A CONTRIBUTION TO A FURTHER UNDERSTANDING OF THE OCCURRENCE OF THE INDIAN PAINT FUNGUS, *ECHINODONTIUM TINCTORIUM* E. and E., IN BRITISH COLUMBIA FORESTS

by

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ABSTRACT

The wood-decaying ability of *Echinodontium tinctorium* E. & E. and the high frequency of occurrence that is sometimes attributed to it has established this fungus as one of the most destructive of fungi that infect the heartwood of coniferous trees in western North America. Considerations of the biological requirements of the fungus by previous investigators were, mainly, incidental to surveys of the purely economic aspects of its decay. Thus, despite local and regional demonstrations of an abundance of *E. tinctorium*, the circumstances whereby it can infest its different suscepts with variable intensities have remained, for the most part, unanswered. Consequently, evaluation of the importance of the fungus in British Columbia forests, with reference to any particular unit of them, has been largely speculative.

A province-wide investigation was conducted to determine the distribution pattern that is peculiar to *E. tinctorium* and, also, to evaluate the factors that regulate its occurrence. Forest units that were comprised entirely or in part of E. tinctorium suscepts were categorised on an ecological basis with the result that 53 habitats were distinguished. The environmental factors peculiar to each habitat were analysed in the light of their apparent effects upon the welfare of the fungus.

E. tinctorium was absent from 13 habitats despite the proximity of them to the 40 in which the fungus occurred regularly. A pronounced degree of inter- and intra-regional variation in the frequency of the fungus was observed that could be traced to the environmental influences specific

to individual habitats. Thus, E. tinctorium was more abundant on each of its suscepts the more remote they were from the influences of a Pacific climate, provided that atmospheric humidities remained high.

Certain of the many factors that regulate the occurrence of the fungus appeared at times to have a greater influence than did others but, apart from that of inherent resistance to infection, seldom did one factor become limiting. Atmospheric temperature and humidity, however, appeared to be the strongest factors of all that influence E. tinctorium. Thus, whenever environmental influences had combined to produce high humidities and high average temperatures for protracted periods, a high incidence of infection by E. tinctorium usually resulted.

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Members of the Faculty of the University of British Columbia, Biology and Botany Department and Forestry Faculty, together have been most helpful as regards the details of the investigation and report. The late Dr. D.C. Buckland, Associate Professor of Forest Pathology, provided technical guidance for all but the final phases of the investigation, for which the author is sincerely grateful. Dr. T.M.C. Taylor, Chairman, Biology and Botany Department, and Dr. F. Dickson, Professor, have been most helpful with their guidance in the final stages of the work and in the preparation of the manuscript.

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X. APPENDICES

VITA

George Philip Thomas was born on November 21, 1920, in North Vancouver, B.C. After graduating from Prince of Wales High School, Vancouver, in 1938, he entered the University of British Columbia. His university studies were interrupted in 1942 by his enlistment in the Canadian Army, with which he served in Canada and Europe until 1946. Upon his discharge from the Army he re-entered the University of British Columbia and received the degree of Bachelor of Arts (Honors, Biology and Forestry Option), in 1947, and the degree of Bachelor of Science in Forestry, with first class standing, in 1948. He was appointed to the Dominion Forest Pathology Laboratory, Victoria, B.C., in May 1948, and has had continuous service as a research officer with this organization since, apart from leaves of absence for graduate studies. He entered the School of Forestry, Yale University, in 1948, as a graduate student, and received the degree of Master of Forestry, cum laude, in 1949. He re-entered the University of British Columbia in 1951, as a graduate student, and held a Canadian Pulp and Paper Association (Western Division) Fellowship in the academic year 1952-53. He is the author of the following publications:

1950. Foster, R.E. and Thomas, G.P. A uniform field procedure for mature timber analysis in forest pathology. Can., Dept. Agr., For. Biol. Lab., Victoria.

1950. Thomas, G.P. Two new outbreaks of Phomopsis lokoyae in British Columbia. Can. J. Res., C, 28:477-481.

1950. Thomas, G.P., Browne, J.E. and Foster, A.T. Decay in western hemlock and amabilis fir in the upper Nitinat region, B.C. Can., Dept. Agr., For. Biol. Lab., Victoria.

VITA (continued)

1951. Foster, R.E. and Thomas, G.P. Pathological classification of mature timber stands. Can., Dept. Agr., For. Biol. Lab., Victoria.

1953. Thomas, G.P. and Podmore, D.G. Studies in forest pathology. XI. Decay in black cottonwood in the middle Fraser region, British Columbia. Can. J. Bot., 31:675-692.

1953. Foster, R.E., Thomas, G.P. and Browne, J.E. A tree decadence classification for mature coniferous stands. For. Chron., 29(4): 359-366.

1954. Thomas, G.P. and Thomas, R.W. Studies in forest pathology. XIV. Decay of Douglas fir in the coastal region of British Columbia. Can. J. Bot., 32:630-653.

INTRODUCTION

Echinodontium tinctorium Ellis and Everhart, commonly named the Indian paint fungus, is the cause of a heart rot in coniferous trees of western North America. Apart from having an extensive suscept range it occurs most frequently in and causes most damage to species of Abies and Tsuga. The destructive nature of the rot caused by *E. tinctorium* and the high frequency of occurrence frequently attributed to it has established the fungus as one of the most destructive fungi that infest western conifers.

The initial concept of the importance of *E. tinctorium* was that the fungus has a distribution essentially commensurate with the ranges of its suscepts and that, wherever it occurs, serious losses in wood volume by reason of its decay can be expected. This evaluation, based as it was on the results of non-representative surveys of western forests, was shown to be grossly in error by later and more complete surveys which indicated that extensive areas within the ranges of its different hosts were free of the fungus. Consequently, regional importance was ascribed to the fungus, its population and effect being regarded as uniform within particular regions. On this basis, for example, the fungus was considered to be of no consequence in stands of the lower coast forest of British Columbia in contrast to its damaging effect in stands of the interior wet-belt forest. More recently, however, and coincident with a more precise evaluation being made of the extent and condition of the forest resources of British Columbia, *E. tinctorium* has been found to vary in its occurrence, both in regions of presumed high abundance and in those of low abundance. So great has been the variation encountered that a concept of regional importance as pertains to this fungus cannot be legitimately applied to British Columbia forests.

The need for a reconsideration of the habits and capabilities of forest fungi, such as those of E. tinctorium is apparent in view of the detailed planning that today features preparations for effective management of forest units. It has become important to learn how to anticipate the occurrence of decay and to appreciate its significance under the range of natural conditions that characterize any particular forest unit. Thus, the purpose of this investigation is two-fold: to study some aspects of the ecology of E. tinctorium in order that a precedent may be set for studies of other similarly important forest fungi, and to ascertain and evaluate some of the major factors that control this fungus, from the view points of its distribution and ability to cause damage, so that its abundant occurrence in nature may be anticipated.

Three approaches were made to the attainment of the objectives of this investigation. A search of pertinent literature was carried out in order to assess our current knowledge of the fungus. The essence of such literature together with an appraisal of its contribution to an understanding of E. tinctorium are presented herein. An examination of British Columbia forests was carried out to the extent that two species known to be suscepts were examined as they occurred in stand form under the range of forest conditions that exists. The examination of stands included records being made of the occurrence, abundance, and fruiting habit of the fungus together with records of the principal features of suscept and fungous habitats. The results of these examinations are embodied herein in the form of habitat descriptions. An evaluation of the factors that control E. tinctorium habitats was made in the light of the physiological requirements of this fungus. The results of this evaluation are presented together with a description of the means whereby critical habitat factors may be recognized in nature.

LITERATURE REVIEW

Historical Record of *Echinodontium tinctorium*

The Indian paint fungus was first described by Ellis and Everhart (14) in 1895 on receipt of a damaged specimen of its fruit body collected by J.G. Swan and F.V. Coville on Admiralty Island, Alaska. It was mistakenly described and named as *Fomes tinctorius* E. and E. by reason of the spines of the fruit body having been broken off and their hollow remains mistaken for pores. Lloyd (26) discovered the hydnaceous character of the fruit body on receipt from C.V. Piper of a more perfect specimen collected on *Abies grandis* (Dougl.) Lindl. at Janesville, Idaho and named the fungus *Hydnum tinctorium*. Ellis, in correspondence with Lloyd, suggested that the Idaho and Alaska collections were undoubtedly of the same fungus, for which he proposed the name *Echinodontium tinctorium* Ellis and Everhart. Subsequent challenges to this name for the fungus were made and it was Banker (1), some years later, who firmly established the name *E. tinctorium*. Some controversy exists as to the systematic arrangement of *E. tinctorium* but, regardless of its being placed in the *Polyporaceae* by Miller (30), most other workers advocate its retention in the *Hydnaceae*.

Life Cycle of Echinodontium tinctorium

Both the hymenophore and spores of the fungus are formed in contact with an aerial environment. Similarly, the spores are disseminated and germinate, and penetration by the fungus is effected into suscept tissue in an aerial environment. Following penetration the fungus develops an intra-cellular mycelium that ramifies throughout the heartwood of its host. The resultant decay (see Plates I and II) is quite distinct from that caused by other fungi with the exception of some of its advanced stages which are similar to the equivalent stages of decay caused by Stereum sanguinolentum Alb. and Schw. ex Fr. The initial and final stages of E. tinctorium decay are normally quite readily distinguishable from those of Stereum sanguinolentum, although Bier et al. (3) have stressed the need for cultural identifications if the two decays are to be distinguished. The early descriptions of E. tinctorium decay given by Hedgcock (19) and Meinecke (20) have been augmented by one given by Weir and Hubert (42) which is as follows:

> "The advance rot of Echinodontium tinctorium is difficult to detect and, unless accompanied by small brownish discolorations or by reddish or brownish streaks, cannot be detected without very close inspection. In the early stages of the decay the wood assumes a faint yellowish, spongy texture. Sometimes this stage is intensified by the presence of small, barely discernible, brownish areas which later develop into the typical decay. The extension of advance rot beyond typical rot varies from about two to six feet in Abies concolor and from about one to five feet in western hemlock. The typical rot has a reddish brown to brownish yellow color, often spotted with areas of a more vivid rust color and occasionally showing streaks of a dark to reddish brown hue. It has a stringy texture. In the last stages of decay the heartwood is entirely disorganized, giving place to large cavities. The stringy nature of the rot can be readily seen in this stage, particularly in the ends of logs.

PLATE I, Figures 1 - 3

PLATE I. *E. tinctorium Decay.*

Figure 1. *Decay in western hemlock.* The restriction of the decay to heartwood and the stringy nature of its advanced stages, as illustrated, are characteristic of *E. tinctorium.*

Figure 2. *Decay in western hemlock.* The invasion of the heartwood of living trees via branch stubs, as illustrated, is a common method of entrance for *E. tinctorium.*

Figure 3. *Decay in alpine fir.* The occurrence of decay in the butt and root regions of alpine fir is a common feature of E. tinctorium infections in this species of suscept. Regardless of whether root infections have occurred, inoculation will have occurred above the ground line.


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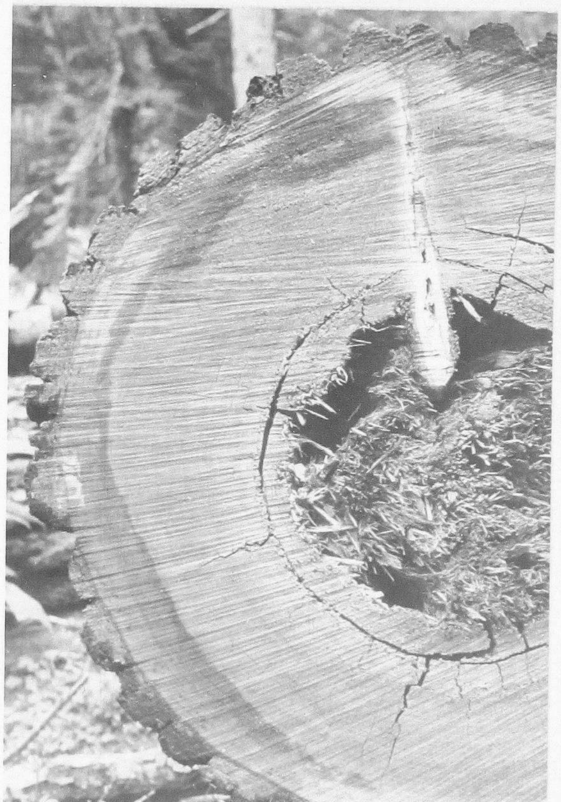
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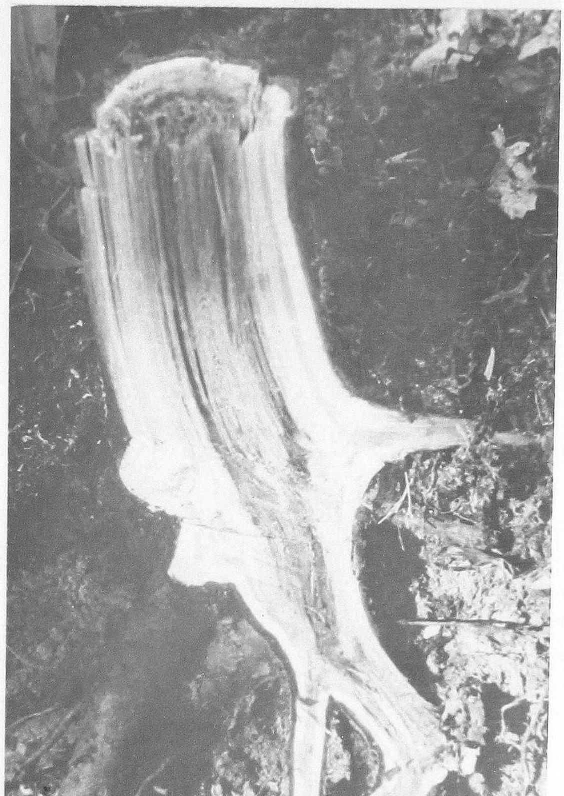
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PLATE II, Figures 4 - 9

PLATE II. *E. tinctorium Decay.*

Figure 4. *Decay in alpine fir.* The series of discs illustrated represent cross-sectional views of a decay column at different points above the ground line, viz., at 18 feet (lower left), 34 feet (lower right), 50 feet (top disc). The stains characteristic of incipient decay, as illustrated in the top disc, normally occur several feet beyond advanced decay.

Figure 5. *Decay in alpine fir.* The stringy nature of advanced decay and the dark streaks or blotches, as illustrated, are typical of E. tinctorium decay.

Figure 6. *Decay in alpine fir.* A tendency to ring rot and lamination, as illustrated, are typical of advanced stages of E. tinctorium decay, although the decay in its final stages usually results in complete destruction of the heartwood.

Figure 7. *Decay in western hemlock.* The darker portions of the heartwood column represent the stain stage of E. tinctorium decay as it occurred at 33 feet above the ground line in a 12-in. tree.

Figure 8. *Decay in western hemlock.* Incipient and advanced decay at 13 feet above the ground line of the same tree as illustrated in Figure 7.

Figure 9. *Decay in western hemlock.* The final stage of E. tinctorium decay as it appears in cross-sectional view.

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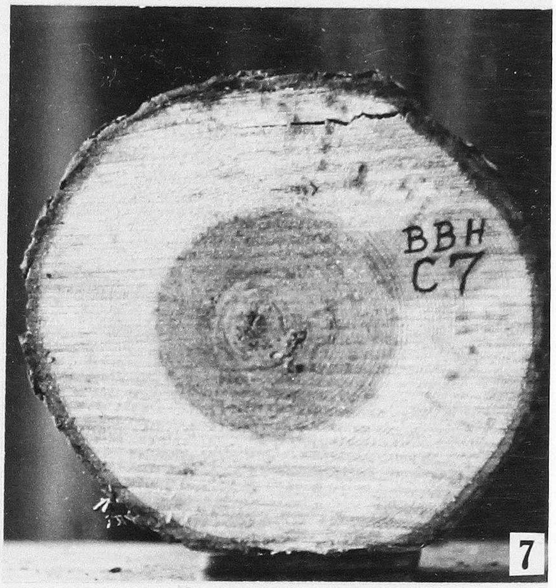

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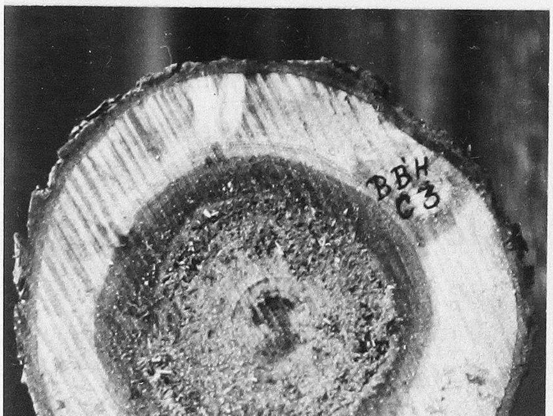

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The brick red color of the sporophores is often found distributed through the typical rot and in branch stubs."

Certain of the microscopic details of the fungus, as apparent in wood in different stages of decay, have been described by Hubert (22) and Mayers (27). Both authors described a difference in hyphae that depended largely upon age; young hyphae are thin, often hyaline, usually with clamps, and usually without constrictions, while the older hyphae are thick, often encrusted with dark brown decomposition products, frequently without clamps, and usually constricted. Likewise, both of these authors observed that the hyphae E. tinctorium concentrate in and adjacent to medullary rays which, in their opinion, are the main avenues of mycelial spread. The red bands that characterize wood decayed by E. tinctorium were observed by Mayers to be the result of plugging of wood cells by mycelium and the diffusion of coloring matter. Certain of the gross and microscopic features of the fungus, as apparent in artificial culture, have been described by Davidson et al. (12) and Nobles (31) both of whom studied the fungus for the purpose of describing its characteristic features in relation to other wood-inhabiting fungi.

Schmitz, in a study of the enzyme activity of E. tinctorium (36), used the mats of tissue cultures from young sporophores to demonstrate the presence of 12 different enzymes and concluded that carbohydrase activity is a dominant phase in the physiology of this fungus. Mayers (27), who reported the occurrence of eight additional enzymes in a further study of the enzyme activity of the fungus, extended his observations to the results of microchemical tests to show whether or not such enzymes functioned in both mycelial growth and passage of hyphae from cell to cell. He concluded on the basis of such tests that the enzymes of *E. tinctorium* function almost entirely in the growth of the fungus.

The mode of attack by the fungus in wood was first suggested by Hedgcock (19) who expressed the opinion that it first attacks the spring wood of each annual ring, causing the wood to separate into flakes, and that finally the wood is for the greater part dissolved and left in a yellow or brown stringy mass. The more detailed works of Hubert (22) and Mayers (27) placed particular stress upon the role of medullary rays in the progress of the decay. Mayers suggested a sequence of decay development for the fungus as follows:

> "The medullary ray cells of the spring wood break down first after which the adjacent tracheids break down to leave a pocket of decay where the medullary ray passes through the spring wood. Such pockets are formed in the spring wood of several adjacent annual rings while the summer wood remains normal."

Concerning the breakdown of individual cells, both Hubert and Mayers concluded that delignification first occurs nearest to the lumen of the cell and proceeds towards the middle lamella, which in many cases remains intact.

After a variable period of years following infection, during which the mycelium exists vegetatively within host trees, hyphae mass beneath the outer bark, generally at the base of a branch stub or on the face of a branch scar, and initiate the formation of sporophores. Fruit body formation occurs throughout the summer and either one or two hymenial layers may be formed each year. The fruit body (see Plates III and IV) is perennial to the extent that for several years

PLATE III, Figures 10 - 13

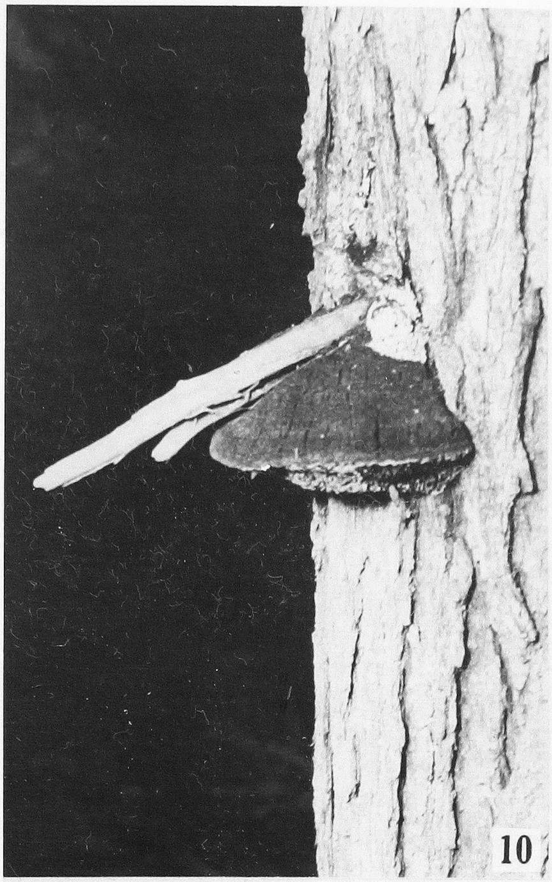
PLATE III. *The Gross Features of E. tinctorium Sporophores.*

Figure 10. *The upper surface.* In older sporophores the upper surface is characteristically black and cracked, as illustrated, but in younger sporophores it is usually brown, smooth, and sometimes velvety.

Figure 11. *The lower surface.* In older sporophores the lower surface consists of vertically arranged teeth, or spines, that are hard and gray. In younger sporophores, as illustrated, or near the margins of older ones the lower surface is typically daedaloid and white to light brown in color.

Figure 12. *The lower surface.* An annual reduction in the extent of the functional portion of the lower surface occurs in older sporophores, as illustrated, to the point where a sporophore ceases to function in sporulation.

Figure 13. *The arrangement of the hymenium.* The hymenium is arranged over the surface of downward-directed spines. Sporulation is most abundant near the ends of the spines in older sporophores and is usually indicated, as illustrated, by a whitish bloom.



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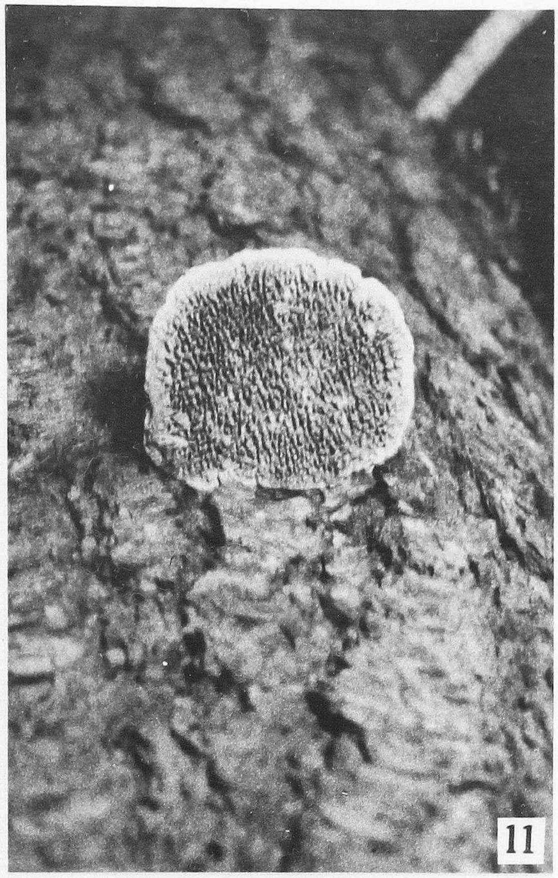

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PLATE IV, Figures 14 - 17

PLATE IV. <u>The fruiting Habit of F. tinctorius</u>.

Figure 14. <u>The region of attachment</u>. Most sporophores are located beneath branch stubs and extend downward in the angle formed by the branch stub and the tree bole. Sporophores are formed in some instances on the lower surface of living branches at variable distances from the bole.

Figure 15. <u>The location of fruiting in stands where favourable conditions for fruiting exist only in the higher canopies</u>. Fruiting is normally most abundant in the upper third of dominant and co-dominant trees in stands such as those of association number 14, as illustrated.

Figure 16. <u>The location of fruiting in stands where favourable conditions exist in all canopies</u>. Fruiting is normally abundant for the full stem length of trees in stands such as those of association number 33, as illustrated.

Figure 17. <u>The location of fruiting in stands where favourable conditions exist only in the lower canopies</u>. Fruiting is normally close to the ground line in stands such as those of association number 35, as illustrated.


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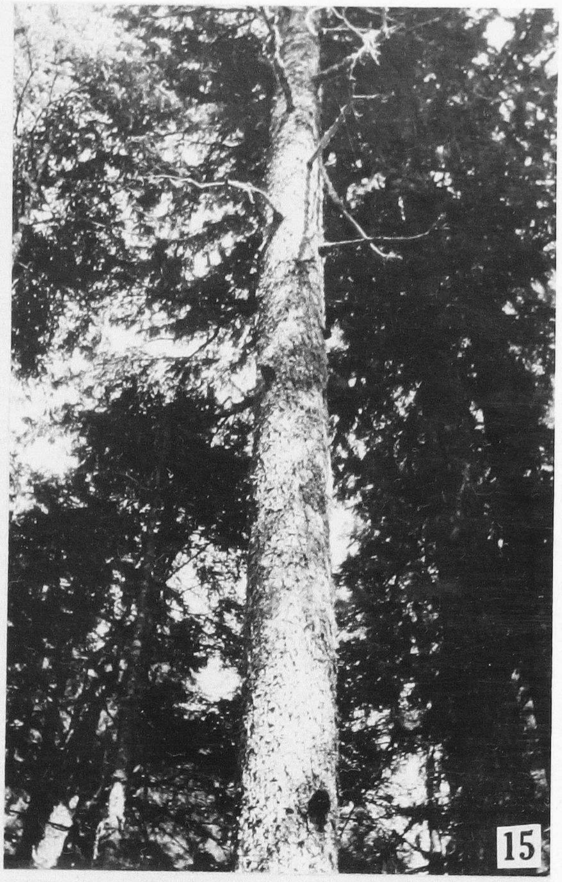
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it can produce a new hymenium that normally covers the lower surface completely. The fruit body has been described by Weir and Hubert (42) as follows:

> "The chief gross character by which the fruiting organ of the fungus may be readily recognized is a hymenium consisting of numerous, firm, thick, sharp-pointed teeth of a light brown color. The upper surface is almost black in old specimens, usually of a lighter color when young, and concentrically zoned, each zone representing a year's growth. In a growing condition the outer zone is white or brown, context solid and of a Mars-orange to orange-rufous color. The minute characteristics of the fruiting organ are; spores hyaline, broadly ellipsoid, 4 x 6 u; teeth covered with colorless setae or with microscopic spines; the hymenium of the young growing fungus is by no means toothed in the beginning but is typically daedaloid."

