AN ABSTRACT OF THE THESIS OF

Nathan Jeremy Poage for the degree of Master of Science in Forest Science presented on September 21, 1994.

Title: Comparison of Stand Development of a Deciduous-Dominated Riparian Forest and a Coniferous-Dominated Riparian Forest in the Oregon Coast Range

Signature redacted for privacy.

Abstract approved: ______________________________
Thomas A. Spies

Riparian forests in the central Oregon Coast Range vary along a coniferous-deciduous compositional continuum. Variations in structure and composition affect water quality, fish and wildlife, biodiversity, timber, and aesthetics. A retrospective approach was taken in this study in order to understand and compare the structure, pattern, and history of an unmanaged, mature, deciduous-dominated riparian forest and an unmanaged, mature, coniferous-dominated riparian forest in the central Oregon Coast Range. Information on forest structure and pattern was acquired by mapping locations of all trees and snags (DBH $\geq$ 5cm) within a 2.0 ha and a 2.25 ha reference stand. The history of each stand was reconstructed through analyses of stand structure and composition, tree

ages, spatial patterns of trees and snags, as well as detailed field observations.

The structure and composition of the two forests is very different. Non-random patterns of trees and snags were observed at multiple scales. Although it is not possible to infer directly the process(es) responsible for observed patterns, point-pattern analysis is a useful tool to detect and describe intra- and interspecific patterns.

Neither forest resulted from a single, stand-replacing fire. Instead, both sites were at least partially burned about 145 years ago, possibly in the same fire(s) which spread across an estimated 500,000 acres between the Siuslaw and Siletz Rivers in the mid-1800's (Morris 1934). There is good evidence to suggest that a second fire occurred at the coniferous-dominated site. One or two other fires may have occurred at the deciduous-dominated site. Evidence of wind, herbivory, flooding, pathogens, mass movement events, and non-stand replacing fire was observed at one or both of the sites.

Seed source availability as affected by disturbance history may have played a role in forest development at both sites. The seed source availability of red alder relative to Douglas-fir may have increased with successive disturbance events at the deciduous-dominated, riparian forest. A local source of western hemlock seed may have been a key factor in the development of the coniferous-dominated, riparian forest.

Master of Science thesis of Nathan Jeremy Poage presented on September 21, 1994

APPROVED:

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Professor of Forest Science in charge of major

Signature redacted for privacy.

Head of Department of Forest Science

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Nathan Jeremy Poage, Author

COMPARISON OF STAND DEVELOPMENT OF A DECIDUOUS-DOMINATED RIPARIAN FOREST AND A CONIFEROUS-DOMINATED RIPARIAN FOREST IN THE OREGON COAST RANGE

by

Nathan Jeremy Poage

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INTRODUCTION

Forest development following disturbance is a complex process which can follow a wide range of successional pathways (Egler 1954, Drury and Nisbet 1973, Pickett et al. 1987, Christensen 1988). Similar sites may be occupied by a variety of relatively stable communities (Niering and Egler 1955, Niering and Goodwin 1974, Botkin 1979, McCune and Allen 1985, Niering 1987). Understanding how different forest communities develop is a question of great ecological importance because differences in stand-level structure and composition can profoundly influence ecosystem-level patterns and processes (Waring and Schlesinger 1985, Pickett et al. 1987).

Riparian, or stream-side, forests in the central Oregon Coast Range vary along a coniferous-deciduous compositional continuum (Hibbs 1987). Variations in structure and composition affect water quality, fish and wildlife, biodiversity, timber, and aesthetics (Moring 1975a,b, Moring and Lantz 1975, Harmon et al. 1986, Oliver and Hinckley 1987, Sedell et al. 1988, Gregory et al. 1991, Swanson and Franklin 1992). For example, large diameter, relatively decay-resistant coniferous coarse woody debris in streams greatly enhances the quality of anadramous fish habitat (Meehan et al. 1977, Bisson et al. 1987, Everest et al. 1987, Sullivan et al. 1987, Sedell et al. 1988). Deciduous stands dominated by nitrogen-fixing red alder (Alnus rubra Bong.) may enhance long-term site productivity and limit the spread of the root rot Phellinus wierii, which can cause mortality in coniferous species such as Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) (Franklin et al. 1968, Hemstrom and Logan 1986). The input of higher quality litter from deciduous-dominated stream-side forests relative to litter from coniferous-dominated riparian forests can have important consequences for stream productivity (Gregory et al. 1991). Understanding the structural and compositional development of different forest stands is, therefore, of great ecological interest.

Patterns of forest communities result from the interaction of many factors or mechanisms (Pickett et al. 1987). Primary among these is disturbance, which makes growing space available by killing or damaging established individuals (Oliver and Larson 1990). The type, scale, intensity, and spatial and temporal frequency of disturbance all influence which species initially occupy a site (Henry and Swan 1974, Connell and Slatyer 1977, Pickett et al. 1987, Oliver and Larson 1990, Veblen 1992). The potential species to occupy open growing space are limited by the availability of viable propagules in the form of seeds, advance regeneration, or vegetative reproduction from stumps, roots, and rhizomes (Oliver 1981, Oliver and Larson 1990). Germination and early growth strongly influence which species will initially dominate growing space (Canham and Marks 1985). Propagule availability, establishment, and growth contribute to the initial floristic composition on a site (Egler 1954), an important determinant of the developmental pathway following disturbance (Pickett et al. 1987).

The forests of the Oregon Coast Range historically have been shaped by fires, windstorms, and, since the mid-1800's, land clearing and logging (Morris 1934, Juday 1977, Hemstrom and Logan 1986, Teensma et al. 1991). For example, an estimated 500,000 acres of forest between the Siuslaw and Siletz Rivers in the Oregon Coast Range were burned in the period 1845-1849 (Morris 1934). While lightning ignitions occur (Agee 1991), human activity has been implicated as the cause of many wildfires in the Oregon Coast Range, both before and after settlement by Euro-Americans (Morris 1934, Spies and Cline 1988, Teensma et al. 1991). The Tillamook Burn of 1933, which burned over 300,000 acres, was started accidentally during a logging operation (Lucia 1983).

Windstorms are another type of major disturbance which affect Coast Range forests (Spies and Cline 1988). Hurricane-force winds occur annually in the Coast Range and can disturb large areas in a single storm event (Badura et al. 1974). For example, 11 billion board feet of timber were blown over in western Oregon and Washington during a single windstorm in 1962 (Orr 1963).

The disturbance history and development of Coast Range forests following a major disturbance such as fire are not well understood. In the conventional view of forest development in the Coast Range, even-aged stands of shade-intolerant Douglas-fir established following catastrophic, stand-replacing wildfires (Munger 1940). These even-aged stands were gradually replaced over a period of several centuries by more shade-tolerant species such as western hemlock, leading to uneven-aged stands (Munger 1940). This idealized view of forest disturbance and succession does not, however, recognize the heterogeneous nature of fire and the complex developmental patterns that result from various biological processes.

Although fires like the Tillamook Burn are popularly regarded as "catastrophic wildfires", the heterogeneous nature of such fires and, in some cases, later reburns can leave surviving trees as isolated individuals or in groups (Isaac and Meahger 1938, Hemstrom and Logan 1986, Spies and Cline 1988, Agee 1991, Teensma et al. 1991). Together with the potentially wide variety of microsites produced by disturbance(s), seed from remnant trees can influence not only which species establish but also where species establish following disturbance. Early competition from woody shrubs such as salmonberry (Rubus spectabilis Pursh) and vine maple (Acer circinatum Pursh) also can severely limit the regeneration of tree species (reviewed by Perry et al. 1985, Hibbs 1987). The regeneration of one species over another may be favored or limited by herbivory, pathogens, annual climatic variation, and geomorphic patterns and processes (Oliver and Larson 1990).

Forest development in the Oregon Coast Range is also influenced greatly by the relative number and spatial distribution of Douglas-fir and red alder which initially establish, as well as by the presence of shade-tolerant conifers such as western hemlock (Tsuga heterophylla (Raf.) Sarg.) and western red cedar (Thuja plicata Donn) (Franklin and Pechanec 1968, Hemstrom and Logan 1986, Oliver and Larson 1990). Although both Douglas-fir and red alder grow best on mesic sites (Oliver and Larson 1990), a higher initial growth rate generally enables red alder to outcompete Douglas-fir on such sites (Newton et al. 1968). Given the general agreement that the survival of Douglas-fir overtopped by red alder is very poor (Franklin and Pechanec 1968, Newton et al. 1968, Perry et al. 1985, Hemstrom and Logan 1986, Oliver and Larson 1990), how do coniferous-dominated forests develop in an environment where red alder is competitive?

Riparian forests of the Coast Range may have more complex disturbance histories and developmental pathways than upland forests. Disturbance regimes near streams are affected not only by fire, wind, and disease which are common in upslope forests, but also by erosion and deposition connected with active streams, and by the movement of sediments and woody materials downslope (Swanson et al. 1988, Gregory et al. 1991). Banks, benches, terraces, and other geomorphic features associated with fluvial activity provide a variety of microsites not found upslope, resulting in a relatively high degree of structural and compositional diversity among riparian plant communities (Swanson et al. 1988, Gregory et al. 1991). Large vertebrates such as beavers can profoundly affect stream-side communities (Waring and Schlesinger 1985, Remillard et al. 1987).

Given the complex disturbance and biotic processes that potentially characterize riparian forests, as well as the lack of basic vegetation studies, there are many unanswered questions about the ecology of these forests. For example, how do structurally and compositionally different riparian forests develop? Are different riparian forests the result of single catastrophic wildfires or can multiple "major" disturbances play a role (e.g., fires and/or windstorms)? What is the role of localized non-fire disturbances in the development of stream-side forests?

This study compares the development of an unmanaged, mature, deciduous-dominated riparian forest (Flynn Creek) and an unmanaged, mature, coniferous-dominated riparian forest (Trout Creek) in the central Oregon Coast Range. Although they are growing on similar sites, these two forests are compositionally and structurally very different. Initial field reconnaissance suggested that fire(s) occurred at both sites in the mid-1800's. Knowledge of a forest's disturbance and establishment history is essential to understanding its development and to predict its response to management practices (Oliver and Larson 1990). A retrospective approach is taken in this study in order to understand how the forests at Flynn Creek and Trout Creek have developed. Information on forest development is acquired by reconstructing the history of each stand through analyses of stand structure and composition, tree ages, and spatial patterns of trees and snags (Henry and Swan 1974, Means 1982, Deal et al. 1991, Moeur 1993).

The use of point-pattern spatial analysis can facilitate the interpretation of forest development. Spatial patterns of aggregation or dispersion indicate that the distribution of establishment and mortality within a stand has been influenced by non-random processes such as competition between species. As summarized by Moeur (1993), the

> spatial patterns of [live and dead] trees in forest stands reflect the complex historical and environmental mosaic imposed by initial establishment patterns, microenvironment differences, climate and sunlight factors, competing vegetation, and the chance success of different species over time depending on their individual life history characteristics.

Hypotheses concerning the nature of spatial patterns which are thought to occur can be tested statistically and used as a line of evidence in the interpretation of forest development.

Management of Coast Range forests on public lands is shifting toward landscape-level planning and watershed analysis to meet ecological goals and legal mandates (FEMAT 1993). Approximately 11 percent of all Federal lands in western Washington, western Oregon, and northwestern California, an area of over one million hectares, have been recently classified as "riparian reserves" in recent federal land management planning efforts (ROD/SAG 1994). The development of late-successional, multi-storied riparian forests dominated by coniferous species has received a great deal of attention in these planning efforts (FEMAT 1993). Understory conifer regeneration is one of the criteria used to define the old-growth structure of forests in the Pacific Northwest (Franklin et al. 1981, Oliver and Larson 1990, Spies and Franklin 1991). The establishment coniferous-dominated forests in riparian areas is of great interest to public and private land managers (Horvath and Tucker 1992, Chan et al. 1993), particularly in light of observations that conifer regeneration is poor along streams in the Oregon Coast Range (Franklin and Pechanec 1968, Henderson 1970, Andrus and Froehlich 1987, Carlton 1988, Minore and Weatherly 1994).

The need to develop management systems for stream-side forests is clear (Hibbs 1987, Oliver and Hinckley 1987, Hibbs et al. 1990, Horvath and Tucker 1992, Chan et al. 1993). This is true not only for coniferous-dominated forests but also for deciduous-dominated and mixed coniferous-deciduous forests. The success of such efforts is heavily dependent upon baseline information about the structure and development of unmanaged riparian stands.

QUESTIONS AND OBJECTIVES

Understanding the structure and development of Coast Range riparian forest is of great ecological and silvicultural importance. Given that no detailed study of riparian stand structure and/or development has been done anywhere in Oregon, the two retrospective case studies at Flynn Creek and Trout Creek have the opportunity to provide valuable information on the structure and development of stream-side forests. The overall question addressed in this study is how does an unmanaged, mature, deciduous-dominated riparian forest differ in structure and development from an unmanaged, mature, coniferous-dominated riparian forest?

The first objective of this study is to characterize and contrast the forest structure and composition of the Flynn Creek and Trout Creek reference stands. Although it is apparent that the stands differ structurally (they were selected on this basis), quantified structure is needed to help set management targets and provide society with models of unmanaged riparian forests.

The second objective of this study is to characterize the interactions within and between species as expressed by spatial patterns. Analysis of spatial patterns can give insights into the processes which influence stand development. Pattern analysis also can augment models of forest structure. Further, species may respond differently to spatial variations in forest structure. For example, the spatial pattern of snags may be important for wildlife.

Several questions have been posed to facilitate the interpretation of spatial point patterns:

1) Are the different species of trees and snags randomly distributed in each stand?
2) Is the spatial distribution of trees from the current stand associated with trees from the prior stand (i.e., snags)?
3) Is the spatial distribution of trees of one species associated with the spatial distribution of other species?
4) What are the spatial patterns of dead trees relative to live trees in the current stand?
5) What are the spatial patterns of understory conifer regeneration relative to trees and snags in the current stand?

The third objective of this study is to determine the disturbance and establishment history of each forest. Differences in stand structure may be the result of differences in disturbance histories. Alternatively, stands may be influenced by the same disturbances but by different biotic processes.

Two questions focusing on disturbance have been posed:

1) Did these two riparian forests result from single catastrophic wildfires or did multiple fires occur?

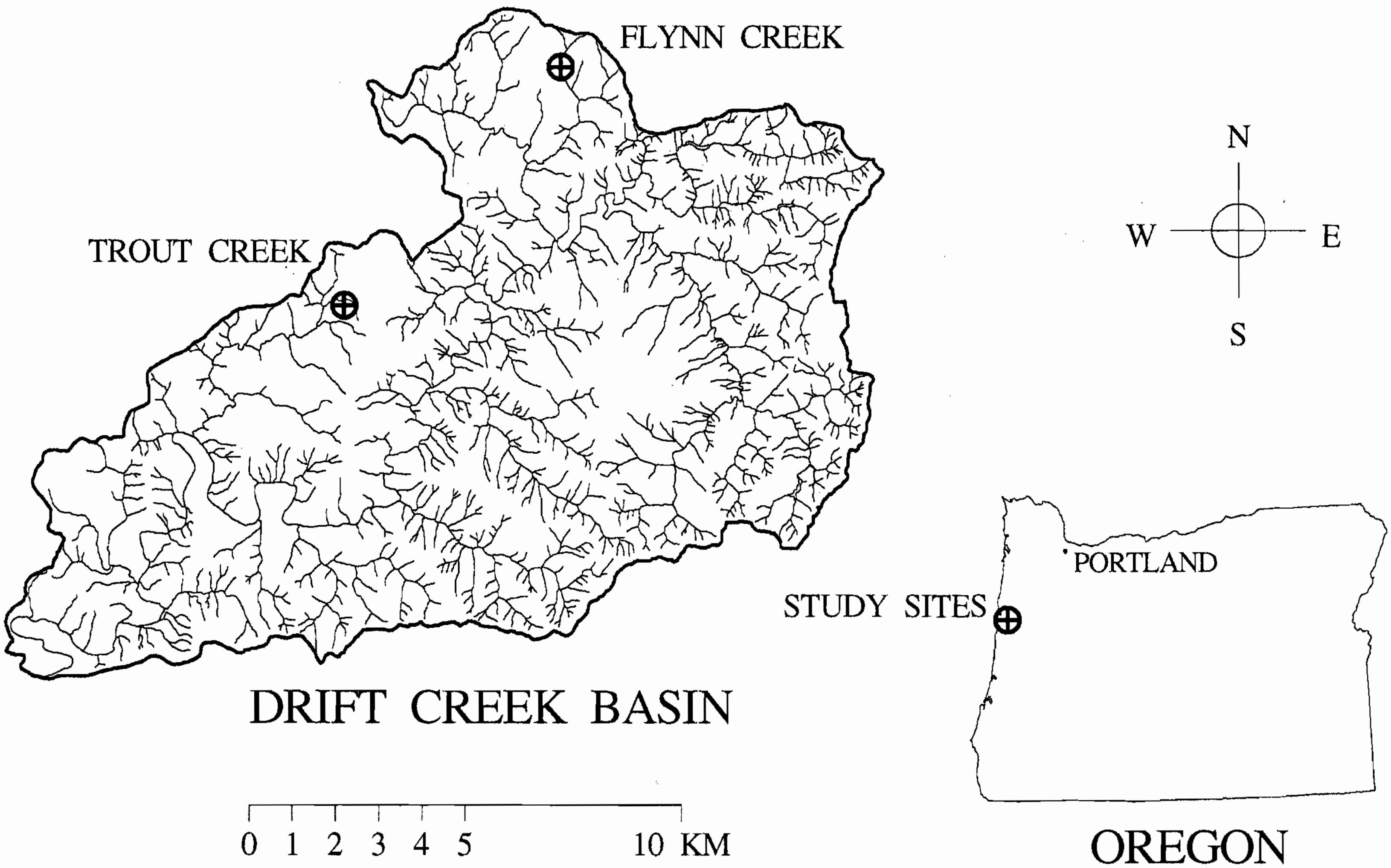
2) What is the role of localized non-fire disturbances (e.g., wind, geomorphic activity, pathogens, and animals) in the development of these two riparian forests?

STUDY SITES

In 1989 and 1990, as part of the Coastal Oregon Productivity Enhancement Program (COPE), permanent reference stands were established in unmanaged, stream-side forests at Flynn Creek and Trout Creek, located in the Drift Creek basin (Figure 1). These reference stands, which represent distinctive compositional and structural phases for riparian forests, were located subjectively by T. Spies following extensive reconnaissance in unmanaged riparian forests of the central Coast Range. The deciduous-dominated reference stand at Flynn Creek (44°32'40"N, 123°51'21"W; legal coordinates T12S, R10W, Section 12) is a 2.25ha area, 225m along by 50m on either side of the second-order stream of the same name. The Trout Creek reference stand (44°29'40"N, 123°55'06"W; legal coordinates T12S, R10W, Section 28) is a 2.0ha section of coniferous-dominated forest, 200m along by 50m on either side of the second-order stream of the same name.

The Flynn Creek and Trout Creek reference stands are located in the Tsuga heterophylla vegetation zone of the Oregon Coast Range (Franklin and Dyrness 1973). Although sites may be dominated for long periods by the shade-intolerant species Douglas-fir, this zone is named for the shade-tolerant species western hemlock, the potential late-successional dominant. Western red cedar, a relatively shade-tolerant conifer, is found in association with both Douglas-fir and western hemlock. Sitka spruce (Picea

Figure 1. Location of the Flynn Creek and Trout Creek reference stands.



sitchensis (Bong.) Carr.) is found within near-coastal portions of this vegetation zone. Deciduous tree species present in the Tsuga heterophylla zone include red alder and big-leaf maple (Acer macrophyllum Pursh). Shrubs found at both sites include salmonberry, vine maple, elderberry (Sambucus racemosa var. arborescens (T. & G.) Gray), and salal (Gaultheria shallon Pursh).

The reference stands are located at an elevation of 170-220m. Average annual precipitation at both sites is approximately 2150-2290mm, falling almost entirely as rain (PRISM/OSU 1993). Summer precipitation accounts for 6-9% of the annual total (Franklin and Dyrness 1973). Average annual temperature is 8-9°C (Franklin and Dyrness 1973).

The soils at both Trout Creek and Flynn Creek are classified as 50-100cm deep, gravely loam soils of the Bohannon-Slickrock soil association (Corliss 1973). The bedrock at both sites is part of the Tyee formation, consisting of bedded sandstones and siltstones of middle Eocene age (Corcoran 1973). Both streams run roughly north to south, with the eastern side of each drainage being steeper than the west. The valley floor at Trout Creek is narrower than that at Flynn Creek, although both contain narrow floodplains.

METHODS

Characterization of Forest Structure and Composition

Stand-Level Mapping and Data Collection

The locations, species, and DBH of all trees and snags $\geq$ 5cm DBH within each reference stand were recorded under the direction of R. Pabst following the procedures outlined by Pabst et al. (in preparation). (DBH, or diameter at breast height, is the diameter of the bole measured at 1.37m above the ground.) Briefly, this consisted of surveying the boundaries of each reference stand, establishing a 25m x 25m grid with permanently marked grid points within the surveyed boundaries, and then mapping the location of all trees and snags by triangulating from two or more of the 25m x 25m grid points. The locations of active stream channels and elevations at selected mapped points within each reference stand also were recorded. The coordinate data for trees and snags were analyzed using the ARC/INFO geographic information system (GIS) (ESRI 1992). Topographic contour lines (2m intervals) were extrapolated from the mapped elevation points using ARC/INFO.

Stand structure and composition were described in terms of species-size distributions of live trees/ha and snags/ha, as well as by summarizing the stem density and basal area of all live trees and snags of DBH $\geq$ 5cm by stand and species. The canopy position of each tree was recorded as dominant, codominant, intermediate, or suppressed relative to all other trees in the stand.

Stand Cross-Sections

Using methods similar to Kuiper (1988), a roughly east-west, 12.5 meter-wide, three dimensional belt-transect was established across each stand to provide additional information about vertical and horizontal stand structure and composition. Each belt-transect was subjectively located to give as representative a cross-section of stand structure as possible. The height of each tree and snag located within the belt-transect was measured using a clinometer, as well as each tree's height-to-lowest and height-to-highest live branch. The vertical projection of each tree's crown center was mapped relative to each tree's bole (the crown center was defined by the horizontal (x,y) coordinates of the top of the tree stem). The vertical projection of each overstory tree crown was mapped by measuring the horizontal distance from the estimated crown center to the edge of each crown along the eight cardinal azimuths (N,NE,E,SE,S,SW,W,NW). The size, decay class (from Maser _et_ _al_. 1988), species (when possible), and location of each piece of coarse woody debris (CWD) with a largest-end diameter $\geq$ 25cm in each belt-transect also were recorded.

Characterization of Spatial Patterns

Overview

To aid in interpreting intra- and interspecific spatial patterns, individual stem maps were produced for trees and for snags of each species with a sufficient number of individuals to conduct spatial analyses. The intraspecific spatial patterns of these trees and snags were characterized using K'(t), a transformation of Ripley's K-function (Ripley 1977, Diggle 1983, Leemans 1991, Moeur 1993). Hamill and Wright's (1986) nearest neighbor method was used to characterize interspecific spatial patterns at each site. These methods of spatial analysis were chosen because the trees and snags mapped in the reference stands represent point-patterns. Further, both methods enable the null hypothesis of spatial randomness to be tested by comparing the observed spatial distributions of individuals to those expected from a similar number of randomly distributed individuals. Both sets of analyses provide statistical tests to assess at what scale(s) the observed spatial patterns differed significantly from patterns of randomly distributed individuals.

The two methods used to analyze intra- and interspecific spatial point patterns are discussed individually below. Detailed examples of intra- and interspecific spatial point pattern analyses using these methods are given following each discussion.

Intraspecific Spatial Patterns

A transformed version of Ripley's K(t) was used to characterize intraspecific spatial patterns. Prior to transformation, the function @K(t) is defined as the expected number of trees within a distance t of an arbitrarily chosen tree, where @ equals the total number of trees in the plot divided by the total plot area, or stem density (Leemans 1991, Moeur 1993). If the individuals are distributed randomly in space (the null hypothesis), the expected value of K(t) is equivalent to $pi*t^2$. Transforming K(t) to K'(t) = { sqrt[(K(t)/pi)] - t }, the expected value of K'(t) under the null hypothesis of a random spatial distribution of individuals becomes zero for each distance t (Leemans 1991, Moeur 1993). K'(t), the notation used by Leemans (1991), is equivalent to L(d) proposed by Besag [in the discussion of Ripley (1977); see Moeur (1993)].

The statistical significance of K'(t) at each distance t was determined by comparing the observed value of K'(t) to a confidence interval of complete spatial randomness calculated using a Monte-Carlo approach (Leemans 1991, Moeur 1993). To calculate a 95% confidence interval, 19 random spatial distributions were generated. Each generated spatial distribution had N individuals (equal to the number of observed individuals) randomly distributed in a square plot of size m x m (equal to the size of the field plot). A positive value of K'(t) falling outside the confidence interval indicated aggregation at that scale; a negative value of K'(t) falling outside the confidence interval indicated a dispersed or regular pattern at that scale. Spatial pattern across a range of scales was shown by plotting K'(t) against t. See Moeur (1993) and Leemans (1991) for more information on this analytical method.

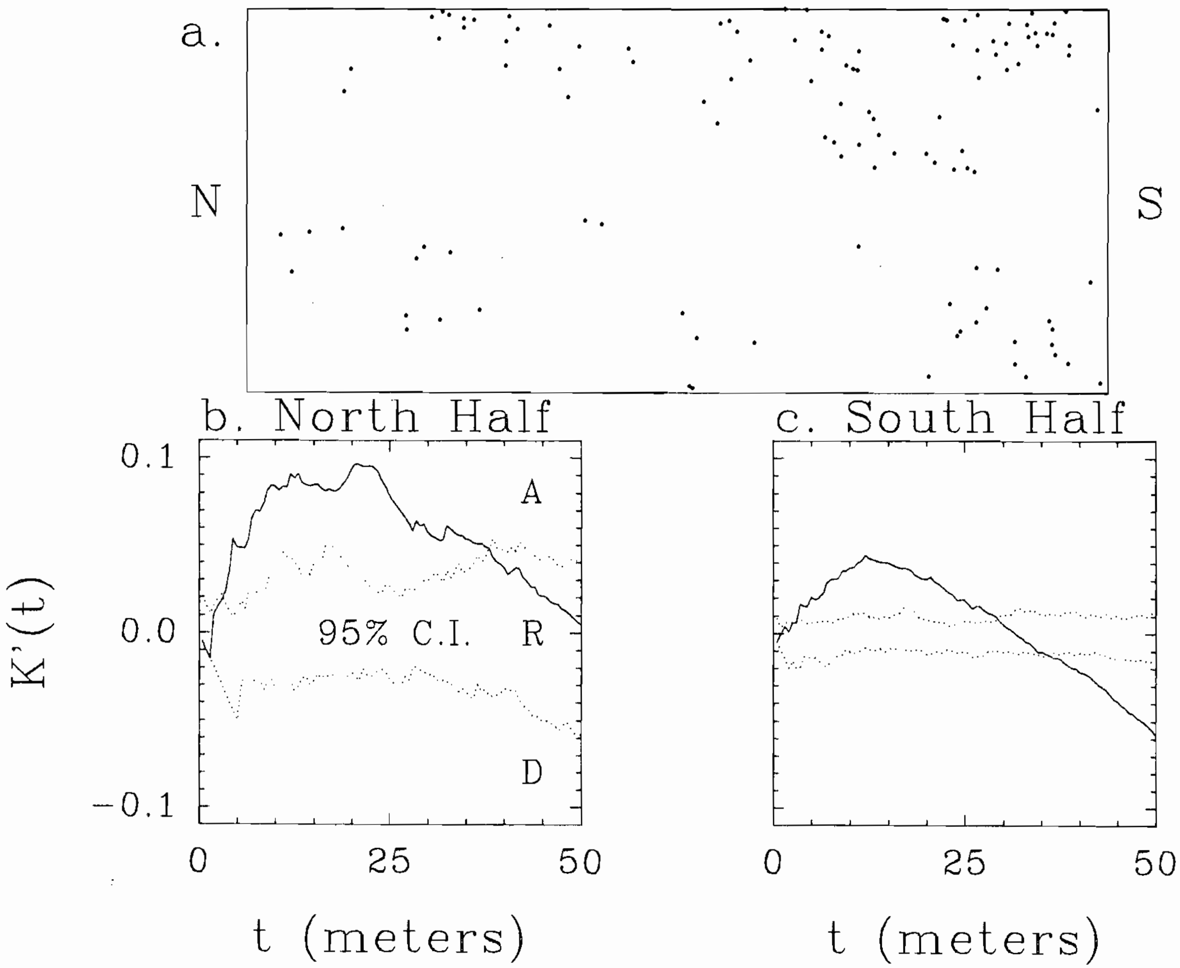
An example illustrating the use of Ripley's K'(t) to analyze the intraspecific point patterns of Douglas-fir trees at the Flynn Creek site is presented in Figure 2. Note that Douglas-fir trees in the south end of the stand appear strongly aggregated at fine to medium scales. As shown in the bottom right graph in Figure 2, the high degree of spatial aggregation at scales of approximately 5-25 meters is reflected by the observed values of K'(t) (solid line) falling above the 95% confidence interval (dotted lines), in the area labeled "A" for aggregated. (Values of K'(t) falling within the areas labeled "R" and "D" indicate scales at which the observed spatial pattern is random or dispersed, respectively.) The null hypothesis that Douglas-fir trees are randomly distributed at Flynn Creek is, therefore, rejected.

Interspecific Spatial Patterns

Originally developed to investigate the spatial pattern of juveniles relative to adults, the nearest-neighbor method developed by Hamill and Wright (1986) was used to analyze the spatial distribution of one group of trees or snags relative to that of another group. The observed probability

Figure 2. Example of intraspecific spatial pattern analysis. The locations of mature Douglas-fir trees (a) and tests of the hypothesis of spatial randomness in the north (b) and south (c) halves of the Flynn Creek reference stand are shown. Heavy lines in Figures 2b,c indicate observed values of K'(t); dotted lines are 95% confidence intervals of complete spatial randomness calculated using a Monte-Carlo simulation. Values of K'(t) above the upper confidence interval indicate aggregation at that scale; values below the lower confidence interval indicate dispersion.

Figure 2.


a.
N
S
b. North Half
c. South Half
0.1
0.0
−0.1
K'(t)
A
95% C.I.
R
D
0
25
50
0
25
50
t (meters)
t (meters)

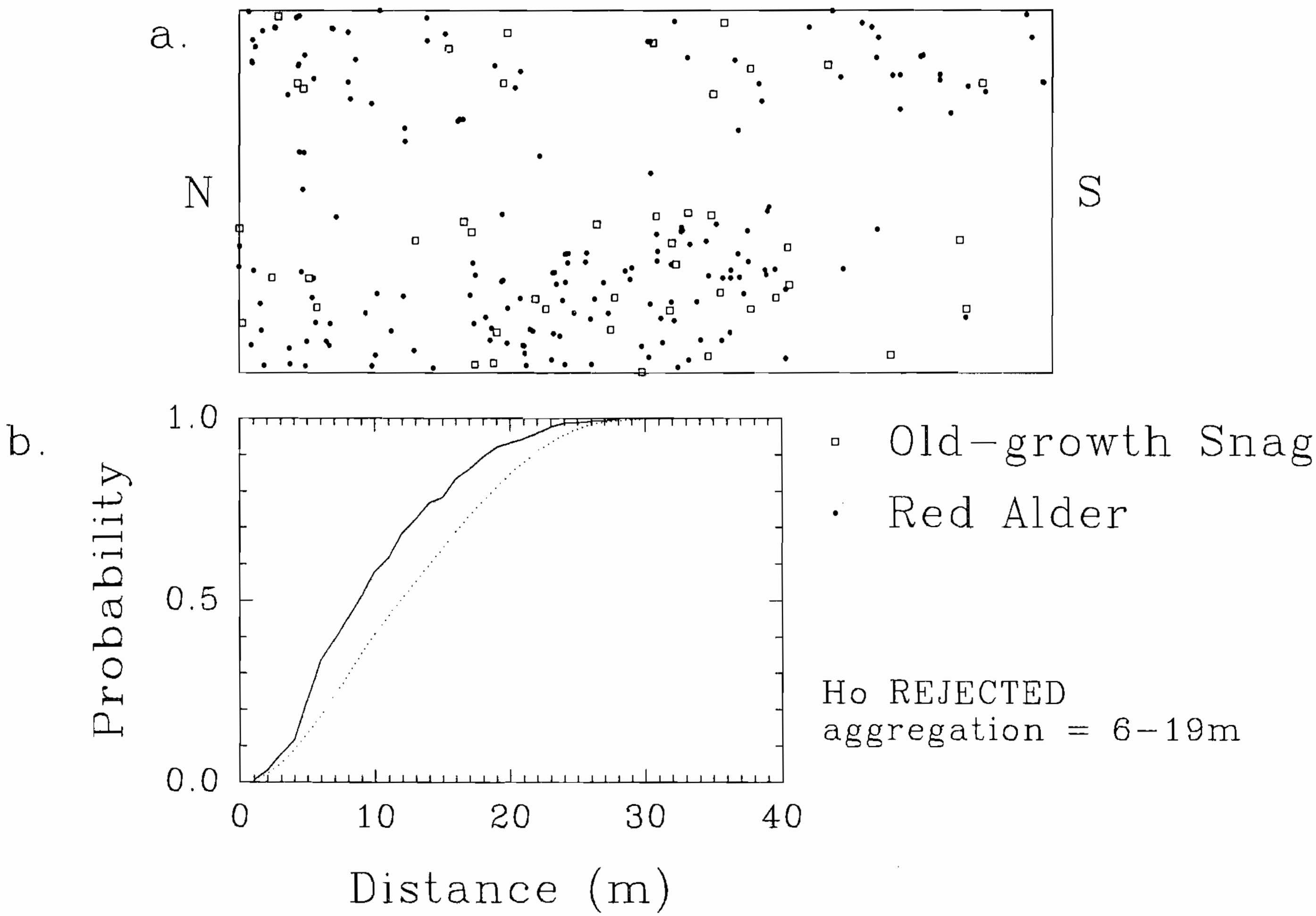
distribution of Class I individuals relative to Class II individuals was generated by calculating the percentage of all Class I individuals found within a given distance (e.g., 1m) of the nearest Class II individuals and then repeating this calculation across a range of distances (e.g., 2m,3m,4m,...). At some distance X, 100% of the Class I individuals were located $\leq$ X meters from the nearest Class II individual. The null probability distribution was generated by calculating the percentage of all Class I individuals which would be expected to be located within a given distance of the nearest Class II individuals, assuming a random distribution of Class I individuals relative to Class II individuals; this calculation was repeated across a range of distances.

