

Spatial and Temporal Dynamics of Fire and Vegetation Change in Thunder Creek
Watershed, North Cascades National Park, Washington

Susan Joy Prichard

A dissertation submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

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2003

Program Authorized to Offer Degree: College of Forest Resources

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Abstract

Spatial and Temporal Dynamics of Fire and Vegetation Change in Thunder Creek Watershed, North Cascades National Park, Washington

Susan Joy Prichard

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Professor David L. Peterson

College of Forest Resources

Little is known about the history of fire and vegetation in the North Cascade Range. I conducted two studies in the lower Thunder Creek watershed, North Cascades National Park to evaluate past fire and forest vegetation dynamics. The first study evaluated forest development following a series of fires c. 150 years ago. Tree species, age and size data were sampled along altitudinal transects. Tree species distributions and relationships with environmental factors were analyzed using multivariate and regression techniques, and forest development was evaluated from tree age and size frequency distributions. The 7.5 km² study area supports an unusually high number of conifer species (12). A combination of steep environmental gradients, slow rates of forest succession, frequent fire, and other disturbances maintain a diversity of species assemblages and structures. The second study reconstructed a Holocene fire and vegetation history at a montane site from lake sediment charcoal, macrofossil and pollen records. During the early Holocene (>10,500 to c. 7700 cal year BP) forests were likely open grown and dominated by *Pinus contorta*. During the mid Holocene (c. 7700 to c. 5200 cal yr BP) *Pinus contorta* became uncommon and *Pseudotsuga menziesii* and *Pinus monticola* were dominant. Shade tolerant species including *Thuja plicata* and *Tsuga heterophylla* first appeared at the beginning of the late Holocene (5200 cal yr BP to present). *Chamaecyparis nootkatensis* appeared most recently at 2000 years BP. Fire frequency does not significantly change over millennial time scales, but fire return intervals are highly variable. Of the 62 detected fires, 39 have a quantifiable response in the macrofossil record. Overall, peaks in charcoal accumulation rates are associated with

an initial peak followed by a drop in macrofossil accumulation rates. Douglas-fir may be favored by fire with a strong peak in accumulation rates following fire events whereas western hemlock and subalpine fir decline following fire events. Together, these studies demonstrate the spatial and temporal variability of fire and vegetation in mountain forests. Climate is a major driver of vegetation change over millennial time scales, and fire and other disturbances are important agents of change at decadal to century time scales.

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CHAPTER 1: OVERVIEW

Fire is a key physical process influencing forested landscapes and vegetation change in North Cascades National Park. Since the end of the last major glaciation (~12,000 BP) fire has interacted with vegetation and affected trajectories of forest succession (Cwynar 1987). As with many regions along the Cascade crest, much of the North Cascades is located in a transitional climate between the maritime (moist) west side and the continental (dry) east side of the mountains. No single fire regime or vegetation type characterizes this region. Fires in the North Cascades generally have shorter return intervals than temperate rainforests farther to the west (80 to 150 years vs. 100 to 500 years) and are highly variable in spatial extent and severity (Agee 1993). Rugged topography mediates wind and weather, creating spatial variability in lightning ignitions and fire spread. Fuel breaks, formed by heterogeneous landforms, further contribute to variable size, magnitude and severity of fire events (Hemstrom and Franklin 1982, Morrison and Swanson 1990).

Although mixed severity fire regimes may be widespread throughout the Cascade Range (Hemstrom and Franklin 1982, Agee et al. 1990, Morrison and Swanson 1990, Agee 1993), few studies of the dynamics of fire and vegetation have been conducted in these systems. During the last century, fire exclusion led to increased fuel loading and greater fire hazard over vast areas of the Inland West (Agee 1999). We know too little about forest ecosystems in the North Cascades to speculate as to whether fire exclusion has substantially modified stand structures and fire susceptibility. However, if mean fire return intervals are generally 100 to 150 years, further fire exclusion clearly could affect landscape patterns and ecosystem dynamics.

North Cascades National Park is part of the second largest contiguous wilderness area in the coterminous United States. Because of its size and remote location, there is a unique opportunity to manage for wildland fire. Smaller parks that are surrounded by private lands or urban areas generally cannot accommodate wildfires because hazards are too great. Managers of NOCA are currently exploring ways to allow fire to occur as an ecological process in the park and surrounding federal lands (North Cascades National Park 2001). Long-term reconstructions of fire regimes are essential elements of effective

fire management plans. In addition, reconstructions of ecological succession following fire will help managers anticipate potential impacts of future fires on forest regeneration and development.

Given recent scenarios of climatic warming in the Pacific Northwest (Mote et al. 1999), park managers also need to evaluate how future climatic variability may affect fire regimes and vegetation change in the North Cascades. Fire histories indicate how the frequency and severity of fires vary with climate. However, what time period adequately captures the historic range of variability in fire regimes? Recorded history of fire and climate in the Cascade Range begins at the time of EuroAmerican settlement, which roughly coincided with the end of the Little Ice Age. Unfortunately, impacts by EuroAmerican settlers on fire regimes and effects of climatic change following the Little Ice Age are indistinguishable (Edmonds et al. 1999). Further, because mean fire return intervals may be greater than 100 years, we need a period of at least several centuries to evaluate long-term trends in fire frequency. Reconstructions should extend over several centuries or millennia to evaluate dynamics among climate, fire and vegetation (Stephenson 1999).

In two separate investigations, I reconstructed the history of fire and forest succession in the lower Thunder Creek Watershed, North Cascades National Park. The first study investigates postfire tree distribution and forest development along an elevation gradient. The second study reconstructs the long-term history of fire and vegetation at a montane forest site. The studies are presented as three stand-alone chapters in this dissertation.

Chapter 2 reports findings from my first investigation. This study quantified species distributions across gradients in elevation and site moisture, interpreted stand dynamics along these gradients, and evaluated how fire and other disturbances may perpetuate heterogeneity in forest composition and structure. Although results are not directly used in my second investigation, knowledge of modern species' distributions and successional dynamics helped instruct my interpretations of long-term vegetation change under broad changes in Holocene climate and responses of vegetation to historic fire events.

Chapter 3 reports findings from my second investigation. This study reconstructed a c. 10,500-year fire and vegetation history of a montane site in Thunder Creek Watershed based on lake sediment charcoal, macrofossil and pollen records. In this study, I evaluated the relative roles of climatic variation and fire on long-term patterns of vegetation assemblages. Few paleoecological investigations have been conducted in the mountains of the Pacific Northwest (Dunwiddie 1986, Pellatt et al. 1998, Pellatt et al. 2000, and Gavin et al. 2001). This study helps fill a void in our knowledge of the Holocene vegetation history of the North Cascade Range. Estimates of historic fire frequency extend far beyond the limits of dendrochronological reconstructions and provide important perspective on short- and long-term variability in fire return intervals over the Holocene.

Chapter 4 is an extension of my analyses in Chapter 3. I used lake sediment charcoal and macrofossil records, sampled at the same high resolution, to evaluate responses in the macrofossil record to fire events delineated from charcoal peaks. Secondary measures of fire, such as responses of vegetation to fire events, help to validate the fire-history reconstruction and indicate shifts in vegetation assemblages associated with specific fire events. Although a number of studies have evaluated historic responses of vegetation to fire using pollen records (Green 1981, Larsen and MacDonald 1998a, b, Tinner et al. 1998, Tinner et al. 1999, Carcaillet et al. 2001), this is the first study to evaluate macrofossil responses to fire events. Macrofossil records have an advantage over pollen records in that they represent a more local signal of vegetation and can thus indicate whether a fire burned in the immediate watershed.

The studies that comprise this dissertation provide data on the dynamics of fire and vegetation in the North Cascade Range. The studies are multi-scalar in that the first investigation highlights the spatial patterns of past fires and subsequent forest development, and the second investigation reconstructs long-term fire and vegetation history of a site using sediment records that have high temporal resolution and span the entire Holocene. Mountains are a dominant feature of the Pacific Northwest, and knowledge of the forest ecology in mountains is critical for understanding factors influencing the current distribution and functions of Pacific Northwest forest as well as

predicting how these forests might change under future warming scenarios (Mote 1999). The North Cascade Range harbors a wide diversity of environments that cannot possibly be captured or represented by a single area. Complementary studies at other locations in the North Cascade Range would improve our understanding of the history of fire and vegetation change in this region.

CHAPTER 2:
SUCCESSIONAL PATHWAYS AND DISTURBANCE IN A
MONTANE FOREST: INTERACTIONS OF FIRE, STAND DYNAMICS, AND
ENVIRONMENTAL GRADIENTS

Introduction

Maintaining biological diversity and landscape heterogeneity are key forest management concerns, particularly as the practice of forest management intensifies in many parts of the world (Hunter 1999, Dale 2001, Hansen et al. 2001). Understanding past ecosystem dynamics can help guide future management for biological diversity and inform predictions of vegetation change under global warming scenarios (Landres et al. 1999, Egan and Howell 2001). Much of the spatial and temporal heterogeneity in forest ecosystems can be explained by historic interactions between climate, landform, disturbance and the life history traits and competitive interactions of species (Smith and Huston 1989, Huston 1994, Clark 1996, Loehle 2000a). Fire and other disturbances are now recognized as important drivers of species and forest patch distributions over space and time (Pickett and White 1985, Turner et al. 1998, Dale et al. 2001). In addition, from reconstructions of vegetation under past climatic variability, we know that species have responded individually to past environmental conditions and that some species have exhibited broader environmental amplitudes than would be expected by their modern distributions (Davis 1986).

Current forest simulation models rely on modern species-environmental relationships and generally do not account for the full range of environmental conditions under which individual species can survive and grow (Loehle and LeBlanc 1996, Loehle 2000a, Hansen 2001). This is partly due to our limited understanding of species' ecophysiology and competitive dynamics. To better understand species' environmental amplitudes, we can assess their dynamics under past climatic variability (Chapter 3, Davis 1986, Brubaker 1991) and investigate their interactions at environmental extremes (i.e. altitudinal or latitudinal limits) (Ohmann and Spies 1998, Thompson 1999, Loehle 2000b, McKenzie et al. 2003).

In this study, we examined the fine-scale dynamics of mountain forest development in relation to fire and the environmental gradients that correlate with tree species distributions. We take advantage of a montane forest landscape in the lower Thunder Creek Watershed, North Cascades National Park where a large number of conifer species occur. Within a relatively small area (7.5 km²) many species exist at the altitudinal or climatic limits of their distributions and coexist in complex assemblages. Because this location is drier than most of the western Cascades and supports a diverse assemblage of tree species, we expected that pathways of forest development would be unlike those described for moist forest assemblages of the Pacific Northwest (Franklin and Hemstrom 1981, Oliver et al. 1984, Stewart 1986, Franklin and Dyrness 1988, Franklin and Spies 1991, Huff 1995, Franklin et al. 2002).

Few studies have investigated secondary forest succession in the mountainous terrain of the Pacific Northwest. In both dry and high-elevation forests, tree recruitment can extend well over 100 yr (Means 1982) and often allows for a high diversity of tree species to establish and codominate stands (Agee and Smith 1984, Franklin et al. 2002). Compared to moist, lowland forests, rates of forest succession (i.e. turnover to shade-tolerant, late successional species) are slow. Delayed rates of succession also can lead to high species diversity in which shade-intolerant pioneers maintain dominance or codominance and form mixed assemblages with late successional species (Romme and Knight 1981, Donnegan and Rebertus 1999). Although simple models of forest development are convenient (Oliver 1981, Oliver and Larson 1990), a myriad of variables that influence tree establishment and survival can lead to multiple pathways of forest succession (Franklin et al. 2002). These include past disturbance extent and severity, climatic variability, available seed sources, landscape heterogeneity, and secondary disturbances (Franklin and Hemstrom 1981, Pickett and White 1985, Franklin et al. 2002). The spatial and temporal scales at which one studies forest successional processes can also affect interpretations of successional pathways (Delcourt and Delcourt 1991, Frelich and Reich 1995).

In this study, our objectives were to 1) quantify tree species distributions across landscape gradients in elevation and site moisture, 2) interpret forest dynamics along

these gradients, and 3) evaluate how fire and other disturbances contribute to heterogeneity in forest composition and structure. Knowledge of how species interact at the limits of their distributions will provide critical detail to the current models of forest succession and simulations of vegetation dynamics under a changing climate.

Study area

North Cascades National Park spans a large portion of the North Cascade Range, and much of the Park is situated within a transitional climatic zone between the maritime west Cascades and inland (continental) east Cascades. Throughout the Cascade Range, uplift has been greatest in the North Cascades and has created varied terrain and steep relief (Tabor and Haugerud 1999). Due to the transitional climate and the steep environmental gradients associated with variable topography, forest vegetation is highly variable, spanning maritime lowland, subalpine, and dry, inland forest types (Agee and Kertis 1987). A majority of forests in the Park have never been harvested, and because mean fire return intervals are generally between 80 and 250 yr (Agee 1993), fire suppression probably has not disrupted forest structures or natural disturbance processes.

Thunder Creek watershed is located in the center of North Cascades National Park and comprises 9% (30,000 ha) of the total park area (Figure 2.1). Although it is west of the Cascade crest, the watershed lies within the rain shadow of several large peaks, and local climate is considerably drier than most west-side sites. Due to the orographic effect of surrounding mountains, a pronounced precipitation gradient exists within the watershed. Based on historic precipitation data (1930-1957), the mouth of the watershed (Diablo Lake) receives 1770 mm of average annual precipitation; 4 km up valley (the upper extent of our study area), annual precipitation is 2540 mm (Larson 1972). At the nearest recorded weather station (Diablo Dam, Washington, 300 m elevation and 5 km west of the study site), mean annual precipitation over the period 1959-2001 was 1910 mm (December high 319 mm, July low 39 mm) and temperatures ranged from an average annual maximum of 14.1 °C (August high 25.1 °C) to an average annual minimum of 4.3 °C (January low -2.6 °C) (Western Regional Climate Center).

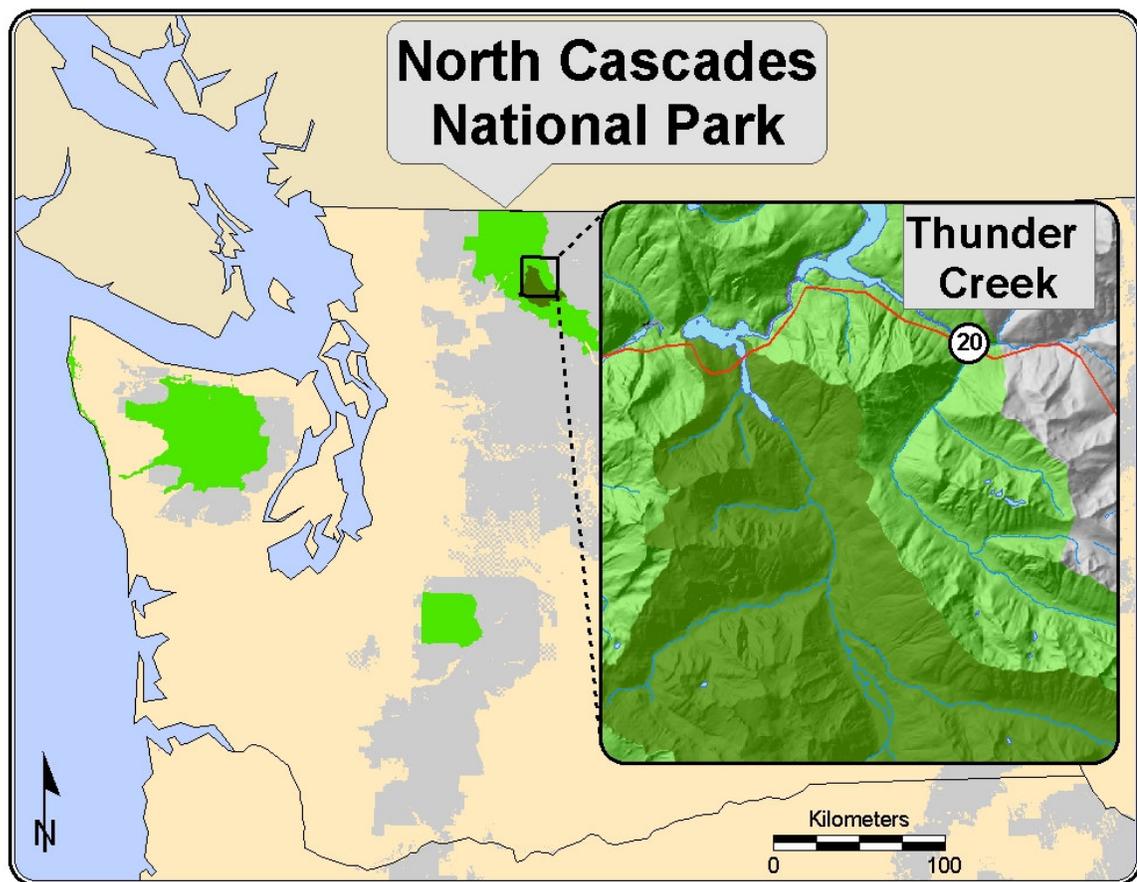


Figure 2.1 Study area location, lower Thunder Creek watershed, North Cascades National Park, Washington

Geology and soils are highly variable in Thunder Creek watershed. During the last ice age, alpine glaciers carved the steep sides of the watershed and left behind rocky benches, a prominent feature of the landscape today. Old gravel-lined river terraces, traces of a preglacial river that once flowed north to the Fraser River, also are a common feature of valley walls (Tabor and Haugerud 1999). Soils are shallow and skeletal throughout much of the study area and are generally classified as Andisols and Spodosols (C. Briggs, personal communication).

Vegetation is transitional, with a flora representing both dry east-side and moist west-side communities of the Cascade Range (Table 2.1). At low elevations (300 to 900 m), forests generally have open structures typical of dry sites and are dominated by Douglas-fir (Figure 2.2) and/or lodgepole pine (*Pinus contorta*) (Figure 2.3) with locally co-dominant western hemlock, western redcedar, and grand fir (*Abies grandis*). At ~ 900 m, lowland forests yield to a transitional montane ecotone characterized by a many coniferous species, including Douglas-fir, lodgepole pine, western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), western white pine (*P. monticola*), Pacific silver fir (*A. amabilis*) mountain hemlock (*Tsuga mertensiana*), Alaska yellow cedar (*Chamaecyparis nootkatensis*) and subalpine fir (*A. lasiocarpa*). Subalpine forests (1050 to 1500 m) are composed of Alaska yellow cedar, subalpine fir, mountain hemlock, and occasional Engelmann spruce (*Picea engelmannii*) and western white pine (Figure 2.4). Rock outcrops and benches are common at all elevations and support mixed stands of lodgepole pine and Douglas-fir in lowland areas and mixed stands of lodgepole pine, western white pine and subalpine fir at higher elevations (> 1200 m).

Agee *et al.* (1989) reconstructed a fire history of Desolation Peak, approximately 25 km north of our study area. They reported mean fire return intervals of 76 yr for lodgepole pine-Douglas-fir forests, 137 yr for Douglas-fir-western hemlock forests, 107 yr for lodgepole pine-subalpine fir forests, and 137 yr for mountain hemlock-Pacific silver fir forests. Desolation Peak has an even drier climate than does Thunder Creek; average annual precipitation ranges from 1000 to 1500 mm (Larson 1972). Thus, mean fire return intervals in Thunder Creek may be somewhat longer, and fires may be more severe. Other major disturbances in Thunder Creek watershed include snow avalanches,



Figure 2.2 Low elevation forest dominated by Douglas-fir.



Figure 2.3 Low elevation forest dominated by lodgepole pine. This stand had evidence of recent bark beetle activity.



Figure 2.4 High elevation sites, 1200- to 1500-m elevation. Note cliff bands and patchy distribution of high elevation forests.

windstorms, insect outbreaks, and diseases. Past snow avalanches are evident at high elevations (>1200 m) and are generally restricted to established avalanche gulleys (Smith 1974). Evidence of wind damage, fungal pathogens (root rot) and insect outbreaks is present on individual trees or small (0.05 ha) groups of trees (S. Prichard, personal observation). Insect-related tree mortality (most likely mountain pine beetle, *Dendroctonus ponderosae*) is particularly common on the scattered western white pine throughout the study area and locally in stands of lodgepole pine. Many western white pine are infected in varying degrees by the exotic fungus, white pine blister rust (*Cronartium ribicola*), and are succumbing to secondary predation by bark beetles.

Methods

Field methods

Several reconnaissance trips were used to locate a large forested area with a fairly consistent elevational range and aspect that had originated from a stand-replacing fire event. A site that satisfied these criteria was found on the west-facing slope of Ruby Mountain. We established four, 1200-m altitudinal transects with plots spaced at 100-m intervals (Figure 2.5). Stream drainages and avalanche tracks were avoided. Although the positions of transects were carefully delineated for safety, start points were selected randomly. Plot locations were determined using a constant compass bearing and altimeter readings. Exceptions were made to avoid riparian areas or cliffs and along transect D where the upper half of the transect was displaced to avoid a series of false ridgetops (Figure 2.5).

At each 0.05-ha plot, we sampled all living and standing dead trees ≥ 10 cm diameter at breast height (dbh) for species, dbh, and height. Tree ages were obtained from increment cores of 20-30 randomly selected trees. Increment cores were extracted perpendicular to the slope and as low to the ground as possible. Rotten cores were discarded, and new trees were randomly selected as replacements. Where plots contained fewer than 20 sound trees, additional trees were selected outside of plot boundaries. Seedlings (<1.5 m in height) and saplings (≥ 1.5 m in height and <10 cm dbh) were sampled over the entire plot if tallies for each group were ≤ 10 , but in a centrally located

Table 2.1 Coniferous tree species of Thunder Creek watershed, their geographic range and basic autecological characteristics.

| Species | Geographic Range | Shade Tolerance | Drought Tolerance | Frost Tolerance |
|--|---|-----------------|-------------------|-----------------|
| Pacific silver fir (PSF) <i>Abies amabilis</i> | coastal BC, Olympics, Cascades | Very high | Very low | Moderate |
| Pacific yew (PY) <i>Taxus brevifolia</i> | southern BC, western WA, OR, Northern CA, northern ID | Very high | Low | Low |
| Western hemlock (WH) <i>Tsuga heterophylla</i> | coastal BC, inland BC, western WA, western OR, northern ID | High | Low | Low |
| Western redcedar (WRC) <i>Thuja plicata</i> | coastal BC, inland BC, western WA, western OR, northern ID | High | Moderate | Low |
| Mountain hemlock (MH) <i>Tsuga mertensiana</i> | coastal BC, Olympics, Cascades, Sierra Nevada, western Rockies | High | Very low | Moderate/High |
| Subalpine fir (SF) <i>Abies lasiocarpa</i> | Yukon, B.C., Olympics, Cascades, Okanogan, Inland West | Moderate/high | Moderate | Moderate |
| Grand fir (GF) <i>Abies grandis</i> | southern BC, WA, OR, northern ID | Moderate/high | Moderate | Moderate |
| Alaska yellow cedar (AYC) <i>Chamaecyparis nootkatensis</i> | coastal BC, Olympics, Cascades | Moderate/high | Low | Moderate |
| Western white pine (WWP) <i>Pinus monticola</i> | southern BC, WA, OR, northern ID, northern CA | Moderate | Moderate | High |
| Engelmann spruce (ES) <i>Picea engelmannii</i> | central & southern BC, Cascades, Rockies, inland West | Moderate | Moderate/High | High |
| Douglas-fir (DF) <i>Pseudotsuga menziesii</i> | central & southern BC, WA, OR, northern CA, inland West, Mexico | Moderate/low | Moderate/High | Low |
| Lodgepole pine (LP) <i>Pinus contorta</i> | Yukon, BC, Alberta, WA, OR, northern CA, Sierras, inland West | Low | High | High |

Table adapted from Minore 1979 and Thompson et al. 1999

0.02 ha subplot if tallies were >10. Seedlings were tallied by species and height, and 10 randomly selected individuals, when present, were destructively sampled to determine age. Saplings were tallied by species and sampled for dbh and height; 10 randomly selected stems, when present, were either cored or destructively sampled to determine age.

Physical data were also collected at each plot. Elevation was recorded using a mechanical altimeter that was calibrated at the beginning of each day and at known topographic positions. Aspect was recorded by taking a bearing perpendicular to the hillslope of each plot. Slope gradient was averaged from upslope and downslope clinometer readings. Landform position was categorized as ridgetop, shoulder slope, upper slope, mid slope, lower slope, bench, and alluvial flat. Geographic position was recorded in UTM coordinates using a hand-held Geographic Positioning System. Finally, upper soil horizons were sampled at three random locations within each plot. As part of each soil survey, we recorded depth of the organic layer and presence of any charcoal within organic or upper mineral horizons. Small (20-cm³) samples of organic and upper mineral soil horizons were collected in air-tight bags for soil moisture calculations. All soil samples were collected in August 2000, during which the study area received no precipitation.

Laboratory and statistical analysis

Aging and crossdating of trees

Increment cores were air dried, then mounted and sanded with progressively finer sandpaper until individual cell walls were discernable under a 64X dissecting microscope. All cores were counted and crossdated according to Stokes and Smiley (1968). Sapling and seedling sections were counted but not crossdated; the last ring near bark was assumed to be year 2000. Of 1125 increment cores of trees, 949 (84%) successfully crossdated. A total of 308 saplings and 278 seedlings ages were determined. Saplings and seedlings that had been sampled in 0.02-ha subplots were extrapolated to the larger 0.05-ha plot area.

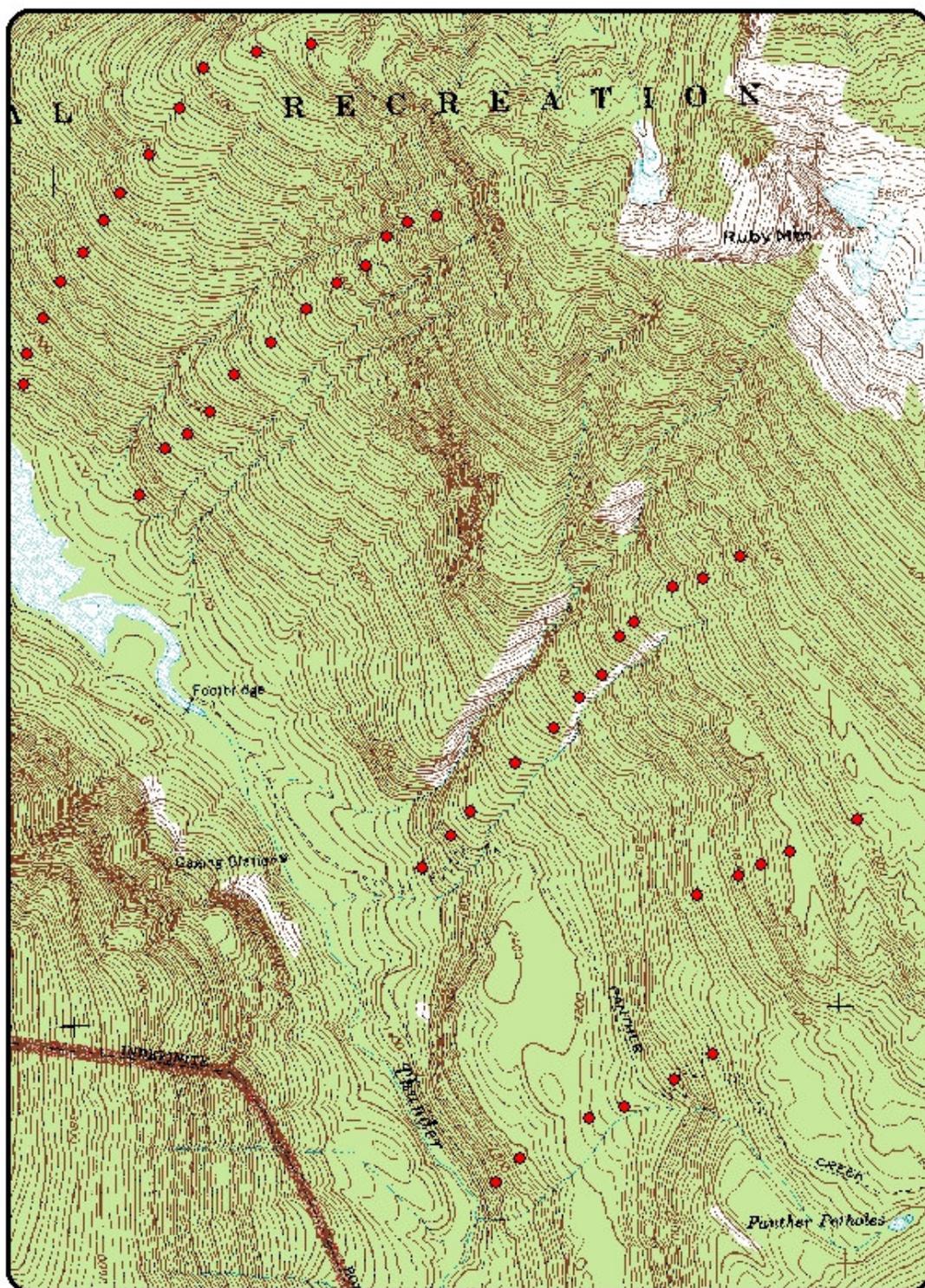


Figure 2.5: Plot locations along transects A through D. GPS locations are overlaid on a USGS 15' quadrangle.