After a few years the extent to which a new hymenium is laid down varies but, in most cases, an annual reduction in the extent of the fruiting layer occurs until the fruit body is rendered functionless and drops to the ground. The spores mature throughout the summer and early fall, one crop being formed for each hymenium laid down. They are liberated into the air to initiate new infections.

Suscepts and Geographic Distribution

E. tinctorium was first reported from Alaska on *Tsuga* sp. (14) and next on *Abies grandis* (Dougl.) Lindl. (grand fir) in Idaho (26). The first authentic report of its occurrence upon *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) was that of Hedgcock (19) who at the same time reported its occurrence on *Abies amabilis* (Dougl.) Forb. (amabilis fir), *A. arizonica* Merr. (corkbark fir), *A. concolor* Lindl. & Gord. (white fir), *A. lasiocarpa* (Hook.) Nutt. (alpine fir), *A. magnifica* A. Murr. (red fir), *A. nobilis* Lindl. (noble fir), *Picea engelmanni* Parry (Engelmann spruce), and *Pseudotsuga taxifolia* (Poir.)

Britton (Douglas fir)[1]. Weir and Hubert (42) report it additionally on *Abies venusta* (Dougl.) Koch. (bristlecone fir) and on *Tsuga mertensiana* (Dong.) Carr. (mountain hemlock) and Tannhauser (38) has reported it on *Picea glauca* (Moench) Voss var. *albertiana* (S. Brown) Sarg. (western white spruce), thus completing, to the author's knowledge, the current known host range of the fungus for North America. It appears, therefore, that of the commercial coniferous tree species native to British Columbia, species of *Chamaecyparis*, *Thuja*, *Larix*, *Pinus*, as well as *Picea sitchensis* (Dong.) Carr. (Sitka spruce) and *P. mariana* (Mill.) B.S.P. (black spruce) are probably not naturally susceptible to E. tinctorium infection but, if so, only to a very minor degree.

Knowledge of the geographic range of *E. tinctorium* stems from the original collections from Alaska (14) and Idaho (26) and from Hedgcock's report of its being very destructive in western hemlock and *Abies* spp. in northwestern United States (19). Meinecke reported it as being very common in California, particularly on white fir (28). Weir and Hubert (42) reported its distribution in North America as being from Alaska to northern Mexico and as far eastward as the limits of grand fir and western hemlock in Canada and Montana. Englerth (15) modified the extensive geographic range claimed for the fungus by Weir and Hubert, in so far as Oregon and Washington are concerned, in his report that the fungus occurs in those states only in the Cascade Mountain region and, then, only rarely in commercial stands. Bourchier

1. The name *Pseudotsuga taxifolia* (Poir.) Britton has been used for purposes of this report although *P. menziesii* (Mirb.) Franco is regarded by some workers as the most acceptable of the two names.

(4) has reported the fungus to occur on alpine fir in the eastern slopes of the Rocky Mountain region in Alberta.

More specific mention of its distribution in British Columbia is given in the reports of Dickson (13), Bier *et al.* (3), and Tannhauser (38) all of whom report it to be common in the upper Fraser region, north and east of Prince George. In addition, Bier (2) encountered the fungus on western hemlock and amabilis fir in north coastal forests, near Kitimat, and Browne *et al.* (7) reported it on the same species in the vicinity of Terrace. Further reports of the fungus are given by Browne (6) for its occurrence on alpine fir and Engelmann spruce in the Spa Hills, near Vernon, by Foster *et al.* (17) for western hemlock in the upper Columbia region, by Foster and Thomas (16) for an isolated occurrence of it on western hemlock on Vancouver Island, and by Ziller and Molnar (44) for its occurrence generally throughout south coastal and south central interior forests.

Susceptibility and Damage

Most of the investigators concerned with one or other aspect of *E. tinctorium* have been able to observe apparent differences in the degree of susceptibility to the fungus that is expressed by its different hosts. In this respect Etheridge (27) made a number of laboratory tests to determine the relative susceptibilities of different woods to attack. His experiments included growing the fungus on media, to which had been added water-soluble extractives of heartwood and sapwood of several different tree species, and exposing wood blocks of the same species to vegetative activity of the fungus. On the basis of these tests he indicated a range of decreasing susceptibility as follows: amabilis fir[1], grand fir, western hemlock, Douglas fir, balsam fir (*Abies balsamea* (L.) Mill.), western red cedar, and Sitka spruce. He observed also that the fungus grew better when water-soluble extractives of heartwood and sapwood of amabilis fir[1], grand fir, western hemlock, and Douglas fir were added to the growing media than without. On the other hand, similar extractives from western red cedar, Sitka spruce, and balsam fir supported only reduced growth of *E. tinctorium* on media to which they had been added.

Early accounts of the destructiveness of the fungus in white fir in California were given by Meinecke (28, 29) who concluded that, in this host it was important almost to the exclusion of other fungi. Weir and Hubert (42) reported a similar situation in the case of western hemlock in the Priest River drainage of Idaho. On the other hand, Englerth (15) found that decay losses in western hemlock resulting from *E. tinctorium* were low in western Oregon and Washington.

Concerning the destructive nature of the fungus in stands under British Columbia conditions, Dickson (13), Bier *et al.* (3), and Tannhauser (38) revealed that losses in stands of *Abies* spp. and western white spruce in the upper Fraser region are generally high but that losses in even-aged stands may be expected to be somewhat less than those in uneven-aged stands. Dickson attributed most of the decay to *E. tinctorium* in his study of decay in *Abies* sp. near Prince George

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1. It is the author's contention that Mayers intended to indicate alpine fir rather than amabilis fir in as much as the wood samples provided to him for the purposes of these tests were gathered in an area in which amabilis fir does not occur.

whereas Bier *et al.* and Tannhauser, working in the same general region, found much of the decay to be caused by *Stereum sanguinolentum*. The predominance of *S. sanguinolentum* encountered by Bier *et al.* led them to speculate that much of the decay in this region that is normally attributed to *E. tinctorium* must in fact be ascribed to the former fungus. In the case of spruce, Tannhauser (38) found *E. tinctorium* to be uncommon in western white spruce in the upper Fraser region and when present in this suscept to occur almost invariably as the cause of butt rot. On the other hand, Browne (6) found the fungus to be common in stands of Engelmann spruce near Vernon in the Spa Hills. In such instances the fungus occurred characteristically as the cause of trunk rot. Browne reported that 10 per cent of the decay in spruce and about 75 per cent of that in alpine fir in the Spa Hills was caused by *E. tinctorium*. Stands of western hemlock and amabilis fir were examined near Terrace by Browne *et al.* (7) who observed the fungus in both species. It was reported by them to cause about 20 per cent of the decay present in hemlock and about 50 per cent of that found in amabilis fir. Foster *et al.* (17) examined stands of western hemlock in the upper Columbia region and reported a generally high, but variable, loss through E. tinctorium decay. The loss recorded by them for different stands ranged from 39 per cent to 74 per cent of the gross volume of hemlock.

The significance of the abundance and size of E. tinctorium fruit bodies has been assessed by a number of investigators. In this regard, Weir (40) found that the fruit bodies on living branches of western hemlock and grand fir in Idaho and Montana could be taken as evidence that most of the heartwood of such trees had been destroyed. Weir and Hubert (42) regarded the occurrence of single fruit bodies on the trunks of western hemlocks and grand firs to be indicative of extensive decay. The same investigators found that when several fruit bodies occurred on a single tree the largest fruit body of the group invariably indicated the area of greatest decay. They found also that the absence of fruit bodies is no criterion of soundness in a tree and that such trees frequently represent cases where fruit bodies have fallen away, the former locations of fruit bodies on them being indicated by discolored bark or by holes left by rotted branches. Dickson (13), in his study of decay in *Abies* sp. found that 25 per cent of the infected trees on his plots bore fruit bodies and that there was a tendency for badly decayed trees to occur in groups with one or more of the group bearing fruit bodies. On the other hand, Bier *et al.* (3) found in the same region as that studied by Dickson that *E. tinctorium* produced fruit bodies in nearly all cases of infection and that many of the trees examined by them that lacked fruit bodies were, in fact, decayed by *Stereum sanguinolentum* and not by *E. tinctorium*.

Factors Influencing the Occurrence of *E. tinctorium*

Meinecke considered suppression to be an important factor in the early establishment of decay and recognized, in the course of an investigation of the pathology of white fir in California (29), three important stages in the life history of this host. The first stage was the age of infection which he placed at 60 years or less. Such trees, unless severely wounded, were found by him to contain negligible amounts of decay. The second stage, the critical stage, was placed at about 130 years and corresponded to a stage after which a combination of pronounced suppression and heavy wounding generally results in serious decay. At this stage, however, wounding alone was found insufficient to counteract thriftiness of growth. The third stage, the "age of decline", was placed at about 150 years and corresponded to a time when even dominant trees were subject to serious decay. Although he regarded suppression as a major factor promoting E. tinctorium decay, Meinecke concluded that decay itself was not responsible for decreased thriftiness of infected trees. Weir and Hubert also stressed the importance of suppression to the establishment of _E. tinctorium_ and, on the basis of observations made of river-bottom stands of hemlock and grand fir in Idaho (42), they formulated a theory of infection with respect to these suscepts. Their theory holds that low vigor, due to overshading of the lower crown and sometimes entire trees, causes the early and numerous formation of shade-killed branches which, in turn, produce the branch stubs which they believed to be responsible for most E. tinctorium infections. The over-shading of the crown, in addition to hastening the formation of branch stubs, was believed by them to create a shade and moisture condition favorable to germination of spores and entrance of the fungus. An adjunct to the conclusions of Weir and Hubert were those of Englerth (15) who stated that E. tinctorium decay in western Oregon and Washington is confined to small trees of low vigor and that poor sites, or badly suppressed trees on good sites, are necessary prerequisites to most infections by this fungus. Bier commented on the conditions that appeared to promote decay in stands of western hemlock and amabilis fir near Kitimat (2), stating that early suppression whereby branch stubs require a longer than normal time to heal, in addition to the killing of branches and tops of trees by dwarf mistletoes (*Arceuthobium* spp.), and the occurrence of scars, frost cracks, and snow breaks, all combined to promote conditions favorable to decay entrance.

Weir and Hubert attempted to extend the results of their study of hemlock at Priest River by interpreting the results of a questionnaire sent by them to foresters and other woodsmen throughout Pacific northwestern United States. Thus, they concluded (42) that *E. tinctorium* may occur on hemlock growing on any type of soil but that it occurs most abundantly on trees growing on wet, undrained sites. The least defective stands were believed to occur on well-drained soils, at upper elevations, and on slopes, whereas the most defective stands were believed to occur on poorly-drained soils, at lower elevations, and on river-bottom lands. As regards the effect of altitude upon the fungus, Weir reported (41) that it follows its suscepts to their absolute upper limits of elevation and that up to about 5000 feet the fruit bodies of this fungus are similar in habit and size but that beyond 5000 feet the fruit bodies are smaller and grow lower on their suscepts. Foster *et al.* (17) reported a situation in stands of western hemlock in the upper Columbia region that is in contrast with that reported by Weir and Hubert for Priest River. These investigators found a marked trend of increasing incidence and importance of *E. tinctorium* in the upper Columbia region that was coincident with decreasing site quality.

The significance of the fungus in young stands and young trees of uneven-aged stands has been commented upon by several investigators for a number of different suscepts. In the case of white fir in California, Meinecke (29) found that infections occurred at 60 years or less although such early infections were most commonly associated with severe wounds, principally those caused by fire. Hedgcock (19) expressed the opinion that E. tinctorium occurs in hemlock and fir (Abies spp.) almost to the exclusion of other heart-rotting fungi by reason of the establishment of it earlier in the life of its suscepts than most other heart-rotting fungi. Weir and Hubert (42) observed a difference in the probable ages of earliest infection in the case of western hemlock growing on river-bottom sites as opposed to stands growing on slopes, the former occurring at 44 years and the latter at 57 years. Englerth (15) made observations in western Oregon and Washington of the ages of the youngest trees infected by E. tinctorium according to the type of infection court associated with each infection. He found that of 44 infections examined the youngest infected tree was 78 years old and that, in general, falling-tree scars were associated with the earliest infections. Dickson (13) determined the probable infection age of Abies sp. in the upper Fraser region to be 115 years, whereas Bier et al. (3), working in uneven-aged stands of the same species in the same region, determined the age of earliest infection to be less than 75 years. Foster et al. (17) found E. tinctorium to be the primary fungus responsible for decay in both immature and mature stands of hemlock in the upper Columbia region and that infections had taken place in some of the trees examined by them at ages of less than 75 years.

In discussing the factors that promote the development of *E. tinctorium* Meinecke (29) commented that, in as much as there must be an optimum, maximum, and minimum percentage of water and air in the cells of heartwood for the development of the fungus, any factor influencing the quota of water and air in the heartwood must be of importance. Thus, he concluded that the admission of air and the evaporation of water via injuries of the nature of fire, frost, lightning, wind, and broken branches are intimately connected with the progress of decay. He concluded, on the basis of an analysis of the probable methods of entrance of *E. tinctorium* into white fir, that fire wounds are the most common and that, as a consequence, decay starts most often in the butts of white fir. Weir and Hubert (42), on the other hand, found in the case of western hemlock and grand fir in Idaho that fire played a very minor role in the establishment of *E. tinctorium* and that by far the greatest percentage of infections was traceable to branch stubs. Meinecke considered frost cracks to be a less important mode of entry than fire wounds but that they functioned later as an important means of rapid vertical spread of the decay from the butt. A similar opinion as to the significance of frost cracks in amabilis fir in the upper Fraser region was expressed by Dickson (13). Hubert (23), commenting upon the longevity of the fungus in its vegetative phase within western hemlock, stated that it will remain alive, although inactive, in lumber stored in the air-dry conditions of a room for more than five years.

Weir and Hubert (43) commented upon the effects of the aerial environment upon the welfare of *E. tinctorium* in its fruiting stage and drew conclusions from observations made of the number and condition of fruit bodies in thinned and uncut stands of hemlock and grand fir in Idaho. They observed in the case of both species that the exposure of trees to drying conditions, such as were obtained in the thinned stands, resulted in the drying out of fruit bodies and retarded the formation of new ones.

EVALUATION OF PREVIOUS INVESTIGATIONS

The most informative and conclusive aspects of the many studies of *E. tinctorium* that were carried out prior to this investigation appear to be an appreciation of its life cycle, its range of natural suscepts, and its ability to cause excessive damage. Although several investigators have made some reference to the conditions in nature under which the fungus exists, there has been no concerted attempt to bring the salient biological properties of the fungus and its suscepts together with the conditions of their habitats. The net result has been our inability to predict the occurrence and abundance of *E. tinctorium* in the light of different suscepts, stands, and localities. Clarification of the ecology of the fungus, being predicated upon knowledge of its suscepts and the forest conditions that support its occurrence, necessitates careful documentation of data contributory to these ends. Perhaps the most outstanding limitation placed upon the usefulness of previous investigations in this regard has been the incomplete and generalized nature of the descriptions afforded the habitats of the fungus and its suscepts. Thus, it is either difficult or impossible to identify many of the earlier observations made of the fungus, in respect of its occurrence and behaviour in nature, with the precise conditions under which the fungus existed at the time and place such observations were made. The degree of variation in the abundance of E. *tinctorium* that appears to occur over very short distances, together with the strong possibility that such variations result from differences between forest conditions, lends emphasis to the necessity of recognising and describing separately the various forest conditions under which the fungus is found. This has not been accomplished by previous investigators with the result that their observations and measurements were neither segregated initially nor finally reassembled upon an equitable basis. Without the provision of appropriate categories within which to assemble observations pertinent to the fungus it has been impossible for previous investigators to assess its capabilities and behaviour to the degree which an adequate understanding of it requires.

In connection with the status of knowledge of E. *tinctorium* as it occurs in British Columbia, it is evident that consideration of its biological requirements has been, to a large degree, incidental to surveys of the purely economic aspects of its decay. Subjugation of biological considerations to those of an economic nature, such as has been done in the case of this fungus by most investigators, has provided an uncertain basis upon which to evaluate the fungus effectively. Consequently, our observations of the fungus, being thus tied to surveys of decay, have been confined for the most part to suscepts, stands, and localities that have entered into the pattern of forest utilization that has prevailed up to the present time. The result has been that the occurrence and destructive capabilities of *E. tinctorium* in British Columbia have been investigated in relatively few areas and, in most cases, to only a very minor degree.

THE OCCURRENCE OF *ECHINODONTIUM TINCTORIUM* IN BRITISH COLUMBIA

General

Abandonment of the concept of regional importance as regards *E. tinctorium* in British Columbia became necessary when both inter- and intra-regional variation in the occurrence and abundance of the fungus became evident. Since no strict geographic limits were indicated for the fungus it was judged appropriate to assess it on the basis of its occurrence under different conditions of forest growth. Such an assessment would be tantamount to demonstrating the complete ecology of the fungus. In the case of *E. tinctorium*, where some essentials of its life cycle were already known, it was considered possible to expand our existing knowledge of some of the ecological aspects of its life history *in lieu* of a more complete study of its life history and yet satisfy the objectives of this investigation. In the event that the selected approach to an understanding of the fungus should prove inadequate it was recognised that a more diverse approach, such as that advocated by Cooke (9), could subsequently be employed.

Acceptance of a limited study of the ecological life history of *E. tinctorium* as being adequate for the purposes of this study demanded recognition of alternatives and priorities as to the actual conduct of the investigation. The two apparent courses open for investigation were either consideration of the aerial environment of the fungus or consideration of the characteristics of its suscepts and, of the two, the former appeared to offer the most expedient starting point. Despite an indicated range in host susceptibility (27), justification for giving primary emphasis to a consideration of the influences of the aerial environment was obtained in the knowledge that such factors exert a direct influence upon the fungus at several critical periods in its life cycle. On the other hand, superimposed over a profusion of potential host influences was the complication of a diversity of suscepts. Thus, it was decided that, in the interim at least, observations of the behaviour of _E. tinctorium_ should be directed towards the influences of its aerial environments.

Distribution and Habitats

General

The decision to investigate the occurrence of _E. tinctorium_ primarily on the basis of specific conditions of forest growth and, secondarily, on the basis of the influences of aerial environments required the segregation of forest cover into discrete and recognizable units of vegetation. It has been indicated that a major limitation placed upon the usefulness of previous investigations has been the incomplete and generalized nature of the descriptions afforded the habitats of _E. tinctorium_ and its suscepts. The single most important reason, of the many that contributed to this situation, seems to lie in the bases used for segregating forest cover into units whereby observations were categorized and later compared. In many instances the basis of forest classification used was essentially mathematical and yielded the investigator, therefore, vegetational units that had little or no bearing upon biological considerations. In other instances the basis was limited, to the extent of including only one or a few habitat characteristics. Such classifications yielded vegetational units that were too general in their scope and which, therefore, could not appreciate many of the environmental changes that occur from one habitat to the next. Consequently, it was evident that consideration should be given to selecting a basis for forest classification that would yield units of forest cover that could be regarded as natural units.

Several systems of forest classification have been developed and used effectively in different phases of forest investigation. The success of each system is unquestioned when each is employed under the circumstances for which it was designed. Misapplication of these systems, on the other hand, has been common practice and has served in some instances to confound investigations based on the forest units they yield, rather than to elucidate them. Such could be the case with climatic-geographic systems as developed by Weaver and Clements (39) and employed by Halliday (18) to describe Canadian forests. Climatic-geographic systems were rejected for the purpose of this investigation for the reason that such systems employ as their fundamental unit of classification a "formation", which is intended to represent vegetation that is in balance with the macro-climate of arbitrary geographic regions. The subordinate units of classification of such systems are intended to express intra-regional differences of macro-climate and, as such, have little application to specific stands or localities. Typological systems represent a group of forest classification systems that vary from those that are based mainly upon edaphic considerations, such as the system of Hills

(20,21), to those that are based on climatic, edaphic, and vegetative conditions but which place their greatest stress upon the significance of one or other consideration, such as the classifications of Cajander (8) and Spilsbury (37). Such systems permit undue reliance being placed upon the value of a particular factor and, also, do not provide the descriptive detail considered necessary to this investigation. Autoecological systems, such as that employed by Cowles (10), regard vegetation as having a constantly changing floristic structure as opposed to the occurrence of vegetative units that are in balance with their environments. Such systems, by failing to recognise any degree of stability of vegetative units, were judged unsuited to the purpose of this study. Mechanical systems of classifying forests, although in constant use in North American forestry, provide neither the necessary description of forest conditions nor do they recognize distinct boundaries between contiguous forest habitats and were, therefore, rejected as a method of stand description.

Ecological or floro-ecological systems, such as that employed by Braun-Blanquet (5) and particularly those of Daubenmire (11) and Oosting (32), appeared to be the best suited of all systems to the purpose of this investigation. Such systems, which utilise an "association" as the fundamental unit of classification, recognise and define their units on the basis of their specific ecotopes, i.e., the characteristics of their vegetative, atmospheric, edaphic, and topographic environments. The vegetative environment of the association is defined on the basis of its constancy with respect to the occurrence, abundance, dominance and vigor of the plants, including trees, of which it is composed. The unit of classification of such systems is, therefore, a natural unit of vegetation that is expressed by its constant floristic structure and which itself

Explanation of Figure 18

__Elevation:__ measured in feet above mean sea level

__Exp.:__ exposure, measured by compass as a cardinal direction

__Slope:__ measured by Abney level in degrees

__Wind:__ wind influence, estimated as to degree of exposure to the maximum wind influence of the area, viz., O, +, ++, !, and !!, indicating increasing exposure to wind

__Snow:__ estimated duration, in months, of continuous snow cover

__Layer:__ A 1 = dominant and co-dominant trees
A 2 = intermediate trees
B 1 = overtopped trees and shrubs taller than six feet
B 2 = overtopped trees and shrubs less than six feet
C = herbs
D = mosses and lichens

__Estimate:__

__abundance and dominance__

+ =solitary
1 =scattered
2 =up to 1/5 of area
3 = 1/5 to 1/2 of area
4 = 1/2 to 3/4 of area
5 = 3/4 to entire area

__sociability__

+= solitary
1= colonies up to one square foot
2= colonies up to one square yard
3= colonies up to 5 square yards
4= colonies up to 100 square yards
5= colonies up to 500 square yards

__vigor__

0 = dead or impending mortality
1 = low vigor
2 = intermediate vigor
3 + maximum vigor for the region

__Soil:__ Ao = humus layer including the litter
A1 = melanized horizon
A2 = podsol horizon
B = enriched horizon
C = parent material
D = gled horizon

__Frequency:__ frequency of __E. tinctorium__ as indicated by the incidence of fruit bodies

$\boxed{X}$ = abundant

$\overline{\underline{X}|}$ = common

$\overline{X|}$ = infrequent

$\overline{X}$ = rare

Habitat Tsuga heterophylla-Dryopteris linnaeana-Aralia nudicaulis-Clintonia uniflora-Cornus canadensis.

Location Falls Creek, west of Taghum and Nelson. **Date** 8.9.55 **Plot** 134

Elevation 4900 **Exp.** W **Slope** 5-20 **Wind** ++-I **Snow** 6-7

Layer	Species	Estimate	Layer	Species	Estimate
A 1	T.heterophylla	3.+.2-3	B 2	T.heterophylla	1-2.+.1
	P.taxifolia	1.+.2-0		T.plicata	2.+.1
	P.engelmanni	1-2.+.2-3		A.lasiocarpa	2.+.1-2
	T.plicata	1-2.+.2		M.ferruginea	1.+-3.2-3
	A.lasiocarpa	1.+.2		L.utahensis	1.+-2.2
	P.monticola	+.+.2-0		etc.	
A 2	T.heterophylla	2.+.2	C	D.linnaeana	3-4.2-4.3
	T.plicata	1-2.+.2		A.filix-femina	2.+-3.2
	A.lasiocarpa	1-2.+.2		C.uniflora	2.+-3.2-3
	P.engelmanni	1.+.1-2		etc.	
B 1	T.heterophylla	3.+.1-2	D	M.punctatum	2-3.1-3.2
	T.plicata	2.+.1-2		M.spinulosum	1-2.1-2.3
	P.engelmanni	1.+.1		M.insigne	1-2.1-2.2
	A.lasiocarpa	2-3.+.2		R.triquetrus	2.1-2.2-3
	A.glabrum	1.+-3.2		etc.	
	S.sitchensis	1.+.2			

A o	**Depth** 3 ins. **Litter** 1/4 in. **Humus Type** thin raw over duff mull
A 1	variable up to 5 ins.
A 2	discontinuous-in pockets
B	**Depth** up to 34 ins. **Color** rusty to yellowish **Texture** sand and gravel loam plus stones **Structure** granular to aggregated to compacted
C	glacial drift
D	absent
Depth Fine Soil- at least 36 in.	
Drainage- generally good	
Moisture- entire profile moist	
Soil Type- podsolized brown	

Host	Crown Class and Frequency	
T.heterophylla	A 1	X-X
	A 2	X
	B 1	X

Remarks the ground line aspect was dry at the time of examination. This stand occupies an upper slope. The area is wind-exposed and seasonally dry, particularly partially-cut stands.

Figure 18. Sample of method used to record field observations upon which suscept and fungous habitat descriptions were based.

settled stage of maturity and, on this basis, were considered to reflect adequately the products of the operative factors of individual habitats.

Although many isolated occurrences of E. tinctorium were encountered, it finally became apparent that such occurrences should not be interpreted as indicative of the fungus having a broad ecological tolerance but, rather, that they should be regarded as being coincident with isolated occurrences of precise habitats that are exemplified in other and more extensive areas of infection. Hence it became evident that the extensive geographic range of this fungus was not necessarily synonymous with an extensive ecological tolerance. On the contrary, it became evident that E. tinctorium suscepts have a much wider ecological tolerance than does the fungus itself.

In the light of a conviction that E. tinctorium has a restricted ecological tolerance from that of its suscepts, a limitation in the extent to which habitat determinations of its suscepts need be made appeared justified. Consequently, it resulted that centres of E. tinctorium infection became the major foci for habitat determinations and, in addition, it was from such foci that habitat determinations were made of conditions that did not favour the occurrence of the fungus. In several instances, however, it was necessary to describe host habitats in areas where E. tinctorium could not be found in order that certain of the habitat determinations could be verified and their descriptions augmented. The province was sampled within the limits indicated above with the exception of its most northerly regions. While it is recognised that all forest associations embodying one or more E. tinctorium suscepts have not been determined for the regions examined, it is believed that most of those that support the occurrence of this fungus have been recorded. Furthermore, it is believed that, of the associations that do not support the occurrence of E. *tinctorium* sufficient of them have been determined and described to permit an adequate evaluation of the factors that operate for and against the welfare of this fungus.