As outlined by Hamill and Wright (1986), analysis consisted of the following steps: 1) the null probability distribution of spatially random Class I-to-nearest-Class II distances was calculated from the plot dimensions and the coordinates of Class II individuals; 2) the observed probability distribution was calculated from Class I and Class II coordinates; and 3) a Kolmogorov-Smirnov (KS) goodness-of-fit test for continuous data was used to test the significance of the maximum difference between the observed and null probability distributions. The observed spatial distribution of Class I individuals was considered significantly non-random for a given confidence level and n Class I individuals if the absolute value of the maximum difference between the observed and null probability distributions was greater than or equal to the published critical value for the KS test (Zar 1984). If the observed probability distribution was greater than the null probability distribution at a given spatial scale, and the absolute value of the maximum difference between the two probability distributions was greater than or equal to the KS critical value, the Class I individuals were considered significantly aggregated with respect to Class II individuals at that spatial scale. Conversely, Class I individuals were spatially dispersed with respect to Class II individuals at a given spatial scale if the observed probability distribution was less than the null probability distribution and the absolute value of the maximum difference between the two probability distributions was greater than or equal to the critical value for the KS test. The null and observed distributions were then plotted together, enabling differences in the probability distributions to be judged visually. See Hamill and Wright (1986) and Moeur (1993) for more information on this method of spatial analysis.

An example illustrating the use of Hamill and Wright's method to analyze the interspecific point patterns of red alder trees (the Class I individuals, above) relative to old-growth coniferous snags (the Class II individuals) at the Flynn Creek site is presented in Figure 3. Note that the red alders are spatially aggregated relative to the old-growth coniferous snags. As shown in the bottom graph in Figure 3,

Figure 3. Example of interspecific spatial pattern analysis. The locations of all red alder trees and old-growth coniferous snags in the Flynn Creek reference stand (a) and probability distributions of red alder relative to old-growth coniferous snags (b) are shown. The dotted line in Figure 3b indicates the proportion of red alder trees expected within a given distance (meters) of the nearest old-growth coniferous snag if the red alder trees were distributed randomly with respect to the old-growth coniferous snags. The heavy line in Figure 3b indicates the observed proportion of red alder trees located within a given distance of the nearest old-growth coniferous snag. Observed values above the expected probability distribution indicate aggregation at that scale; observed values below the expected probability distribution indicate dispersion. The null hypothesis of complete spatial randomness can be tested by using a Kolmogorov-Smirnov (KS) test to determine the significance of the difference between the observed and expected probability distributions in Figure 3b.

Figure 3.



a.
N
S
b.
1.0
0.5
0.0
Probability
0
10
20
30
40
Distance (m)
Old-growth Snag
Red Alder
Ho REJECTED
aggregation = 6-19m

this spatial aggregation between species is reflected by the location of the observed probability distribution (solid line) above the null probability distribution (dotted line). The KS test indicates that the differences at scales of 6-19m are significant (95% confidence interval), with a maximum difference between the observed and null distributions at 12m. The null hypothesis that red alder trees are distributed randomly in space with respect to the old-growth coniferous snags at Flynn Creek is, therefore, rejected.

The program to run Ripley's K′(t) was obtained from P.J. Diggle by L. Lopez-Mata and R. Busing and was, in turn, made available for use in this study. Hamill and Wright's program was also obtained by L. Lopez-Mata and R. Busing from those authors. Both programs correct for edge effects. Although Hamill and Wright's program works for individuals in any sized rectangular plot, the program to calculate Ripley's K′(t) only works on square plots. Therefore, analyses using Ripley's K′(t) were performed on two, 100m x 100m, non-overlapping portions of each stand. Analyses using Hamill and Wright's method were done using the full reference stands at Trout Creek (200m x 100m) and Flynn Creek (225m x 100m).

Characterization of Disturbance and Establishment

Field Observations

Evidence of burned snags and trees, charcoal, coarse woody debris, tree form (branchiness as an indicator of past growth habitat), root rot, mass movement, wind damage, as well as beaver (Castor canadensis), mountain beaver (Aplodontia rufa), and elk (Cervus elaphus) activity were noted as encountered in the reference stands.

Evidence of Historical Disturbance

Published literature of historically known disturbances which might have impacted either of the study sites was reviewed.

Dendrochronological Analysis

Increment cores were extracted from a subsample of trees subjectively chosen to cover the entire spatial extent of each reference stand. Cores were collected from all species present in each stand. At Flynn Creek 182 cores were collected from 124 (of 322) trees; at Trout Creek 152 cores from were collected from 87 (of 409) trees. Trees were cored as close to the ground as possible. Because of concerns about injury to small trees (these are permanent reference stands), coring was generally confined to trees > 20cm DBH. The increment cores were prepared using standard dendrochronological techniques and then dated by counting the number of rings (Stokes and Smiley 1968, Fritts 1976). Patterns of suppression and release were noted during the core-dating process, enabling more accurate tree ages to be obtained by cross-dating between cores and trees. An establishment timeline was developed for each species using age data for each cored individual. Stem maps showing the spatial patterns of establishment were developed using ARC/INFO.

RESULTS

Characterization of Forest Structure and Composition

Stem Maps

The overall appearance of the Flynn Creek and Trout Creek reference stands suggests that the two sites differ with respect to horizontal structure as well as composition (Figures 4-6). Trees and snags at both sites exhibit varied degrees of patchiness. For example, Douglas-fir and red alder at Flynn Creek appear to be distributed in largely monospecific patches of different sizes (Figure 4). A relatively large patch of red alder occurs on the west side of the reference stand, a medium-sized patch of Douglas-fir occupies the southwest corner, and smaller, largely monospecific patches of red alder and Douglas-fir are found in the southeast part of the stand (Figure 4). The stem map of the Trout Creek reference stand suggests a structurally and compositionally more complex picture at Trout Creek (Figure 5). Trees and snags at both sites tend to be located on the upslope, away from the main stream channel.

Stand Cross-Sections

The stand cross-sections demonstrate the vertical layering characteristic at each site (Figures 7-9). Although the cross-sections were subjectively located within each

Figure 4. Stem map of the Flynn Creek reference stand. See Figure 6 for symbol key.

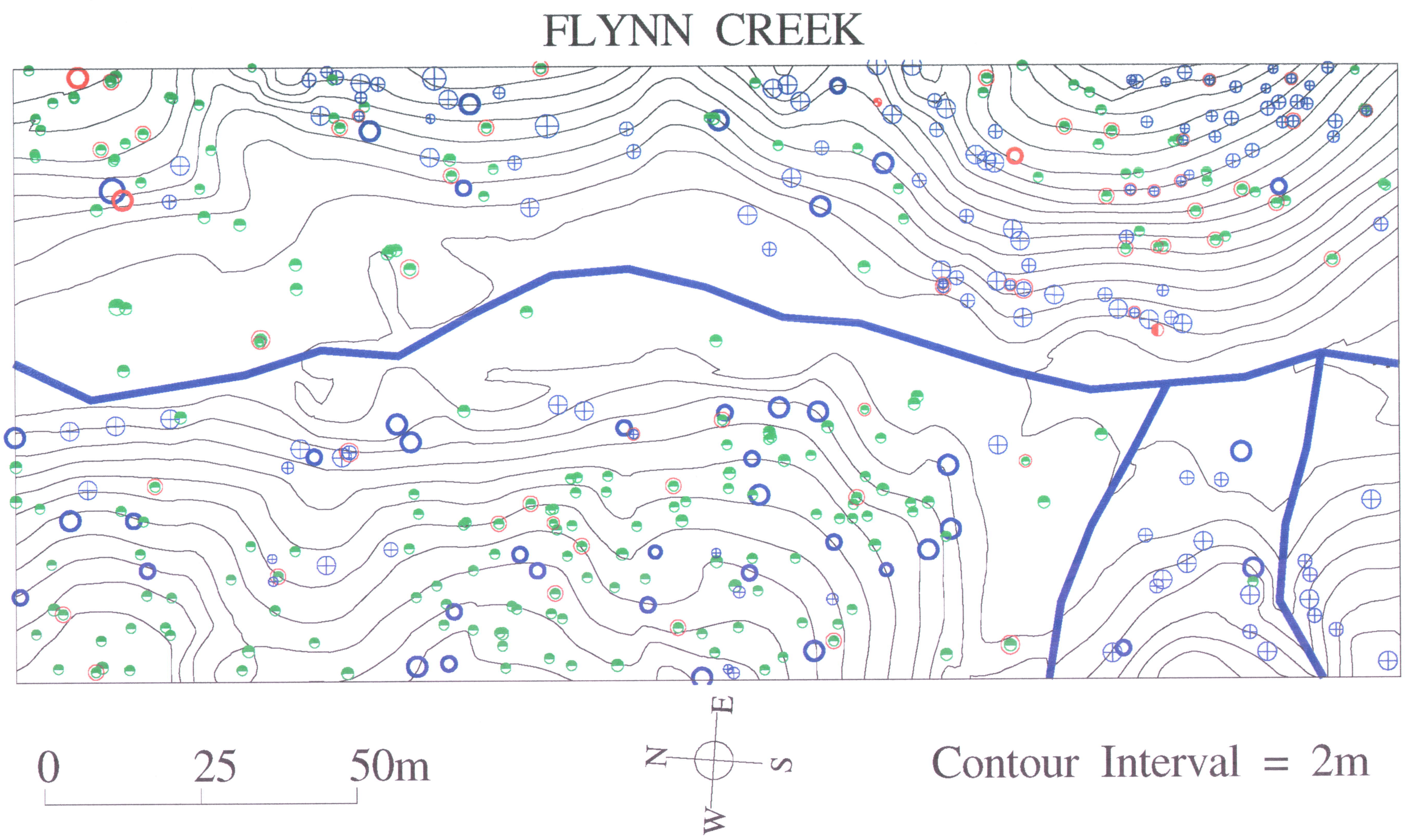


Figure 5. Stem map of the Trout Creek reference stand. See Figure 6 for symbol key.

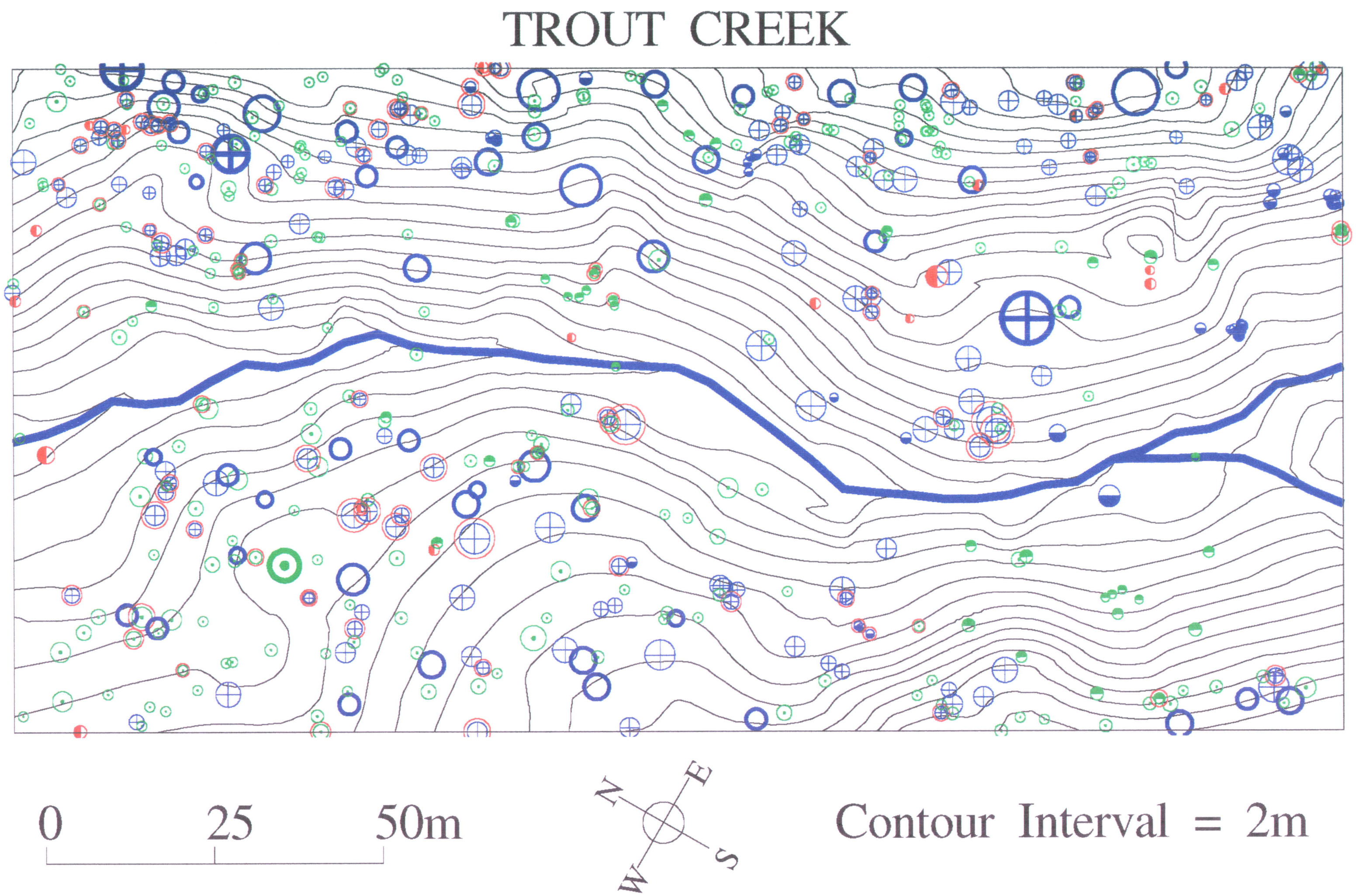


Figure 6. Symbol key for Figures 4 and 5.

KEY TO SYMBOLS

Douglas-fir, live

Douglas-fir, dead

Douglas-fir, live, old – growth

Douglas-fir, dead, old – growth

Western Hemlock, live

Western Hemlock, dead

Western Hemlock, live, old – growth

Western Red Cedar, live

Western Red Cedar, dead

Western Red Cedar, dead, old – growth

Sitka Spruce, live

Red Alder, live

Red Alder, dead

Big-leaf Maple, live

Big-leaf Maple, dead

Diameter Classes (DBH)

5 – 25 cm

25 – 50 cm

50 – 75 cm

75 – 100 cm

100 – 125 cm

125 – 150 cm

150 – 175 cm

175 – 200 cm

200 – 225 cm

225+ cm

Figure 7. Stand profile of the Flynn Creek reference stand. See Figures 6 and 9 for symbol keys.

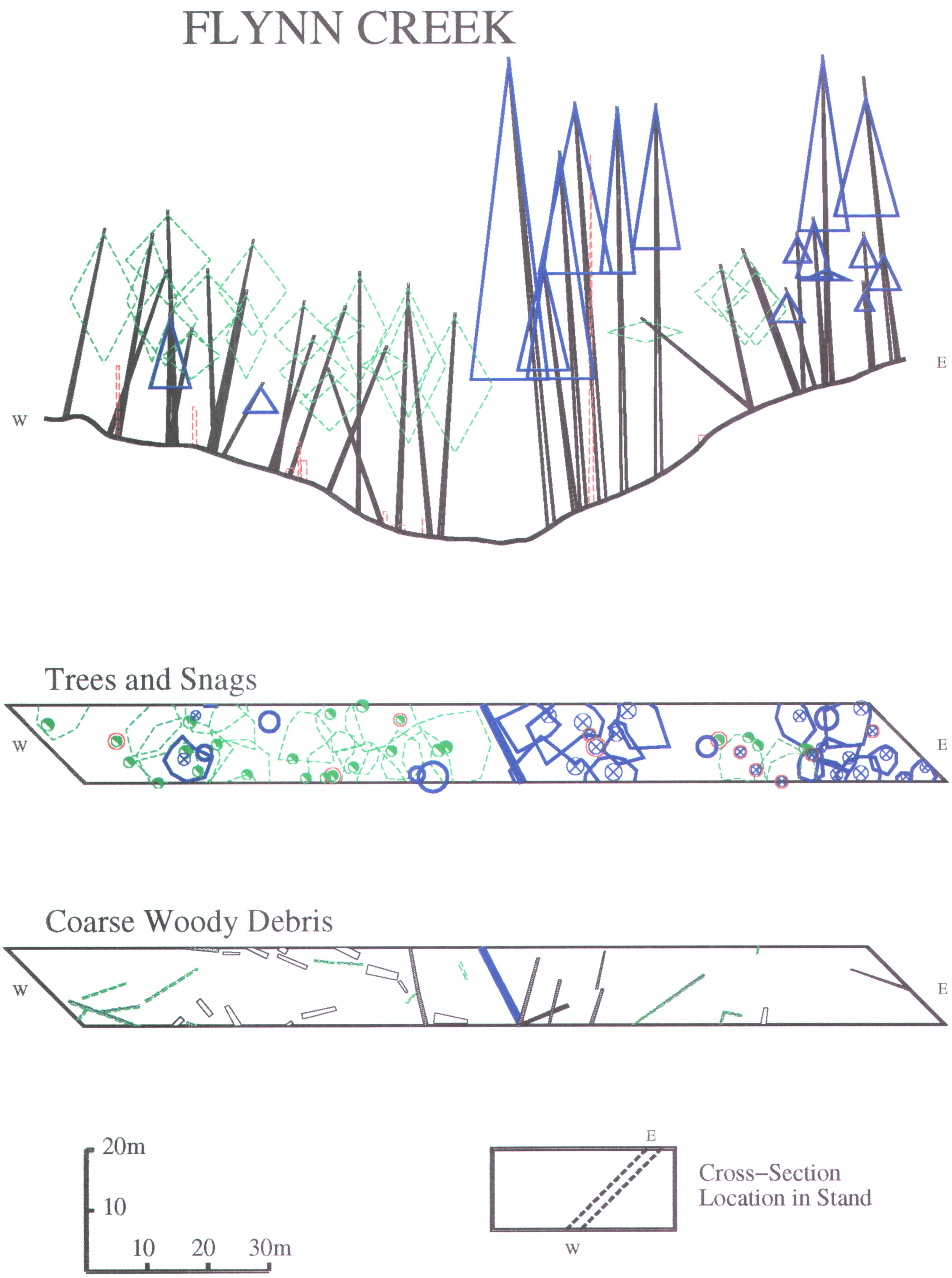


Figure 8. Stand profile of the Trout Creek reference stand. See Figures 6 and 9 for symbol keys.

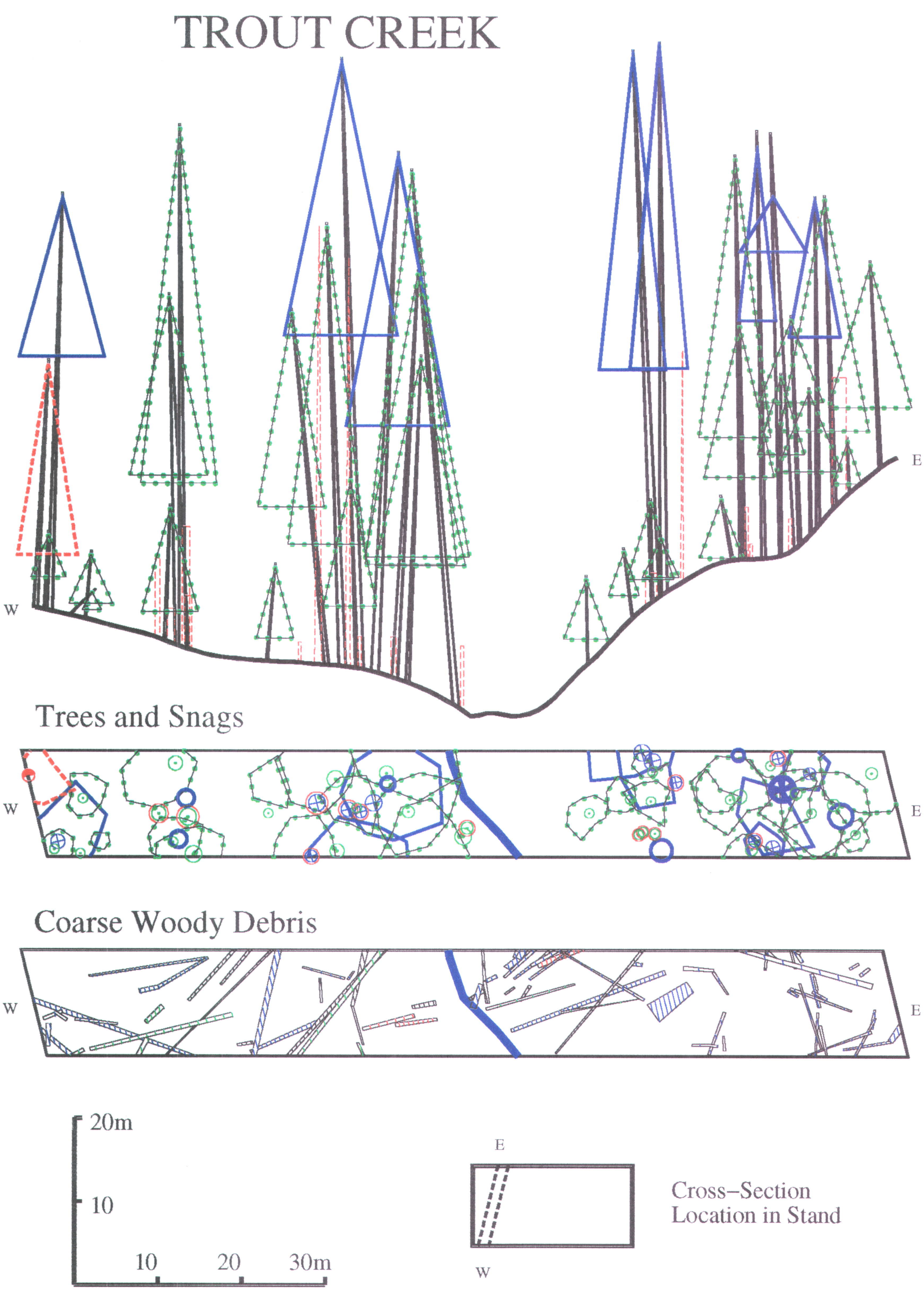
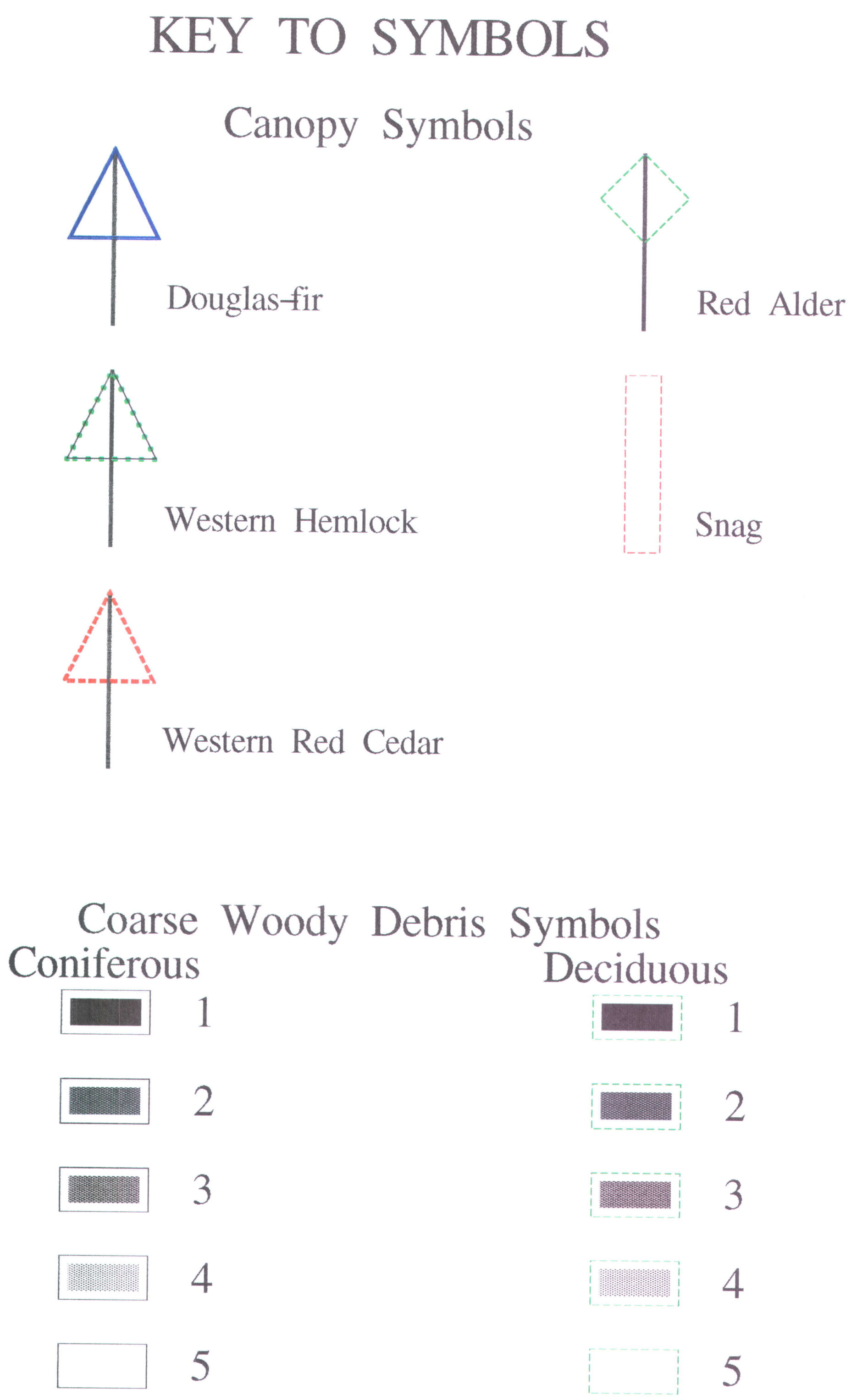


Figure 9. Symbol key for Figures 7 and 8.



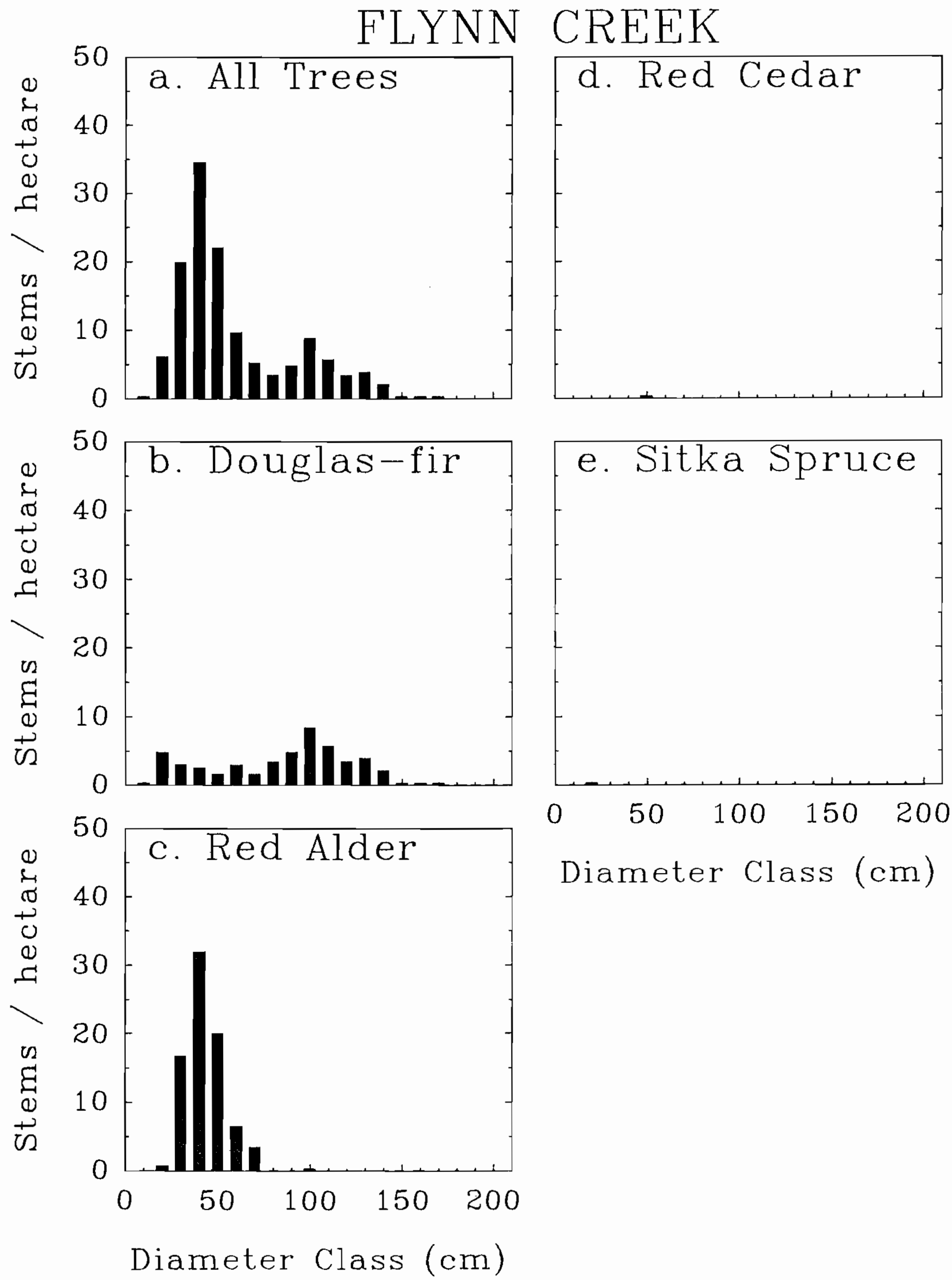
stand, several observations can be made which reflect general patterns in each stand as a whole. The trees in the Flynn Creek cross-section occur in largely monospecific patches of either Douglas-fir or red alder (Figure 7). Distinct, largely monospecific canopy layers are formed by the Douglas-fir and red alder at Flynn Creek. In contrast, Douglas-fir, western hemlock, and western red cedar appear to be both vertically and horizontally mixed in the cross-section at Trout Creek (Figure 8).

Although the total amount of coarse woody debris (CWD) was not quantified at either site, it is apparent that more coarse woody debris is present in the belt-transect at Trout Creek than at Flynn Creek (Figures 7,8). This difference appears to be due to the greater amount of mature coniferous CWD present in the belt-transect at Trout Creek compared to Flynn Creek. The amount of old-growth coniferous CWD appears comparable in the belt-transects at both sites. Deciduous CWD is present in the Flynn Creek belt-transect, but is not located in the Trout Creek belt-transect (although deciduous CWD is found in other parts of the Trout Creek reference stand).

Diameter Distributions

The diameter distribution of all live trees at Flynn Creek exhibit a strong peak at about 40cm and a second, lower peak at 100cm (Figure 10a). The peak at 100cm is primarily composed of Douglas-fir, which has a bimodal distribution

Figure 10. Diameter distributions by 10cm DBH size classes for trees in the Flynn Creek reference stand.



