced when fewer than 80 to 90% of the pits are aspirated.

Although the increase in pit aspiration that occurs during the seasoning of wood can be altered by choice of a particular seasoning method, every seasoning method studied here resulted in an increase in numbers of aspirated bordered pits compared with never-dried wood. Solvent seasoning proved most effective, but a significant number of pits still became aspirated, probably because of the choice of solvent system used.

Earlywood pit aspiration can be used to explain observed differences in permeability for wood within a discrete sample. How-

ever, when wood from different trees is compared, the effect of pit aspiration on permeability should be considered in relation to certain other important anatomical characteristics of the wood being permeated. Tracheid length, number of bordered pits per tracheid, and number of tracheids per unit area determine intrinsic or never-dried sapwood permeability. Shorter tracheids and a smaller number of pits per tracheid render wood relatively less permeable, while a greater number of tracheids per square millimeter, which determines the number of parallel-flow paths through wood, serves to increase permeability. A more detailed analysis of the effect of these factors is necessary before a final conclusion can be reached as to their relative importance. However, on the basis of the available evidence, the combined effect of tracheid length and number of pits per tracheid appears to have the greatest effect on permeability, especially when the proportion of aspirated pits increases, and likely is responsible for the lesser permeability of interior wood studied here.

An extension of these findings to a general comparison of coastal and interior Douglas-fir cannot be made until more data are obtained regarding average tracheid length, number of pits per tracheid, and number of tracheids per square millimeter for both coastal and interior material.

APPENDIX

The final probability equation, used to determine the proportion of fluid-filled tracheids at various levels within a permeability sample, was derived as follows by W. G. Warren.

If n is the average number of pits per tracheid, and if the pits are evenly distributed on each of the four tracheid-tracheid contact faces shown in Fig. 3, there will be $n/4$ pits per tracheid-tracheid contact face. Suppose that the probability that a pit is open is p and the probability that a pit is closed is q, where $p + q = 1$. The probability that all pits on a given contact face are aspirated is $q^{n/4}$. Therefore, the probability of one or more pits being open is $1 - q^{n/4}$.

If (A) is the event that there is a fluid in A, $(C/A, B)$ is the event that there is a fluid in C given that there is a fluid in both A and B, and $(C/A,\overline{B})$ is the event that there is fluid in C, given that there is fluid in A but not in B, etc., then the probability of occurrence of each of these events can be written thus:

$$P(C/A, B) = 1 - q^{n/2};$$
$$P(C/A, \overline{B}) = 1 - q^{n/4};$$
$$P(C/\overline{A}, B) = 1 - q^{n/4};$$
$$P(C/\overline{A}, \overline{B}) = 0.$$

The unconditioned probability that there is fluid in C is, therefore, $P(C) = P(C/A,B) P(A,B) + P(C/A,\overline{B})P(A,\overline{B}) + P(C/\overline{A},B) P(\overline{A},B)$, which because of the symmetry of the system reduces to $P(C) = P(C/A,B) P(A,B) + 2P(C/A,\overline{B})P(A,\overline{B})$.

If we suppose that A and B in Fig. 3 are at the ith level, then C is at the $(i + 1)^{th}$ level. Further, if p_i is the probability that there is fluid in any given tracheid in the ith level, then

$$P(A,B) = p_i^2$$
and $$P(A,\overline{B}) = p_i(1 - p_i).$$

Therefore, the probability of the fluid arriving at the $(i + 1)^{th}$ level is

$$p_{i+1} = (1 - q^{n/2})p_i^2 + 2(1 - q^{n/4})p_i(1 - p_i).$$

If we assume that the fluid is freely available outside the first level of tracheids, then $p_0 = 1$, and

$$p_1 = (1 - q^{n/2});$$
$$p_2 = (1 - q^{n/2})^3 + 2(1 - q^{n/4}) q^{n/2}(1 - q^{n/2}),$$

etc. Since it is impractical to write an explicit equation for p_i, we must compute sequentially for any given level of n and q, the probabilities p_1, p_2, p_3, etc. For purposes of calculation, it is most convenient to write the probability relationship in the form:

$$p_{i+1} = p_i(1 - q^{n/4})[2 - p_i(1 - q^{n/4})].$$

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