Age-to-core-height was estimated using species-specific relationships developed by Agee (1993). However, relationships were lacking for many species. Douglas-fir core height corrections were used for species typical of low to moderate elevations, including hardwood species, Pacific yew, grand fir, western white pine, western redcedar, and western hemlock. Corrections for mountain hemlock were used to estimate age-to-core-height for high-elevation species, including Alaska yellow cedar, Engelmann spruce and Pacific silver fir (Appendix A).

Soil moisture calculations

Soil samples were weighed, oven dried at 105°C for 36 hr, and reweighed until a constant weight was achieved to calculate soil moisture. Samples were visually reexamined to identify presence of charcoal that might have been overlooked in the field.

Statistical Analyses

Environmental distributions of tree species

Multivariate and regression analyses were used to evaluate gradients in tree species distributions and their relationships with environmental and site factors. Multivariate techniques, including Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA), were used to explore gradients in vegetation composition and to determine whether these patterns could be explained by linear relationships with site factors. Simple and multiple regression models were then constructed to evaluate species-specific relationships with site factors. Tree species basal area ($\text{m}^2 \text{ha}^{-1}$) and density (trees ha^{-1}) were used separately as measures of abundance. Environmental gradients were subjectively inferred from DCA, and linear relationships between environmental factors and tree basal area and density were analyzed using CCA. Site CCA scores were standardized using centering and normalizing, and Monte Carlo tests of significance were conducted. Environmental factors included elevation, aspect, slope gradient, Parker's topographic relief moisture index (TRMI) (Parker 1982), depth of organic soil horizon, and percentage moisture of organic and upper mineral soil horizons. Parker's TRMI is derived from a combination of elevation, aspect, slope

gradient and landform position. DCA and CCA were conducted with PCOrd v4.0 (McCune and Mefford 1999).

Linear regression models were constructed in S-Plus to predict relative tree basal area (%) and relative density (%) of individual tree species from environmental variables (Table 2.2). Relative basal area and density data were first transformed using an arcsine square-root transformation.

Stand dynamics

Patterns of forest development were inferred from age- and size-class (dbh and height) frequency distributions. Age-class distributions were tallied in 5-yr bins, and size-class distributions in 2-m height and 5-cm dbh bins. Age samples of trees, saplings and seedlings were not extrapolated to actual plot densities.

Results

Tree species distributions

A total of 17 tree species was recorded, including 12 conifers and 5 hardwoods (Appendix B). Tree species distributions are continuous from low to high elevations (Figure 2.6). Species typical of low-elevations, including Douglas-fir, western hemlock, and western redcedar, decrease in relative abundance and basal area above ~1100 m and coexist with subalpine species, including Alaska yellow cedar, Engelmann spruce, mountain hemlock, Pacific silver fir and subalpine fir, ~ 1100 m elevation. Douglas-fir is dominant in relative basal area on most plots ($n=25$) and has the broadest elevational range of any tree species except lodgepole pine. It dominates most low-elevation plots with exceptions of plot B4 (dominated by bitter cherry), where lodgepole pine is locally abundant, and a few plots on transect D with higher basal area and/or relative densities of western hemlock and western redcedar (Figure 2.7). At high-elevations (plots 10-11), Douglas-fir is not the most abundant tree species but in many cases still has the highest basal area. Douglas-fir is rare or absent from plot 12 in each transect (1500 m). Lodgepole pine has an even broader distribution than Douglas-fir and is found on all transects and at all elevations. However, it rarely dominant in terms of basal area.

Subalpine species increase in abundance above ~1100 m. Seedlings and saplings of high elevation species, including Alaska yellow cedar and Pacific silver fir, occur at lower elevations than do mature trees of the same species (Figure 2.8).

Tree species distributions also differ between transects with a greater dominance of shade-tolerant species, including Pacific silver fir, western hemlock, and western redcedar and decreased abundance of lodgepole pine on transect D relative to transects A, B and C (Figure 2.9). Saplings and seedlings of western hemlock and western redcedar are uncommon on transects A and B, common on transect C, and the most abundant understory species in most plots in transect D. On transect A, lodgepole pine either dominates or is codominant with Douglas-fir in many plots. It is locally abundant on transects B and C, virtually absent from low-elevation transect D plots, and sparsely represented on high-elevation plots on transect D.

Several species are either common throughout the study area with low densities within plots or have narrow distributions across the study area with high local abundance. Western white pine is found on many plots, spanning low to high elevations, but most often as understory saplings and seedlings and rarely as mature trees. Grand fir is present on a few mid-elevation plots on transect B. Engelmann spruce is rare throughout the study area and is confined to high-elevation plots on transects C and D. Hardwood species, including bitter cherry, bigleaf maple, paper birch, red alder and western dogwood, are uncommon to rare throughout the study area but are occasionally abundant within plots.

Multivariate analyses

DCA ordinations suggest that tree species distributions correlate with gradients in elevation and site moisture. Ordination based on tree basal area (Figure 2.10), separated plots by elevation (low to high) along Axis 1. Montane (10 and 11) and subalpine plots (12) are the most distinct group on this axis. Axis 2 appears to represent a moisture gradient; plots dominated by lodgepole pine, which tolerates dry soils, have low scores, and plots with a large component of western redcedar and western hemlock, which are more mesic species, have high scores. Ordination based on tree density showed a similar

pattern. Environmental factors used in CCA explain some of the variation in tree species distributions. In the CCA of species basal area (Figure 2.11), the percent variance explained by three canonical axes (Axis 1, 2 and 3) is 30%. Axis 1 accounts for half of the explained variance and ordines species and plots from low to high elevations ($r = -0.73$). Axis 2 is correlated with slope gradient ($r = 0.87$).

Linear regression models

Simple linear regressions of relative basal area or density of individual species and landform factors are weak but corroborate trends found in multivariate analyses (Table 2.3). Species typical of high elevations (Alaska yellow cedar, Pacific silver fir, and subalpine fir) are positively correlated with elevation, while Douglas-fir, typically found on lowland sites, is negatively correlated with elevation. Lodgepole pine and western white pine are both negatively correlated with slope gradient, while Douglas-fir is positively correlated with slope gradient. Western hemlock and western redcedar both are positively correlated with TRMI, and western hemlock is also positively correlated with moisture in organic and mineral soil horizons.

Disturbance history

Periods of tree establishment are synchronous among many of the 47 plots (Figure 2.12). Most recently, plots A1, A2, and B1 regenerated between 1950 and 1970. Over the four transects, some plots had a wide establishment period beginning in 1920. Many stands established or have a primary establishment pulse between 1880 and 1900. This pulse dominates much of transect A and B but is occasional in transect C and absent in all but the lowest elevation plot on transect D. Another establishment window in 1860-1880 is present on all transects, particularly at high elevations and throughout transect D. An 1830-1860 establishment window dominates plots within transect D but is occasional on high-elevation plots of transects A - C. Finally, individual trees (predominantly Douglas-fir) predating the 1800s were found on all transects. No fire scars, injuries or corresponding abrupt changes in growth patterns were found on these residual trees. Charcoal was found in upper soil horizons in 44 of the 47 plots.

Stand Dynamics

A variety of stand structures exist in terms of tree establishment dates and tree size distributions. Few plots have a narrow, unimodal distribution of tree establishment dates (e.g., Figure 2.13, Plot A5). Distributions are typically wide and either unimodal with extended tree recruitment (e.g., Figure 2.13, Plot B11) or multi-modal with multiple establishment pulses (e.g., Figure 2.13, Plot D3). Diameter and height structures generally exhibit a wide range of size and height classes.

Where Douglas-fir is dominant, it generally established early and is among the oldest and tallest trees. With the exception of transect D, Douglas-fir is also recruiting in many low- to mid-elevation (Plots 1-9) understories as seedlings and saplings. In three plots (Appendix C, A1, A3 and B4), hardwood species, including bitter cherry, bigleaf maple and paper birch, co-established with Douglas-fir. In all three cases, stands are succeeding to Douglas-fir with continued recruitment of this species.

Although it is not currently dominant on most plots, lodgepole pine was an early seral species on 31 of the 47 plots. Where Douglas-fir and lodgepole coexist, Douglas-fir is generally much taller and has greater relative basal area (e.g., Figure 2.14). Lodgepole pine also exhibits higher recent mortality than Douglas-fir. On a few plots (Appendix C, A5, A9, A11), lodgepole pine is nearly monodominant with sparse understory of other species including Douglas-fir on A5 and A9 and subalpine fir on A11.

On low- to mid-elevation plots on Transect D, western hemlock and western redcedar generally co-established with Douglas-fir. Stands are dense, multi-layered, and Douglas-fir is uncommon in understories. Western hemlock and western redcedar are common recruits in forest understories at low to mid-elevations on Transects C and D.

At high-elevation plots tree recruitment has spanned over 150 yr, and most stands have not reached canopy closure. No single forest assemblage characterizes high elevation plots, and a variety of conifer species coexist at these sites. Douglas-fir established early on several high elevation plots (A10, B11, C10-11, D11), but is not present in later cohorts. In three of these plots (A10, C10, and D11) western hemlock also established in the first few decades following the stand-replacing disturbance.

Table 2.2 Environmental factors and soil properties by plot.

| Plot ID | Elevation (m) | Aspect (°) | Slope gradient (°) | TRMI | O-horizon depth (cm) | O-horizon moisture (%) | Mineral soil moisture (%) |
|-----------|---------------|--------------|--------------------|------------|----------------------|------------------------|---------------------------|
| A01 | 495 | 165 | 30 | 21.5 | 2.3 | 1.8 | 11.8 |
| A02 | 560 | 220 | 29 | 22 | 2.1 | 1.8 | 14.8 |
| A03 | 650 | 212 | 34 | 16 | 2.7 | 9.5 | 14.6 |
| A04 | 780 | 225 | 32 | 22 | 8.0 | 2.9 | 8.6 |
| A05 | 870 | 252 | 27 | 21 | 2.3 | 1.9 | 5.5 |
| A06 | 960 | 218 | 36 | 17 | 2.8 | 9.3 | 7.7 |
| A07 | 1050 | 234 | 36 | 18 | 1.8 | 2.0 | 3.7 |
| A08 | 1145 | 250 | 32 | 20 | 2.5 | 2.4 | 5.9 |
| A09 | 1235 | 237 | 22 | 22 | 0.5 | 2.1 | 7.5 |
| A10 | 1325 | 217 | 20 | 19 | 6.2 | 3.7 | 13.2 |
| A11 | 1420 | 200 | 16 | 18 | 4.5 | 5.2 | 5.8 |
| A12 | 1510 | 260 | 39 | 16 | 1.7 | 3.6 | 15.7 |
| Mean ± SD | | 224.2 ± 25.8 | 29.4 ± 7.0 | 19.4 ± 2.3 | 3.1 ± 2.1 | 3.9 ± 2.8 | 9.6 ± 4.2 |
| B01 | 460 | 218 | 33 | 18 | 2.7 | 1.9 | 5.3 |
| B02 | 595 | 243 | 32 | 19 | 3.7 | 2.2 | 4.7 |
| B03 | 665 | 222 | 32 | 17 | 11.3 | 5.1 | 14.7 |
| B04 | 760 | 222 | 35 | 17 | 3.3 | 1.8 | 6.5 |
| B05 | 855 | 211 | 35 | 16 | 6.2 | 2.9 | 6.5 |
| B06 | 955 | 244 | 35 | 20 | 2.4 | 2.3 | 4.7 |
| B07 | 1050 | 226 | 33 | 15 | 4.2 | 5.6 | 5.7 |
| B08 | 1140 | 240 | 31 | 19 | 2.5 | 2.8 | 4.9 |
| B09 | 1230 | 230 | 32 | 18 | 4.5 | 3.1 | 17.0 |
| B10 | 1320 | 269 | 46 | 17 | 5.2 | 2.5 | 6.8 |
| B11 | 1410 | 222 | 36 | 12 | 1.8 | 2.2 | 8.9 |
| B12 | 1525 | 310 | 35 | 17 | 13.3 | 12.5 | n/a |
| Mean ± SD | | 238.1 ± 27.5 | 34.6 ± 3.9 | 17.1 ± 2.1 | 5.1 ± 3.6 | 3.7 ± 3.0 | 7.8 ± 4.2 |

Table 2.2 continued.

| Plot ID | Elevation (m) | Aspect (°) | Slope gradient (°) | TRMI | O-horizon depth (cm) | O-horizon moisture (%) | Mineral soil moisture (%) |
|-----------|---------------|--------------|--------------------|------------|----------------------|------------------------|---------------------------|
| C01 | 460 | 272 | 29 | 24 | 4.4 | n/a | n/a |
| C02 | 560 | 260 | 42 | 21 | 0.7 | 1.6 | 5.1 |
| C03 | 660 | 240 | 24 | 16 | 1.2 | 2.5 | 6.4 |
| C04 | 760 | 193 | 30 | 16 | 3.0 | 1.6 | 3.0 |
| C05 | 865 | 219 | 15 | 17 | 3.0 | 1.4 | 3.6 |
| C06 | 955 | 244 | 27 | 16 | 8.7 | 9.7 | 6.8 |
| C07 | 1045 | 222 | 24 | 14 | 4.8 | 4.6 | 8.0 |
| C08 | 1140 | 226 | 29 | 14 | 7.3 | 3.7 | 5.2 |
| C09 | 1205 | 234 | 30 | 18 | 4.4 | 4.2 | 6.3 |
| C10 | 1310 | 280 | 32 | 24 | 4.4 | 12.7 | 15.4 |
| C11 | 1415 | 260 | 30 | 16 | 5.2 | 5.0 | 9.3 |
| C12 | 1500 | 260 | 31 | 11 | 3.7 | 5.7 | 15.5 |
| Mean ± SD | | 242.5 ± 25.2 | 28.6 ± 6.3 | 17.3 ± 4.0 | 4.2 ± 2.3 | 4.8 ± 3.6 | 7.7 ± 4.2 |
| D01 | 460 | 266 | 35 | 30 | 13.0 | 4.9 | 12.0 |
| D02 | 560 | 249 | 31 | 20 | 3.8 | 5.8 | 5.6 |
| D03 | 655 | 280 | 29 | 30 | 3.8 | 6.1 | 12.3 |
| D04 | 760 | 240 | 23 | 22 | 7.7 | 8.6 | 15.4 |
| D05 | 860 | 235 | 35 | 19 | 5.7 | 3.2 | 11.2 |
| D06 | 965 | 256 | 27 | 22 | 4.0 | 2.8 | 7.8 |
| D07 | 1055 | 235 | 24 | 31 | 7.6 | 8.1 | 39.3 |
| D08 | 1160 | 263 | 37 | 22 | 2.5 | 0.8 | 6.2 |
| D09 | 1230 | 239 | 40 | 19 | 2.0 | 6.6 | 5.8 |
| D10 | 1320 | 276 | 7 | 21 | 4.0 | 11.4 | 10.5 |
| D11 | 1410 | 225 | 29 | 8 | 3.3 | 9.6 | 11.4 |
| Mean ± SD | | 232.4 ± 67.5 | 26.9 ± 10.8 | 20.7 ± 8.2 | 5.0 ± 3.1 | 6.0 ± 3.1 | 11.8 ± 9.3 |

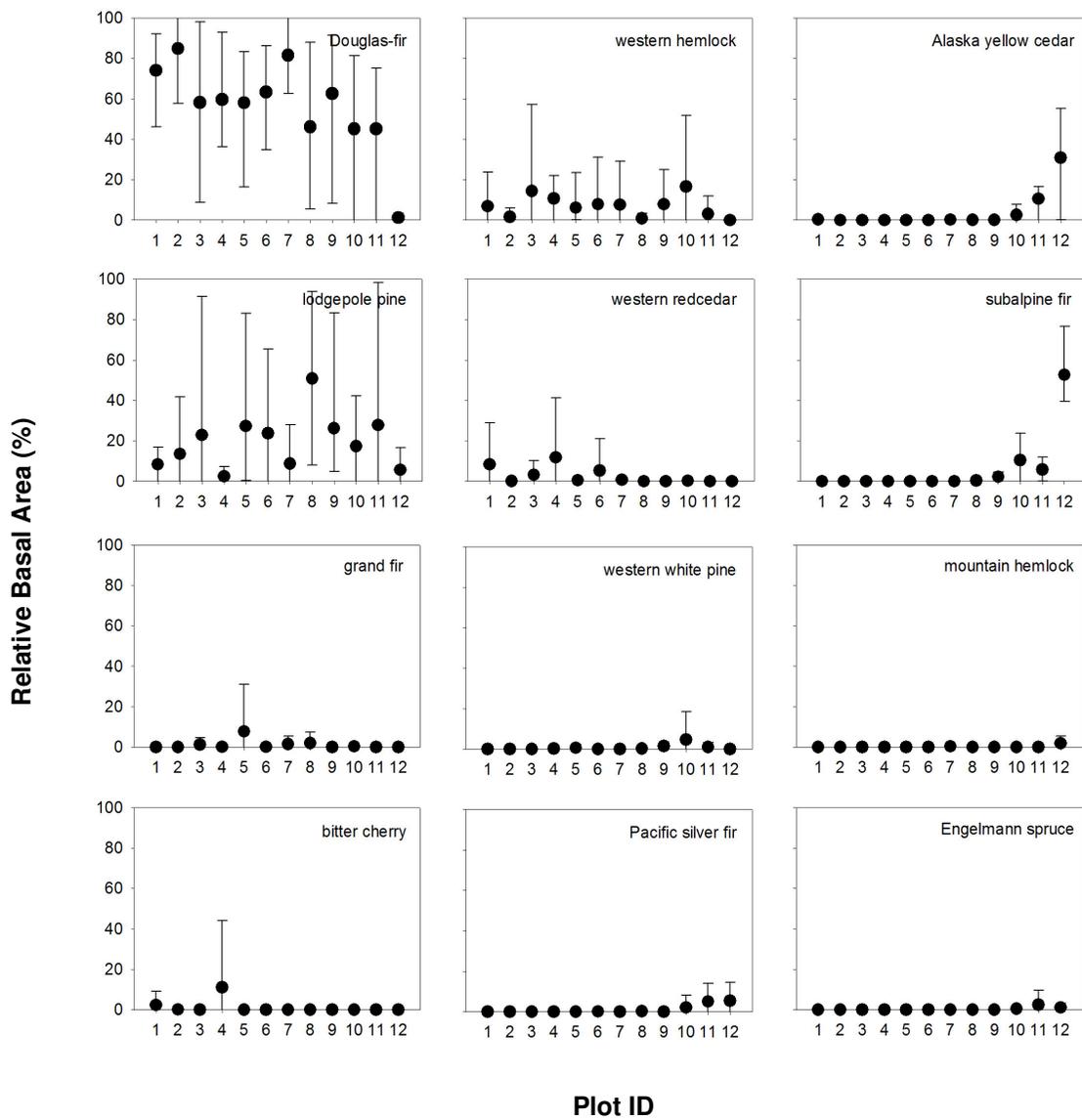


Figure 2.6 Relative (%) basal area of tree species averaged over the four transects. Error bars represent minimum and maximum percentages.

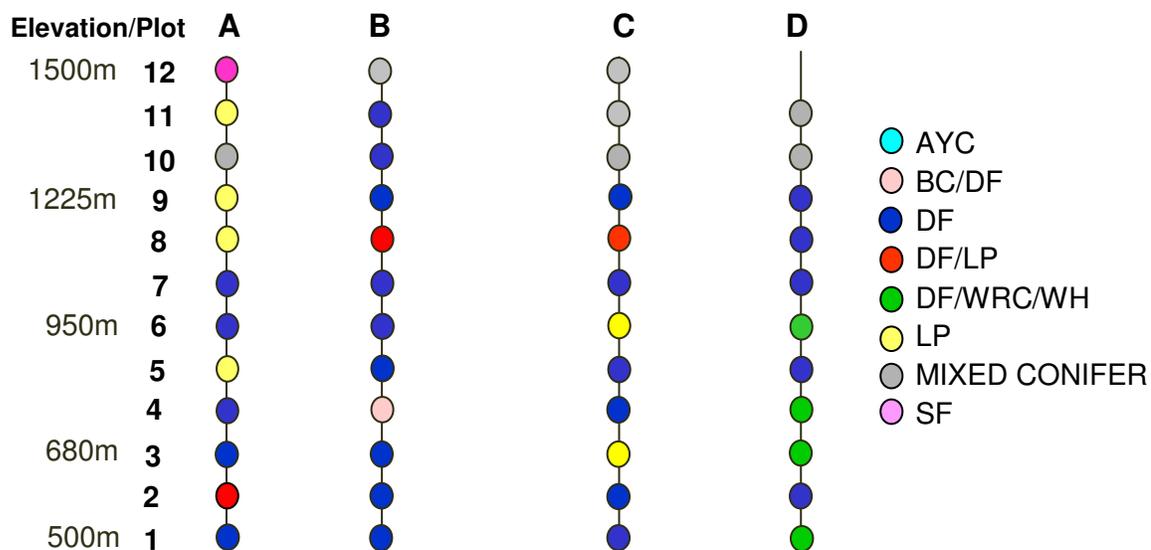


Figure 2.7 Stand types designated by dominant tree species or group of tree species comprising > 60% basal area. AYC = Alaska yellow cedar, BC = bitter cherry, DF = Douglas-fir, LP = lodgepole pine, SF = subalpine fir, WH = western hemlock, WRC = western redcedar.

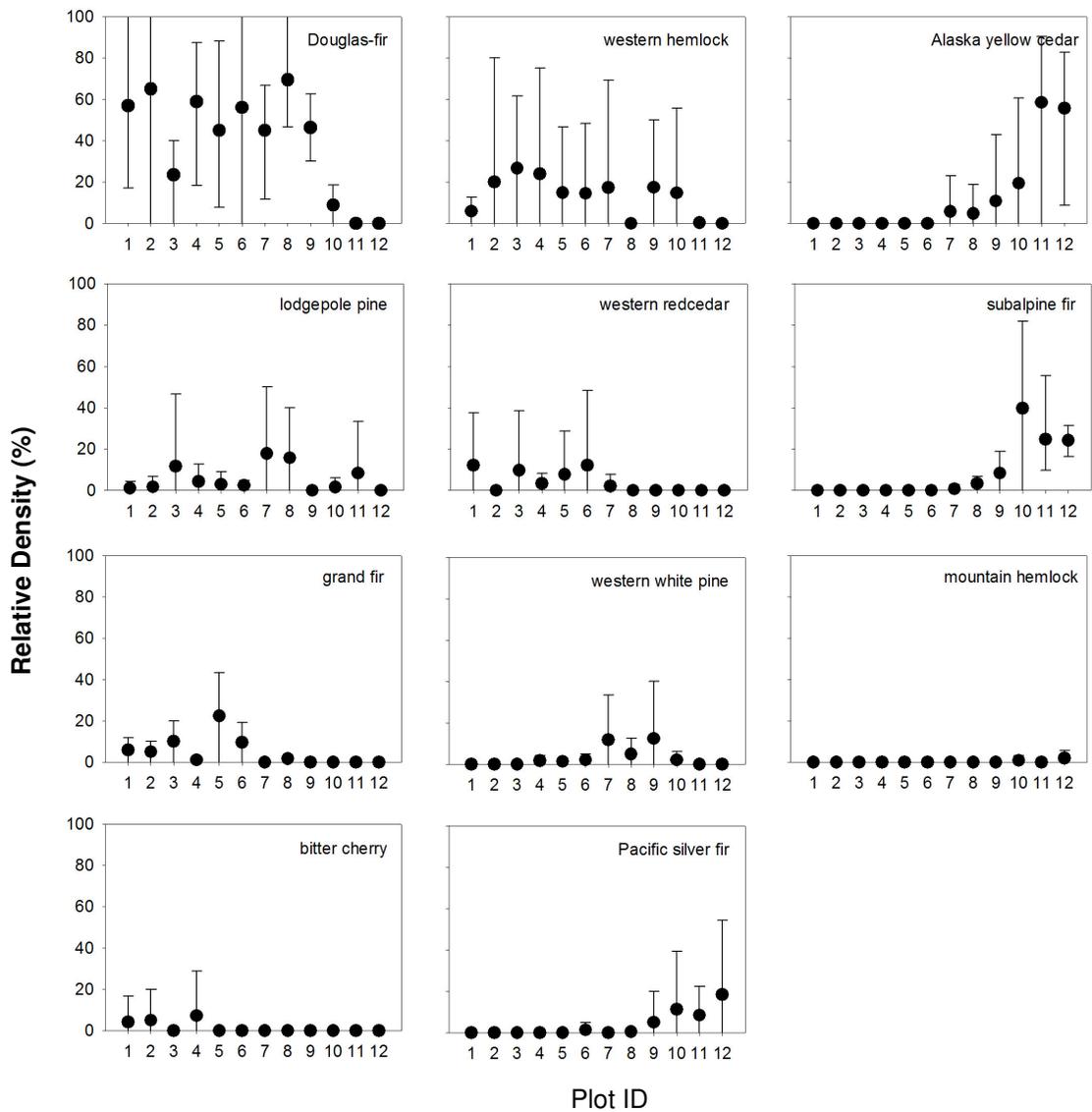


Figure 2.8 Relative (%) density tree seedlings and saplings averaged over the four transects. Error bars represent minimum and maximum percentages. Engelmann spruce was absent in seedling and sapling classes.