Certain of the 53 associations and sub-associations recognized in the course of this investigation were determined by previous investigators (24,25,33,34,35) while others were determined by the author[1]. Regardless of the origin of its determination, however, each association was verified by the author to his own satisfaction before its acceptance. Modifications to original determinations were sometimes required in addition to the derivation of new associations. While descriptions of all of the associations recognized in the course of the investigation have not been included in this report, 40 of them have been described in some detail in later sections. The associations that have been described correspond to those in which E. *tinctorium* occurs. The remaining associations have been listed, together with those in which the fungus occurs, as an appendix to this report (see Appendix II) and each association so listed has been numbered to facilitate reference to it in subsequent sections of the report. The occurrence of suscepts according to the tree layers which they occupied in each of the associations and sub-associations is presented in summary form in Table I.

1. The reporting procedure employed in the Annual Report of the Forest Service, Department of Lands and Forests, Victoria, does not permit the author to cite directly the contributions of R.L. Schmidt and J.W.C. Arlidge to site-type classifications in coast and interior forests respectively.

TABLE I. THE OCCURRENCE OF E. TINCTORIUM SUSCEPTS WITHIN CERTAIN FOREST ASSOCIATIONS IN BRITISH COLUMBIA FORESTS

Tree layer	Occurrence (association number)
	Western hemlock
A 1	1,2,3,5,6,8-16(sub-assoc.),18-21,29-35,38-42
A 2	1-22,29-43
B 1	1-22,26,27,29-43,45-48
B 2	1-22,26,27,29-43,45-48
	Mountain hemlock
A 1	16,17
A 2	16,17,19,19(sub-assoc.)
B 1	16,17,19,19(sub-assoc.),24,26,27
B 2	16,17,19,19(sub-assoc.),24,26,27
	Grand fir
A 1	1,2-5,32,34
A 2	1,2,3,5,32,34
B 1	1,2,3,7,32,34
B 2	2,3,5,7,32,34
	Amabilis fir
A 1	1(sub-assoc.),12-19,20,21,38-41
A 2	1(sub-assoc.),9-22,38-41
B 1	1(sub-assoc.),8-23,26,38-42
B 2	1(sub-assoc.),8-23,26,38-42
	Alpine fir
A 1	19(sub-assoc.),23-31,35-37,44-48
A 2	19(sub-assoc.),23-31,33,35-37,44-48
B 1	19(sub-assoc.),23-31,33,35-37,44-48
B 2	19(sub-assoc.),23-31,33,35-37,44-48
	Douglas fir
A 1	1,3-16,18-22,29,31-35,45,46,47(sub-assoc.)
A 2	3,5-7,9,11,21,22,32-35,45,47(sub-assoc.)
B 1	6,7,11,22,32-35,47(sub-assoc.)
B 2	7,19,22,32-34
	Western white spruce
A 1	44-48
A 2	44-48
B 1	44-48
B 2	44-48
	Engelmann spruce
A 1	18-19(sub-assoc.),22-34,36,37
A 2	18,19(sub-assoc.),22-34,36,37
B 1	18,23-34,36,37
B 2	18,23-32,34,36,37

E. tinctorium distribution and habitats.

Sufficient records of the occurrence of E. tinctorium in Pacific northwestern United States and British Columbia have resulted from previous investigations to indicate a fairly general distribution for the fungus. The distribution so indicated was, however, based largely upon the results of a limited number of investigations of a local nature. Consequently, the occurrence of the fungus on similar suscepts in areas other than those specifically examined has been largely a matter of speculation. The outstanding deficiency of such an evaluation of the distribution of E. tinctorium lies in the failure of previous investigations to demonstrate the requisite conditions for the fungus to occur and, also, the means whereby such conditions may be recognised in nature.

The current investigation has endeavoured to correct this deficiency by defining suscept habitats and recording their occurrence in the province and, at the same time, associating with each habitat either the presence or absence of the fungus. As the result of this procedure 40 of 53 suscept habitats were found to support growth of the fungus to some or other degree. The fungus was not observed in the remaining 13 habitats despite a diligent search for it and despite the fact that the 13 habitats in question normally occur in close proximity to those in which the fungus regularly occurs. The ecotopes specific to each habitat in which E. tinctorium was found are described in Appendix III. The authorities for the naming of individual plants in the descriptions of specific ecotopes are given in Appendix I. Those habitats in which the fungus was most abundant are illustrated in Plates V-XI.

PLATE V, Figures 19 - 22

PLATE V. E. tinctorium Habitats Common to Coast Forests.

Figure 19. Association number 8. E. tinctorium occurs in this association with fair regularity but in low frequency. Its occurrence is confined to trees of the lower canopies or to the butt region of trees of higher canopies. Stands of this association frequently occupy the margins of stagnant lakes.

Figure 20. Association number 13. E. tinctorium occurs regularly in this association except in stands of the western slope of Vancouver Island. It occurs characteristically in the upper half of the bole of dominant and co-dominant trees.

Figure 21. Association number 14. E. tinctorium occurs regularly in this association but mainly on dominant and co-dominant amabilis firs. Such trees normally occur with reduced vigor in this association.

Figure 22. Association number 16. E. tinctorium is most abundant in the coast region in this association. Stands of association number 16 regularly occur on well drained upper slopes, as illustrated, at elevations of from 1600 to 3800 feet above sea level.


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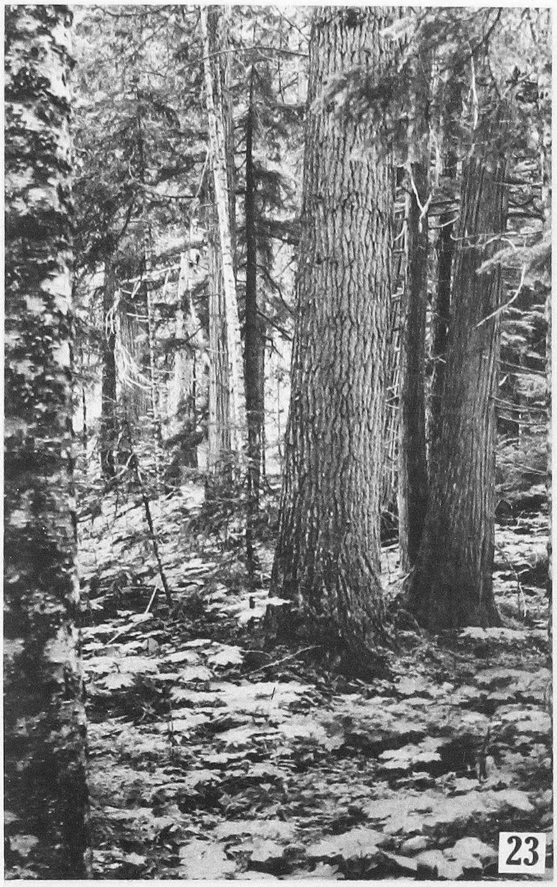
PLATE VI, Figures 23 - 26

PLATE VI. *E. tinctorium Habitats Common to the Cascade Mountains Region.*

Figure 23. *Association number 18.* Stands of this association are often fragmentary. They regularly border and occupy the confluence of mountain streams. *E. tinctorium* occurs regularly in this association but with a lesser frequency than in adjoining associations.

Figure 24. *Association number 19.* Stands of this association represent maximum conditions for E. tinctorium infection in western hemlock for the Cascade region.

Figures 25 and 26. *Association number 20.* Stands of this association represent maximum conditions for E. tinctorium infection in amabilis fir for the Cascade region.


23


24


25

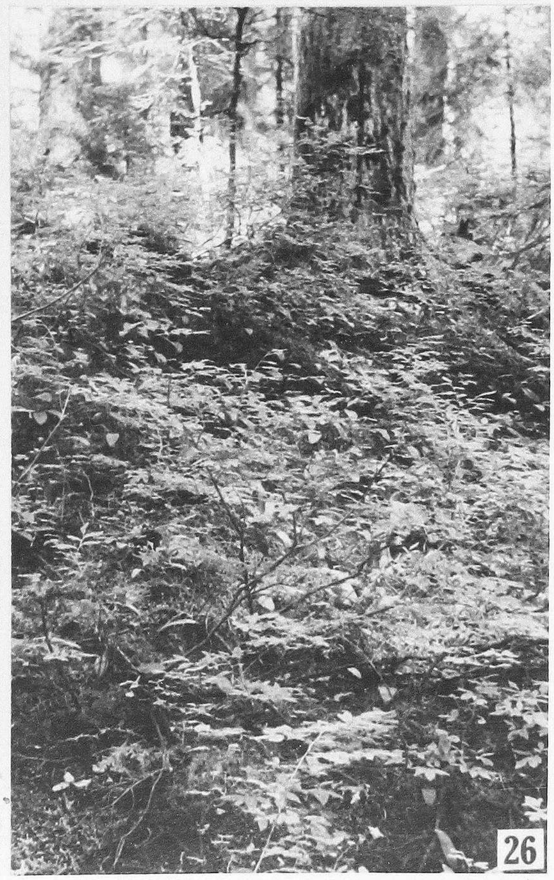

26

PLATE VII, Figures 27 - 30

PLATE VII. _E. tinctorium Habitats Common to the Sub-alpine Forests of the Cascade Mountains and Southern Interior._

Figure 27. _Association number 23._ _E. tinctorium_ occurs regularly in this association on alpine fir. It normally fruits higher above ground in this association than it does in adjacent associations.

Figure 28. _Association number 24._ Stands of this association represent maximum conditions for E. tinctorium infection for the region.

Figure 29. _Association number 25._ _E. tinctorium_ is confined usually to a fairly shallow stratum above the ground line in stands of this association.

Figure 30. _Association number 26._ Stands of this association are usually damaged less by _E. tinctorium_ than are those of association number 24. Infections occur closer to the ground in this association, although in about the same frequency, than they do in stands of association number 24.


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PLATE VIII, Figures 31 - 34

PLATE VIII. _E. tinctorium Habitats Common to the Monashee and Selkirk Mountains Region._

Figure 31. _Association number 29._ _E. tinctorium_ occurs in stands of this association mainly in the upper half of the stem length of dominant and co-dominant trees. It has a high frequency only in very old stands.

Figure 32. _Association number 31._ _E. tinctorium_ occurs with greater frequency in young stands of this association than in those of comparable ages of association number 29, although even in this association the fungus has a high frequency only in older stands.

Figures 33 and 34. _Association number 33._ _E. tinctorium_ reaches its maximum development for the region in stands of this association. It occurs regularly on western hemlock in all canopies.


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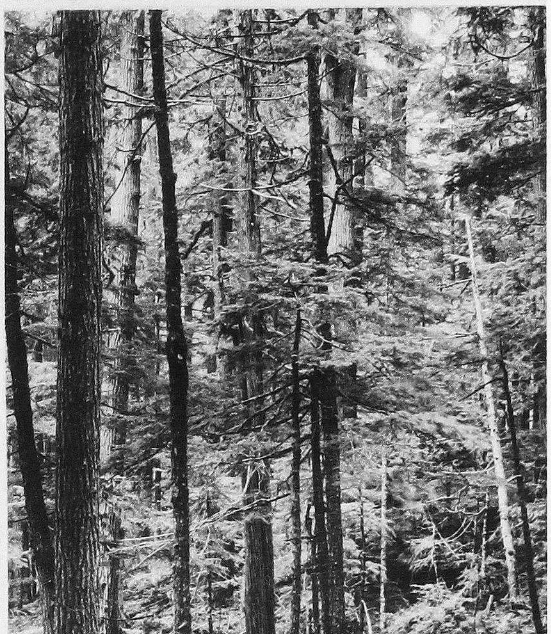
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PLATE IX, Figures 35 - 38

PLATE IX. E. tinctorium Habitats Common to the Central Interior Plateau Region.

Figure 35. Association number 45. E. tinctorium has, in general, a lesser frequency in stands of this association than in some adjacent associations but its occurrence higher on trees of this association results usually in heavy losses.

Figure 36. Association number 46. The eco-climate characteristic of stands of this association is less conducive to Echinodontium infection than are those of associations number 45 and 47, being seasonally dry and hot for most of the stem length of trees.

Figure 37. Association number 47 (sub-association). Stands of this sub-association are infected by E. tinctorium somewhat less than are those of the association proper. Association number 47 is the most seriously damaged association for the region.

Figure 38. Association number 48. E. tinctorium has its highest frequency for the region in stands of this association but is less damaging than in most of the adjacent associations. It occurs in this association only at heights up to about those of the shrub layer.

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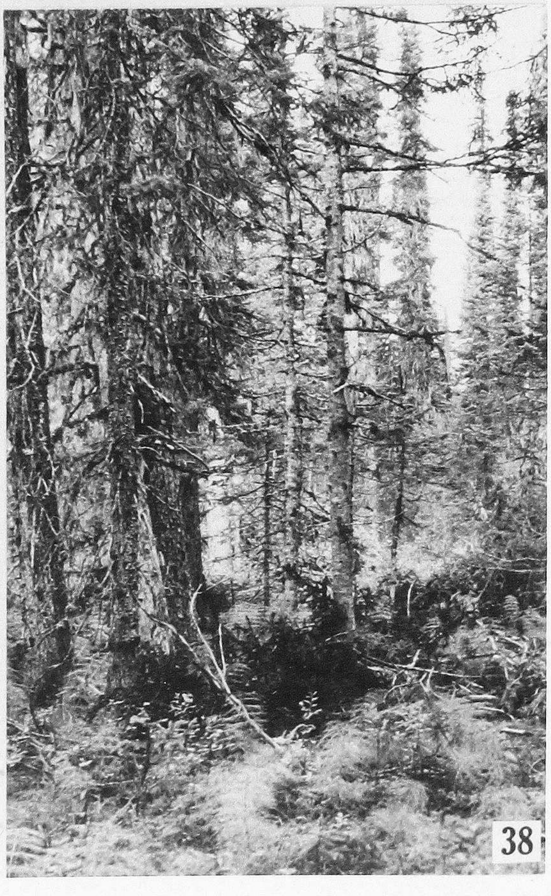

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PLATE X, Figure 39

PLATE X. An E. tinctorium Habitat Common to the Central and Northern Cascade Mountains Region.

Figure 39. Association number 22. This association, together with its sub-association, provides maximum conditions for E. tinctorium development for the region. The stand illustrated represents a stage of stand development in which very old western hemlocks are being replaced by old, but smaller-sized, amabilis firs. Stands that are older than the one illustrated have a much higher frequency of large-sized amabilis firs that are, in general, younger than western hemlocks of the same size.

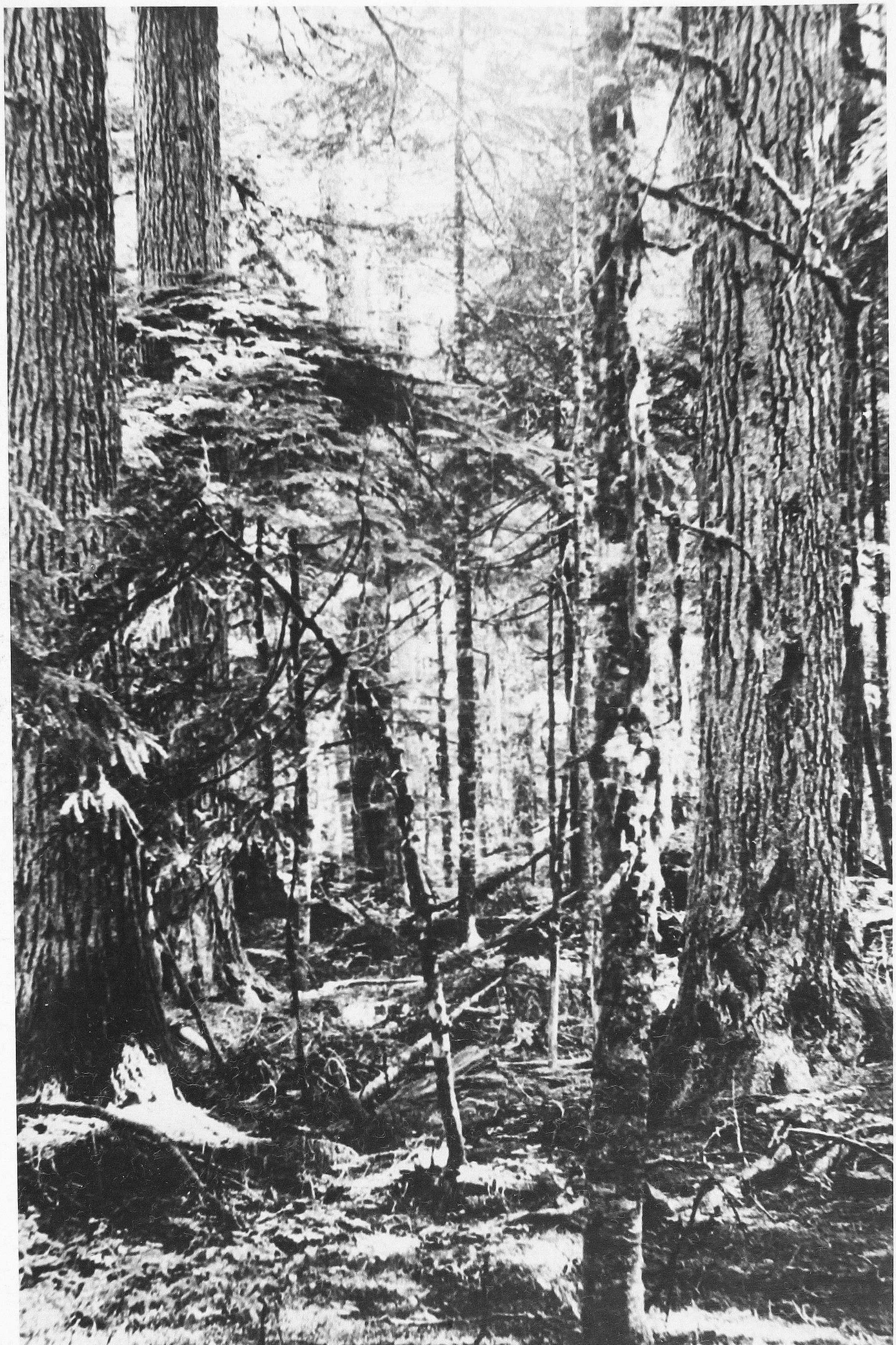

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PLATE XI, Figure 40

PLATE XI. <u>An E. tinctorium Habitat Common to the Central and Northern Cascade Mountains Region</u>.

Figure 40. <u>Association number 41</u>. Stands of this association represent conditions that are, in general, less conducive to E. tinctorium infection than are those of association number 40. Summer temperatures in stands of this association are lower than those requisite to maximum infection for the region. Certain of the frequencies of infection obtained by E. <u>tinctorium</u> in association number 40 are replaced in this association by Fomes pini infections (<u>F. pini</u> (Thore) Lloyd) in the case of western hemlock and by infections associated with a species of <u>Hericium</u> in the case of amabilis fir.


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On the basis of the regular occurrence of the fungus in certain habitats and its absence from others it would appear that the fungus has a definite distribution pattern despite its extensive geographic distribution. With sufficient evidence on hand to demonstrate that the fungus has an ecologic tolerance much restricted from those indicated for its different hosts it becomes entirely incorrect to assume a greater distribution for the fungus than it may appear to have. On the other hand, it is equally incorrect to assume that the fungus does not occur in a region until it has also been demonstrated that at least none of the habitats described in Appendix III occur in that region. This feature of the distribution of E. tinctorium is illustrated by a consideration of the lower coast region of British Columbia in which the fungus was at one time believed to be either absent or extremely rare. The present investigation has demonstrated that its suscept habitats occur regularly throughout the region and that wherever certain of them are found the fungus will invariably occur. Thus it has been found that, of 19 suscept habitats defined for the lower coast forest, E. tinctorium occurs in 10 of them.

A definite distribution pattern is indicated for the fungus not only by its occurrence in some habitats and its absence from others but, also, by the manner of its occurrence in the different tree layers of its habitats and by the manner of its occurrence on either one or more than one of its different suscepts within individual habitats. Table II presents a summary of the occurrence of E. tinctorium on its different suscepts according to the tree layers which they occupy in individual habitats. Table II may be considered an adjunct to Table I.

TABLE II. THE OCCURRENCE OF E. TINCTORIUM WITHIN CERTAIN FOREST ASSOCIATIONS IN BRITISH COLUMBIA[1]

Tree layer	Occurrence (association number)
	on western hemlock
A 1	8,13-16(sub-assoc.),18-21,29-36,38-42
A 2	8,11,13,16,18-21,29-42
B 1	18-21,27,29-38,40-42,45,47
	on mountain hemlock
A 1	17,19,36
A 2	19,36
B 1	24,27,36
	on grand fir
A 1	32,34
A 2	32,34
B 1	32,34
	on amabilis fir
A 1	1(sub-assoc.),13-21,38-41
A 2	13-16,18-21,38-42
B 1	13-16,18-21,38-42
	on alpine fir
A 1	19(sub-assoc.),23,24,26,27,29,30,36,37,45-48
A 2	19(sub-assoc.),23,24,26,29,30,36,37,45-48
B 1	23-26,29,30,36,37,45-48
	on Douglas fir
A 1	14
A 2	absent
B 1	absent
	on western white spruce
A 1	absent
A 2	absent
B 1	absent
	on engelmann spruce
A 1	absent
A 2	absent
B 1	absent

1. The occurrence of the fungus was based on the occurrence of its fruit bodies.

Examination of Tables I and II throws some doubt as to the advisability of evaluating the occurrence of *E. tinctorium* on the basis of the single criterion of habitat. It is quite evident that degrees of susceptibility to E. tinctorium infection may be attached to its different suscepts depending upon not only their occurrence within specific habitats but, also, according to the circumstances under which they occur in individual habits. Thus, it has been observed that western hemlock occupies dominant and co-dominant positions in 31 of 53 host habitats but only in 22 of these has *E. tinctorium* been recorded. In the case of Douglas fir 29 of 53 habitats regularly feature this species in the dominant and co-dominant levels but only in one habitat was the fungus recorded on dominant and co-dominant trees. An even more extreme case exists in the observation that, despite the occurrence of engelmann spruce as dominant and co-dominant trees in 18 of 53 host habitats, E. tinctorium fruit bodies were not observed on this species in any of them. That *E. tinctorium* is known to infect Douglas fir, engelmann spruce, and western white spruce more frequently than is indicated by the incidence of fruit bodies has been demonstrated by isolating its decay in culture from these species. In consequence of such wide variations in the distribution pattern of the fungus within individual habitats it would appear advisable, when predicting the occurrence of this fungus, to consider each suscept habitat separately.

Frequency of *E. tinctorium*

The mere presence of *E. tinctorium* in individual stands appears to bear little relation to the consequences of its decay to the management of such stands unless the fact of its presence can be qualified on the basis of frequency of occurrence. Estimates of the importance of E. tinctorium decay in individual stands of south coast forests, for example, could be very misleading were they based only on the presence or absence of the fungus for in this region E. tinctorium appears to be of little importance other than in the case of grandis fir and, then, only under special circumstances. In other forested regions of the province a different situation exists, to the extent that several of its suscepts are seriously and consistently affected by this fungus. It appeared advisable, therefore, to recognize such inter-and intra-regional differences by attempting to evaluate the occurrence of the fungus from the aspect of the frequency of its occurrence.

Suitable measures of frequency under the circumstances of this investigation were difficult to obtain; the measure actually used was an arbitrary one. The frequency of the fungus was judged on the basis of the production of fruit bodies in stands that had reached the stage of maturity indicated in the habitat descriptions elsewhere in this report (see Appendix III). The incidence of fruiting was recorded by means of temporary plots for each of the habitats in which the fungus was encountered. Minimum samples of 100 trees of each species were obtained for this purpose, although the extent of sampling was in most cases very much greater. The results of this approach to a measure of E. tinctorium frequency are presented in Table III.

Such a measure of frequency is admittedly conservative for it became apparent early in the course of the investigation that, in most cases, incidence of infection is greater than is that of fruiting.

TABLE III. FREQUENCY OF R. [illegible] WITHIN CERTAIN FOREST ASSOCIATIONS IN BRITISH COLUMBIA [1]

Association number	Suscept and Tree Layer														
	western hemlock			mountain hemlock			grand fir			amabilis fir			alpine fir		
	A1	A2	B1	A1	A2	B1	A1	A2	B1	A1	A2	B1	A1	A2	B1
1(sub-assoc.)	-	-	-	-	-	-	-	-	-	I	R	-	-	-	-
8	I	R	-	-	-	-	-	-	-	-	-	-	-	-	-
11	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
13	R	R	-	-	-	-	-	-	-	C	I	R	-	-	-
14	R	-	-	-	-	-	-	-	-	A	C	I	-	-	-
15	I	-	-	-	-	-	-	-	-	C	I	R	-	-	-
16	R	R	-	-	-	-	-	-	-	A	A	C	-	-	-
16(sub-assoc.)	R	-	-	-	-	-	-	-	-	I	I	I	-	-	-
17	-	-	-	R	R	-	-	-	-	I	R	-	-	-	-
18	C	C	I	-	-	-	-	-	-	C	I	R	-	-	-
19	A	C	C	-	R	-	-	-	-	C	I	I	-	-	-
19(sub-assoc.)	I	R	R	-	-	-	-	-	-	I	R	R	C	I	-
20	C	I	R	-	-	-	-	-	-	A	A	C	-	-	-
21	C	I	R	-	-	-	-	-	-	I	I	I	-	-	-
23	-	-	-	-	-	-	-	-	-	-	-	-	C	C	I
24	-	-	-	-	-	I	-	-	-	-	-	-	A	C	C
25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I
26	-	-	-	-	-	-	-	-	-	-	-	-	A	C	I
27	-	-	R	-	-	R	-	-	-	-	-	-	I	-	-
29	A	C	I	-	-	-	-	-	-	-	-	-	I	R	R
30	C	I	I	-	-	-	-	-	-	-	-	-	R	R	I
31	A	C	I	-	-	-	-	-	-	-	-	-	-	-	-
32	A	C	C	-	-	-	A	A	C	-	-	-	-	-	-
33	A	A	C	-	-	-	-	-	-	-	-	-	-	-	-
34	A	A	C	-	-	-	A	A	C	-	-	-	-	-	-
35	I	I	I	-	-	-	-	-	-	-	-	-	-	-	-
36	C	C	I	I	I	R	-	-	-	-	-	-	I	I	I
37	-	I	I	-	-	-	-	-	-	-	-	-	A	C	I
38	I	I	R	-	-	-	-	-	-	I	I	R	-	-	-
39	C	I	I	-	-	-	-	-	-	I	I	R	-	-	-
40	C	C	I	-	-	-	-	-	-	C	C	I	-	-	-
40(sub-assoc.)	C	C	C	-	-	-	-	-	-	A	C	C	-	-	-
41	C	I	I	-	-	-	-	-	-	C	C	-	-	-	-
42	I	C	C	-	-	-	-	-	-	-	I	R	-	-	-
45	-	-	C	-	-	-	-	-	-	-	-	-	A	C	I
46	-	-	-	-	-	-	-	-	-	-	-	-	C	I	I

TABLE III. (continued)

Association number	Suscept and Tree Layer				
	western hemlock	mountain hemlock	grand fir	amabilis fir	alpine fir
	A1-A2-B1	A1-A2-B1	A1-A2-B1	A1-A2-B1	A1-A2-B1
47	- - C	- - -	- - -	- - -	A C C
47(sub-assoc.)	- - -	- - -	- - -	- - -	C C I
48	- - -	- - -	- - -	- - -	A C C

1. Based on the occurrence of fruit bodies.
   R = rare = up to one per cent of trees bearing fruit bodies
   I = infrequent = from two to five per cent of trees with fruit bodies
   C = common = from six to 25 per cent of trees with fruit bodies
   A = abundant = more than 25 per cent of trees with fruit bodies

A higher incidence of infection over that of fruiting was apparent mainly in the case of both very young and very old trees and it is with such classes of trees that estimates of the frequency of E. tinctorium can be seriously in error. Despite a difference between the incidences of infection and fruiting it was found that incidence of fruiting provides a reasonably good basis for estimates of frequency for this fungus for, unlike many other fungi that cause decay, E. tinctorium characteristically fruits soon after significant volumes of rot have occurred. In this connection and on the basis of examining 151 small-sized western hemlocks in both young stands and in the understory of older stands of association number 33, fruiting was found to occur on trees down to an age of 54 years. The incidence and volume of rot at such an early age are both characteristically very low, even under maximum conditions of infection as can be provided by association number 33.

