5836 Old West Saanich Rd.
R.R. 7, Victoria, B.C.
Canada V8X 3X3
(604) 479-0016

Arenaria
Research & Interpretation

The Habitat Conditions of *Allotropa virgata* and *Hemitomes congestum* - Two Species at Risk from the Conversion of Forests from Old-Growth to Second-Growth

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Prepared for: V. Marshall, Project Leader
Pacific Forestry Centre
506 West Burnside Rd.
Victoria, B.C.

Prepared by: Michael W. Ryan M.Sc. and David F. Fraser, M.Sc. R.P.Bio.
Arenaria Research and Interpretation
5836 Old West Saanich Rd.
RR#7, Victoria, B.C.
V8X 3X3

Summary

Based a previous examination of the biodiversity of the vegetation of *Pseudotsuga menziesii* stands on southeastern Vancouver Island, a number of vascular species are believed to be sensitive to logging operations because of their confinement to mature and old-growth stands (Ryan and Fraser 1992). Two of these species, *Allotropa virgata* and *Hemitomes congestum*, which are endemic to the west coast of North America and are uncommon throughout their respective ranges, were selected for further investigation in the present study.

Following a review of the literature (Ryan and Fraser 1993), it became apparent that there was a dearth of information regarding the ecology and biology of these two species. Both species are non-chlorophyllous and are suspected of obtaining energy for growth and reproduction indirectly through associated mycorrhizae that are also connected to the roots of trees. The purpose of the current investigation was to provide some information on the habitat conditions in which these species occur and attempt to identify characteristics of the vegetation and environment which influence the presence or absence of either species at a given site.

Because of budget and time constraints, the investigation was limited to a search of mature and old-growth *Pseudotsuga menziesii* stands on southeastern Vancouver Island. Individuals of both species were searched for in stands along transects placed at 5 m intervals. Located specimens were used to identify the centres of small plots in which all vascular and cryptogamic species and their respective cover values were recorded. The distance between *Allotropa* or *Hemitomes* and the nearest four mature trees was recorded. Information, including the species, height, age, and circumference at breast height, was recorded for these four trees. Site information including aspect, slope, elevation, and distance to the edge of the stand and substrate conditions including humus type and depth, the rooting depth of *Allotropa* or *Hemitomes*, the presence of juvenile shoots, and characteristics of the soil were recorded.

The vegetation information was analyzed using detrended correspondence analysis followed by further analysis with the site and substrate information using detrended canonical correspondence analysis.

The vegetation in which *Allotropa* and *Hemitomes* occurred comprised open stands of *Pseudotsuga menziesii* varying in age from about 70 years to over 350 years. The understorey was dominated by a high cover of *Gaultheria shallon* with an average height of less than one meter. *Gaultheria* surrounding individual stems of *Allotropa* and *Hemitomes* was often spindly in appearance and never completely shaded these species. In some instances, *Allotropa* and *Hemitomes* were located under dense regenerating *Tsuga heterophylla* or *Thuja plicata*. There were very few species of herbs and bryophyte cover was variable; usually the moss, *Eurhynchium oreganum* was the most abundant species.

Site and soil conditions were variable but all plots were located in relatively dry areas where slopes were either moderately steep or soils shallow and well-drained. The base of flowering

shoots of *Allotropa* and *Hemitomes* were surrounded by abundant greyish organic matter which appeared to consist of fine roots and decaying mycelia . The number of juvenile shoots located in the soil profile occurred in about 40% of the plots. There appeared to be no correlation between the number of juvenile shoots and above-ground flowering shoots.

The results of the detrended correspondence analysis showed no discernable relationship between the occurrence of either *Allotropa* or *Hemitomes* at a given plot and variation in the vegetation. Similar results were also obtained when site and soil factors were included in the detrended canonical correspondence analysis. However, site factors which appear to correspond to variation in the vegetation included slope, stand age, average tree height, minimum distance between *Allotropa* or *Hemitomes* and the nearest tree, and plot location.

The limitations of this study are discussed including recommendations for further research.

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Introduction

Diminishing old-growth forests and the methods by which they are harvested has resulted in increasing levels of public concern over the manner in which the forests of British Columbia are managed and the extent to which management decisions consider the range of societal values regarding old-growth forest and their conversion to second-growth stands. Much of the debate in British Columbia, as well as that in the United States (e.g. Forestry Ecosystems Management Assessment Team 1993), has focused on the biodiversity of old-growth forests and how it is altered by logging. Although substantial efforts have been directed towards providing a framework based on the ecological classification of the forest vegetation by which forest management practices are carried out, much less is known regarding the dynamic processes by which the components of the forest ecosystem change over time, the mechanisms underlying these changes, and how both are altered by logging practices. In particular, information is sorely lacking on the roles of non-commercial plant species in the functioning of the forest ecosystem and how these groups influence the species richness and abundance of other organisms including insects and other invertebrates.

In an attempt to meet some of these challenges, a multidisciplinary study was initiated to provide a preliminary assessment of the biodiversity of *Psuedotsuga menziesii* forests on southeast Vancouver Island. The selection of *Pseudotsuga menziesii* stands was particularly critical given its limited range in coastal British Columbia and the extent to which *Psuedotsuga menziesii* old-growth stands have been eliminated by logging. The vegetation of *Pseudotsuga menziesii* stands was compared at three sites between four stages of succession (regeneration: 5-10 yrs.; immature 40-60 yrs.; mature 75-85 yrs.; and old-growth 160+ yrs.). The results of this work (see Ryan and Fraser 1992) indicated that a number of non-chlorophyllous species appeared to be very sensitive to logging as these species were found only in mature and old-growth stands. As a result of these investigations, it was decided further information was required on two of these species, *Allotropa virgata* and *Hemitomes congestum*, which are endemic to the west coast of North America and appear to be limited in Canada to southern British Columbia where they both appear to be most abundant on southern Vancouver Island. Although neither species is listed as rare and endangered by the Conservation Data Centre (B.C. Ministry of Lands, Parks and Housing), both species are likely threatened given their limited range in British Columbia and their tendency to be most abundant in mature and old-growth coastal *Pseudotsuga menziesii* forests which are being eliminated at a rapid rate.

After reviewing the literature regarding *Allotropa* and *Hemitomes* (see Ryan and Fraser 1993), a small field survey was conducted to provide additional information on the ecology of these species. Unfortunately, because of budget constraints and time limitations, the study was confined to a limited area on southeastern Vancouver Island largely comprising those areas in which the biodiversity of *Pseudotsuga menziesii* forests had been previously studied. Furthermore, the short duration of the study prevented a examination of several factors which had been identified in the literature as important areas of investigation because of missing or inadequate information. These comprised many of the life-history characteristics of these species including pollination, seed dispersal, seedling establishment, modes of nutrition, and their

relationship to mycorrhizal fungi and other vascular plants. It is believed that *Allotropa* and *Hemitomes* are epiparasites in that they form mycorrhizal associations with fungal species that are also associated with the roots of trees from which *Allotropa* and *Hemitomes* indirectly parasitize as an energy source for growth and reproduction (Wallace 1975).

The purpose of the field survey was to examine the occurrence of *Allotropa* and *Hemitomes* in mature and old-growth *Pseudotsuga menziesii* forests and attempt to provide further information on the habitat conditions surrounding individual plants including characteristics of the adjacent vegetation and environmental factors (including characteristics of the substrate) which may influence the occurrence of either species at a given site.

Methods

Field Investigations

Three areas were intensively searched where previous field work (Ryan and Fraser 1993) had indicated the occurrence of both species. They included the portion of the Greater Victoria Watershed east of Shawnigan Lake (South), the northwestern portion of the Greater Victoria Watershed and adjacent lands (outside of the watershed) (North), and Eagle Ridge on MacMillan Bloedel property southwest of Duncan (Koksilah) (Fig.1).

Within each area, mature and old-growth forests were systematically searched along transects of differing lengths set at approximately 5 m intervals. The locations of *Allotropa* and *Hemitomes* were flagged and small 4 m x 4 m plots were established using *Allotropa* or *Hemitomes* as the centre point of the plot.

Information recorded at each plot included site features such as slope, aspect, elevation, slope position, microtopography, general characteristics of the vegetation and general moisture conditions. The identification and estimates of cover values of all vascular and cryptogamic species were made using the methods outlined in "Describing Ecosystems in the Field" (Walmsley *et al.* 1980). The distance between *Allotropa* or *Hemitomes* and the nearest four mature trees was recorded. Information was also collected on each of these four trees which included the species, height, and circumference at breast height (c.b.h.). Furthermore, cores, using an increment bore, were collected from each tree and subsequently examined to estimate the age of each tree.

General information on the *Allotropa* or *Hemitomes* specimen located at the centre of each plot was collected which included the number of visible flowering shoots and the vegetation immediately adjacent to each specimen. The soil around each plant was removed and information was recorded on humus depth, the position in the soil horizon of the flower stem(s), and the number of *Allotropa* or *Hemitomes* juvenile shoots and their position in the soil horizons. Additional information was also recorded on general soil characteristics including the colour and texture of the soil horizons, the location of roots, and soil conditions immediately around the
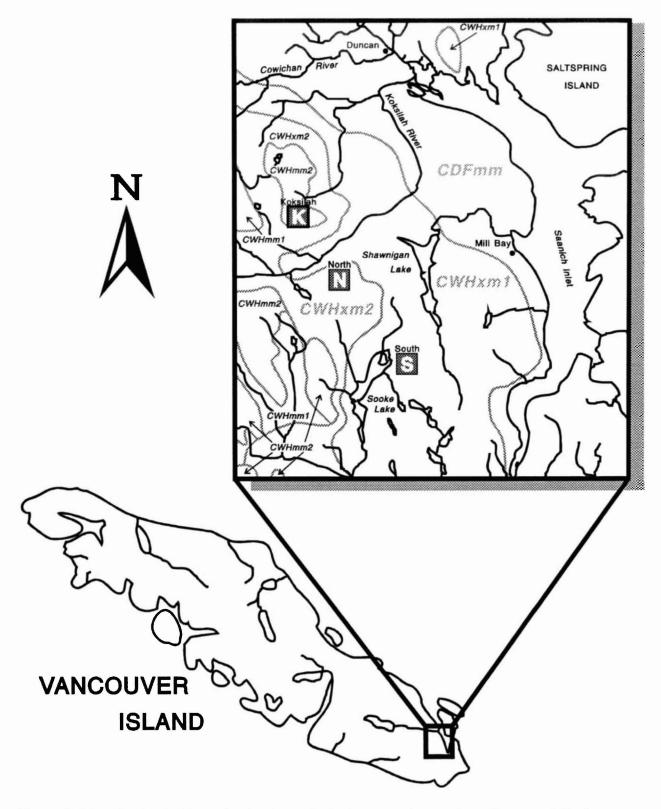
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Figure 1. Maps showing the biogeoclimatic subzones in the three general areas where *Allotropa* and *Hemitomes* were searched for (South, North, and Koksilah watersheds).

flower stems and juvenile shoots of *Allotropa* and *Hemitomes*.