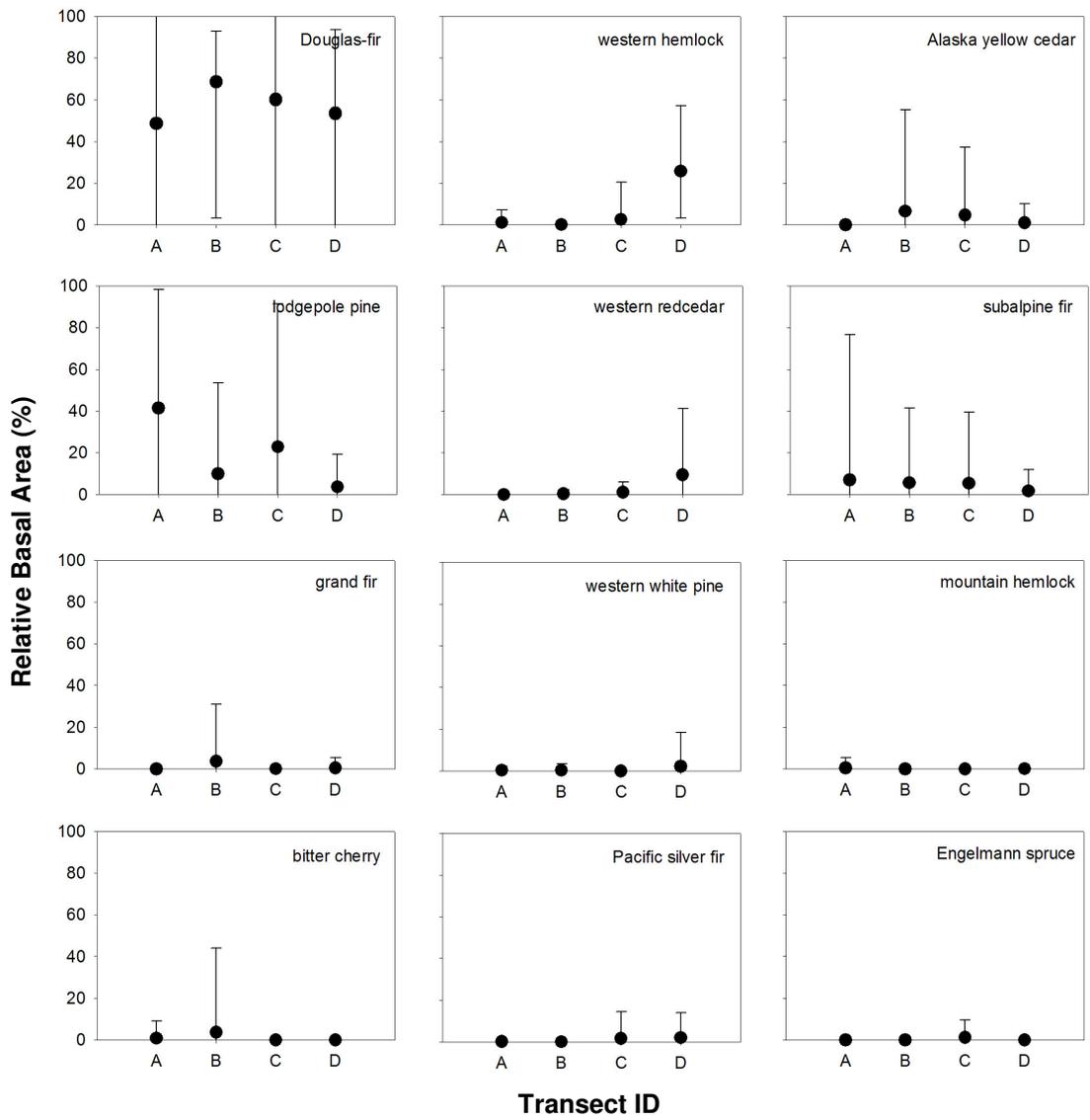


Figure 2.9 Relative (%) tree basal area averaged over all plots within each transect. Error bars represent minimum and maximum percentages.

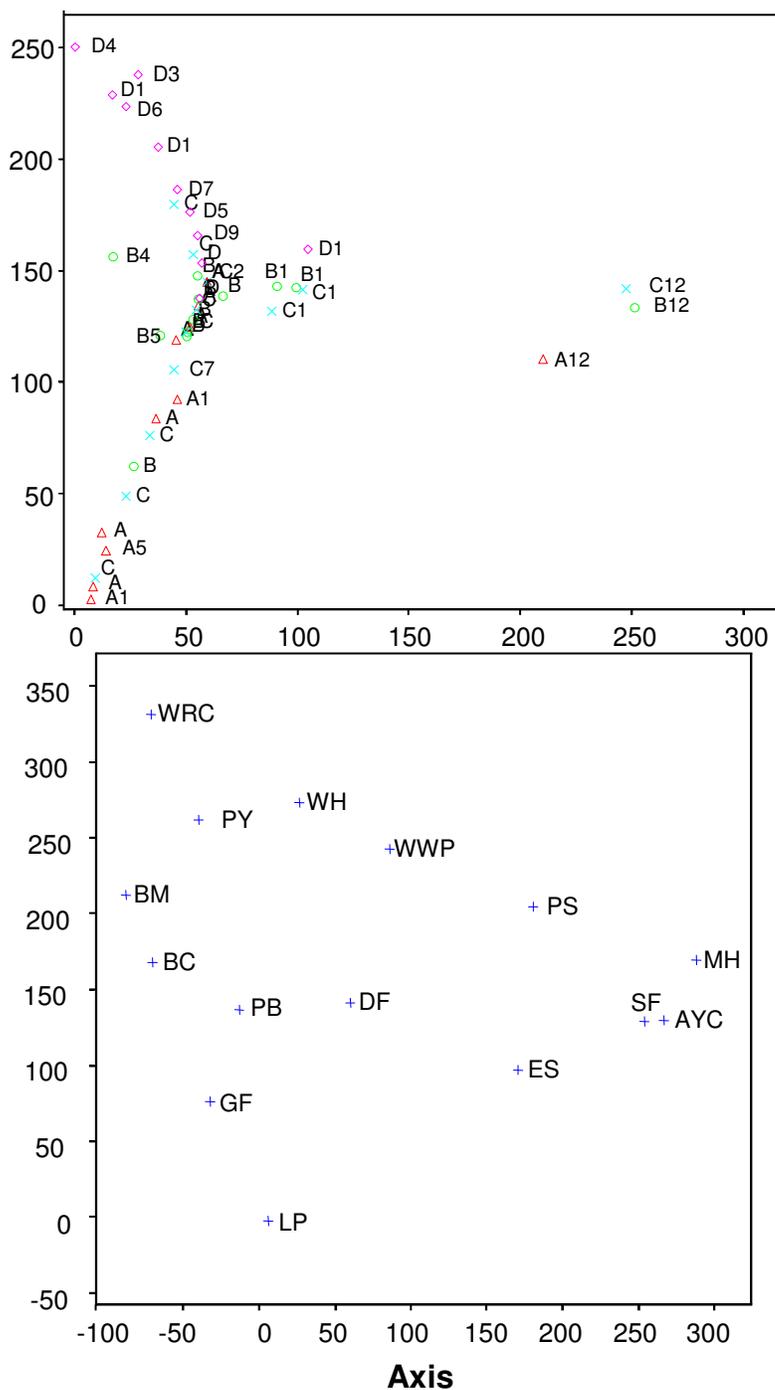


Figure 2.10 DCA ordination of samples and species based on tree basal area.
 AYC = Alaska yellow cedar, BC = bitter cherry, BM = bigleaf maple,
 DF = Douglas-fir, ES = Engelmann spruce, GF = grand fir,
 LP = lodgepole pine, MH = mountain hemlock, PSF = Pacific silver fir, PY =
 Pacific yew, SF = subalpine fir, WH = western hemlock, WRC = western
 redcedar, WWP = western white pine.

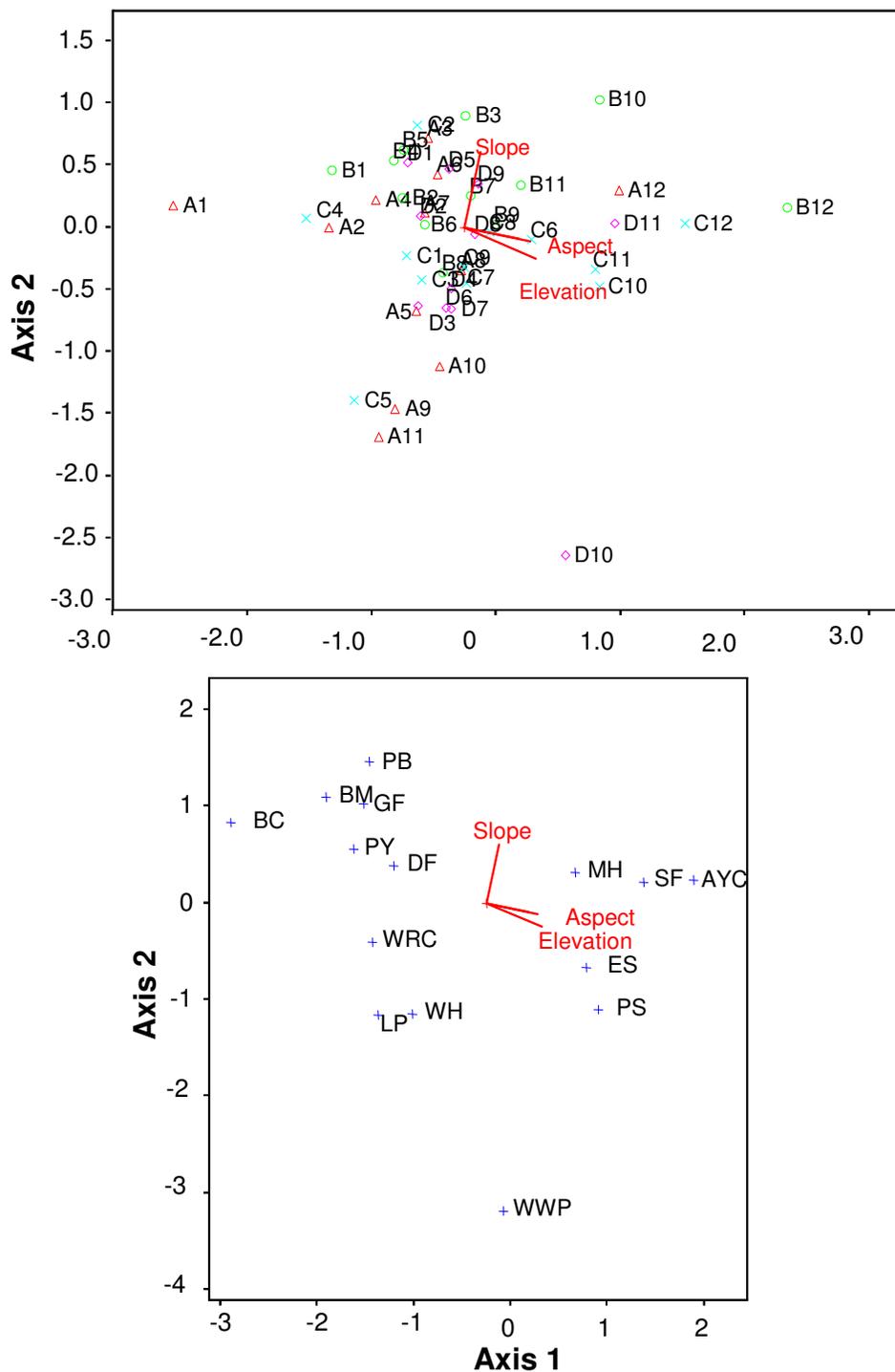


Figure 2.11 CCA ordination of samples and species based on tree basal area. AYC = Alaska yellow cedar, BC = bitter cherry, DF = Douglas-fir, GF = grand fir, LP = lodgepole pine, MH = mountain hemlock, PSF = Pacific silver fir, SF = subalpine fir, WH = western hemlock, WRC = western redcedar, WWP = western white pine.

Table 2.3 Simple linear regression models. Correlation coefficients (r) for relative basal area (%) of tree species vs. environmental factors. Only those coefficients with significant correlations ($p < 0.05$) are shown.

| Species | Elevation | Aspect | Slope | TRMI | Organic horizon depth | % Moisture organic soil | % Moisture mineral soil |
|-----------------------------------|-----------|--------|-------|-------|-----------------------|-------------------------|-------------------------|
| Alaska yellow cedar (n = 9/8)* | 0.52 | 0.42 | | -0.37 | | | |
| Douglas-fir (n = 43/41) | -0.46 | | 0.42 | | | | |
| lodgepole pine (n = 31/31) | | | -0.43 | | | | |
| Pacific silver fir (n = 5/5) | 0.45 | | | -0.40 | | 0.36 | 0.30 |
| subalpine fir (n = 12/11) | 0.62 | 0.37 | | -0.29 | | | 0.42 |
| Western hemlock (n = 18/17) | | | -0.30 | 0.52 | | 0.39 | 0.32 |
| western redcedar (n = 13/12) | -0.34 | | | 0.46 | 0.47 | | |
| Western white pine (n = 7/7) | | | -0.51 | | | 0.31 | |

* Sample size for landform factors (elevation, aspect, slope, TRMI) and soil data, respectively.

| Plot ID | 1500 s | 1600 s | 1700 s | 1800 | 1810 | 1820 | 1830 | 1840 | 1850 | 1860 | 1870 | 1880 | 1890 | 1900 | 1910 | 1920 | 1930 | 1940 | 1950 | 1960 | 1970 | 1980 |
|---------|--------|--------|--------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| A1 | | | | | | | | | | | | | | | X | | | X | | | | |
| A2 | | | | | | | | | | | | | | | X | | | | X | | | |
| A3 | | | | | | | | | | | | | | | X | X | | | | | | |
| A4 | | | | X | | | | | X | | | | X | | | | | | | | | |
| A5 | | | | | | | | | | | | | | | | | | | | | | |
| A6 | | | | | | | | | | | | | | | X | | | | X | | | |
| A7 | | | | | | | | | | | | | | | | | | | | | | |
| A8 | | | | | | | | | | | | | | X | X | X | | X | | | | |
| A9 | | | | | | | | | | | | X | X | | | | | | | | | |
| A10 | | | | | | | | | | | | | | | | | | | | | | |
| A11 | | | | | | | | | | X | | | | | | | | | | | | |
| A12 | | | | | | | | | | | | | | X | | | | | | | | |
| B1 | | | | | | | | | | | | | | | | | | X | | | | |
| B2 | | | | | | | | | | | | | X | | | | | | X | | | |
| B3 | | | | | | | | | | | | | | | | | | | | | | |
| B4 | | | | | | | | | | | | | | X | X | | | | | X | | |
| B5 | | | | | | | | | | | | | | | | X | X | X | X | | | |
| B6 | | | | | | | | | | | | X | | | | | X | | X | | | |
| B7 | | | | | | | | | | | | | | | | X | | | X | X | | |
| B8 | | | | | | | | | | | | | | | | | | | | | | |
| B9 | | | | | | | | | | | | | | | X | | | | | | | |
| B10 | | | | | | | | | | | | | | | | | | | | | | |
| B11 | | X | | | | | | | | | | | | X | X | X | X | | | | | |
| B12 | | | | | | X | | | | X | X | | X | | | | | | | | | |

Figure 2.12 Periods of tree establishment interpreted from age-class frequency histograms. “Xs” represent individual trees and gray shading indicates multiple trees (≥ 2).

| Plot ID | 1500s | 1600s | 1700s | 1800 | 1810 | 1820 | 1830 | 1840 | 1850 | 1860 | 1870 | 1880 | 1890 | 1900 | 1910 | 1920 | 1930 | 1940 | 1950 | 1960 | 1970 | 1980 |
|---------|-------|-------|-------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| C1 | X | | | | | | | X | | | | | | | | X | X | X | | | | |
| C2 | | | | | | | | | | | | | X | | | X | | | | | | |
| C3 | | | | | | | | | | | | X | X | | | | | | | | | |
| C4 | | | | | | | | | | | | | | | X | X | X | | | | | |
| C5 | | | | | | | | | | | | | | | | X | | | | | | |
| C6 | | | | | | | | | | | | | | | | | | | X | | | |
| C7 | | | | | | | | | | | | X | X | | | X | | | | | | |
| C8 | | | | | | | | X | | | | | | | | | | | | | | |
| C9 | | | | | | | | | | | X | | | | | | | | | | | |
| C10 | | | | | | | | X | | | | | | | | | | | | | | |
| C11 | | | | | | | | | | | X | | | | X | | | | | | | |
| C12 | | | | | | | | | X | | X | | | | | | | | | | | |
| D1 | | | | | | | | | X | | X | | | | | | | X | | | | |
| D2 | | | | | | | X | | | | X | X | X | | | X | | | | | | |
| D3 | | | | X | | X | | | | | | | | | | | | | | | | |
| D4 | | | | | X | | | | X | | | | | X | X | X | | | | X | | |
| D5 | | | | | | | X | | | | | | | X | | | | | | | | |
| D6 | | | | | | | | | | | | | X | | X | | | | | | | |
| D7 | | | | | | | | | | | | | | | X | | X | X | X | | | |
| D8 | | | | | | | X | | | | | | X | | | | | | | | | |
| D9 | X | X | | | | X | | | | | | | X | | | | | | | | | |
| D10 | | | | | | | | | | | X | X | | | | | | | | | | |
| D11 | X | | | | | X | | | | | | X | | | X | X | | | | | | |

Figure 2.12 Continued.

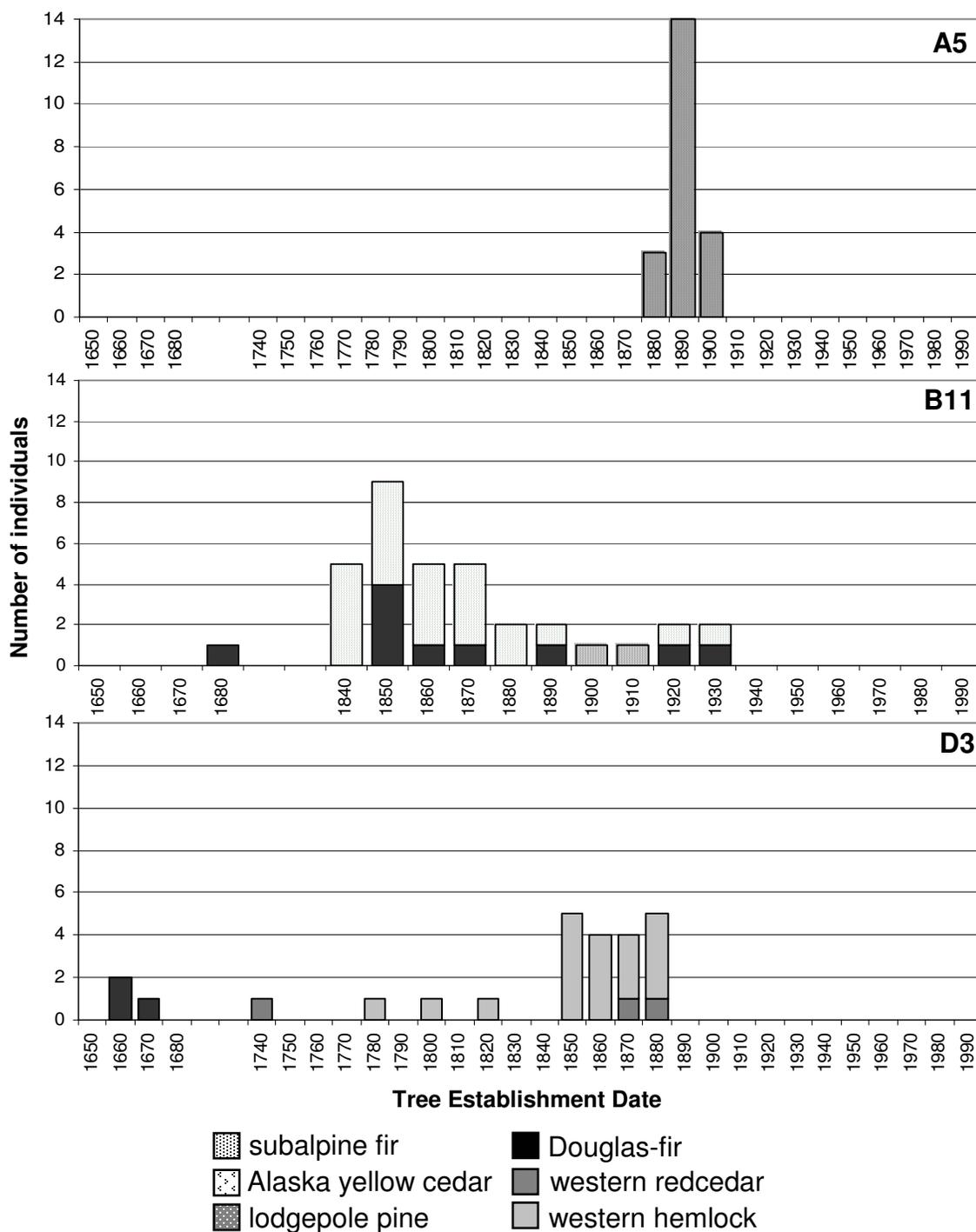


Figure 2.13 Age-class frequency distributions of plot A5 which has a narrow distribution of tree establishment, plot B11 with a wide distribution of tree establishment, and plot D3 with multiple periods of tree establishment.

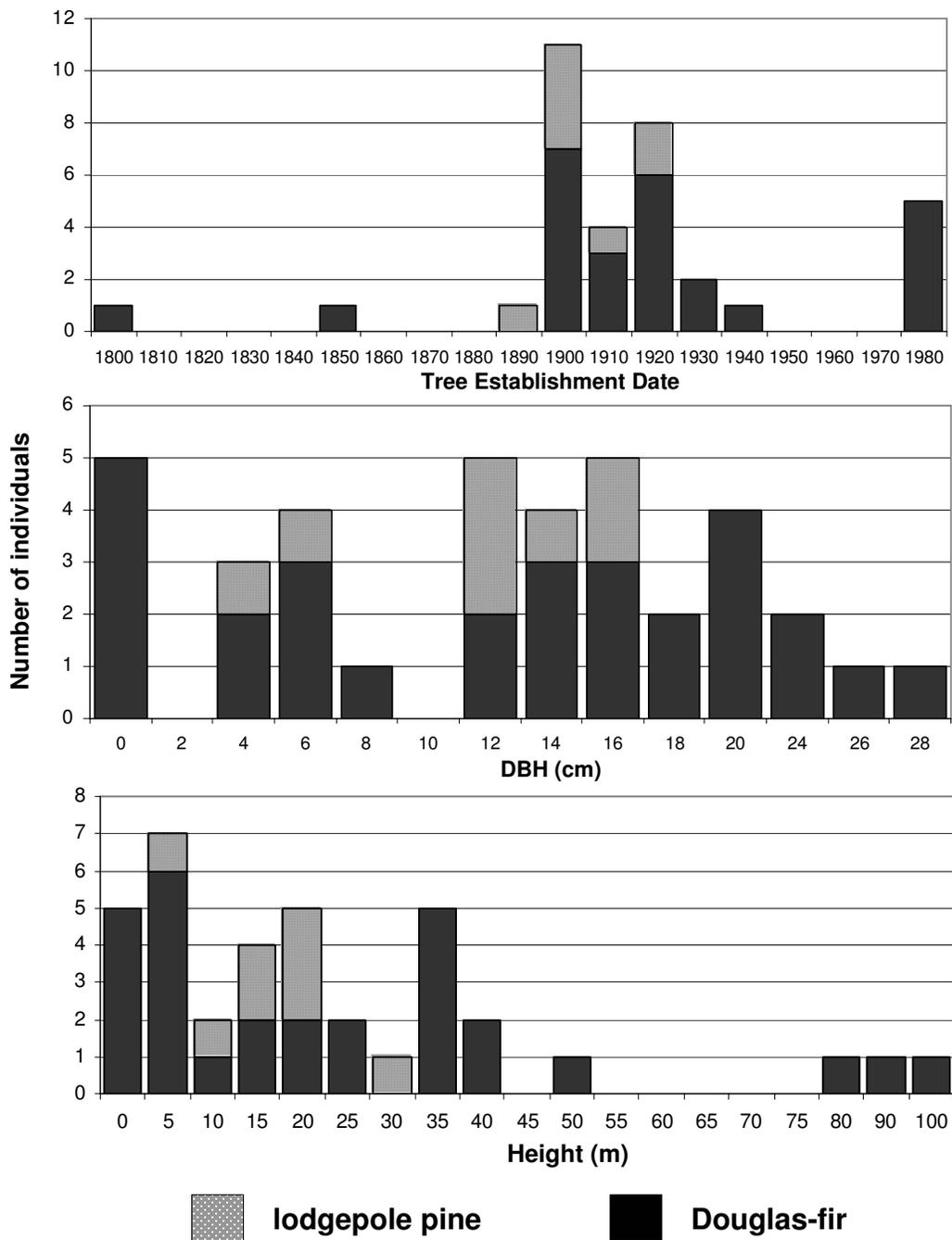


Figure 2.14 Age- and size-class frequency distributions of plot A4.

Discussion

Environmental distributions of tree species

Our study area is approximately 7.5 km², yet is rich in tree species and supports forest structures not typically described on the west side of the Cascade Range (Franklin and Dyrness 1988). Because transects were selected to represent planar slopes and specifically avoided riparian areas and extreme topography (cliffs, avalanche tracks), this estimate of community diversity is conservative; riparian corridors and avalanche tracks may contain additional species and stand assemblages. In addition, the overall study area is located on the west face of Ruby Mountain. Other aspects in the general vicinity likely have different tree assemblages and forest disturbance histories. For example, forests on the opposite side of Thunder Creek with an east-facing aspect appear to be much older and have a more mesic forest assemblage than our those in the study area (S. Prichard, personal observation).

We did not take direct measures of site moisture and temperature, but correlations between landform features (elevation, aspect, slope, and TRMI) and forest composition indicate that gradients temperature and moisture, driven by landform, shape the distributions of tree species. In their ordination of forest communities of North Cascades National Park, Agee and Kertis (1987) inferred that forest composition reflects strong gradients in temperature (DCA Axis 1) and moisture (Axis 2). We found similar patterns in Thunder Creek. The primary axis in our ordinations correlates with elevation along which temperature declines and snowpack increases. The secondary axis is more complex and suggests a gradient in moisture availability, increasing from transect A to D and, possibly, from steep, planar slopes to more gradual ones. Although transects span less than 4-km along Thunder Creek watershed, precipitation may vary considerably from transect A to D, thereby influencing species distributions (Larson 1972).

All transects have an ecotone between low elevation and montane forests at 1200-1400 m (Plots 9-11). This ecotone lies at a consistent elevation across the four transects, although transects appear to differ in moisture availability. Montane ecotones support the highest diversity and represent the convergence of low-elevation species at their upper

limit and subalpine species at their lower limit. Neither low-elevation nor subalpine species appear to have competitive dominance within this zone (Huston 1994, Loehle 1998).

Soils and topography may also influence moisture availability along individual transects. For example, lodgepole pine is more dominant on shallower slopes ($< 27^\circ$) and drier soils, which characterize glacially carved benches with thin, excessively drained soils. In contrast, western redcedar, western hemlock, western white pine, and Pacific silver fir have greater dominance on Transect D and on gradual toe slopes with high soil moisture. These patterns of local tree distribution are consistent with individual species autecologies (Minore 1979, Franklin and Dyrness 1988).

Disturbance

Our study area was selected to encompass a single, large, stand-replacing disturbance event but tree ages suggest multiple disturbances. Stand origin dates estimated from age of the oldest trees range from 50 to 160 yr. The oldest stands are located at high elevations and along transects C and D. These stands appear to have regenerated from a single fire ca. 1830 or multiple fires and/or other disturbance events between 1830 and 1860. Nearly half (22) of all stands regenerated from a large fire in 1880, which spanned low to moderate elevations from transects A to C. Unfortunately, we were unable to locate any fire scars to verify these estimated fire dates. Although tree age distributions only approximate fire dates, it is unlikely that the 1830 and 1880 establishment pulses followed the same fire event. Inferred fire dates at high elevation sites may be conservative because tree establishment after fire in these environmentally stressful locations (Agee and Smith 1984, Little et al. 1994). Many residual (> 200 year old) trees are scattered throughout the study area (Figure 2.12) and suggest that past fires were of mixed severity. Because charcoal was found in upper soil horizons on 44 of the 47 plots, fire has likely been a major disturbance agent throughout the study area.

More recent periods of tree establishment are not strongly synchronous across the landscape and may represent small, stand-level disturbances such as wind, small fires,

insect outbreaks, and fungal pathogens. For example, the lowest elevation plots on transect A (plots 1 and 2) and B (plot 1) have a major recruitment period at 1950. The presence of logs, snags and residual trees indicate that ~ 1950, a disturbance such as wind and or insect outbreak occurred. Finally, a few stands in which lodgepole pine is present are currently undergoing a mountain pine beetle outbreak (e.g., A5, A8 and A9), while several others have undergone substantial mortality, from stem exclusion, windthrow and/or past insect outbreaks (e.g., A6, B6, B7, C6, and C7) (Appendix C).

Stand dynamics

Histograms of tree age and size structures allow closer inspection of competitive and successional dynamics within forests. However, static age and size structures cannot account for past mortality of trees at all life stages (Lorimer 1984, Johnson *et al.* 1994). Within our study area, snags and logs were too decomposed to extract increment cores for crossdating. In addition, current seedling and sapling occurrence and distribution must be interpreted with caution, because continual recruitment and mortality of individuals within the forest understory may have occurred in the past and may well occur in the future.