(Figure 10b). The peak at 40cm is primarily composed of red alder, which is unimodal in its diameter distribution (Figure 10c). The single individuals of Sitka spruce and western red cedar found at Flynn Creek fall within the 20cm and 50cm DBH classes, respectively (Figures 10d,e).

Live trees at Trout Creek exhibit a diameter distribution characterized by a peak in the smallest size class and decline in frequency in successively larger size classes (Figure 11a). The largest diameter classes are dominated almost entirely by Douglas-fir (Figure 11b). The smallest diameter classes are dominated by western hemlock, with some red alder, western red cedar, and big-leaf maple also present (Figures 11c-f).

An occasional western hemlock, western red cedar, and big-leaf maple attained a DBH $\geq$ 100cm. All species are represented in the mid-sized diameter classes.

The mature coniferous snags at both Flynn Creek (Figure 12a) and Trout Creek (Figure 12b) tend to be found in the smaller diameter classes, while the old-growth coniferous snags are concentrated in the larger diameter classes. Although the number of old-growth coniferous snags at both sites is similar, there are larger diameter old-growth coniferous snags at Trout Creek than at Flynn Creek. The number of mature coniferous snags is greater at Trout Creek than at Flynn Creek and there are larger diameter mature coniferous snags at Trout Creek than at Flynn Creek.

Figure 11. Diameter distributions by 10cm DBH size classes for trees in the Trout Creek reference stand.

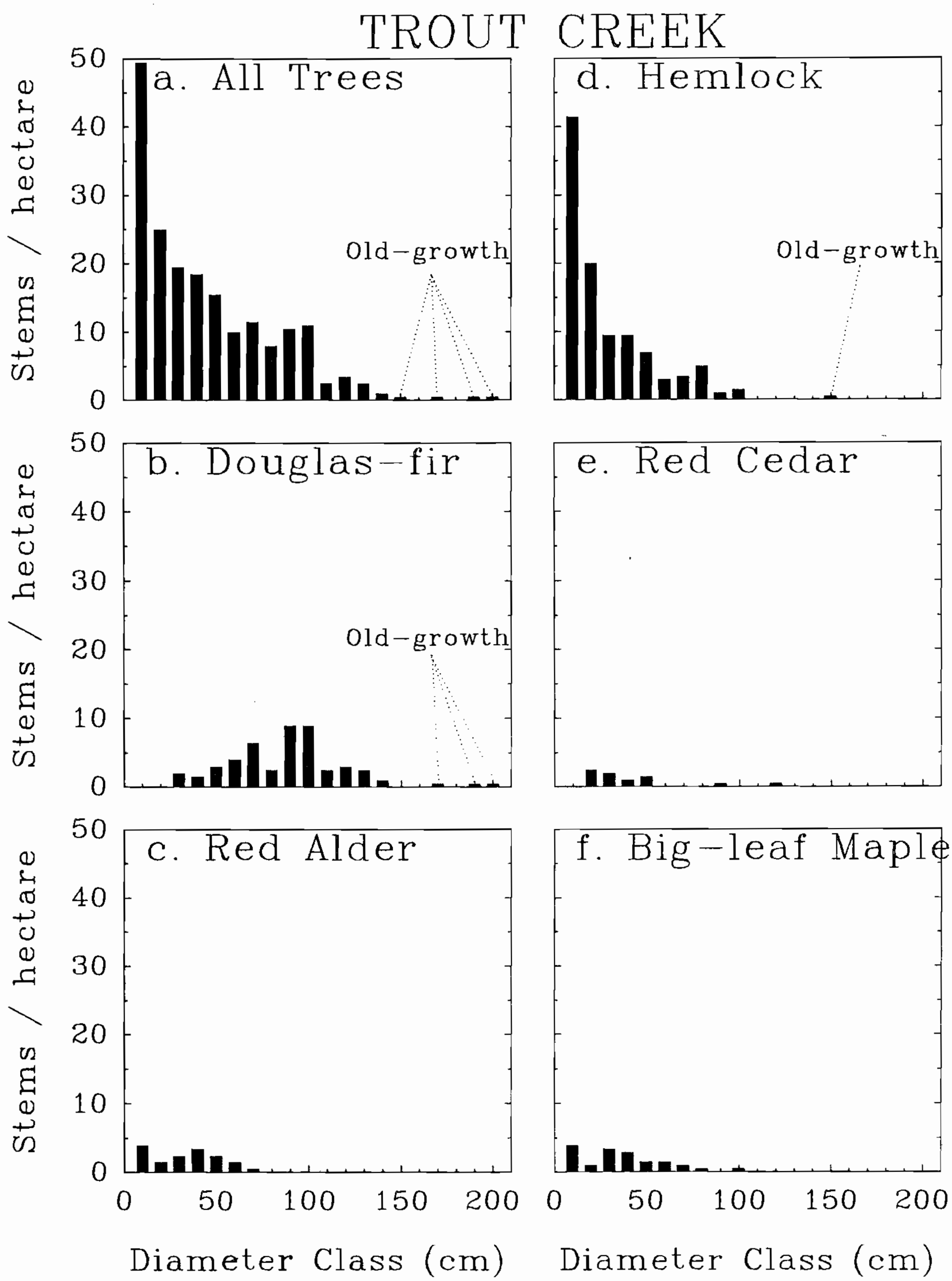
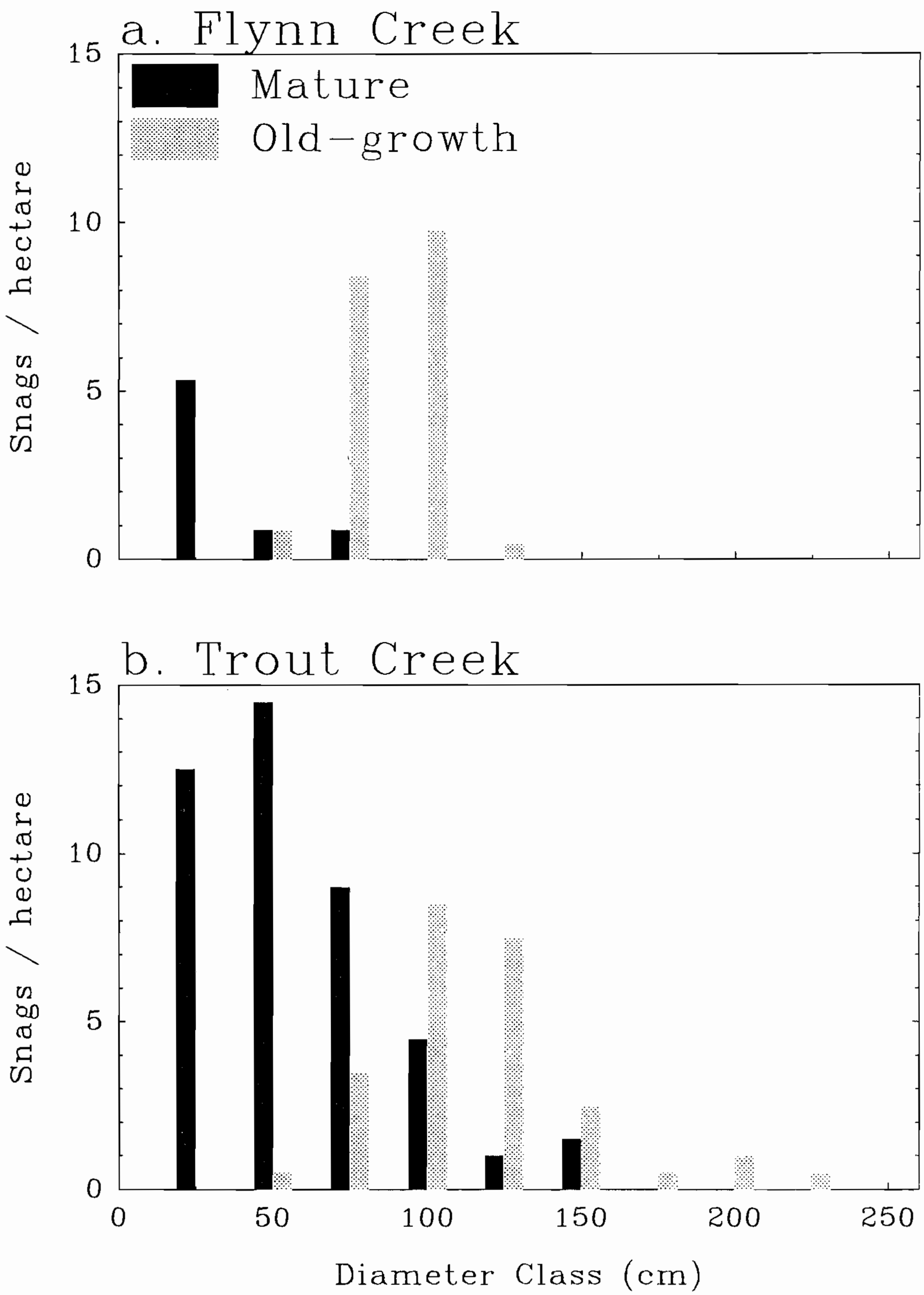


Figure 12. Diameter distributions by 25cm DBH size classes for coniferous snags in the Flynn Creek and Trout Creek reference stands.



The deciduous snags at both Flynn Creek and Trout Creek are concentrated in the smaller diameter classes (Figure 13a). Not surprisingly, the deciduous-dominated Flynn Creek has many more deciduous snags than the coniferous-dominated Trout Creek (Figure 13b).

Stem Density and Basal Area

Both stem density and basal area per unit area are greater at Trout Creek than at Flynn Creek (Table 1). Basal area of Douglas-fir is approximately equal in both stands and represents the greatest contribution by a single species to the live basal area of each stand. Red alder represents the second greatest contribution to live basal area at Flynn Creek (26.5% of total), but accounts for only 3.5% of basal area at Trout Creek. Other conifers, hemlock and western red cedar, account for 25.3% of the total basal area at Trout Creek, but are almost entirely absent from Flynn Creek (no hemlock; 0.10 m^2/ha western red cedar). Big-leaf maple, 4.7% of the Trout Creek basal area, is absent at Flynn Creek.

Snag basal area forms a higher proportion of the total basal area at Trout Creek than at Flynn Creek (Table 1). Conifer snags account for the majority of standing dead wood basal area at both sites, although stem density of conifer snags at Trout Creek is nearly twice that of Flynn Creek. The number of old-growth coniferous snags is similar at Trout Creek (25.0/ha) and Flynn Creek (19.6/ha). All old-growth coniferous snags at Trout Creek are Douglas-fir. Although

Figure 13. Diameter distributions by 25cm DBH size classes for deciduous snags in the Flynn Creek and Trout Creek reference stands.

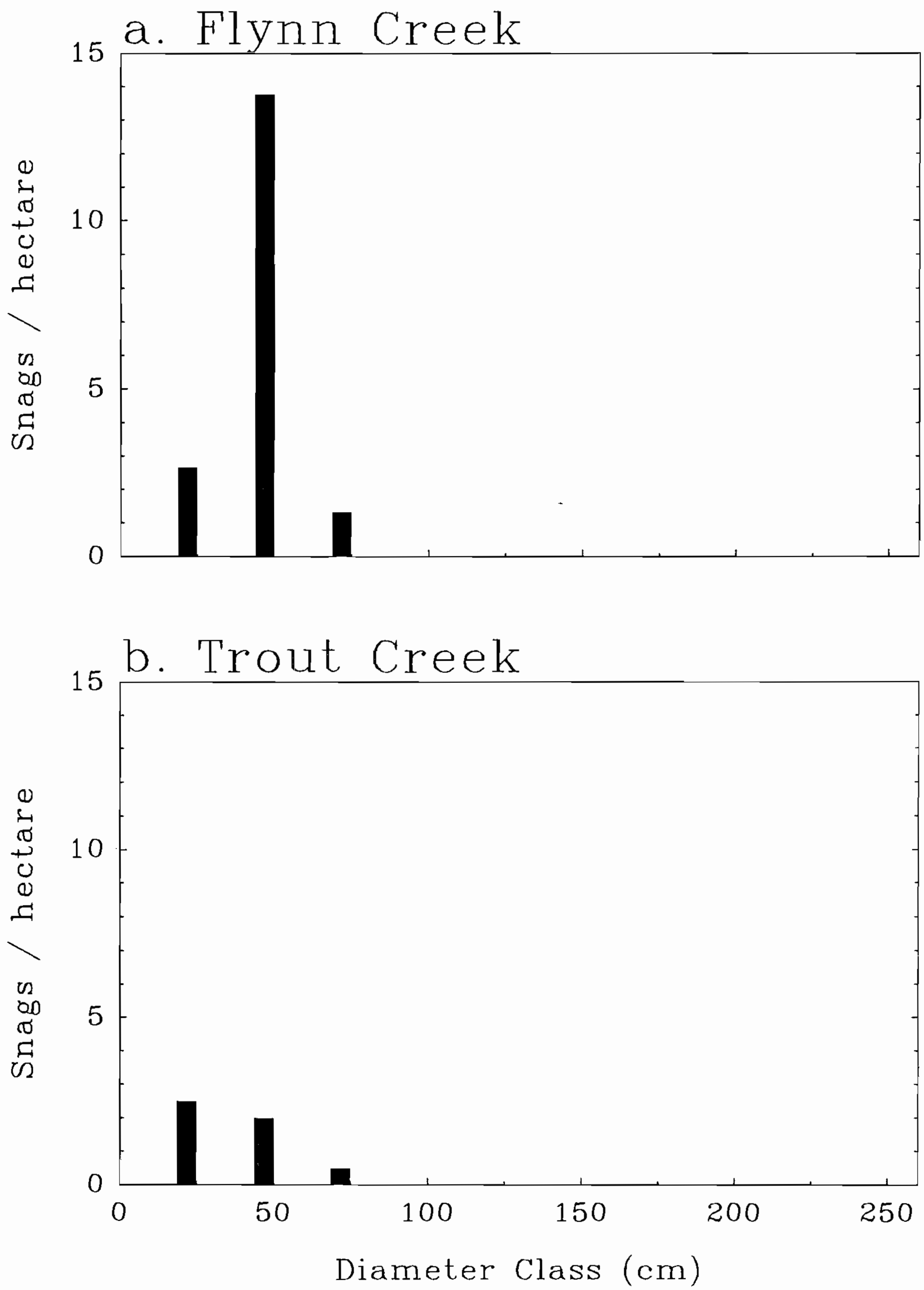


Table 1. Stem density and basal area of trees and snags in the Flynn Creek and Trout Creek reference stands.

	Stem Density (stems/ha)		Basal Area (m^2/ha)	
	FLYNN	TROUT	FLYNN	TROUT
Coniferous Trees				
Douglas-fir	51.6	48.0	34.96	33.87
Sitka Spruce	0.4	0.0	0.02	0.00
Western Red cedar	0.4	8.0	0.10	1.43
Western Hemlock	0.0	102.0	0.00	11.49
subtotal	**52.4**	**158.0**	**35.08**	**46.79**
Deciduous Trees				
Big-leaf Maple	0.0	16.5	0.00	2.41
Red Alder	80.4	16.0	12.67	1.78
subtotal	**80.4**	**32.5**	**12.67**	**4.19**
Tree Subtotal	**132.8**	**190.5**	**47.75**	**50.98**
Snags				
Coniferous	26.7	68.0	16.97	33.70
Deciduous	17.8	4.5	1.90	0.24
Snag Subtotal	**44.5**	**72.5**	**18.87**	**33.94**
STAND TOTAL	**177.3**	**263.0**	**66.62**	**84.92**

the majority of old-growth coniferous snags are Douglas-firs (18.2/ha), old-growth western red cedar snags (1.4/ha) are also present at Flynn Creek. Old-growth western hemlock snags are not present at either site. Mature, current stand conifer snags are six times more abundant at Trout Creek (43.0/ha) than at Flynn Creek (7.1/ha). All mature coniferous snags at Flynn Creek are Douglas-fir. In contrast, the mature coniferous snags at Trout Creek are Douglas-fir (32.5/ha), western hemlock (9.5/ha), and western red cedar (1.0/ha). Approximately two-thirds of the total conifer snag basal area at each site is comprised of decay class 4 and 5 snags which originated from the previous stand.

Deciduous snags at Trout Creek are red alder (3.3/ha) and big-leaf maple (1.2/ha). All deciduous snags at Flynn Creek are red alder.

Canopy Position

As noted above for the stand cross-sections, the canopy at Flynn Creek is two-layered, while that at Trout Creek is multi-layered (Table 2). Douglas-fir occupies the dominant and codominant canopy positions at both sites. Although the canopy of each stand is dominated by Douglas-fir, red alder at Flynn Creek are more abundant in the codominant canopy class than are Douglas-fir. More intermediate and suppressed Douglas-fir are present at Flynn Creek than Trout Creek, as are intermediate and suppressed red alder. The majority of intermediate and suppressed trees at Trout Creek are western

Table 2. Stem density of live trees by canopy position in the Flynn Creek and Trout Creek reference stands.

	Dominant (stems/ha)		Codominant (stems/ha)	
	FLYNN	TROUT	FLYNN	TROUT
Douglas-fir	12.4	12.0	24.0	27.0
Sitka Spruce	0.0	0.0	0.0	0.0
Western Red cedar	0.0	0.0	0.0	0.5
Western Hemlock	0.0	2.0	0.0	8.0
Big-leaf Maple	0.0	0.0	0.0	0.0
Red Alder	0.4	0.0	55.6	0.5

	Intermediate (stems/ha)		Suppressed (stems/ha)	
	FLYNN	TROUT	FLYNN	TROUT
Douglas-fir	8.9	6.5	6.2	2.5
Sitka Spruce	0.0	0.0	0.4	0.0
Western Red cedar	0.4	5.5	0.0	2.0
Western Hemlock	0.0	61.5	0.0	30.5
Big-leaf Maple	0.0	12.0	0.0	4.5
Red Alder	20.9	13.0	3.6	2.5

hemlock. Both big-leaf maple and red alder are more common than Douglas-fir in the intermediate and suppressed canopy classes at Trout Creek. The species least common at Trout Creek in the codominant, intermediate, and suppressed canopy classes is western red cedar.

Characterization of Spatial Patterns

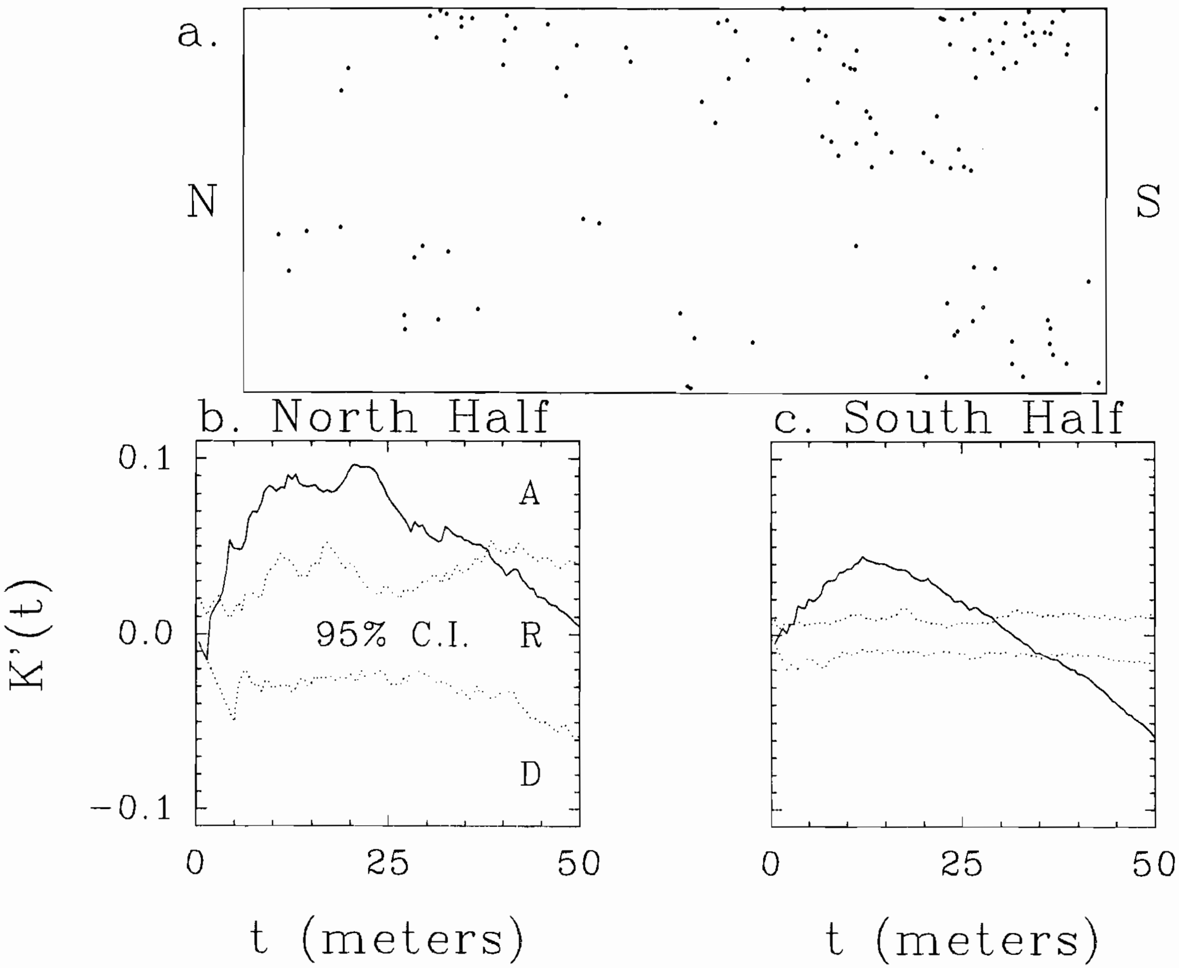
Intraspecific Spatial Patterns

Are the different species of trees and snags randomly distributed in each stand?

Analyses of the individual stem maps produced for each species reject the null hypothesis that the spatial distributions of tree and snag species were random. The intraspecific distributions of mature Douglas-fir were significantly different from random at both sites (95% confidence interval of spatial randomness). Analysis of the Flynn Creek stand indicates that Douglas-fir are spatially aggregated at scales of 5-35m (north half of the stand) and 5-30m (south half) (Figure 14). At coarser scales, however, Douglas-fir appear to be more evenly distributed than expected under a random distribution. The value of K'(t) for Douglas-fir at Flynn Creek more strongly deviates from the expected distribution than at Trout Creek (Figure 15). If just the large (DBH $\geq$ 50cm), mature Douglas-fir at Trout Creek are examined, the distribution of trees in the north

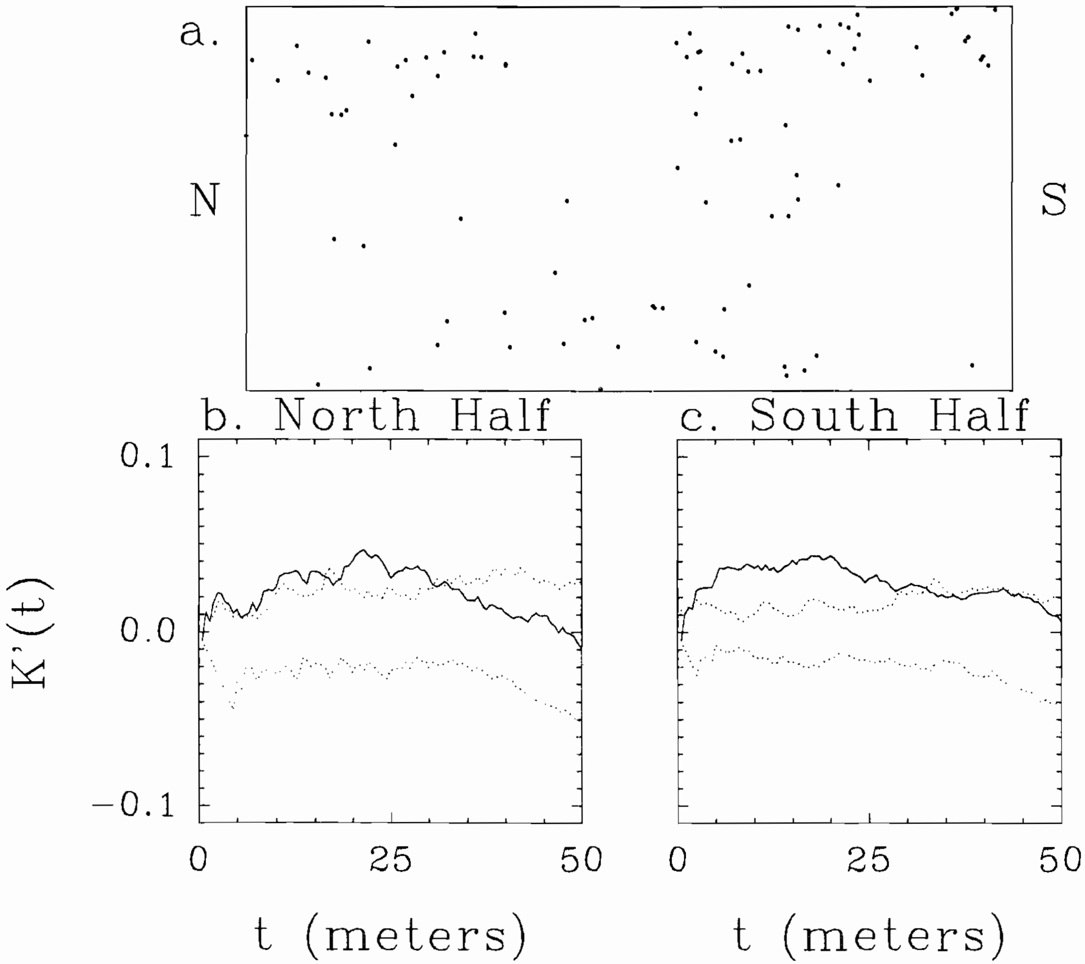
Figure 14. Intraspecific point-pattern analysis of the spatial distribution of mature (current stand) Douglas-fir in the Flynn Creek reference stand. The locations of mature Douglas-fir trees (a) and tests of the hypothesis of spatial randomness in the north (b) and south (c) halves of the reference stand are shown. Heavy lines in Figures 14b,c indicate observed values of K'(t); dotted lines are 95% confidence intervals of complete spatial randomness calculated using a Monte-Carlo simulation. Values of K'(t) above the upper confidence interval indicate aggregation at that scale; values below the lower confidence interval indicate dispersion.

Figure 14.



a.
N
S
b. North Half
c. South Half
0.1
0.0
−0.1
K'(t)
A
R
D
95% C.I.
0
25
50
t (meters)
0
25
50
t (meters)

Figure 15. Intraspecific point-pattern analysis of the spatial distribution of all mature Douglas-fir in the Trout Creek reference stand. See Figure 14 for details of the analyses.



half of the stand does not significantly deviate from a random distribution, while the trees in the south half of the stand appear more spatially aggregated than expected (Figure 16).

Red alders at Flynn Creek appear to be aggregated over spatial scales less than 40m and dispersed at scales of 45-50m (Figure 17). Although the distribution of red alders at Trout Creek indicates spatial aggregation in the stand, the degree of deviation from expected values is more variable than at Flynn Creek and not as consistent between the halves of the stand (Figure 18). The wide confidence intervals for red alder at Trout Creek reflect the low number of red alder present in each half of the stand.

The spatial pattern of old-growth coniferous snags at Flynn Creek is not significantly different from a random pattern at scales less than 35-40m, but tends toward a dispersed pattern at the coarsest scales (Figure 19). The old-growth snag distribution at Trout Creek does not differ strongly from random, although there is a suggestion of aggregation at medium scales in the south half of the stand (Figure 20).

The distribution of mature (current stand) coniferous snags in the south half of the Flynn Creek stand appears weakly aggregated at less than 25m and strongly aggregated at scales greater than 25m (Figure 21). Too few mature coniferous snags are located in the north half of the Flynn Creek reference stand to conduct a spatial analysis. At

Figure 16. Intraspecific point-pattern analysis of the spatial distribution of large (DBH ≥ 50cm), mature Douglas-fir in the Trout Creek reference stand. See Figure 14 for details of the analyses.

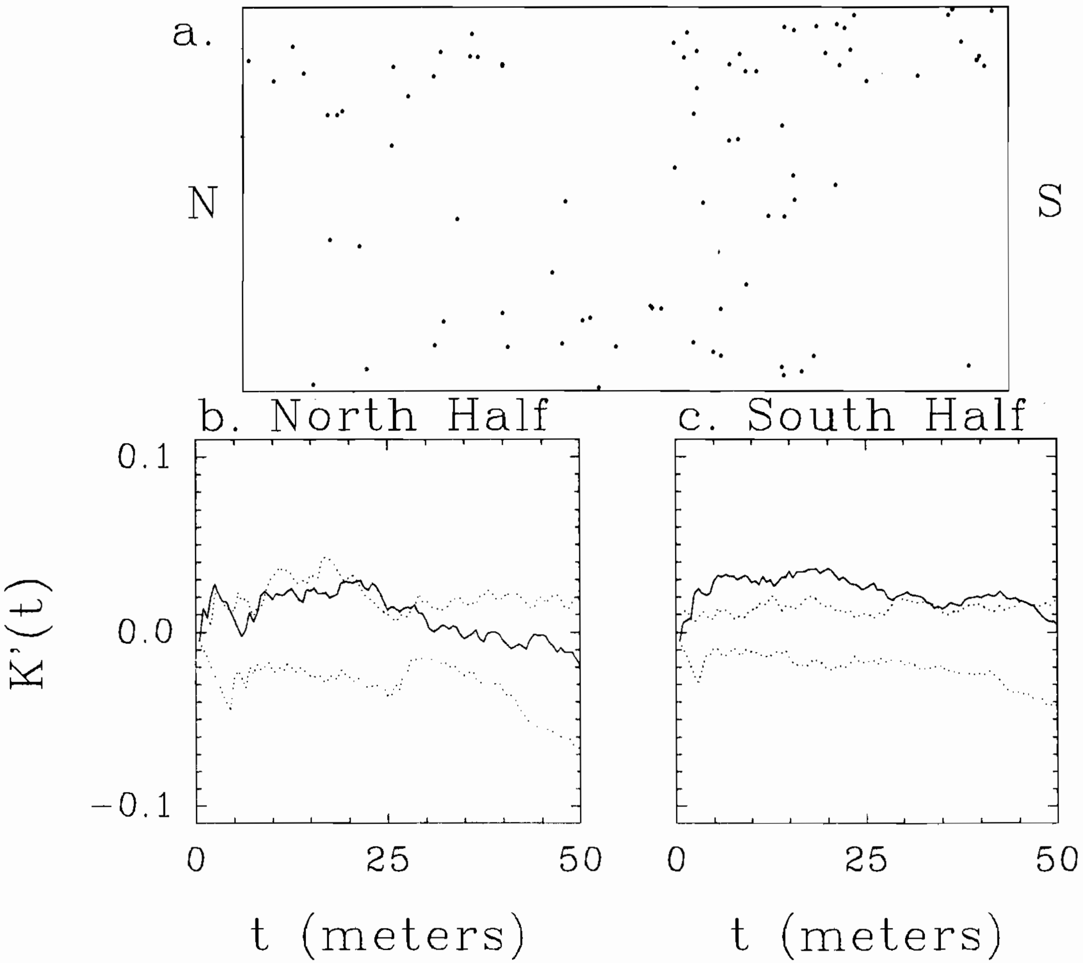


Figure 17. Intraspecific point-pattern analysis of the spatial distribution of red alder in the Flynn Creek reference stand. See Figure 14 for details of the analyses.