Information was collected from a total of 33 plots of which 21 plots contained *Allotropa* and 12 contained *Hemitomes*.

Data Analysis

The cover values for identified species in each plot were analyzed using detrended correspondence analysis (DCA) to determine if there were any discernable differences in the composition and structure of the vegetation amongst the three sample areas (South, North, and Koksilah) as well as between those plots occupied by *Allotropa* and those occupied by *Hemitomes*. The data were also subjected to multi-response permutation procedure (MRPP) to determine if there were statistically significant differences between the three sample areas and between *Allotropa* and *Hemitomes* plots.

To examine the influence of environmental factors on the structure and composition of the vegetation, the vegetation data and thirteen site factors were subjected to detrended canonical correspondence analysis (DCCA). The factors used included distance to stand edge, slope, aspect, elevation, cover of humus, rock, and rotten wood within each plot, tree age, average c.b.h., average tree height, distance from *Allotropa* or *Hemitomes* to the nearest tree, humus depth, and the location of the plot (South, North and Koksilah). Because a number of trees were either too large or rotten near the centre, an accurate estimate of tree age could not be made. Hence, for the purposes of the DCCA analysis, each plot was assigned to one of the following categories based on the estimated age of the oldest tree: 1 (50-150 years), 2 (151-250 years), 3 (251-350 years), and 4 (351-450 years).

DCA and DCCA analyses were carried out using the computer program, CANOCO (Ter Braak 1988) whereas the computer program PC-ORD (McCune 1991) was used to perform the MRPP analysis. Default parameters were used in all analyses.

Results

Vegetation

The types of habitats in which *Allotropa* and *Hemitomes* were collected were remarkably similar. The vegetation in almost all areas where these two species were located comprised a stand of *Pseudotsuga menziesii* (with an average height that varied between 20 and 45 m) usually with a component of *Tsuga heterophylla* and occasionally *Thuja plicata* located beneath the main canopy. Although the canopy cover of *Pseudotsuga menziesii* was usually quite high (>80%), it often contained a large number of canopy gaps allowing for a high levels of incidental light in the understorey (see Appendix I for a list of species located in all plots and Appendix II showing the species composition and cover values for each plot)..

Although the age of some trees could not be estimated either because the tree diameter exceeded the length of the increment bore or wood at the centre of the tree was rotten, all stands were found to have an average age often approaching or exceeding 200 years except for the plots located in a mature stand outside the north watershed (M2[1] -71 to 81 years), and a mature stand located in the Koksilah (M3 - 76 years). The oldest trees were between 360 and 390 years and were located in old growth stands in the north watershed (O2) and in the Koksilah watershed (O3). Tree height varied from an average height of 13 m in the youngest aged stand (M3) in the Koksilah watershed to 49 m in the south watershed (O1); most stands were between 20 and 30 m in height with a c.d.h. of 140 to 200 cm (see Appendix III and IV).

The understorey vegetation in almost all cases comprised a shrub layer dominated by *Gaultheria shallon*. Often a minor component of *Mahonia nervosa, Chimaphila umbellata, Rosa gymnocarpa, Vaccinium parvifolium* was present. Forbs and grasses were sometimes present but in small amounts and included the species *Moehringia macrophylla (Arenaria macrophylla), Boschniaka hookeri, Festuca occidentalis, Linnaea borealis, Melica subulata, Monotropa uniflora, Trientalis latifolia,* and *Viola sempevirens*. Bryophytes were variable and ranged in cover from <1% to 90%. The most abundant species was usually *Eurhynchium oreganum* (formerly *Kindbergia oregana*) although *Hylocomium splendens* was also very abundant in some locations. Other common species included *Dicranum scoparium, Rhytidiopsis robusta,* and *Trachybryum megaptilium*. Mosses were most abundant on drier sites where soils were shallow.

In a number of plots, dense *Tsuga heterophylla* regeneration shaded the understorey to such an extent that *Gaultheria shallon* was almost completely absent, as were most other species of herbs and mosses.

The vegetation immediately adjacent to *Allotropa* and *Hemitomes* stems was either absent or, more often, composed of *Gaultheria shallon*, usually between 0.2 - 0.7 m in height with a spindly appearance that only partially shaded *Allotropa* or *Hemitomes*. Interestingly, although *Gaultheria shallon* was the dominant understorey species at all sites with a high cover, it rarely formed a dense, tall layer like that often observed elsewhere in coastal rain forests; individual plants were often less than 1 m tall usually with sparse branching which permitted some incidental light to reach the forest floor. Even in those sites where *Gaultheria* was relatively tall and dense, plants located near *Allotropa* or *Hemitomes* were shorter and spindly in appearance. The forest floor around *Allotropa* and *Hemitomes* stems was often bare but sometimes bryophytes, usually *Eurhynchium oreganum*, were present.

The distance between *Allotropa* or *Hemitomes* and the closest tree varied between 0 and 6 m. In almost every instance, the four closest trees in every plot were *Pseudotsuga menziesii*.

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[1] "M" and "O" refers to the mature and old-growth plots, respectively, which had been inventoried in a previous investigation (Ryan and Fraser 1992). The number following the letter "M" or "O" refers to the location of the plot as follows: 1- South, 2 - North, 3 - Koksilah.

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Site Conditions

The general site conditions in which the plots were located were similar for some factors but extremely variable for others (see Appendix V). Aspect showed little relationship to the location of *Allotropa* and *Hemitomes*; plots appeared to be equally located in all directions. Likewise, plots were located on slopes that varied from gentle (10%) to moderately steep (60%). However, all plots appeared to be located on water-shedding sites in which soils were relatively porous and water drainage rapid; even those plots located on gentle slopes were either located on relatively dry plateaus (e.g. M2 outside the north watershed) or in areas where soils were shallow as indicated by the abundance of exposed bedrock (e.g. O3 in the Koksilah drainage). Even those plots located at the wettest site (O1 in the southern part of the watershed) were located on relatively steep slopes near the summits of ridges running parallel to the main slope where water drainage would be rapid.

Elevation varied substantially between 250 m and 700 m. a.s.l. However, it should be noted that neither species has been collected in the lowlands on eastern Vancouver Island with the exception of a single collection of *Allotropa* from the Royal Oak area in Victoria.

The location of *Allotropa* and *Hemitomes* did not appear to be strongly influenced by its proximity to the edge of the stand (e.g. distance to adjacent clearcut, road, or other major form of disturbance). Distance between the plots and edge of stands ranged from 18 m to over 300 m with most plots located less than 100 m from stand edges. It was noticed at all sites there appeared to be no change in the composition of the vegetation near the edge of a stand to that found in the interior of the stand. In some instances, some species such as *Gaultheria shallon* or *Tsuga heterophylla* showed signs of increased vigour near the edge of a stand, but generally, the levels of incidental light reaching the forest understorey were sufficiently high within the stands that little change was apparent in the vegetation near the edges of stands. However, because no plots were located less than 18 m from the edge of a stand, it is not possible to rule out potential negative impacts on *Allotropa* and *Hemitomes* resulting from large-scale disturbances in nearby adjacent areas.

Soil Conditions

As would be expected, the forest floor within each plot was comprised primarily of humus with occasionally a minor component of rotten wood, and to a lesser extent, bedrock or stones. There appeared to be no difference in the substrate surrounding *Allotropa* or *Hemitomes* and that found elsewhere in the stand.

Humus depth varied substantially between plots and ranged from 2 to 10 cm (appendix V). In general, plots located in the south watershed (O1) were usually thinner than those located elsewhere. The humus layers were composed of unconsolidated, peaty organic material, often containing fungal hyphae, which typically characterizes a mor humus form.

The soil horizons varied from light-coloured tan brunisols, particularly in the driest plots, to

typical podzols in which the B horizon is dark orange from the deposition of iron. Mineral soil immediately beneath the overlying humus usually comprised a narrow dark brown horizon with some organic matter mixed in; in a few instances there was some evidence of a thin white eluviated A horizon. In a number of plots, particularly those on steep slopes, the mineral soil also contained a large number of angular stones and rocks (comprising as much as 50% of the soil volume) likely derived from colluvial processes. Mineral soil showed little structure and appeared to be primarily a sandy loam..

Allotropa and *Hemitomes*

The degree of association exhibited by *Allotropa* and *Hemitomes* stems varied between sites (Appendix V). In about 90% of the plots, only a single stem was present although other stems were sometimes located within a few meters. In a few instances, clumps of stems of both species were present; as many as 17 and 16 stems of *Allotropa* and *Hemitomes* stems were counted in two plots, respectively. There appeared to be no relation between the number of stems and site conditions.

During August, when the field work was conducted, both *Allotropa* and *Hemitomes* had finished flowering. Almost all *Allotropa* stems were wilted and dead whereas *Hemitomes* and some *Allotropa* stems (particularly those found in high-elevation plots) were beginning to show signs of decay but were still relatively firm and hydrated.

Below the surface of the soil, *Allotropa* stems often terminated just below the humus layer, but in some instances, particularly on steep slopes, the stems extended to depths of 10 cm or more. The remarkable feature of the soil conditions surrounding most stems was that the soil contained much organic material, greyish in colour, that appeared to be comprised of fine roots and abundant decaying fungal hyphae. Hence, the soil surrounding the stems comprised a mixture of mineral soil and abundant greyish organic matter that gave the soil a light peaty texture. In some instances the organic matter was so abundant that the soil had the texture of peat moss in that the soil did not break apart when disturbed but instead formed a cohesive mat that could be torn apart.

The base of *Hemitomes* stems were also often surrounded by abundant organic matter which appeared to comprise decaying fungal hyphae and fine roots. Unlike *Allotropa*, the base of stems always terminated in the uppermost layer of mineral soil just beneath the overlying humus. Although, fungal hyphae was a common component of the humus layer, that observed around the base of *Hemitomes* was much more abundant than that typically observed elsewhere in the same soil horizons.