Circumstances did not permit for the detection of possible relationships between rot incidence and incidence of fruiting for all species and habitats. In order to be assured that such differences occur, however, western hemlock and amabilis fir were examined for this specific purpose in two regions and in several habitats. The results of this examination are summarized in Table IV.

The advisability of considering each habitat separately, when predicting the occurrence and frequency of E. tinctorium, is emphasized by the indication that, of 10 host habitats in the lower coast forest in which the fungus regularly occurs, in no habitat is the incidence of the fungus on western hemlock greater than infrequent. In the same region the frequency of E. tinctorium appears to be abundant on amabilis fir in only two habitats, although generally higher than that on western hemlock in most habitats. In the case of sub-alpine forests of the Cascade Mountains and south central interior British Columbia, it appears that of the five habitats recognizable for this region in only two of them is E. tinctorium abundant on alpine fir. In two others its frequency appears to be very low. Intra-regional differences such as those indicated for the sub-alpine forests of interior British Columbia, and for other regions as well, appear to be sufficiently great and consistent as to throw doubt upon the advisability of treating such forests as a single unit.

FACTORS CONTROLLING THE DISTRIBUTION AND FREQUENCY OF E. TINCTORIUM IN BRITISH COLUMBIA

General

The factors that control the distribution and frequency of E. tinctorium in British Columbia are seemingly numerous. While certain

TABLE IV. THE COMPARATIVE INCIDENCES OF E. TINCTORIUM FRUIT BODIES AND ROT IN WESTERN HEMLOCK AND AMABILIS FIR

Association number	Tree layer	Number of trees examined	Average age (years)	Average diameter (inches)[1]	Percentage of trees with fruit bodies	Percentage of trees with rot
			western hemlock			
29	A 1	65	280	30	52.3	67.7
	A 2	9	151	15	33.3	33.3
	B 1	14	172	13	7.1	21.4
31	A 1	83	205	25	50.6	68.1
	A 2	33	175	16	27.3	31.4
	B 1	144	178	8	14.6	19.9
39	A 1	109	207	20	71.1	72.5
	A 2	18	194	14	38.9	41.9
	B 1	14	164	8	21.4	50.1
40	A 1	113	326	27	21.3	32.7
	A 2	23	224	15	4.3	4.3
	B 1	18	171	12	0.0	5.6
41	A 1	104	362	33	10.6	29.8
	A 2	38	275	20	10.5	21.1
	B 1	56	225	14	1.8	14.3
			amabilis fir			
40	A 1	102	365	30	8.8	15.7
	A 2	28	251	18	7.1	7.1
	B 1	31	219	13	3.2	6.5
41	A 1	98	336	32	36.7	45.9
	A 2	9	263	17	22.2	22.2
	B 1	28	180	12	7.1	13.9

1. Measured at breast height, outside bark.(= 4.5 ft. above ground level).

of these factors appear at times to have a greater regulatory effect upon the welfare of the fungus than do others, it is equally apparent that seldom does one factor become limiting. Such factors as air temperature, atmospheric humidity, inherent susceptibilities of different trees to infection and decay, and many others, are apparently so interrelated in their effects upon E. tinctorium that the separate influence of each is rarely of paramount importance. Under the circumstances of integration of habitat factors, to such a degree as is demonstrated in the case of E. tinctorium suscept habitats, the evaluation of any single factor becomes a very difficult process. So integrated were the factors that control the distribution and frequency of the fungus, it appeared quite unlikely that particular study of any one of them could prove to serve a vital purpose. It was decided, therefore, to make separate assessments of factors for individual habitats only in relative terms and not in terms of actual values. In this way, for example, atmospheric humidity was interpreted for any one habitat as being either more or less higher than that for other habitats, or so much higher than that of a completely exposed area in the same region. Factors other than atmospheric humidity were considered in essentially the same manner.

When dealing with a habitat that is in itself composed of a multiplicity of micro-habitats, such as are those of E. tinctorium hosts, the feasibility of obtaining adequate measurement data was very much in doubt and the utility of interpreting data drawn from only one or a few micro-habitats within a much larger composite habitat appeared equally doubtful. It was decided, therefore, that reliance upon actual values of individual factors for purposes of this investigation, apart from the difficulty of obtaining them, could prove to be more misleading than enlightening. *In lieu* of measuring or otherwise recording actual values of habitat factors, relative values of them were either estimated directly, as in the case of such factors as those of soil, wind influence, and ages of trees or stands, or interpreted indirectly according to their effect upon the vegetation of specific ecotopes, as in the case of such factors as atmospheric temperature, humidity, and host vigor.

Certain factors appeared to act directly upon the welfare of the fungus, whereas the influences of others appeared to be carried out indirectly through their modifying influences upon other factors. The indirect influences of certain factors were observed to either augment or counteract the direct influences of others, such as inherent susceptibility to infection, air temperature, and humidity. Factors whose influences upon the fungus were exerted for the most part indirectly were of the nature of suppression through over-topping of trees, tree or stand vigor, and soil factors. Although the following sections of this report are devoted to a discussion of some of the individual factors that operate to control the distribution and frequency of *E. tinctorium*, it should be borne in mind that only rarely can the influences of separate factors be considered as mutually exclusive.

Relative Susceptibilities of E. tinctorium Hosts

While the inherent susceptibility on the part of some tree species to infection by *E. tinctorium* and resistance to infection on the part of others are unquestionably the basic reasons for the distribution pattern that can be ascribed to this fungus, the fact remains that degrees of susceptibility exist both between and within host species. The occurrence of the fungus on western hemlock in seven of 19 habitats observed for this suscept in coast forests and the occurrence of it on amabilis fir in eight of 13 coast forest habitats indicates, for this region at least, not only a higher degree of susceptibility for amabilis fir but also a range in susceptibility within each host. A further demonstration of a range in susceptibility within these two hosts occurs in the observation that nowhere in the coast region is the intensity of *E. tinctorium* greater than infrequent on western hemlock whereas, in the case of amabilis fir, the fungus has an abundant occurrence in at least two habitats. Grand fir demonstrates an even more extreme range in its susceptibility to infection by the total absence of the fungus from its five coastal habitats and the abundant occurrence of the fungus in both of its two interior habitats.

The quality of resistance to infection by *E. tinctorium*, although partly imparted by the inherent characteristics of the woods of different species, cannot be ascribed to this source alone for all through the course of the investigation the presence of physical barriers to inoculation and infection of otherwise susceptible species was apparent. Extremes of summer temperature and humidity were noteworthy in this respect. While it may be impossible to segregate the separate influences of inherent resistance and physical barriers upon E. tinctorium distribution and frequency, it is safe to assume that inherent resistance does occur, both in an absolute sense in the case of species of pines and in a relative sense, as in the case of such a species as amabilis fir.

Geographic Isolation of Suscepts

The feature of isolation of known E. tinctorium suscepts has a possible demonstration in the apparent absence of the fungus from the Queen Charlotte Islands of British Columbia. Other than the case cited, however, there is no evidence to indicate that geographic isolation can be considered a factor in limiting the occurrence of this fungus. Even in the case of the Queen Charlotte Islands it is doubtful whether geographic isolation alone is responsible for the absence of E. tinctorium for the results of both the current and previous investigations have shown that the fungus does not occur in areas that are fully exposed to the Pacific climate. This feature of the distribution of the fungus can be demonstrated by the absence of it from the extremities of coastal inlets and its presence at the heads of the same inlets. Thus, it is possible that exclusion of the fungus from the Queen Charlotte Islands is due to both geographic isolation and climatic influences.

Atmospheric Temperature

The factor of atmospheric temperature appears to be one of the strongest factors that influences the distribution of E. tinctorium.

Although temperature influences are pronounced, they are almost always closely integrated with the influences of other factors, notably those of atmospheric humidity. Thus, air temperature both modifies and is modified by other habitat factors.

Air temperature, as a separate influence, has a direct effect upon the reproductive phases of the life cycle of E. *tinctorium* that are exposed to an aerial environment. Thus, there are critical temperatures above or below which reproduction cannot occur and between which reproduction is either enhanced or retarded. It is apparent that minimum periods of favourable temperatures are required for reproduction to occur and that the more extended the period of favourable temperatures is the more efficient will be the fungus from the aspect of reproduction.

Circumstances did not permit detection of the actual extremes of temperature at which reproduction is inhibited nor the actual minimum periods of time over which favourable temperatures must occur. *In lieu* of actual measurements it was observed that maximum infection was achieved under temperature conditions represented by mature stands of certain associations. When temperatures were observed to either exceed or fall short of those exhibited by associations having maximum infection the frequency of infection declined accordingly. The conditions of temperature that were the most conducive to E. tinctorium infection in its major hosts were observed to occur as follows:

western hemlock .....associations number 33 and 34
mountain hemlock ....association number 36
grand fir ....associations number 32 and 34
amabilis fir ....associations number 16 and 20
alpine fir ....associations number 24, 47, and 48

The associations listed as providing maximum conditions of temperature for infection were found to be uniform to the extent that high average summer temperatures persist for extended periods over all or at least part of the stem length of trees. Depending upon both the duration of such favourable temperatures and the proportion of the stem length of trees over which such temperatures persist, the intensity of infection varied from one habitat to the next. Thus, in the case of western hemlock stands, maximum infection occurred when protracted periods of high summer temperatures were observed to prevail from the tops of dominant trees to the ground line. Such was the condition in associations number 33 and 34. Any restriction in either the duration of favourable temperatures or in the proportion of the stem length over which such temperatures prevail was observed to decrease the intensity of infection, as in the case of associations number 30 and 35. In cases where favourable temperatures prevailed mainly in the higher canopies of trees infections rarely occurred in trees of the lower canopies. In cases where favourable temperatures existed only in the lower canopies, as in association number 25, infections were invariably centred close to the ground.

Temperature was observed to affect not only the extent and location of fruiting but also the size of fruit bodies and the condition of their hymenial surfaces. Extreme high temperatures were observed to reduce both the size of fruit bodies and the longevity of their hymenial surfaces, whereas extreme low temperatures retarded the maturation of fruit bodies or even inhibited their formation.

Atmospheric Humidity

The factor of atmospheric humidity appears to be as vital to the welfare of E. *tinctorium* as is that of air temperature, although requisite conditions of humidity are more commonly met with than are those of temperature. Thus, it is a combined condition of temperature and humidity that either favours or retards E. tinctorium development.

Atmospheric humidity is conditioned by many habitat factors, most noteworthy among which are air drainage, surface accumulations of water or snow, the supply of ground water that is available to plants, and the efficiency of transpiration of herbs and shrubs. When either of the conditions indicated were able to maintain a constantly humid atmosphere within a stand infections normally resulted, provided the requirements of temperature and inherent susceptibility were satisfied. That the provision of requisite conditions of humidity alone are insufficient to meet the requirements of E. *tinctorium* can be demonstrated by the absence of the fungus from the western slope of Vancouver Island and at low elevations on the eastern slope in contrast with its occurrence at medium and high elevations on the eastern slope. Thus, for example, the fungus was observed in association number 12 only in those instances where stands of this association occurred in the "rain shadow" of Vancouver Island and coast mountains. Under such conditions the climate was continental, or interior, as opposed to oceanic, or Pacific.

Relative conditions of atmospheric humidity and temperature could be recognised in stands of different associations according to the occurrence, distribution, and frequency of xerophytic mosses and lichens on trees and according to the type and vigor of ground vegetation. It was possible by such means to recognize a fairly definite pattern of stratification of atmospheric conditions for each habitat. Stratification of such a nature was particularly well demonstrated in cases of stands of sub-alpine and central interior plateau forests. The resultant effect of such a stratification of atmospheric conditions within a stand was fairly regular, incidence and location of fruiting and luxuriance of growth of individual sporophores being enhanced by warm and humid atmospheres and decreased by hot and dry atmospheres. A comparison of the fruiting habit of E. *tinctorium* between sub-alpine forests and those of lower elevations showed marked differences. Extreme examples of each type of forest existed in associations number 27 and 33. In the case of association number 27, fruit bodies were characteristically small, few in number per tree, and restricted to a shallow stratum that corresponded to about the height of shrubs. In the case of association number 33, fruit bodies were characteristically large, many per tree, and located over all but the tops of dominant and co-dominant trees.

Evidence of stratification of atmospheric conditions and the resultant effect upon E. tinctorium fruiting can be demonstrated for different stands of the same association as well as for stands of different associations. Thus, stands of association number 23 that occur in the Spa Hills and Fly Hills regions were similar to those that occurred in the mountains west of Kelowna in so far as their soils and vegetative structures were concerned but differed markedly in the relative dryness of their atmospheres during summer months. Stands of this association located in the mountains west of Kelowna had a much drier atmosphere during summer months than did those in either the Spa Hills or Fly Hills, possibly for the reason that stands near Kelowna are more exposed to the influences of a grassland climate than are those located elsewhere. Whatever the cause of such differences in atmospheric humidity may be, the fact remains that E. tinctorium was less abundant and fruited closer to the ground in stands west of Kelowna than was the case in stands of other areas.

Suscept Vigor

The most abundant occurrence of E. tinctorium in any particular region appeared to be coincident with reduced vigor of its suscepts, although not usually with their least vigorous condition. This trend can be demonstrated, in the case of the Selkirk and Monashee Mountains region, by relating the incidence of the fungus on western hemlock in associations number 31, 33, and 35 (see Table III) to the comparative vigors of this suscept in each of the three habitats. Western hemlock obtains its maximum development for the region indicated in stands of association number 31, in which habitat the incidence of E. tinctorium is characteristically reduced from that of associations number 33 and 35. The fact that the highest incidence of the fungus is not necessarily related to the least vigorous condition of its suscepts is demonstrated by the reduced occurrence of the fungus in association number 35 from that characteristic of both associations number 31 and 33, association number 35 representing conditions that are the least favourable for growth of western hemlock for the region indicated. Similar trends can be demonstrated for other regions as, for example, the reduced occurrence of the fungus in stands of association number 21 from that in stands of association number 19 in the Cascade Mountains, or the absence of the fungus on western hemlock from stands of association number five and its occurrence in association number eight in coast forests.

Reduced vigor used in the sense as in the above examples does not refer to sub-par growth by reason of over-topping but, rather, to the particular ability of a suscept species to occupy and develop in a specific habitat. That reduced vigour resulting from suppression through over-topping is, however, related to a high incidence of E. tinctorium infection is demonstrated in the observation that infection is characteristically greater in trees that have sustained over-topping than in trees of the same age that have not been consistently suppressed. The circumstances whereby suppression appeared to be an important factor as a conditioner to a high incidence of infection by E. tinctorium were limited, being confined to those habitats in which conditions favourable to infection extended into the lower canopies. It would be inadvisable, therefore, to assume that suppression, in respect of its confining individual trees to the lower canopies, is as equally an important factor in stands of, say, association number 30 as in stands of associations number 33 and 34 because conditions that favour E. tinctorium are concentrated higher above ground in association number 30 than they are in the other two habitats. It is apparently for this reason that stands having environments similar to those characteristic of associations number 33 and 34 and in which overstories of large, old, dominant trees occur are usually infected to a much greater degree than are stands in which such an overstory does not occur.

Suscept Age

Suscept age is unquestionably a major factor among all others that control the incidence of infection by E. tinctorium but, as a single factor, age does not appear to operate exclusively of other factors. It has been observed, for example, that under some circumstances trees of the same age may have either a greater or lesser incidence of E. tinctorium according to the degree to which they have been subjected to suppression by over-topping. The influence of host age on the incidence of E. tinctorium may be generalized upon, however, to the extent that, the older trees and stands become, the greater is the frequency of infection in them and the less pronounced are the differences in intensity of infection between different habitats of the same region.

One of the basic reasons for a levelling off in the incidence of infection in older stands of different habitats appears to be that most older stands, regardless of their specific habitat, have an open structure sufficient to the extent that atmospheric conditions within them are more uniformly favourable to E. tinctorium development than they are in the case of younger stands. Thus, for example, there may be very little difference between the incidence of infection in older stands of associations number 31 and 33 despite a pronounced difference in this regard between younger stands of the same associations. A further influence of increasing age, supplementary to that of providing a more favourable atmospheric environment for the fungus, in the mere fact of an increased period of time over which infections can occur and during which the number of infection courts is invariably increased.

When considering the influence of host age upon the incidence of E. tinctorium it would be logical to speculate upon possible differences in this regard between young trees of young stands and trees of the same age of older stands. Observations were not carried out in the course of this investigation for this express purpose but, on the basis of observations that were incidental to observations made mainly of older stands, it appeared that very little difference exists between the two conditions. A similar indication was gained by Foster et al. (17) in the course of their work in young and old stands of western hemlock in the Columbia River region. It appeared, therefore, that, apart from a minimum period before which infection could not occur under any circumstance, young trees of young stands are equally susceptible to infection than are trees of the same age in older stands of the same habitat and, if differences do occur, it is probable that they are of little magnitude.

Inhibition of Fruiting

The frequency and luxuriance of E. tinctorium fruit bodies appeared to be fairly closely related to the incidence of infection by this fungus in most of the stands examined. Thus, it was observed that, when infections had taken place in a stand, fruit bodies could almost invariably be found. A possible exception to this relationship exists in the cases of engelmann and western white spruce. Although fruit bodies were observed on neither of these suscepts, in all instances where infections in them had occurred they were growing in mixture with alpine fir and, sometimes, western hemlock, both of which species were heavily infected and bore fruit bodies.

Incidence of fruiting was regularly observed to lag behind that of infection, even in stands where conditions were highly conducive to fruiting. The difference between incidences of fruiting and infection was, however, less pronounced in older trees and stands than in young stands. This was particularly so under habitat conditions that provided for maximum conditions for fruiting to occur.

Inhibition of fruiting, as a limiting factor in the incidence of infection by _E. tinctorium_, was most apparent in habitats and regions where the fungus was least abundant or where the activity of the fungus was confined to a limited portion of the stem length of trees. Thus, it was observed, in the case of sub-alpine and central interior plateau habitats, while a low incidence of fruiting invariably indicated a higher incidence of infection, the incidence of infection was not greatly in excess of that of fruiting. When fruiting had not occurred in a particular habitat but had occurred in adjacent habitats, infections could invariably be found in the habitat in which fruiting had not occurred, although usually in a reduced frequency from that of habitats in which fruiting had occurred. Furthermore, as fruiting became increasingly inhibited in a habitat, area, or region, the frequency of infection was increasingly less the more remote a particular stand was from a stand in which fruiting had occurred, ultimately to the point where infections did not occur.

Soil Characteristics

Although soils were examined only as regards their gross characteristics in the course of this investigation, it was apparent that their physical and chemical properties have a considerable influence upon the occurrence and frequency of E. *tinctorium*. Thus, the soils characteristic of different habitats were observed to impart an influence upon both the welfare of suscepts and the condition of the atmosphere within stands. The respective qualities of the soils that are characteristic of different habitats were observed to impose definite limitations upon the occurrence of trees of different species and, also, upon their vigor and, by so doing, they appeared to condition E. tinctorium suscepts to a greater or lesser incidence of infection. The exclusion of a host species from the higher canopies of a stand, or its admission into the higher canopies only in greatly reduced vigor, can be accomplished through the medium of soil characteristics as, for example, in the case of amabilis fir in stands of association number 11. Should the requisite conditions for E. *tinctorium* to occur prevail only in the upper canopies, as they do in association number 11, it follows that trees that are confined to lower canopies will be relatively free from infection.

Apart from the admission of trees of different species into specific habitats and their admission into or exclusion from the respective canopies of individual stands, because of the nature of the soils peculiar to these habitats, the limitations imposed by soil upon the vigor of trees is pronounced. The consequence of reduced vigor, as has already been indicated, is usually a higher incidence of E.

tinctorium than that characteristic of vigorous stands. Thus, soils of association number 19 permit western hemlock to occur only with a vigor that is reduced from that which it obtains in association number 21. The results of observations made in stands of both of these habitats showed a consistently higher incidence of *E. tinctorium* in association number 19.

The ability of soil to influence the condition of the atmosphere within stands, mainly as regards humidity, was quite evident. Since the maintenance of continuously high humidities during the summer months appears to be a requisite for a high incidence of infection, it is certain that the water relationship of soils will at times play a prominent role in the provision of such a requirement of the fungus. Thus, any aspect of soil that provides for a continuous emission of moisture into the atmosphere within a stand will enhance the possibility of a high incidence of infection.

DISCUSSION

The results of this investigation have served to emphasize that, despite its suscepts having in aggregate a broad ecological tolerance, *E. tinctorium* has an ecological tolerance that is much less broad. The possible confusion of the extensive geographic distribution that is peculiar to this fungus with its having a broader ecological tolerance than it in fact has can be dispensed with in the knowledge that the fungus appears to occur under rather precise conditions, irrespective of the region in which it is observed. While the fungus may be encountered in different regions, on different hosts, and under what may appear to be radically different forest conditions, it can be demonstrated that the actual conditions under which it occurs are, in fact, quite similar. The conditions that permit the fungus to occur in the Horseshoe Mountains on western hemlock from close to the ground line to close to the tops of co-dominant trees, for example, are not greatly different from those which permit its occurrence in coast forests on amabilis fir in the upper third of the stem length of dominant trees. Thus, conditions that permit E. tinctorium to occur are quite similar despite great differences in the over-all aspects of individual habitats, such as occur between, say, associations number 13 and 33. It is for such reasons that estimates of the probable occurrence of the fungus should be based not only on the recognition of specific habitats but, also, on the range of conditions which each habitat exemplifies.

It has been indicated earlier in this report (see page 50) that a forest habitat, or association, is in reality a composite group of micro-habitats. Furthermore, the results of this investigation have indicated that the conditions that define and regulate such micro-habitats are, in all likelihood, the conditions which regulate the occurrence of E. tinctorium. Credence is lent to this hypothesis by the great similarity between micro-habitats that permit the fungus to occur. Similarities between micro-habitats that are conducive to E. tinctorium occurrence may be observed in a comparison of, say, that portion of association number eight in which the fungus is found with association number 48 or, say, associations number 20 and 31. Consequently, the differences that exist between forest habitats, or macro-habitats, are more readily apparent and profound than appear to be the differences between the micro-habitats, or precise conditions, that determine the distribution of E. *tinctorium*.

Apart from consideration of the conditions that permit the mere occurrence of the fungus, a separate consideration exists in the matter of its frequency of occurrence. The fact that its frequency, or abundance, is neither a product of chance nor, in most cases, a result of geographic isolation of its hosts is demonstrated by the definite pattern of occurrence and frequency that may be attached to this fungus. Thus, conditions may be recognised and described that are either more or less conducive to a high frequency of it for any forest region of the province. Some of the factors that appear to contribute to the frequency pattern that is recognizable for E. *tinctorium* have already been listed, along with the means whereby they can be detected and evaluated in nature. Some of these factors, such as those of atmospheric temperature and humidity, appeared to be consistently stronger than others but, in general, it must be confessed that all factors, apart from inherent resistance to the fungus, are inter-acting. The water relationships of the soils of different habitats, for example, can influence the frequency of E. *tinctorium* in a number of recognizable, even if indirect, ways such as their effects on host vigor, density of stocking, amount of surface evaporation of water, and amount of water that is transpired into the atmosphere. It appears, therefore, that it is the influences of such factors, whether they be exerted directly or indirectly, that provide the specific characteristics of micro-habitats which, in turn, act upon the welfare of the fungus.

Although the results of examinations made of stands throughout the province emphasized the fact of precise environments being necessary for *E. tinctorium* to occur, it is possible to derive some practical benefit from a comparison of the occurrence of the fungus in the different regions of the province. Hence, the fungus has a characteristically greater frequency in some regions than in others. In general it can be safely said that the fungus is least abundant in regions that are exposed to the influences of a Pacific climate and is most abundant in regions that are exposed to a modified Pacific climate, i.e., a more continental climate such as is obtained east of the Coast Mountains. Thus, in the case of each of its suscepts, it appears that *E. tinctorium* becomes more abundant the more remote its suscepts are from the influences of a Pacific climate, provided that atmospheric humidity is maintained at a constant high level.

Certain differences as regards the frequency of *E. tinctorium* have been ascribed by previous investigators to north and south coast forests which, in fact, have proven to be less pronounced than was formerly believed. The current investigation has shown that the fungus has a fairly uniform distribution throughout north and south coast forests to the extent that it does not appear to occur in either of these regions in stands that are fully exposed to the influences of the Pacific climate. Thus, *E. tinctorium* occurs in both regions only when some measure of protection is afforded from the low summer temperatures that characterize the Pacific climate. Consequently, the fact of the fungus having a high frequency in north coast forests may be ascribed to the broken terrain that characterizes this region. The essential difference between north and south coast forests, as regards the occurrence of E. tinctorium, appears to stem from this feature of both regions and not to a uniform distribution of the fungus in north coast forests alone. The exposed extremities of north coast inlets are virtually free from the fungus, just as is the western slope of Vancouver Island, whereas the sheltered extremities of the same inlets and the valleys tributary to them normally provide conditions that are highly conducive to E. tinctorium development.