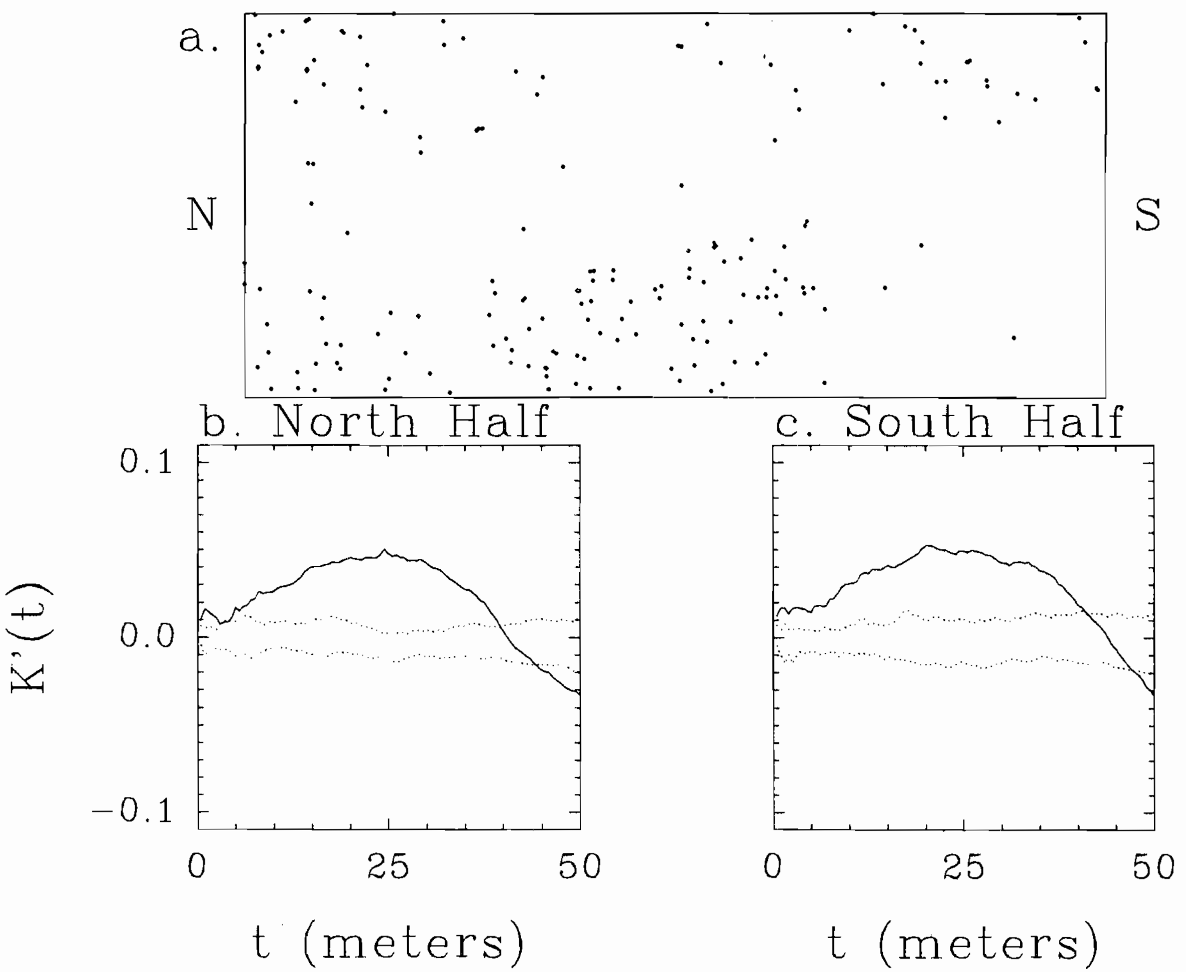


Figure 18. Intraspecific point-pattern analysis of the spatial distribution of red alder in the Trout Creek reference stand. See Figure 14 for details of the analyses.

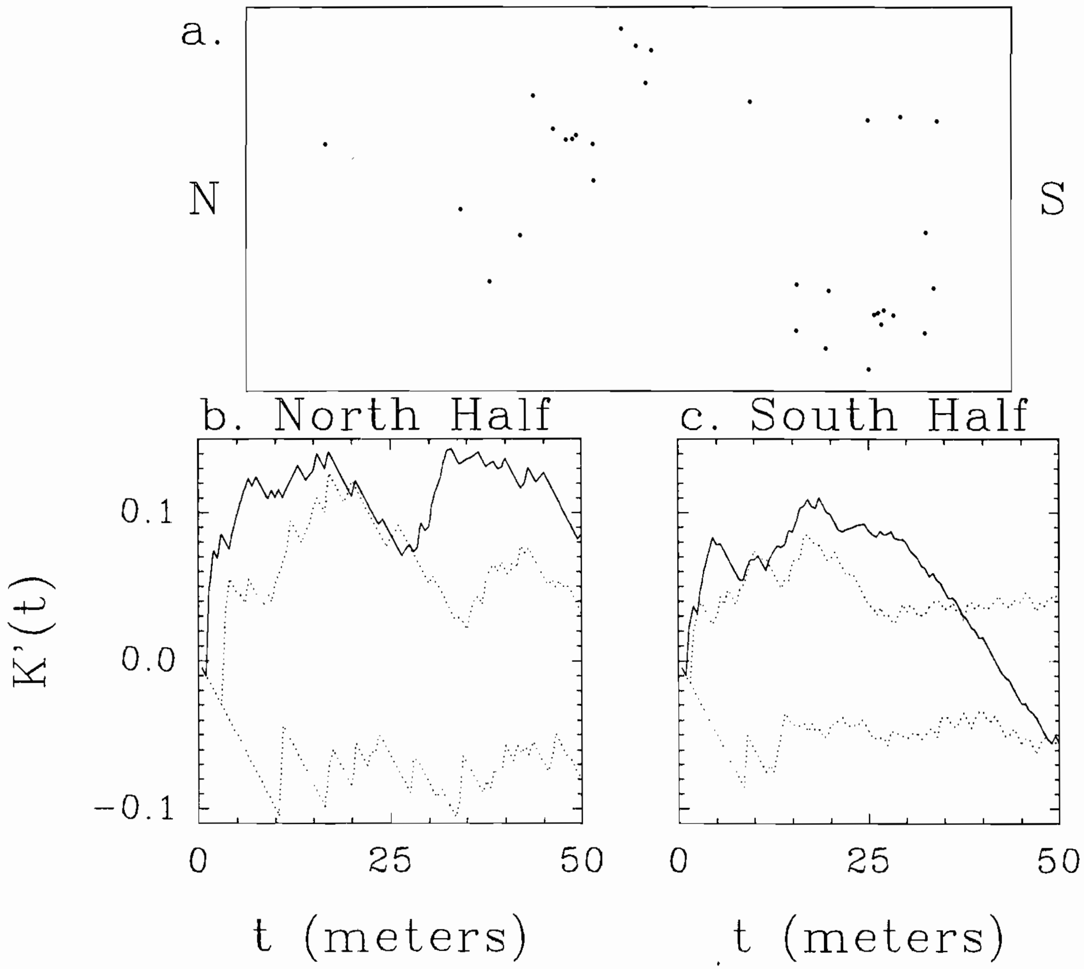


Figure 19. Intraspecific point-pattern analysis of the spatial distribution of old-growth coniferous snags in the Flynn Creek reference stand. See Figure 14 for details of the analyses.

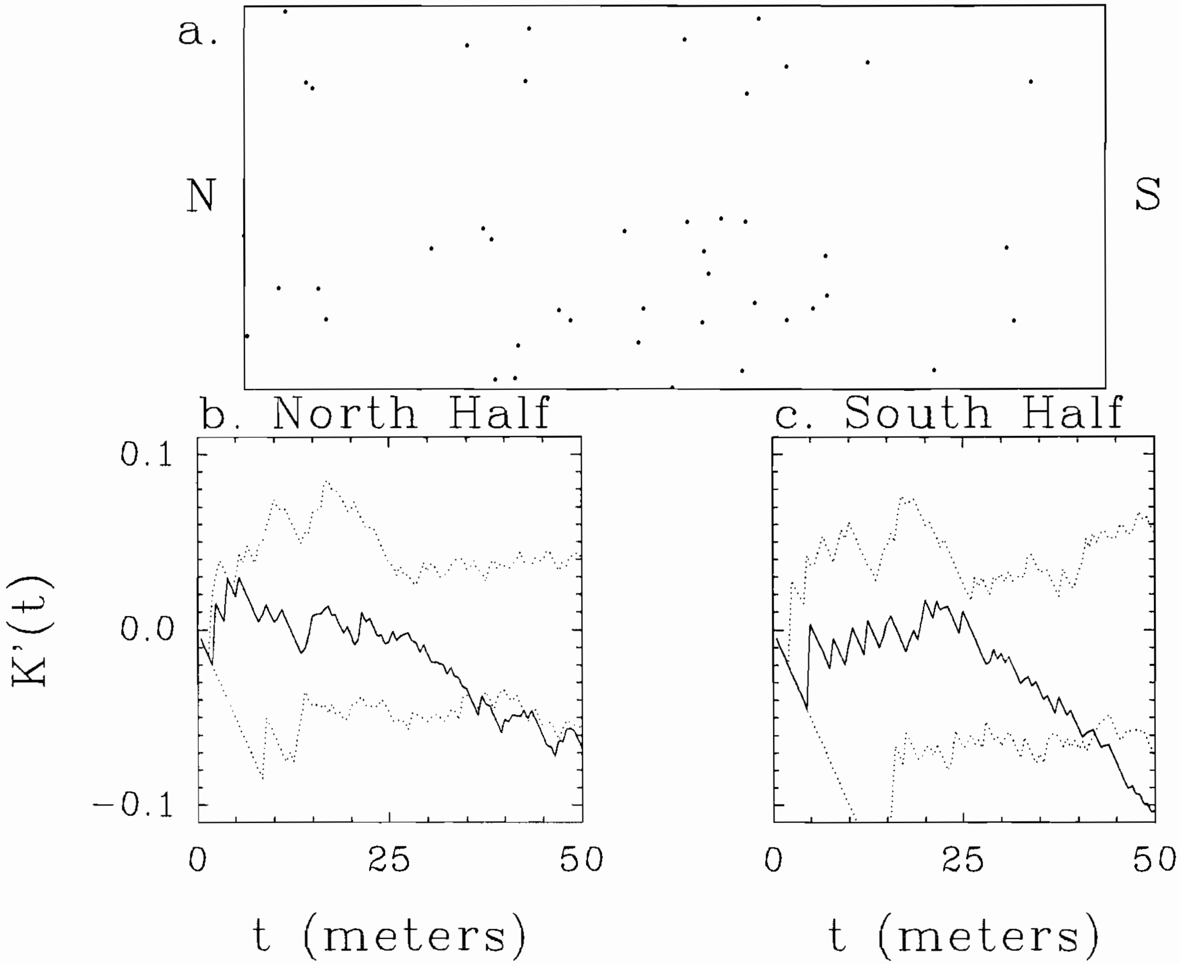


Figure 20. Intraspecific point-pattern analysis of the spatial distribution of old-growth coniferous snags in the Trout Creek reference stand. See Figure 14 for details of the analyses.

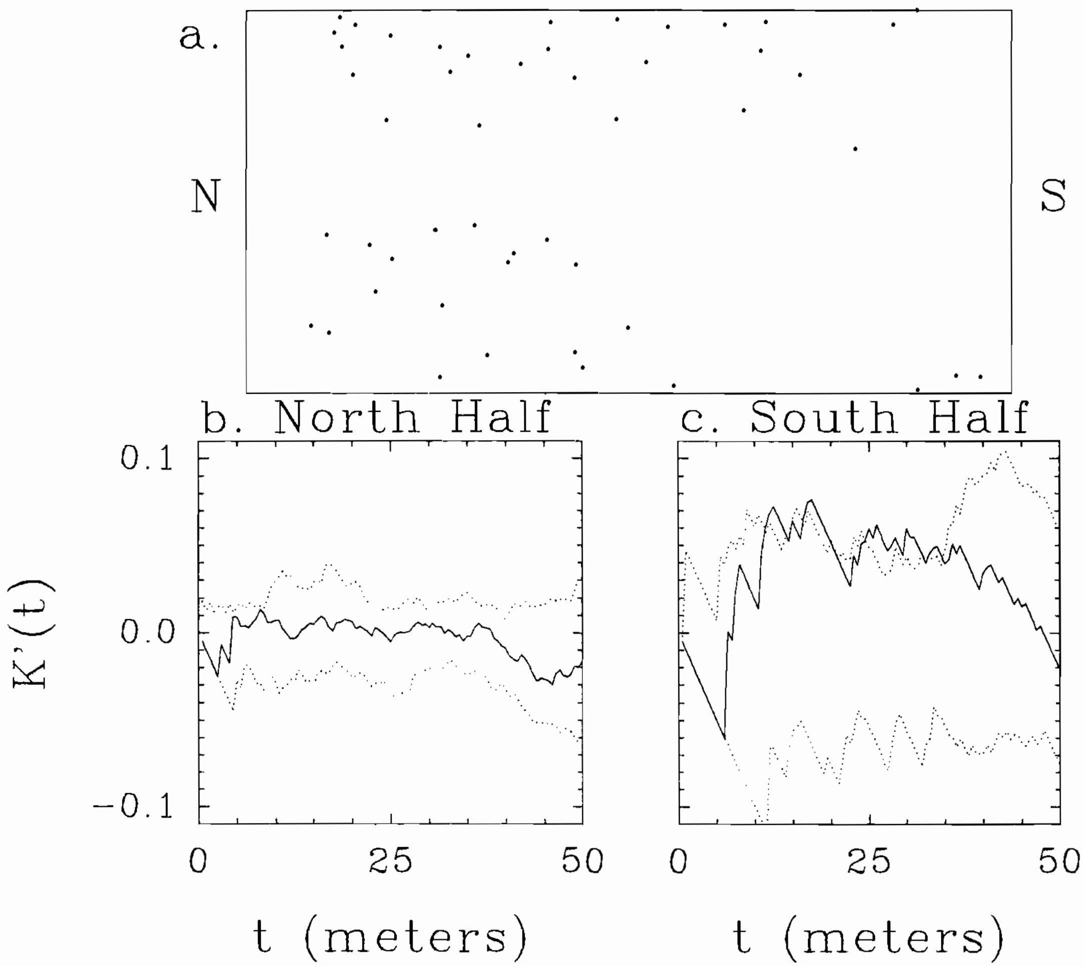
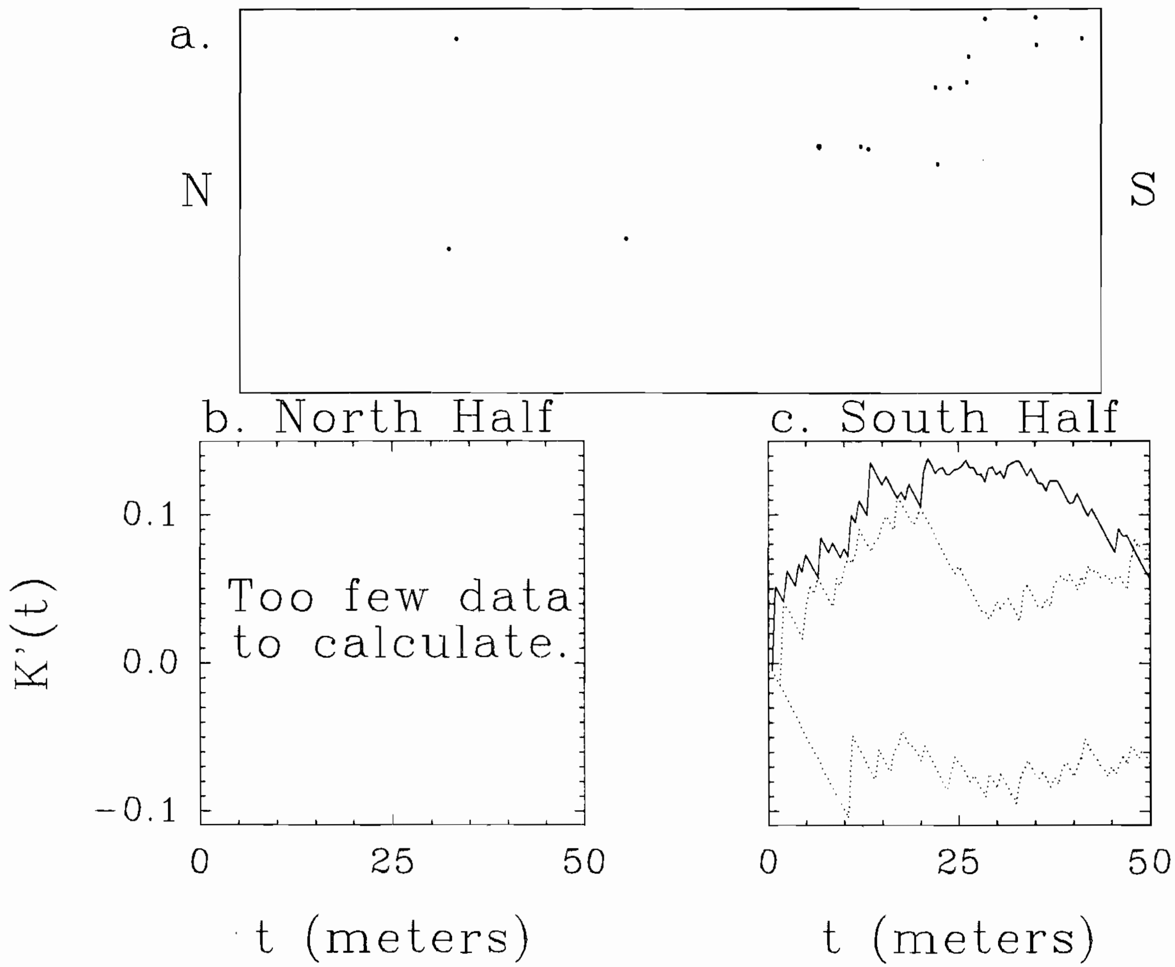


Figure 21. Intraspecific point-pattern analysis of the spatial distribution of mature (current stand) coniferous snags in the Flynn Creek reference stand. See Figure 14 for details of the analyses.



Trout Creek the mature coniferous snags appear to be aggregated at fine scales but do not appear to be distributed significantly different from random at coarser scales (Figure 22). The high density of mature coniferous snags in the northwest corner of the Trout Creek stand is characteristic of the mortality caused by the root rot Phellinus wierii (the majority of these snags are Douglas-fir).

The distributions of deciduous snags at Flynn Creek (all from the current stand) are significantly aggregated at fine scales in both halves of the stand (Figure 23). In the north half of the stand, deciduous snags tend toward a dispersed spacing at scales greater than 30m. Deciduous snags in the south half appear more aggregated than expected at medium scales. There are too few deciduous snags at Trout Creek to conduct a spatial analysis.

Although the distributions of western hemlock at Trout Creek are more spatially aggregated than expected at fine and medium scales, the degree of aggregation varies with tree size (Figure 24). The distributions of large western hemlock (DBH $\geq$ 50cm) are not significantly different from random at fine-medium scales in both halves of the stand and appear slightly more aggregated than expected at coarse scales in the north half of the Trout Creek reference stand (Figure 25). In contrast to the large hemlocks, small western hemlock (DBH 5-10cm) are significantly aggregated at fine and medium scales (Figure 26). Western hemlock older than two years are not present at Flynn Creek.

Figure 22. Intraspecific point-pattern analysis of the spatial distribution of mature (current stand) coniferous snags in the Trout Creek reference stand. See Figure 14 for details of the analyses.

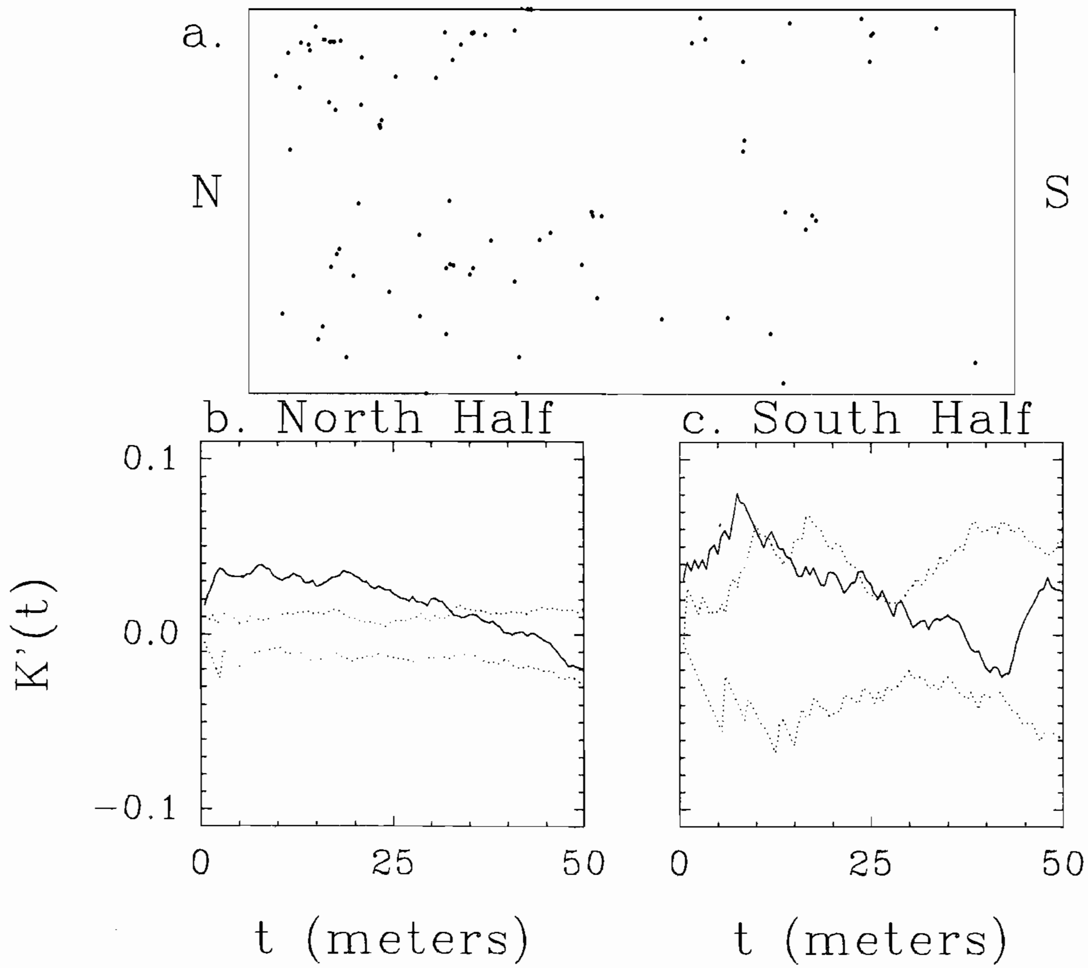


Figure 23. Intraspecific point-pattern analysis of the spatial distribution of deciduous snags in the Flynn Creek reference stand. See Figure 14 for details of the analyses.

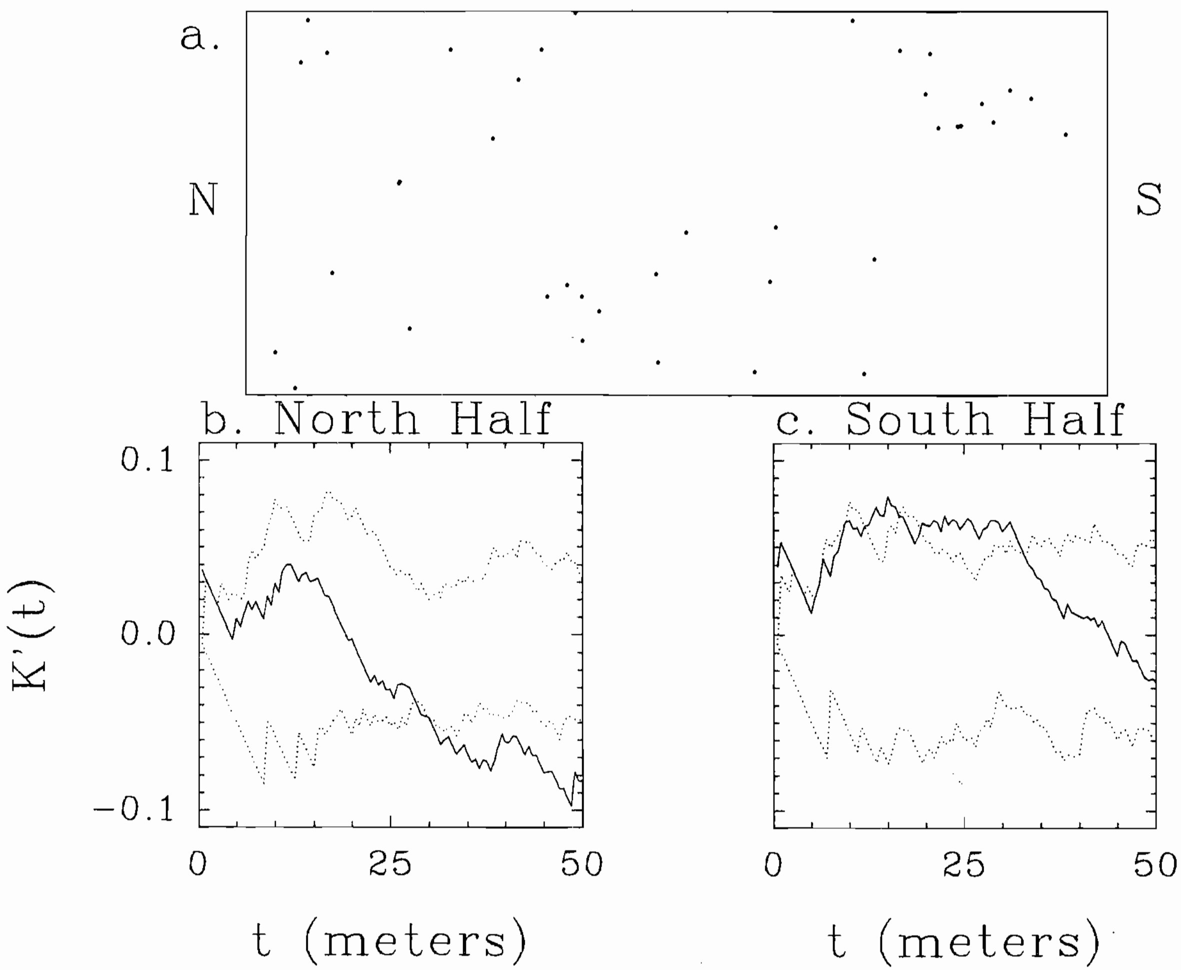


Figure 24. Intraspecific point-pattern analysis of the spatial distribution of all western hemlock in the Trout Creek reference stand. See Figure 14 for details of the analyses.

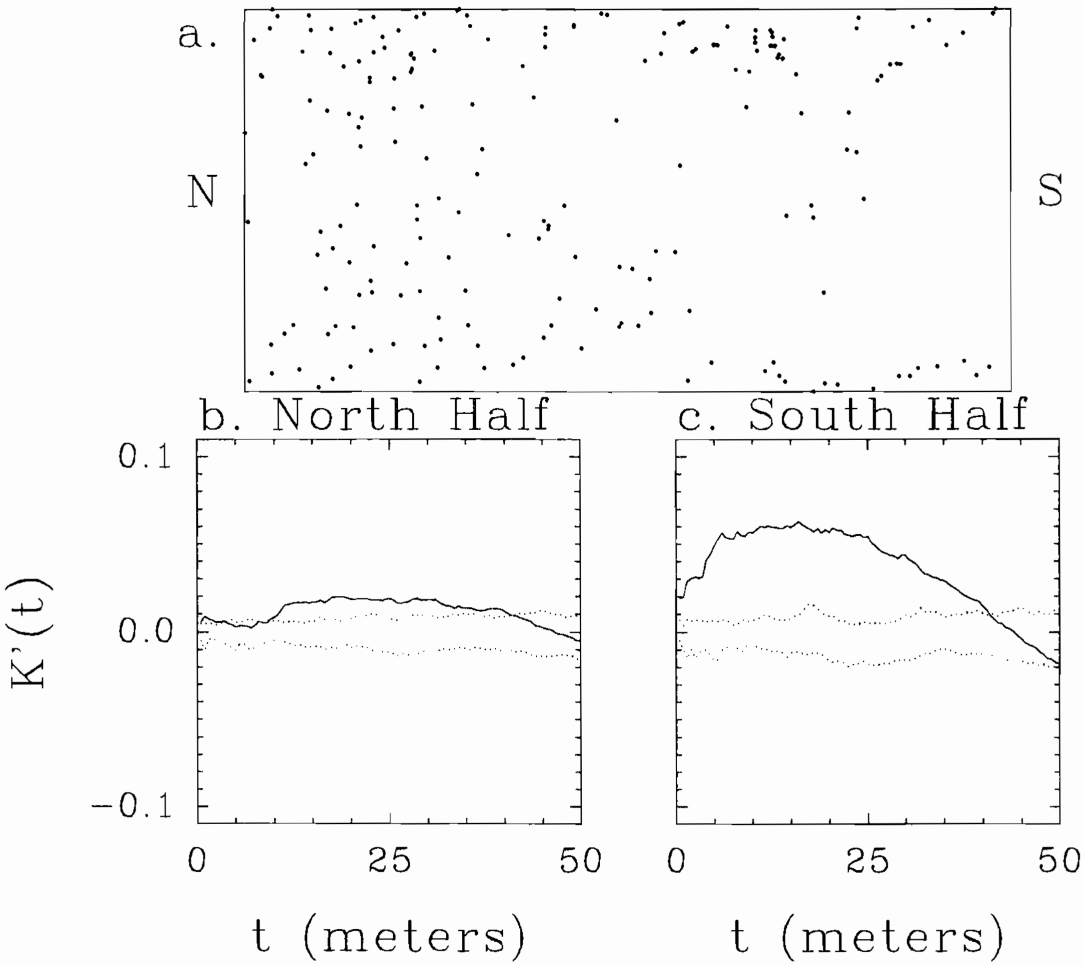


Figure 25. Intraspecific point-pattern analysis of the spatial distribution of large (DBH ≥ 50cm) western hemlock in the Trout Creek reference stand. See Figure 14 for details of the analyses.

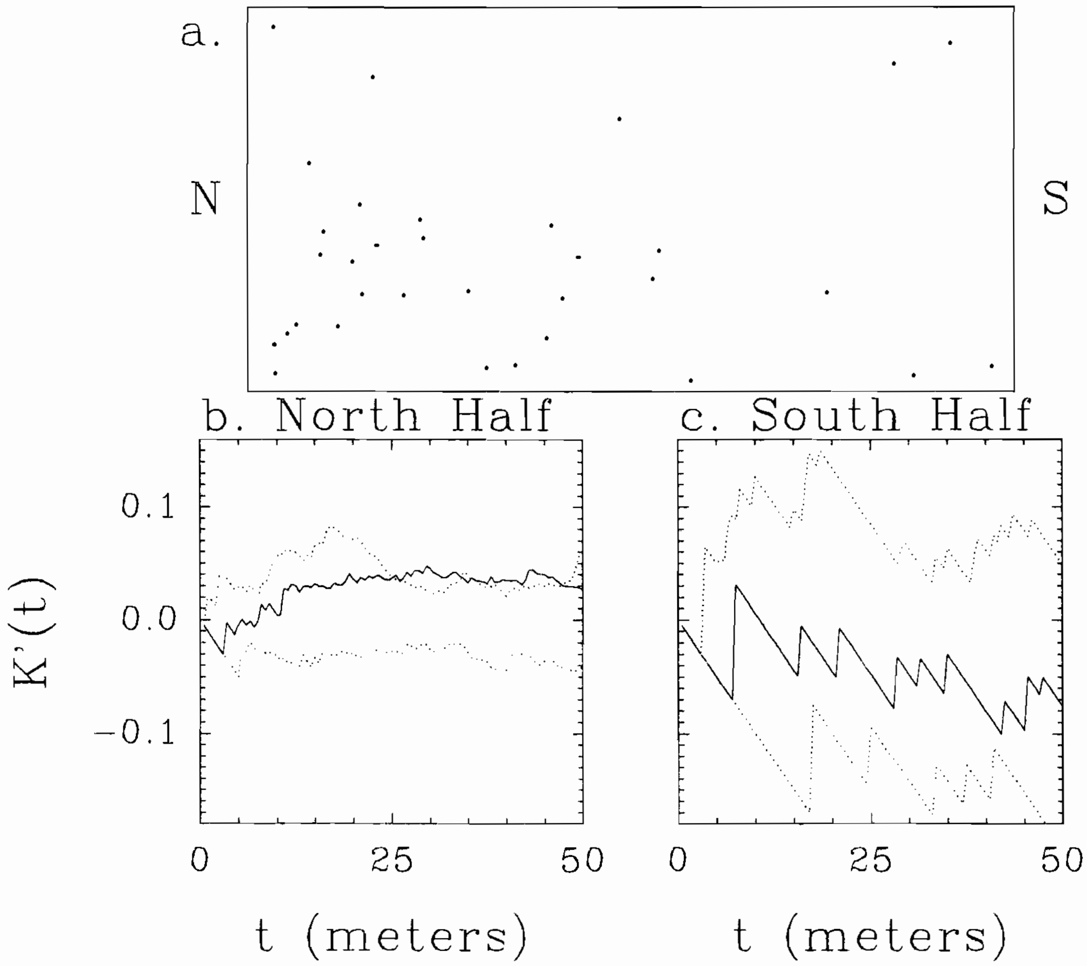
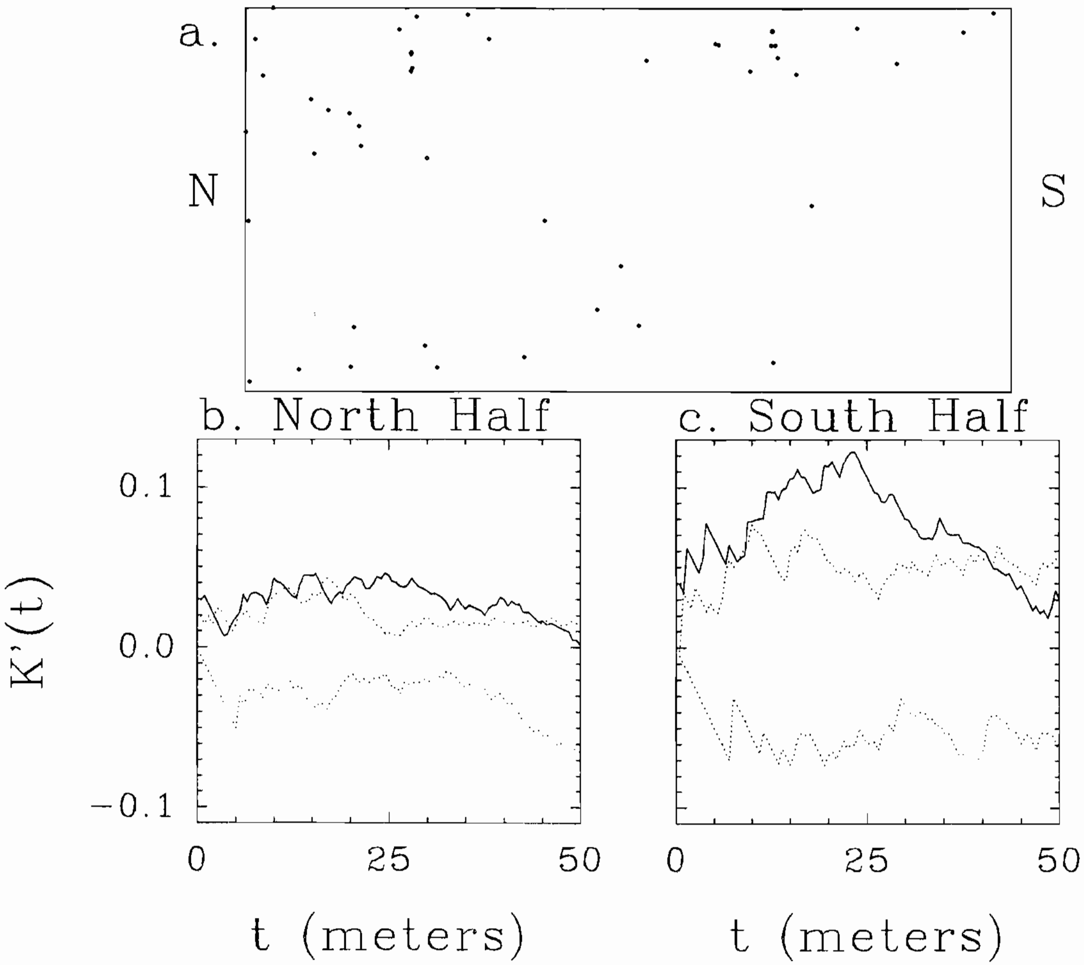


Figure 26. Intraspecific point-pattern analysis of the spatial distribution of small (5-10cm DBH) western hemlock in the Trout Creek reference stand. See Figure 14 for details of the analyses.