Mature flowering stems of both species appear to be annual structures that do not last for more than a single growing season. However, in about a third of the plots, when the stems were excavated, dormant juvenile shoots were found near the base of mature stems which may have been formed during the current season. The dormant shoots of *Allotropa* were firm, fleshy white shoots about 2-3 cm thick and about 10 cm long whereas those of *Hemitomes* were much smaller

- about 1 cm thick and about 5 cm long. Both shoots showed little tissue differentiation and were similar in appearance to the underground tubers of other flowering plants. The number of dormant shoots varied in number between one and five and did not appear to be closely correlated to the number of mature stems present. In some instances, there were more dormant shoots than above-ground stems whereas in other plots, the number of above-ground stems exceeded the number of the dormant shoots.

Allotropa shoots at two plots and *Hemitomes* shoots at four plots were rooted in mineral soil that contained abundant decayed rotten wood which had been incorporated into the soil a long time ago as there was no indication at the soil surface (e.g. mounded appearance) that rotten wood would be present in the soil horizons.

Data Analyses

The results of the DCA ordination for the first two axes are shown in fig. 2. Here, the ordination graphically displays differences in the vegetation between plots by placing plots with similar vegetation near one another whereas those plots with dissimilar vegetation are placed far apart. Only the first two axis are displayed as they account for the greatest amount of variation in the data (first column of data - Table 1). Remarkably, when the percent variation accounted for by the first four axes is summed, 98% of the variation in the data is accounted for. However, much of this variation is attributed to the strong dissimilarity between plots 15, 16, 20, and 21, and the remaining plots which are compacted into a tight cluster near the lower corner of the ordination. This strong dissimilarity is due to the large amount of regenerating *Tsuga heterophylla* or *Thuja plicata*, less than 10 meters in height, found in these four plots. As a result, the understorey layer also differed in that it tended to be much sparser than that typically observed in most other plots.

Table 1. Percent Variation Accounted for by the First Four Ordination Axes

Axis	Detrended Correspondence Analysis		Detrended Canonical Correspondence Analysis	
	All Plots	Exclude Plots 15,16, 20, & 21	All Plots	Exclude Plot 26
1	38.0	30.0	29.5	29.2
2	25.8	19.6	14.4	17.0
3	23.9	11.0	6.0	8.4
4	10.4	5.9	4.5	6.3
Total	98.1	66.5	54.4	60.9

Axis 2

21

15

16

24

25
20
267 11 12
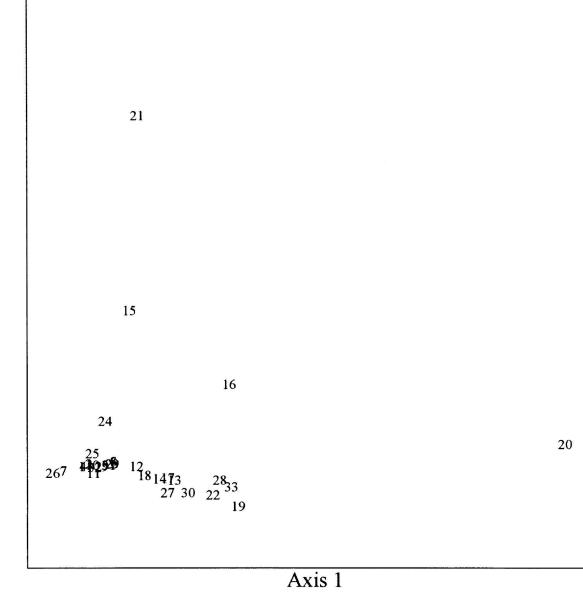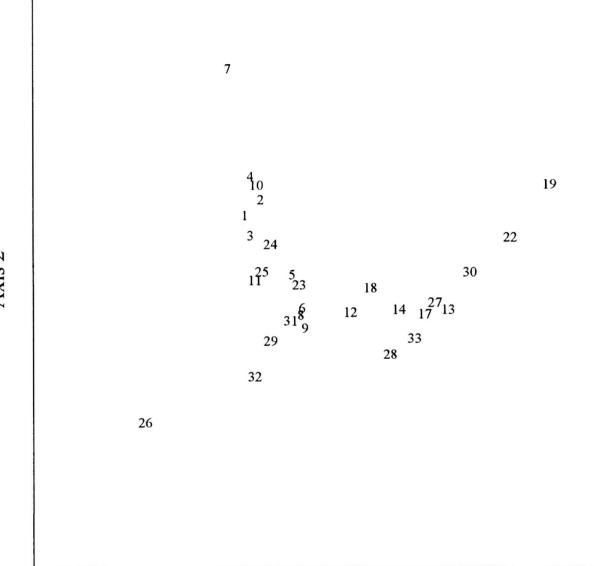18 14 13
27 30 22 28 33
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Axis 1

Figure 2. Detrended correspondence analysis of the vegetation.   Plots positioned near one another are more similar than those positioned far apart.

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To obtain a better understanding of the relationships between the 29 tightly clustered plots, the data were reanalyzed excluding the four dissimilar plots (Fig. 3). Here, the first four axes of the ordination accounted for 66.5% of the variation in the remaining 29 plots. Removing the four dissimilar plots resulted in a better dispersion of the plots but the axes accounted for much less variation in the data. There appears to be no discernable pattern in the data. When the presence of *Allotropa* (A) or *Hemitomes* (H) for each plot is displayed (Fig. 4), there appears to be no differences in the composition and structure of the vegetation between these two species. Similarly, when the locations of the plots (South, North, Koksilah) are displayed (Fig. 5), there are no obvious differences in the vegetation based on location except the South plots tend to form a cluster in the middle of the ordination.

The lack of difference in the vegetation between plots based either on the presence of *Allotropa* and *Hemitomes* or plot location is also partially supported by the MRPP results. It was found that the likelihood of dividing the plots into two groups that are more dissimilar than those based on the presence of *Allotropa* or *Hemitomes* was 45% when all plots were included in the analysis and 48% when the four dissimilar plots (15, 16, 20, and 21) were excluded. Hence there appears to be no correlation between the occurrence of either *Allotropa* or *Hemitomes* and the composition of the vegetation. Alternatively, the chances of dividing the plots into three groups that are more dissimilar than those groups formed on the basis of plot location is 0.4% when all plots are considered in the analysis and 0.5% when the four dissimilar plots are excluded. Although these results likely reflect the relatively tight cluster formed by South plots, the likelihood of forming two groups more dissimilar than those between the North and Koksilah plots is only 16.6% when the procedure is repeated excluding the South plots. This low value may reflect the tighter cluster formed by most Koksilah plots when compared to the broader dispersion of North plots. However, the extent of overlap between these two groups in the ordination suggests that these differences may not be so much a reflection of differences in the vegetation between North and Koksilah plots but reflect the greater degree of heterogeneity in the vegetation of North plots compared to that of the Koksilah plots. Similarly, the MRPP results may simply reflect the greater degree of homogeneity in the vegetation among the South plots to that found in the North and Koksilah plots but do not reflect actual compositional differences in the vegetation.

Although the DCA is a useful method in identifying natural groupings (if there are any) among the vegetation plots, it is often difficult to identify what environmental factors are responsible for the dispersion of the plots in the ordination. A more useful approach to examining the influence of environment on the composition and structure of the vegetation is shown in the biplot displayed in fig. 6 produced by the DCCA results. Here, the plots are again represented by numbers in which plots containing similar vegetation are placed near one another whereas dissimilar plots are placed far apart. Overlaid on this biplot are the environmental factors recorded in this study. The abbreviations used for the environmental factors are as follows: Min. Dist. - minimum distance between the *Allotropa* or *Hemitomes* and the nearest mature tree, Elev. - elevation of the plot; Asp. - aspect of the plot; Slope - slope of the plot; Hum. Depth - humus depth at plot centre; Edge - distance from the centre of the plot to the edge of the stand; Avg. CBH - average circumference at breast height of measured trees; Age Class - the age class of

Figure 3. Detrended correspondence of the vegetation after excluding plots 15, 16, 20, and 21.
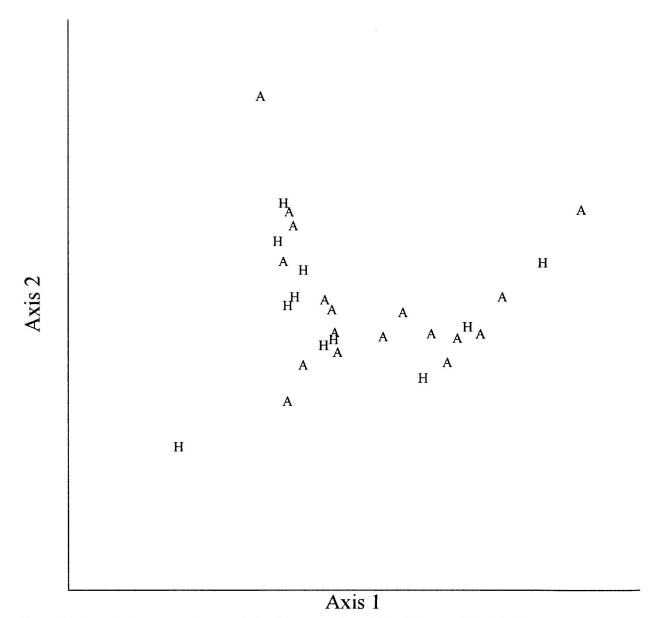
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Figure 4. Detrended correspondence analysis of the vegetation. "A" - *Allotropa*, "H" - *Hemitomes*.
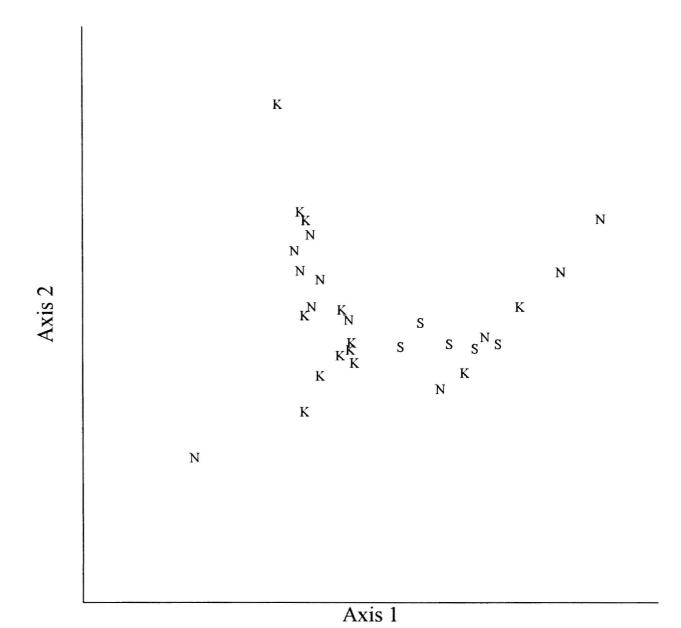
Figure 5. Detrended canonical correspondence analysis of the vegetation. "S" - South, "N" - North, "K" - Koksilah.
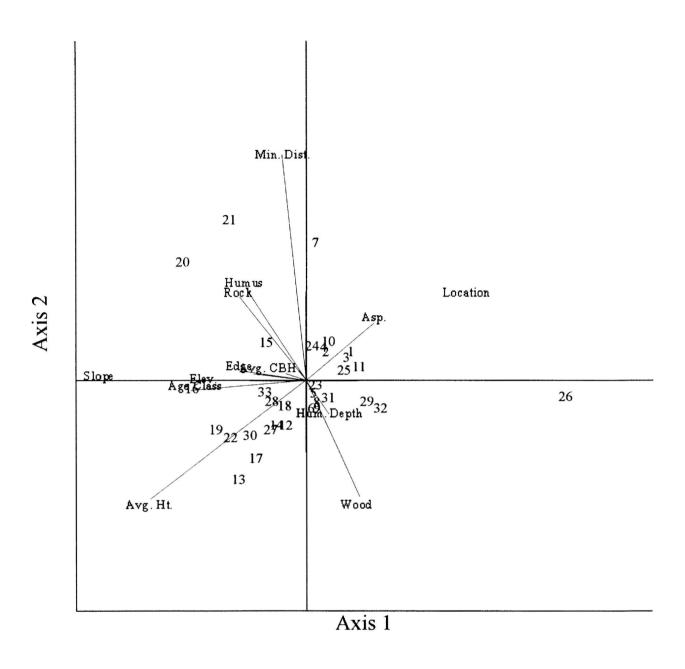
Figure 6. Detrended canonical correspondence analysis of the vegetation data with environmental factors.