The southern Cascade Mountains as well as their northern extensions represent conditions that are, in general, more conducive to a high incidence of the fungus than are those of the coast region. Thus, western hemlock is at times very seriously damaged by E. tinctorium in the Cascade Mountains, as in association number 19, whereas it is only slightly damaged in coast forests. The incidence of the fungus on each of its suscepts in the Cascade Mountains may be regarded as being intermediate between that of the coast region and that of the Selkirk and Monashee Mountains region. The essential difference that appears to exist between the Cascade region and the Selkirk and Monashee region is that only in a very limited number of habitats is E. tinctorium consistently abundant in the Cascade region, whereas it is more uniformly abundant in a greater number of habitats in the Selkirk and Monashee Mountains.

The investigation revealed that considerable similarity may be anticipated as regards the occurrence of E. tinctorium in sub-alpine stands of the Cascade Mountains and the southern interior generally and in stands of the central interior plateau. In no other region of the province was the incidence of the fungus so well defined as in the alpine fir stands of the regions indicated, probably for the reason that extremes of local climate, soil, and other environmental factors occur with great regularity over very short distances. The general high incidence of *E. tinctorium* that has been ascribed to alpine fir stands possibly stems from the mosaic of sites, or habitats, that characterizes the regions in which they occur. The validity of applying a general high incidence of the fungus to alpine fir stands is questionable in the light of the outstanding habitat differences such as were encountered in the course of this investigation, particularly if a type of forest management is envisaged that will take into account the occurrence of different sites or habitats.

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APPENDIX I

LIST OF PLANTS COMPRISING THE VEGETATION THAT IS DIAGNOSTIC OF ECHINODONTIUM TINCTORIUM HABITATS IN BRITISH COLUMBIA FORESTS

Abies amabilis (Dougl.) Forb.
A. grandis (Dougl.) Lindl.
A. lasiocarpa (Hook.) Nutt.
Acer glabrum Torr. var. *douglasii* (Hook.) Dipp.
A. macrophyllum Pursh
Achlys triphylla (Smith) DC.
Actaea arguta Nutt.
Adenocaulon bicolor Hook.
Adiantum pedatum L.
Alnus oregona Nutt.
A. tenuifolia Nutt.
Amelanchier florida Lindl.
Apocynum androsaemifolium L.
Aralia nudicaulis L.
Arctostaphylos uva-ursi (L.) Spreng.
Arnica latifolia Bong.
Asarum caudatum Lindl.
Athyrium filix-femina (L.) Roth

Betula occidentalis Hook.
B. papyrifera Marsh.
Blechnum spicant (L.) J.E. Smith

Calliergonella schreberi (Bruch & Schimp.) Grout
Camptothecium megaptilum Sull.
Chamaecyparis nootkatensis (D. Don) Spach
Chimaphila menziesii (R.Br.) Spreng.
C. umbellata (L.) Nutt.
Cinna latifolia (Torr.) Griseb.
Circaea alpina L.
Clintonia uniflora (Schult.) Kunth.
Conocephalum conicum (L.) Dumort.
Cornus canadensis L.
C. stolonifera Michx.
Corylus californica (A. DC.) Rose
C. rostrata Ait.

Dicranum fuscescens Turn.
D. scoparium Hedw.
Disporum oreganum (S. Wats.) Benth. & Hook.
Drosera longifolia L.
D. rotundifolia L.
Dryopteris dilatata (Hoffm.) A. Gray
D. linnaeana C. Chr.
Equisetum arvense L.
E. palustre L.
E. pratense Ehrh.
E. sylvaticum L.
Eurhynchium oreganum (Sull.) Lesq. & James
E. stokesii (Turn.) Bruch & Schimp.

Galium triflorum Michx.
Gaultheria ovatifolia Gray
G. shallon Pursh
Goodyera decipiens (Hook.) F.T. Hubbard

Heracleum lanatum Michx.
Hieracium albiflorum Hook.
Hylocomium splendens (Hedw.) Bruch & Schimp.

Kalmia polifolia Wang.

Larix occidentalis Nutt.
Ledum groenlandicum Oedr.
Linnaea borealis L.
Listera nephrophylla Rydb.
Lonicera involucrata Banks.
L. utahensis Wats.
Lycopodium annotinum L.
L. obscurum L.
L. selago L.
Lysichitum americanum Hulten & St. John

Mahonia aquifolium (Pursh) Nutt.
Maianthemum dilatatum (Wood) Abrams

APPENDIX I (Cont'd)

Menziesia ferruginea Hook.
Mitella caulescens Nutt.
Mnium affine Bland.
M. insigne Mitt.
M. menziesii (Hook.) C.M.
M. punctatum Hedw.
M. spinulosum Bruch & Schimp.
Moneses uniflora (L.) Gray
Myrica gale L.

Oplopanax horridus (J.E. Smith) Miq.

Pachystima myrsinites (Pursh) Raf.
Pedicularis racemosa Dougl.
P. [illegible] Gray
Peltigera aphthosa (L.) Ach.
P. canina (L.) Willd.
Petasites speciosa (Nutt.) Piper
Picea engelmanni Parry
P. glauca (Moench) Voss var. *albertiana* (S.Brown) Sarg.
P. mariana (Mill.) B.S.P.
P. sitchensis (Bong.) Carr.
Pinus contorta Dougl.
P. monticola Dougl.
Plagiothecium undulatum (Hedw.) Bruch & Schimp.
Polystichum munitum (Kaulf.) Presl.
Polytrichum juniperinum Hedw.
Populus tremuloides Michx.
P. trichocarpa Torr. & Gray
Pseudotsuga taxifolia (Poir.) Britt.
Pteretis nodulosa (Michx.) Nieuwl.
Ptilium crista-castrensis (Hedw.) DN.
Pyrola bracteata Hook.
P. chlorantha Sw.
P. secunda L.

Rhacomitrium canescens Brid.
Rhododendron albiflorum Hook.
Rhytidiadelphus loreus (Hedw.) Warnst.
R. triquetrus (Hedw.) Warnst.
Rhytidiopsis robusta (Hook.) Broth.
Ribes lacustre (Pers.) Poir.
R. sanguineum Pursh
Rosa gymnocarpa Nutt.
Rubus leucodermis Dougl.
R. parviflorus Nutt.
R. nodatus Smith
R. spectabilis Pursh
R. strigosus Michx.

Sambucus melanocarpa Gray
S. pubens Michx.
Smilacina racemosa (L.) Desf.
Sorbus sitchensis Roem.
Sphagnum capillaceum (Weiss.) Schrank.
S. fuscum (Schimp.) Kling
S. recurvum Beauv.
S. rubellum Wils.
S. squarrosum Crome.
Spiraea lucida Dougl.
Stachys ciliata Dougl.
Streptopus amplexifolius (L.) DC.
Streptopus roseus Michx.
Symphoricarpos albus (L.) Blake

Taxus brevifolia Nutt.
Thalictrum occidentale Gray
Thuja plicata D. Don
Tiarella laciniata Hook.
T. trifoliata L.
T. unifoliata Hook.
Trientalis arctica Fisch.
Trillium ovatum Pursh
Tsuga heterophylla (Raf.) Sarg.
T. mertensiana (Bong.) Carr.

Vaccinium caespitosum Michx.
V. membranaceum Dougl.
V. ovalifolium J.E. Smith
V. oxycoccus L.
V. parvifolium J.E. Smith
V. uliginosum L.
Valeriana sitchensis Bong.
Veratrum eschscholtzii A. Gray
Viburnum pauciflorum Pyl.
Viola glabella Nutt.
V. orbiculata Geyer

APPENDIX II

FOREST ASSOCIATIONS AND SUB-ASSOCIATIONS OF BRITISH COLUMBIA FORESTS THAT EMBODY ECHINODONTIUM TINCTORIUM SUSCEPTS [1]

1. *Thuja plicata*-(*Pseudotsuga taxifolia*)-*Abies grandis*-*Adiantum pedatum*.

   Thuja plicata - (*Pseudotsuga taxifolia*)-*Abies amabilis*-*Adiantum pedatum*. (Sub-association)

2. *Picea sitchensis*-*Thuja plicata*-*Rubus spectabilis*-*Polystichum munitum*.

3. *Pseudotsuga taxifolia*-(*Tsuga heterophylla*)-*Polystichum munitum*.

4. *Thuja plicata*-*Alnus oregona*-*Lysichitum americanum*.

5. *Pseudotsuga taxifolia*-*Tsuga heterophylla*-*Eurhynchium oreganum*-*Hylocomium splendens*.

6. *Pseudotsuga taxifolia*-(*Tsuga heterophylla*)-*Gaultheria shallon*.

7. *Pseudotsuga taxifolia* (*Tsuga heterophylla*)-*Pinus contorta*-*Peltigera canina*-*Peltigera aphthosa*.

* 8. *Pinus contorta*-*Ledum groenlandicum*-*Sphagnum* spp.

9. *Pseudotsuga taxifolia*-*Tsuga heterophylla*-*Dryopteris linnaeana*-*Achlys triphylla*.

10. *Thuja plicata*-*Tsuga heterophylla*-*Veratrum eschscholtzii*-*Mnium punctatum*.

* 11. *Tsuga heterophylla*-(*Pseudotsuga taxifolia*)-*Gaultheria shallon*-*Camptothecium megaptilum*-*Hylocomium splendens*-*Rhytidiopsis robusta*.

* 12. *Tsuga heterophylla*-*Abies amabilis*-*Blechnum spicant*-*Tiarella trifoliata*.

* 13. *Tsuga heterophylla*-(*Thuja plicata*)-*Abies amabilis*-*Vaccinium parvifolium*-*Vaccinium ovalifolium*-*Hylocomium splendens*-*Rhytidiadelphus loreus*.

* 14. *Tsuga heterophylla*-(*Abies amabilis*)-*Thuja plicata*-*Vaccinium parvifolium*-*Vaccinium ovalifolium*-*Gaultheria shallon*-*Cornus canadensis*.

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[1] Associations prefixed with an asterisk are those in which *Echinodontium tinctorium* has been recorded.

APPENDIX II (cont'd)

* 15. *Tsuga heterophylla*-(*Pinus monticola*)-*Chamaecyparis nootkatensis*-*Gaultheria shallon*-*Cornus canadensis*-*Sphagnum* spp.

* 16. *Tsuga heterophylla*-*Abies amabilis*-*Vaccinium ovalifolium*-*Cornus canadensis*-*Rubus pedatus*-*Rhytidiadelphus loreus*-*Rhytidiopsis robusta*.

* *Tsuga heterophylla*-*Abies amabilis*-*Vaccinium ovalifolium*-*Cornus canadensis*-*Rubus pedatus*-*Sphagnum* spp. (Sub-association)

* 17. *Tsuga mertensiana*-(*Tsuga heterophylla*)-*Abies amabilis*-*Vaccinium ovalifolium*-*Vaccinium membranaceum*-*Rhytidiopsis robusta*.

* 18. *Thuja plicata*-(*Tsuga heterophylla*)-*Oplopanax horridus*-*Dryopteris linnaeana*.

* 19. *Tsuga heterophylla*-(*Abies amabilis*)-*Pachystima myrsinites*-*Hylocomium splendens*-*Rhytidiopsis robusta*-*Calliergonella schreberi*.

* *Tsuga heterophylla*-(*Abies lasiocarpa*)-*Pachystima myrsinites*-*Rhytidiopsis robusta*-*Calliergonella schreberi*. (Sub-association)

* 20. *Tsuga heterophylla*-*Abies amabilis*-*Vaccinium ovalifolium*-*Clintonia uniflora*-*Cornus canadensis*.

* 21. *Tsuga heterophylla*-(*Abies amabilis*)-*Thuja plicata*-*Dryopteris linnaeana*-*Mnium punctatum*.

22. *Pseudotsuga taxifolia*-(*Tsuga heterophylla*)-*Pinus monticola*-*Vaccinium membranaceum*-*Pachystima myrsinites*-*Cladonia* spp.

* 23. *Picea engelmanni*-*Abies lasiocarpa*-*Thalictrum occidentale*-*Tiarella unifoliata*.

* 24. *Picea engelmanni*-*Abies lasiocarpa*-*Vaccinium ovalifolium*-*Dryopteris linnaeana*-*Mnium punctatum*.

* 25. *Picea engelmanni*-*Abies lasiocarpa*-*Menziesia ferruginea*-*Equisetum palustre*-*Sphagnum recurvum*.

* 26. *Picea engelmanni*-*Abies lasiocarpa*-*Vaccinium membranaceum*-*Rubus pedatus*.

* 27. *Picea engelmanni*-*Abies lasiocarpa*-*Vaccinium membranaceum*-*Dicranum scoparium*-*Dicranum fuscescens*.

28. *Populus trichocarpa*-*Picea engelmanni*-*Corylus californica*-*Cornus stolonifera*.

APPENDIX II (cont'd)

* 29. Thuja plicata-Oplopanax horridus-Dryopteris linnaeana.

* 30. Thuja plicata-Athyrium filix-femina-Lysichitum americanum.

* 31. Tsuga heterophylla-Dryopteris linnaeana-Aralia nudicaulis-Clintonia uniflora-Cornus canadensis.

* 32. Tsuga heterophylla-Abies grandis-Dryopteris linnaeana-Aralia nudicaulis-Clintonia uniflora-Cornus canadensis.

* 33. Tsuga heterophylla-Pachystima myrsinites-Calliergonella

* 34. Tsuga heterophylla-Abies grandis-Pachystima myrsinites-Calliergonella schreberi.

* 35. Pseudotsuga taxifolia-Vaccinium membranaceum-Arctostaphylos uva-ursi-Dicranum scoparium-Peltigera canina.

* 36. Thuja plicata-Picea engelmanni-Abies lasiocarpa-Oplopanax horridus-Dryopteris linnaeana.

* 37. Picea engelmanni-Abies lasiocarpa-Pachystima myrsinites-Vaccinium membranaceum-Calliergonella schreberi.

* 38. Picea sitchensis-(Populus trichocarpa)-Oplopanax horridus-Athyrium filix-femina.

* 39. Thuja plicata-Tsuga heterophylla-Oplopanax horridus-Dryopteris linnaeana-Mnium spp.

* 40. Tsuga heterophylla-Abies amabilis-Vaccinium ovalifolium-Hylocomium splendens-Rhytidiadelphus loreus-Rhytidiopsis robusta.

* Tsuga heterophylla-Abies amabilis-Vaccinium ovalifolium-Sphagnum spp. (Sub-association)

* 41. Tsuga heterophylla-Abies amabilis-Dryopteris dilatata-Dryopteris linnaeana-Mnium punctatum.

* 42. Tsuga heterophylla-(Pinus contorta)-Menziesia ferruginea-Hylocomium splendens-Calliergonella schreberi.

43. Pinus contorta-(Tsuga heterophylla)-Vaccinium membranaceum-Peltigera spp.

44. Picea glauca-Alnus tenuifolia-Lonicera involucrata-Athyrium filix-femina.

APPENDIX II (cont'd)

* 45. Picea glauca-Abies lasiocarpa-Oplopanax horridus-Athyrium filix-femina.

* 46. Picea glauca-Abies lasiocarpa-Rubus parviflorus-Disporum oreganum.

* 47. Picea glauca-Abies lasiocarpa-Dryopteris linnaeana-Aralia nudicaulis.

* Picea glauca-Abies lasiocarpa-Vaccinium membranaceum-Cornus canadensis-Rhytidiadelphus triquetrus-Calliergonella schreberi. (Sub-association)

* 48. Picea glauca-(Picea mariana)-Abies lasiocarpa-Alnus tenuifolia-Equisetum sylvaticum-Sphagnum recurvum-Sphagnum squarrosum.

APPENDIX III

ECOTOPES SPECIFIC TO HABITATS WITHIN WHICH ECHINODONTIUM TINCTORIUM OCCURS IN BRITISH COLUMBIA

Association number. 1 (sub-association)

Name. Thuja plicata-(Pseudotsuga taxifolia)-Abies amabilis-Adiantum pedatum.

Occurrence. Coast Mountains and the western slopes of the Cascade mountains on alluvial benches formed by seasonal or periodic flooding but which are currently above flood level. Stands of this sub-association occur at elevations of from 700 to about 1500 feet above sea level.

Vegetation.

1. Trees. Thuja plicata has excellent development in all canopies, particularly in lower elevation stands.

   Abies amabilis has very good development up to co-dominant level above which it has reduced vigor.

   Pseudotsuga taxifolia occurs in very good vigor in the higher canopies but usually on only those portions of the sub-association that are raised above the level of the general area.

   Tsuga heterophylla has a variable occurrence that is usually confined to the lower canopies.

   Acer macrophyllum has a variable occurrence but will assume and retain dominance on denuded areas where coniferous regeneration is lacking. It has its greatest abundance at low elevations.

   Alnus oregona is a short-lived pioneer species that eventually loses dominance to either maple or coniferous species.

2. Lesser vegetation. The shrub layer varies from being complete to discontinuous but is invariably represented by Sambucus pubens, Rubus parviflorus, and R. spectabilis. Usually present are R. leucodermis and Oplopanax horridus. The herb layer is usually complete and invariably present in this layer are Adiantum pedatum, Dryopteris linnaeana, Athyrium filix-femina, Veratrum eschscholtzii, Stachys ciliata, Achlys

triphylla, Tiarella trifoliata, T. laciniata. Dominant among the mosses are Mnium punctatum, M. insigne, M. menziesii, and Plagiothecium undulatum.

Topography and soil. The topography is generally flat with low dissecting ridges. The soil is of alluvial origin and lacks stratification other than a fairly distinct humus layer. Beneath the thin layer of duff mull humus the soil has earth-mull characteristics. Sub-surface drainage is good but the soil is permanently moist.

Eco-climate. Stands of this sub-association have an aerial aspect that is continuously humid and cool, other than in the tops of dominant trees where seasonal warm temperatures occur.

Association number. 8.

Name. Pinus contorta-Ledum groenlandicum-Sphagnum spp.

Occurrence. Eastern slopes of the Coast Mountains and western slopes of the Cascade Mountains in areas immediately tributary to stagnant lakes. This association may either develop from associations number 5 and 10, in the event that sub-surface drainage is impeded, or may develop into associations 6 and 11 should unrestricted drainage ensue. It occurs from nearly sea level to about 2500 feet.

Vegetation.

1. Trees. This is a non-commercial forest association which is, however, normally adjacent to stands of other associations of economic importance. Low vigor and overstocking of trees is a normal feature of this association. Pinus contorta and P. monticola dominate the highest canopy whereas Tsuga heterophylla and Thuja plicata dominate in the lower canopies at low elevations and Tsuga mertensiana and Chamaecyparis nootkatensis at higher elevations.

2. Lesser vegetation. The shrub layer is normally well developed and invariably present are Ledum groenlandicum, Kalmia polifolia, Gaultheria shallon and Vaccinium oxycoccus. Usually present are Myrica gale and Vaccinium uliginosum. The herb layer is less well developed although invariably present are Cornus canadensis, Drosera rotundifolia, D. longifolia, Trientalis arctica, Maianthemum

APPENDIX III (cont'd)

dilatatum and Eriophorum sp. The moss layer is usually complete and is dominated by Sphagnum capillaceum, S. fuscum, S. recurvum, S. rubellum, Hylocomium splendens, Calliergonella schreberi and Polytrichum juniperinum. Corticolous lichens are abundant from close to the ground line to the tops of trees.

Topography and soil. The topography varies from flat to gently sloping. The soil is continuously wet other than for a seasonal drying of the upper layers of humus. The humus layer is thick, peaty and overlies a mineralized soil that has the consistency of black muck. Such soils are very acid.

Eco-climate. The higher canopies of stands of this association are open and have a very dry seasonal aspect. The lower canopies, shrub, herb, and moss layers are more sheltered and exhibit constant high humidities and moderate temperatures.

Association number. 11.

Name. Tsuga heterophylla-(Pseudotsuga taxifolia)-Gaultheria shallon-Camptothecium megaptilum-Hylocomium splendens-Rhytidiopsis robusta.

Occurrence. Eastern slopes of the Coast Mountains and western slopes of the Cascade Mountains on upper slopes and on the crests of gently rolling hills. It occurs at elevations of from about 1500 feet to about 3000 feet above sea level.

Vegetation.

1. Trees. Tsuga heterophylla occurs in all canopies in fair vigor. It rarely occupies the highest canopy in young stands where Douglas fir dominates.

   Pseudotsuga taxifolia is often the dominant species in young stands, together with western white pine, but it leaves the association at an early age other than for a few scattered trees.

   Abies amabilis remains in the lower canopies for so long as Douglas fir remains co-dominant with western hemlock but it eventually follows hemlock into the highest canopy. It occurs only in reduced vigor.

   Pinus monticola has a low frequency in the highest canopy of older stands but has a greater abundance in younger stands.

APPENDIX III (cont'd)

Thuja plicata has fairly good vigor and abundance up to co-dominant level but does not occur in the highest canopy in older stands.

Chamaecyparis nootkatensis occurs only sporadically and in the lower canopies.

2. Lesser vegetation. The shrub layer is often nearly complete. Invariably present in this layer are *Gaultheria shallon*, *G. ovatifolia*, *Vaccinium ovalifolium*, *V. parvifolium*, and *V. membranaceum*. The herbs are few in species and normally low in abundance. Usually present in this layer are *Chimaphila umbellata*, *Viola orbiculata*, *Listera nephrophylla*, *Goodyera decipiens*, *Linnaea borealis* and *Pyrola* spp. The moss layer is usually complete and is dominated by *Camptothecium megaptilum*, *Hylocomium splendens* and *Rhytidiopsis robusta*.

Topography and soil. The topography varies from being flat to slopes of moderate steepness. Podzolised brown soils, usually of glacial origin, characterize this association. A raw humus layer that varies up to four inches in thickness may overlie a thin layer of duff mull humus. Leaching may occur in a continuous horizon but more commonly occurs in pockets in proximity to stones and roots. The mineralised portion of the soil has a sand and gravel texture and a granular to cemented structure. Cementation occurs usually below 18 inches if at all. If an orstein is present there is usually some evidence of gleization. The profile is seasonally dry down to about 20 inches, below which it is continuously moist.

Eco-climate. Stands of this association are often exposed to near maximum wind influence for the region and as a consequence have a seasonally dry aerial aspect. Temperature and humidity extremes for the region regularly occur in this association, for most of such stands are fairly open, particularly in the higher canopies.

Association number. 12.

Name. *Tsuga heterophylla*-*Abies amabilis*-*Blechnum spicant*-*Tiarella trifoliata*.

Occurrence. Coast Mountains and the western slopes of the Cascade Mountains on the lower portions of slopes

APPENDIX III (cont'd)

or on well-drained alluvial flats. It occurs at elevations of from about 200 to 2000 feet above sea level, reaching its highest elevations on the eastern slopes of the Coast Mountains.

Vegetation.

1. Trees. This is a highly productive site from the aspect of tree growth.

Tsuga heterophylla occurs regularly in all canopies in excellent vigor.

Pseudotsuga taxifolia is often present in the highest canopy. It has a sporadic occurrence in older stands but may have a good distribution in younger stands.

Abies amabilis occurs regularly in all canopies and usually in good vigor. It sometimes is the major species in the lower canopies.

Thuja plicata usually has a regular occurrence in all canopies, but is usually much less abundant than are western hemlock and amabilis fir.

Picea sitchensis has a fairly regular occurrence in low elevation stands but occurs only in the highest canopy and with sporadic frequency.

Alnus oregona usually pioneers denuded areas of this association but does not occur in mature stands.

2. Lesser vegetation. The shrub layer is often discontinuous, except in the more moist and open portions of stands where Rubus spectabilis and Sambucus pubens dominate. This layer is otherwise represented by a low frequency of Vaccinium parvifolium, V. ovalifolium. The herb layer is almost always well developed. It is dominated by Blechnum spicant, Dryopteris dilatata, D. linnaeana, Achlys triphylla and Tiarella trifoliata. The moss layer is likewise often complete. It is dominated by Mnium punctatum, M. insigne, Eurhynchium oreganum, and Rhytidiadelphus loreus.

Topography and soil. The topography varies from being flat to slopes of considerable steepness. Weakly podzolised brown soils characterise this association. They may be either of glacial or alluvial origin, although the latter predominate. The humus layer is distinct and varies up to at least five inches in depth. It is either of duff-mull quality or raw humus, in which case there is usually a thin underlying layer of duff mull. Most of such soils are deep, lack a

APPENDIX III (cont'd)

distinct podzol horizon and are either silty-sands or sand and gravel loams. They are continuously moist throughout their depth and are seasonally wet at the surface. Gleization occurs regularly and usually within 18 inches of the soil surface.

Eco-climate. Most stands of this association are reasonably sheltered from wind influences other than in the tops of the higher tree canopies by reason of both their topographic location and the density of stocking. Such stands have aerial aspects that are continuously humid and cool.

Association number. 13.

Name. Tsuga heterophylla-(Thuja plicata)-Abies amabilis-Vaccinium parvifolium-V. ovalifolium-Hylocomium splendens-Rhytidiadelphus loreus.

Occurrence. Coast Mountains and the western slopes of the Cascade Mountains on well-drained benches or slopes at elevations of from about 1000 to 2500 feet above sea level. Stands of this association occur at their lowest elevations on the western slope of the Coast Mountains and are often fragmentary within larger areas of association number 12.

Vegetation.

1. Trees. Tsuga heterophylla is characteristically the major species by volume and frequency. It has good vigor in all canopies, although slightly reduced from that in association number 12.

Abies amabilis occurs in good vigor in all canopies but has its greatest frequency in the lower canopies.

Thuja plicata occurs in all canopies in most stands but does not normally compete successfully with western hemlock and amabilis fir in mature stands.

Pseudotsuga taxifolia is a minor species of low vigor in older stands but is sometimes a major dominant in young stands, provided such stands have had their origin in denuded areas.

Pinus monticola has a similar occurrence and development to that of Douglas fir.

APPENDIX III (cont'd)

2. Lesser vegetation. The shrub layer is characteristically fully developed and is dominated by *Vaccinium ovalifolium* and *V. parvifolium*. Usually present in this layer are *Gaultheria shallon*. and *Mahonia nervosa*. The herb layer is normally poorly developed and often almost lacking. When herbs occur, invariably present are *Cornus canadensis*, *Rubus pedatus* and *Achlys triphylla*, while usually present are *Linnaea borealis*, *Pyrola secunda*, *Listera nephrophylla*, and *Dryopteris linnaeana*. The moss layer is normally complete and is dominated by *Hylocomium splendens*, and *Rhytidiadelphus loreus*. Of less frequent occurrence are *Rhytidiopsis robusta* and *Plagiothecium undulatum*.