With the exception of transect D, many plots below 1300 m (Plot 10) are dominated either by Douglas-fir or lodgepole pine or both. These dry, low elevation forest types generally have a wide establishment period, in which the marginally shade-tolerant Douglas-fir recruits under forest canopies. Competitive interactions between Douglas-fir and lodgepole pine are complex. In lodgepole pine ecosystems near Ross and Diablo Lakes, North Cascades National Park, Larson (1972) postulated that pine can out-compete Douglas-fir in height growth on the most xeric sites, whereas Douglas-fir dominates mesic sites; the two species then potentially coexist on intermediate sites. Our findings agree with this model. On many plots in which either lodgepole pine or a mix of lodgepole pine and Douglas-fir pioneered, both species persist. However, Douglas-fir often exceeds lodgepole pine in height and in some stands may be out-competing lodgepole pine for light. On the most mesic sites (transects C and D), early seral

lodgepole pine has yielded to mixed stands of Douglas-fir, western hemlock and western redcedar. However, lodgepole pine is still dominant primarily on ridgeline benches with shallow soils.

In general, only the low-elevation forests on transect D have similar composition and dynamics to lowland forests of the maritime Pacific Northwest (Franklin and Hemstrom 1981, Agee and Smith 1984, Oliver 1984, Stewart 1986, Agee *et al.* 1990, Huff 1995). Low to moderate elevation plots on transect D have more closed canopies and understories dominated by shade-tolerant species including western hemlock, western redcedar and Pacific yew. On these plots, Douglas-fir generally behaves as a shade-intolerant, early seral species and is absent or uncommon in the understory.

At sites higher than 1200 m elevation, tree species diversity is generally highest, with a mix of lowland and subalpine species. These high-elevation sites generally have had continuous recruitment following stand-replacing fires, spanning 130-170 yr. Some stands have reached canopy closure whereas others are still undergoing recruitment. Cold winter temperatures, ice storms, strong winds, and excessively-drained soils markedly reduce the annual productivity of these sites (Fonda and Bliss 1969, Peterson 1998). Because site productivity is low and environmental conditions favorable for tree establishment are sporadic, recruitment following a stand-replacing disturbance can extend over a century or more (Agee and Smith 1984, Agee 1993, Little *et al.* 1994). These high elevation sites favor species more adapted to cold, snow-dominated environments including Alaska yellow cedar, Engelmann spruce, lodgepole pine, mountain hemlock, Pacific silver fir, and subalpine fir. Douglas-fir and western hemlock, which are typically associated with low elevations, appear to have established at some of these high elevation sites immediately following stand-replacing disturbance events. Open conditions, which may have resulted in earlier spring snowmelt, and recently disturbed soils may have allowed these low-elevation species an opportunity to establish.

In summary, except for the most mesic sites, rates of forest succession, or replacement of pioneers by shade-tolerant species, are slow. At high elevations, a prolonged establishment phase allows both shade-intolerant and shade-tolerant species to

coexist. At low to moderate elevations, dry site conditions likely prevent shade-tolerant species such as western hemlock and western redcedar from establishing and surviving. In a study of limber pine (*Pinus flexilis*)-Engelmann spruce-subalpine fir forests of the Rocky Mountains, Donnegan and Rebertus (1999) reported more rapid rates of forest succession on mesic than on xeric sites in which pioneering species maintained dominance. Similar patterns were described by Romme and Knight (1981) in similar subalpine forest types of the Medicine Bow Mountains of Wyoming. Our study area contains a greater diversity of species and stand types, but we see similar variation in rates of recruitment, causing multiple trajectories of forest development across the landscape.

Conceptual Model of Forest Succession

Disturbances, especially fire, contribute to forest heterogeneity in the North Cascade Range. Because rates of forest succession are slow in dry and high-elevation types, fire return intervals of 75-125 yr (Agee *et al.* 1990) would continually reset succession, maintaining early seral communities. Even in the western Olympic Mountains, which have the highest precipitation in the maritime Pacific Northwest, Huff (1995) concluded that western hemlock and western redcedar were successfully recruiting into post-fire stands only after 150 yr of development. In Thunder Creek, in which sites are drier than in the western Olympics, succession toward dominance by shade-tolerant species is much slower. A combination of slow rates of species replacement and frequent fire maintains diverse stand composition and structures.

Based on our understanding of past fire and current successional trends, we have developed a conceptual model of fire and forest succession for this mountain landscape (Figure 15). At low to moderate elevations (500 to 1150 m), most forests follow convergent successional trajectories (*sensu* Frelich and Reich 1995). Although many species can establish after fire, succession tends toward dominance by Douglas-fir with codominance by western hemlock and western redcedar. Rates of succession are markedly slower on dry than on mesic sites. On the most xeric sites, lodgepole pine still

dominates 100-160 yr after fire; over time and without major disturbance events, Douglas-fir would likely recruit in the understory. However, it is unlikely that western hemlock and western redcedar would ever become significant components of these xeric forest types. On more mesic sites, Douglas-fir establishes with lodgepole pine or hardwood species, including bitter cherry and paper birch. Because Douglas-fir has more rapid height growth and greater longevity, forests gradually succeed to Douglas-fir dominance with some recruitment of western hemlock and/or western redcedar. On moist sites at low to moderate elevations, western hemlock and western redcedar either co-establish with Douglas-fir or recruit soon afterward to become codominant. Thus, in the absence of fire or other disturbances, most forests at low to moderate elevations might converge in composition, but xeric sites would likely maintain open stands of lodgepole pine and Douglas-fir. Stand-replacing fire, the primary disturbance agent in this watershed, appears to play a role in maintaining landscape heterogeneity by resetting forest succession and allowing a broad range of shade-intolerant and shade-tolerant species to coexist. Other potential sources of forest heterogeneity include disturbance agents not necessarily evident in static age structures, such as wind, bark beetles, and *Armillaria* or *Phellinus* root rot (Edmonds et al. 2000).

At high elevations, forest development patterns do not support a convergent model of succession. Harsh growing conditions, including cold temperatures, ice and wind storms, and persistent snowpack, all favor slow-growing subalpine species over Douglas-fir and other low-elevation conifers that lack adaptations to cold, snowy environments. High elevation environments likely prevent any individual species from becoming dominant because chance establishment in microsites plays an important role in species occurrence and survival (Agee and Smith 1984, Little *et al.* 1994). In general, recruitment periods are longest at high-elevation sites, and because establishment is often stochastic, forests follow multiple successional pathways, dictated by unique establishment histories.

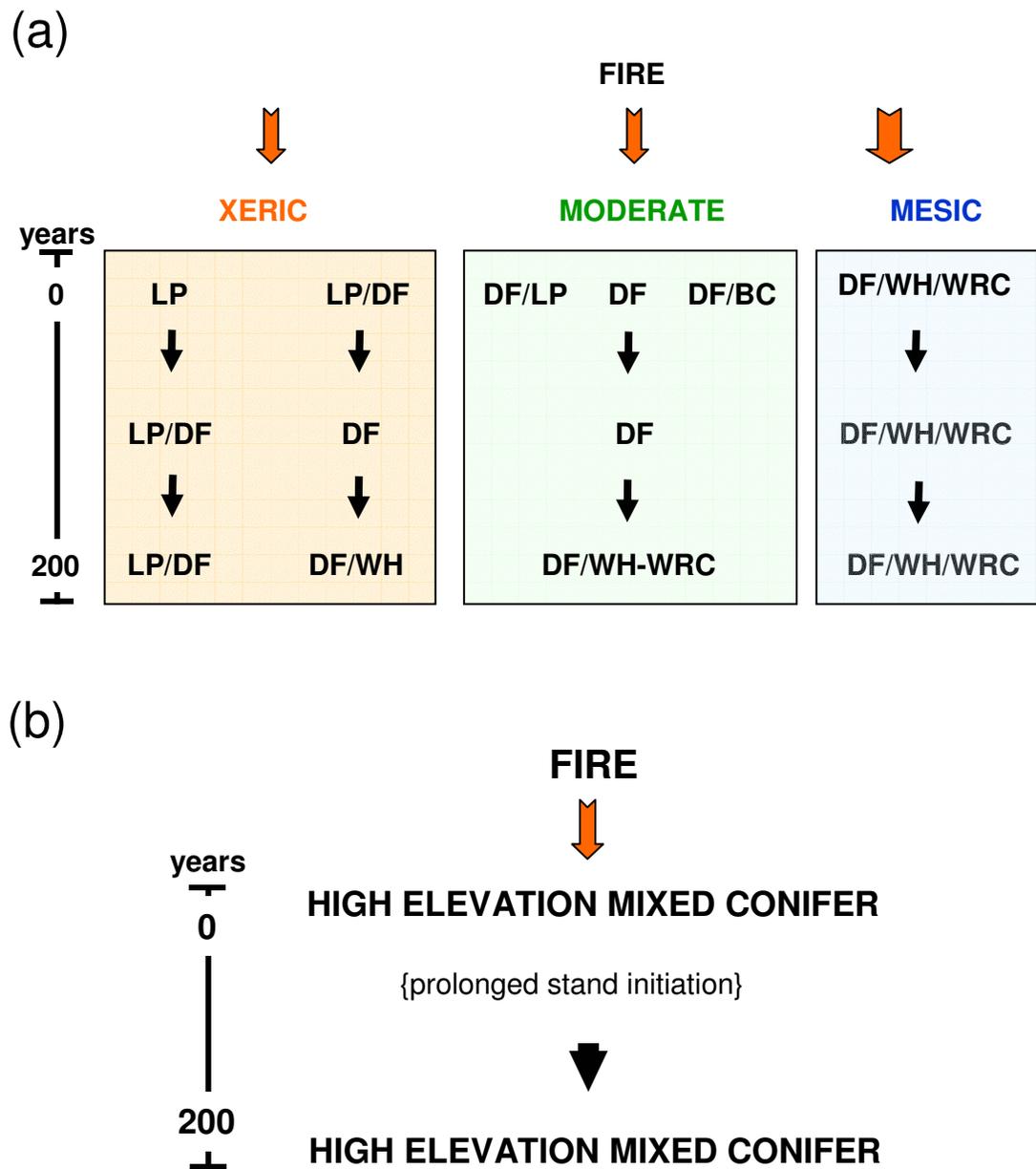


Figure 2.15 Conceptual model of successional trajectories following fire in a) low elevation and b) high elevation sites. BC = bitter cherry, DF = Douglas-fir, LP = lodgepole pine, WH = western hemlock, and WRC = western red cedar.

Conclusions

Mountain forests may be particularly sensitive to global warming (Armand 1992, Slatyer and Noble 1992, Zolbrod and Peterson 1999). Coarse resolution analyses, such as habitat classifications and simulations of vegetation change under climatic scenarios, currently overlook fine-scale gradients and inherent complexity in mountain ecosystems (Cook 1995, Neilson 1995, Bugmann and Solomon 2000). Understanding species dynamics along environmental gradients in space and time is necessary to simulate effects of climatic change on vegetation dynamics (Neilson and Marks 1994, Woodward *et al.* 1995, Waring and Running 1998). However, these models rely on coarse resolution environmental data that may be appropriate for latitudinal gradients but fail to capture local environmental heterogeneity in mountain forests (Waring and Running 1998, Bugmann and Solomon 2000).

An advantage of evaluating forest dynamics in mountainous areas is that large portions of the landscape are protected and have not been greatly affected by human activities, such as timber harvesting. In the Pacific Northwest region of North America, only a small fraction of the original forestland remains undeveloped and unharvested, much of which is contained within mountain reserves (Spies and Franklin 1988). Forested landscapes with intact disturbance regimes and ecosystems, such as those within North Cascades National Park, are vital to our knowledge of ecosystem structure and function. These sites provide important reference data, including historic range of variability in fire regimes and forest development following fire, for restoration and management of forest landscapes (Frelich and Puettmann 1999, Egan and Howell 2001).

CHAPTER 3: HOLOCENE FIRE AND VEGETATION DYNAMICS IN A MONTANE FOREST, NORTH CASCADES NATIONAL PARK, WASHINGTON

Introduction

With their complex topography and steep environmental gradients, mountains are important refuges for biological diversity (Peterson 1998, Delcourt and Delcourt 1998). Over relatively small areas, a wide range of environments and life zones are supported by abrupt shifts in elevation and aspect (e.g., Peterson et al. 1997). The fine-scale complexity of mountain systems may also make them especially sensitive to climatic change (Delcourt and Delcourt 1998, Hansen et al. 2001, Gitay et al. 2002). At high elevations, many species exist at altitudinal limits of their distribution and are particularly responsive to growth-limiting factors such as snowpack duration, growing degree days, site moisture, and local disturbance regimes (Graumlich 1991, Little et al. 1994, Ettl & Peterson 1995, Peterson 1998, Peterson & Peterson 2001). Rapid changes in climate associated with global warming (McCarthy et al. 2001) may catalyze shifts in mountain environments, and in the case of species associated with subalpine or alpine areas, may restrict or eliminate their available growing space (Delcourt and Delcourt 1998, Iverson and Prasad 2001, Gitay et al. 2002). Fire regimes may also be responsive to changes in climate and influence vegetation assemblages (Clark 1990, Dale 2001). Understanding how mountain environments responded to past changes in climate may help us to interpret current patterns and drivers of biological diversity in mountains and to predict how these systems may respond to future climatic change (Webb 1992, Bartlein et al. 1997, Delcourt & Delcourt 1998, Shafer et al. 2001).

The Pacific Northwest is dominated by prominent mountain ranges, but we know little about the contemporary vegetation in mountains relative to low elevations and even less about the long-term history of vegetation. Few paleoecological reconstructions have focused on high elevations in the Pacific Northwest (but see Dunwiddie 1986, Pellatt et al. 1998, Pellatt et al. 2000, and Gavin et al. 2001), and there is a particular lack of information on the North Cascade Range. Our understanding of Holocene climate-

vegetation dynamics in the Pacific Northwest is mostly instructed from studies at low elevation sites in western Washington, western Oregon and southwestern British Columbia (see Brubaker 1991, Whitlock 1992 and Thompson et al. 1993 for reviews) and simulations of late Quaternary climatic change (Thompson et al. 1993). At the end of continental glaciation, regional climate warmed rapidly. During the early Holocene warm period, (c. 10,000 to 6000 radiocarbon years before present (BP)), *Pseudotsuga menziesii* and *Alnus rubra* were prominent in the lowlands, and based on lake sediment charcoal records, fires may have been more frequent than today (Cwynar 1987, McLachlan & Brubaker 1995, Long et al. 1998, Brown and Hebda 2002). Modern forest assemblages, which included late successional species such as *Tsuga heterophylla* and *Thuja plicata*, began to establish c. 8000 BP as regional climate shifted toward the cooler and moister conditions typical of the present-day coastal Pacific Northwest. In the interior Pacific Northwest, the onset of modern cool-moist climatic conditions appears to have been delayed. Paleoecological investigations in northeastern Washington and southern-interior British Columbia suggest that the Holocene warm period extended until c. 4500 to 2500 BP (Mack et al. 1978, 1979, Mehringer 1985, Mathewes and King 1989, Hebda 1995, Pellatt et al. 1998, 2000).

Although regional climatic forcings were likely important in mountain environments, the type and timing of vegetation changes may not have been analogous to lowland sites due to differences in elevation, heterogeneous terrain, and more extreme growing conditions. For example, at a high-elevation site in the central Olympic Mountains, alpine tundra persisted throughout the early Holocene and was not invaded by conifers until c. 7000 BP, whereas subalpine forests expanded during the same time period at a site in the northeastern Olympic Mountains (Gavin et al. 2001). At a dry, subalpine site in the northernmost extent of the Cascade Range, Pellatt et al. (1998, 2000) interpreted a warm-moist period of high forest productivity from c. 6700 to 3500 BP. So few Holocene records are available in mountainous areas that we do not have an adequate understanding of the regional vegetation history in mountains.

In this study, we reconstructed fire and vegetation history from a c. 10,500 cal yr (9300 BP) sediment record sampled from a small (0.4 ha) montane lake in the North Cascade Range. The site is located near the Cascade crest, and climate is transitional between the coastal and inland sides of the mountains. In addition, the montane forest surrounding our study site has eleven conifer species, an unusually high diversity for Pacific Northwest forests (Waring & Franklin 1979, Franklin & Dyrness 1988), are present. Vegetation is likely to be sensitive to climatic variability because many tree species exist at regional or altitudinal limits of their distribution. Our main objectives were to 1) to reconstruct the local history of fire and vegetation at this montane site in the North Cascades and 2) evaluate how this long-term record compares with other paleoecological records in the Pacific Northwest and contributes to the regional vegetation history in mountains.

Pollen and abundant macrofossils of conifer needles made it possible to construct a record of both local and regional vegetation. Macrofossil and fossil pollen records generally contribute similar information to reconstructions of vegetation but differ in terms of spatial signal, abundance, and taxonomic specificity. Macrofossils tend to represent local vegetation within 30 m of lakes (Dunwiddie 1987), are usually identifiable to species, and when abundant, their relative abundance may correspond to the relative basal area of local conifers (Dunwiddie 1987). Fossil pollen from lake sediments produces a broader, regional signal of vegetation and generally has less taxonomic resolution (Faegri and Iversen 1975, Prentice 1985, Sugita 1994). When combined, macrofossil and fossil pollen records are complementary; macrofossils represent local vegetation with high taxonomic resolution and fossil pollen provides a regional context of the local macrofossil record (e.g., Dunwiddie 1986, Wainman & Mathewes 1987).

We reconstructed historic fire events from high resolution lake sediment charcoal records to evaluate changes in fire regimes over the Holocene and possible interactions with vegetation. Fire histories based on lake sediment charcoal rely on the

decomposition of a slowly varying background charcoal accumulation rate and a rapidly varying peak component, which represent fire events (Long et al. 1998, Whitlock & Anderson 2003). In the Pacific Northwest a few other long-term fire history records have been constructed from lake sediment charcoal records (Long et al. 1998, Fujikawa 2002, Hallett et al. 2002) and allow for a comparison with results of this study.

Study area

The study area is located in a mixed conifer forest on Fourth of July Pass, elevation 1100 m, near the center of North Cascades National Park (48° 39' N, 121° 02' W) (Figure 3.1). Climate is transitional between the maritime (moist) west-side and inland (dry) east-side of the Cascades. At the nearest recorded weather station (Diablo Dam, Washington, 300 m elevation and 5 km west of the study site), mean annual precipitation over the period 1959-2001 was 191.0 cm (December high 31.9 cm, July low 3.9 cm) and temperature ranged from an average annual maximum temperatures of 14.1°C (August high 25.1°C) to average annual minimum temperatures of 4.3°C (January low -2.6 °C) (Western Regional Climate Center, <http://www.wrcc.dri.edu>). Approximately 90% of average annual precipitation falls between October and May.

Sediment cores were extracted from one of the Panther Potholes, a set of small lakes situated on Fourth of July Pass. The mountain pass was carved by alpine glaciers during the Fraser Glaciation, and local site geology is part of the Skagit Gneiss Complex (Tabor & Hagerud 1999). The lake is small (< 0.5 ha), shallow (1 to 5 m), fed by an intermittent stream that connects the two lakes, and has a small outlet. The immediate watershed is mostly forested with interspersed talus fields and cliffs.

The montane forest surrounding the Panther Potholes is ecotonal between low-elevation assemblages of *P. menziesii*, *Taxus brevifolia*, *T. plicata* and *T. heterophylla*, and high elevation assemblages of *Abies amabilis*, *A. lasiocarpa*, *Chamaecyparis nootkatensis*, *Picea engelmannii*, *Pinus monticola*, and *Tsuga mertensiana*. *A. lasiocarpa* is common along the lakeshore, and *A. amabilis*, *P. menziesii*, *T. plicata*, and *T.*

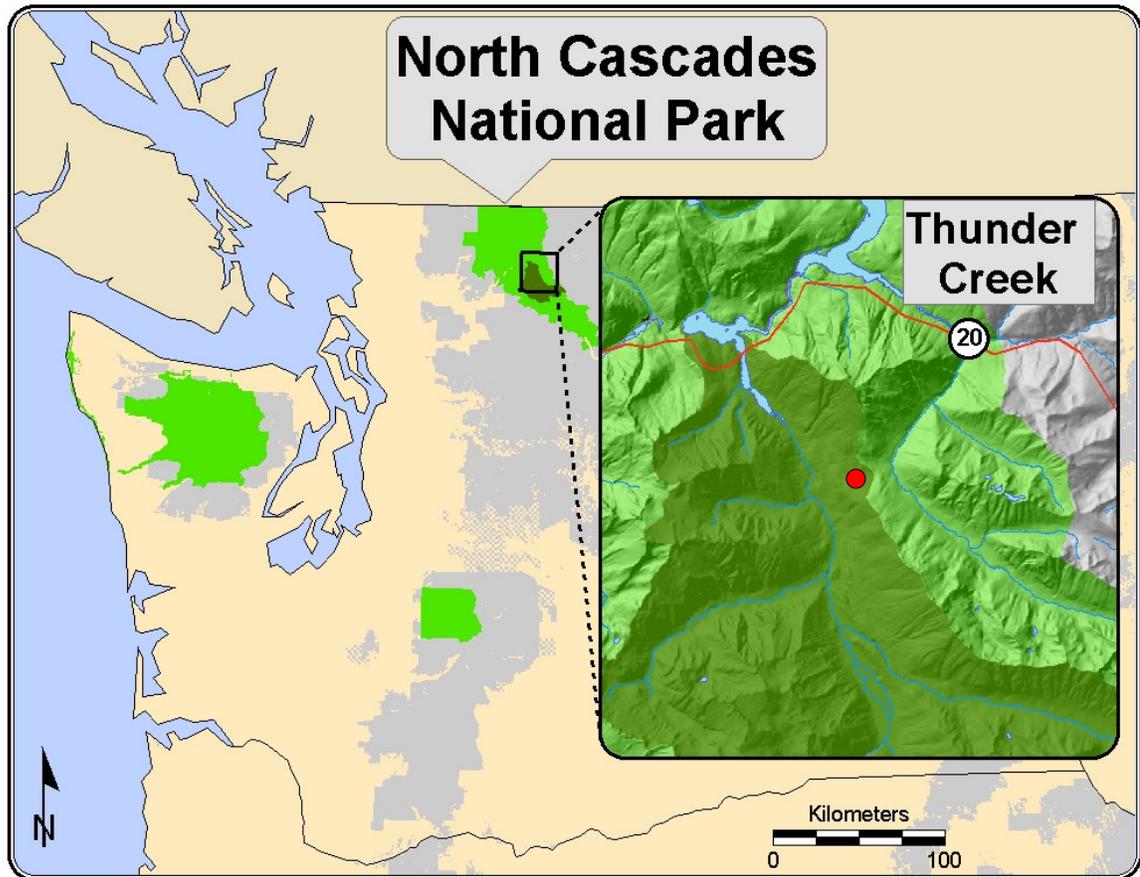


Figure 3.1 Study area.

heterophylla are associated with the upland forest. Numerous snags of *P. monticola* indicate that this species was until recently a common stand associate. *P. contorta* is not present within the immediate study area but is locally abundant within 0.5 km of the study site. *Alnus sinuata* is present on the lakeshore but is absent in upland forests. Understory and/or lakeside shrub and herbaceous species include: *Cornus canadensis*, *Clintonia uniflora*, *Mahonia nervosa*, *Menziesia ferruginea*, *Pyrola asarifolia*, *Vaccinium membranaceum*, *V. parvifolium*, and *Viburnum edule*.

Methods

Lake sediment sampling

At the deepest location of the lake (Figure 3.2), two parallel sediment cores were extracted approximately 1 m apart with a 5-cm diameter modified Livingston piston sampler (Wright et al. 1984). The top 0.5 m of sediment, including the mud-water interface, was sampled with a clear plastic, 7.6-cm diameter tube, held vertically and immediately sectioned into 1-cm intervals. The remainder of the cores were extruded horizontally in the field, wrapped in plastic wrap and aluminum foil, and encased in PVC piping. Cores were air lifted out of the backcountry via helicopter and transported to cold storage (4 °C) at the University of Washington.

Modern vegetation sampling

The modern forest surrounding the Panther Potholes was sampled for species composition, density, basal area and tree age. Five belt transects (10m by 100m), radiating from approximately equidistant locations of each lake, were sampled for tree species and diameter at breast height (dbh). A 0.05-ha circular plot was established at 50 m along each transect. Within each plot, all trees were identified and measured for dbh, and a subsample of 10-20 trees was cored to construct age structures.

Additional tree age and fire scar data were collected to calibrate sediment charcoal peaks with known fires surrounding the lake basins. Stand boundaries within an approximately 10-km² area around the Panther Potholes were mapped using aerial

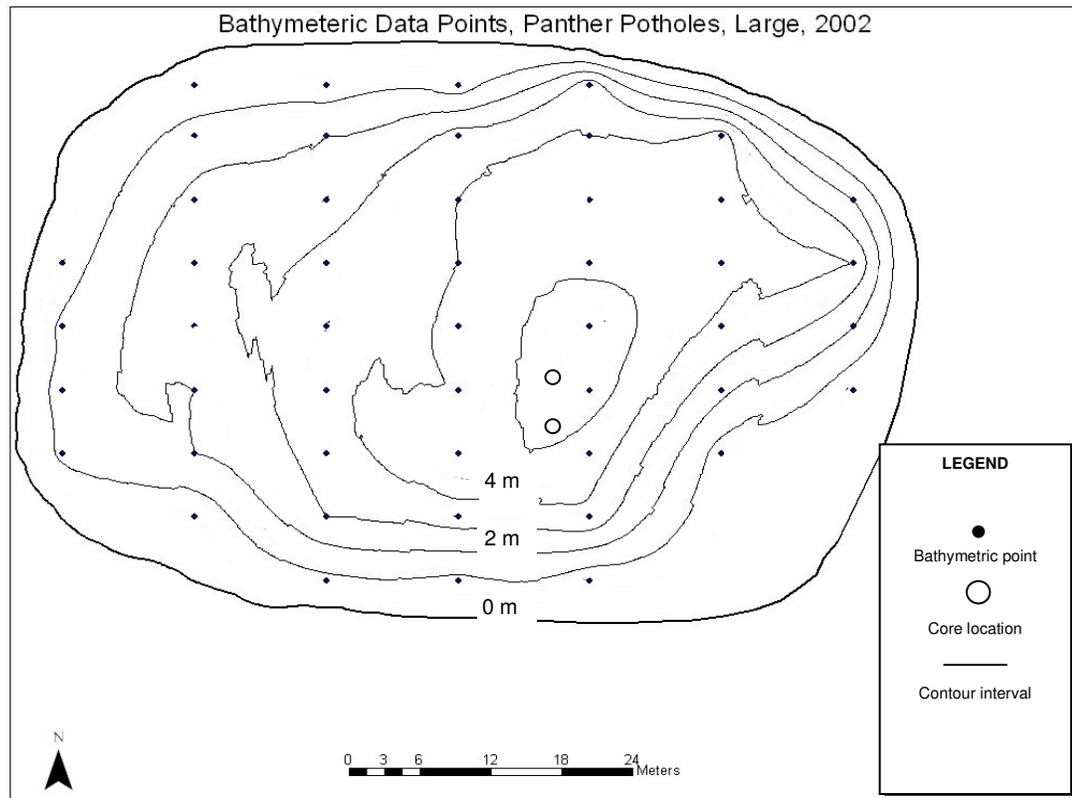


Figure 3.2 Bathymetric map with 0.5-m contours.

photos, and increment cores were extracted from randomly-selected dominant trees within delineated stands. Two fire scars were located and sampled with increment borers (Agee 1993). Tree cores were air dried, then mounted and sanded with progressively finer sandpaper until individual cell walls were discernible under a dissecting microscope. All tree cores were visually cross dated according to Stokes & Smiley (1968).