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the measured trees; Avg. Ht. - average height of measured trees; Humus - percent cover of humus in the plot; Wood - percent cover of logs in the plot; Rock - percent cover of rock (stones and bedrock) in the plot; Location - location of the plot (North, South, Koksilah).

An examination of the plots indicates that plot 26 is very dissimilar from all other plots. It was noted that this plot was dominated by the moss *Hylocomium splendens* which was either absent or much less abundant in other plots. It was evident from the numerical results of the DCCA analysis that this species was given much more weight than all other species (almost twice that of the next most heavily weighted species *Thuja plicata*) along Axis 1, so that plot 26 with its high cover of *Hylocomium splendens* would be placed near the far right-hand side of the axis.

The amount of variation explained by the first four axes for the DCCA is 54.4% (third column of Table 1) of which the first two axes account for the greatest amount of variation (43.9%). The correlations between each environmental factor and the four axes are shown in Table 2. It is evident that some factors are more strongly correlated with one of the environmental axes than other factors. Slope of the plot, followed by the average tree height are negatively associated with the first axis whereas plot location is positively associated with this axis. For the second axis, the minimum distance between *Allotropa* and *Hemitomes* and the nearest tree is the most highly correlated factor followed by average tree height and the amount of rotten wood in the plot. The amount of humus and rock and plot location also show a correlation with this axis. The remaining factors are less strongly correlated with either axis and appear to be less important in explaining the variation in the vegetation composition of the plots.

These environmental factors are also superimposed in the biplot of fig. 6. In general, the direction and distance of the environmental factor from the origin of the biplot provides some indication of the extent to which it is correlated with each axis. Those factors which are placed farthest from the origin (and have the longest lines) are usually the most strongly associated factors with differences in the vegetation (as indicated by the correlations in Table 2). Furthermore, the closer an environmental factor is positioned near an axis indicates the extent to which it is usually associated with the variation in the vegetation data along that particular axis. All environmental factors are displayed by lines which meet at the origin with the exception of nominal environmental factors which is represented in this study by "plot location" (in the upper right corner of the biplot). Hence, based on the information contained in fig. 6 and Table 2, slope, age class, average tree height, minimum distance between *Allotropa* or *Hemitomes* and the nearest tree, and plot location appear to be the most important factors associated with variation in the vegetation composition and structure.

To better observe the relationships among the plots tightly clustered near the centre of the biplot, the data was reanalyzed excluding plot 26. The results of this analysis are displayed in the biplot of fig. 7. About 60% of the variation in the vegetation data was accounted for by the first four axes (fourth column - Table 1). Again, many of the same environmental factors which were most strongly correlated with the biplot axes of fig. 5 remain important factors after plot 26 is excluded. However, some factors become more closely associated with the second axis and include elevation and distance to the edge of the stand. Alternatively, the amount of humus and

rotten wood within the plots and the average tree height become less important along the second axis.

Table 2. Pearson correlation coefficients between environmental factors and the first two axes of the DCCA biplots.

Environmental Factor	DCCA of All Plots		DCCA Excluding Plot 26	
	Axis 1	Axis 2	Axis 1	Axis 2
Edge	-.13	.04	.13	-.28
Slope	-.40	.01	-.73	.04
Aspect	.14	.16	-.25	.35
Elevation	-.20	.00	.00	.28
Humus	-.12	.25	.01	.07
Wood	.10	.32	-.05	-.21
Rock	-.13	.23	-.07	.33
Age Class	-.22	-.01	-.53	.15
Average CBH	-.07	.03	.09	-.09
Average Height	-.31	-.32	-.73	-.24
Min. Distance	-.04	.59	-.06	.54
Humus Depth	.05	-.08	-.19	.02
Location	.31	.23	.59	.33

Although the DCCA analyses provide some indication of those environmental variables that are most closely associated with variation in the vegetation data, there is no distinguishable pattern in the position of the plots with respect to the occurrence of *Allotropa* or *Hemitomes* and with the locations of the plots as shown in figs.8 and 9 (The environmental factors have been removed from these figures so as to provide less cluttered images). Both figures are similar to those displaying the results of the DCA ordinations in that no pattern is discernable with respect to the occurrence of *Allotropa* and *Hemitomes* and only the South plots show a tendency to cluster in the lower half of the biplot.
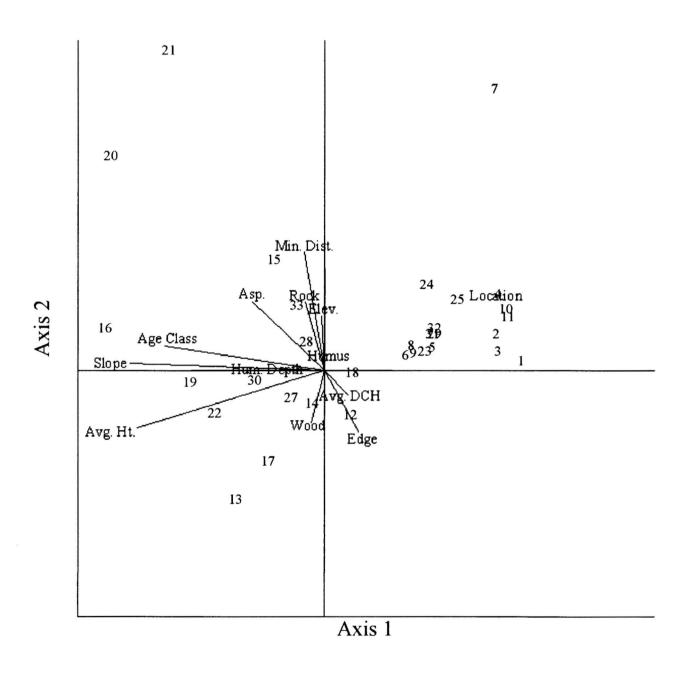
16

Figure 7. Detrended canonical correspondence analysis of the vegetation with environmental factors excluding plot 26.

17
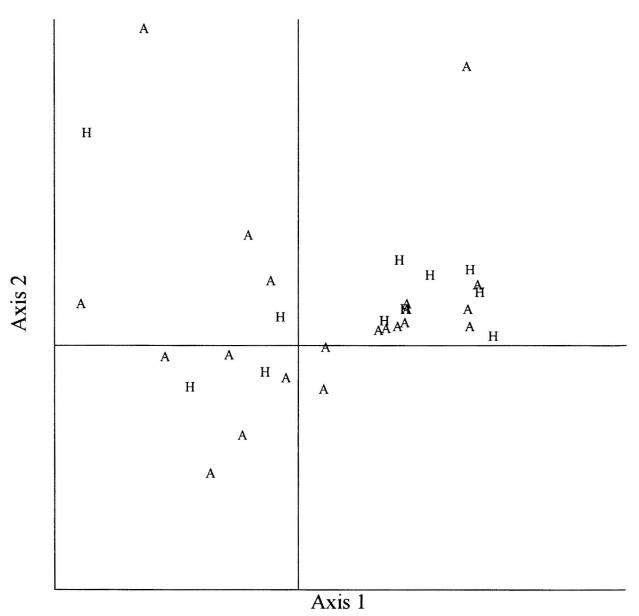
Figure 8. Detrended canonical correspondence biplot excluding plot 26. "A" - *Allotropa*; "H"- *Hemitomes*.

18
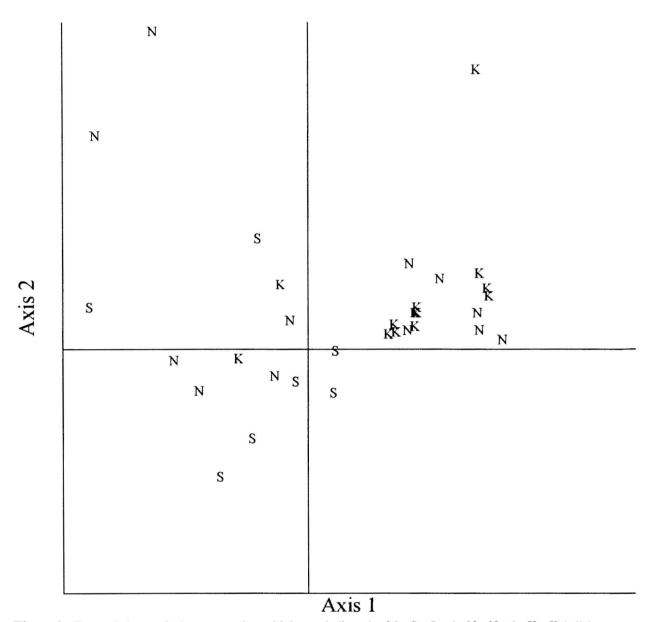
Figure 9. Detrended canonical correspondence biplot excluding plot 26. S - South; N - North; K - Koksilah.