Topography and soil. The topography varies from being flat to steeply sloping, although most stands of this association occur on gentle slopes. Podzolized brown soils that are mainly of glacial origin characterize this association. Such soils have a thick, raw humus that varies up to 14 inches in depth and a distinct podzol horizon of about one inch deep. The mineralized portion of the soil is usually a sand and gravel loam, and has a granular structure at the surface that changes to being either compacted or cemented in the depth. These soils may be of either glacial or alluvial origin. Those of alluvial origin are deep while those of glacial origin are often shallow. Subsurface drainage is very good, although sub-surface irrigation is equally good and is effective for most of the soil depth throughout the year. Gleization often occurs deep in the profile, frequently above an ortstein layer.

Eco-climate. A combination of increased wind influence and a more open structure in stands of this association, from those of association number 12, normally results in a seasonally dry aerial environment that reaches down to the co-dominant level of trees.

Association number. 14.

Name. *Tsuga heterophylla*-(*Abies amabilis*)-*Thuja plicata*-*Vaccinium ovalifolium*-*V. parvifolium*-*Gaultheria shallon*-*Cornus canadensis*.

Occurrence. Coast Mountains and on the western slope of the Cascade Mountains. Stands of this association occur mainly

APPENDIX III (cont'd)

on steep slopes at elevations of from 1000 to 3000 feet above sea level. They occur at their lower elevations in the Coast Mountains and at their higher elevations in the Cascade Mountains.

Vegetation.

1. Trees. Tree growth is reduced from that obtained in associations number 12 and 13, particularly as to height growth.

Tsuga heterophylla occurs in all canopies and in mature stands is normally the major species by volume and frequency.

Thuja plicata occurs in all canopies in good vigor except at the higher elevations where it tends to be replaced by yellow cypress.

Abies amabilis occurs in all canopies but has its greatest frequency and vigor in the lower canopies.

Chamaecyparis nootkatensis has increasing abundance with increasing altitude and occurs only in the lower canopies at lower elevations.

Pseudotsuga taxifolia has only a sporadic occurrence in mature stands, always in the highest canopy and in reduced vigor. It is often absent, particularly at higher elevations.

Pinus monticola has a similar occurrence to that of Douglas fir.

Taxus brevifolia occurs in the lower canopies in good vigor and often in good abundance.

2. Lesser vegetation. The shrub layer is invariably well developed and is dominated by *Vaccinium ovalifolum*, *V. parvifolium* and *Gaultheria shallon*. The herb layer varies greatly as to its luxuriance but invariably present are *Cornus canadensis*, *Achlys triphylla*, *Blechnum spicant*, *Listera nephrophylla*, *Linnaea borealis* and *Goodyera decipiens*. Usually present are *Pyrola uniflora* and *Chimaphila menziesii*. The moss layer is often complete. It is dominated by *Rhytidiadelphus loreus*, *Eurhynchium oreganum*, and *Hylocomium splendens*. At higher elevations *Rhytidiopsis robusta* is

present. Sphagnum recurvum has a scattered occurrence in areas where surface drainage is impeded.

Topography and soil. Stands of this association regularly occur on moderate to very steep slopes. Podzolized brown soils of glacial origin are characteristic. The parent material may be either glacial deposit or alluvial deposit from glacial rivers. Bedrock is often close to the surface and outcrops are common. There is a distinct raw humus layer that varies from two up to 12 inches in depth. Leaching is usually evident as a distinct horizon but often penetrates to more than 12 inches, depending largely upon the stoniness of the ground. The texture of the mineral portion of the soil is sand and gravel loam with silts sometimes present. They are normally granular near the surface and vary from aggregated to densely compacted in the depth. Cementation is uncommon as is gleization. Subsurface drainage is usually good but is sometimes impeded according to the arrangement of large stones and the configuration of the bedrock. Most of these soils are consistently moist and are often wet in their depth.

Eco-climate. Most stands of this association have unrestricted air drainage in the higher canopies only. Air temperatures are consistently moderate in the lower canopies but are seasonally high above. Atmospheric humidities are consistently high in the lower canopies but are much less so in the higher canopies.

Association number. 15.

Name. Tsuga heterophylla-(Pinus monticola)-Chamaecyparis nootkatensis-Gaultheria shallon-Cornus canadensis-Sphagnum spp.

Occurrence. Coast Mountains and the western slopes of the Cascade Mountains on poorly-drained soils resulting from the configuration of the bedrock which lies close to the soil surface. Stands of this association occur at elevations of from about 1500 to 3000 feet above sea level. The association often occurs as fragments within more extensive areas of associations number 13 and 14.

Vegetation.

1. Trees. Tsuga heterophylla occurs in all canopies but in low vigor, particularly in the highest canopy.

Pinus monticola occurs in the higher canopies but usually in low vigor. It has a scattered

APPENDIX III (cont'd)

distribution in older stands but may be abundant in young stands.

Chamaecyparis nootkatensis normally occurs in all canopies but only in moderate vigor. It has its greatest abundance at higher elevations and may be replaced at lower elevations by western red cedar.

Thuja plicata has its greatest frequency in the lower canopies. It has extreme low vigor in the highest canopy.

Tsuga mertensiana has a high frequency in high-elevation stands where it occurs in the lower canopies, except in very old stands where it may occupy the dominant canopy.

Abies amabilis has an extremely variable distribution. When it is present it is usually confined to the lower canopies where it has low vigor.

Pseudotsuga taxifolia has its greatest frequency in young stands and if present in older stands it will occur infrequently and in low vigor.

Taxus brevifolia occurs only in the lower canopies in low vigor.

2. Lesser vegetation. The association presents a luxuriant aspect by reason of a fully developed shrub layer. Invariably present are Vaccinium ovalifolium and Gaultheria shallon and usually present are Vaccinium parvifolium and Ribes sanguineum. The herb layer is usually less well developed but often has a good distribution of Cornus canadensis and Rubus pedatus. Other herbs that are usually present are Lysichitum americanum, Clintonia uniflora, Lycopodium annotinum and Veratrum eschscholtzii. The moss layer is usually complete except for rock outcrops and is dominated by Hylocomium splendens, Rhytidiadelphus loreus and Rhytidiopsis robusta in the better drained areas and by Sphagnum spp., Plagiothecium undulatum, Mnium punctatum and M. insigne in the wetter areas.

Topography and soil. The topography is usually flat but with numerous low hummocks. The soil is of glacial origin and may consist mainly of humus

APPENDIX III (cont'd)

accumulations over a very shallow layer of mineralised soil. The humus varies up to eight inches thick and is of very poor quality. Podsolisation invariably occurs and may reach downward for more than 14 inches in proximity to roots and stones. Bedrock is usually close to the surface and rock outcrops are normal. Such soils are wet and are acid throughout their depth by reason of ground water accumulation.

Eco-climate. Most stands of this association are wind-exposed. Extreme drying conditions occur seasonally down to the top of the shrub layer, below which a constantly humid atmosphere occurs.

Association Number. 16.

Name. Tsuga heterophylla-Abies amabilis-Vaccinium ovalifolium-Cornus canadensis-Rubus pedatus-Rhytidiadelphus loreus-Rhytidiopsis robusta.

Occurrence. Coast Mountains and the western slopes of the Cascade Mountains at altitudes of from 1600 to about 3800 feet above sea level. Stands of this association are either intermixed with associations number 13, 14, 15, and 17 or lie above them.

Vegetation.

1. Trees. Tsuga heterophylla is interchangeable with amabilis fir as the major species. It has a high frequency and good vigor in all canopies but lacks the height growth it attains in associations number 13 and 14.

Abies amabilis occurs in all canopies and with good vigor.

Chamaecyparis nootkatensis reaches its maximum development in this association where it occurs in all canopies.

Thuja plicata has at best a scattered occurrence in this association. It has poor vigor.

Tsuga mertensiana has its greates frequency up to co-dominant level and if present in the dominant canopy it occurs in reduced vigor.

Pseudotsuga taxifolia is normally absent but if present it occurs in low vigor and frequency in the highest canopy.

APPENDIX III (cont'd)

Pinus monticola is often present as a scattered species in the highest canopy.

Taxus brevifolia is rarely present but, if so, it occurs in low vigor in the lowest canopy.

2. Lesser vegetation. The shrub layer is well developed. Invariably present in this layer are Vaccinium ovalifolium and, at low elevations, V. parvifolium. Usually present are Gaultheria shallon, G. ovatifolia, and Mahonia nervosa. The herb layer is usually well developed. Invariably present in this layer are Rubus pedatus, Pyrola secunda, Cornus canadensis, Linnaea borealis, Blechnum spicant and Chimaphila menziesii. Usually present are Clintonia uniflora, Listera nephrophylla, Chimaphila umbellata and Moneses uniflora. The moss layer is usually well developed and is sometimes complete. It is dominated by Rhytidiopsis robusta and Rhytidiadelphus loreus. Usually present are Hylocomium splendens, Mnium punctatum and Dicranum fuscescens.

Topography and soil. Stands of this association occur on steep to moderate slopes and on benches, provided sub-surface drainage is good. When sub-surface drainage is seriously impeded the association is replaced by either a Sphagnum variation of it or by association number 15. The soil is of glacial origin and is usually strongly podzolised and acid in its upper layers. There is a raw humus layer of from six to 12 inches thickness. Except for the occurrence of large stones the soil is usually 30 or more inches deep. The texture of the soil is almost invariably sand and gravel loam. Such soils are permanently moist and are usually gleisate in the depth.

Eco-climate. Most stands of this association are wind exposed and tend to have an open structure in their higher canopies at maturity. Such stands have a seasonally warm aerial aspect from above the shrub layer to the tops of trees. Atmospheric humidities are consistently high by reason of protracted and heavy snow cover, abundant soil moisture and a high evaporation rate.

Association number. 16 (sub-association)

Name. Tsuga heterophylla-Abies amabilis-Vaccinium ovalifolium-Cornus canadensis-Rubus pedatus-Sphagnum spp.

Occurrence. Stands of this association occur usually as fragments within more extensive areas of association number 16. They occur in circumstances where sub-surface drainage is impeded to the extent that surface accumulations of water persist for most of the year. Such stands have an open structure in all stages of their development to maturity. Tree growth is much reduced from that of surrounding associations.

Association number. 17.

Name. Tsuga mertensiana-(Tsuga heterophylla)-Abies amabilis-Vaccinium ovalifolium-V. membranaceum-Rhytidiopsis robusta.

Occurrence. Coast Mountains and the western slopes of the Cascade Mountains at elevations normally above 3500 feet. Stands of this association represent approximately the upper limits of merchantable stands in the coast forest region.

Vegetation.

1. Trees. Tsuga mertensiana is the main species by volume in the highest canopy. It occurs in good vigor in all canopies except at the highest elevations.

Abies amabilis has limited distribution in the dominant canopy but often has a high frequency in the lower canopies. Its vigor in all canopies is low.

Tsuga heterophylla does not occur in the highest canopy and has only a sporadic occurrence in the lower canopies.

Pinus monticola sometimes occurs in the highest canopy, but only in low frequency.

2. Lesser vegetation. The shrub layer is extremely variable as to its continuity. Invariably present, however, are Vaccinium ovalifolium, V. membranaceum, and Rhododendron albiflorum. The herb layer is poorly developed both as to the number of species and their frequency but usually present are Rubus pedatus, Viola orbiculata, and Pyrola secunda. The moss layer is usually complete. Rhytidiopsis robusta dominates this layer and Mnium spinulosum and Dicranum fuscescens occur in lower frequency.

APPENDIX III (cont'd)

Topography and soil. The topography varies from moderate to very steep slopes and occasionally to well drained benches. The soil is a mountain podsol with a thick raw humus. The podsol horizon is continuous and varies up to five inches in thickness. The soil is of glacial origin, has a sand and gravel loam texture and is normally shallow, not exceeding 18 inches in depth. The soil is seasonally very dry at the surface but is continuously moist in its depth.

Eco-climate. Stands of this association have close to maximum wind exposure for the region. They have a seasonally dry atmosphere above the intermediate level of trees but have a continuously humid climate below.

Association number. 18.

Name. Thuja plicata- (Tsuga heterophylla)-Oplopanax horridus-Dryopteris linnaeana.

Occurrence. Cascade Mountains at elevations of from 1000 feet to more than 3000 feet above sea level on alluvial flood plains bordering and at the confluence of mountain streams. Stands of this association are often fragmentary, particularly at higher elevations.

Vegetation.

1. Trees. Thuja plicata is the major species in the highest canopy and has generally very good vigor. It is sometimes replaced to a large degree in older stands by western hemlock.

Tsuga heterophylla usually reaches the highest canopy only with a scattered occurrence. It has a good distribution and good vigor in the lower canopies.

Pseudotsuga taxifolia does not occur in the oldest stands nor at the highest elevations. It has a scattered occurrence at low elevations and sometimes a good distribution in younger stands.

Picea engelmanni occurs at higher elevations in the highest canopy only. It has only a scattered frequency and is eventually replaced by western red cedar.

Abies amabilis occurs mainly in the lower canopies and usually only in low vigor and frequency.

APPENDIX III (cont'd)

Acer glabrum occurs only in the lower canopies in older stands but is often the dominant plant in young stands or in openings of older stands.

2. Lesser vegetation. The shrub layer is luxuriant mainly by reason of the occurrence of _Oplopanax horridus_. Less common but usually present are _Sorbus sitchensis_, _Vaccinium ovalifolium_, _Rubus parviflorus_, _R. spectabilis_, and _Cornus stolonifera_. The herb layer is usually complete. Invariably present and dominant are _Dryopteris linnaeana_, _Tiarella unifoliata_, _Streptopus roseus_, _Clintonia uniflora_, and _Cornus canadensis_. Usually present in this layer are _Athyrium filix-femina_, and _Trillium ovatum_. The moss layer is fairly complete with _Mnium punctatum_, _M. spinulosum_, _M. insigne_ and _Rhytidiadelphus triquetrus_ dominating.

Topography and soil. The topography is either flat or very gently sloping. Scattered low hummocks often occur throughout a generally low-lying and flat area. The soil is deep and has a definite raw humus that overlies a thinner layer of duff mull. A shallow and discontinuous podsol horizon overlies a deep sand and gravel or silty loam. The soil is moist throughout its depth but has excellent sub-surface drainage.

Eco-climate. Stands of this association are usually well sheltered from wind influences. Being situated in a region of high summer temperatures, such stands have a seasonally warm and continuously humid aerial aspect.

Association number. 19.

Name. _Tsuga heterophylla_-(_Abies amabilis_)-_Pachystima myrsinites_-_Hylocomium splendens_-_Rhytidiopsis robusta_-_Calliergonella schreberi_.

Occurrence. Cascade Mountains at elevations of from 1400 to 4000 feet above sea level. Stands of this association occur on well drained but sub-irrigated slopes and benches. Such stands normally lie adjacent to or above association number 18.

Vegetation.

1. Trees. _Tsuga heterophylla_ occurs in all canopies with fair vigor, being the major species by volume and frequency in the highest canopy.

APPENDIX III (cont'd)

Abies amabilis occurs in all canopies but has its greatest vigor and abundance below co-dominant level.

Picea engelmanni is often absent and has only a scattered distribution in the highest canopy when present.

Pseudotsuga taxifolia often has a good occurrence in young stands but is gradually and completely replaced by western hemlock. It has good vigor in young stands.

Pinus monticola has a similar occurrence to that of Douglas fir but is more persistent in older stands.

Thuja plicata has a variable occurrence in all canopies. It has its greatest frequency and vigor in the lower canopies and at lower elevations.

Taxus brevifolia has a consistent occurrence and very good vigor in the lower canopies.

2. Lesser vegetation. The shrub layer is usually well developed, being dominated by Pachystima myrsinites, Vaccinium membranaceum, and V. ovalifolium. Usually present but in lower frequency are Rhododendron albiflorum, Rosa gymnocarpa, and Sorbus sitchensis. The herb layer varies considerably as to its luxuriance but is invariably represented by Linnaea borealis, Clintonia uniflora, Cornus canadensis, Chimaphila umbellata, and Pyrola bracteata. Less common but usually present are Rubus pedatus, Pyrola secunda, Listera nephrophylla, and Chimaphila menziesii. The moss layer is usually complete. Always present in this layer are Calliergonella schreberi, Rhytidiopsis robusta, and Hylocomium splendens and usually present are Rhytidiadelphus triquetrus and Ptilium crista-castrensis.

Topography and soil. The topography varies from flat to slopes of from five up to 60 degrees. The soil is strongly podsolized, of glacial or alluvial origin, and has a raw humus layer that varies in thickness up to 10 inches. The podsol horizon varies from one-quarter inch to at least five inches thick and often penetrates in pockets to much greater depths. Sand and gravel loams predominate and soil depths vary from 14 to 40 inches. Gleization often occurs but always deep in the profile. The soil structure is usually

APPENDIX III (cont'd)

granular at the surface becoming aggregated or compacted in the depth. Cementation sometimes occurs but is not a regular feature of these soils. Sub-surface drainage is good as is sub-surface irrigation. Such soils are continuously moist in their depth and are seasonally dry only in the moss and humus layers.

Eco-climate. Stands of this association vary considerably in their exposure to wind although a heavy and protracted snow cover, abundant soil moisture, and generally high summer temperatures contribute to a seasonally warm, humid, aerial aspect from the ground line to the tops of trees.

Association number. 19 (sub-association)

Name. Tsuga heterophylla-(Abies lasiocarpa)-Pachystima myrsinites-Rhytidiopsis robusta-Calliergonella schreberi.

Occurrence. Stands of this sub-association occur normally above those of association number 19 and often as fragments within more extensive areas of associations number 23-27 inclusive. They occur normally above 4000 feet to about 4800 feet above sea level.

Association number. 20.

Name. Tsuga heterophylla-Abies amabilis-Vaccinium ovalifolium-Clintonia uniflora-Cornus canadensis.

Occurrence. Cascade Mountains at elevations of from 1000 to 3800 feet above sea level on well drained slopes. Stands of this association represent conditions that are the most favorable to growth of western hemlock and amabilis fir in the southern portion of the Cascade Mountain region.

Vegetation.

1. Trees. Tsuga heterophylla occurs in all canopies in excellent vigor. It shares the dominant canopy with amabilis fir by which it is sometimes replaced in very old stands.

Abies amabilis occurs in all canopies with excellent vigor.

Thuja plicata is often lacking in very old stands but usually occurs in mature stands in all canopies even though in reduced vigor.

APPENDIX III (cont'd)

Pseudotsuga taxifolia may have a high frequency in the highest canopy of young stands but is either absent from older stands or has at best only a sporadic occurrence.

Taxus brevifolia has a variable occurrence that is always confined to the lower canopies.

2. Lesser vegetation. The shrub layer is often complete with *Vaccinium ovalifolium* dominating. Usually present in this layer are *V. membranaceum*, *Oplopanax horridus*, *Rhododendron albiflorum*, *Sorbus sitchensis*, and *Rubus spectabilis*. The herb layer is luxuriant both as to the number of species and their frequency. Always present and dominating are *Clintonia uniflora*, *Cornus canadensis*, *Tiarella unifoliata*, and *Pyrola secunda*. Usually present are *Rubus pedatus*, *Linnaea borealis*, *Lycopodium annotinum*, *Chimaphila menziesii*, *Streptopus roseus*, and *Listera nephrophylla*. The moss layer varies from being almost complete to "nudum". When mosses occur *Rhytidiopsis robusta* and *Calliergonella schreberi* are always present. Usually present are *Rhytidiadelphus loreus*, *R. triquetrus*, and *Hylocomium splendens*.

Topography and soil. The topography varies from gentle to very steep slopes and considerable variation may be experienced within a single stand. The soil may be of either glacial or alluvial origin, usually the former, and has a raw humus that varies up to eight inches thick but which is usually of good quality. There is a well defined podsol layer that varies up to four inches in depth, although leaching often penetrates to much greater depths around stones and roots. The mineral portion of the soil varies from 18 inches to more than 36 inches. A sand and gravel loam texture is normal for these soils. The soil is granular near the surface, becoming aggregated, compacted, or cemented in the depth. Gleization is common, particularly in old alluvial soils. The profile is continuously moist and seasonally wet.

Eco-climate. Most of such stands are sheltered from wind influences. Summer temperatures are normally high and atmospheric humidities are consistently high by reason of heavy and protracted snow cover which may persist for more than seven months.

APPENDIX III (cont'd)

Association number. 21.

Name. Tsuga heterophylla-(Abies amabilis)-Thuja plicata-Dryopteris linnaeana-Mnium punctatum.

Occurrence. Cascade Mountains on the lower slopes of steep hills and adjacent to but above the flood influence of mountain streams. This association occurs in close proximity to either association number 18, from which it may develop, or associations number 19 and 20. Tree growth is generally very good in this association.

Vegetation.

1. Trees. Tsuga heterophylla occurs regularly in all canopies with very good vigor.

   Pseudotsuga taxifolia occurs regularly in the highest canopy in young stands but is replaced by western hemlock and western red cedar in older stands.

   Thuja plicata occurs regularly in all canopies and in good vigor.

   Abies amabilis occurs only irregularly in the dominant canopy but is regularly present in lower canopies. It has low vigor even in the lower canopies.

   Taxus brevifolia occurs irregularly and always in the lower canopies, but with good vigor.

2. Lesser vegetation. The extent and luxuriance of shrub cover varies greatly and reaches its maximum development in stand openings. Oplopanax horridus, Vaccinium ovalifolium, Ribes lacustre, Rubus spectabilis, R. parviflorus, and Sambucus pubens are normally present. The herb layer is invariably well developed. Dryopteris linnaeana, Athyrium filix-femina, Tiarella unifoliata, Clintonia uniflora, Cornus canadensis, Galium triflorum, Linnaea borealis, Rubus pedatus, and Streptopus roseus are invariably present. Usually present are S. amplexifolius, Viola glabella, Disporum oreganum and Blechnum spicant. The extent of moss cover varies considerably. In the more moist areas Mnium punctatum, M. insigne, M. affine, and Eurhynchium stokesii dominate while in the drier areas of the same stand Rhytidiadelphus triquetrus, Rhytidiopsis robusta and Mnium spinulosum dominate.

Topography and soil. The topography may be either flat or steeply sloping. The soils are either of glacial

APPENDIX III (cont'd)

or alluvial origin but in all cases are continuously moist and, usually, with seasonal accumulations of surface water. There is usually a deep raw humus that overlies a thinner layer of duff mull. Leaching occurs, but not always in a well defined horizon. The mineral soil is usually deep and has a sand and gravel loam texture with some silts often present. The structure varies from granular at the surface to compacted in the depth. Ortstein formation is uncommon. Gleization often occurs and sometimes close to the surface. Sub-surface irrigation and drainage is normally excellent.

Eco-climate. Atmospheric humidities are consistently high and temperatures are seasonally warm, particularly in the upper canopies.

Association number. 23.

Name. Picea engelmanni-Abies lasiocarpa-Thalictrum occidentale-Tiarella unifoliata.

Occurrence. Sub-alpine portions of the Cascade Mountains and high elevation forests of south central interior plateaux at elevations of from 4300 to 5600 feet above sea level. Stands of this association are located on former flood plains of streams and lakes but are at present above the level of seasonal or periodic flooding.

Vegetation.

1. Trees. Picea engelmanni attains its maximum development for the region in this association. It occurs with good vigor in all canopies other than in the lowest canopy where its frequency and vigor are less.

Abies lasiocarpa attains very good development in all canopies and in older stands it may completely replace engelmann spruce.

Abies amabilis has a sporadic occurrence in the Cascade Mountain stands of this association where it occurs only in the lower canopies and with low vigor.

Alnus tenuifolia has an irregular occurrence but often pioneers the association on denuded areas. It occurs mainly in openings in older stands.

2. Lesser vegetation. The shrub layer is often very well developed. Invariably present are

APPENDIX III (cont'd)

Menziesia ferruginea, *Vaccinium membranaceum*, *Lonicera utahensis*, and *Ribes lacustre*. Usually present are *Rhododendron albiflorum*, *Sorbus sitchensis*, *Rubus parviflorus*, *Oplopanax horridus*, and *Cornus stolonifera*. The herb layer is normally complete. Invariably present are *Thalictrum occidentale*, *Tiarella unifoliata*, *Streptopus amplexifolius*, *S. roseus*, *Valeriana sitchensis*, *Viola glabella*, *Rubus pedatus*, *Arnica latifolia*, *Pedicularis scopulorum*, and *Listera nephrophylla*. Usually present are *Heracleum lanatum*, *Dryopteris linnaeana*, *Cornus canadensis*, *Athyrium filix-femina*, and *Equisetum palustre*. The extent of the moss layer varies considerably, although *Mnium punctatum* and *Brachythecium* spp. are invariably present. Usually present but in lesser abundance are *Mnium affine* and *M. spinulosum*.

Topography and soil. The topography is either flat or gently sloping. Most of the soils are of an alluvial origin and have a thin raw humus over a thicker layer of duff mull. Leaching occurs but is seldom expressed as an horizon. The soil texture is silty-sand and the structure is granular, with compaction and incipient ortstein formation occurring in the depth. Gleization is invariably present and often close to the surface. The soil is deep and consistently moist.

Eco-climate. Stands of this association have a continuously humid atmosphere up to, and usually including, the dominant tree level. Air temperatures are seasonally warm in the higher canopies but are continuously cool below. Air drainage is normally restricted other than in the tops of dominant trees.

Association number. 24.

Name. *Picea engelmanni*-*Abies lasiocarpa*-*Vaccinium ovalifolium*-*Dryopteris linnaeana*-*Mnium punctatum*.

Occurrence. Sub-alpine portions of the Cascade Mountains and high elevation forests of south central interior plateaux at elevations of from 4800 to 5500 feet above sea level. Stands of this association occur on the lower slopes of hills where ground water movement is free and conspicuous in its influence upon the soil.

Vegetation.

1. Trees. *Picea engelmanni* has close to maximum growth for the region in stands of this association. It has its greatest abundance and vigor in the higher canopies but normally occurs in all canopies.

APPENDIX III (cont'd)

Abies lasiocarpa has very good development in all canopies and sometimes replaces engelmann spruce to a large extent in older stands.

Pinus contorta has only a very sporadic occurrence in older stands, always in the highest canopy. It often pioneers denuded areas.

Thuja plicata has very low vigor and usually only a sporadic occurrence in the lower canopies.

Tsuga mertensiana has a variable occurrence up to co-dominant level in stands of the Cascade Mountain region.

2. Lesser vegetation. The shrub layer is well developed and invariably includes *Menziesia ferruginea*, *Vaccinium ovalifolium*, and *V. membranaceum*. Usually present in this layer are *Cornus stolonifera*, *Sorbus sitchensis*, *Ribes lacustre*, and *Lonicera utahensis*. The herb layer is equally well developed and invariably includes *Dryopteris linnaeana*, *Streptopus roseus*, *Rubus pedatus*, *Tiarella unifoliata*, *Lycopodium annotinum* and *Valeriana sitchensis*. Usually present are *Clintonia uniflora*, *Viola glabella*, *Veratrum eschscholtzii*, *Cornus canadensis*, *Listera nephrophylla*, and *Pedicularis racemosa*. The moss layer is rarely complete but invariably present are *Mnium punctatum*, *Brachythecium* spp., *Calliergonella schreberi*, and *Ptilium crista-castrensis*.