Western red cedar, big-leaf maple, and Sitka spruce are either absent or too few in number to conduct spatial analyses at either site.

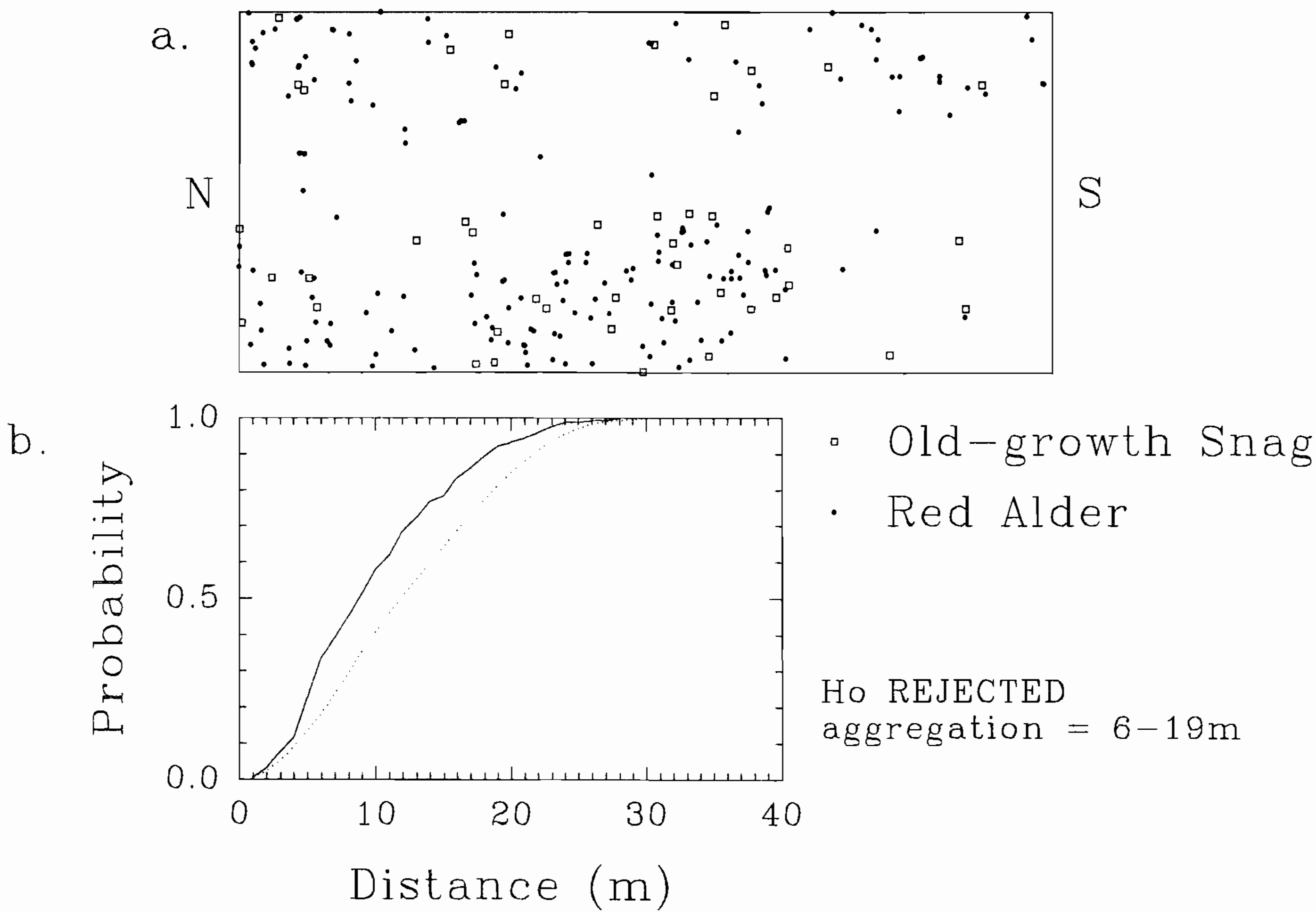
Interspecific Spatial Patterns

Is the spatial distribution of trees from the current stand associated with trees from the prior stand (i.e., snags)?

Red alder are significantly closer to old-growth coniferous snags at Flynn Creek than expected at scales of 6-19m, with the maximum difference between the observed and expected distributions occurring at a distance of 12m (two-sided KS test, alpha $\leq$ 0.001; Figure 27). In contrast, the distribution of red alder relative to old-growth coniferous snags at Trout Creek is not significantly different from random (Figure 28). The distributions of mature Douglas-fir (DBH $\geq$ 50cm) with respect to old-growth coniferous snags at both Flynn Creek and Trout Creek are not significantly different from random (Figures 29,30). Large western hemlock (DBH > 50cm) are closer to old-growth coniferous snags than expected at scales of 5-9m and 11-14m at Trout Creek, with the maximum difference between the observed and expected distributions occurring at a distance of 8m (two-sided KS test, alpha $\leq$ 0.01; Figure 31).

Figure 27. Interspecific point-pattern analysis of the spatial distribution of red alder relative to old-growth coniferous snags in the Flynn Creek reference stand. The locations of all red alder trees and old-growth coniferous snags in the reference stand (a) and probability distributions of red alder relative to old-growth coniferous snags (b) are shown. The dotted line in Figure 27b indicates the proportion of red alder trees expected within a given distance (meters) of the nearest old-growth coniferous snag if the red alder trees were distributed randomly with respect to the old-growth coniferous snags. The heavy line in Figure 27b indicates the observed proportion of red alder trees located within a given distance of the nearest old-growth coniferous snag. Observed values above the expected probability distribution indicate aggregation at that scale; observed values below the expected probability distribution indicate dispersion. The null hypothesis of complete spatial randomness can be tested by using a Kolmogorov-Smirnov (KS) test to determine the significance of the difference between the observed and expected probability distributions in Figure 27b.

Figure 27.



a.
N
S
b.
1.0
0.5
0.0
Probability
0
10
20
30
40
Distance (m)
Old-growth Snag
Red Alder
Ho REJECTED
aggregation = 6-19m

Figure 28. Interspecific point-pattern analysis of the spatial distribution of red alder relative to old-growth coniferous snags in the Trout Creek reference stand. See Figure 27 for details of the analyses.

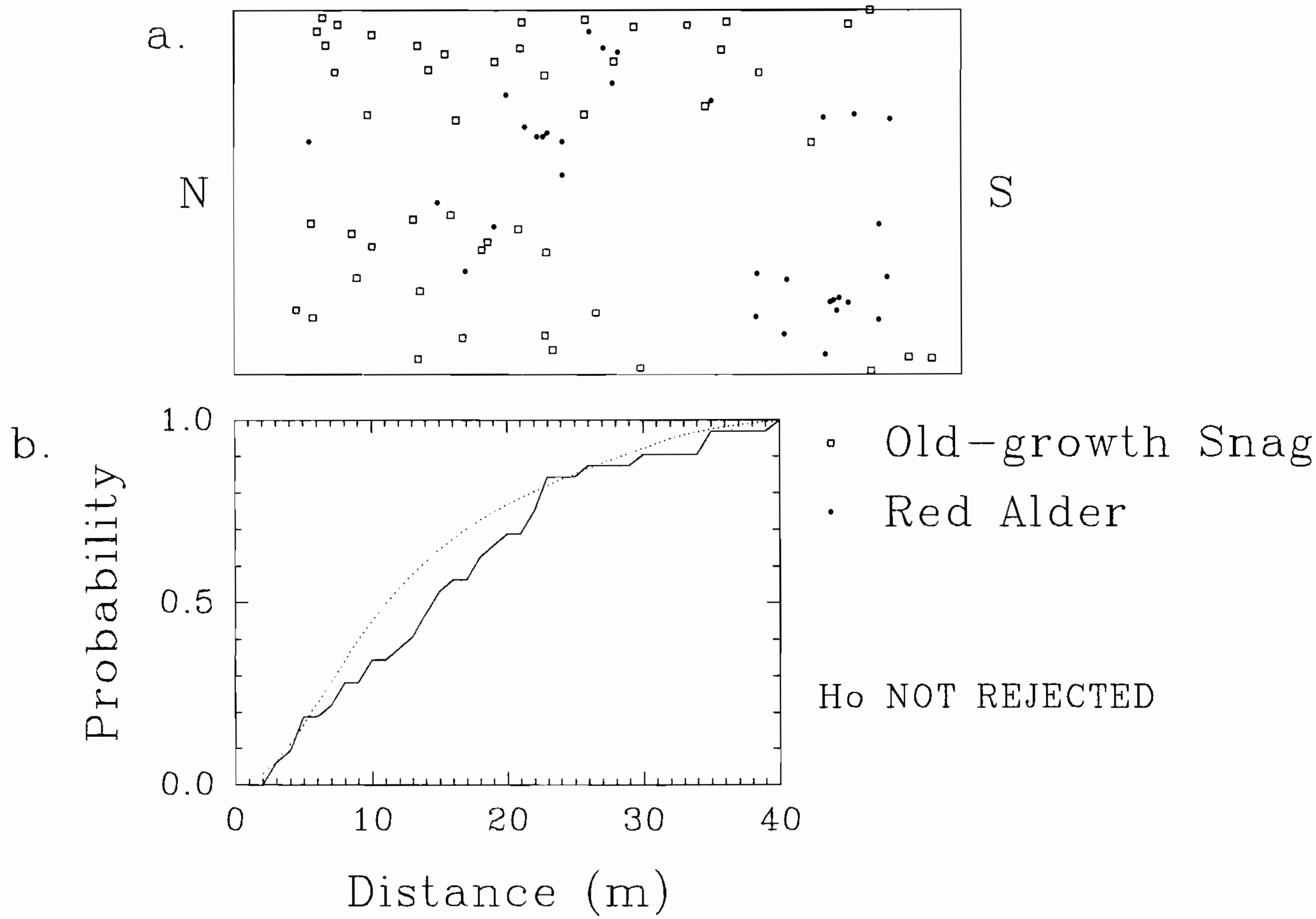


Figure 29. Interspecific point-pattern analysis of the spatial distribution of mature Douglas-fir relative to old-growth coniferous snags in the Flynn Creek reference stand. See Figure 27 for details of the analyses.

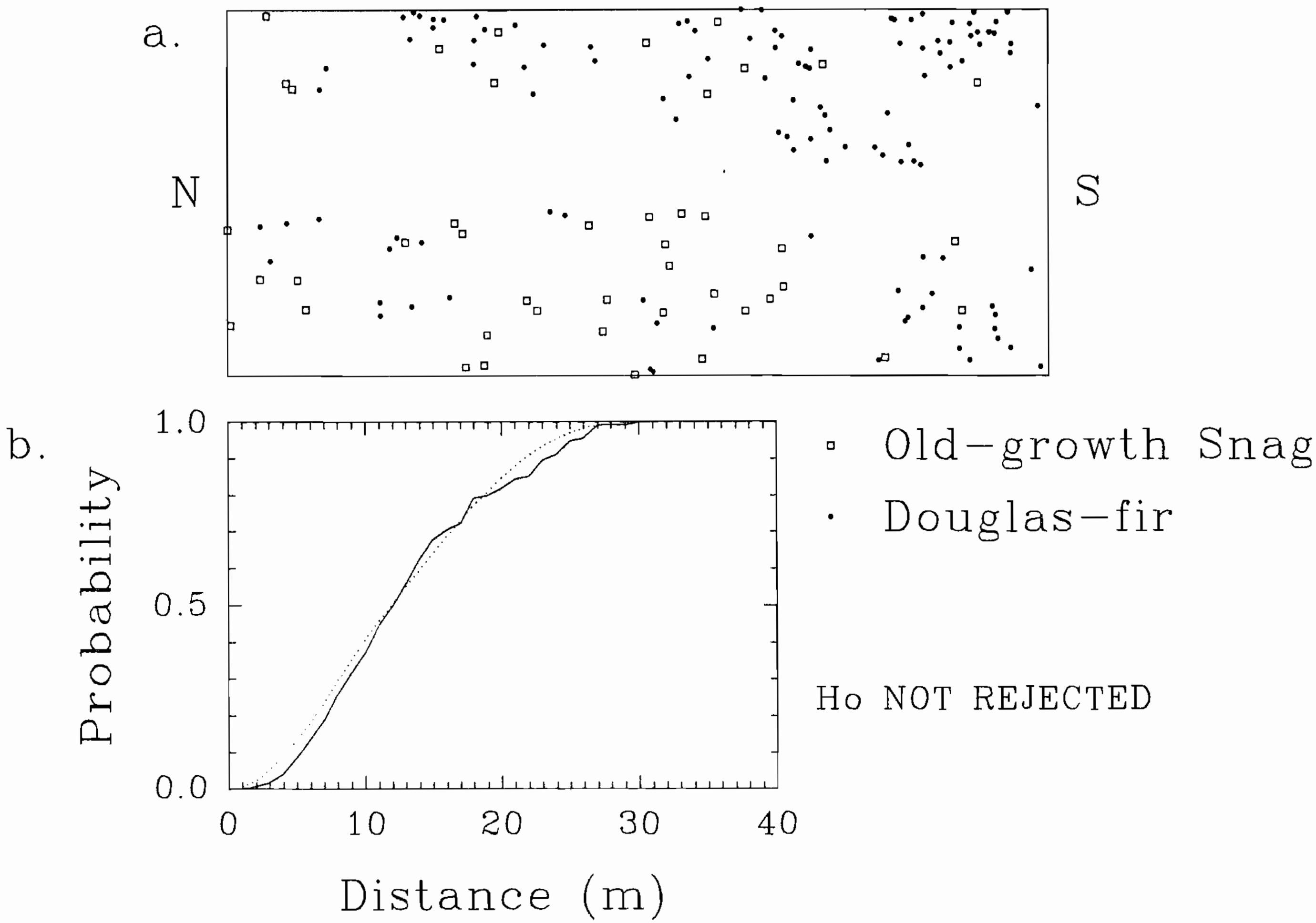


Figure 30. Interspecific point-pattern analysis of the spatial distribution of large (DBH ≥ 50cm), mature Douglas-fir relative to old-growth coniferous snags in the Trout Creek reference stand. See Figure 27 for details of the analyses.

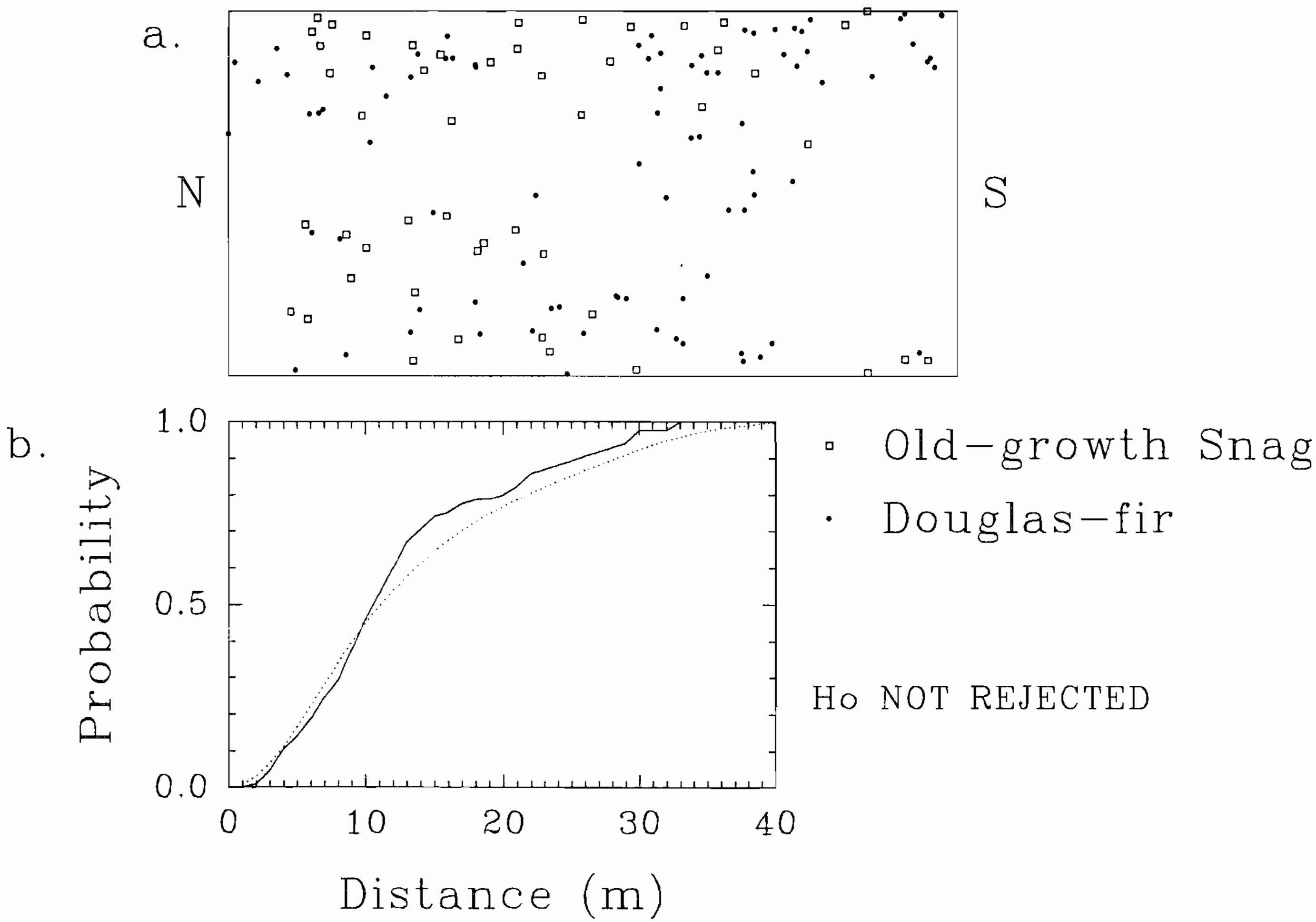
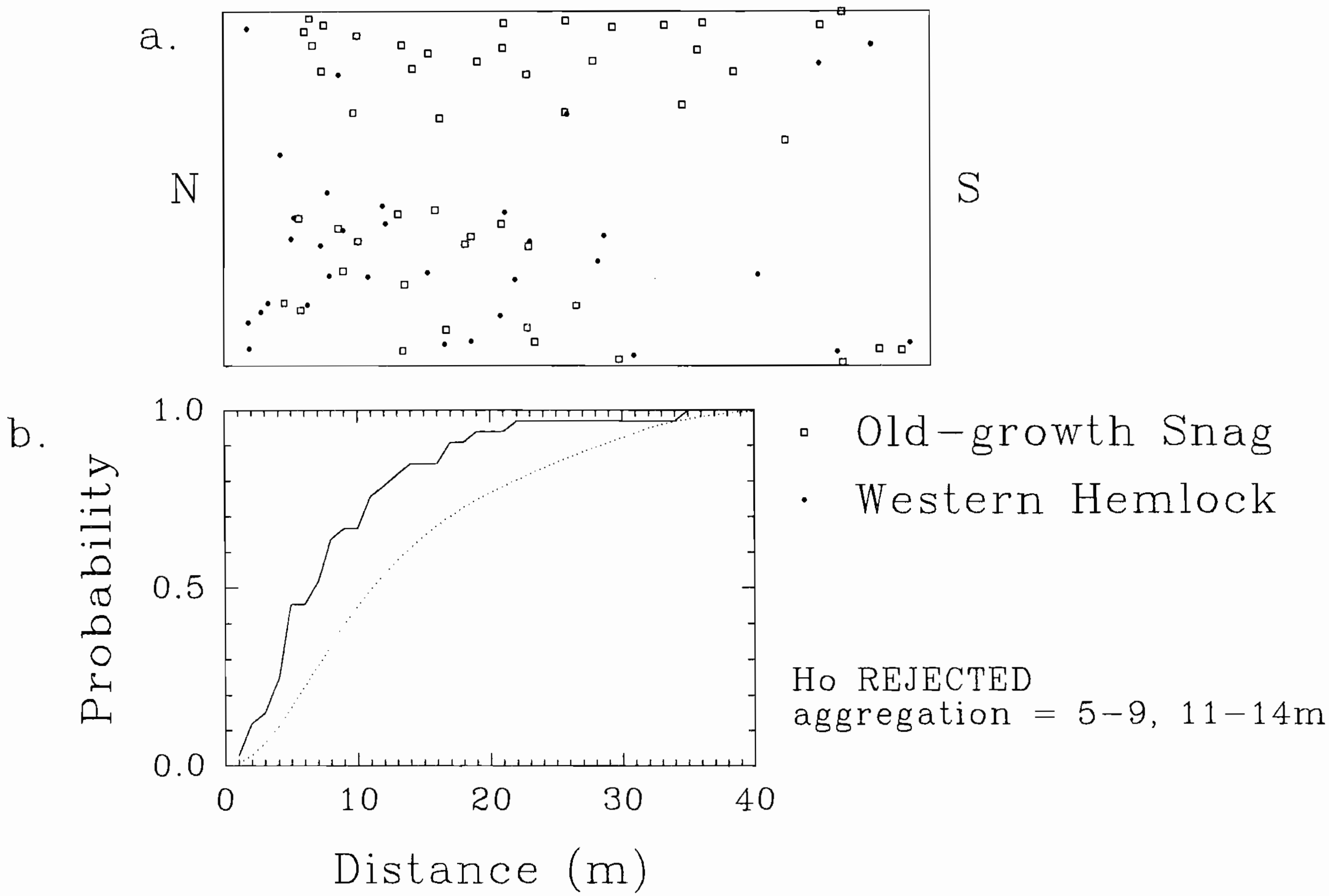


Figure 31. Interspecific point-pattern analysis of the spatial distribution of large (DBH ≥ 50cm) western hemlock relative to old-growth coniferous snags in the Trout Creek reference stand. See Figure 27 for details of the analyses.



Is the spatial distribution of trees of one species associated with the spatial distribution of other species?

Red alder are farther away from mature Douglas-fir at Flynn Creek than expected at scales of 6-19m under the null hypothesis of spatial randomness, with the maximum difference occurring at a distance of 10m (two-sided KS test, alpha $\leq$ 0.001; Figure 32). A similar result occurs at Trout Creek where red alder are significantly dispersed relative to mature Douglas-fir at scales of 6-14m, with the maximum difference in probability distributions at 12m (two-sided KS test, alpha $\leq$ 0.001; Figure 33). The distribution of large western hemlock relative to large, mature Douglas-fir is not significantly different from random at Trout Creek (Figure 34).

What are the spatial patterns of dead trees relative to live trees in the current stand?

Mature (current stand) coniferous snags are closer to large, mature Douglas-fir at both Flynn Creek and Trout Creek than expected (two-sided KS test, alpha < 0.001 in both cases; Figures 35,36). However, the distribution of mature coniferous snags relative to large western hemlock is not significantly different from random at Trout Creek (Figure 37). Deciduous snags (all red alder) are closer to red alder than expected at scales of 4-9m and 11m at Flynn Creek, with the maximum difference in probability distributions at 5m

Figure 32. Interspecific point-pattern analysis of the spatial distribution of red alder relative to mature Douglas-fir in the Flynn Creek reference stand. See Figure 27 for details of the analyses.

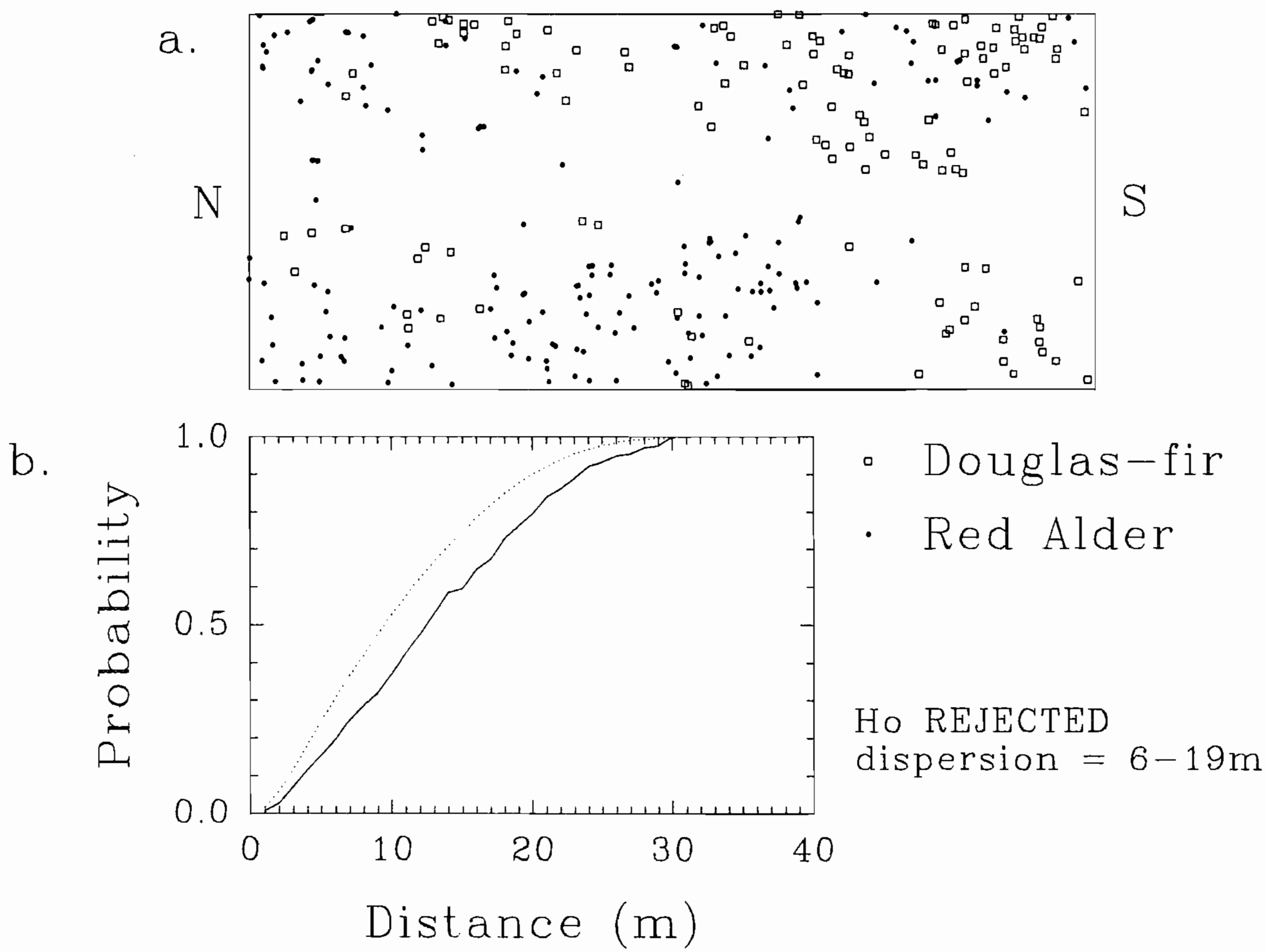


Figure 33. Interspecific point-pattern analysis of the spatial distribution of red alder relative to all mature Douglas-fir in the Trout Creek reference stand. See Figure 27 for details of the analyses.

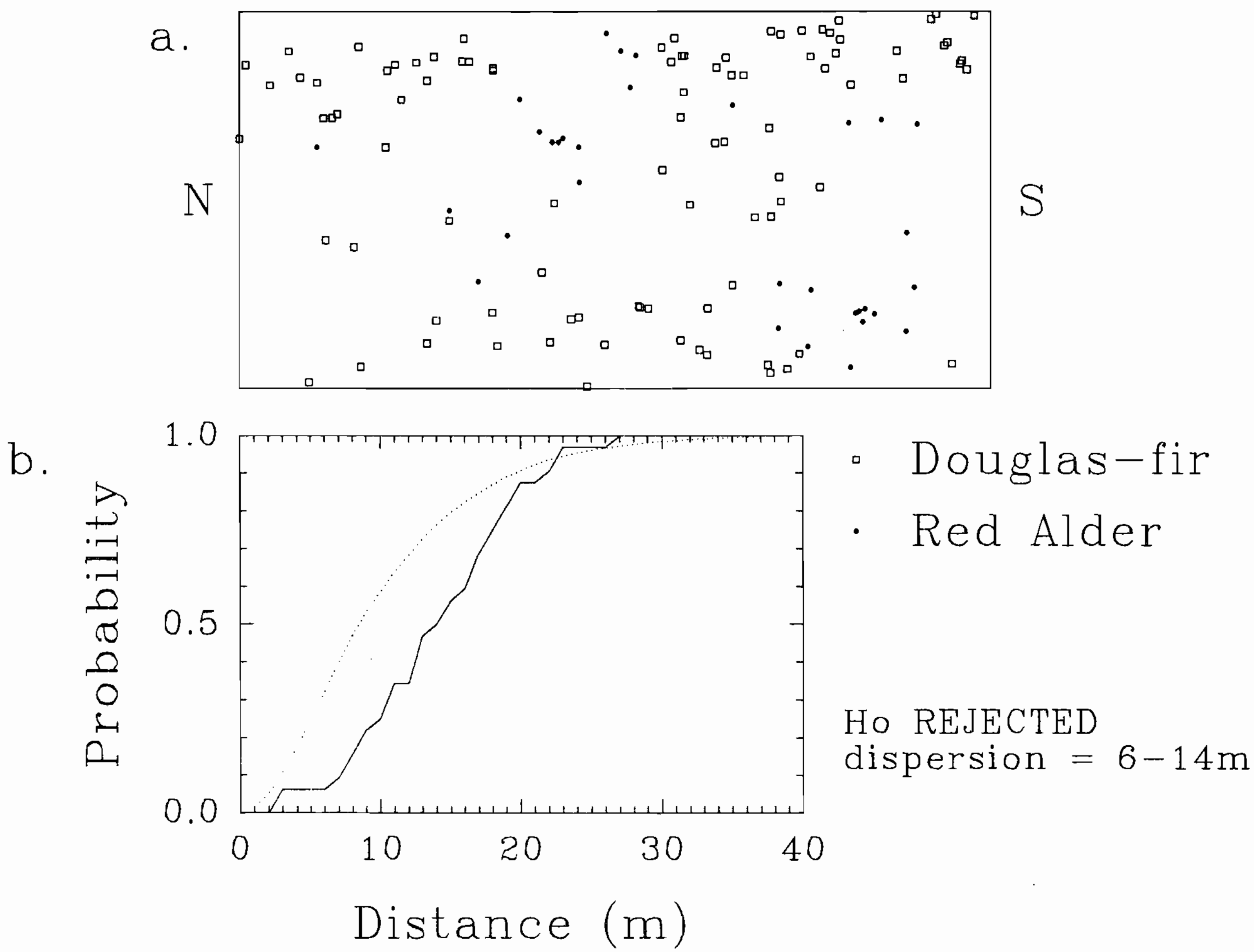


Figure 34. Interspecific point-pattern analysis of the spatial distribution of large (DBH ≥ 50cm) western hemlock relative to large (DBH ≥ 50cm), mature Douglas-fir in the Trout Creek reference stand. See Figure 27 for details of the analyses.