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Discussion

Time and budget constraints largely limited the search of *Allotropa* and *Hemitomes* to mature and old growth *Pseudotsuga menziesii* stands in which these species would be expected to be found. As a result, it is possible we have failed to fully characterize the range of habitats in which both species may occur. It would have been useful to fully search numerous immature *Pseudotsuga menziesii* stands as well as wetter stands with a greater component of *Tsuga heterophylla* and *Thuja plicata* to provide a better notion of the habitat limitations of *Allotropa* and *Hemitomes*. Likewise, it would have been useful to sample the vegetation in areas in which both species were absent and include these data in the DCA and DCCA analyses. By incorporating this information in the analyses, it may have clearly identified those factors which are most closely associated with the presence or absence of one or both species at a given site.

Despite these limitations, a few stands were searched in which neither *Allotropa* and *Hemitomes* were found. These included several old growth stands where the closely-related species *Monotropa hypopitys* was often present but not *Allotropa* and *Hemitomes*. *Tsuga heterophylla* was much more abundant in these stands and heavily shaded the understorey which lacked shrubs and most herbaceous species; instead, much of the forest floor was dominated by bryophytes. These stands appeared to be wetter than those stands in which *Allotropa* and *Hemitomes* were found. A number of immature *Pseudotsuga menziesii* stands dominated in the understorey by *Gaultheria shallon* were also searched without success. These stands were similar to older *Pseudotsuga menziesii* stands in which *Allotropa* and *Hemitomes* were located but differed in that they were younger in age and tended to be characterized by a denser forest canopy with few canopy gaps.

The absence of non-chlorophyllous vascular species on immature and regeneration sites has also been observed by Mueller-Dombois (1965) in a study of the changes in *Tsuga heterophylla* and *Pseudotsuga menziesii* stands near Nanaimo. Similar results have also been reported in Oregon in *Pseudotsuga menziesii* forests where two non-chlorophyllous species, *Corallorhiza mertensiana* and *Pterospora andromedea*, appeared to be the only vascular species eradicated as a result of logging (Schoonaker and McKee 1988) (also see Ryan and Fraser 1992). There appears to be no reports in the literature of *Allotropa* or *Hemitomes* occurring in immature stands although *Allotropa* was recently observed growing in a ditch adjacent to a young *Pseudotsuga menziesii* stand in the southern part of the Greater Victoria Water District (Andrew Harcombe pers. comm.). Recently, non-chlorophyllous ericaceous (including *Allotropa* and *Hemitomes*) and orchidaceous species were cited as being particularly vulnerable to forest management activities in Washington, Oregon, and northern California and are believed to be more vulnerable than most other vascular species to logging. A number of these species are believed to be closely associated with mature and old-growth forests and are rarely observed in stands younger than 80 years (Forest Ecosystem Management Assessment Team 1993).

Based on the limited data set used in this investigation, it appears that on southern Vancouver Island, *Allotropa* and *Hemitomes* appear to be restricted to, or most abundant in, mature and old growth *Pseudotsuga menziesii* stands which are characterized in the understorey by a high cover

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of *Gaultheria shallon* which, according to Klinka *et al* (1989) and Haeussler *et al.* (1990), is most strongly associated with nitrogen-poor soils on water-shedding sites. On more nutrient-rich or wetter sites *Gaultheria* is largely restricted to rotten wood on the forest floor. In the areas investigated in this study, it was found that although the cover of *Gaultheria shallon* was often extremely high, it rarely formed tall, dense, impenetrable thickets. Instead, it comprised a relatively short (< 1 m tall) continuous, but somewhat sparse, shrub layer which allowed for the occurrence of other shrub species such as *Mahonia nervosa* and herbaceous and bryophyte species.

Allotropa and *Hemitomes* are also found in other types of habitats throughout their range which extends southwards to California. According to Wallace (1975) *Allotropa* is associated with *Pinus contorta* var. *contorta*, *P. lambertina*, *P. monticola*, *Pseudotsuga menziesii*, *Tsuga mertensiana*, *Abies magnifica*, *Lithocarpus densiflorus* var. *densiflorus*, *Chrysolepis chrysophylla*, *Arbutus menziesii*, *Gaultheria shallon*, *Arctostaphylos uva-ursi*, *A. columbiana*, *A. tomentosa*, *Chimaphila menziesii*, *Hypopitys monotropa*, *Pterospora andromedea*, and *Goodyera oblongifolia*. It is also known to occur on stabilized sand dunes in Oregon. Hence, the range of habitats in which this species is found is broader than that considered in the present study although in Canada, *Pseudotsuga menziesii - Gaultheria shallon* vegetation appears to be the most common type of habitat in which this species is found. Likewise, *Hemitomes* also appears to occupy a substantial number of different habitats throughout its range; Wallace (1975) reports *Hemitomes* is associated with the species *Picea sitchensis, Pseudotsuga menziesii, Sequoia sempervirens, Sequoiadendron giganteum, Pinus lambertina, Calocedrus decurrens, Arbutus menziesii, Lithocarpus densiflorus* var. *densiflorus, Gaultheria shallon, Vaccinium ovatum, Polystichum munitum, Hypopithys monotropa, Pityopus californicus, Pterospora andromedea,* and *Pleuricospora fimbriolata*. However, in Canada this species appears to occur most frequently in *Pseudotsuga menziesii - Gaultheria shallon* stands.

Klinka *et al.* (1989) reports that *Hemitomes* occurs on moist nitrogen-medium soils in dryish stands whereas *Allotropa* occurs on nitrogen-poor soils. This may be the case when these species are examined over a broad range of habitat types, but the results of the DCA and DCCA analyses suggest that there is substantial overlap in their respective habitats as both species were found growing in similar sites which could not be separated using DCA or DCCA analyses based on differences in the vegetation and site conditions. In several instances both species were found at a number of the same sites growing within a few meters of one another. (Soil nutrient analysis of collected soil samples may be completed in 1994).

Although the DCA and DCCA results failed to make any distinction between the type of vegetation and environment in which these two species are found, the results indicated that changes in the vegetation appeared to be most closely associated with the environmental factors, slope, stand age, average tree height, minimum distance between *Allotropa* or *Hemitomes* and the nearest tree, and plot location. Plot location is not a specific recognizable factor which can be measured in the field although it is likely to be correlated to a set of environmental factors that differed between the three sampled areas (South, North and Koksilah). This was indicated in a previous inventory of these areas (Ryan and Fraser 1992), where it was shown that the

vegetation at these sites appears to be more closely correlated to differences in location rather than differences in the age of the stands and that the South sites are wetter than the North sites which are, in turn, wetter than the Koksilah sites. Hence, moisture may be a factor that is correlated with stand location and may be an important factor in the distribution of *Allotropa* and *Hemitomes*. If a broader range of vegetation types were included in the above analyses (including those habitats in which both species are absent), it is possible that some of these factors may also be highly correlated with the presence or absence of either species at a given site. It is already known that stand age appears to be an important factor given the fact that the studies cited above reported the absence of non-chlorophyllous species on immature and regeneration sites.

What factors control the distribution of these two species remains unknown. Although Klinka *et al.* (1989) describe *Allotropa* as a shade-intolerant species and *Hemitomes* as shade intolerant/tolerant species, this is somewhat misleading as both species are non-chlorophyllous and, therefore, do not use light as an energy source. Instead, they are likely referring to the type of habitat in which these species are found rather than suggesting a connection between light and physiological requirements of these species. Although both species were most often found in open stands of *Pseudotsuga menziesii* dominated in the understorey by *Gaultheria shallon*, some specimens were located under dense conifer regeneration which heavily shaded the forest understorey to such an extent that almost all chlorophyllous species were absent including *Gaultheria shallon*. Hence neither species can truly be considered to be shade-intolerant although they were most often found in open stands whereby a large amount of incidental light reaches the forest understorey.

Allotropa and *Hemitomes* was not found in large numbers at any of the areas investigated and this appears to hold true for both species in the United States where they are listed as rare (Forest Ecosystem Management Assessment Team 1993). Why these species may be present at one microsite yet absent from adjacent similar microsites remains to be investigated. Unfortunately, there appears to be no observable site factors which appear to differ between those sites at which either species was found to adjacent areas where both species were absent. There are a number of non-exclusive factors which could explain the absence of either species from apparently suitable habitats:

1) There may be subtle differences in some environmental factor(s) which render similar sites inhospitable to the occurrence of either species at some stage in their life-cycle.

2) There may be no suitable mycorrhizal species at these sites either because they have not yet had the opportunity to become established or because some feature(s) of these habitats renders them unsuitable for their occurrence.

3) Those sites at which *Allotropa* and *Hemitomes* are absent may be suitable habitats but seeds of these species has not yet been deposited at these sites.

It is unlikely the last factor is importance because the seeds of *Allotropa* and *Hemitomes* are dust-like and are easily transported over large distances by air currents.

Unfortunately, very little is known regarding the habitat requirements of both species. They are assumed to be epiparasites on the roots of trees whereby the roots of *Allotropa* and *Hemitomes* form associations with mycorrhizae that are also associated with the roots of trees from which *Allotropa* and *Hemitomes* indirectly use as a source of energy for growth and reproduction to make up for the loss of carbon fixation associated with photosynthesis. This has been shown to occur in the closely related species *Monotropa hypopitys* (Björkman 1960, Furman 1966) and *Sarcodes sanguinea* (Vreeland *et al.* 1981). Although this has yet to be proven in *Allotropa* and *Hemitomes*, Furman and Trappe (1971) contend that the productivity rates of these species cannot be maintained by a saprophytic lifestyle. However, assuming *Allotropa* and *Hemitomes* are epiparasites, very little is known regarding the nature of this relationship and whether or not these species are limited to specific sites based on the availability of compatible mycorrhizae or specific habitat conditions. It has been noticed that other species belonging to Monotropoideae are much more widespread and occupy a greater variety of habitats than these species. For example, *Monotropa uniflora* has been observed on southern Vancouver Island in habitats occupied by *Allotropa* and *Hemitomes* as well as wetter nutrient rich sites and drier nutrient poor sites including pure stands of *Quercus garryana* (pers. obs. 1993). It is unknown if the broader range of *Monotropa* is a result of its adaptability to a broader range of habitat conditions or if it has the ability to form associations with a wide variety of mycorrhizal species (or a few wide-ranging mycorrhizal species) thus allowing it to occupy a wide range of habitats. Unfortunately, the mycorrhizae with which *Allotropa* and *Hemitomes* are associated with have not been reported in the literature and remain unknown. However, an examination of some of the samples collected in this study indicates that *Hemitomes* appears to be associated with an unidentified mycorrhizae that has also been isolated from the roots of *Pseudotsuga menziesii* (Doug Goodman, pers. comm.).