Laboratory analysis

Sediment sampling

We selected the longer of the two sediment cores for further analysis. The sediment core was sectioned into 1-cm, contiguous samples, and 1-cm³ from each sample was archived for pollen analysis. Prior to processing, magnetic susceptibility (in electromagnetic units (emu)) was measured on all samples using a Sapphire SI-2 magnetic susceptibility meter with a coil-cup sampling device (Thompson & Oldfield 1986, Millspaugh et al. 2000). Magnetic susceptibility is a rapid measure of bulk sediments that can detect the presence of minerals deposited following fire events (Patterson et al. 1987, Millspaugh & Whitlock 1995). Because the sediment core was sampled in 1-m drives, contamination between drives was unavoidable. Contamination was detected by visual inspection and by peaks of magnetic susceptibility at the top of drives, which detected tephra particles that had settled from upper sediments. Contaminated samples were excluded from all subsequent analyses.

Charcoal

Samples were soaked for 72 hours in a known volume of 10% sodium metaphosphate solution to aid in sediment dispersal. Prior to sieving, the total volume of sediment in solution was measured to calculate the actual sediment volume (i.e., total volume minus known volume of dispersal agent). Sediments were then gently washed through 500- and 150- μ m sieves. Prior to charcoal counting, the 150 to 500- μ m sieve fraction was bleached with an 8% hydrogen peroxide solution for 8 hours and rewashed to terminate the bleaching process. Charcoal fragments were identified and tallied using

a stereomicroscope at 10-40X magnification. Because charcoal fragments in the >500- μm fraction were rare, they were combined with the 150 to 500- μm fraction for subsequent analyses.

Macrofossils

Macrofossils of conifer needles were collected from the >500- μm fraction and identified to species using a published key (Dunwiddie 1985) and a modern reference collection. Needle fragments (tips and bases) were tallied as needle equivalents and identified to species with the following exceptions. *P. contorta* and *P. monticola* needle fragments were too numerous to reconstruct into needle equivalents. Instead, fascicles were tallied as needle equivalents (after Dunwiddie 1987). Branchlets (i.e., clusters of two or more scales) of *C. nootkatensis* and *T. plicata* were tallied as needle equivalents. *A. amabilis* and *A. grandis* are indistinguishable by needle morphology; *Abies* needles other than *A. lasiocarpa* were classified to genus.

Pollen

A total of 60 1-cm³ subsamples was selected for pollen analysis. Pollen samples were prepared for analysis using standard methodology (Faegri & Iversen 1975). Tablets containing *Lycopodium* spores were added to allow measurement of pollen concentrations and estimation of pollen accumulation rates (Stockmarr 1971). Pollen residues were mounted in silicon oil, and pollen grains and spores were counted at 400X or 1000X magnification. At least 300 pollen grains of terrestrial taxa were counted for each sample, and all pollen and spore percentages are expressed as a percentage of the sum of identified and unidentified pollen grains. Based on 25-30 pollen grains per sample, *A. sinuata*-type and *A. rubra*-type pollen grains were separated by pore morphology (Sugita 1990), and *Pinus* pollen was separated into diploxylon and haploxylon types (McAndrews et al. 1973).

Sediment Chronology

A sediment core chronology was created using AMS radiocarbon, ^{210}Pb and tephra dates. Three tephra layers were identified using glass chemistry analysis (N. Foit, Washington State University Electron Microbeam and X-ray Analysis Labs, Pullman, WA). Radiocarbon dates were obtained for six macrofossils (conifer needles and seeds) using Accelerated Mass Spectrography (AMS) and were calibrated using a 2- σ calibration (95% probability) (Talma et al. 1993). ^{210}Pb activity was measured on 7 samples in the upper 35 cm of the mud-water interface, and sedimentation rates were modeled using slope regression model and constant rate of supply (CRS) models, both of which yielded similar results (Flett Research Ltd., Manitoba, Canada). A third-order quadratic age-depth model was constructed from tephra and AMS radiocarbon dates ($r^2 = 0.99$). To account for rapid sedimentation rates for the top 35 cm, a linear model was constructed from five ^{210}Pb dates. The two chronologies were linked at lowest modeled ^{210}Pb date, c. 85 years.

Analytical methods

Macrofossil source area

The relative abundance of macrofossils was summarized over the first 500 years of the sediment record and compared with the relative basal area of tree species at 0-25m and 0-100m distances from the lake.

Calculation of CHAR, MFAR and EMAR

Sedimentation rates based on the sediment chronology were used to convert charcoal and macrofossil concentrations (pieces or needles equivalents cm^{-3}) to accumulation rates (CHAR – charcoal pieces $\text{cm}^{-2} \text{yr}^{-1}$, MFAR – macrofossil needle equivalents $\text{cm}^{-2} \text{yr}^{-1}$). Macrofossil accumulation rates were calculated by species and total needle equivalents. Magnetic susceptibility (emu) was also converted from emu cm^{-3} to $\text{emu cm}^{-2} \text{yr}^{-1}$. Accumulation rates were interpolated to evenly spaced 10-year

intervals, which approximates the mean sedimentation rate of the core ($9.2 \pm 1.9 \text{ cm}^{-2} \text{ yr}^{-1}$).

Fire history interpretation

CHAR peaks were decomposed into background and peak components using Charcoal Analysis Programs (CHAPS) detailed in Whitlock and Anderson (2003). This decomposition method is based on the calculation of background CHAR with a locally weighted running mean and selection of a threshold ratio for peak detection. More specifically, background CHAR is multiplied by the threshold ratio, and charcoal peaks exceeding this value are delineated as fire events. Background levels were evaluated by calculating a series of weighted running means on log-transformed CHAR over varied window widths (250, 600, 750, 1000, 1250 and 1500 years). Based on visual inspection, the number of CHAR peaks above the running mean stabilized between 500 and 1200 years. A mid-range window width of 750 years was then selected to evaluate a range of threshold ratios (1-3). Because the entire range of threshold ratios detected recent, known fire events, we evaluated CHAR frequency distributions over the range in threshold ratios to determine which thresholds captured the second mode (right tail) of CHAR distributions (Chapter 4). A threshold ratio of 1.4 and multiplied by the CHAR background to delineate fire events. Fire event frequency was summarized by calculating a locally-weighted mean frequency of fires from a binary time series (1 = fire event, 0 = no fire event) smoothed with a 2000-year window width (Whitlock and Anderson 2003). Mean fire return intervals (MFRI) were summarized by major vegetation zone time periods, and significant differences were tested using a Kruskal-Wallis test at $p = 0.1$.

Results and interpretation

Macrofossil source area

Macrofossils from the first 500 years of lake sediments correspond fairly well to estimates of tree basal area from vegetation surveys (Figure 3.3). Tree basal area from 100-m transects has a better correspondence to the macrofossil record than that of the

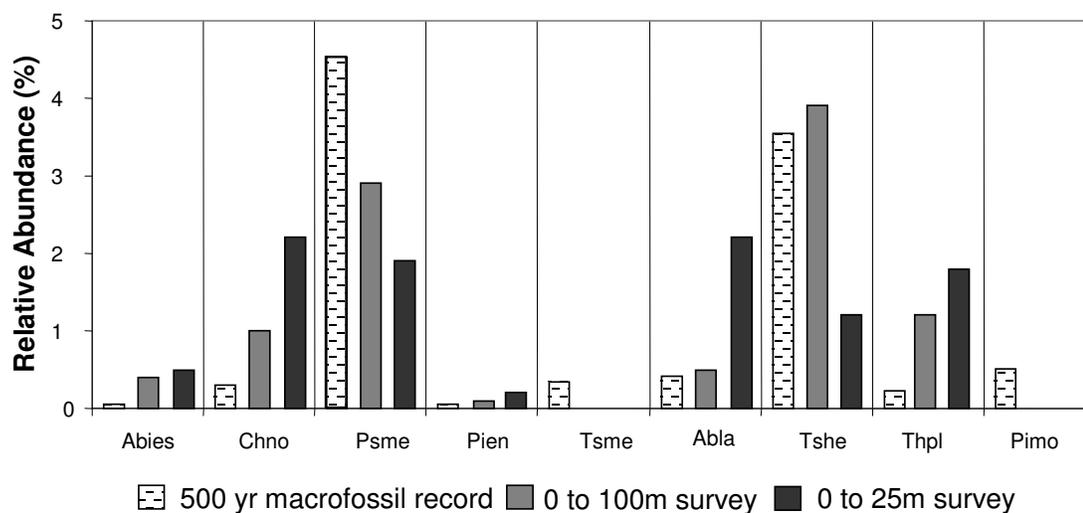


Figure 3.3 Relative abundance (%) of tree species in the most recent 500-year macrofossil record and relative tree basal area (%) in the 0-to-100-m and 0-to-25-m belt transect surveys. Abies = Pacific silver fir in modern vegetation surveys, Chno = Alaska yellow cedar, Psme = Douglas-fir, Pien = Engelmann spruce, Tsme = mountain hemlock, Abla = subalpine fir, Tshe = western hemlock, Thpl = western redcedar, and Pimo = western white pine.

0-to-25-m belt transect distance. The relative basal area of *A. amabilis*, *C. nootkatensis*, and *T. plicata* are underrepresented in the macrofossil record and *P. menziesii* is overrepresented. This may be explained by the height difference between *Pseudotsuga menziesii* and the other two species (S. Prichard, personal observation); taller trees with larger canopies may have a disproportionate contribution to the macrofossil record. Leaf turnover rates may also be greater in *Pseudotsuga menziesii* than these shade-tolerant species (T. Hinckley, University of Washington, personal communication).

Core stratigraphy and chronology

The sediment core consists almost entirely of uniform fine detritus gyttja. Magnetic susceptibility levels are mostly undetectable; major peaks are associated with tephra deposits. Three tephra layers were present and identified as Mount St. Helens W at 303-308 cm (470 cal BP), Mount St. Helens Y at 396-406 cm (2930-3510 BP, 3300-4000 cal BP), and Mazama Climactic at 623-639 cm (6850 BP, 7610-7690 cal BP) (Table 3.1). All tephra layers matched known standards with high similarity coefficients (r^2 0.99, 0.97, and 0.99, respectively). However, the Mount St. Helens W was a clear outlier in the age-depth model (Figure 3.4) and could have been misidentified. Given that its depth falls around 2800 yrs cal BP on the age-depth curve, this tephra layer may actually be Mount St Helens B or P, although the current match is inconclusive (N. Foit, Washington State University, personal communication). The six AMS radiocarbon dates (Table 3.2) range from the basal date of 9370 ± 40 BP ($10,545 \pm 115$ cal BP) at 864 cm to the most recent date of 1950 ± 50 (1895 ± 95 cal BP) at 214 cm. All AMS radiocarbon dates and two of the tephra layers fall on a straight line (Figure 3.4). The oldest modeled ^{210}Pb date (Table 3.3) is 85 years BP at 35 cm.

Vegetation history

Four major vegetation zones (Table 3.4) were subjectively delineated based on broad changes in macrofossil assemblages (Figure 3.5).

Early Holocene Zone (EH) (c. 9300 to 7100 ^{14}C BP, c. 10,500 to 7700 cal BP). *P. contorta* dominates the early Holocene macrofossil record and is particularly dominant between c. 9000 and 8000 cal BP (Figure 3.6). *A. lasiocarpa*, *P. monticola*, and *P. menziesii* are less important but have higher macrofossil accumulation rates than at any other time in the Holocene. Macrofossils of *P. engelmannii*, *T. mertensiana* and *Abies* species other than *A. lasiocarpa* are present but uncommon throughout this zone. Pollen percentages of diploxylon-type pine are high in this zone, corroborating the dominance of *P. contorta* (Figure 3.7, 3.8). *Abies* and *Pseudotsuga*-type pollen percentages are low (5-10% respectively); individuals of these taxa are low pollen producers and are typically underrepresented in pollen records (Pellatt et al. 1997). Although *P. monticola* was common in the macrofossil record, haploxylon-type pollen is notably absent or rare throughout much of this zone. *Alnus* pollen percentages are high (30-60%) in the early Holocene with a greater contribution from *A. sinuata*-type than *A. rubra*-type. Of the nonarborescent taxa, the relative abundance of Rosaceae and *Artemisia* pollen is highest in this zone. Background charcoal accumulation rates (CHAR) are at their highest levels in this zone, but fire frequency, based on detected CHAR peaks, is not significantly different than the mid- or late-Holocene periods. Fire return intervals are highly variable, and the mean fire return interval for this period is 201 ± 110 yr (Table 3.5).

At the Panther Potholes, the early Holocene is distinguished by a mixed conifer assemblage of *P. contorta*, *P. menziesii*, *P. monticola* and *A. lasiocarpa*. Based on species composition, this assemblage is more similar to xeric, subalpine communities currently found in the eastern Cascade Range (Franklin and Dyrness 1973) or Rocky Mountains (Alexander 1987, Smith and Fisher 1997) than to the modern forest assemblage at Panther Potholes. At c. 9000 cal BP, forest composition appears to have shifted from a mixed conifer forest to one dominated by *P. contorta* with a minor component of, *A. lasiocarpa*, *P. monticola*, and *P. menziesii*. The relatively high percentages of *Artemisia* and Rosaceae pollen throughout this zone suggest that forest canopies were open and supported understories of these taxa (Figure 3.7). As is the case today, *A. lasiocarpa* may have been localized in the cold air drainage of the Panther

Potholes watershed (Fonda & Bliss 1969, Franklin & Dryness 1988). Pollen from deciduous taxa, including *A. rubra*, *Populus* and *Betula* may have originated from lower elevations, likely the riparian forest along Thunder Creek. Although *A. rubra*-type and *Betula* pollen are present in the uppermost sediments at Panther Potholes, the nearest current populations of *A. rubra* and *B. papyrifera* are located at lower elevations near Thunder Creek (S. Prichard, personal observation).

During the early Holocene, summers were likely warmer than they are today while winters were colder due to differences in seasonal insolation (Thompson et al. 1993). Warm, dry summers probably perpetuated a dry, montane forest assemblage dominated by *P. contorta*. High levels of *Alnus* pollen may have originated from large patches of *A. sinuata* (Franklin & Dryness 1988, Gavin et al. 2001). Heine (1998) reports evidence of glacial advances from c. 10,900 to 9950 cal BP at Mount Rainier, indicating greater snow accumulation during this period. Snow avalanches may have been more common in the early Holocene and supported a greater abundance of *A. sinuata* (Gavin et al. 2001).

An early Holocene warm period is distinct in most interpretations of Holocene vegetation in high- and low-elevation sites throughout western Washington and southern British Columbia. Most low elevation sites tell a similar story: during the early Holocene, a high relative abundance of *P. menziesii* is associated with high accumulations of lake sediment charcoal. A common interpretation is that short fire intervals perpetuated the dominance of early seral species over *T. heterophylla* on the lowland landscape (Barnosky 1981, Leopold et al. 1982, Cwynar 1987, McLachlan & Brubaker 1995, Brown & Hebda 2002).

The few existing Holocene reconstructions at subalpine sites demonstrate vegetation responses to the early Holocene warm period, but patterns of vegetation change are more site specific. At a subalpine site in southwestern interior BC, where the current climate is considerably drier than at our study area, Pellat et al. (2000) describe the replacement of alpine tundra with a subalpine parkland of *A. lasiocarpa*, *P.*

engelmannii, and *P. albicaulis* c. 11,500 to 7800 cal BP. They also note high levels of *A. sinuata*-type pollen and maximum lake sediment charcoal concentrations during this period. At a subalpine site in the northeastern Olympic Mountains, Gavin et al. (2001) report an expansion of subalpine forest into alpine tundra, high levels of *Alnus* pollen, and an increase in charcoal concentrations during the period between c. 13,000 and 8500 cal BP. In contrast, a subalpine site in the central Olympics remained dominated by alpine tundra during this period, possibly due to high snow accumulations and shorter growing seasons during much of the early Holocene (Gavin et al. 2001).

The presence of *P. monticola* at the Panther Potholes during the early Holocene is somewhat surprising, considering that it appeared later at other sites in western Washington and western Oregon. Based on the few existing records in western Washington and Oregon (Barnosky 1981, Cwynar 1987, MacDonald et al. 1998), *P. monticola* appears to have arrived in the southern Puget lowland c. 8300 cal BP (Barnosky 1981) and northern Puget Lowland c. 7800 cal BP (Cwynar 1987) several thousand years later than is reported here. In general, the post-glacial record of *P. monticola* is sparse (MacDonald et al. 1998). Previous studies suggest that *P. monticola* survived the glacial maximum in the coast mountains of Oregon (Critchfield 1984, MacDonald et al. 1998). However, there may have been refugial populations on the east side of the Cascade Range (Mack et al. 1979) that were responsible for the early arrival of *P. monticola* at the Panther Potholes. An alternative explanation is that macrofossils of this species may have been misidentified in the early Holocene. Most *Pinus* needle fragments were poorly preserved in the early Holocene sediment record. Even under ideal circumstances it is difficult to distinguish between *P. monticola* and *P. albicaulis* solely on needle morphology. It is possible that there was an early Holocene population of *P. albicaulis* at this site.

Mid Holocene Zone (MH) (c. 7100 to 4500 ¹⁴C BP, c. 7700 to 5200 cal BP). The start of the mid Holocene zone c. 7700 cal BP (Figure 3.8) is marked by an abrupt decrease in *P. contorta* macrofossil accumulation rates. Although macrofossil

accumulation rates of all species are substantially lower than in the early Holocene, *A. lasiocarpa*, *P. monticola*, and *P. menziesii* remain important. In contrast to *P. contorta* macrofossil record, diploxylon-type pine percentages are high throughout this zone (Figure 3.7). Around 7600 BP, *Alnus* pollen drops from approximately 40% to 10-15%. Percentages of *Pseudotsuga*-type, *Abies*, and haploxylon-type pollen increase throughout this zone. *T. heterophylla* gradually increases in the pollen record starting c. 7000 cal BP but is absent from the macrofossil record until c. 5000 cal BP. Background CHAR decreases during the mid Holocene, and peak amplitudes are markedly lower than in the early Holocene. Fire frequency is somewhat higher than the early Holocene (Figure 3.5) but the difference in mean fire return intervals between these periods is not significant (Table 3.5). Although the drop in background CHAR could have resulted in an artificially high frequency during the mid Holocene, the trend in higher fire frequency is insensitive to a wide range of threshold ratios.

There is a pronounced drop in both CHAR and MFAR from c. 7500 cal yr BP to c. 4000 cal yr BP (Figure 3.5). The core chronology indicates no major change in sedimentation rates that would explain this change in accumulation rates. The drop is initially associated with the Mazama tephra layer, but CHAR and MFAR remain low for several millennia. It is possible that the forests surrounding the Panther Potholes during the mid Holocene were relatively open and contributed lower macrofossil input than in the early and late Holocene periods. Lower fuel loads also could have resulted in low background and peak CHAR values.

Around 7700 cal BP, the forest assemblage around Panther Potholes underwent a major transition from a dry forest type dominated by *P. contorta* to mixed conifer forests of *A. lasiocarpa*, *P. monticola*, *P. menziesii* and a relatively small component of *P. contorta*. Although *T. heterophylla* does not appear in the macrofossil record until around 5000 cal BP, its gradual rise in the pollen record starting around 7000 cal BP suggests it became more important in the general vicinity, likely at lower elevations. The decrease in *Alnus* pollen suggests that it was less important in the general vicinity.

Changes in regional climate may have been responsible for the shifts in vegetation during the mid Holocene. Pollen records in northern Washington and southern British Columbia document a major shift in vegetation around 7800 cal BP, suggesting climatic forcing of regional vegetation change. At low elevations sites pollen of late successional species including *T. plicata* and *T. heterophylla* increased while *P. menziesii* and *A. rubra* pollen and lake sediment charcoal accumulation rates declined (Cwynar 1987, Wainman & Mathewes 1987, McLachlan & Brubaker 1995, Brown & Hebda 2002). At a subalpine site in interior BC, Pellatt et al. (2000) documented an increase in conifer abundance starting c. 7800 cal BP, indicating more closed canopy conditions, which they attribute to warmer and moister climatic conditions than at present. In the northeastern and central Olympic Mountains Gavin et al. (2001) described a gradual decrease in *Alnus* and an increase in conifer species including Cupressaceae (likely *C. nootkatensis*) c. 8500 cal BP and *Pinus*, *T. heterophylla*, and *T. mertensiana* c. 7800 cal BP. Climatic conditions east of the Cascades may have remained relatively hot and dry for a few millennia longer than that west of the Cascades (Mack et al. 1979, Dunwiddie 1986). In the Okanogan Valley east of the North Cascade Range, Mack et al. (1979) report that xeric, *Artemisia* shrub-steppe was not replaced by modern forests dominated by *P. menziesii* until c. 5700 cal BP.

Late Holocene Zone a (LHa) (c. 4500 to 2000 ¹⁴C BP, c. 5200 to 2000 cal BP). *T. plicata* and *T. heterophylla* macrofossils appear nearly synchronously at the start of this zone (Figure 3.9). Accumulation rates of *A. lasiocarpa*, *P. monticola*, and *P. menziesii* macrofossils are similar to those of the mid Holocene, whereas *P. contorta* macrofossils are rare. *T. heterophylla* pollen percentages rise markedly c. 4800 cal BP, supporting macrofossil evidence that populations established near the Panther Potholes around this time (Figure 3.7). Cupressaceae pollen gradually increases throughout this zone and corresponds well with increasing abundances of *T. plicata* macrofossils. Diploxylon type pollen generally decreases throughout this zone. Background CHAR increases slightly and peak amplitudes are higher in the late Holocene, starting c 4000 cal

BP. The MFRI for this period is 182 ± 96 (SE) years, and there is no significant change in fire frequency from the mid to late Holocene periods (Table 3.5).

Late Holocene Zone b (LHb) (*c.* 2000 cal BP to present). *C. nootkatensis* first appears in the macrofossil record *c.* 2000 cal BP (Figure 3.10). A small cluster of *C. nootkatensis* branchlets was identified much earlier in the record, *c.* 5000 cal BP but probably represents a rare individual. Cupressaceae and *T. heterophylla* pollen generally increases over the last 2000 years while *Pinus* and *Alnus* pollen generally decrease (Figure 3.7). *T. heterophylla* markedly increases in both macrofossil and pollen records around 500 cal BP. Although macrofossil evidence of *T. mertensiana* is scarce, there is a slight increase of *T. mertensiana* pollen percentages throughout this zone. There is also a small increase in the occurrence of Ericaceae pollen in the last 1000 years. No appreciable changes are apparent in the charcoal record during this period.

During the last *c.* 5000 years the forest assemblage at the Panther Potholes shifted to its modern species composition, suggesting a change toward a cooler, moister climate. *T. plicata* and *T. heterophylla* first appeared at the site *c.* 5200 cal BP and gradually increased in relative abundance to present. Forests may have grown denser in the late Holocene based on the increase in late successional species, such as *T. plicata* and *T. heterophylla*, and low representation of nonarboreal taxa. *C. nootkatensis* arrived last, *c.* 2000 cal BP. *T. mertensiana* has never been abundant at the Panther Potholes, but its increase in the pollen record in the last 2000 years along with the increase in *C. nootkatensis* may indicate that the last two millennia have been particularly cool and moist. Both species are typically found at high elevations on moist sites in the Pacific Northwest (Franklin & Dyrness 1988). The greater occurrence of Ericaceae pollen in the last 1000 years also suggests cooler, moister climatic conditions. The modern forest assemblage has the highest diversity of tree species of any time in the Holocene and may be the result of neoglacial cooling over the last 2000 years (Porter et al. 1967, Pellatt et al. 2000).

Regional climatic changes appear to have been responsible for the major vegetation changes at the Panther Potholes. The onset of cooler, moister climatic conditions in the late Holocene is commonly interpreted from pollen records of late Holocene vegetation change in western Washington and southern British Columbia. Some studies (McLachlan & Brubaker 1995, Wainman & Mathewes 1987, Gavin et al. 2001) describe the mid and late Holocene as a gradual transition to modern assemblages. Others note a shift to even more mesic, late successional forest assemblages in the late Holocene beginning *c.* 3800 cal BP (Dunwiddie 1986, Pellatt et al. 2000) and *c.* 2000 cal BP (Fujikawa 2002). The *c.* 5200 cal BP transition to modern vegetation is also noted in studies by Pellatt (1998, 2000) at subalpine sites in southwestern British Columbia and by Mack (1978) in the Okanogan Valley, Washington.

Fire History

A total of 62 fire events was detected throughout the Holocene record (Figure 3.5). The dates of the most recent fires detected in the sediment record correspond to dates of fires inferred from tree and stand age distributions near the Panther Potholes. The 100-150 year tree ages on the steep, west-facing slope approximately 0.25 km from the Panther Potholes (Chapter 2) corresponds to the age of the most recent charcoal peak. Similarly, a 520-500 year cohort of dominant *P. menziesii* trees, located within 50 m of the lake corresponds well with the age of the second-most recent CHAR peak (Figure 11). Dates of delineated charcoal peaks suggest that fire frequency did not vary much over the entire Holocene. Calculated fire return intervals are highly variable, and do not differ significantly between early-, mid-, and late-Holocene zones at $p = 0.1$ (Table 3.5). Although not significant, the mid Holocene MFRI is shorter than that of the early and late Holocene periods.

Fire and Vegetation Dynamics

Because the major vegetation changes at our site correspond to region-wide vegetation changes, climate is clearly the key driver of vegetation change at broad time

scales. At shorter time scales, it appears as though fire and other disturbances may have played an important role in shaping species assemblages and forest successional dynamics. In particular, most charcoal peaks are associated with peaks in the macrofossil accumulation rates (Chapter 4). This correspondence likely indicates that many peaks detected in the charcoal record represent local fire events that caused tree mortality and tree needle deposition in lake sediments. It also appears that individual fires caused short-term changes in tree species composition. For example, prominent gaps in the macrofossil record occur following specific fire events in the late Holocene, and this is particularly evident for shade-tolerant species such as *T. plicata* and *T. heterophylla* (Figure 3.10). Disturbances other than fire (i.e., insects, disease and weather events) may have also been important agents of vegetation change. For example, peaks in *P. contorta* macrofossil accumulation rates are regular during the early Holocene. Many of these appear to be associated with charcoal peaks. However, several do not correspond to charcoal peaks and could conceivably have been caused by mountain pine beetle outbreaks or other disturbances including low-severity fire or windstorms. Relationships between charcoal peaks and evidence of local fire events in the macrofossil record are further addressed in Chapter 4.

Fire and other disturbances are often cited as having the potential to accelerate vegetation responses to climatic change (Brubaker 1988, Sprugel 1991, Agee 1993, Dale et al. 2001). A common interpretation of early Holocene lowland Pacific Northwest landscapes is that *P. menziesii* and grassland communities were perpetuated by frequent fires in the warm, dry summers (Brubaker 1991, Whitlock 1992). Estimated fire frequencies at Panther Potholes do not necessarily reflect this interpretation. The difference in mean fire return intervals among the major vegetation zones is insignificant. It is possible that fire regimes did not substantially change over the Holocene at this high elevation site.