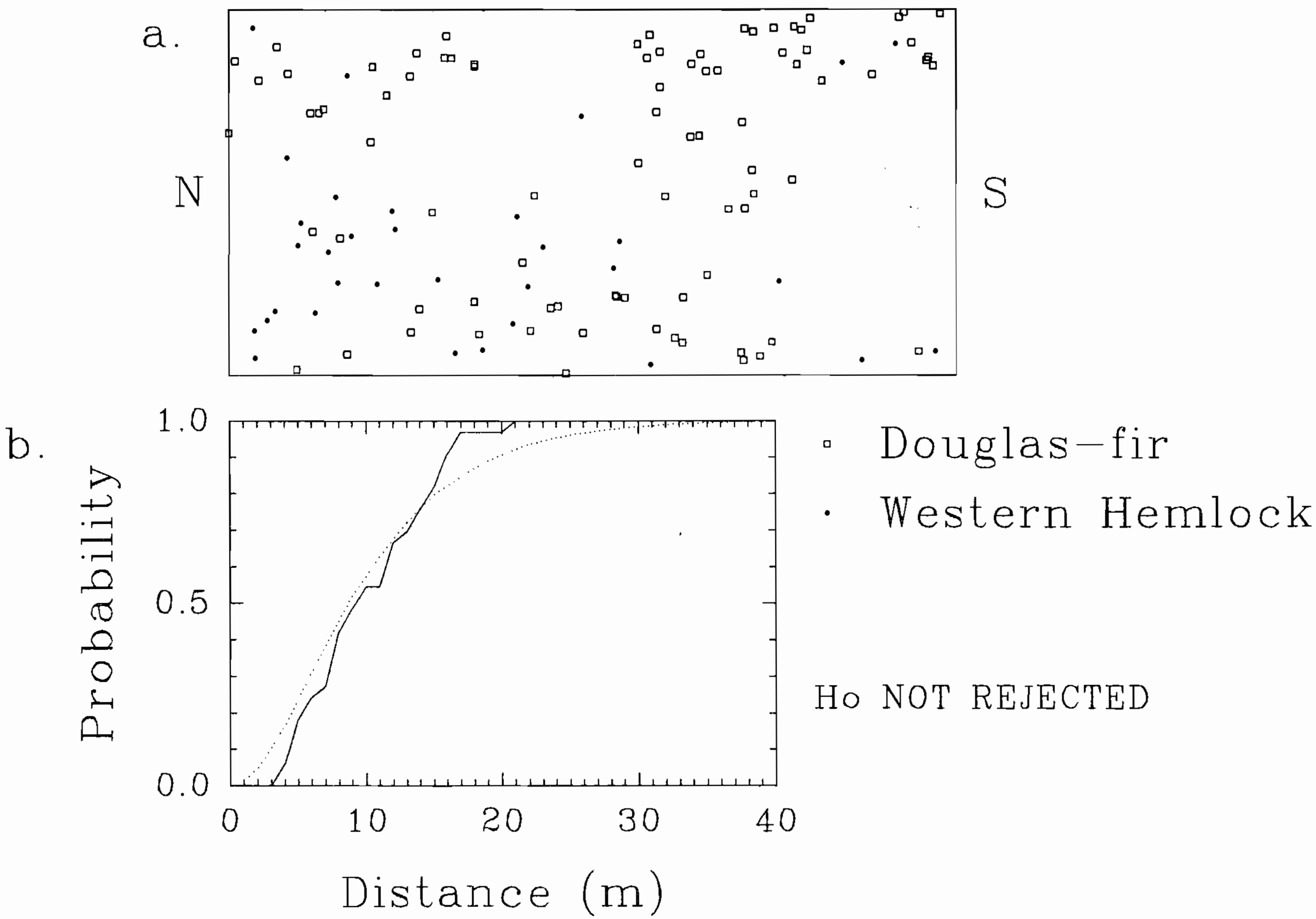


Figure 35. Interspecific point-pattern analysis of the spatial distribution of mature (current stand) coniferous snags relative to mature Douglas-fir in the Flynn Creek reference stand. See Figure 27 for details of the analyses.

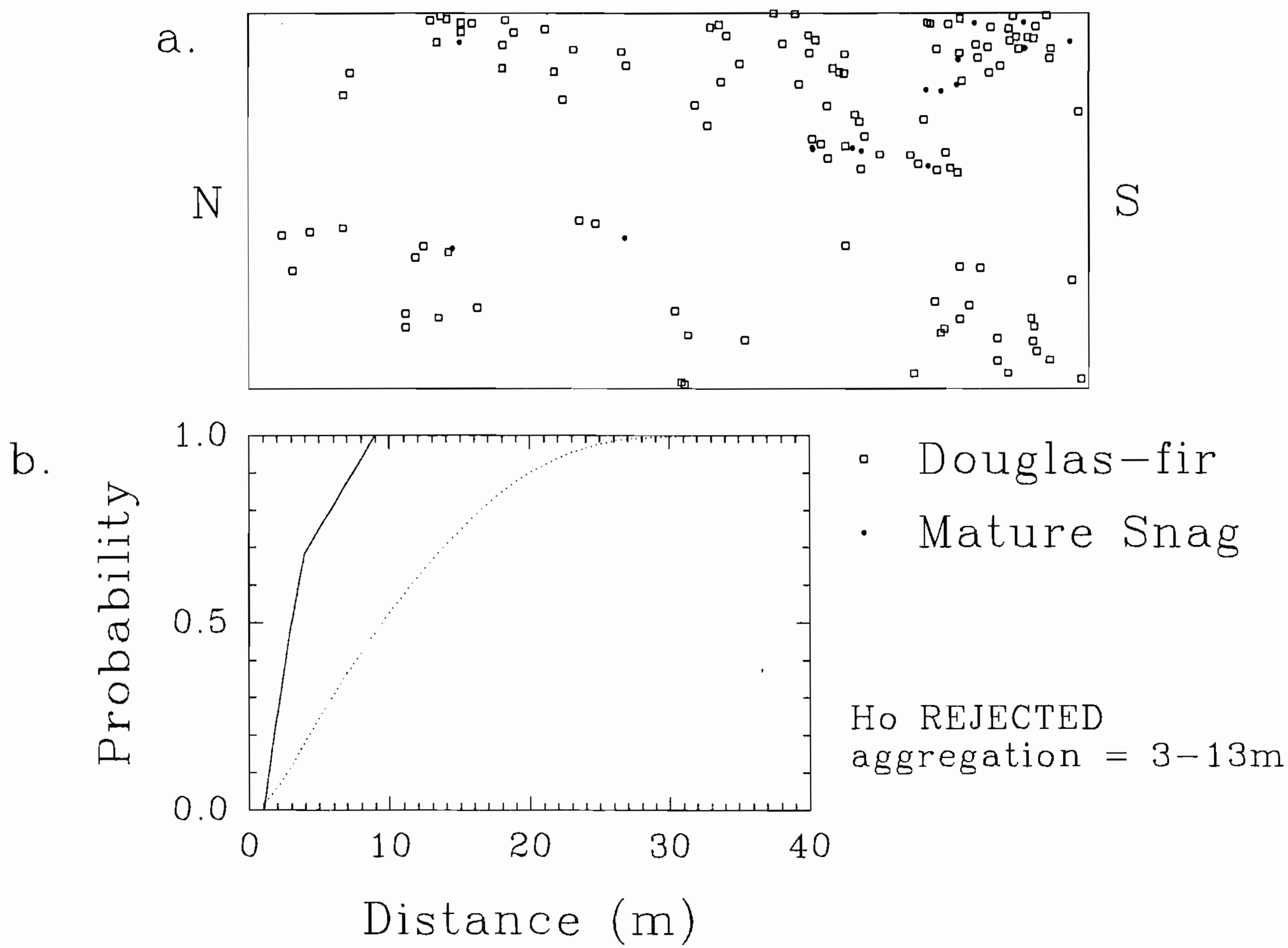


Figure 36. Interspecific point-pattern analysis of the spatial distribution of mature (current stand) coniferous snags relative to large (DBH ≥ 50cm), mature Douglas-fir in the Trout Creek reference stand. See Figure 27 for details of the analyses.

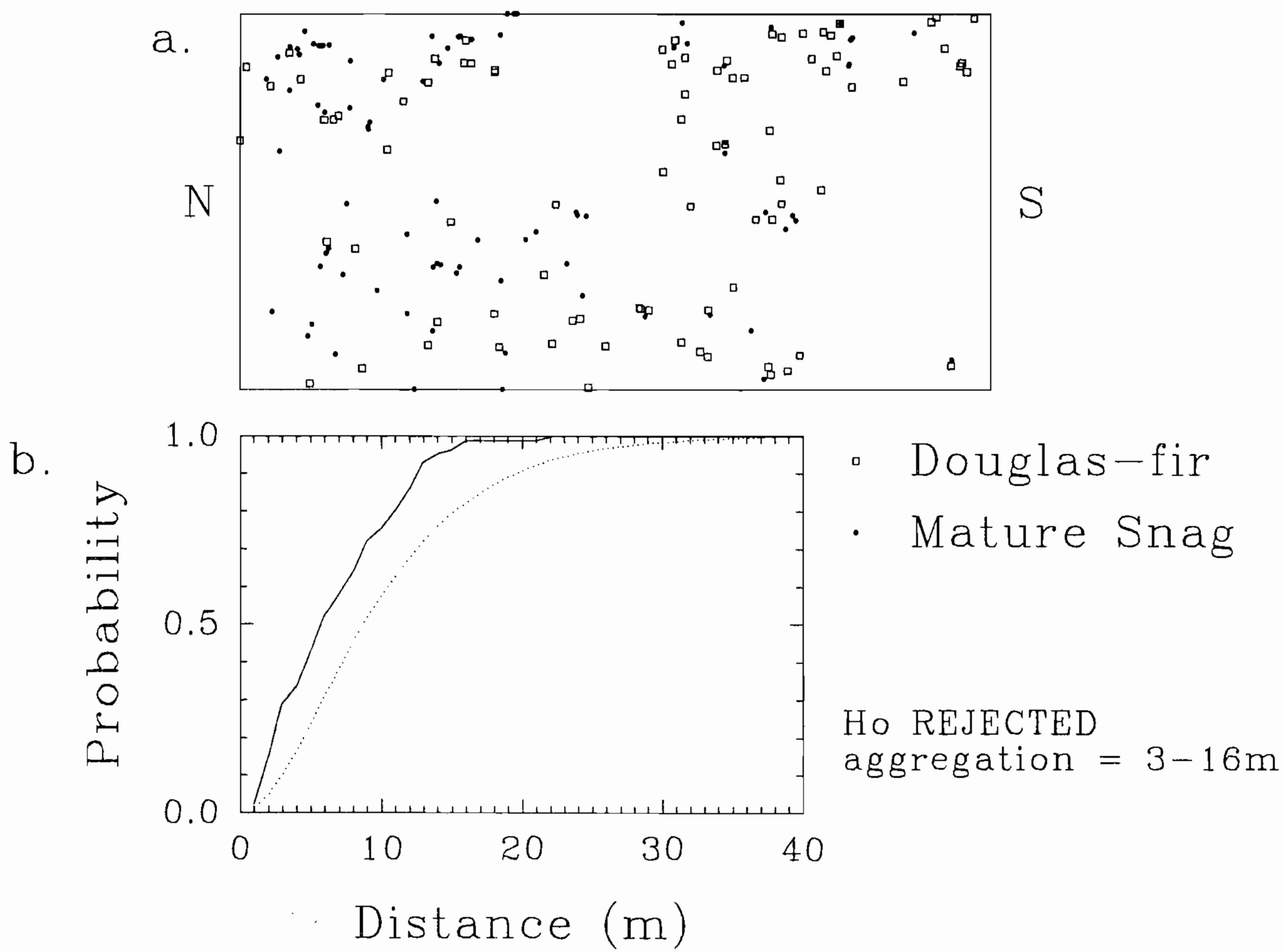
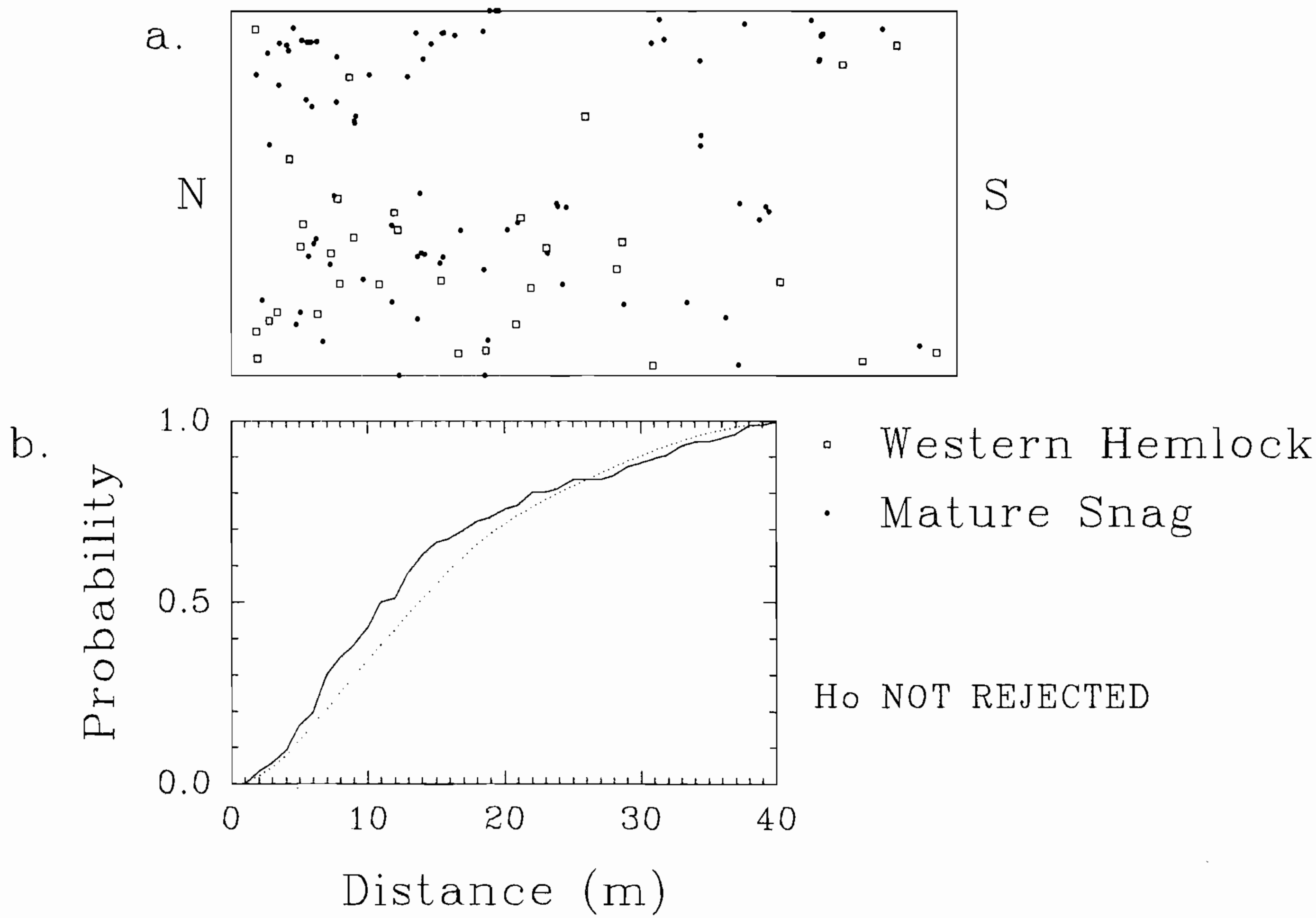


Figure 37. Interspecific point-pattern analysis of the spatial distribution of mature (current stand) coniferous snags relative to large (DBH ≥ 50cm) western hemlock in the Trout Creek reference stand. See Figure 27 for details of the analyses.



(two-sided KS test, alpha $\leq$ 0.001; Figure 38). There are not enough deciduous snags at Trout Creek to conduct spatial analyses.

What are the spatial patterns of understory conifer regeneration relative to trees and snags in the current stand?

Understory western hemlock regeneration (DBH 5-10cm) is significantly aggregated with respect to large, mature Douglas-fir at scales of 6-14m at Trout Creek, with the maximum difference between the observed and expected distributions occurring at a distance of 6m (two-sided KS test, alpha $\leq$ 0.001; Figure 39). Interestingly, the distribution of western hemlock regeneration relative to large western hemlock is not significantly different from random (Figure 40). The distribution of western hemlock regeneration relative to old-growth coniferous snags is not significantly different from random at Trout Creek (Figure 41). However, when compared with mature coniferous snags, the distribution of western hemlock regeneration is significantly aggregated at scales of 8-16m at Trout Creek (two-sided KS test, alpha $\leq$ 0.001; Figure 42). There are too few understory western red cedar at Trout Creek to conduct spatial analyses. Understory conifer regeneration in the 5-10cm DBH size class is not present at Flynn Creek (although several two-year old western hemlock seedlings were observed growing on a downed red alder log within the stand).

Figure 38. Interspecific point-pattern analysis of the spatial distribution of deciduous snags relative to red alder in the Flynn Creek reference stand. See Figure 27 for details of the analyses.

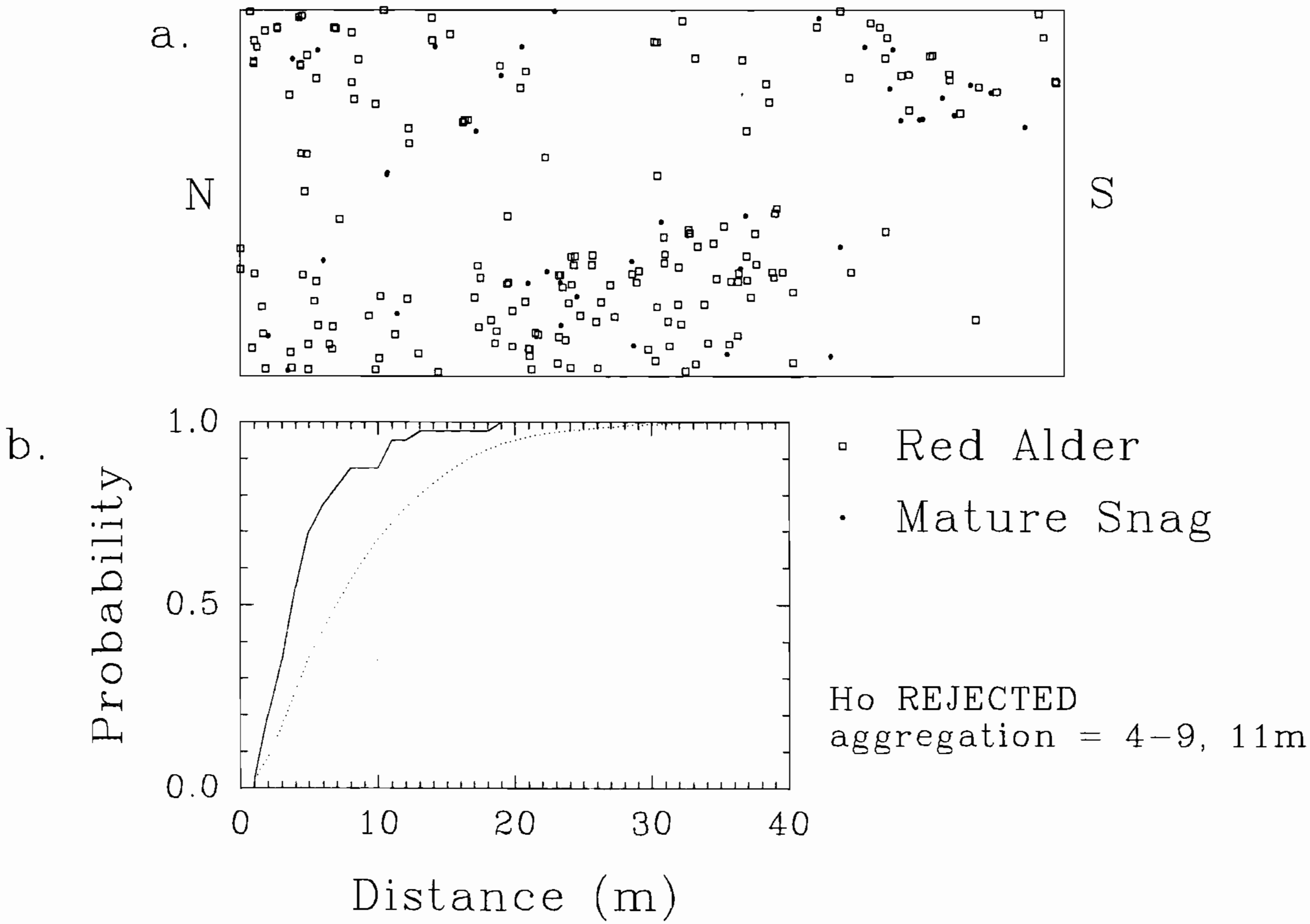


Figure 39. Interspecific point-pattern analysis of the spatial distribution of small (5-10cm DBH) western hemlock relative to large (DBH ≥ 50cm), mature Douglas-fir in the Trout Creek reference stand. See Figure 27 for details of the analyses.

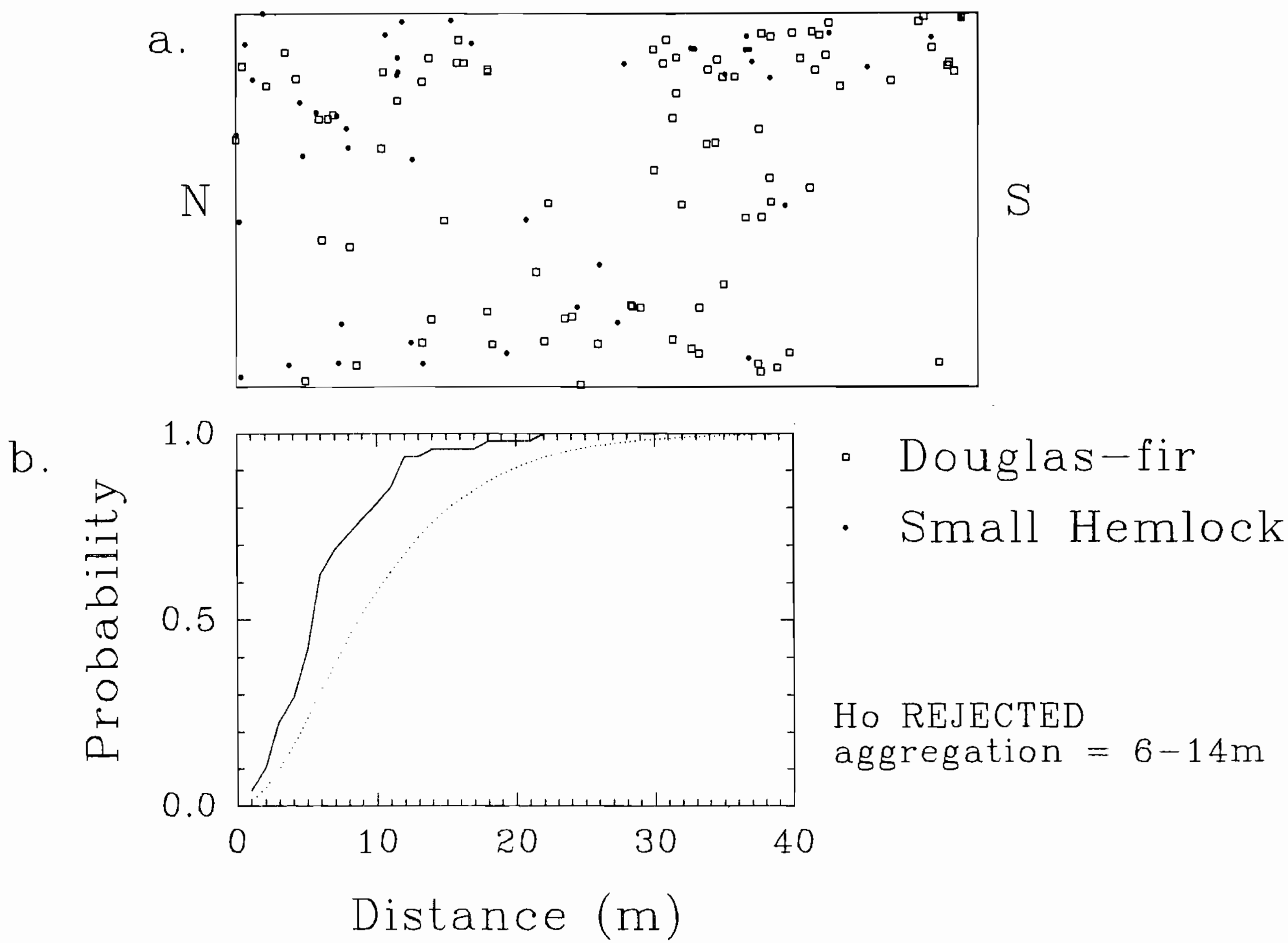


Figure 40. Interspecific point-pattern analysis of the spatial distribution of small (5-10cm DBH) western hemlock relative to large (DBH ≥ 50cm) western hemlock in the Trout Creek reference stand. See Figure 27 for details of the analyses.

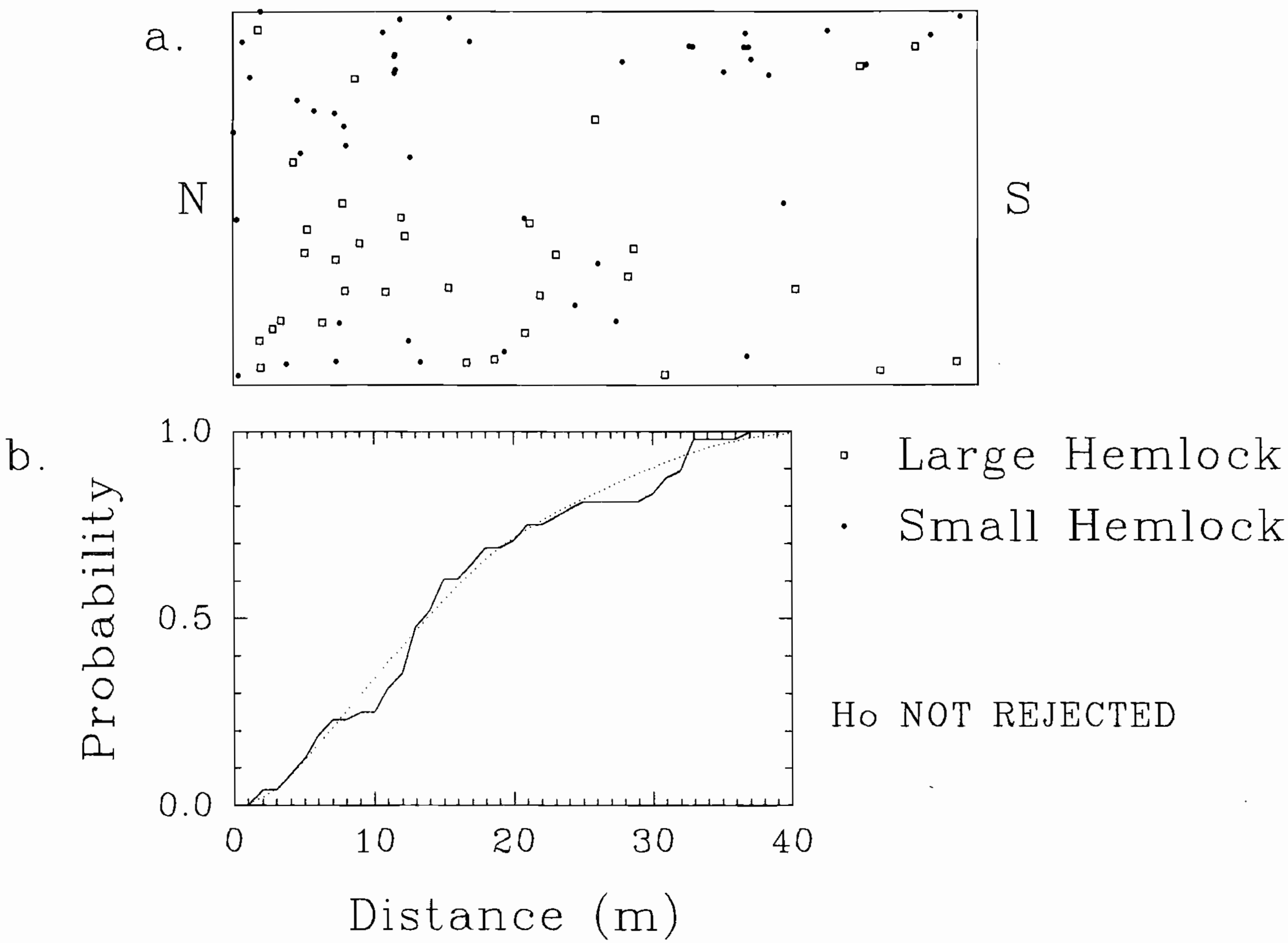


Figure 41. Interspecific point-pattern analysis of the spatial distribution of small (5-10cm DBH) western hemlock relative to old-growth coniferous snags in the Trout Creek reference stand. See Figure 27 for details of the analyses.