Many characteristics of the life history of both species remains unknown. Although Wallace (1975) reports that the above-ground shoots are annual and arise from a perennating root mass, it was found that for the specimens excavated in this study, that the root mass of both species was extremely difficult to distinguish from the organic debris and mycelia surrounding the basal portions of flowering shoots. Unfortunately, there was no definite structure to the root mass; instead of a large tap root with smaller secondary roots as is the case with many vascular plants, the roots constituted a mass of fine roots which did not form a distinct homogenous structure that could easily be distinguished from the hyphae and roots of other plants located in the soil. Furthermore, the connection between the stem and root mass was very fragile because, despite careful excavation, most stems were easily detached from the root mass and appeared to have very few connective roots.

In over a third of the plots, juvenile shoots were found beneath the soil surface. It is not certain how long these shoots have existed in the soil or if they will emerge the following year. If it is assumed that these juvenile shoots represent flowering shoots that will appear the following year, then it is likely that the reappearance of either species at a given plot by the next growing season

is about 40%. Although the uncertainty to which these species reappear at a given site on an annual basis has not been documented in the literature, Soyrinki (1986) has reported on the unpredictable reappearance of other non-chlorophyllous plants including the closely-related species *Monotropa hypopitys*. Similar observations during the current investigation were also made regarding *Monotropa uniflora*. This species produces shoots that decay relatively slowly so that shoots produced during the previous year are still apparent a year later. During this investigation it was noticed that some clumps of *Monotropa* emerged at sites in which shoots from the previous year were visible whereas other clumps emerged where no shoots had been produced the previous year. Furthermore, several clumps were composed of shoots which had been produced the previous year but lacked shoots produced during the current growing season. It is likely, that both *Allotropa* and *Hemitomes* also follow a similar unpredictable pattern but this cannot be readily observed in the field because the shoots of these species decay within a year so that it is not possible to determine if shoots had been produced the previous year at any of the plots sampled this year; only in one plot were some shoot fragments of *Allotropa* present which appeared to have been produced the previous year.

Other than the dense network of roots and mycelia surrounding the base of *Allotropa* and *Hemitomes* stems, there appears to be no other unique soil characteristics that are consistent between plots. It has been suggested that *Allotropa* requires substrates composed of rotten wood in order to become established at a site (Forest Ecosystem Management Assessment Team 1993), however, rotten wood was only found in the soil at six of the 33 plots which suggests it is not a prerequisite for the establishment of either species at a given site.

Conclusions and Recommendations

The results of this investigation have provided further information on the ecology of *Allotropa* and *Hemitomes*. It appears that both species are commonly associated with relatively dry *Pseudotsuga menziesii* forests in which *Gaultheria shallon* is the dominant understorey species. However, there appears to be little difference in the habitat requirements of both species at least within the range of sites investigated in this study. Further work is required in which more sites are investigated over a broader area to better identify the habitat limits of these two species within British Columbia and determine if there are distinct differences in the habitat requirements of these species over a broader range of habitat types.

Although both species are not currently considered to be rare and endangered in British Columbia according to the Conservation Data Centre (B.C. Ministry of Lands, Parks and Housing), both species may be at risk in the near future. Although they have no commercial value they remain important for several reasons:

1) The subfamily Monotropoideae, to which *Allotropa* and *Hemitomes* belong, reaches its greatest diversity in western North America. Hence, British Columbia and the western coastal United States represent the richest Monotropoideae sites in the world.

2) Both species are listed as closely associated with late-successional and old-growth forests in Washington, Oregon and California where they are considered to be rare (see Appendix table IV-A-4 in Forest Ecosystem Management Assessment Team 1993) and rarely occur in stands less than 80 years old. They are believed to be more at risk than most other species of plants because they have complex life histories involving fungal symbionts, other vascular plants and, possibly, unidentified seed disseminators.

3) Both species appear to be limited to mature and old growth forests primarily on southern Vancouver Island which has been heavily logged within the last fifty years. Because both species are most abundant in this area, current activities will likely see a decline in the number and size of populations in British Columbia as forests are converted to second-growth forests with rotation periods that are likely to be too short for these species to become established at a given site before it is eradicated by logging activities. Hence, there is a serious concern regarding the future of these two species in British Columbia.

4) Unfortunately, even if the sites in which these species are known to occur were not logged, it is possible that these populations may decline in the future. These *Pseudotsuga menziesii* stands are believed to represent a fire-climax forest whereby fires occasionally kill much of the understorey vegetation including regenerating *Tsuga heterophylla* and *Thuja plicata*. However, with the suppression of fire over the past 100 years, it is expected that the proportion of *Tsuga heterophylla* and *Thuja plicata* will increase as individual *Pseudotsuga menziesii* trees die and are replaced by *Tsuga heterophylla* and *Thuja plicata* regeneration in the understorey. Although some *Pseudotsuga menziesii* may persist and continue to be a component of the vegetation, it is likely that these stands will be sufficiently altered that they may not provide either suitable habitats or suitable mycorrhizal hosts for the establishment and growth of *Allotropa* and *Hemitomes*, particularly if both species are limited to mycorrhizal species that are associated with *Pseudotsuga menziesii*.

5) The populations located on Vancouver Island represent the northern limits of the ranges of both species. It is likely that these populations rarely exchange genetic material with populations located in the United States, hence, they may represent genetically distinct populations that possess physiological or genetic characteristics that are not found elsewhere.

6) Both species produce small dust-like seeds which likely require contact with suitable mycorrhizae in order to germinate and are unlikely to remain viable in the soil for more than a short period of time. Hence, it is unlikely that either species is a seed banker and can rely on buried viable seed to maintain the population during periods of stress. Unfortunately, this makes both species vulnerable to extirpation during stressful periods including logging activities or other impacts which alters the habitats in which current populations are located. This threat is further accentuated by the fact that neither species is capable of spreading by vegetative propagation.

There are a number of areas on the ecology of *Allotropa* and *Hemitomes* which require further investigation and include:

1) Most importantly, because both species are likely to be epiparasites, it is essential that the mycorrhizal species with which they are associated with are identified and studied. This is of critical importance because it is likely these species are extremely important and may be responsible for the limited distribution of *Allotropa* and *Hemitomes* with respect to the types of habitats in which both species are found and their overall distributions within British Columbia. It is possible that the absence of *Allotropa* and *Hemitomes* from immature and regeneration sites may result from the absence of suitable mycorrhizal species rather than differences in habitat conditions. Unfortunately, until this work is completed, we only have a partial picture of the ecology of *Allotropa* and *Hemitomes*.

2) It is important to establish permanent plots containing a number of *Allotropa* and *Hemitomes* stems and monitor these sites annually to determine how frequently and consistently shoots reappear on an annual basis. This will also provide some information on the annual reproductive output of these species.

3) Seed should be collected from flowering plants and studied to determine what factors control the germination of seeds and whether or not they require contact with a suitable species of mycorrhizae.

4) Once the mycorrhizal species have been identified, experiments should be conducted to determine if *Allotropa* and *Hemitomes* can be cultured by exposing seeds to the proper mycorrhizal hosts and associated tree species.

5) The habitat limits of both species should be more clearly defined by searching for these species over a broad range of habitat types in southern British Columbia. This work may be facilitated by reexamining locations cited on old herbarium specimens.

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Appendix I

List of species encountered in sampled plots. Nomenclature follows Douglas, G.W., G.B. Straley, and D. Meidinger. 1989-1994 (in press). The Vascular Plants of British Columbia. Part 1-4. B.C. Ministry of Forests, Victoria.

Allotropa virgata	*Mnium spinulosum*
Arctostaphylos columbiana	*Moehringia macrophylla*
Boschniaka hookeri	*Monotropa uniflora*
Campanula scouleri	*Peltigera aphthosa*
Chimaphila umbellata ssp. *occidentalis*	*Polystichum munitum*
Dicranum scoparium	*Pseudotsuga menziesii*
Eurhynchium oreganum	*Pteridium aquilinum*
Festuca occidentalis	*Pyrola picta*
Gaultheria shallon	*Rhytidiadelphus loreus*
Goodyera oblongifolia	*Rhytidiadelphus triquetrus*
Hemitomes congestum	*Rhytidiopsis robusta*
Hieracium albiflorum	*Rosa gymnocarpa*
Holodiscus discolor	*Rubus ursinus*
Hylocomium splendens	*Symphoricarpos mollis*
Isothecium myosuroides	*Thuja plicata*
Lacuca muralis	*Trachybryum megaptilium*
Linnea borealis	*Trientalis latifolia*
Lonicera ciliosa	*Tsuga heterophylla*
Madia spp.	*Vaccinium parvifolium*
Mahonia aquifolium	*Viola sempevirens*
Mahonia nervosa	
Melica subulata	

Appendix II

Species occurrences and their respective cover values (%) in each plot. Species codes comprise the first three letters of the genus and species names except for tree species which were encountered in both the tree and shrub layers. For these species, the last letter of the six-letter code indicates in which vegetation layer the species was encountered ("T" tree layer, "S" shrub layer).