Although fire frequency does not appear to have shifted substantially over the Holocene, low to moderate severity fires may have been common in the early- to mid-

Table 3.1 Tephra dates based on glass chemistry analysis (N. Foit, Washington State University Electron Microbeam and X-ray Analysis Labs, Pullman, WA).

| Tephra Depth (cm) | Probable Correlation | Similarity Coefficient | Measured Date | Calibrated Date | Lab ID |
|--------------------------|-----------------------------|-------------------------------|---|------------------------|-----------------|
| 303-308 | Mount St Helens W | 0.99 | | 470 cal BP | Prichard PPBIIC |
| 396-406 | Mount St Helens Y | 0.97 | 2930-3510 ¹⁴ C BP < 3900 | 4000-3300 cal BP | Prichard PPBIID |
| 623-639 | Mazama Climactic | 0.99 | 6850 ¹⁴ C BP | 7690-7610 cal BP | Prichard PPBIIG |

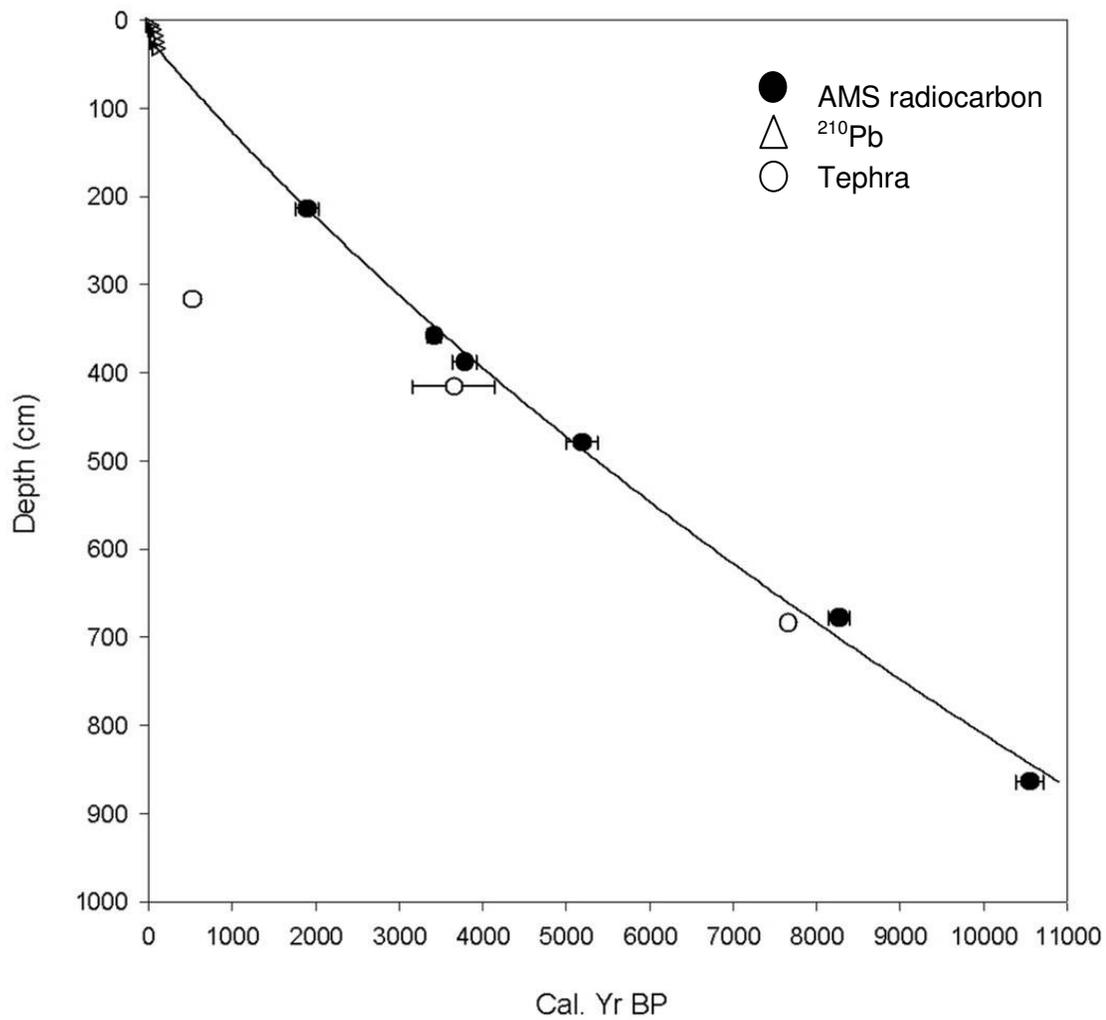


Figure 3.4 AMS radiocarbon, tephra, and ^{210}Pb dates. Error bars indicate one standard deviation.

Table 3.2 AMS Radiocarbon dates. Samples were analyzed and calibrated by Beta Analytic, Inc.

| Depth (cm) | Measured Radiocarbon Date | 2- σ Calibrated Date | Laboratory no. | Sample type |
|------------|---------------------------|-----------------------------|----------------|--|
| PPB2 219 | 1950 (+/- 50) BP | 1800 to 1990 cal BP | Beta-172005 | Conifer seed |
| PPB2 378 | 3260 (+/- 40) BP | 3470 to 3350 cal BP | Beta-169623 | Seed |
| PPB2 404 | 3520 (+/- 40) BP | 3880 to 3680 cal BP | Beta-169624 | Pollen cone |
| PPB2 504 | 4500 (+/- 40) BP | 5320 to 5050 cal BP | Beta-169207 | Pollen cone |
| PPB2 756 | 7330 (+/- 40) BP | 8350 to 8170 cal BP | Beta-169208 | Seed |
| PPB2 972 | 9370 (+/- 40) BP | 10,660 to 10,430 cal BP | Beta-169625 | Needle fragments (<i>Pinus contorta</i>) |

Table 3.3 ^{210}Pb dates based on CRS age-depth model (Flett Research Ltd., Winnipeg, Canada).

| Depth (cm) | Total Activity | Error (1 SD) | Modeled Date |
|------------|----------------|--------------|--------------|
| 3 | 29.69 | 2.87 | |
| 7 | 32.55 | 3.47 | 12.3 |
| 14 | 8.30 | 1.15 | 40 |
| 21 | 2.68 | 0.72 | 61 |
| 28 | 3.22 | 0.74 | 70 |
| 35 | 3.76 | 0.77 | 85 |

Table 3.4 Major vegetation types throughout the Holocene.

| Pollen zone | ¹⁴ C yr BP | Cal. yr BP | Vegetation type | Dominant trees (decreasing importance) |
|-------------|-----------------------|-----------------------|------------------------------|--|
| EH | c. 9300 to 7100 BP | c. 10,500 to 7700 BP | Dry montane conifer forest | <i>Pinus contorta</i> , <i>Pseudotsuga menziesii</i> and <i>Abies lasiocarpa</i> |
| MH | c. 7100 to 4500 BP | c. 7700 to 5200 BP | Dry montane conifer forest | <i>Pinus monticola</i> , <i>Pseudotsuga menziesii</i> and <i>Abies lasiocarpa</i> |
| LH1 | c. 4500 to 2000 BP | c. 5200 to 2000 BP | Moist montane conifer forest | <i>Pseudotsuga menziesii</i> , <i>Pinus monticola</i> , <i>Thuja plicata</i> and <i>Tsuga heterophylla</i> |
| LH2 | c. 2000 BP to present | c. 2000 BP to present | Moist montane conifer forest | <i>Pseudotsuga menziesii</i> , <i>Pinus monticola</i> , <i>Chamaecyparis nootkatensis</i> , <i>Tsuga heterophylla</i> and <i>Thuja plicata</i> . |

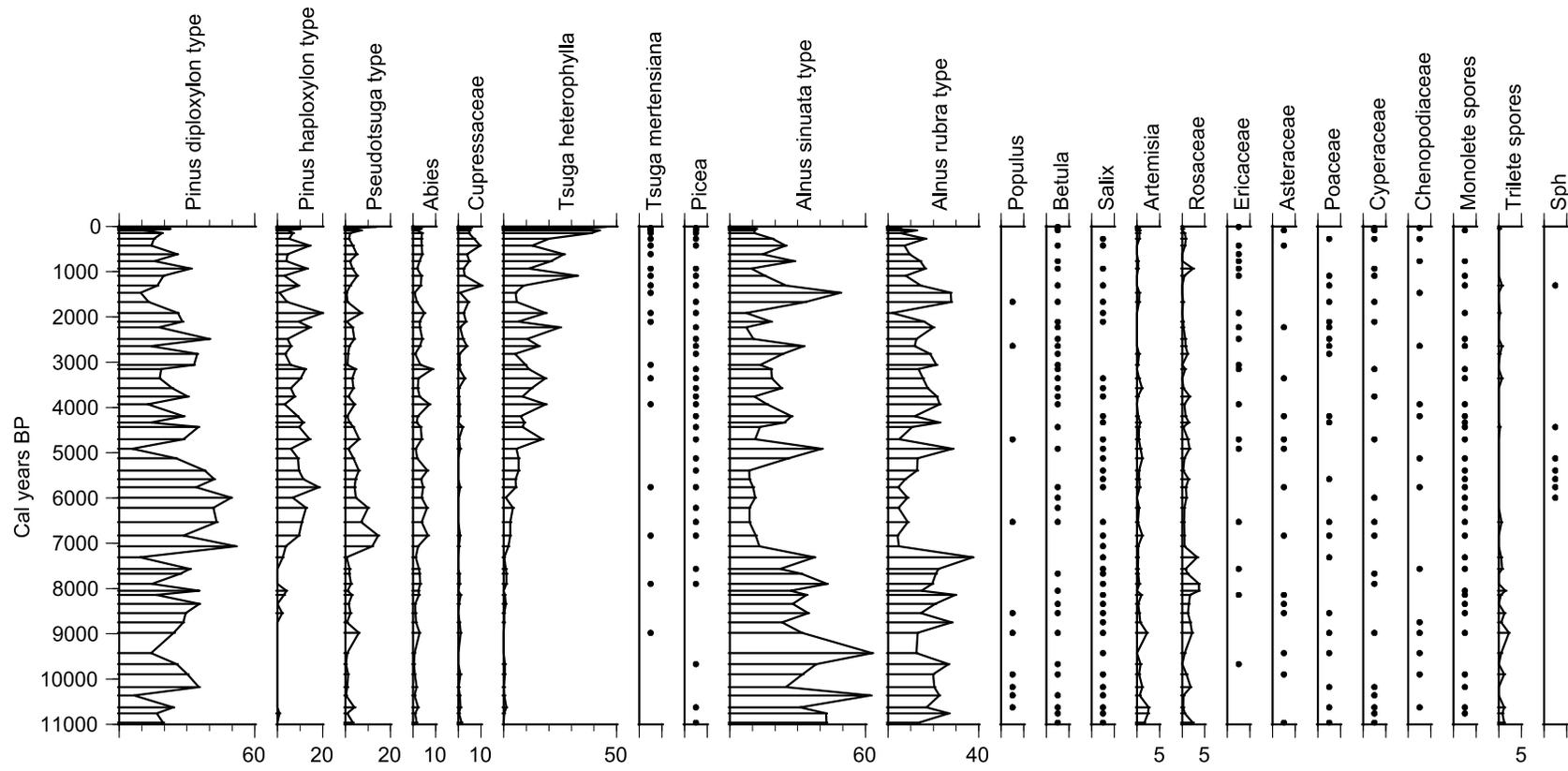


Figure 3.6 Pollen percentage diagram.

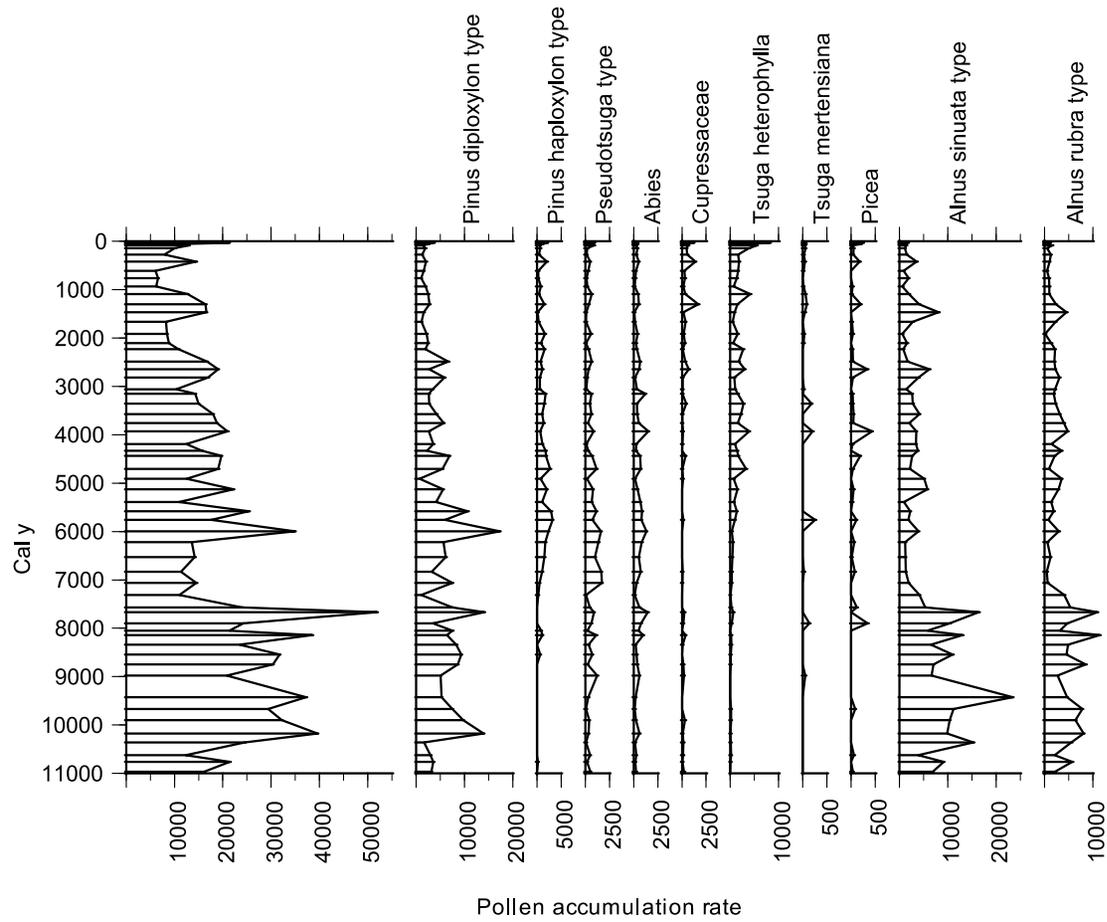


Figure 3.7 Pollen accumulation rate diagram.

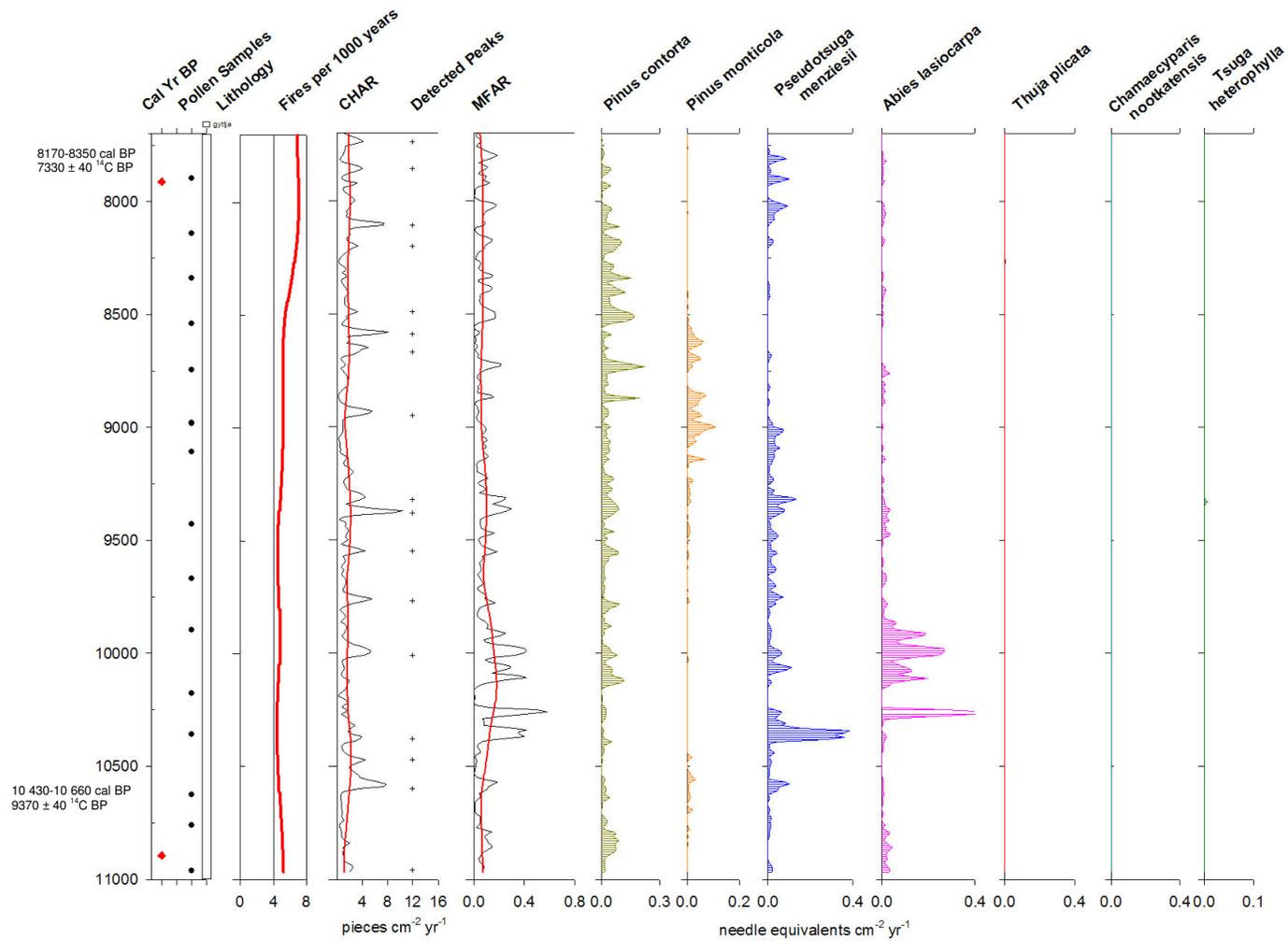


Figure 3.8 Macrofossil and charcoal records of the Early Holocene. Charcoal (CHAR), macrofossil (MFAR) and macrofossil accumulation rate by species. CHAR threshold line is indicated in red.

Table 3.5 Mean fire return interval, standard deviation and number of fires by Holocene periods, calculated from the CHAR-based reconstruction of fire events.

| Interval (cal BP) | MFRI (\pm SD) years | Min years | Max Years | # fires |
|------------------------------|---|----------------------|----------------------|----------------|
| Entire Record | 177 \pm 97 | 30 | 410 | 62 |
| c. 10600 to 7700 | 201 \pm 110 | 60 | 370 | 16 |
| c. 7700 to 5200 | 146 \pm 84 | 30 | 300 | 17 |
| 5200 to present | 182 \pm 96 | 30 | 410 | 28 |

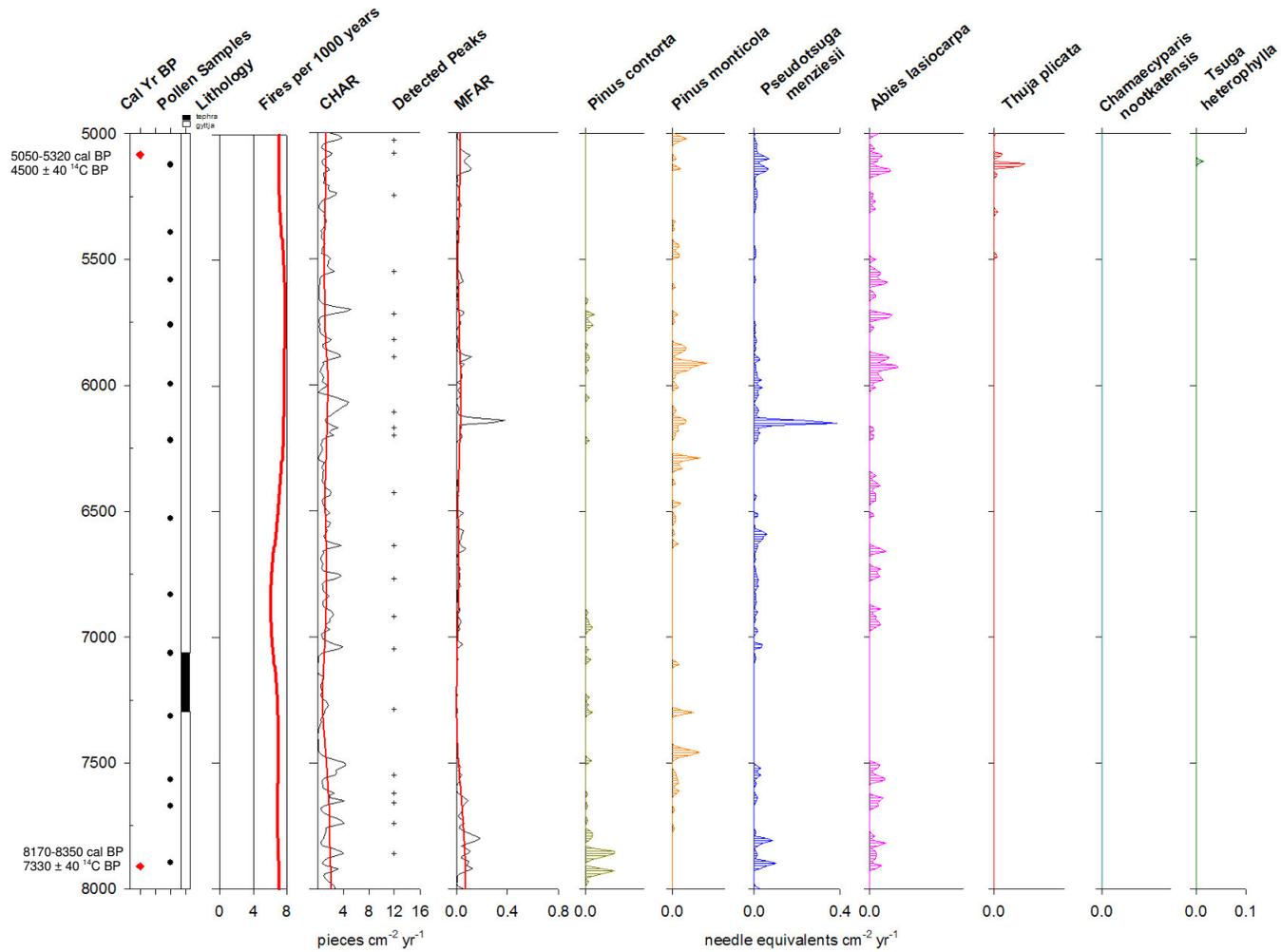


Figure 3.9 Macrofossil and charcoal records of the mid Holocene. Charcoal (CHAR), macrofossil (MFAR) and macrofossil accumulation rate by species. CHAR threshold line is indicated in red.

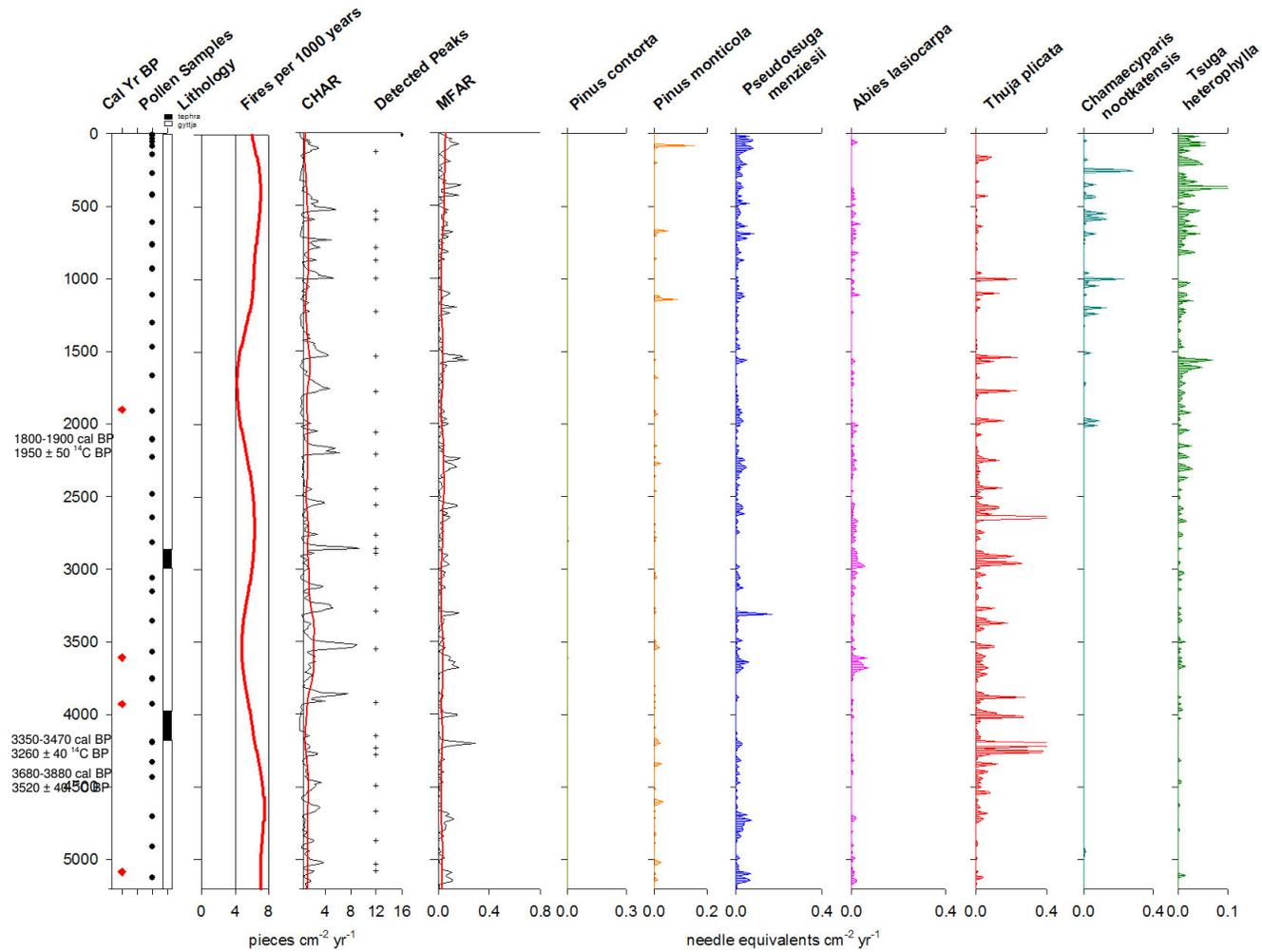


Figure 3.10 Charcoal and macrofossil records of the Late Holocene. Charcoal (CHAR), macrofossil (MFAR) and macrofossil accumulation rate by species. CHAR threshold line is indicated in red.

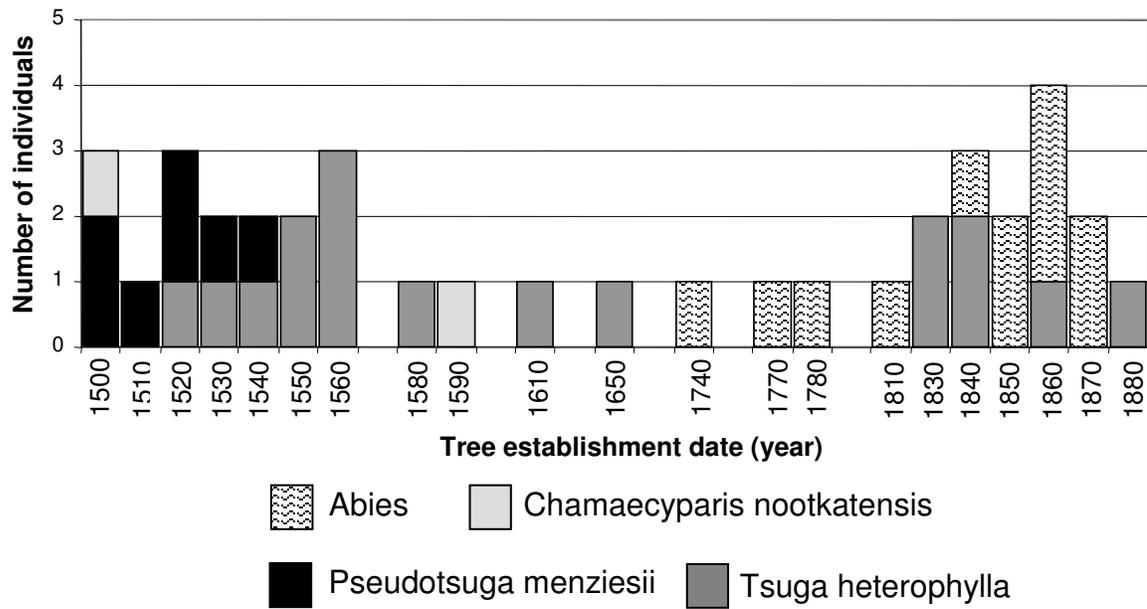


Figure 3.11 Age class frequency distributions of a survey of three 0.05-ha plots near Panther Pothole B.