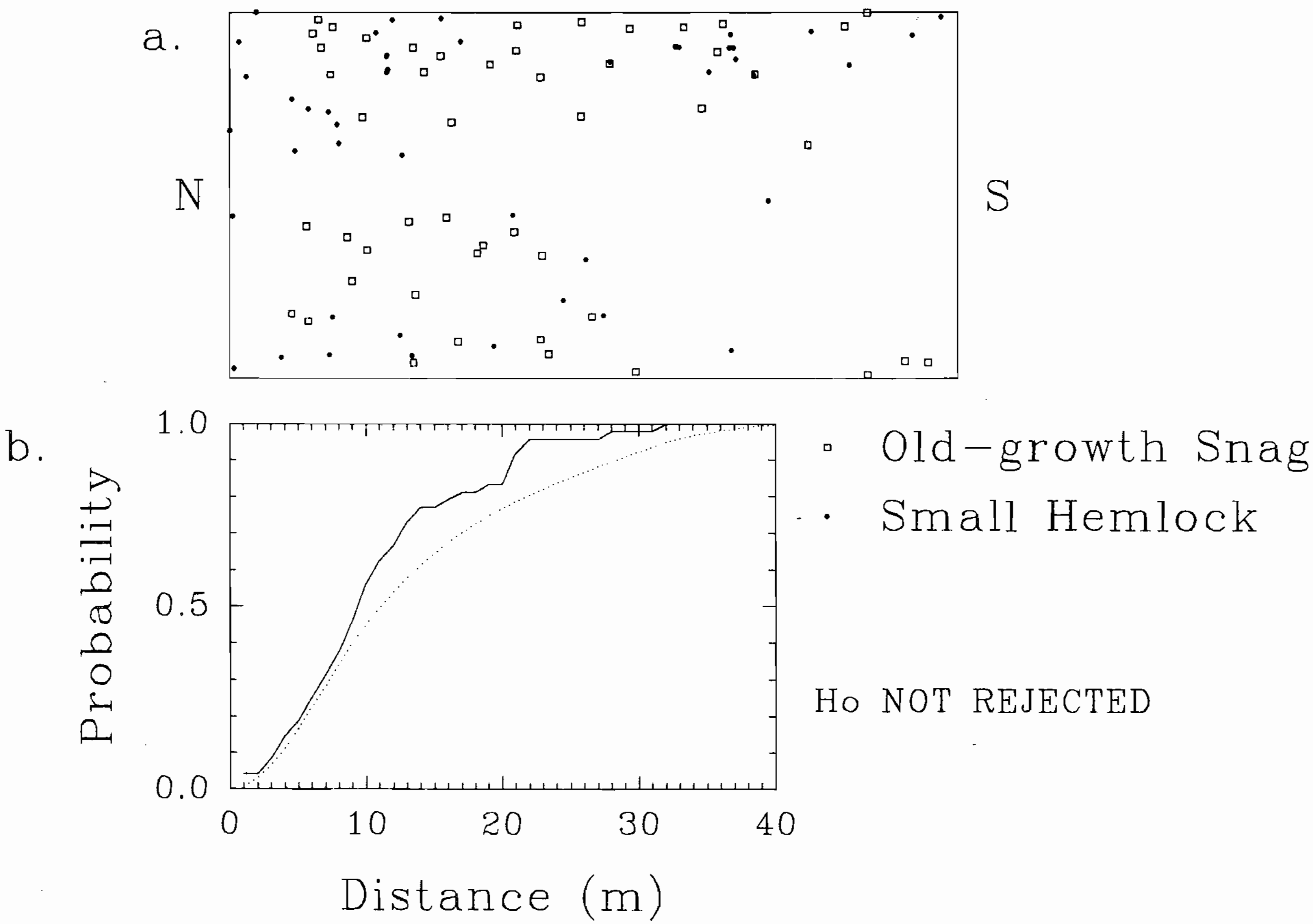
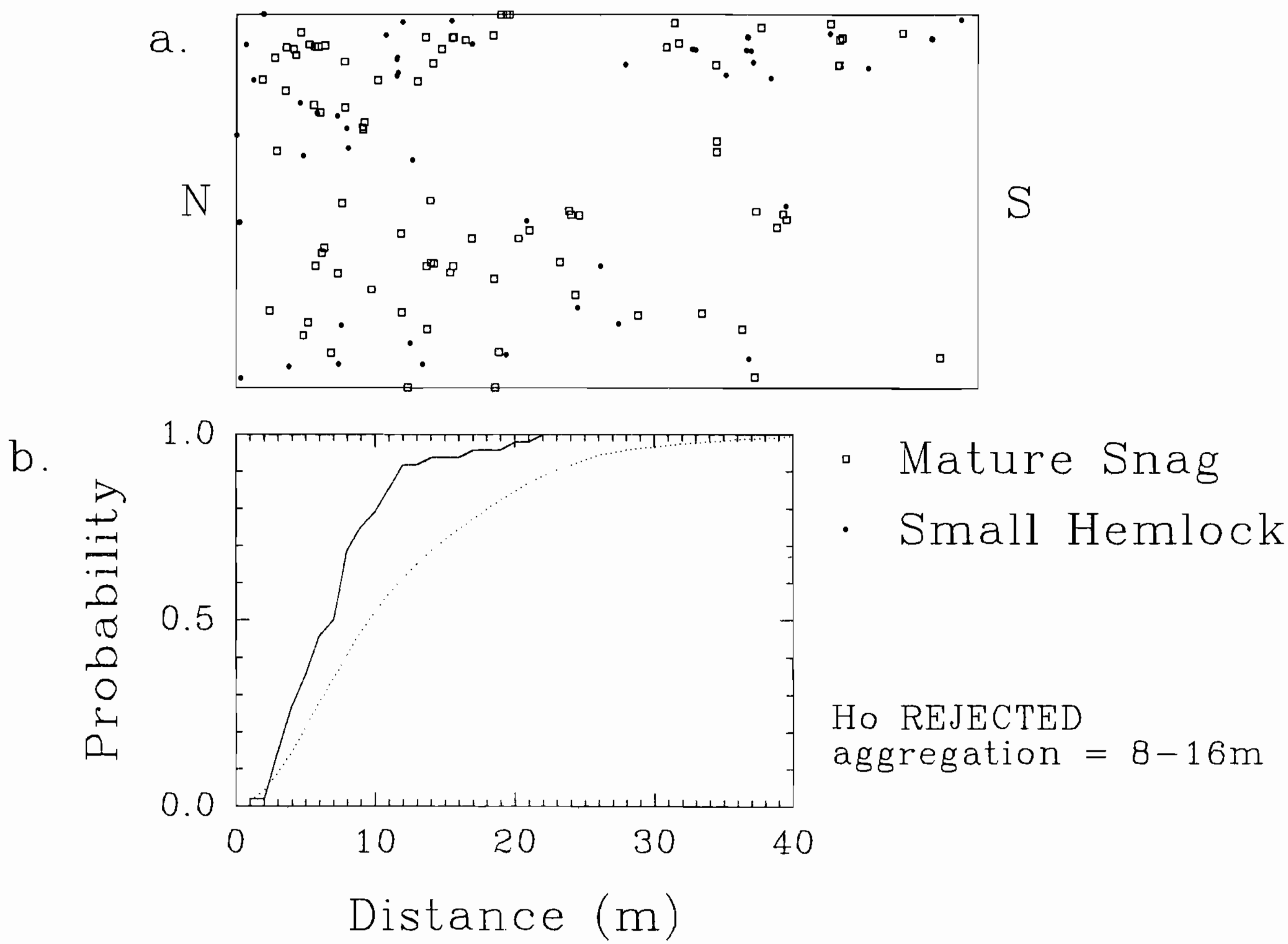


Figure 42. Interspecific point-pattern analysis of the spatial distribution of small (5-10cm DBH) western hemlock relative to mature (current stand) coniferous snags in the Trout Creek reference stand. See Figure 27 for details of the analyses.



Characterization of Disturbance and Establishment

Field Observations

Evidence of fire was noted at both Flynn Creek and Trout Creek. Charcoal was observed on the ground, on downed coniferous coarse woody debris, and on old-growth coniferous snags at both sites. One of the live old-growth Douglas-firs and the old-growth western hemlock at Trout Creek have visible fire scars. Fire scarring also was observed on old-growth trees outside of the Trout Creek reference stand (including an old-growth western red cedar). No fire scars were observed on mature trees at either Trout Creek or Flynn Creek. No live old-growth trees, burned or otherwise, were found in or around the Flynn Creek reference stand.

Old-growth coniferous, mature coniferous, and hardwood coarse woody debris generally reflects the patterns observed in the stand cross-sections at both sites. Although the amount of old-growth coniferous woody debris appears comparable at both sites, the amount of mature coniferous coarse woody debris is greater at Trout Creek than Flynn Creek. The opposite pattern is observed for deciduous coarse woody debris; more deciduous coarse woody debris was noted at Flynn Creek. This was particularly noticeable on the valley floor at Flynn Creek where downed red alder logs were found under a shrub layer of salmonberry, elderberry, and vine maple.

Branching patterns of trees may indicate the presence and/or absence of competition and/or disturbance(s) in the past. For example, the old-growth Douglas-firs at Trout Creek have broken, irregular tops which suggest past damage from windstorms. The branch-free, smooth boles of mature Douglas-firs presently growing under open conditions along the valley floor at Flynn Creek suggest that past growing conditions suppressed lateral branch development, perhaps as a result of competition from red alders which are now dead and form deciduous coarse woody debris on the valley floor.

A patch of conifer mortality symptomatic of the presence of the root rot Phellinus wierii was noted in the northeast corner of the Trout Creek reference stand (Figure 43). Patterns of mortality characteristic of root rot were not observed at Flynn Creek.

Evidence of recent mass movement events was observed at both sites but is more apparent at Trout Creek than Flynn Creek (Figures 43,44). Portions of the hillslopes along the length of the Trout Creek reference stand appear to have slid at one or more times in the recent past (Figure 43). It is likely that other geomorphic disturbances have occurred in the more distant past as evidenced by coarse textured deposits on the valley floor and hillslope profiles, suggesting slumps and other earth movements. Deciduous species, red alder and big-leaf maple, tend to occupy these mass movement areas at Trout Creek. Interestingly, old-growth coniferous snags are absent from these areas of mass

Figure 43. Field observations of recent non-fire disturbances in the Trout Creek reference stand. Areas of root rot, mass movement, and animal activity are indicated.

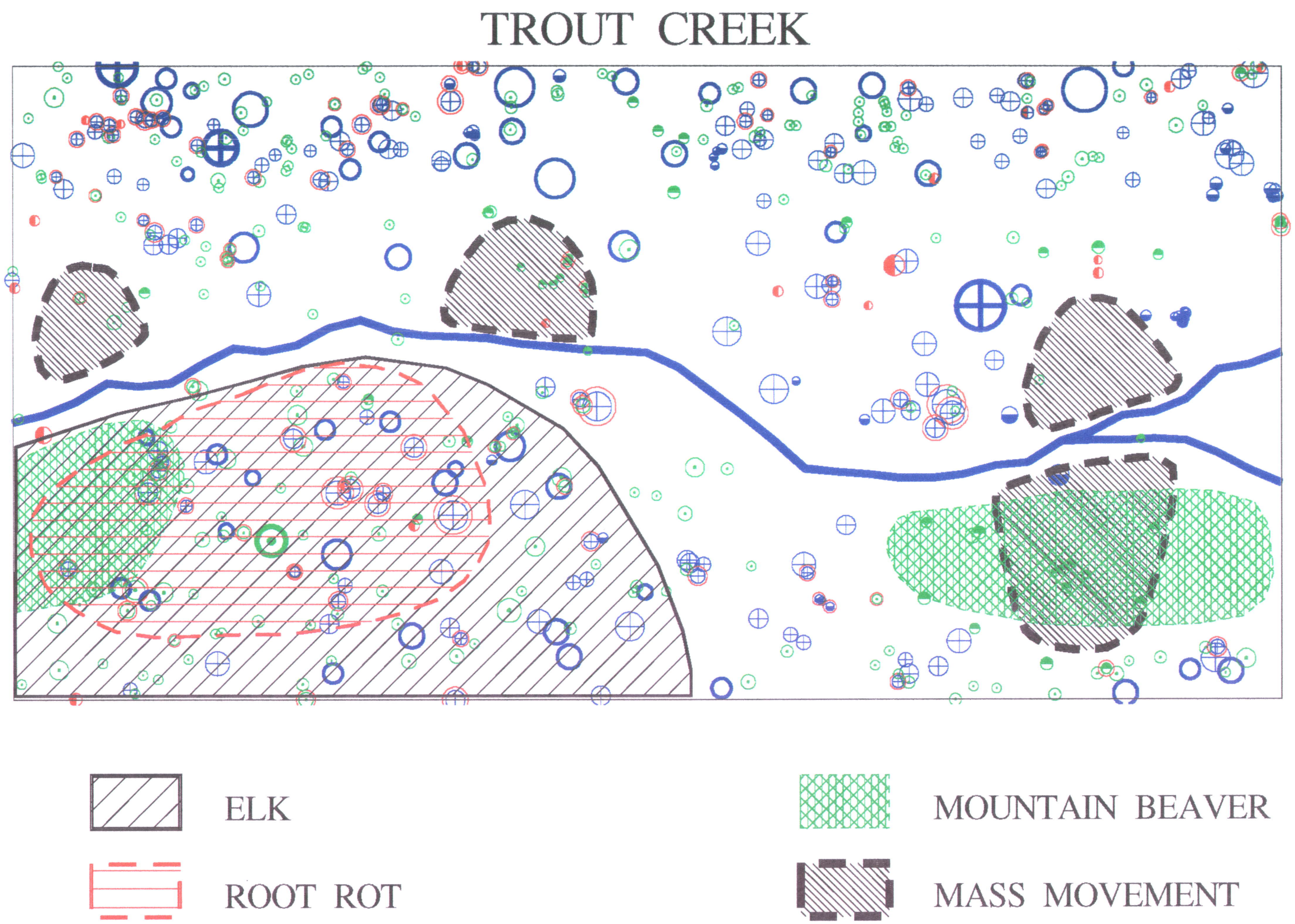
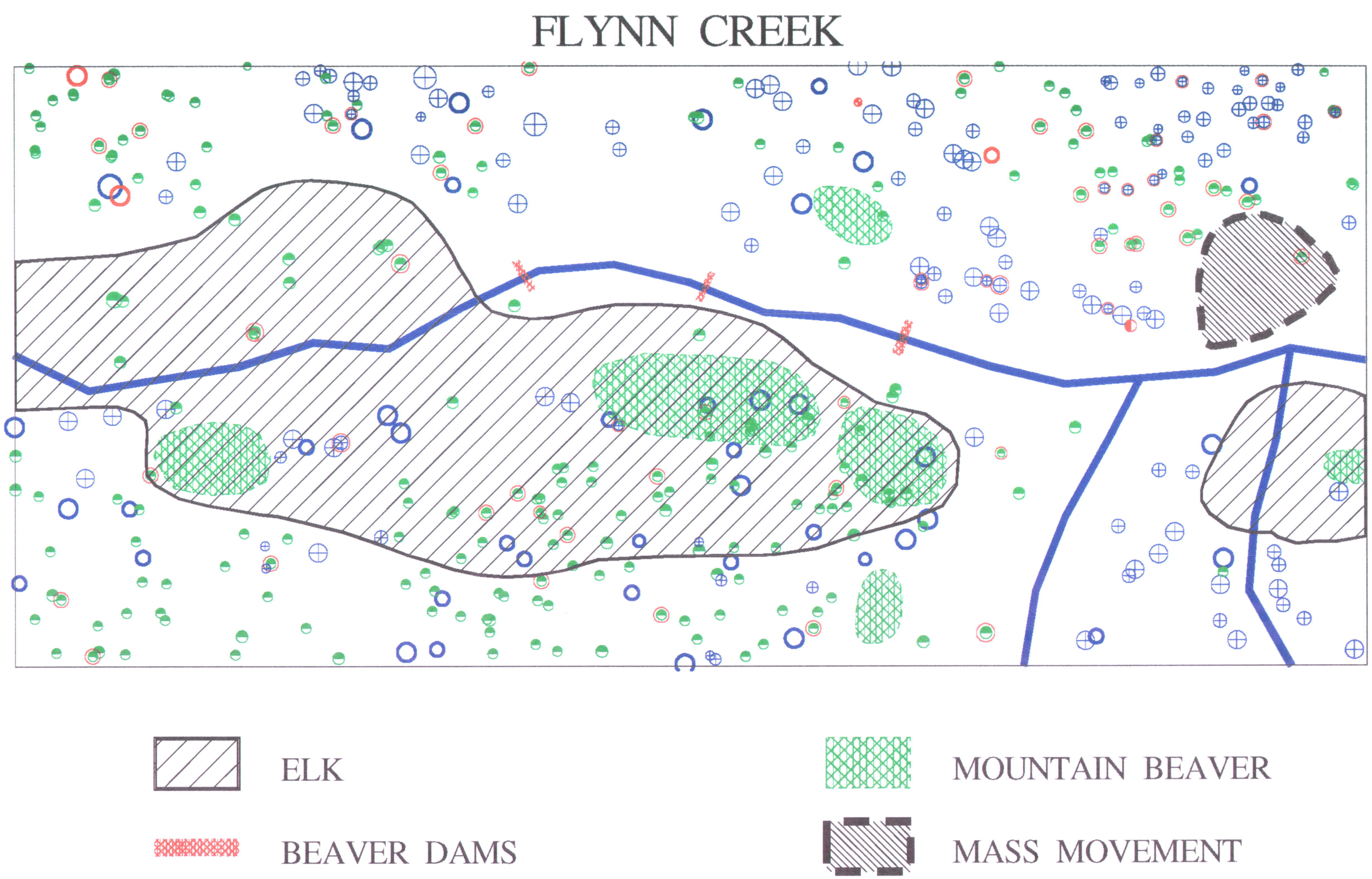


Figure 44. Field observations of recent non-fire disturbances in the Flynn Creek reference stand. Areas of mass movement and animal activity are indicated.



movement. Possible explanations for this observation include: 1) individuals were removed by past mass movement events (while either living or dead), 2) individuals were prevented from establishing by competition from deciduous trees or shrubs, and/or 3) these areas slid because the absence of coniferous species (for whatever reason) and their associated root systems prevented effective slope stabilization. Red alders established in the early-1960's may have done so following mass movement events and/or partial canopy breakup associated with the Columbus Day Storm of 1962 (Orr 1963). Relatively wide points on the valley floor at Trout Creek may represent geomorphic deposits associated with hillslope sliding and/or flooding. Evidence of recent mass movement is apparent in the southern end of the Flynn Creek reference stand (Figure 44).

Evidence of beaver activity was observed in and around both reference stands (Figures 43,44). Beaver activity in the Flynn Creek reference stand first was observed in the spring of 1993 when beavers migrated into the reference stand and began constructing small dams, primarily of salmonberry canes, across the main stream channel. Portions the valley floor shrub layer were killed in the past year by flooding associated with the beaver dams. Beavers do not appear to be active at present in the Trout Creek reference stand. However, beaver activity at Trout Creek in the past is suggested by the presence of characteristic chip marks found on a low Sitka spruce snag just south of the reference stand.

Evidence of mountain beaver and elk herbivory as well as burrowing by mountain beavers was observed in and around both reference stands (Figures 43,44). Herbivory on understory shrubs is characterized by chisel-shaped clipped stems to a height of at least 2m. Mountain beaver have been observed clipping vine-maple branches 1.8m above the ground elsewhere in western Oregon (personal observation). High levels of herbivory on salmonberry, vine-maple, and Vaccinium species were observed around mountain beaver burrows, suggesting that mountain beaver and/or elk may alter the local understory vegetation community. For example, herbivory close to the ground may favor the regeneration of tree species such as western hemlock and western red cedar on snags and elevated coarse woody debris.

Evidence of Historical Disturbance

Two historically recorded fire events may have impacted one or both of these riparian forests. The first is the series of fires of 1845-1849 which burned over an estimated 500,000 acres of forest between the Siuslaw and Siletz Rivers in 1845-1849, an area which contains the study sites (Morris 1934, Juday 1977). Fires also burned around Yaquina Bay and in the Alsea Basin in 1868 (Morris 1934, Juday 1977). Human caused ignitions, accidental or otherwise, may have been responsible for one or more of these fires. Fires related to landclearing activities have been documented (Morris 1934). Given that homesteading began in the area around the Flynn

Creek reference stand in the latter half of the 1800's, it is not impossible that pasturing and fire related to landclearing may have disturbed the study site at Flynn Creek (R. Pabst, personal comment). However, no cut stumps or old road beds were observed in either of the reference stands. The relatively steep topography and inaccessibility of the area around Trout Creek suggest that homesteading was unlikely to have had the same potential impact at Trout Creek, and no direct evidence of logging or roads was observed.

Dendrochronological Analysis

Age distributions for Douglas-fir, red alder, and western hemlock indicate that most trees (DBH > 10cm) established between 1850 and 1895 at Flynn Creek and Trout Creek (Figures 45,46). However, there small but possibly important differences between the two stands. Establishment dates calculated from tree cores indicate that no trees presently alive at the Flynn Creek site established before 1850 (Figure 45). In contrast, the three live old-growth Douglas-fir and the live old-growth western hemlock at Trout Creek all established prior to 1850 (Figure 46). The rotten center of the old-growth western hemlock made an accurate estimate of age impossible (it was only possible to date tree rings to 1869). However, tree size and canopy morphology suggest that this tree established well before 1850 (hence the question mark in Figure 46b).

Figure 45. Temporal establishment of tree species in the Flynn Creek reference stand. Arrows indicate historically documented fires in the area.

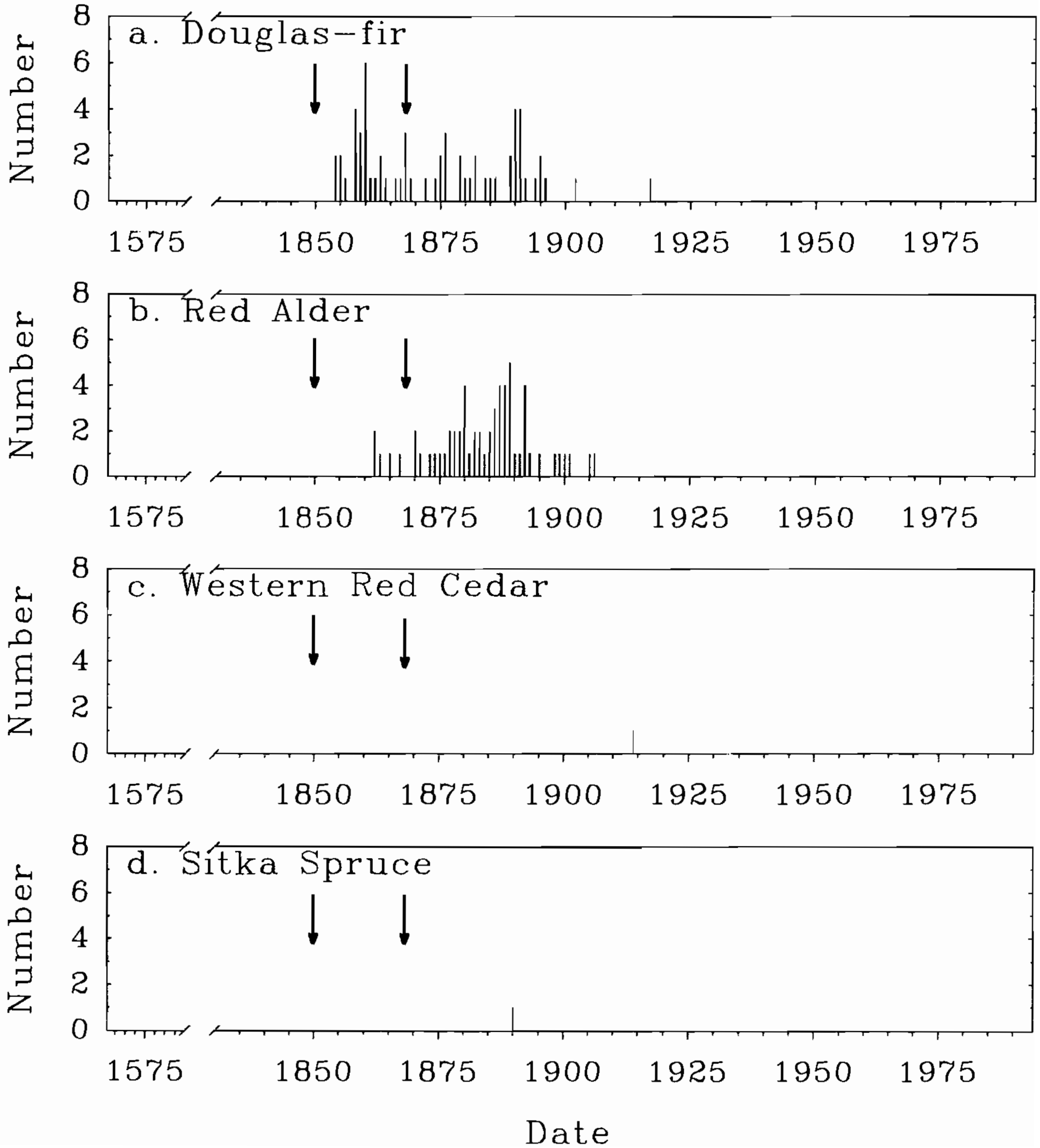
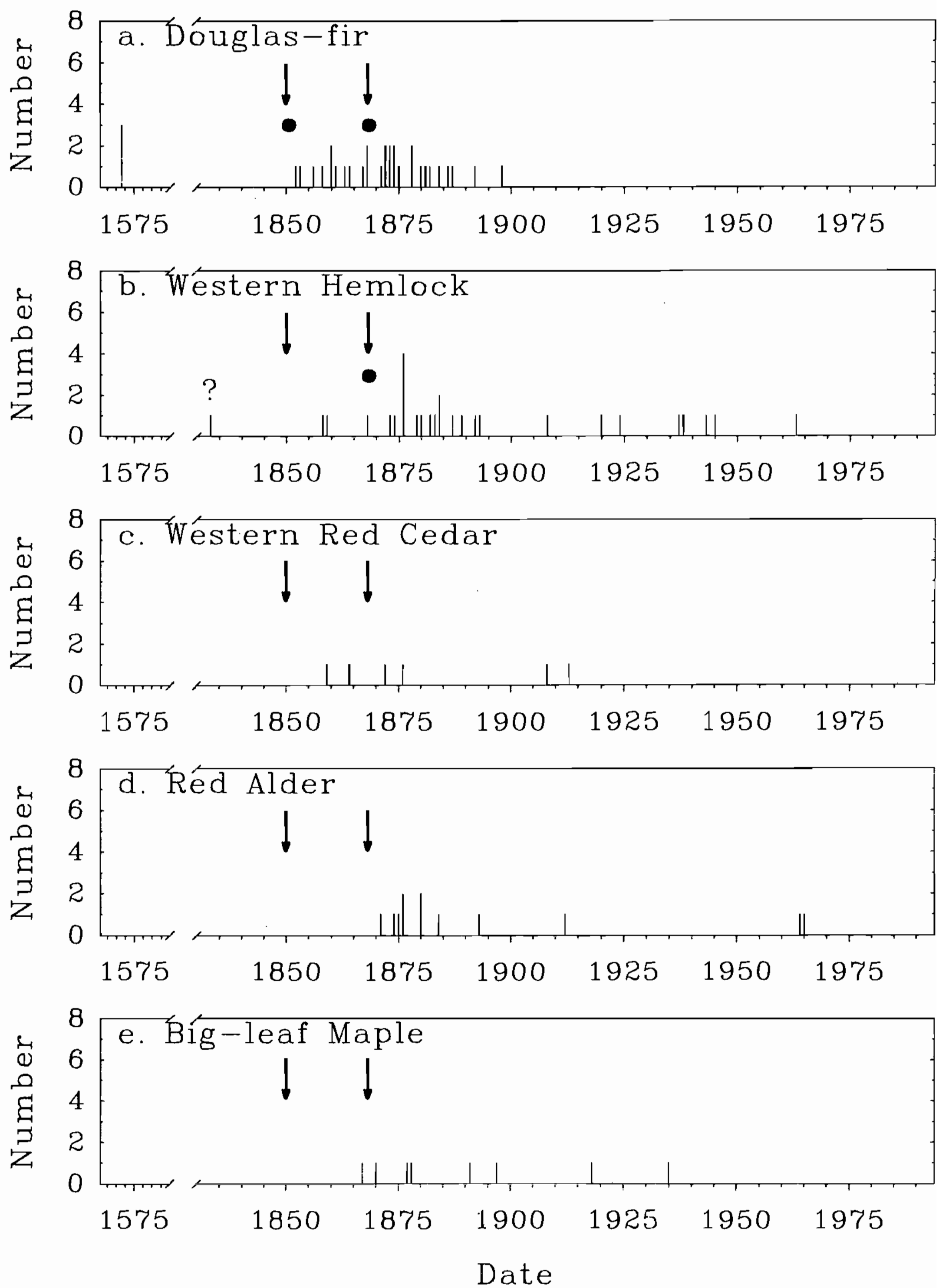


Figure 46. Temporal establishment of tree species in the Trout Creek reference stand. Arrows indicate historically documented fires in the area. Solid circles indicate fire scars in the stand.



Several lines of dendrochronological evidence suggest that a major disturbance occurred at each site in about 1850, possibly the fire(s) noted above which burned in this area in the late-1840's (Morris 1934, Juday 1977). Sudden changes, both increases and decreases, were observed in the radial growth patterns of old-growth trees at Trout Creek around 1850, suggesting response to disturbance or sudden environmental change (there are no live old-growth trees at Flynn Creek). Cores extracted from two of the live old-growth Douglas-fir (one of which was dated to at least 1568) indicate that a sudden depression of radial growth occurred in 1850-1. A fire scar was observed on the third live old-growth Douglas-fir but could be dated back only as far as 1852, suggesting that a fire may have occurred in or before that year (although the tree was estimated to be over 400 years old, the tree center was too rotten to date earlier than 1852). Cross-dating an old-growth Douglas-fir snag (death occurred in 1990) revealed that a sudden increase in radial growth occurred in 1852.

A wave of establishment began in about 1850 at both the Flynn Creek and Trout Creek sites, suggesting a sudden change in the amount of growing space available at that time. I hypothesize that the creation of space for establishment and growth was due to fire(s) and perhaps associated disturbances such as landslides. Both Douglas-fir and red alder established at Flynn Creek in the 1850's and early-1860's (Figure 45). The ages of red alder are a bit younger than those of Douglas-fir, suggesting that if red alder established in the early-1850's, 1) the oldest red alder have died, 2) subsequent fire(s) removed the first red alder that established, and/or 3) red alder established slightly after the Douglas-fir. Core dates from mature (current stand) Douglas-fir, western hemlock, western red cedar, and big-leaf maple indicate that individuals of each of these species established during this time period at Trout Creek (Figure 46).

The spatial patterns of establishment presently visible from the 1850 establishment wave appear different in the Flynn Creek and Trout Creek reference stands (Figures 47,48). The pattern at Flynn Creek appears more patchy than at Trout Creek. The differences between sites may due to differences in initial disturbance(s), initial establishment, subsequent disturbance(s), subsequent establishment. As noted above, there is considerable evidence that localized, non-fire disturbances (e.g., wind, geomorphic activity, pathogens, and animals) other than fire have occurred in these stands. It is likely that they have influenced the development these forests at points in the past without leaving definitive evidence of their having occurred.

Tree establishment in the 1850's and early-1860's occurred on both sides of the main stream channel at each study site. Douglas-fir which established at this time and which have survived to the present are found at all distances from the main stream channel at both Flynn Creek and Trout

Figure 47. Spatial establishment of tree species in the Flynn Creek reference stand. See Figure 6 for symbol key.