SPECIES	PLOT	COVER	SPECIES	PLOT	COVER
EURORE	1	60	SYMMOL	4	0.1
GAUSHA	1	75	TRAMEG	4	2
HEMCON	1	0.5	TRILAT	4	0.5
HYLSPL	1	5	VIOSEM	4	0.1
MAHAQU	1	8	ALLVIR	5	0.1
PSEMES	1	1	AREMAC	5	0.5
PSEMET	1	65	CHIUMB	5	0.5
PTEAQU	1	5	EURORE	5	30
ALLVIR	2	0.1	FESOCC	5	0.5
EURORE	2	90	GAUSHA	5	55
GAUSHA	2	65	ISOMYO	5	0.5
MAHNER	2	5	LACMUR	5	0.5
PSEMES	2	1	LINBOR	5	0.5
PSEMET	2	80	MAHNER	5	10
PTEAQU	2	3	MNISPI	5	0.5
ALLVIR	3	0.1	PSEMET	5	70
EURORE	3	65	RHYTRI	5	0.5
GAUSHA	3	55	ROSGYM	5	0.5
MAHAQU	3	2	TRAMEG	5	3
PSEMET	3	90	TRILAT	5	0.5
PTEAQU	3	5	VIOSEM	5	0.5
THUPLT	3	10	ALLVIR	6	0.1
AREMAC	4	0.5	AREMAC	6	0.5
CAMSCO	4	0.1	BOSHOO	6	0.5
EURORE	4	70	DICSCO	6	0.5
FESOCC	4	1	EURORE	6	8
GAUSHA	4	60	GAUSHA	6	65
HEMCON	4	0.1	LINBOR	6	0.5
HIEALB	4	0.1	MADSPP	6	0.1
LACMUR	4	1	MAHNER	6	5
LINBOR	4	0.5	MELSUB	6	0.5
MAHNER	4	2	PSEMES	6	2
MELSUB	4	1	PSEMET	6	85
POLMUN	4	0.1	ROSGYM	6	2
PSEMES	4	12	TRAMEG	6	2
PSEMET	4	65	ALLVIR	7	0.1

SPECIES	PLOT	COVER	SPECIES	PLOT	COVER
AREMAC	7	0.5	TRAMEG	9	8
DICSCO	7	0.5	TRILAT	9	0.5
EURORE	7	40	ALLVIR	10	0.1
FESOCC	7	0.5	EURORE	10	85
GAUSHA	7	65	FESOCC	10	0.1
HOLDIS	7	20	GAUSHA	10	20
LINBOR	7	0.5	GOOOBL	10	0.5
MAHNER	7	3	HOLDIS	10	0.1
MELSUB	7	0.5	HYLSPL	10	1
PSEMES	7	3	MAHNER	10	1
PSEMET	7	30	PELAPH	10	0.5
RHYTRI	7	3	PSEMET	10	80
ROSGYM	7	0.5	RHYROB	10	4
TRAMEG	7	2	ROSGYM	10	0.5
TRILAT	7	0.5	VACPAR	10	0.5
VACPAR	7	1	VIOSEM	10	0.1
CHIUMB	8	0.5	CHIUMB	11	2
EURORE	8	7	EURORE	11	55
FESOCC	8	0.5	GAUSHA	11	60
GAUSHA	8	70	HEMCON	11	0.5
HEMCON	8	0.1	HYLSPL	11	11
HYLSPL	8	0.1	LINBOR	11	0.5
LINBOR	8	0.5	MAHNER	11	2
MAHNER	8	1	MAHAQU	11	0.1
MNISPI	8	0.1	MNISPI	11	0.5
PSEMET	8	75	PSEMET	11	85
SYMMOL	8	0.5	RHYROB	11	2
TRAMEG	8	1	RUBURS	11	0.1
TRILAT	8	0.5	TRAMEG	11	30
ALLVIR	9	0.1	ALLVIR	12	0.5
BOSHOO	9	0.1	EURORE	12	13
CHIUMB	9	0.5	GAUSHA	12	35
DICSCO	9	0.1	MAHNER	12	12
EURORE	9	2	MONUNI	12	0.5
GAUSHA	9	70	POLMUN	12	0.5
GOOOBL	9	0.1	PSEMET	12	85
LINBOR	9	0.5	TSUHET	12	10
MAHNER	9	2	ALLVIR	13	0.1
MELSUB	9	0.5	EURORE	13	5
PSEMET	9	80	GAUSHA	13	25
PYRPIC	9	0.5	MAHNER	13	35
ROSGYM	9	0.5	MONUNI	13	0.1

SPECIES	PLOT	COVER	SPECIES	PLOT	COVER
POLMUN	13	0.1	TSUHET	18	30
PSEMET	13	80	ALLVIR	19	0.1
TSUHET	13	35	EURORE	19	15
ALLVIR	14	0.1	GAUSHA	19	15
EURORE	14	8	PSEMET	19	40
GAUSHA	14	50	PYRPIC	19	0.5
HYLSPL	14	1	THUPLS	19	3
MAHNER	14	5	TSUHET	19	80
POLMUN	14	0.1	EURORE	20	5
PSEMET	14	80	GAUSHA	20	0.1
RHYROB	14	1	HEMCON	20	0.1
TSUHET	14	35	PSEMET	20	75
ALLVIR	15	0.1	THUPLS	20	90
DICSCO	15	0.5	TSUHET	20	20
EURORE	15	3	ALLVIR	21	0.1
GAUSHA	15	50	CHIUMB	21	0.1
MAHNER	15	10	EURORE	21	8
MONUNI	15	0.1	GAUSHA	21	30
PSEMET	15	80	HEMCON	21	0.1
TSUHES	15	30	HYLSPL	21	0.5
ALLVIR	16	0.1	PSEMET	21	75
EURORE	16	1	TSUHES	21	75
GAUSHA	16	6	EURORE	22	7
MAHNER	16	2	GAUSHA	22	10
PSEMET	16	65	HEMCON	22	0.1
TSUHES	16	25	PSEMET	22	70
TSUHET	16	90	TSUHET	22	65
ALLVIR	17	0.1	ALLVIR	23	0.1
EURORE	17	4	BOSHOO	23	0.1
GAUSHA	17	30	EURORE	23	25
HYLSPL	17	1	GAUSHA	23	65
MAHNER	17	25	PSEMET	23	75
MONUNI	17	0.1	TSUHET	23	4
PSEMET	17	90	EURORE	24	45
TSUHET	17	35	GAUSHA	24	75
VIOSEM	17	0.1	HEMCON	24	0.1
ALLVIR	18	0.5	PSEMET	24	70
CHIUMB	18	0.1	THUPLS	24	1
EURORE	18	25	TSUHES	24	10
GAUSHA	18	50	VACPAR	24	0.1
MAHNER	18	4	EURORE	25	30
PSEMET	18	80	GAUSHA	25	70

SPECIES	PLOT	COVER	SPECIES	PLOT	COVER
HEMCON	25	0.1	LONCIL	30	0.1
HYLSPL	25	5	PSEMET	30	70
PSEMET	25	50	TSUHET	30	80
TSUHES	25	2	BOSHOO	31	0.5
BOSHOO	26	0.1	CHIUMB	31	0.5
EURORE	26	2	EURORE	31	10
GAUSHA	26	70	GAUSHA	31	80
HEMCON	26	0.1	HEMCON	31	0.1
HYLSPL	26	85	HYLSPL	31	2
MAHNER	26	1	LINBOR	31	0.5
PSEMET	26	85	PSEMET	31	75
THUPLT	26	20	RHYLOR	31	0.5
GAUSHA	27	85	RHYROB	31	1
HEMCON	27	0.1	SYMMOL	31	0.1
HYLSPL	27	1	TRAMEG	31	7
LINBOR	27	0.5	ALLVIR	32	0.1
PSEMET	27	30	BOSHOO	32	0.1
RHYROB	27	3	EURORE	32	0.5
TSUHET	27	50	GAUSHA	32	80
CHIUMB	28	0.5	GOOOBL	32	0.1
GAUSHA	28	30	HYLSPL	32	3
HEMCON	28	0.5	MAHNER	32	0.5
PSEMET	28	85	PSEMET	32	80
RHYROB	28	10	THUPLT	32	25
THUPLS	28	12	TRAMEG	32	5
TRAMEG	28	3	ALLVIR	33	0.1
TSUHET	28	15	ARCUVA	33	1
ALLVIR	29	0.5	GAUSHA	33	70
BOSHOO	29	0.5	MNISPI	33	0.5
EURORE	29	12	PSEMET	33	85
GAUSHA	29	80	RHYROB	33	1
HYLSPL	29	15	THUPLS	33	20
ISOMYO	29	3	TRAMEG	33	12
PSEMET	29	90	TSUHET	33	40
RHYROB	29	2	VACPAR	33	0.5
RHYTRI	29	1			
ROSGYM	29	0.5			
RUBURS	29	0.5			
TSUHET	29	2			
ALLVIR	30	0.1			
EURORE	30	5			
GAUSHA	30	70			

Appendix III

Measurements of the four closest mature trees to the plot centre where either *Allotropa* or *Hemitomes* was present. The word "incomplete" which, in some instances, follows the species name indicates that an accurate estimate of the tree age could not be made either because the trunk radius exceeded that of the increment borer or the centre of the trunk was rotten.

Plot 1

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		73	92	19.82	1.60
Df		60	72	23.17	3.60
Df		48	34	9.45	1.70
Df		82	129	28.66	6.50
Df		92	188	31.10	8.00
Average		71	103.00	22.44	4.28

Plot 2

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		69	58	23.48	2.50
Df		73	91	25.61	3.70
Df		79	86	21.65	4.50
Df		102	155	31.10	5.40
Average		81	97.50	25.46	4.03

Plot 3

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	67	136	26.83	2.40
Df		74	124	25.91	3.00
Df		70	77	17.38	3.30
Df		61	52	17.38	3.50
Df		86	180	32.32	7.20
Average		72	113.80	23.96	3.88

Plot 4

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		329	150	27.44	2.10
Df	incomplete	298	170	23.17	3.30
Df		282	195	28.96	3.80
Df		379	220	26.83	2.80
Average		322	183.75	26.60	3.00

Plot 5

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		240	205	31.71	1.00
Df	incomplete	235	175	23.17	7.00
Df	incomplete	322	225	24.70	8.60
Df	incomplete	135	228	24.70	7.20
Average		233	208.25	26.07	5.95

Plot 6

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		288	115	24.09	1.50
Df		279	191	27.13	2.80
Df	incomplete	294	205	32.32	6.60
Df	incomplete	345	229	33.84	5.90
Average		302	185.00	29.34	4.20

Plot 7

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		270	107	25.61	6.00
Df	incomplete	225	217	33.54	8.00
Df		294	205	32.32	6.80
Df		288	115	24.09	6.80
Average		269	161.00	28.89	6.90

Plot 8

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	295	208	28.96	0.80
Df	incomplete	282	146	24.70	4.40
Df	incomplete	227	108	18.60	5.50
Df		366	188	29.27	7.00
Average		292	162.50	25.38	4.43

Plot 9

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	295	208	28.96	1.50
Df	incomplete	282	146	24.70	6.50
Df	incomplete	227	108	18.60	3.80
Df		366	188	29.27	7.20
Average		292	162.50	25.38	4.75

Plot 10

Species	Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	70	49	10.06	1.00
Df	81	57	10.67	1.50
Df	70	55	13.41	1.70
Df	85	110	17.38	1.60
Average	76	67.75	12.88	1.45