Holocene periods but not detected in lake sediments. Reconstructions of fire history based on lake sediment charcoal likely underestimate moderate and low severity fire events (Mohr et al. 2000, Higuera 2002). Low and moderate severity fires may produce less charcoal than high severity fires, and depending on the prevailing wind direction and location of the fire event, may not be recorded as charcoal peaks in lake sediments (Mohr et al. 2000, Higuera 2002). During the early and mid Holocene, seasonal low to moderate fires may have been more common with warmer drier summers. The potential underrepresentation of low to moderate severity fire events is probably less of an issue in the late Holocene. The continuous presence of late successional species during the late Holocene makes it unlikely that frequent, low severity fires were a major part of the fire regime.

Conclusions

Over the past *c.* 10,500 years, vegetation has changed considerably at the Panther Potholes, and patterns of these vegetation changes correspond well to major changes of climate and vegetation in the Pacific Northwest (Mack et al. 1979, Barnosky 1981, Mathewes & Heusser 1981, Leopold et al. 1982, Cwynar 1987, Wainman & Mathewes 1987, McLachlan & Brubaker 1995, Long et al. 1998, Pellat et al. 2000, Gavin et al. 2001, Brown & Hebda 2002). This study helps to fill a void in paleoecological data for the North Cascades Range and provides a comparison of vegetation change in a mountainous area to reconstructions other sites throughout the region. Over millennial time scales, climate appears to be the major driver of vegetation change, whereas fire and other disturbances were likely important agents of vegetation change at decadal to century time scales.

Paleoecological reconstructions demonstrate that vegetation has varied dynamically with changing climatic and disturbance regimes over the Holocene (Clark 1990, Delcourt & Delcourt 1991, Whitlock 1992, Clark et al. 1996). Climate itself varies continuously (Davis 1986, Thompson et al. 1993), and while it may be tempting to manage natural resources for historical conditions, it is important to consider longer time

scales to appreciate the range of variability in ecosystem dynamics, including changing vegetation assemblages, forest structure and disturbance regimes. Future climatic change may cause ecosystems and fire regimes to shift outside of their historical range of variability (Paine et al. 1998, Hansen 2001, Dale 2001). Climatic scenarios for the Pacific Northwest over the next 50-100 years predict warm, dry summers and warm wet winters (Mote et al. 1999), a combination which does not appear to be analogous at least to the broad-scale climatic regimes over the Holocene. A rapid climatic shift, coupled with stand-replacing fires and other disturbances, could conceivably result in new vegetation assemblages with no historic analogues.

Recent paleoecological studies of high elevation sites in the Pacific Northwest, including this study, demonstrate that during major climatic changes over the Holocene, responses of forests at high elevations appear to have been very site dependent, whereas at low elevation, more broad generalizations about species responses to climatic change are possible. The Pacific Northwest is dominated by topographically complex mountain systems. Any analysis of the effects of climatic change on vegetation, past or present, must acknowledge the variability of sites and growing conditions of mountain forests in this region.

CHAPTER 4: A RECONSTRUCTION OF HOLOCENE FIRE HISTORY IN THE NORTH CASCADES RANGE, WASHINGTON USING LAKE SEDIMENT CHARCOAL AND MACROFOSSIL RECORDS

Introduction

The importance of fire history on forest vegetation is well documented (Johnson 1992, Agee 1993, Whelan 1995). However, most reconstructions of historic fire regimes are based on tree ring records and do not span century to millennial scale climatic variation (e.g., Heinselman 1973, Hemstrom and Franklin 1982, Johnson and Larsen 1991, Grissino-Mayer and Swetnam 2000). In the absence of long-term records, we lack information about the range of variability in fire regimes under past climates and have little basis to predict the effects of global warming on future fire and vegetation dynamics. Recent paleoecological reconstructions of fire have sampled sediment charcoal at contiguous, fine intervals and have resolved individual fire events from peaks in charcoal accumulation rates (CHAR) (e.g., Clark 1990, Clark and Royall 1996, Larsen and MacDonald 1998a, b, Long et al. 1998, Tinner et al. 1998, Tinner et al. 1999, Mohr et al. 2000, Long and Whitlock 2002, Hallett et al. 2003). Many of these records span c. 10,000 yr and have been used to reconstruct fire and vegetation dynamics over long-term fluctuations in Holocene climatic regimes.

A standard methodology for detecting fire events from macroscopic charcoal in sediments is to decompose the record into background and peak components (e.g., Clark and Royall 1995, Long et al. 1998). The background component represents charcoal accumulation from a variety of sources, including regional fires, secondary deposition from surface runoff, littoral zone erosion and/or sediment mixing, and variation in charcoal production related to fluctuation in forest fuels (Patterson et al. 1987, Whitlock and Millspaugh 1996, Clark et al. 1998, Gardner and Whitlock 2001). Charcoal peaks exceeding background levels are interpreted as local fire events, i.e., fires that occurred within the immediate watershed or within close proximity (Whitlock and Millspaugh 1996, Clark et al. 1998, Gardner and Whitlock 2001). Charcoal source areas are not well

defined. Delineation of local fire events is usually validated by comparing dates of known fires to those detected in the sediment charcoal record and/or to estimated fire return intervals (Clark 1990, Millspaugh and Whitlock 1995, Long et al. 1998, Whitlock and Anderson 2003). Such validation relies on the assumption that variables influencing charcoal deposition did not substantially change over time. A number of variables potentially affect CHAR, including distance and position of the fire relative to the lake basin, wind direction at the time of individual fire events, fire severity, and fuel biomass (Patterson et al. 1987, Whitlock and Millspaugh 1996, Clark et al. 1998, Gardner and Whitlock 2001). Ideally, a secondary measure of fire would be available in lake sediment records to corroborate the interpretation of local fire events.

A number of studies have sampled fossil pollen at the same interval as charcoal and found a correspondence between charcoal peaks and distinct changes in pollen stratigraphy (Green 1981, Larsen and MacDonald 1998a, b, Tinner et al. 1998, Tinner et al. 1999, Carcaillet et al. 2001). A problem with using pollen as an indicator of local fires is that the spatial resolution is vague, and non-local pollen can mask the signal of local vegetation (Sugita 1994). For example, correspondence between pollen accumulation rates and charcoal peaks could result from fires that were regionally widespread and/or local fire events (e.g., Carcaillet et al. 2001). Plant macrofossils represent a much more localized signal of past vegetation than pollen (Dunwiddie 1985a) but are generally not sufficiently numerous in lake sediments to detect responses to fire events. In small lakes surrounded by coniferous forests macrofossils of conifer needles can be quite abundant (Dunwiddie 1985a) and theoretically could record a local fire event through peaks in needle deposition associated with tree death and/or low needle deposition during forest regeneration following stand-replacing fire events. High resolution macrofossil records also can be used to evaluate the impacts of fire on vegetation assemblages and succession over long time periods.

As part of a reconstruction of Holocene fire and vegetation history of a montane forest in the North Cascades Range (Chapter 3), we analyzed correspondences between lake sediment charcoal and macrofossil accumulation rates from the same high-resolution

record. We sampled sediments from a small (< 0.5 ha) lake and analyzed macroscopic charcoal (>150 μ m) to capture a signal of local fires recorded as charcoal peaks (Clark et al. 1998, Whitlock and Anderson 2003). Abundant macrofossils, primarily consisting of conifer needles, provided a unique opportunity to evaluate the response of local vegetation to reconstructed fire events. Key questions guiding this study were: 1) Is there a correspondence between peaks in CHAR and macrofossil accumulation rates? 2) Do tree species, as represented by macrofossil accumulation rates, respond differentially to fire events, and 3) Did fire frequency, estimated from peaks in charcoal accumulation rates, vary over broad changes in Holocene climate?

Study area

Lake basin characteristics

Sediments were sampled from the larger of two small (~ 0.3 ha) montane lakes called the Panther Potholes in North Cascades National Park, Washington (Figure 4.1). The Panther Potholes are located at 1100 m elevation on Fourth of July Pass (48° 39' N, 121° 02' W), a glacially-carved notch between two mountain peaks (Tabor and Haugerud 1999). Local site geology is part of the Skagit Gneiss Complex. The immediate watershed (approximately 25 ha) is dominated by a montane coniferous forest with interspersing talus and cliff bands. The lake is shallow with a maximum water depth of 5 m, has a small outlet, and is connected to a smaller lake via an intermittent channel.

Climate

The study area is located near the crest of the North Cascades Range, and local climate is transitional between the moist, maritime west-side and dry, continental east-side climate of the Cascades. The nearest weather station is located at Diablo Dam, 5 km to the west at 300 m elevation (Western Regional Climate Center, <http://www.wrcc.dri.edu>). Mean annual precipitation is 191.0 cm, and average annual temperatures range from 4.3 to 14.1 °C. Winters are cool and wet, and summers are mild and dry. Approximately 90% of average annual precipitation falls between October and May.

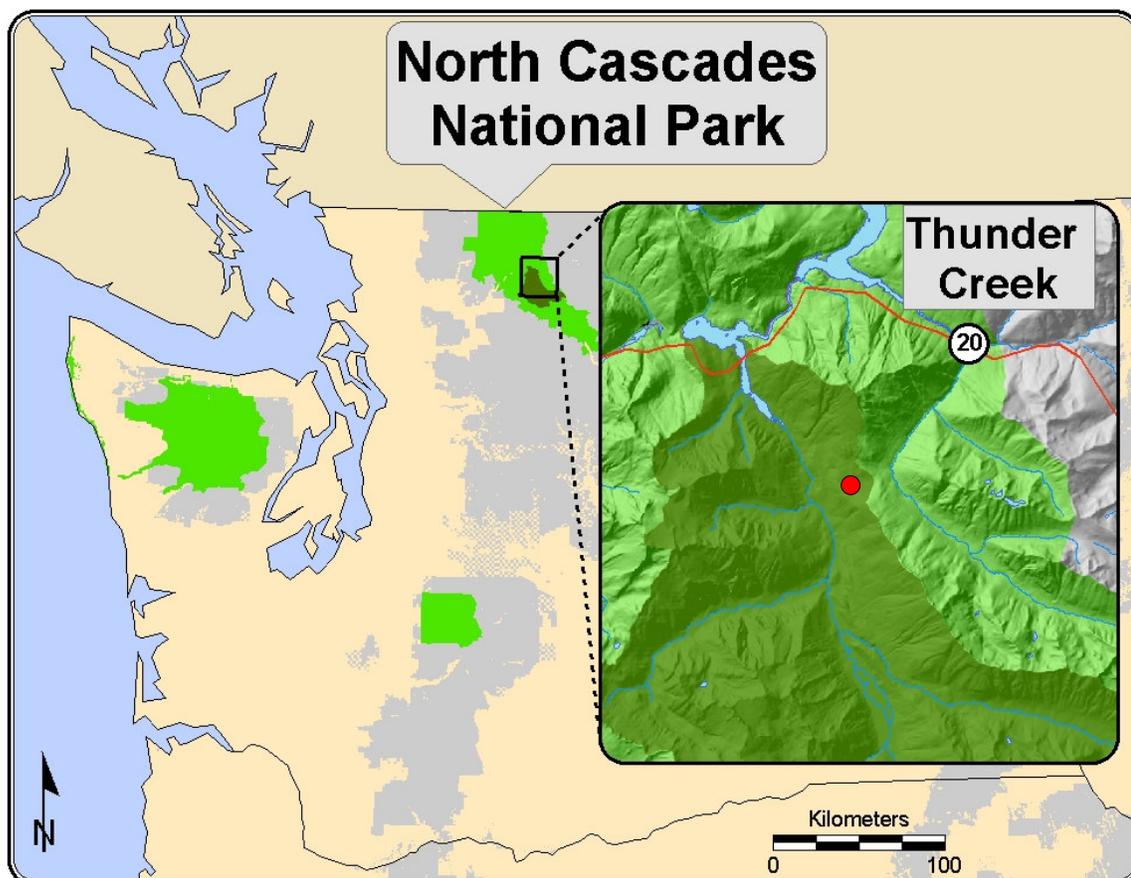


Figure 4.1 Study area.

Modern vegetation and recent fire history

The surrounding montane forest has a high diversity of conifer species (see Chapter 2 for a more complete description of modern vegetation). Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*T. heterophylla*), western redcedar (*Thuja plicata*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), and Pacific silver fir (*Abies amabilis*) are common stand associates in lakeside and upland forests. Subalpine fir (*Abies lasiocarpa*) is mostly confined to the immediate lake basin. Engelmann spruce (*Picea engelmannii*), mountain hemlock (*T. mertensiana*), western white pine (*Pinus monticola*), and Pacific yew (*Taxus brevifolia*) are rare throughout the study area, and the nearest population of lodgepole pine (*Pinus contorta*) is located approximately 0.5 km from the Panther Potholes.

Evidence of recent fire events is present in the vicinity of our study area. Tree age distributions, sampled within 100-m of the Panther Potholes, indicate a pulse of Douglas-fir establishment from 500-540 yr BP and no evidence of a more recent fire (Chapter 2). Stand age distributions were sampled within 0.25 to 4 km from our study area and have spatially-variable establishment dates of ~160, ~120, and ~100 yr BP. Fire scars are rare but record fires 160 and 100 yr BP within 2 km of the study area.

Approximately 25 km north of our study area, Agee et al. (1990) reconstructed a 400-year fire history based on fire scar and stand-origin mapping at Desolation Peak. Large fire events occurred in 427, 185, 149, 120, and 74 yr BP. They also constructed natural fire rotations from stand origin mapping and reported a 100-year natural fire rotation overall and 137 yr for mountain hemlock-Pacific silver fir forests, the closest analogue to the forest assemblage at the Panther Potholes.

Methods

Lake sediment sampling and processing

The sediment core was sampled from the deepest location of the lake with a 5-cm diameter modified Livingston piston sampler (Wright et al. 1984). The top 0.4-m were sampled with a clear plastic 7.6-cm diameter tube, which was held vertically and

immediately sectioned into 1-cm intervals. Additional sediment cores were sampled, including a parallel core extracted 1 m from the one reported here, and two parallel cores from the smaller lake, Panther Pothole A. Sediment cores were stored at 4 °C prior to processing.

Lake sediments were described in the lab and sectioned into 1-cm intervals. Before sediments were processed for macrofossil and charcoal analysis, we measured magnetic susceptibility (in electromagnetic units (emu)) on bulk samples using a Sapphire SI-2 magnetic susceptibility meter with a coil-cup sampling device (Thompson and Oldfield 1986, Millspaugh et al. 2000). Samples were then disaggregated for 72 hours in a known volume of 10% sodium metaphosphate solution. Prior to sieving, the total volume of sediment in solution was measured to calculate the actual sediment volume (i.e., total volume minus known volume of dispersal agent). Sediments were gently washed through 500- and 150- μm sieves. Macrofossils of conifer needles were collected from the >500- μm fraction and identified to species using a published key (Dunwiddie 1985b) and a modern reference collection. Macrofossils were tallied as needle equivalents (i.e., whole needles, tip + base of needle fragments, pine needle fascicles, and clusters of 2 or more scales of Alaska yellow cedar and western redcedar) and as total fragments. Charcoal in the 150- to 500- μm fraction was bleached with an 8% hydrogen peroxide solution for 8 hours and rewashed through sieves to terminate the bleaching process. Charcoal pieces were identified and tallied on a gridded Petri dish under 10-40X magnification. Charcoal was rare in the >500- μm fraction and combined with the 150- to 500- μm tally for data analysis. During processing, 16 samples of the 150- to 500- μm sieve fraction, spanning drive depths 44-59 cm, were lost. Fortunately, the uppermost 150 cm of sediment, sampled from the adjacent lake, Panther Pothole A, had been sectioned, processed and analyzed for charcoal as a practice run. Charcoal records from the two lakes are very similar, and it appears that no charcoal peaks were present in the lost samples (Figure 4.2).

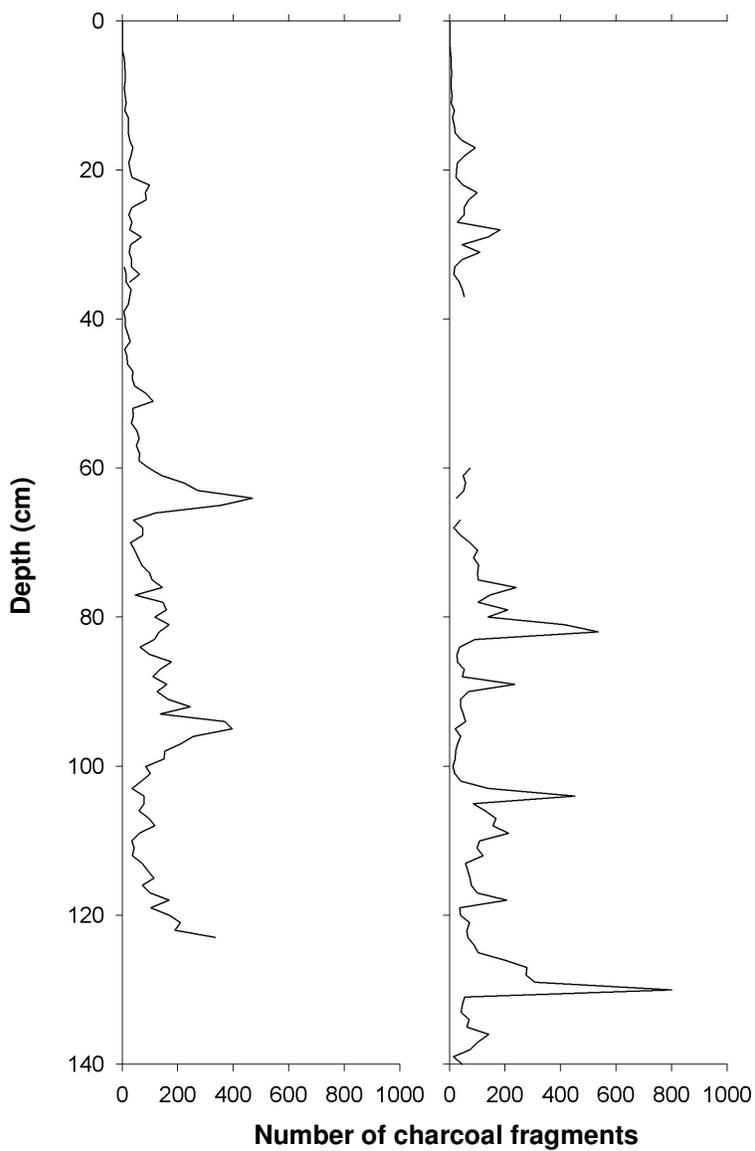


Figure 4.2 Comparison of raw charcoal counts in the upper 140 cm of Panther Pothole A and Panther Pothole B. Peaks are offset because Panther Pothole B has a faster sedimentation rate.

Sediment chronology

Three dating tools were used to create an age-depth model for the sediment core. Three tephra layers were identified using glass chemistry analysis (N. Foit, Washington State University Electron Microbeam and X-ray Analysis Labs, Pullman, WA). Radiocarbon dates were obtained for six macrofossils (conifer needles and seeds) using Accelerated Mass Spectrography (AMS) and were calibrated using a 2- σ calibration (Beta Analytic, Inc., Miami, Florida). ^{210}Pb activity was measured on 7 samples in the upper 35 cm of the mud-water interface, and sedimentation rates were modeled using slope regression model and constant rate of supply (CRS) models, both of which yielded similar results (Flett Research Ltd., Manitoba, Canada). A third-order quadratic age-depth model was constructed from tephra and AMS radiocarbon dates ($r^2 = 0.99$). To account for rapid sedimentation rates for the top 35 cm, a linear model was constructed from five ^{210}Pb dates.

Calculation of CHAR, MFAR and EMAR

Sedimentation rates based on the sediment chronology were used to convert charcoal and macrofossil concentrations (pieces or needles equivalents cm^{-3}) to accumulation rates (CHAR – charcoal pieces $\text{cm}^{-2} \text{yr}^{-1}$, MFAR – macrofossils $\text{cm}^{-2} \text{yr}^{-1}$). Macrofossil accumulation rates were calculated by species, total needle equivalents, and as tallies of all needle fragments. Magnetic susceptibility (emu) was also converted from emu cm^{-3} to $\text{emu cm}^{-2} \text{yr}^{-1}$. Accumulation rates were interpolated to a 10-year increment.

Detection of individual fire events

CHAR peaks were decomposed into background and peak components using Charcoal Analysis Programs (CHAPS) developed by P. Bartlein, Department of Geography, University of Oregon, and detailed in Whitlock and Anderson (2003). This method delineates background CHARs with a locally weighted running mean and multiplies the background by a threshold ratio for peak detection. This method was selected because it is widely used in sediment charcoal-based reconstructions of fire in western North America and accounts for low frequency fluctuations in charcoal signals

(Long et al. 1998, Hallett and Walker 2000, Millspaugh et al. 2000, Mohr et al. 2000, Long and Whitlock 2002, Hallett et al. 2003). CHAR values were log transformed, and background CHAR was estimated by calculating a series of weighted running means over varied window widths (250, 600, 750, 1000, 1250 and 1500 yr). The number of CHAR peaks did not vary between 500 and 1200 year window widths. A mid-range window width of 750 yr was selected to evaluate a range of threshold ratios from 1.0 to 3.25 at 0.125 increments. CHARs for the last 540 yr were compared with the 2 local fire scar and tree age dates at c. 100-160 yr BP and c. 500-540 yr BP, and all threshold ratios detected these known fire events. To help define a threshold ratio, we evaluated standardized CHAR frequency distributions. Assuming that background CHAR is normally distributed, we determined that a threshold ratio of 1.4 captures the second mode (right tail) of CHAR distributions is appropriate for CHAR peak delineations (Figure 4.3).

Estimation of fire frequency

The frequency of fire events was summarized by calculating a locally-weighted mean frequency of fires from a binary time series (1 = fire event, 0 = no fire event). Fire frequencies were smoothed at a 400-year window width, which represents the longest fire free interval in our record. We also smoothed fire frequencies with a standard 2000-year window width to compare with other studies (Whitlock and Anderson 2003). Mean fire return intervals were summarized by early-, mid-, and late-Holocene periods, and we tested for a significant difference in fire return intervals between periods ($p = 0.1$) using a Kruskal-Wallis test (Zar 1999).

Macrofossil response to fire events

Superposed epoch analysis was used to evaluate relationships between macrofossil accumulation rates (MFAR) and fire events delineated from CHAR peaks. MFARs were first detrended using a cubic smoothing spline with a 50 percent frequency cutoff of 500 yr (Cook and Peters 1981). MFAR anomalies (in standard deviations) were calculated at 100-year leads and lags at 10-year increments surrounding fire event years.

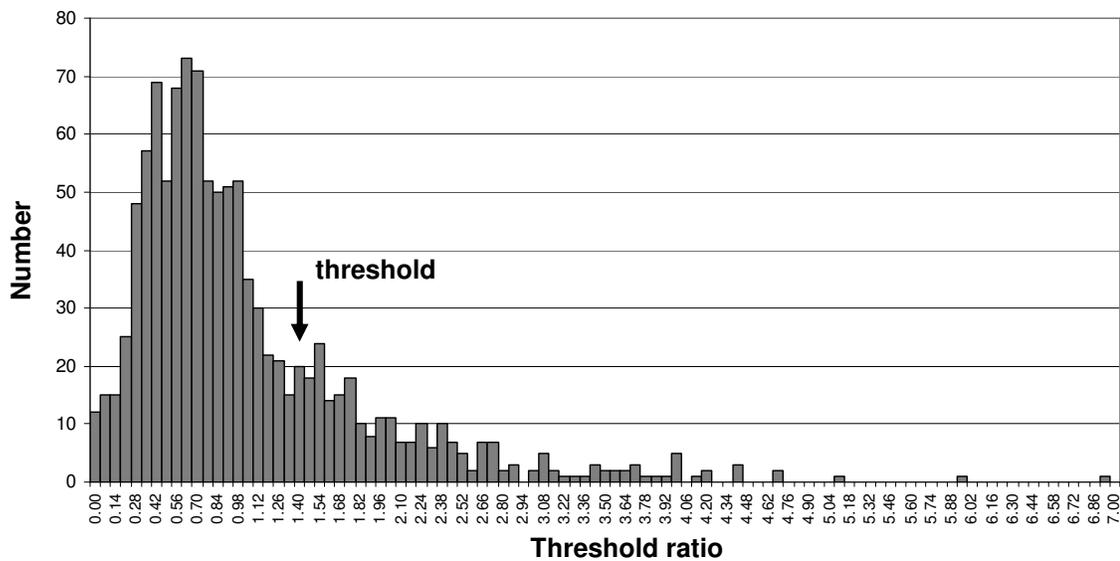


Figure 4.3 Frequency distribution of standardized CHAR (minus background). A threshold of 1.4 indicates the beginning of the right tail of the CHAR distribution.

Anomalies were defined as an initial peak followed by a drop in MFAR associated with fire events. Macrofossil accumulation rates of total fragments and needle equivalents were included in this analysis. We also evaluated MFAR anomalies by individual species (as needle equivalents) to determine whether there were any differences in responses to fire events. At each 10-year lead/lag, 90% confidence limits were calculated on the MFAR anomaly.

To determine which fire events had a corresponding macrofossil response (i.e., peak at the time of a fire and negative anomalies following a fire event), we calculated the covariance between MFAR responses (in terms of total fragments) to each individual fire event and the mean response. The critical covariance value, above which it is statistically unlikely that the observed relationship would occur by chance, was calculated for two random series of length 21, mean of zero, standard deviation of 1.0, with a 90 percent confidence level.

Results

Lithology and sedimentation rates

Lake sediments consisted of uniform, dark brown gyttja. The mean sedimentation rate of the entire core is $9.2 \pm 1.9 \text{ yr cm}^{-1}$ with faster sedimentation at the top 200 cm of the core ($3\text{-}9 \text{ yr cm}^{-1}$) and slower sedimentation from 200 cm to the base of the core at 860 cm ($9\text{-}12 \text{ yr cm}^{-1}$) (Figure 4.4). Other than the three tephra layers, mineral deposits are rare. Magnetic susceptibility levels of sediment are mostly undetectable, and there is no correspondence between magnetic susceptibility peaks and CHAR peaks (data not shown).

CHAR-based reconstruction of fire

A total of 62 fire events were interpreted as fire events (Figure 4.5). With a smoothing window of 2000 years, the number of fire events per 1000 yr ranges from 4 to 8 throughout the Holocene with 4-5 per 1000 yrs in the early Holocene (>10,000 to c. 8500 cal yr BP), 6-8 per 1000 yrs in the mid Holocene (c. 8500 cal yr BP to 4500 cal yr

BP), and 4 to 7 in the late Holocene (c. 4500 cal yr BP to present) (Figure 4.5). Fire return intervals are highly variable (Figure 4.6) and there are no significant differences between early-, mid-, and late-Holocene periods (Table 4.1). Although differences are not significant, the mid Holocene MFRI is shorter than the early Holocene and late Holocene periods. Background CHAR drops markedly between c. 7500 and 4000 cal yr BP. Likewise, there is a noticeable drop in CHAR peak amplitudes c. 8000 cal yr BP and a sharp rise in peak amplitudes c. 4000 cal yr BP. Although the drop in background CHAR during the mid Holocene could have resulted in an artificially high estimation of fire events, the trend of higher frequency of fires in the mid Holocene is evident over a wide range of threshold ratios.