Topography and soil. The topography is either flat or gently sloping. The soils are of either glacial or alluvial origin and are slightly podzolized, although a distinct podzol horizon is often lacking. The humus varies from up to eight inches of raw humus above a thinner layer of duff mull to only two inches of raw humus. The mineral soil varies from 18 to more than 30 inches in depth, has a sand and gravel and, sometimes, silty texture, and varies from being granular at the surface to either aggregated, compacted or, rarely, cemented in the depth. Gleization normally occurs, often high in the mineral soil zone. Such soils are moist throughout their depth for most of the year and are seasonally wet. Sub-surface drainage is usually good but is sometimes impeded by accumulations of glacial rocks.

Eco-climate. Stands of this association are often very wind-exposed. They have an open aspect at maturity, particularly in the upper canopies, that results in seasonally warm temperatures and low humidities in the upper tree layers.

APPENDIX III (cont'd)

On the other hand, there is a continuously humid and seasonally warm stratum of air that blankets the lower levels of trees.

Association number. 25.

Name. *Picea engelmanni-Abies lasiocarpa-Menziesia ferruginea-Equisetum palustre-Sphagnum recurvum.*

Occurrence. Sub-alpine portions of the Cascade Mountains and high elevation forests of south central interior plateaux at elevations similar to those of associations 23 and 24. Stands of this association often occur as fragments within larger areas of associations number 23, 24, and 26.

Vegetation.

1. Trees. *Picea engelmanni* occurs in all canopies with low vigor.

   Abies lasiocarpa occurs in all canopies in low vigor. It has a greater frequency in the lower canopies than does engelmann spruce.

   Alnus tenuifolia occurs regularly in stands of all ages but has its greatest frequency in young stands.

2. Lesser vegetation. The shrub layer is usually well developed and is dominated by *Menziesia ferriginea*, *Vaccinium ovalifolium*, and *Rhododendron albiflorum*. The herb layer is also well developed and invariably present in this layer are *Equisetum palustre*, *E. pratense*, *Veratrum eschscholtzii*, *Streptopus roseus*, and *Tiarella unifoliata*. Less common but usually present are *Habenaria* spp., *Lycopodium annotinum*, *Rubus pedatus*, and *Listera cordata*. The moss layer is usually complete by reason of the abundance of *Sphagnum recurvum*. *Mnium punctatum*, *M. affine*, and *Calliergonella schreberi* are usually present, although less common.

Topography and soil. The topography is either flat or very gently sloping. The soil lacks definite stratification other than a fairly distinct raw to duff mull humus. The remainder of the soil is composed of cumulose deposit that has been mineralized to a variable degree. Such soils are continuously wet and are very acid. Sub-surface drainage is greatly impeded, usually by the configuration of underlying bedrock.

APPENDIX III (cont'd)

Meso-climate. The open structure of stands of this association contribute to a seasonally dry and warm aerial aspect other than for a low stratum of warm humid air that reaches up to about the level of the shrub layer.

Association number. 26.

Name. Picea engelmanni-Abies lasiocarpa-Vaccinium membranaceum-Rubus pedatus.

Occurrence. Sub-alpine portions of the Cascade Mountains and high elevation stands of south central interior plateaux. Stands of this association occur at elevations similar to those of association number 24 on well-drained slopes and on the crests of gently sloping hills.

Vegetation.

1. Trees. Picea engelmanni occurs mainly in the upper canopies and has sub-optimal vigor. It occurs in the lower canopies mainly in stand openings.

Pinus contorta has a sporadic occurrence in older stands where it occupies the dominant canopy. It often pioneers young stands.

Abies lasiocarpa occurs in all canopies with fair vigor. It is more aggressive in this association than is engelmann spruce and may replace it almost completely in older stands.

Tsuga heterophylla has a very low frequency and vigor in the lower canopies.

Pinus monticola has a low frequency in the higher canopies of some older stands but is normally absent.

2. Lesser vegetation. The shrub layer is normally complete and invariably present are Rhododendron albiflorum, Menziesia ferruginea, Vaccinium membranaceum and Sorbus sitchensis. Usually present in this layer are Vaccinium ovalifolium, Ribes lacustre, Pachystima myrsinites, and Lonicera utahensis. The herb layer is often complete. Invariably present are Rubus pedatus, Clintonia uniflora, Tiarella unifoliata, Lycopodium annotinum, and Listera nephrophylla. Usually present Cornus canadensis, Streptopus roseus, Valeriana sitchensis, Pyrola secunda, and Veratrum eschscholtzii. The moss layer is usually complete and is dominated by

Calliergonella schreberi, Rhytidiadelphus triquestrus, Dicranum fuscescens, and Peltigera spp.

Topography and soil. The topography varies from being flat to slopes of about 15 degrees. Stands of this association are located on soils where sub-surface drainage is seasonally extreme and where sub-surface irrigation is restricted to the lower levels of the soil during summer months. Most of the soils are sub-alpine podzols of either glacial or alluvial origin. There is a thin raw humus layer that is seasonally very dry. Leaching is pronounced and is carried into the soil depth around roots and stones although a distinct podzol horizon may be lacking. The mineralized soil varies from either silty-sands to sand and gravel loams. The structure is usually granular at the surface and variously aggregated, compacted, or cemented in the depth. Ortstein often occurs within 14 inches of the soil surface although in most of such cases the ortstein is in an incipient stage of development. These soils are seasonally very dry at the surface and only slightly moist in the depth.

Eco-climate. Stands of this association have a seasonally dry aspect for most of the stem length of trees, particularly in cases of stands that are completely wind-exposed. Heavy and protracted snow cover and frequent summer rains provide for a shallow stratum of warm humid air above the shrub layer during summer months.

Association number. 27.

Name. Picea engelmanni-Abies lasiocarpa-Vaccinium membranaceum-Dicranum fuscescens-Dicranum scoparium.

Occurrence. Sub-alpine portions of the Cascade, Monashee, and Selkirk Mountains and high elevation forests of south central interior plateaux. Stands of this association occupy areas of extreme drainage such as the crests of hills, ridges, and in the vicinity of rock outcrops. Tree growth is characteristically very poor.

Vegetation.

1. Trees. Picea engelmanni has a high frequency in all canopies other than in the lowest canopy where it is largely replaced by alpine fir. It has very low vigor in all canopies.

Abies lasiocarpa occurs in all canopies but has its greatest frequency and best vigor below the co-dominant level.

APPENDIX III (cont'd)

Pinus contorta normally occurs in the highest canopy although its frequency may be low. It is often the major dominant species in young stands.

2. Lesser vegetation. The shrub layer is usually complete although the vigor of plants is sub-optimal in most cases. Invariably present are Vaccinium membranaceum, Lonicera utahensis, and Pachystima myrsinites and usually present are Menziesia ferruginea, Rhododendron albiflorum, Vaccinium caespitosum, and Sorbus sitchensis. The herb layer is often discontinuous but invariably present are Valeriana sitchensis, Viola orbiculata, and Pyrola secunda. Usually present in this layer are Hieracium albiflorum, Linnaea borealis, and Cornus canadensis. Moss and lichen cover on the ground is usually complete. Invariably present are Calliergonella schreberi, Dicranum scoparium, D. fuscescens, and Cladonia spp. Usually present are Polytrichum juniperinum and Rhytidiadelphus triquetrus.

Topography and soil. The topography varies from being flat to slopes up to about 30 degrees. The soils are often shallow and have a thin raw humus layer that lies immediately above a well defined podzol horizon. Leaching is invariably carried deep into such soils. Sand and gravel loams, usually with an admixture of glacial rocks, are normal for this association. The structure of such soils is usually granular or aggregated at the surface to densely compacted in the depth. The complete profile is seasonally very dry.

Eco-climate. Stands of this association are usually the most wind exposed of the region. They are seasonally very dry and warm other than for a very shallow stratum of warm humid air that blankets the moss and herb layers.

Association number. 29.

Name. Thuja plicata-Oplopanax horridus-Dryopteris linnaeana.

Occurrence. In the Monashee and Selkirk Mountains on moist steep slopes and on more gentle slopes that border or occupy the confluence of mountain streams. Stands of this association are often fragmentary in larger areas of association number 31. The association is formed within an elevation range of from 1500 to 4000 feet above sea level.

APPENDIX III (cont'd)

Vegetation.

1. Trees. Thuja plicata occurs in all canopies and attains its maximum vigor for the region in this association.

Tsuga heterophylla has a sporadic occurrence up to the co-dominant level. It has its best frequency and vigor in this association at the perimeter of stands that are in proximity to stands of association number 31.

Pseudotsuga taxifolia may have a low frequency in the dominant canopy but is usually absent from mature stands.

Picea engelmanni has a sporadic occurrence but very good vigor in the highest canopy.

Populus trichocarpa may have a high frequency in the dominant canopy of young stands but is eventually replaced by western red cedar.

Abies lasiocarpa has a sporadic occurrence, mainly in the lower canopies and at higher elevations.

Acer glabrum varies from having a low to high frequency, occupying stand openings with very good vigor.

2. Lesser vegetation. The shrub layer is well-developed mainly by reason of the occurrence of Oplopanax horridus, although Corylus californica, Menziesia ferruginea, and Vaccinium ovalifolium are usually present. The herb layer is luxuriant both as to the number of species and their abundance. Invariably present are Dryopteris linnaeana, Athyrium filix-femina, Streptopus amplexifolius, S. roseus, Tiarella unifoliata, Smilacina racemosa, Veratrum eschscholtzii, Trillium ovatum, Viola glabella, and Clintonia uniflora. Frequently present are Circaea alpina, Asarum caudatum, Habenaria sp., and Adenocaulon bicolor. Mosses and liverworts are usually well-developed on the ground. Dominant in this layer are Mnium punctatum, M. spinulosum, M. affine, and Conocephalum conicum.

Topography and soil. The topography varies from very steep slopes to gently sloping stream margins. The soil is continuously moist throughout its depth and is seasonally wet at the surface by reason of seepage water. The humus layer may be either duff mull or a thin layer of raw humus above a thicker layer of duff mull. Leaching is sometimes pronounced, although a distinct podsol horizon is normally absent. Mineralised humus usually occurs for several inches above the mineral soil proper. Most of such soils are of alluvial origin, have a silty-sand texture and a granular structure. Gleization occurs regularly and usually up to the top of the mineral soil. Sub-surface drainage is normally good despite a continuously moist profile.

Eco-climate. Stands of this association normally have a cool moist aerial aspect other than in the tops of dominant and co-dominant trees where high humidities and seasonally warm temperatures prevail.

Association number. 30.

Name. Thuja plicata-Athyrium filix femina-Lysichitum americanum.

Vegetation.

1. Trees. Thuja plicata occurs in all canopies with good vigor but somewhat reduced from that in association number 29. It is normally the major species by volume and frequency in the association.

Tsuga heterophylla reaches the highest canopy only in older stands. Its occurrence in this association is closely dependent upon accumulations of decaying wood which, if in short supply, limits its frequency.

Pinus monticola may have a sporadic occurrence in the highest canopy of older stands.

Abies lasiocarpa has a similar occurrence to that of western hemlock but at higher elevations.

Taxus brevifolia may have a high frequency and good vigor in the lower canopies.

2. Lesser vegetation. The extent of shrub cover varies considerably but invariably present are Oplopanax horridus and Vaccinium ovalifolium and usually present are Rubus parviflorus, Cornus stolonifera, and Lonicera utahensis. The herb layer is usually complete. Invariably present in this layer are Athyrium filix-femina, Lysichitum americanum, Valeriana sitchensis, Circaea alpina, Mitella caulescens, and Dryopteris linnaeana. Usually present but less abundant are Adenocaulon bicolor, Listera nephrophylla, Equisetum arvense, E. pratense, and Veratrum eschscholtzii. The moss layer is often complete and is dominated by Mnium punctatum, Brachythecium sp., Bryum sp., and Rhytidiadelphus squarrosus.

APPENDIX III (cont'd)

Topography and soil. The topography is generally only slightly sloping. The soils are of either alluvial or glacial origin and are characteristically alpha-gleizate, the glei horizon lying directly beneath a thick, black-muck humus. The texture of the mineral soil is sand and gravel loam and the structure is granular to pasty. Such soils are permanently wet throughout their depth for most of the year.

Eco-climate. Similarly to association number 29, stands of this association have a permanently cool and humid aerial aspect other than in the tops of dominant and co-dominant trees.

Association number. 31.

Name. Tsuga heterophylla-Dryopteris linnaeana-Aralia nudicaulis-Clintonia uniflora-Cornus canadensis.

Occurrence. In the Monashee and Selkirk Mountains on well irrigated slopes and benches at elevations of from 1500 to 4800 feet above sea level. Most of such stands lie below 4000 feet. It is possible to segregate this association into at least three sub-associations, each reflecting different soil acidities, viz., Cornus canadensis-Clintonia uniflora, Dryopteris linnaeana, and Aralia nudicaulis sub-associations in order of decreasing soil acidity. They are, however, frequently so intermixed as to prevent their separation on a practical basis.

Vegetation.

1. Trees. Tsuga heterophylla attains its maximum development for the region in this association. It occurs in all canopies in maximum vigor, being the main species by frequency and volumes.

Pseudotsuga taxifolia has very good growth in the dominant canopy but eventually loses its place in older stand to western hemlock.

Pinus monticola has a similar occurrence to that of Douglas fir but persists longer in older stands than does Douglas fir.

Thuja plicata occurs in all canopies with good vigor other than in the dominant canopy where its vigor is sub-optimal.

APPENDIX III (cont'd)

Taxus brevifolia has a consistent occurrence in the lower canopies.

Betula papyrifera often pioneers young stands but is replaced in older stands first by Douglas fir and western white pine and, later, usually completely by western hemlock and western red cedar.

Populus tremuloides has a similar, although more short-lived, occurrence to that of western white birch.

2. Lesser vegetation. The extent of the shrub layer varies from "nudum" to almost complete. When shrubs occur, invariably present are *Pachystima myrsinites*, and *Vaccinium membranaceum* while usually present are *V. ovalifolium*, *Lonicera utahensis*, *Sorbus sitchensis* and *Oplopanax horridus*. Sometimes present are *Rubus parviflorus*, *Menziesia ferruginea*, *Rosa gymnocarpa*, and *Corylus californica*. The herb layer is usually complete although in young stands it may be almost lacking. Invariably present under mature stands are *Dryopteris linnaeana*, *Clintonia uniflora*, *Linnaea borealis*, and *Tiarella unifoliata*. Usually present and often abundant are *Aralia nudicaulis*, *Cornus canadensis*, *Streptopus roseus*, *Goodyera decipiens*, *Rubus pedatus*, *Pyrola secunda*, and *Viola orbiculata*. Frequently present but low in abundance are *Dryopteris dilatata*, *Pyrola bracteata*, *Streptopus amplexifolius*, and *Athyrium filix-femina*. The moss layer varies from being complete to "nudum". When mosses occur, normally included are *Mnium punctatum*, *M. spinulosum*, *Rhytidiopsis robusta*, and *Calliergonella schreberi*. Frequently present and sometimes dominant in this layer are *Hylocomium splendens*, *Rhytidiadelphus triquetrus*, and *Ptilium crista-castrensis*.

Topography and soil. The topography varies from being flat to sloping up to about 40 degrees. Most soils of this association have a variably thick raw humus that sometimes lies above a thinner layer of duff mull. A definite podsol horizon is usually present although leaching is commonly carried to greater depths. These soils may be of either glacial or alluvial origin. They have a silty-sand or sand and gravel texture and are granular or aggregated near the surface to compacted or cemented in the depth. Gleization normally occurs but usually not so close to the surface as in association number 29. The soils are normally moist throughout their depth for the entire year and differ in this respect from those of association number 29 mainly in

APPENDIX III (cont'd)

that they exhibit a greater seasonal fluctuation in the ground water level.

Eco-climate. Stands of this association have a continuously humid aerial aspect throughout the stem length of the tree cover. Air temperatures are seasonally warm within stands depending upon the degree of stocking. In very old stands where stocking is reduced from that normal to younger stands, a warm and humid aerial aspect reaches to ground level. In younger and more densely stocked stands a stratum of cool humid air occurs up to about the level of intermediate trees.

Association number. 32.

Name. Tsuga heterophylla-Abies grandis-Dryopteris linnaeana-Aralia nudicaulis-Clintonia uniflora-Cornus canadensis

Occurrence. In the southern portion of the Monashee and Selkirk Mountains co-incident with the northern limits of grand fir in interior British Columbia. Stands of this association occur at elevations generally below 3000 feet.

Vegetation.

1. Trees. Tsuga heterophylla occurs in all canopies with good vigor, although somewhat reduced from that in association number 31. It is normally the major species by volume and frequency in the higher canopies but sometimes loses its major status to grand fir in very old stands.

Abies grandis occurs in all canopies with maximum vigor for this species for the region.

Pseudotsuga taxifolia has only a sporadic occurrence in the higher canopies of older stands but may have a greater frequency in young stands.

Thuja plicata normally occurs in all canopies but reaches its best development in this association in the lower canopies.

Picea engelmanni has a similar occurrence to that of Douglas fir although it is even more transitory.

Larix occidentalis has a similar occurrence to that of Douglas fir other than being even more intolerant to conditions of the lower canopies.

APPENDIX III (cont'd)

Pinus monticola has a similar occurrence to that of Douglas fir other than its being more persistent in older stands.

Taxus brevifolia occurs mainly in shrub form.

2. Lesser vegetation. The shrub layer corresponds very closely to that of association number 31 both as to composition and extent. The herb layer also conforms closely to that of association number 31 with the exception of a more consistent and abundant occurrence of Aralia nudicaulis. The moss layer is similar to that of association number 31 with possibly a greater frequency of Rhytidiadelphus triquetrus.

Topography and soil. The topography varies from being flat to steeply sloping. The soils are similar in all visible respects to those of association number 31.

Eco-climate. A continuously humid and seasonally warm aerial aspect features stands of this association. The occurrence and depth of a cool humid stratum of air above the ground line varies directly with the density of stocking of individual stands, older and more open stands having a warm humid aerial aspect that penetrates to the ground line.

Association number. 33.

Name. Tsuga heterophylla-Pachystima myrsinites-Calliergonella schreberi.

Occurrence. In the Monashee and Selkirk Mountains at elevations of from 1500 to 4500 feet above sea level on benches and slopes where sub-surface irrigation is sufficiently remote so as to have no influence upon the growth of plants during most of the summer months.

Vegetation.

1. Trees. Tsuga heterophylla regularly occurs in all canopies and, in older stands, is the major species by volume and frequency. Its vigor is much less than that which it attains in association number 31.

Thuja plicata has its greates frequency in the lower canopies where it has fair vigor, although much reduced from that in associations number 29, 30, and 31.

APPENDIX III (cont'd)

Pseudotsuga taxifolia is a regular component of the higher canopies of all but the oldest stands. It competes with western white pine for supremacy in younger stands of this association.

Pinus monticola is a regular component of the higher canopies even in very old stands although in such stands its occurrence is sporadic. It is almost invariably a major component of young stands.

Taxus brevifolia occurs in shrub form in the lowest canopy.

Betula papyrifera sometimes pioneers denuded areas but eventually gives way to Douglas fir, western hemlock, western red cedar, and western white pine. Its vigor is reduced from that which it attains in association number 31.

Populus tremuloides is a short-lived pioneer species and rarely occurs in stands of this association when western hemlock has reached the status of being the dominant tree.

2. Lesser vegetation. The shrub layer varies in its completeness from highly irregular to nearly complete, although invariably present are Pachystima myrsinites, Vaccinium membranaceum, and Lonicera utahensis. Usually present are Vaccinium ovalifolium, Sorbus sitchensis, and Rosa gymnocarpa. The herb layer is often discontinuous, but invariably present are Chimaphila umbellata, Clintonia uniflora, Pyrola secunda, Linnaea borealis, and Goodyera decipiens. Usually present are Cornus canadensis, Tiarella unifoliata, Viola orbiculata, Pyrola bracteata, and P. chlorantha. The moss layer is normally complete and invariably present and dominating are Calliergonella schreberi, Rhytidiopsis robusta, and Hylocomium splendens. Commonly present and sometimes abundant are Ptilium crista-castrensis, Rhytidiadelphus triquetrus, Dicranum scoparium, D. fuscescens, and Peltigera aphthosa.

Topography and soil. The topography varies from flat to very steep slopes. Podsolized brown soils of glacial, alluvial, or residual origin characterize the association. There is a raw humus that varies up to five inches in thickness and a distinct podsol horizon that varies up to three inches thick. Leaching action is carried to much greater depths than that indicated by the podsol horizon, mainly in proximity to roots and stones. The mineral zone of the soil varies from

APPENDIX III (cont'd)

eight inches to at least 40 inches in depth. Its structure is either granular or aggregated near the surface and compacted or cemented below. Ortstein occurs quite regularly and sometimes very close to the surface. Gleization is usually evident in a shallow zone immediately above the ortstein layer. The texture of the mineral soil varies from silty-sands to sand and gravel loam. Large glacial boulders occur in some soils. Sub-surface drainage is extreme to the extent that the upper portions of the soil are seasonally very dry although most soils are continuously moist in their depth.

Eco-climate. Stands of this association have a continuously humid climate by reason of heavy and protracted snow cover and frequent summer rains. They have a seasonally warm aerial aspect that reaches to the ground line, particularly in mature stands.

Association number. 34.

Name. Tsuga heterophylla-Abies grandis-Pachystima myrsinites-Calliergonella schreberi.

Occurrence. Southern portions of the Monashee and Selkirk Mountains coincident with the northern limits of Abies grandis. Stands of this association occur at elevations generally below 3000 feet on either benches or well-drained slopes.

Vegetation.

1. Trees. Tsuga heterophylla occurs in all canopies with a high frequency but with reduced vigor.

Abies grandis occurs in all canopies and sometimes replaces western hemlock to a large degree. It occurs with reduced vigor.

Pseudotsuga taxifolia occurs in at least the higher canopies and usually in all canopies. It has fair vigor and has a scattered distribution in older stands.

Pinus monticola has a similar occurrence to that of Douglas fir other than having greater persistence in older stands.

Picea engelmanni has its greatest vigor and frequency at higher elevations but is eventually replaced by western hemlock and grand fir.

APPENDIX III (cont'd)

Larix occidentalis is often abundant in the higher canopies of young stands but is gradually replaced by western hemlock and grand fir in older stands.

Thuja plicata has an irregular occurrence in all canopies. It has its greatest frequency and vigor up to co-dominant level but its vigor in this association in any canopy is very much reduced.

Pinus contorta often pioneers young stands but is usually absent from older stands.

2. Lesser vegetation. The shrub layer varies greatly in its luxuriance but is invariably present, even if discontinuous. It is dominated by *Pachystima myrsinites* and *Vaccinium membranaceum* but usually present are *Mahonia aquifolium*, *Amelanchier florida*, *Rosa gymnocarpa*, *Vaccinium caespitosum*, and *Arctostaphylos uva-ursi*. The herb layer is very similar to that of association number 33. The moss layer is regularly complete and similar in all respects to that of association number 33 other than having a reduced occurrence of *Hylocomium splendens*.

Topography and soil. The topography varies from being flat to sloping. The soils of this association are similar in all visible respects to those of association number 33 other than that they are regularly drier during the summer months.

Eco-climate. The eco-climate of stands of this association is similar to that of association number 33 other than that summer temperatures are generally higher.

Association number. 35.

Name. *Pseudotsuga taxifolia*-*Vaccinium membranaceum*-*Arctostaphylos uva-ursi*-*Dicranum scoparium*-*Peltigera* spp.

Occurrence. In the Monashee and Selkirk Mountains at elevations of from 1500 to about 4500 feet above sea level. Stands of this association occur in exposed areas that have extreme sub-surface drainage throughout the year.

Vegetation.

1. Trees. *Pseudotsuga taxifolia* has a high frequency in all canopies. It has very reduced vigor.

APPENDIX III (cont'd)

<u>Tsuga</u> <u>heterophylla</u> rarely occurs in the higher canopies. It may have a high frequency in the lower canopies but its vigor is consistently very low.

<u>Abies</u> <u>lasiocarpa</u> has its best development at high elevations but usually occurs only in the lower canopies and in low vigor. It is often absent from low elevation stands.

<u>Thuja</u> <u>plicata</u> is often absent and, when present, occurs mainly in the lower canopies with reduced vigor.

<u>Picea</u> <u>engelmanni</u> has an irregular occurrence in all canopies. It is frequently absent and has general low vigor.

<u>Pinus</u> <u>monticola</u> has an occurrence similar to that of Douglas fir.

<u>Pinus</u> <u>contorta</u> has a sporadic occurrence in older stands but often has a high frequency as a dominant species in young stands. It has low vigor.

2. Lesser vegetation. The shrub layer is generally well developed and continuous except for rock outcrops. It is dominated by <u>Vaccinium</u> <u>membranaceum</u>, <u>Pachystima</u> <u>myrsinites</u>, <u>Arctostaphylos</u> <u>uva-ursi</u> and usually has a lesser occurrence of <u>Mahonia</u> <u>aquifolium</u>, <u>Spiraea</u> <u>lucida</u>, and <u>Gaultheria</u> <u>ovatifolia</u>. The herb layer is less well developed but is usually represented by <u>Chimaphila</u> <u>umbellata</u>, <u>Apocynum</u> <u>androsaemifolium</u>, <u>Hieracium</u> <u>albiflorum</u>, and <u>Festuca</u> sp. The moss layer is often complete and is dominated by <u>Dicranum</u> <u>scoparium</u>, <u>D.</u> <u>fuscescens</u>, <u>Polytrichum</u> <u>juniperinum</u>, <u>Rhacomitrium</u> <u>canescens</u>, <u>Calliergonella</u> <u>schreberi</u>, <u>Peltigera</u> spp., and <u>Cladonia</u> spp.

Topography and soil. The topography varies from steep to gentle slopes. Stands of this association usually occupy exposed and rocky ridges and the crests of hills. They are often fragmentary within more extensive areas of associations number 33 and 34. The soils are strongly podzolized, shallow, stony, and seasonally very dry. Both surface run-off and sub-surface drainage are extreme. There is a thin layer of raw humus that becomes mineralized very rapidly.

Eco-climate. A seasonally dry and very hot aerial aspect from the ground line to the tops of trees features stands of this association. Heavy and protracted snow cover and frequent summer rains combine to assist in the maintenance of a shallow stratum of warm humid air above the ground line during the early part of the summer.