Plot 11

Species	Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	70	54	13.57	1.00
Df	81	68	16.31	1.40
Df	70	54	15.85	1.10
Df	85	43	15.55	1.00
Average	76	54.75	15.32	1.13

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Plot 12

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	259	204	46.04	1.50
Df	incomplete	316	264	50.00	2.80
Df	incomplete	230	270	48.48	5.70
Df	incomplete	225	266	43.60	5.20
Average		258	251.00	47.03	3.80

Plot 13

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	259	204	46.04	1.50
Df	incomplete	316	264	50.00	2.80
Df	incomplete	230	270	48.48	5.70
Df	incomplete	225	266	43.60	5.20
Average		257	251.00	47.03	3.80

Plot 14

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	227	225	47.56	1.60
Df	incomplete	160	210	48.78	2.80
Df		227	160	44.82	7.40
Cw	incomplete	155	178	37.50	8.80
Average		192	193.25	44.66	5.15

Plot 15

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	227	225	47.56	1.20
Df	incomplete	160	210	48.78	2.00
Df		227	160	44.82	7.20
Cw	incomplete	155	178	37.50	8.80
Average		192	193.25	44.66	4.80

Plot 16

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	225	264	50.00	5.30
Df	incomplete	259	204	46.04	5.80
Df	incomplete	236	264	50.00	7.50
Df	incomplete	230	270	48.48	8.00
Average		238	250.50	48.63	6.65

Plot 17

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	205	312	47.87	1.00
Df		107	90	24.09	4.20
Df		224	172	35.37	6.70
Df	incomplete	223	229	48.78	8.20
Average		190	200.75	39.02	5.03

Plot 18

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		250	266	38.41	1.50
Df		206	219	36.89	3.00
Df		230	167	48.78	4.40
Df	incomplete		266	46.04	6.50
*******only first three used					
Average		229	217.33	41.36	2.97

Plot 19

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	320	239	45.73	1.30
Df	incomplete	321	251	44.51	4.50
Df	incomplete	267	272	45.43	5.10
Df		387	227	35.06	7.00
Average		303	254.00	45.22	3.63

Plot 20

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		387	227	35.06	1.70
Df		253	121	30.79	3.50
Df		317	142	31.71	4.30
Df		307	193	35.37	6.50
Average		319	163.33	32.52	3.17

Plot 21

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		275	100	25.61	2.40
Df		321	171	34.76	2.40
Df		281	170	36.89	5.00
Df		295	158	30.49	4.00
Average		292	147.00	32.42	3.27

Plot 22

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		275	100	25.61	1.00
Df		321	171	34.76	2.80
Df		281	170	36.89	7.00
Df		387	227	35.06	4.30
Average		292	147.00	32.42	3.60

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Plot 23

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		321	171	34.76	1.00
Df		205	100	25.61	3.20
Df		295	158	30.49	5.20
Df		289	157	32.93	3.70
Average		274	143.00	30.28	3.13

Plot 24

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		328	189	33.54	1.20
Df		307	161	35.37	4.80
Df		293	145	30.79	6.40
Df		266	100	32.32	3.80
Average		309	165.00	33.23	4.13

Plot 25

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		302	238	38.41	1.90
Df		309	180	35.67	3.20
Df		254	176	35.98	7.00
Df	incomplete	328	306	39.63	6.80
Average		288	198.00	36.69	4.03

Plot 26

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	177	129	30.18	2.20
Df		290	184	42.68	4.00
Df		213	110	34.76	6.50
Df		356	157	30.49	6.50
Average		227	141.00	35.87	4.23

Plot 27

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		334	154	28.05	1.70
Df		222	97	29.57	2.60
Hw		228	113	29.27	2.90
Hw		271	125	28.05	4.60
Average		261	121.33	28.96	2.40

Plot 28

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df		297	159	26.22	0.50
Df		303	220	31.10	1.60
Df		316	112	21.95	2.00
Df		306	202	31.10	4.00
Average		305	163.67	26.42	1.37

Plot 29

Species	Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	176	184	32.93	0.80
Df	168	127	28.05	2.60
Df	170	120	25.91	3.80
Df	179	186	34.45	4.50
Average	171	143.67	28.96	2.40

Plot 30

Species	Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	85	72	18.90	0.00
Df	148	137	28.05	1.10
Df	123	130	26.52	3.00
Df	112	80	25.61	3.20
Average	119	113.00	24.49	1.37

Plot 31

Species	Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	146	106	23.78	1.20
Df	149	113	24.70	2.50
Df	170	95	22.56	5.60
Df	151	134	26.52	5.10
Average	155	104.67	23.68	3.10

Plot 32

Species	Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	118	115	26.52	0.80
Df	130	133	29.57	1.70
Df	162	144	28.66	3.50
Df	163	111	25.00	4.00
	137	130.67	28.25	2.00

Plot 33

Species		Age (yr)	D.C.H. (cm)	Height (m)	Dist. to Plant (m)
Df	incomplete	225	133	18.90	1.50
Hw	incomplete	80	78	14.33	2.40
Df	incomplete	200	153	21.34	3.40
Df	incomplete	245	213	25.00	3.70
		168	121.33	18.19	2.43

Appendix IV

Age class and average measurements used in the DCCA analysis based on individual tree measurements listed in Appendix III. Values listed under age class refer to the upper age limit used to delineate the age class to which each plot was assigned. Minimum distance to the plot centre (column 6) rather than average distance to the plot centre (column 5) was used in the DCCA analysis.

Plot	Age Class	Avg. DCH. (cm)	Avg. Ht. (m)	Avg. Dist. (m)	Min. Dist. (m)
1	150	103	22.4	4.3	1.6
2	150	97.5	25.46	4	2.5
3	150	113.8	23.96	3.9	2.4
4	350	183.75	26.6	3	2.1
5	250	208.25	26.1	6	1
6	350	185	29.3	4.2	1.5
7	350	161	28.9	7	6
8	350	162.5	25.4	4.4	0.8
9	450	162.5	25.4	4.8	1.5
10	150	67.75	12.9	1.4	1
11	150	54.75	15.3	1.1	1
12	350	251	47	3.8	1.5
13	350	251	47	3.8	1.5
14	250	193.25	44.7	5.2	1.6
15	250	193.25	44.7	4.8	1.2
16	350	250.5	48.6	6.6	5.3
17	250	200.75	39	5	1
18	250	217.33	41.4	3	1.5
19	450	254	45.2	3.6	1.3
20	350	163.33	32.5	3.2	1.7
21	350	147	32.4	3.3	2.4
22	350	147	32.4	3.6	1
23	350	143	30.3	3.1	1
24	350	165	33.2	4.1	1.2
25	350	198	36.7	4	1.9
26	350	141	35.9	4.2	2.2

Plot	Age Class	Avg. DCH. (cm)	Avg. Ht. (m)	Avg. Dist. (m)	Min. Dist. (m)
27	350	121.33	29	2.4	1.7
28	350	163.67	26.4	1.4	0.5
29	250	143.67	29	2.4	0.8
30	150	113	25	1.4	0
31	250	104.67	23.7	3.1	1.2
32	150	130.67	28.3	2	0.8
33	250	121.33	18.2	2.4	1.5

Appendix V

The following table lists the environmental factors recorded at each plot. The column "Species" identifies whether *Allotropa*-"a" or *Hemitomes*-"h" was recorded at each plot. The column "Edge" refers to the distance between the plot and the edge of the stand. The last two columns refer to the number of mature flowering stems (#Stem) and the number of immature shoots (#Im.) recorded for each plot.

Plot	Loc.	Species	Humus Depth (cm)	Asp. (°)	Slope (%)	Elev. (m)	Edge (m)	Humus (%)	Wood (%)	Rock (%)	#Stem	#Im.
1	North m2q2	h	10	30	20	250	300+	95	5	0	1	0
2	North m2q3	a	8	35	25	250	300+	90	10	0	1	0
3	North m2q1	a	5	25	15	250	300+	95	5	0	2	0
4	Koksil o3q1	h	10	167	25	620	41	94	5	1	1	0
5	Koksil o3q1	a	4	160	20	620	48	80	15	5	1	0
6	Koksil o3q2	a	10	140	15	620	47	95	5	0	1	0
7	Koksil o3q4	a	7	93	25	620	50	98	1	1	6	0
8	Koksil o3q2	h	5	142	20	620	25	85	10	5	1	0
9	Koksil o3q2	a	8	133	20	620	27	87	10	3	1	0
10	Koksil m3q2	a	5	200	28	550	45	98	2	0	17	4
11	Koksil m3q2	h	10	212	28	550	45	94	5	1	2	1
12	South o1q1	a	4	85	50	375	170	97	3	0	1	0
13	South o1q1	a	3	65	50	375	170	98	2	0	6	3
14	South o1q1	a	2	50	50	375	180	91	8	1	3	0
15	South o1q1	a	3	358	55	375	180	85	10	5	11	0
16	South o1q1	a	6	61	45	375	170	97	3	0	1	2
17	South o1q1	a	5	40	65	375	180	96	1	3	2	5
18	South o1q2	a	7	36	45	375	120	97	1	2	1	0
19	North o2q4	a	10	280	45	500	75	95	5	0	1	1

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Plot	Loc.	Species	Humus Depth (cm)	Asp. (°)	Slope (%)	Elev. (m)	Edge (m)	Humus (%)	Wood (%)	Rock (%)	#Stem	#Im.
20	North o2q2	h	6	287	60	500	80	93	5	2	1	2
21	North o2q2	a	5	273	60	500	80	94	0	6	2	2
22	North o2q2	h	8	273	60	500	85	94	4	2	3	0
23	North m2q1	a	5	268	45	500	80	95	0	5	1	0
24	North o2q2	h	8	298	50	500	85	95	0	5	1	1
25	North o2q3	h	8	352	42	500	110	84	1	15	1	1
26	North RE2	h	10	277	35	300	20	90	10	0	16	0
27	North border	h	10	65	37	620	18	75	25	0	1	1
28	North border	h	rotten wood	47	15	620	33	65	35	0	1	0
29	Koksil L70	a	8	243	40	600	77	75	4	1	2	0
30	Koksil L70	a	2	224	30	600	64	85	15	0	10	0
31	Koksil L70	h	2	215	40	600	36	99	1	0	10	0
32	Koksil L70	a	10	210	28	600	61	80	20	0	1	4
33	Koksil l92a	a	3	115	10	800	34	87	3	10	5	3