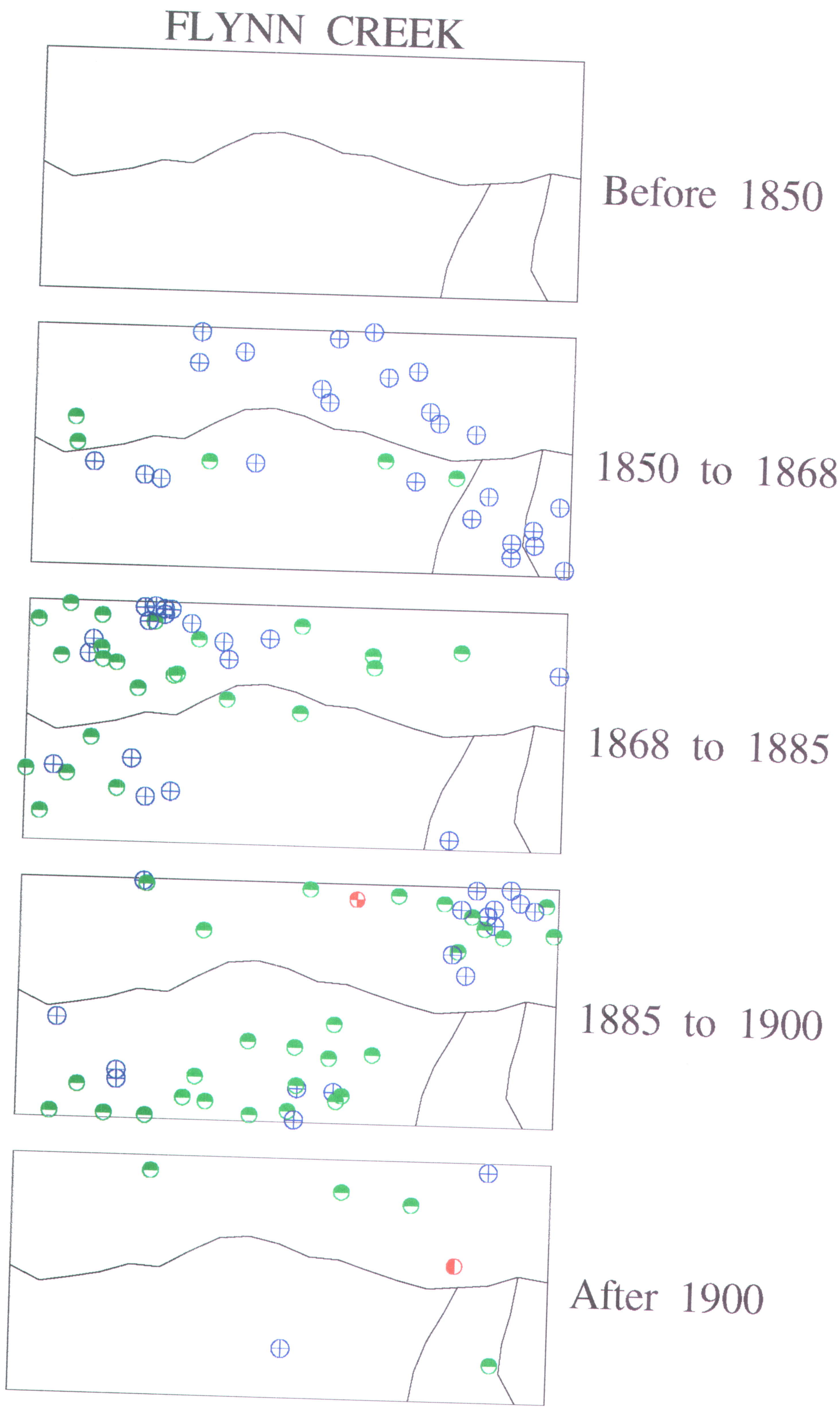
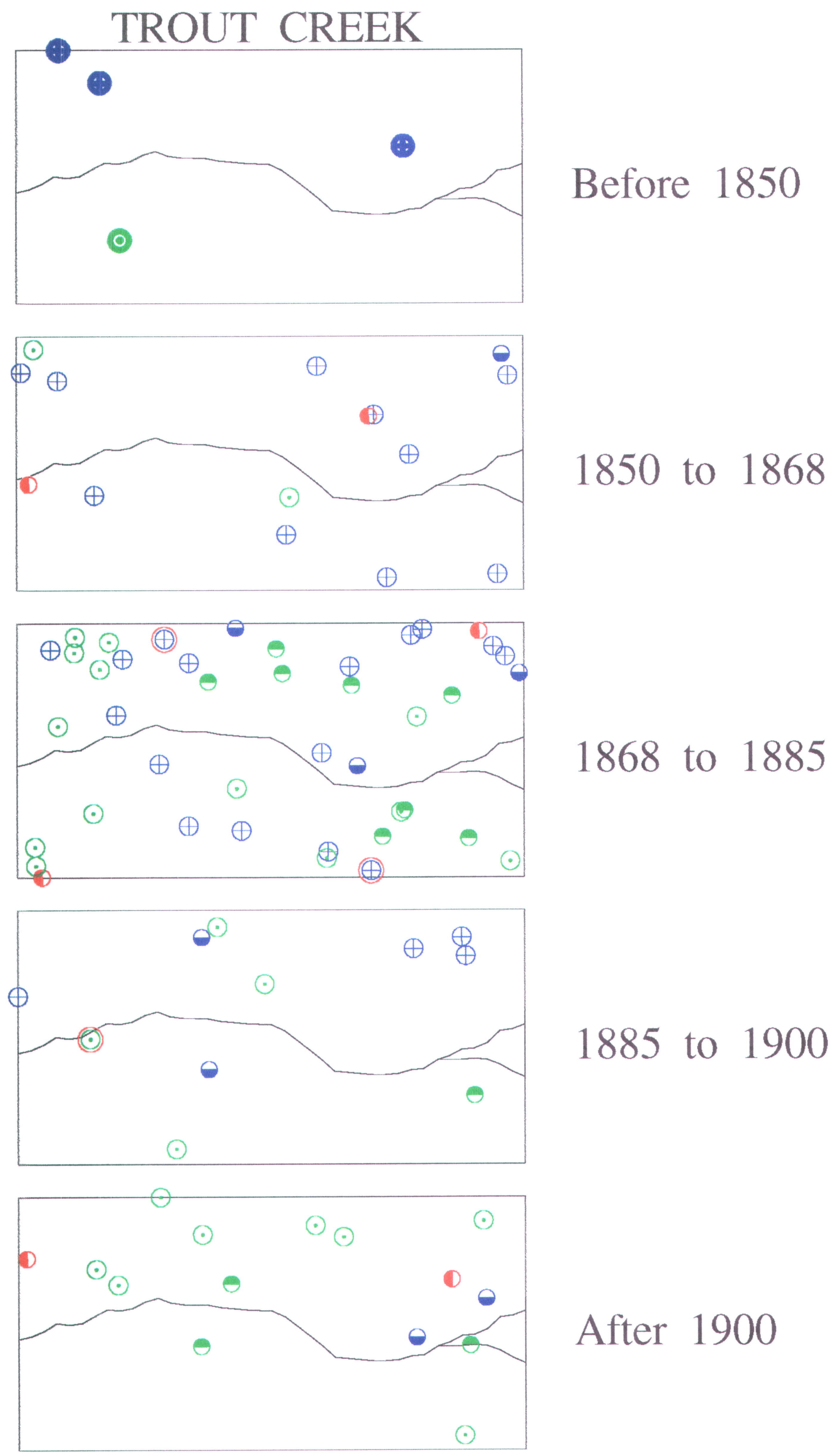


Figure 48. Spatial establishment of tree species in the Trout Creek reference stand. See Figure 6 for symbol key.



Creek (Figures 47,48). However, surviving red alder which established at Flynn Creek during this period are found on or near the valley floor, but not upslope.

A second period of relatively high establishment may have begun in the late-1860's at both Flynn Creek and Trout Creek (Figures 45,46). Relatively large numbers of Douglas-fir and red alder established at Flynn Creek during this period, as did Douglas-fir, western hemlock, western red cedar, red alder, and big-leaf maple at Trout Creek (Figures 45,46). As was the case in the 1850's and early-1860's, tree establishment in the late-1860's and early-1870's occurred on both sides of the main stream channel at each study site (Figures 47,48). The current spatial patterns of establishment dating from this period also appear more patchy at Flynn Creek than at Trout Creek. Douglas-fir and red alder which established during this period at Flynn Creek are concentrated in the north half of the reference stand. Although fine-scale aggregations of trees are apparent, establishment at Trout Creek occurred over the extent of the reference stand.

Without dendrochronological records from living old-growth trees, it is difficult to be certain if fire was the cause of this second establishment wave at Flynn Creek. The disturbance(s) in the mid-1800's may have killed all trees established prior to 1850 at Flynn Creek. For example, the burned old-growth coniferous snags in the northern half of the stand may have been the result of earlier fire(s). Other factors such as herbivory (e.g., elk, beaver, cattle) may have prevented regeneration from occurring locally at Flynn Creek for a period of almost 20 years following fire(s) in the mid-1800's. If fire did occur at Flynn Creek in the late-1860's, it may have been associated with the historically recorded fire(s) which burned in the Alsea Basin in 1868 (Morris 1934, Juday 1977).

Dendrochronological evidence strongly suggests, however, that at least one fire occurred at Trout Creek in the late-1860's. The old-growth western hemlock at Trout Creek has a fire scar which dated to 1868. Two of the old-growth Douglas-fir trees and the snag cored above exhibited sudden changes in radial growth in the period 1868-1870. One of these old-growth Douglas-fir has a fire scar which dated to this time. Several mature trees also experienced dramatic changes in radial growth during the late-1860's (both increases and decreases were observed). For example, the radial growth of a Douglas-fir which established in 1852 decreased suddenly in 1869. Assuming that fire(s) did occur at Trout Creek in the late-1860's, it (they) may have been associated with the historically recorded and dendrochronologically documented Yaquina Bay fire which burned in this section of the Coast Range in 1868 (Morris 1934, Juday 1977).

A third period of frequent tree establishment at Flynn Creek began in the mid-1880's, and presently occurs as a largely monospecific patch of red alders in the western half of the stand and a mixed patch of Douglas-firs and red alders in the southeastern corner of the stand (Figures 45,47). As was the case in the earlier two establishment events, tree establishment in the mid-1880's at Flynn Creek occurred on both sides of the main stream channel. Again, the spatial pattern at Flynn Creek is relatively patchy. As in the case of the second period of establishment in the late-1860's and early-1870's, it is uncertain whether fire played a role in this third establishment period. It is interesting to note, however, that the highest density of old-growth coniferous snags at Flynn Creek spatially overlap with the largely monospecific patch of red alders in the western half of the reference stand (Figure 4; see also Figure 27 for the interspecific point-pattern analysis of the spatial distribution of red alder relative to old-growth coniferous snags in the Flynn Creek reference stand). Although almost all of these snags are visibly burned, these are the least decayed old-growth coniferous snags in the stand. This may indicate that a fire occurred in this part of the stand as recently as the mid-1880's and that the snags have been decaying for a relatively short period of time. An alternative scenario is that these snags were from trees burned by one or more earlier fires but not immediately killed.

There does not appear to have been a well-defined third wave of establishment in the mid-1880's at Trout Creek (Figures 46,48). Instead, tree establishment appears to have occurred sporadically since the late-1800's, with establishment of western hemlock occurring most frequently and continuously of all tree species. With the exception of Douglas-fir, one or more individuals of each of the tree species found at Trout Creek have established after 1900 (Figure 46). As noted above, scattered clumps of young red alder dated to the early-1960's may have established following mass movement events as well as partial overstory breakup following the Columbus Day Storm of 1962 (Figures 43,48).

In contrast to Trout Creek, tree establishment after 1900 at Flynn Creek appears only to have occurred prior to 1920 (Figure 45).

DISCUSSION

Development of the Deciduous-Dominated Forest at Flynn Creek

At least three major periods of establishment appear to have occurred since the mid-1800's at Flynn Creek (beginning in the early-1850's, late-1860's, and mid-1880's). Other periods of establishment may have occurred but may have been erased by subsequent disturbance. These three waves of establishment are most apparent in the temporal and spatial patterns of Douglas-fir and red alder establishment. It is interesting to note that these three establishment periods occurred at 15-20 intervals, with Douglas-fir and red alder establishing on both sides of the main stream channel each time. All three establishment periods appear to span several years.

It is likely that the first wave of establishment at Flynn Creek was initiated by fire(s) in about 1850, possibly in the series of historically documented fires which burned in this part of the Oregon Coast Range in 1845-1849 (Morris 1934, Juday 1977). It is possible that the second establishment wave at Flynn Creek was initiated by historically documented fires in the late-1860's. Alternatively, factors such as herbivory and seed source limitations may have delayed successful establishment for years following an initial major disturbance in the early-1850's.

The spatially aggregated and largely monospecific patches of Douglas-fir and red alder at Flynn Creek may have resulted from several mechanisms. Differences in microsite conditions, seed availability and dispersal, density, competition, and/or other factors may have favored the local establishment and dominance of one species over the other. A higher juvenile growth rate generally enables red alder to outcompete Douglas-fir on mesic sites (Newton et al. 1968). The observation that Douglas-fir presently overtopped by red alder have survived since at least the late-1800's suggests that the initial density of red alder establishment may have been relatively low at Flynn Creek (M. Newton, personal comment). This suggests that the initial source of red alder seed at Flynn Creek may have been limited (D. Hibbs, personal comment). Most dominant red alder trees reach sexual maturity by age 6-8, while the minimum cone-bearing age of Douglas-fir is about 20 (Harrington 1990, Hermann and Lavender 1990). Given these species' life history differences, the seed source availability of red alder relative to Douglas-fir may have actually increased over time with each successive wave of establishment at Flynn Creek.

Competition from red alder (and possibly shrubs) may have excluded Douglas-fir from the more mesic valley floor sites. This interpretation is supported by the presence of large-diameter pieces of red alder coarse woody debris from trees which grew on the valley floor and also by the unusually clear (no evidence of branch stubs) boles of

Douglas-fir growing just upslope of the slopebreak, suggesting that past vegetative competition inhibited lateral crown development. Periodic flooding by beavers and/or severe rainstorms at one or more points in the past may have also favored the survival of red alder over Douglas-fir on the valley floor at Flynn Creek (Minore 1968, 1970).

Both Douglas-fir and red alder established upslope at Flynn Creek. This spatial pattern has been observed elsewhere in the Coast Range (Andrus and Froehlich 1987). In addition to factors such as seed availability and herbivory, microsite differences may influence where different species establish. For example, the establishment of red alder is greatly favored by exposed mineral soil and adequate soil moisture (Newton et al. 1968, Haeussler et al. in preparation). Sufficient mineral soil may have been exposed by disturbances such as fire and/or mass movement to permit upslope establishment of red alder on favorable microsites. In the southeast corner of the Flynn Creek reference stand locally higher soil-moisture levels on the more northern (moister) side of the hillslope also may have enabled a small patch of red alder to outcompete Douglas-fir established at the same time (Figures 4,47). Douglas-fir of the same age are presently found on the more southern (drier) exposure. Although evidence of recent mass movement is apparent in the southern end of the Flynn Creek reference stand, the establishment of tree species on the hillslopes does not appear to have been associated with mass movement events, as evidenced by topographic profiles and surface topography.

The significant spatial association of red alder established in the mid-1880's and old-growth coniferous snags may reflect a facilitation mechanism or simply a correlation with some factor affecting establishment other than the presence of snags. Shade from the locally high density of old-growth coniferous snags (40 snags/ha) might have reduced surface temperature extremes by providing shade and/or lowering the probability of frost damage to young red alder (D. Minore, personal comment). Compared to Douglas-fir, red alder seedlings are relatively sensitive to temperature extremes and frost (Haeussler et al. in preparation). Alternatively, this pattern may reflect the availability of favorable seed beds and/or seed sources in the past.

Field observations suggest that density-dependent mortality within the largely monospecific patches of Douglas-fir and red alder (i.e., self-thinning) is responsible for the observed spatial patterns of current stand coniferous and deciduous snags. This interpretation is supported by point-pattern analyses that indicate that mature coniferous snags (all Douglas-fir) are spatially aggregated around mature Douglas-fir trees and that deciduous snags (all red alder) are spatially aggregated around red alder trees, suggesting mortality associated with crowding (Figures 35,38). Patterns of mortality characteristic of the root rot Phellinus wierii were not observed at Flynn Creek.

Virtually all of the trees growing in the deciduous-dominated forest at Flynn Creek are considered shade-intolerant (Harrington 1990, Hermann and Lavender 1990). I hypothesize that establishment of shade-tolerant species such as western hemlock did not occur because all local seed sources were eliminated by fire(s) and/or other non-fire disturbances. Alternatively, local seed sources of western hemlock may not have been present in the stand and local landscape in the mid-1800's. Although old-growth snags of western red cedar have been found, the only western red cedar tree located in the reference stand established after 1850. If regeneration of shade-tolerant species occurred, new recruits may have been almost entirely eliminated by herbivory and/or other subsequent disturbances.

The absence of shade-tolerant regeneration raises the interesting question of how stand development will proceed at Flynn Creek. Red alder is a relatively short-lived species, attaining maximum ages of about 150 years. Many authors have speculated that salmonberry and other shrubs will replace red alder following breakup of the deciduous overstory (Newton et al. 1968, Henderson 1970, Hemstrom and Logan 1986, Carlton 1988). This appears to have happened on the valley floor at Flynn Creek.

Rhizomatous shrub species such as salmonberry appear able to occupy favorable sites for long periods through the annual production of new stems, often leading to an uneven-aged distribution of aerial stems (Balogh and Grigal 1987, Kurmis and Sucoff 1989, Tappeiner and Alaback 1989, Tappeiner et al. 1991, Huffman et al. 1994). It is unlikely, however, that the "brushfield" at Flynn Creek will persist for centuries because disturbances such as flooding and local accumulations of large, dead Douglas-fir may create sites that are available for tree establishment. Since the spring of 1993, flooding caused by beaver activity within the reference stand has led to local mortality of shrubs on the valley floor.

The development of upslope patches of red alder is uncertain, particularly on the west side of the reference stand. This patch established approximately 110 years ago and the overstory is beginning to break up, suggesting that fine-scale disturbances such as gap formation may play an important role in forest development at Flynn Creek. The understory consists primarily of salmonberry and vine-maple. In the absence of other factors, these species might completely replace the red alder. However, several Douglas-fir which established with or after the red alder, but which have been largely overtopped by them, are responding to the breakup of the red alder overstory with new leader growth. These Douglas-fir may release to form an understocked patch of conifers. Further, browsing by elk and mountain beaver has created small areas (>20m^2) free of above-ground stems of shrubs. Shade-tolerant species may be able to successfully establish and grow in these openings (M. Newton, personal comment). Two-year old seedlings of western hemlock have been observed growing on red alder logs within the Flynn Creek reference stand, suggesting that at least some western hemlock seed is available. A few, isolated intermediate and suppressed western hemlock trees (< 0.25 stems/ha) have been located outside of the reference stand, but no codominant or dominant individuals have been found in the surrounding area. The single western red cedar (54.0cm DBH) and Sitka spruce (24.1cm DBH) found within the reference stand represent potential future seed sources.

Development of the Coniferous-Dominated Forest at Trout Creek

At least two periods of establishment may have occurred since the mid-1800's at Trout Creek. It is likely that the first establishment wave was initiated by fire(s) in about 1850, possibly in the same fire(s) which burned at Flynn Creek at this time. There is good evidence that the second wave of establishment at Trout Creek was initiated by fire(s) in the late-1860's, probably in 1868. This latter fire event may have been associated with the Yaquina Bay fire which burned in this section of the Coast Range in 1868 (Morris 1934, Juday 1977).

Based on the presence of surviving, live, fire-scarred, old-growth conifers (Douglas-fir and a single western hemlock) at Trout Creek, it appears that the fires at Trout Creek were, at least locally, less intense than at Flynn Creek (where no live old-growth trees are present). This difference in past disturbances at the two sites may have had profound consequences in terms of stand development because it may have meant that a local source of western hemlock and Douglas-fir seed always was present at Trout Creek. At Flynn Creek, no local seed source has survived to the present.

The "inverse-J" diameter distribution of the conifer-dominated forest at Trout Creek is largely a reflection of the large number of western hemlock present in the small to medium diameter classes. The stand cross-sections and summaries of live tree density by species and canopy position indicate that, relative to Flynn Creek, the high degree of vertical stand structure at Trout Creek is due to the presence of shade-tolerant western hemlock in all canopy strata.

Dendrochronological evidence indicates that Douglas-fir, western hemlock, and western red cedar established at Trout Creek following both the initial fire in the mid-1800's and the second fire in the late-1860's. Although point-pattern analysis suggests that the overall spatial pattern of large, mature western hemlock is random with respect to large, mature Douglas-fir, there is a tendency toward fine-scale dispersion and coarse-scale aggregation. This suggests that these species established and developed together as a mixed-species stand.

Although there is not a recognizable third period of establishment at Trout Creek, the apparently continuous recruitment of western hemlock since the late-1800's as well as the absence of historical and local evidence of fire suggests that the establishment of western hemlock was not dependent on large-scale scale disturbances at this site. Western hemlock may establish in response to the formation of canopy gaps; while western hemlock regeneration can occur in the absence of canopy gaps, it is unlikely that even shade-tolerant species can grow into the overstory without encountering one or more canopy gaps (Stewart 1986, Spies and Franklin 1989, Poage and Peart 1993). Alternatively, the continuous "recruitment" of western hemlock at Trout Creek may actually represent the response of long-suppressed individuals to the formation of canopy gaps.

Biologically, it is possible that individuals might have established immediately after one of the two fires at Trout Creek, only to remain suppressed for decades thereafter (Packee 1990). This raises the possibility that establishment dates determined from tree cores may underestimate the actual age of shade-tolerant tree species such as western hemlock. (Completely accurate cross-dating of such species can only be accomplished by removing of cross-sections from the bole at ground level, a dendrochronological method not permitted in these permanent reference stands.) Regardless of whether or not the cored western hemlock originated immediately following one of the fires, the observation that western hemlock is found at all levels in the canopy may suggest that canopy gaps and events that create available seed beds play an important role in forest development at Trout Creek. Until a major disturbance impacts the forest, the process of stand development appears likely to result in an ever-increasing of proportion of shade-tolerant individuals at Trout Creek.

The establishment of western hemlock following the two fires was strongly aggregated around old-growth coniferous snags at Trout Creek (Figure 31). Although this pattern only indicates spatial correlation, it is possible that this pattern is the result of interactions between the disturbance and the prior stand which created microsite and/or other conditions that favored the post-fire establishment of western hemlock near the old-growth coniferous snags. For example, rhizomatous shrubs established prior to a disturbance may have been able to survive the disturbance and then invade the open growing space between killed or dying trees more rapidly than seedlings. Shrub competition could have prevented western hemlock from establishing at a distance from the old-growth coniferous snags (shrub competition following disturbance may also explain the pattern of red alder and old-growth coniferous snags at Flynn Creek). Shade from snags and woody debris associated with snags, aspect and slope effects, and seed source availability also may have influenced the distribution of western hemlock.

Field observations and point-pattern analysis indicate that mature coniferous snags are aggregated around mature Douglas-fir trees, suggesting that density-dependent mortality is largely responsible for the observed spatial pattern of mature coniferous snags. However, as noted above, the spatial pattern of mortality in the northwest corner of the Trout Creek stand is characteristic of that associated with the root rot Phellinus wierii (i.e., a patch of dead overstory trees). Although western hemlock is susceptible to attack by P. wierii, most of the mortality has occurred among overstory Douglas-fir. This may suggest that Douglas-fir is more susceptible to attack by P. wierii than is western hemlock (see also comments by Packee (1990)). Understory western hemlock have, at least temporarily, been released as a result of this disease-related overstory mortality, suggesting that P. wierii may play an important role in forest development at Trout Creek. Overall, the spatial pattern of understory conifer regeneration is strongly associated with the patterns of mortality of current stand conifers at Trout Creek.

No red alder or big-leaf maple were found which established following the initial fire in the mid-1800's at Trout Creek. However, small patches of red alder and big-leaf maple did establish at various times following the fire in the late-1860's, apparently as a result of episodic disturbances from mass movement and wind (e.g., red alders that established following the Columbus Day Storm of 1962). This suggests that these non-fire disturbances may play an important role in forest development at Trout Creek.

Despite the presence of red alder at the coniferous-dominated Trout Creek site, red alder did not established to the degree observed at the deciduous-dominated Flynn Creek.

In contrast to the spatial pattern observed at Flynn Creek, red alder at Trout Creek are randomly distributed relative to old-growth coniferous snags. This may suggest that at least some of the factors responsible for the establishment of red alder differed between the two sites. At Trout Creek, less intense burns may have failed to expose sufficient mineral soil for widespread upslope establishment of red alder. Relative to Flynn Creek, the narrower valley floor at Trout Creek also might have reduced the number of optimal sites for the establishment of red alder, a pattern observed elsewhere in the Coast Range (Minore and Weatherly 1994). The local seed source of red alder at Trout Creek may have always been limited relative to Flynn Creek, thereby decreasing the odds that red alder would establish as heavily at Trout Creek as it did at Flynn Creek.

Ecological Implications

Three ecological implications of this study are the role of disturbance in forest development, seed source availability, and the relationship between pattern and process. The role of disturbance in forest development is a fundamental ecological question (Bormann and Likens 1979, Oliver and Larson 1990, Pickett et al. 1994). Within the overall framework of vegetation dynamics, changes in site availability are influenced by the size, severity, timing, and dispersion of disturbances (Oliver and Larson 1990, Pickett et al. 1994). Disturbances such as fire, wind, mass movement, pathogens, and animal activity have strongly influenced the structure and development of the forests at Flynn Creek and Trout Creek. These results support the conclusions of other authors that disturbances play a key role in forest development (Watt 1947, Oliver 1981, Hemstrom and Franklin 1982, Remillard et al. 1987, Christensen 1988, Lorimer 1989, Spies and Franklin 1989, Morrison and Swanson 1990, Oliver and Larson 1990, Poage and Peart 1993).

Differences in seed source availability, possibly as a result of differences in disturbances, also appear to have helped to propel these stream-side forests along very different developmental pathways. At Trout Creek, for example, the fire(s) may have been of a low enough intensity that at least one western hemlock was able to survive to the present. The presence of a local seed source of a shade-tolerant tree species may have facilitated the development of the multi-layered, coniferous-dominated forest at Trout Creek. Conversely, if western hemlock existed at Flynn Creek in the mid-1800's, successive disturbances may have eliminated all local seed sources of this shade-tolerant species. Further, dispersion of western hemlock into an area may be a slow process once a local source of western hemlock seed has been eliminated. Although studies of the dispersion of western hemlock across landscapes have not been published, modeling work on the seed dispersal of the related eastern hemlock (*Tsuga canadensis*) suggests that the spread of hemlock over large distances may be a relatively slow process (Pacala and Hurtt 1993).

Similarly, spatial and temporal differences in the availability of red alder seed may have influenced forest development at both sites. In contrast to western hemlock, successive disturbances, a high juvenile growth rate, and a low age of sexual maturity may have lead to an increase over time in the relative seed availability of red alder at Flynn Creek.

The quantification of the patterns of distributions of plants and understanding the causes of the patterns have been recent focuses of ecological research (Grieg-Smith 1983). The analysis of spatial point-patterns is useful as a tool to quantify and highlight patterns that are not immediately apparent from casual observation. An example of such a pattern is the aggregation of red alder trees around old-growth coniferous snags in the Flynn Creek reference stand.

The analytical methods used in this study enable the statistical significance of patterns to be assessed. Pattern analysis is also a tool by which to generate testable hypotheses about vegetation processes. It is difficult, however, to infer the processes responsible for the observed patterns from the patterns themselves (Cale et al. 1989). This conclusion is supported by the results of this study.

Management Implications

The results of this study indicate that disturbance history, as well as hypothesized differences in seed source availability, have played a role in the development of structurally and compositionally different forests at Flynn Creek and Trout Creek. Even similar disturbances may have unique developmental consequences at different sites. For example, the presence of a shade-tolerant species may have enabled a multi-storied forest to develop at Trout Creek through the process of fine-scale canopy gap formation. At Flynn Creek, where western hemlock is absent, the formation of fine-scale canopy gaps may simply result in increased growth of shrubs in the understory. This suggests that managers interested in promoting different forest structures and compositions must craft their prescriptions on a site-by-site basis, taking into account all processes operating in vegetation dynamics. The patchy distributions of trees and snags, the cumulative effects of successive disturbances (fire and non-fire), and the implications of seed source availability are all examples of factors that must be considered when establishing management objectives.

Recent federal land management planning efforts have called for the establishment of a riparian reserve network, within which management activities are severely curtailed (FEMAT 1993, ROD/SOG 1994). Concurrently, there is a great deal of interest in promoting the development of late-successional, multi-storied riparian forests dominated by coniferous species (similar, perhaps, to Trout Creek). However, the developmental history of Trout Creek suggests that it may be very difficult to develop coniferous-dominated, multi-storied forests in riparian areas that are structurally and compositionally similar to Flynn Creek. Without active management, the development of coniferous-dominated forests from deciduous-dominated forests may take considerably longer than if silvicultural practices such as the planting and release of shade-tolerant species are employed in riparian areas. Further, without active management, it seems unlikely that a continuous supply of coniferous coarse woody debris to streams will be obtained from riparian forests such as Flynn Creek in the near future.

The spatial and temporal patterns of establishment at both Flynn Creek and Trout Creek suggest that, at these sites, disturbances such as fire may be able to spread across the valley floor from one hillslope to the other. The complete absence of old-growth trees at Flynn Creek may indicate this. Similarly, although fire also occurred at the Trout Creek site, old-growth trees are found growing on both sides of Trout Creek and at a range of distances from the stream channel. These observations may be of interest to managers interested in promoting riparian vegetation as firebreaks.

Future Research

There is a great need to better understand the role of initial conditions and floristic composition in forest development. If the individuals that initially establish following disturbances can exclude other individuals for long periods, the potential future development of a forest may be largely determined by the patterns of establishment during the first few years following the release of growing space. Stand development must be investigated at the scale of the individual, beginning with the establishment of individuals and following their development over time.

How structurally and compositionally different riparian stands respond to different disturbances at different points in their development needs to be investigated in both managed and unmanaged settings. This is particularly true with respect to the role of "understory" vegetation in forest development. How likely is it, for example, that tree species can be excluded from an area for centuries by shrub species such as salmonberry? Can localized non-fire disturbances such as animal browsing create gaps of sufficient size in a shrub layer to permit the establishment of tree species?

New methods of reconstructing past disturbances must be developed. For example, how resistant is a partially burned snag to decay and/or subsequent fire? Based on charcoal, is it possible to identify species which otherwise decay relatively quickly when unburned (i.e., western hemlock)?

This might be used to determine whether western hemlock existed at Flynn Creek prior to the mid-1800's.

Finally, what is the role of single, isolated remnant trees in forest development? Are, for example, all the mature western hemlock in the Trout Creek reference stand the progeny of the single old-growth western hemlock which survived the fires at Trout Creek? More generally, how high is the intraspecific genetic diversity of the forests in the Coast Range? What does this suggest about the susceptibility of such a population to introduced pathogens?

CONCLUSION

As expected, the forest structure and composition of the deciduous-dominated riparian forest at Flynn Creek are very different than of the coniferous-dominated riparian forest at Trout Creek. For example, the coniferous-dominated forest had many more standing dead trees and a higher size diversity of live trees than did the deciduous-dominated forest. This study is the first to quantify such basic information for riparian forests in the Oregon Coast Range. This information also may help to set management targets by providing models of unmanaged riparian forests.

Many intra- and interspecific non-random patterns of trees and snags were observed in the Flynn Creek and Trout Creek reference stands. Aggregated and dispersed patterns were observed at multiple scales. For example, red alder tend to be aggregated around old-growth coniferous snags at Flynn Creek. Although it is not possible to infer directly the process(es) responsible for observed patterns, the value of point-pattern analysis is as a tool used to detect and describe intra- and interspecific patterns that are not immediately apparent from casual observation. Further, point-pattern analysis may be used to generate testable hypotheses about vegetation processes.

The disturbance and establishment history of the deciduous-dominated riparian forest at Flynn Creek is very different than that of the coniferous-dominated riparian forest at Trout Creek. Neither forest resulted from a single, stand-replacing fire. Instead, both sites were at least partially burned about 145 years ago, possibly in the same fire(s) which spread across an estimated 500,000 acres between the Siuslaw and Siletz Rivers in the mid-1800's (Morris 1934). There is good evidence to suggest that a second fire occurred at Trout Creek. One or two other fires may have occurred at Flynn Creek, although the evidence is less convincing than at Trout Creek. Evidence of wind, herbivory, flooding, pathogens, mass movement events, and non-stand replacing fires were observed at one or both of the sites. Locally, the influence of any one of these "minor" disturbances may have had as great an influence on forest development as "major" disturbances.

Differences in past disturbances and stand conditions appear to have favored the establishment of different species at these sites, most notably red alder at Flynn Creek and western hemlock and western red cedar at Trout Creek. Seed source availability also may have played a role in forest development. For example, the seed source availability of red alder relative to Douglas-fir may have increased with successive disturbance events at Flynn Creek. I hypothesize further that a local source of western hemlock seed has been a key factor in the development of the conifer-dominated, stream-side forest at Trout Creek.

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APPENDICES

Appendix 1.

Table A.1.1. Stem density and basal area of snags by decay class in the Flynn Creek and Trout Creek reference stands. Decay classes are taken from Maser et al. (1988).

	Stem Density (stems/ha)		**Basal Area** (m^2/ha)	
Coniferous Snags	FLYNN	TROUT	FLYNN	TROUT
Decay Class				
1	3.6	15.0	0.47	5.96
2	2.7	16.0	0.14	6.12
3	4.9	12.5	3.58	1.61
4	11.1	17.5	10.53	15.82
5	4.4	7.0	2.25	4.19
subtotal	**26.7**	**68.0**	**16.97**	**33.70**
Deciduous Snags	FLYNN	TROUT	FLYNN	TROUT
Decay Class				
1	10.2	4.0	1.00	0.21
2	2.2	0.0	0.17	0.00
3	4.9	0.5	0.71	0.03
4	0.4	0.0	0.02	0.00
5	0.0	0.0	0.00	0.00
subtotal	**17.7**	**4.5**	**1.90**	**0.24**
STAND TOTAL	**44.44**	**72.5**	**18.87**	**33.94**

Appendix 2.

Table A.2.1. Mean diameters at breast height of trees and snags in the Flynn Creek and Trout Creek reference stands.

	Diameter ± S.E. (N) (cm)	
	FLYNN CREEK	TROUT CREEK
Coniferous Trees		
Douglas-fir	84.6 ± 3.6 (116)	89.0 ± 3.4 (96)
Sitka Spruce	24.1 ± 0.0 (1)	(0)
Western Hemlock	(0)	28.7 ± 1.7 (204)
Western Red cedar	54.0 ± 0.0 (1)	39.9 ± 6.8 (16)
Deciduous Trees		
Big-leaf Maple	(0)	36.6 ± 4.0 (33)
Red Alder	43.4 ± 0.8 (181)	32.9 ± 3.3 (32)
Snags		
Coniferous	80.3 ± 5.3 (60)	66.9 ± 3.7 (136)
Deciduous	34.1 ± 2.3 (40)	21.3 ± 5.4 (9)

Appendix 3.

Table A.3.1. Mean diameters at breast height of snags by decay class in the Flynn Creek and Trout Creek reference stands. Decay classes are taken from Maser _et_ _al_. (1988).

	Diameter ± S.E. (N) (cm)	
	FLYNN CREEK	TROUT CREEK
Coniferous Snags		
1	33.1 ± 9.1 (8)	53.7 ± 8.7 (30)
2	24.7 ± 3.1 (6)	56.1 ± 7.5 (32)
3	84.9 ± 14.6 (11)	36.9 ± 3.4 (25)
4	108.1 ± 4.0 (25)	103.0 ± 5.1 (35)
5	77.0 ± 7.6 (10)	83.4 ± 7.1 (14)
Deciduous Snags		
1	32.5 ± 2.9 (23)	20.3 ± 6.0 (8)
2	29.6 ± 5.0 (5)	(0)
3	40.1 ± 4.9 (11)	29.5 ± 0.0 (1)
4	26.2 ± 0.0 (1)	(0)
5	(0)	(0)