APPENDIX III (cont'd)

Association number. 36.

Name. Thuja plicata-Picea engelmanni-Abies lasiocarpa-Oplopanax horridus-Dryopteris linnaeana.

Occurrence. In the Monashee and Selkirk Mountains on well irrigated slopes and benches or bordering and at the confluence of mountain streams at elevations of from 3800 to about 5100 feet above sea level. Stands of this association represent the upper altitudinal limits of western red cedar as a major species in this region. Western red cedar is often replaced in the higher canopies of older stands by western hemlock and alpine fir at lower elevations and by mountain hemlock and alpine fir at the higher elevations. The following trees are regularly present in this association, although in varying frequencies and vigor: Thuja plicata, Tsuga heterophylla, T. mertensiana, Picea engelmanni, and Abies lasiocarpa. Circumstances did not permit a full evaluation of this association.

Association number. 37.

Name. Picea engelmannii-Abies lasiocarpa-Vaccinium membranaceum-Pachystima myrsinites-Calliergonella schreberi.

Occurrence. In the Monashee and, mainly, in the Selkirk Mountains on well-drained soils at elevations of from 2500 to 4000 feet above sea level.

Vegetation.

1. Trees. Picea engelmanni has a high frequency and fair vigor in all canopies.

Abies lasiocarpa occurs in all canopies in good vigor, it usually has its greatest vigor and frequency in the lower canopies. It sometimes replaces engelmann spruce to a very large degree.

Pinus contorta frequently pioneers this association and occurs usually only in the highest canopy. It has good vigor.

Thuja plicata has an irregular occurrence and general low vigor in the lower canopies.

Tsuga heterophylla occurs with very low vigor in the lower canopies, rarely reaching the intermediate level of trees.

APPENDIX III (cont'd)

2. Lesser vegetation. There is a well developed shrub layer that is usually continuous. It is dominated by Vaccinium membranaceum and Pachystima myrsinites and is represented to a lesser extent by Viburnum pauciflorum, Lonicera utahensis, Symphoricarpos albus, Ribes lacustre, and Rubus parviflorus. The herb layer is rarely complete but is invariably represented by Lycopodium annotinum, L. selago, Linnaea borealis, Viola orbiculata, Pyrola chlorantha, and P. secunda. The moss layer is regularly complete and is dominated by Calliergonella schreberi and Ptilium crista-castrensis.

Topography and soil. The topography is either gently sloping or flat. Stands of this association regularly occupy very old alluvial soils, probably the flood plains of glacial rivers and lakes. They are deep, have a silty-sand or sand and gravel structure. Sub-surface drainage is usually extreme and such soils are seasonally very dry near the surface. Leaching is pronounced and is indicated by a distinct podsol horizon as well as by continued leaching below this horizon in the form of pockets that reach for considerable depths into the soil.

Eco-climate. Stands of this association are characteristically open at maturity and have a seasonally dry and warm aerial aspect above the intermediate level of trees. The aerial aspect below this level is seasonally warm but continuously humid, other than in stand openings where drier conditions prevail.

Association number. 38.

Name. Picea sitchensis-(Populus trichocarpa)-Oplopanax horridus-Athyrium filix-femina.

Occurrence. Central and northern portions of the Cascade Mountains at elevations of from sea level to about 300 feet. Stands of this association occur mainly on alluvial flood plains of rivers and lakes. They are generally above seasonal flood levels but are periodically subject to flooding of a minor nature.

Vegetation.

1. Trees. Picea sitchensis is the main species by volume and frequency in the upper canopies where it has very good vigor. It is replaced in older stands by western red cedar and western hemlock.

APPENDIX III (cont'd)

Thuja plicata occurs regularly in all canopies in older stands in good vigor and frequency. It has its greatest frequency in young stands in the lower canopies.

Tsuga heterophylla has its greatest frequency in the lower canopies and in older stands. It has fair vigor but is generally overtopped by either sitka spruce or western red cedar.

Abies amabilis occurs mainly in older stands where it has only a sporadic occurrence in the higher canopies. Its frequency in all canopies is extremely variable and its vigor is sub-optimal.

Populus trichocarpa is generally the major dominant species in stands that occupy newly formed soils. It has excellent vigor, but is replaced eventually by sitka spruce and western red cedar.

2. Lesser vegetation. The shrub layer is often very dense, particularly in stands where black cottonwood forms the dominant canopy. Invariably present in this layer are *Sambucus melanocarpa*, *Cornus stolonifera*, *Rubus spectabilis*, *R. parviflorus*, and *Oplopanax horridus*. Frequently present are *Vaccinium ovalifolium*, *Menziesia ferruginea*, and *Rubus strigosus*. The herb layer is invariably well developed and is dominated by *Athyrium filix-femina*, *Dryopteris linnaeana*, *Tiarella unifoliata*, *Dryopteris dilitata*, *Clintonia uniflora*, and *Cornus canadensis*. The moss layer is similarly well developed, although obscured by the luxuriance of the herbs. It is dominated by *Mnium punctatum*, *M. insigne*, *Hylocomium splendens*, and *Fontenalis* sp.

Topography and soil. The topography is flat other than for low dissecting hummocks. The soil is usually an immature alluvial soil that lacks stratification other than for a layer of duff mull humus. The texture is either silty-sand or sand and gravel loam and the structure is usually granular. Such soils are consistently moist, although generally well drained.

Eco-climate. Stands of this association have a consistently humid aerial aspect. Air temperatures are seasonally warm, depending largely upon the density of tree growth. Snow cover is heavy and protracted and summer rains are frequent.

APPENDIX III (cont'd)

Association number. 39.

Name. Thuja plicata-Tsuga heterophylla-Oplopanax horridus-Dryopteris linnaeana-Mnium spp.

Occurrence. Central and northern portions of the Cascade Mountains at elevations of from close to sea level to about 700 feet. Stands of this association occur regularly on alluvial benches and at the bases of slopes.

Vegetation.

1. Trees. Thuja plicata is generally the major species by volume and frequency, although in young stands it sometimes competes with sitka spruce and aspen.

Tsuga heterophylla occurs in all canopies with excellent vigor. It has its greatest frequency in the lower canopies of young stands but usually shares the higher canopies of older stands with western red cedar.

Picea sitchensis has an irregular occurrence in older stands, where it occurs in the highest canopy, but may have a greater frequency in young stands. It has good vigor, although reduced from that which it attains in association number 38.

Abies amabilis occurs regularly in all canopies but has its greatest frequency and vigor in the lower canopies.

Populus trichocarpa is usually absent from older stands but often occurs in the dominant canopy of young stands. It has reduced vigor in this association.

2. Lesser vegetation. The shrub layer is well developed, although sometimes less so than beneath stands of association number 38. Invariably present are Oplopanax horridus, Cornus stolonifera, Rubus spectabilis, and R. parviflorus. Usually present are Sambucus melanocarpa, Menziesia ferruginea, and Vaccinium ovalifolium. The herb layer is similarly well developed and invariably present in this layer are Athyrium filix-femina, Dryopteris linnaeana, D. dilitata, Tiarella unifoliata, Clintonia uniflora, and Cornus canadensis. Usually present are Pteritis nodulosa, Tiarella trifoliata and T. laciniata. The moss layer is well developed and is dominated by Mnium punctatum and M. insigne.

APPENDIX III (cont'd)

Topography and soil. The topography varies from flat to steeply sloping. The soil is weakly podzolized and is of either alluvial or glacial origin. The podzol horizon is usually distinct even if sometimes discontinuous. There is a duff mull humus that varies up to about two inches thick. The mineral portion of the soil is usually very deep and varies in its texture from silty-sands to sand and gravel loam. Gleization occurs regularly and usually very close to the soil surface. Such soils are continuously moist and are seasonally wet.

Eco-climate. Stands of this association have an eco-climate similar to that of association number 38 with the exception that the more dense stocking of trees that characterizes this association preserves a cool humid stratum of air from above the ground to at least the intermediate level of trees.

Association number. 40.

Name. Tsuga heterophylla-Abies amabilis-Vaccinium ovalifolium-Hylocomium splendens-Rhytidiadelphus loreus-Rhytidiopsis robusta.

Occurrence. Central and northern portions of the Cascade Mountains on well-drained slopes and benches at elevations of from 1000 to 3500 feet above sea level.

Vegetation.

1. Trees. Tsuga heterophylla occurs with good vigor and high frequency in all canopies, although it is less tolerant to overtopping in this association than is amabilis fir and tends to be replaced by this species in the higher canopies of very old stands.

Abies amabilis occurs with excellent vigor in all canopies, probably attaining its best development for the region in this association.

Picea sitchensis has a sporadic occurrence in low elevation stands where it occurs in the highest canopy with poor vigor.

Thuja plicata occurs mainly in the lower canopies and when exposed to the highest canopy it has greatly reduced vigor.

Populus tremuloides sometimes pioneers denuded areas but does not occur in older stands.

APPENDIX III (cont'd)

2. Lesser vegetation. The shrub layer is usually well developed, mainly by reason of the regular occurrence of *Vaccinium ovalifolium*. Other shrubs that are usually present are *Sambucus melanocarpa*, *Menziesia ferruginea*, and *Vaccinium parvifolium*. The herb layer varies considerably in its development but invariably present are *Cornus canadensis*, *Clintonia uniflora*, and *Pyrola secunda*. Usually present are *Dryopteris linnaeana*, *D. dilitata*, *Rubus pedatus*, *Lycopodium annotinum*, and *Goodyera decipiens*. The moss layer is usually complete and is dominated by *Hylocomium splendens*, *Rhytidiadelphus loreus*, and *Rhytidiopsis robusta*. Usually present, but in lesser abundance are *Calliergonella schreberi*, *Dicranum scoparium*, and *D. fuscescens*.

Topography and soil. The topography varies from being flat to sloping but, under either circumstance, sub-surface drainage is good. Strongly podsolized brown soils that are of either glacial or alluvial origin predominate in this association. There is a layer of raw humus that varies from three to 12 inches in thickness. Leaching is invariably indicated by a podsol horizon, although it penetrates in pockets to depths of at least 18 inches. The depth of the mineral soil varies from a few inches to more than 36 inches. The soil texture is either silty-sand or sand and gravel loam. The soil structure is either granular or aggregated near the surface, becoming either compacted or cemented below. Sub-surface irrigation is generally low in the profile during summer months and most of such soils are surface dry at this season of the year.

Eco-climate. Stands of this association have a constantly humid aerial aspect except in the tops of dominant trees. Air temperatures are seasonally warm except in densely stocked stands. Depending upon degree of stocking and exposure to winds, stands of this association are seasonally dry.

Association number. 40 (sub-association)

Name. *Tsuga heterophylla*-*Abies amabilis*-*Vaccinium ovalifolium*-*Sphagnum* spp.

Occurrence. In similar localities as stands of association number 40 but under circumstances whereby sub-surface drainage is impeded and where sub-surface

APPENDIX III (cont'd)

irrigation regularly occurs near the soil surface. Stands of this sub-association may be extensive but they have their greatest frequency as fragments within larger areas of associations number 40 and 41.

Association number. 41.

Name. _Tsuga heterophylla-Abies amabilis-Dryopteris dilitata-Dryopteris linnaeana-Mnium punctatum_.

Occurrence. Central and northern portions of the Cascade Mountains at elevations of from about 700 to 3500 feet above sea level on well irrigated but well-drained benches and slopes.

Vegetation.

1. Trees. _Tsuga heterophylla_ occurs in all canopies with excellent vigor. It attains its best development for the region in this association.

   Abies amabilis occurs in all canopies with good vigor and sometimes replaces western hemlock as the major species, first in the lower canopies and later in the higher canopies.

   Thuja plicata usually has only a sporadic occurrence in this association and, when present, it almost invariably occupies select local sites within a general area of association number 41.

2. Lesser vegetation. The shrub layer is very well developed on denuded areas and in older stands but is often discontinuous in stands at intermediate stages of their development. Invariably present in this layer are _Sambucus melanocarpa_, _Oplopanax horridus_, and _Rubus parviflorus_, and usually present is _Vaccinium ovalifolium_. The herb layer is usually complete. Invariably present in this layer are _Dryopteris dilitata_, _D. linnaeana_, _Athyrium filix-femina_, _Tiarella unifoliata_, _Streptopus roseus_, _Clintonia unifelora_, _Cornus canadensis_, and _Rubus pedatus_. The moss layer is also well developed. _Mnium punctatum_ is always present while _Rhytidiadelphus loreus_, _Rhytidiopsis robusta_, and _Brachythecium_ sp. are usually present but in lesser abundance.

Topography and soil. The topography varies from nearly flat to moderately sloping. Podzolized brown soils of either alluvial or glacial origin characterize this association. The humus layer varies up to seven inches in depth and consists of a layer of raw humus above a layer of duff mull. The podsol horizon may be discontinuous. There is usually a deep mineral soil zone that has either a silty-sand or sand and gravel texture and a granular to lightly compacted structure. Most of these soils are beta-gleizate, although sometimes alpha-gleizate. The entire profile is continuously moist and is seasonally wet.

Eco-climate. Stands of this association tend to have a continuously humid aerial aspect from the ground line to the tops of trees. Seasonally warm air temperatures are confined more to the upper canopies than in the case of association number 40.

Association number. 42.

Name. Tsuga heterophylla-(Pinus contorta)-Menziesia ferruginea-Hylocomium splendens-Calliergonella schreberi.

Occurrence. Central and northern portions of the Cascade Mountains, generally at elevations up to 1000 feet on very well drained slopes or benches where the movement of ground water laterally through the soil influences the upper portions of the profile for only short periods of the year.

Vegetation.

1. Trees. Tsuga heterophylla is the major species by volume and frequency. It has its greatest vigor below the dominant level but its vigor in all canopies is low.

Abies lasiocarpa only rarely occurs in the highest canopy and has only a low frequency in the lower canopies. It has very poor vigor.

Thuja plicata has a sporadic occurrence in the higher canopies where it has extremely poor vigor. It occasionally has a greater frequency in the lower canopies but, still, with poor vigor.

Pinus contorta is often the major dominant species in young stands where it has generally good vigor. In older stands it is replaced almost completely by western hemlock.

APPENDIX III (cont'd)

2. Lesser vegetation. The shrub layer is usually very well developed in older stands but is often discontinuous in young stands. Invariably present and dominating are _Menziesia ferruginea_, _Vaccinium ovalifolium_, and _V. membranaceum_ while usually present are _V. parvifolium_ and _Pachystima myrsinites_. The herb layer is much less developed but invariably present are _Cornus canadensis_ and _Chimaphila umbellata_. Usually present but in scattered frequency and often with low vigor are _Pyrola bracteata_, _Clintonia uniflora_, _Linnaea borealis_, _Lycopodium obscurum_, and _Goodyera decipiens_. The moss layer is usually complete and is dominated by _Calliergonella schreberi_ and _Hylocomium splendens_. Other mosses that occur, but in lesser abundance, are _Rhytidiopsis robusta_, _Rhytidiadelphus triquetrus_, _R. loreus_, _Dicranum fuscescens_, and _Ptilium crista-castrensis_.

Topography and soil. The topography is usually flat but may be sloping provided that sub-surface drainage is extreme. Strongly podzolized brown soils of either glacial or alluvial origin characterise this association. There is a thick layer of raw humus that lies above a distinct podzol horizon that may reach a thickness of four inches. The mineral portion of the profile may be shallow but usually is more than 24 inches in depth. Texture varies from silty-sands to sand and gravel loams and the structure varies from granular near the surface to compacted or cemented below. When ortstein occurs there is usually some evidence of gleization. Such soils are surface dry for most of the growing season and are only slightly moist in the depth of the profile.

Eco-climate. Stands of this association have a seasonally warm aerial aspect for the full stem length of trees. Atmospheric humidity is usually high up to about the intermediate level of trees, above which point it is seasonally low.

Association number. 45.

Name. _Picea glauca-Abies lasiocarpa-Oplopanax horridus-Athyrium filix-femina_.

Occurrence. Central interior plateau forests on either level ground or gentle slopes that have a permanently high water table. Stands of this association are open at maturity and are much subject to windthrow.

APPENDIX III (cont'd)

Vegetation.

1. Trees. *Picea glauca* occurs with good vigor in all canopies but is often replaced to a very large extent in older stands by alpine fir.

Abies lasiocarpa occurs with good vigor in all canopies but is usually secondary to western white spruce in all but the oldest of stands.

Pseudotsuga taxifolia has a very limited occurrence in this association and only in the highest canopy. It has good vigor.

Tsuga heterophylla has a limited occurrence and only in the lower canopies where it has very poor vigor.

Betula papyrifera may have a high frequency in young stands where it occurs in the higher canopies with good vigor. It is replaced in older stands by alpine fir and western white spruce.

Alnus tenuifolia has a limited but consistent occurrence in the lower canopies where it often assumes a shrub form.

2. Lesser vegetation. The shrub layer is always well developed and invariably present and dominating are *Oplopanax horridus* and *Cornus stolonifera*. Usually present in this layer are *Rubus parviflorus*, *Viburnum pauciflorum*, *Lonicera involucrata*, *Sambucus melanocarpa*, *Sorbus sitchensis*, *Ribes lacustre*, *Rosa* sp., *Vaccinium membranaceum*, and *Symphoricarpos albus*. The herb layer is similarly well developed. Invariably present are *Athyrium filix-femina*, *Dryopteris dilitata*, *D. linnaeana*, *Aralia nudicaulis*, *Cornus canadensis*, *Tiarella unifoliata*, *Clintonia uniflora*, *Equisetum sylvaticum*, *Mitella* sp., and *Circaea alpina*. The moss layer is often complete but is seconded to the luxuriance of herbs and shrubs. Invariably present in this layer are *Mnium punctatum*, *M. insigne*, *M. spinulosum*, *Rhytidiadelphus triquetrus*, *Brachythecium* sp., and *Ptilium crista-castrensis*.

Topography and soil. The topography is generally flat or gently sloping. The characteristic soil of this association is weakly podzolized, alpha- or beta-gleisate, and has a silty-sand texture. There is usually a very thin layer of raw humus that overlies a thicker layer of duff mull. The soil structure

APPENDIX III (cont'd)

varies from aggregated in the upper 10 inches of mineral soil to pasty or compacted in the depth. The upper layer of crumb structure is very easily compacted in such a soil, as often occurs during logging operations. The soil is continuously moist throughout its depth and is seasonally wet. Such soils are of alluvial origin.

Eco-climate. Stands of this association have a continuously humid aerial aspect from the ground line to the tops of trees. Air temperatures vary greatly with the density of stocking and the age of stands but are generally cool in the lower canopies and seasonally warm in the upper canopies.

Association number. 46.

Name. _Picea glauca-Abies lasiocarpa-Rubus parviflorus-Disporum oreganum_.

Occurrence. Central interior plateau forests on well-drained slopes. Stands of this association normally lie above those of associations number 45 and 47, in situations where sub-surface drainage is unrestricted but where sub-surface irrigation is seasonally effective as regards the growth of trees.

Vegetation.

1. Trees. _Picea glauca_ occurs in all canopies with fair to good vigor. It has much better development in associations number 45 and 47 than it has in this association.

Abies lasiocarpa occurs in all canopies with good vigor. It has less tendency to replace spruce in this association than in association number 45.

Pseudotsuga taxifolia has its greatest frequency for the region in stands of this association although its occurrence in older stands is only sporadic.

Betula papyrifera may have a high frequency in the higher canopies of young stands but has only a sporadic occurrence in older stands.

Populus tremuloides often pioneers denuded areas together with lodgepole pine but has only a sporadic occurrence and very low vigor in older stands.

APPENDIX III (cont'd)

Pinus contorta is a longer lived pioneer species of denuded areas than is aspen. It persists in the highest canopy of all but the oldest stands.

2. Lesser vegetation. The shrub layer is normally well developed and invariably present are Rubus parviflorus and Viburnum pauciflorum. Usually present and often in high abundance are Corylus rostrata, Sorbus sitchensis, Rosa sp., Symphoricarpos albus, Ribes lacustre, and Spiraea lucida. The herb layer is usually complete and is dominated by Disporum oreganum, Tiarella unifoliata, Streptopus roseus, Petasites speciosa, Cornus canadensis, and Dryopteris linnaeana. Less abundant, but often present, in the herb layer are Clintonia uniflora, Mitella sp., Actaea arguta, and Pyrola bracteata. The moss layer is also well developed, mainly by reason of the occurrence of Rhytidiadelphus triquetrus and Ptilium crista-castrensis. Less abundant but usually present are Mnium insigne and M. spinulosum.

Topography and soil. The topography varies from gentle to steep slopes under circumstances whereby the ground water level is remote from the soil surface for extended periods that include the greater part of the growing season. There is a layer of raw humus of from two up to five inches thick that sometimes has duff mull qualities in its depth. Leaching is indicated by a distinct podsol horizon of varying depth. The texture of the mineral soil is either silty-sand or pure sands and its structure varies from granular to aggregated near the surface to compacted in the depth. Such soils are usually very deep. The profile is continuously moist in its depth but is seasonally dry for several inches below the surface.

Eco-climate. Stands of this association have a seasonally warm aspect from above the shrub layer to the tops of trees. The humidity of the air within stands is continuously high up to about the intermediate level of trees, above which point it is seasonally dry.

Association number. 47.

Name. Picea glauca-Abies lasiocarpa-Dryopteris linnaeana-Aralia nudicaulis.

Occurrence. Central interior plateau forests on or at the bases of slopes in places where ground water influences

APPENDIX III (cont'd)

are intermediate between those that feature associations number 45 and 46.

Vegetation.

1. Trees. Picea glauca has a high frequency in all canopies. Its vigor is generally higher than that which it attains in association number 46 but somewhat reduced from that in association number 45.

Abies lasiocarpa has a high frequency and good vigor in all canopies.

Pseudotsuga taxifolia has a sporadic occurrence in the higher canopies.

Picea mariana has only a sporadic occurrence in lower canopies and is often absent.

Tsuga heterophylla has its greatest development for the region in this association. It occurs only in the lower canopies and with low vigor.

Betula papyrifera has a similar occurrence to that which it attains in association number 45.

2. Lesser vegetation. The shrub layer varies considerably in its development but is invariably indicated by the occurrence of Vaccinium membranaceum, Lonicera involucrata, Viburnum pauciflorum, Spiraea lucida, and Rubus parviflorus. The herb layer is more consistently well developed than is the shrub layer. Invariably present are Dryopteris linnaeana, Aralia nudicaulis, Tiarella unifoliata, Streptopus roseus, Clintonia uniflora, Cornus canadensis, Linnaea borealis, and Pyrola secunda. Usually present in this layer are Rubus pedatus, Petasites speciosa, Viola orbiculata, Lycopodium obscurum, and Disporum oreganum. The moss layer is usually complete. Invariably present and dominating are Ptilium crista-castrensis, Rhytidiadelphus triquetrus, and Calliergonella schreberi. Less common but usually present are Hylocomium splendens, Mnium punctatum, M. insigne, M. spinulosum, and Brachythecium sp.

Topography and soil. The topography is usually sloping. The soil may be either alluvial or glacial in its origin and has a thick layer of raw humus that sometimes lies above a thinner layer of duff mull. The podsol horizon is sometimes discontinuous but leaching is strong in this association and may be carried to considerable depths in pockets around roots. The depth of the mineral soil varies up to more than 30 inches but is usually less. The soil texture varies from

APPENDIX III (cont'd)

silty-sands to sand and gravel loam. The soil structure is granular near the surface and either compacted or cemented in the depth. Gleization is common but is not invariably present. Such soils are continuously moist throughout most of their profile and are seasonally dry only very close to the surface.

Eco-climate. Stands of this association have an aerial aspect that is more uniformly humid than that of association number 46 but less so than in association number 45. Seasonally warm temperatures penetrate closer to the ground in this association than they characteristically do in association number 45, but less so than in association number 46.

Association number. 47 (sub-association).

Name. Picea glauca-Abies lasiocarpa-Vaccinium membranaceum-Cornus canadensis-Rhytidiadelphus triquetrus-Calliergonella schreberi.

Occurrence. Stands of this sub-association occur in areas of slightly better sub-surface drainage than is characteristic of areas supporting association number 47. It frequently occurs that stands of association number 47 are temporarily converted to this sub-association when their degree of stocking is for some reason seriously reduced. Such stands have a seasonally dry aerial aspect from above the shrubs to the tops of trees.

Association number. 48.

Name. Picea glauca-(Picea mariana)-Abies lasiocarpa-Alnus tenuifolia-Equisetum sylvaticum-Sphagnum recurvum-Sphagnum squarrosum.

Occurrence. Central interior plateau forests in areas of abundant soil moisture but restricted sub-surface drainage. Stands of this association often occur as fragments within more extensive areas of other associations.

Vegetation.

1. Trees. Picea glauca has a high frequency but very low vigor in all canopies. It is replaced to varying degrees by black spruce from the intermediate level downward.

Picea mariana usually does not occur in the highest canopy of well-stocked stands. It has its

APPENDIX III (cont'd)

greatest frequency, although only moderate vigor, in the lower canopies.

Pinus contorta often has a high frequency in young stands and usually persists in the higher canopies of all but the oldest stands. It has low vigor.

Tsuga heterophylla has a consistent low frequency in the lower canopies where it occurs with very poor vigor.

Betula papyrifera occurs with very low vigor and a variable frequency in the higher canopies.

Alnus tenuifolia usually has a high frequency in the lower canopies where it often occurs in shrub form.

2. Lesser vegetation. The shrub layer is often very dense. Usually present in this layer are *Alnus tenuifolia*, *Vaccinium membranaceum*, *V. ovalifolium*, *V. caespitosum*, *Ledum groenlandicum* and, less regularly, *Spiraea* sp., *Sorbus sitchensis*, and *Cornus stolonifera*. The herb layer is usually well developed and invariably present are *Equisetum sylvaticum*, *E. pratense*, *Cinna latifolia*, *Listera nephrophylla*, *Cornus canadensis*, *Rubus pedatus*, *Linnaea borealis*, *Lycopodium obscurum*, and *L. annotinum*. The moss layer is usually complete. Invariably present and dominating in this layer are *Sphagnum recurvum*, *S. squarrosum*, *S. rubellum*, and *Calliergonella schreberi*.

Topography and soil. The topography is generally flat or cupped. Stands of this association most frequently occupy areas that constitute snow pockets. Thick, peaty, humus that lies directly above a thick podzol horizon is usual for this association. The mineral portion of the soil is usually deep, has a clay to silty-sand texture and a structure that varies from either granular to crumb at the surface to compacted in the depth. Most of such soils are alpha-gleizate. The humus layer is seasonally very dry but the mineral portion of the soil varies from continuously moist to wet.

Eco-climate. Stands of this association are characteristically open at maturity and present an aerial aspect that is seasonally very dry and warm above the level of the shrubs.