Macrofossil response to fire events

There is a clear macrofossil response to fire events delineated from CHAR peaks. If all macrofossil fragments of conifer needles are included in the MFAR, there is a significant peak in MFAR anomalies centered on fire events and decade prior to the fire events ($p = 0.1$) (Figure 4.7). In addition, there is a significant drop in macrofossils in the fourth decade following fires. A total of 39 fire events have a positive covariance with the canonical macrofossil anomaly above the critical value (Figure 4.8). Of the 23 fire events that have a covariance below the critical value, 15 have low CHARs (< 3.0). If only needle equivalents are considered, the same patterns of macrofossil anomalies are evident, but they are not statistically significant (Figure 4.7).

Individual species, based on accumulation rates of needle equivalents, vary in their response to fire events (Figure 4.7). Overall, the peak in MFAR associated with fire events and drop in MFAR following fire events represents the combined response of many species and is not driven by any single species. However, there are a few differences between species responses to fire. For example, Douglas-fir exhibits a significant MFAR peak following fire events. In contrast, MFARs of western hemlock and subalpine fir significantly drop following fire events.

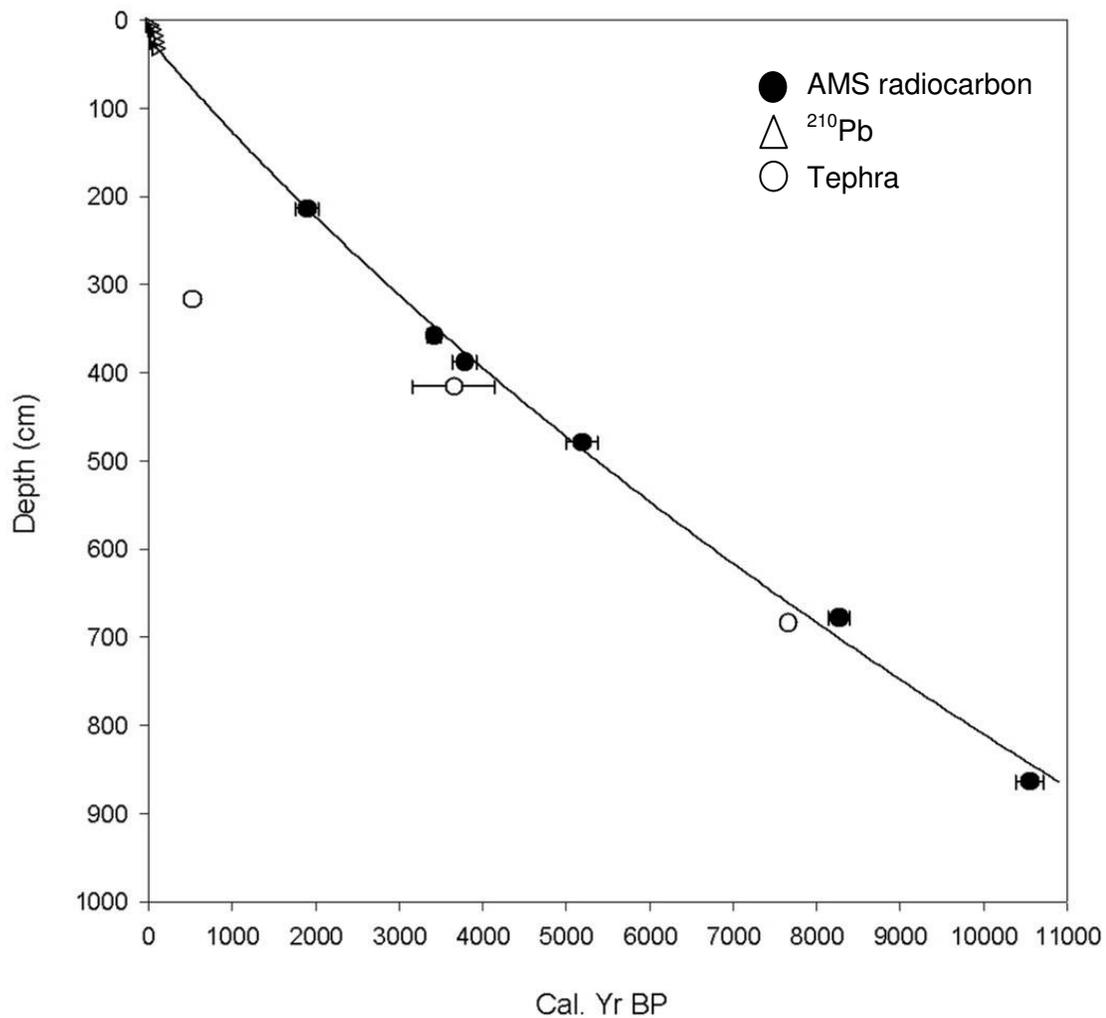


Figure 4.4 AMS radiocarbon, tephra, and ^{210}Pb dates. Error bars indicate one standard deviation. One tephra was a clear outlier and was not included in the age-depth model.

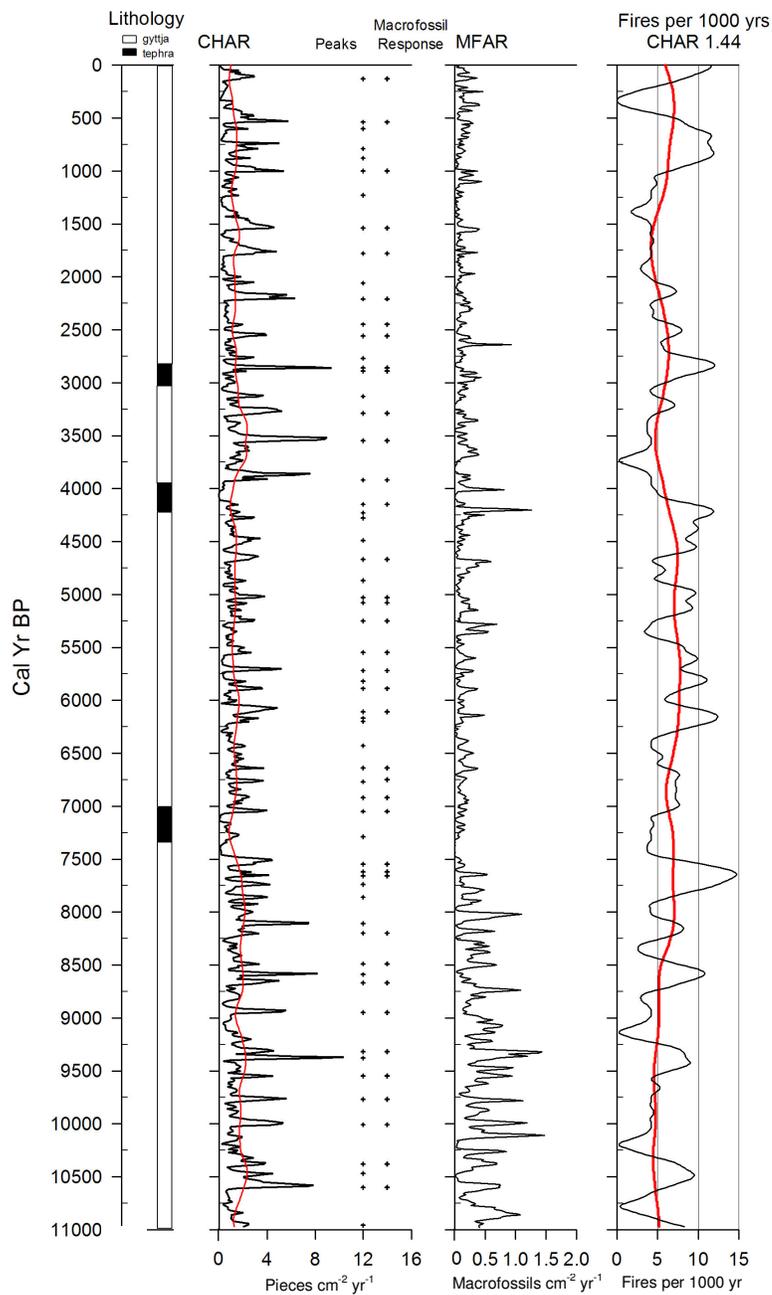


Figure 4.5 Lithology, CHAR, detected peaks, peaks with a macrofossil response, MFAR, and fires per 1000 years over the sediment record.

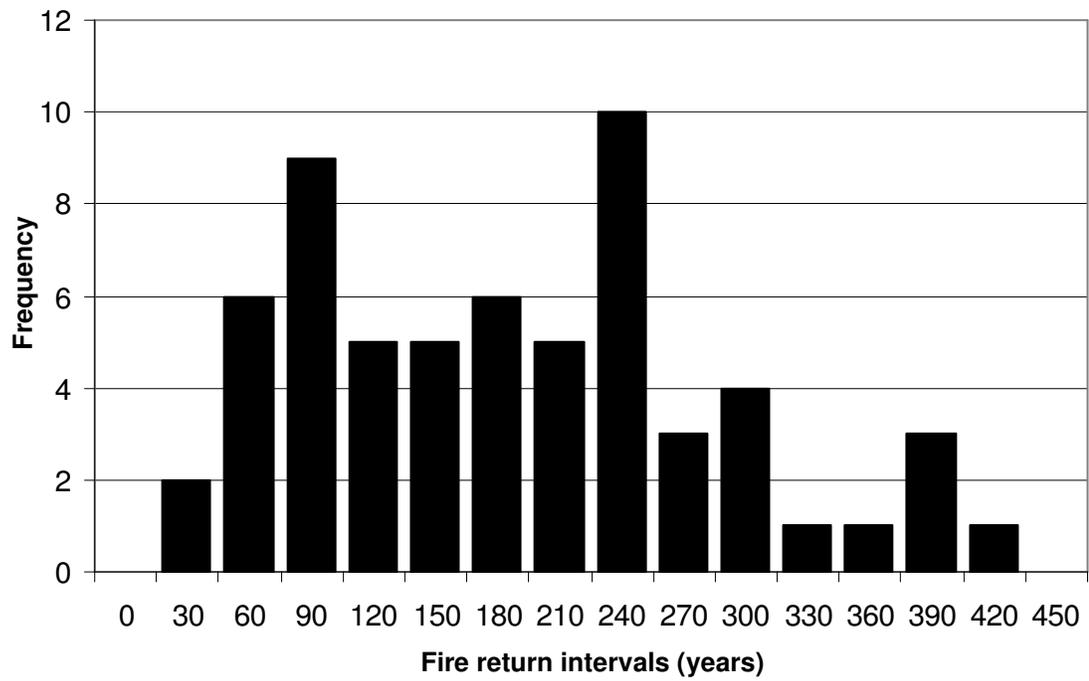


Figure 4.6 Frequency distribution of fire return intervals.

Table 4.1 Mean fire return interval, standard deviation, minimum and maximum fire return intervals, and number of fires by Holocene periods, calculated from the CHAR-based reconstruction of fire events.

| Holocene period (cal yr BP) | MFRI (\pm SD) years | Min years | Max years | Number of fires |
|---|---------------------------|--------------|--------------|--------------------|
| Entire Holocene | 178 \pm 97 | 30 | 410 | 62 |
| Early Holocene (>10,000 to c. 8500 cal BP) | 215 \pm 119 | 60 | 370 | 12 |
| Mid Holocene (c. 8500 to 4500 cal BP) | 151 \pm 81 | 30 | 300 | 26 |
| Late Holocene (c. 4500 cal BP to present) | 189 \pm 100 | 30 | 410 | 24 |

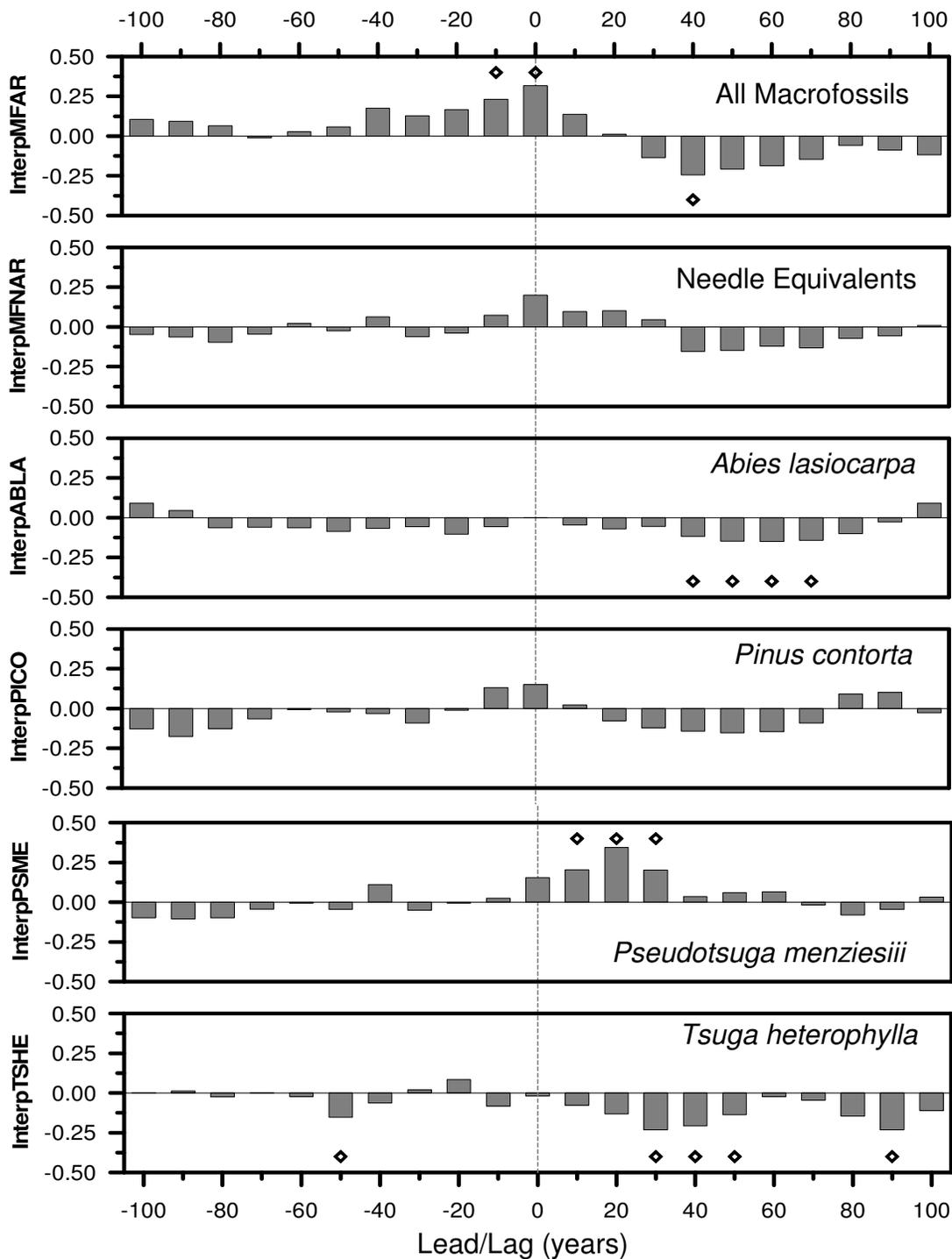


Figure 4.7 Results from superposed epoch analysis. Diamonds indicate significant responses within a 90% confidence interval.

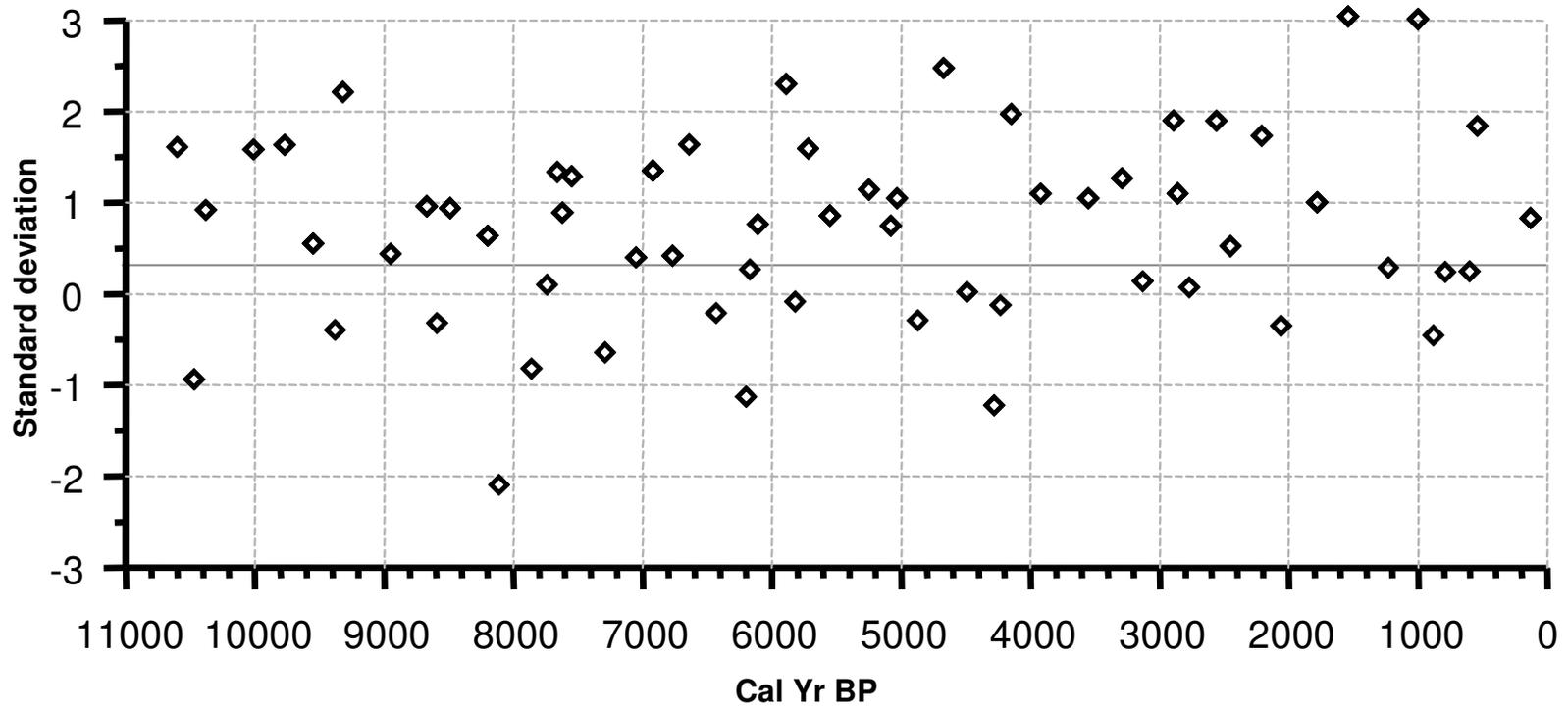


Figure 4.8 Covariance between canonical fire events and macrofossil accumulation rates (MFAR). The line at 0.34 represents the critical value at $p = 0.10$.

Discussion

Holocene reconstruction of fire frequency

Based on our lake sediment charcoal record, fire frequency has been highly variable at this site throughout the Holocene. Fire return intervals range from 30 to 400 yr, and there is no significant difference in mean fire return intervals between the early-, mid-, and late-Holocene periods. Two other reconstructions of Holocene fire frequency from high resolution lake sediment charcoal records have been conducted in the Pacific Northwest and can serve as a comparison to this study (Long et al. 1998, Hallett et al. 2003). Long et al. (1998) reconstructed a 9000-year fire history in the Coast Range of Oregon, and Hallett et al. (2003) reconstructed an 11,000-year fire history from mountain sites in southwestern British Columbia. Both studies interpreted more frequent fires in the early Holocene, likely as a result of warmer, drier summers associated with high summer insolation (Thompson 1993).

In this study, there appears to be no major changes in fire frequency over the >10,000 year record. Fire regimes may not substantially change over the Holocene at this montane site. However, previous studies have demonstrated that sediment charcoal records do not reliably record low to moderate severity fire events (Mohr et al. 2000, Higuera 2002). During the late Holocene, the continuous presence of late successional species including western hemlock and western redcedar make it unlikely that low severity fires were common during this period (Chapter 2). In the early and mid Holocene, dry forest assemblages including lodgepole pine, Douglas-fir and western white pine (Chapter 2), could have accommodated a low to moderate severity fire regime not detected by our charcoal record. High background CHAR in the early Holocene might represent charcoal accumulations from low to moderate severity fire events and/or distant fire events that were not recorded as peaks in the sediment record.

Although there are no major changes in estimated fire frequency over the Holocene, there is a noticeable drop in CHAR background levels from c. 7500 cal yr BP to c. 4000 cal yr BP. This drop in CHAR is paralleled in the macrofossil record. Changes in sedimentation rates during this period are probably not responsible for drops

in CHAR and MFAR. The core chronology indicates no major change in sedimentation rates, and there is adequate dating control to trust the chronology. Instead, the explanation for shifts in background CHAR and MFAR may be ecological. It is possible that the forests surrounding the Panther Potholes during the mid Holocene were relatively open and contributed lower macrofossil input than in the early and late Holocene periods. Lower fuel loads also could have resulted in low background and peak CHAR values.

The high variability in fire return intervals throughout the Holocene is notable in our record. Mean fire return intervals are generally calculated from multiple point locations or across spatially-defined landscapes (Agee 1993). Historic fire return intervals from lake sediment charcoal, which represents a vague spatial area, should probably be used to evaluate changes over time rather than to represent actual fire frequency (Hallett et al. 2003). Even so, the variability in historic fire return intervals at Panther Potholes suggests that mean fire return intervals sampled from tree-ring reconstructions may not adequately represent the variability in historic fire frequencies and should be treated with caution. Most estimates of mean fire return intervals span a few centuries at most. Estimation of fire frequency from any 300-400 year period in our record would yield markedly different estimates and be highly dependent on the selected time period. Long-term charcoal-based reconstructions of fire frequency are our best method to assess the historic range of variability in fire regimes and may help to determine whether tree-ring reconstructions of fire frequency adequately capture this variability. In the case of our study area, a fire history based on tree-ring reconstructions would likely underrepresent the variability in fire return intervals.

Although broad climatic trends are not apparent in our fire record, the most recent fires at Panther Potholes fall within time periods when large fires occurred throughout the maritime Pacific Northwest. Recent studies suggest that climatic forcings may be responsible for regional wildfire years of the Pacific Northwest and elsewhere (Clark 1988, 1990, Hallett et al. 2003, Gedalof *submitted*). Correspondence of fire periods between this study and others, summarized in Weisberg and Swanson (2003), suggests that the fire history at Panther Potholes is linked to regional-wide fire years. For

example, the most recent fires in the lake sediment record, c. 130, 540, and 600 years BP, match periods in which Weisberg and Swanson (2003) report regional fires.

Macrofossil response to fire events

Many detected CHAR peaks are associated with a response in the macrofossil record. This association corroborates our interpretation that delineated CHAR peaks mostly represent local fire events (i.e., fire events occurring at or near the lake basin). The initial peak in macrofossils associated with CHAR peaks suggests high needle influx following high-severity fires. Similarly, a drop in mean MFAR following fire events is likely caused by low needle influx during the first few decades of stand regeneration. Throughout the Holocene, forest regeneration following stand-replacing fires could have been slow due to short growing seasons at this montane site and resulted in this drop in MFAR following CHAR peaks.

Fire delineations by the standard CHAR decomposition method probably represent a mixed signal of local and extralocal fires, which incorporates the fire history of forests on both sides of Fourth of July Pass. Modern charcoal source area studies (Millspaugh and Whitlock 1995, Clark et al. 1998, Gardner and Whitlock 2001) have demonstrated that watersheds downwind of extralocal fire events (i.e., in a nearby watershed) record CHAR peaks. It is conceivable that charcoal peaks with a macrofossil response represent local fire events and that most other fire events were extralocal and/or of moderate to low severity. Of the 23 CHAR peaks that did not have a macrofossil response, 15 were relatively small peaks and could have been extralocal or low to moderate severity fires that did not impact local vegetation. We also cannot know if all local fire events had a corresponding peak in macrofossils or if some of these matches are coincidental.

The differential response of individual tree species to fire events suggests that fires may have altered forest assemblages and influenced successional dynamics. Stand-replacing fire events likely favored the initial establishment of Douglas-fir over late-

successional species that are less adapted to fire. In particular, Douglas-fir exhibits a significant peak following fire whereas western hemlock and subalpine fir exhibit significant drops following fire.

Many peaks in MFAR are not associated with CHAR peaks and could be the result of noise, other disturbance agents such as windstorms, low severity fires not detected in the sediment record, and/or tree mortality associated with insects or diseases. For example, during the early Holocene when lodgepole pine is especially dominant (c. 9000 to 8000 cal BP) (Chapter 2), several MFAR peaks are not associated with CHAR peaks and may reflect other disturbances such as mountain pine beetle outbreaks or low severity fire events.

Conclusions

Long-term charcoal records are the only method for reconstructing fire histories beyond the time limits of dendrochronological reconstructions. However, they are not without problems. Determining a threshold for peak detection is often based on known fire events, which represent only a fraction of the entire record and may not adequately represent past fires. Complementary indicators of fire such as soil charcoal dates (Gavin et al. 2002, Hallett et al. 2003) or pollen/macrofossil responses to fire lend confidence to our interpretation of charcoal records. Macrofossils, in particular, represent a local signal of vegetation and may be useful in the determination of local fire events.

We found a significant correspondence between fires detected by standard CHAR decomposition techniques and responses in the macrofossil record. Macrofossil evidence indicates that most charcoal peaks represent local fire events. Reconstructed fire intervals are highly variable and suggest that mean fire return intervals alone would not adequately characterize the temporal dynamics of fire. Fire frequency has fluctuated somewhat through broad time periods of the Holocene and was somewhat higher in mid Holocene than the late Holocene. These estimates are probably conservative because low to moderate severity fires may not have been recorded.

A number of management applications may be taken from this study. First, the high range of variability in Holocene fire return intervals suggests that local managers should treat mean fire return intervals with caution, particularly in light of global warming scenarios. To adequately characterize the historic range of variability of fire regimes in the North Cascades Mountains, records that extend beyond the scale of tree-ring reconstructions are probably necessary. Second, fire histories based on long-term charcoal records may be most useful for locations in which fire regimes are characterized by infrequent, high severity fires. In our study area, fires were probably of mixed frequency and severity (Agee et al. 1990), and low-severity fires may have been missed in the sediment record. Finally, factors affecting vegetation assemblages may be scale dependent. Millennial-scale changes in vegetation over the Holocene appear to be associated with broad changes in Holocene climatic regimes (Chapter 3). Over decadal to century-scales, fire appears to have influenced vegetation assemblages and reset successional trajectories. In particular, late successional species, including western hemlock and subalpine fir exhibit drops in MFAR following fire events, whereas Douglas-fir appears to have been initially favored by past fire events.

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APPENDIX A: AGE-TO-CORE-HEIGHT CORRECTIONS ¹

| Core Height (cm) | Subalpine fir | Lodgepole pine (dry) | Lodgepole pine (subalpine) | Douglas-fir (Site V) ² | Mountain hemlock (dry) ³ |
|------------------|---------------|----------------------|----------------------------|-----------------------------------|-------------------------------------|
| 5 | 3 | | | 1 | 4 |
| 10 | 4 | 1 | 2 | 2 | 6 |
| 20 | 5 | 2 | 3 | 3 | 8 |
| 30 | 6 | 3 | 4 | 3 | 11 |
| 40 | 7 | 3 | 5 | 4 | 16 |
| 50 | 9 | 4 | 6 | 5 | 16 |
| 60 | 9 | 4 | 6 | 6 | 16 |
| 70 | 10 | 4 | 6 | 7 | 17 |
| 80 | 11 | 5 | 7 | 8 | 18 |
| 90 | 12 | 5 | 7 | 9 | 19 |
| 100 | 13 | 5 | 8 | 9 | 20 |
| 110 | | 5 | | 10 | |
| 120 | | 5 | | 10 | |
| 130 | | 6 | | 11 | |
| 140 | | 7 | | 11 | |
| 150 | | 7 | | 11 | |
| 180 | | | | 12 | |

¹ Bold values were taken directly from Agee (1993). Other values were extrapolated.

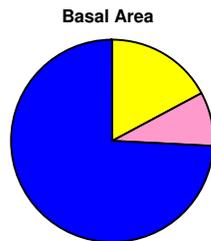
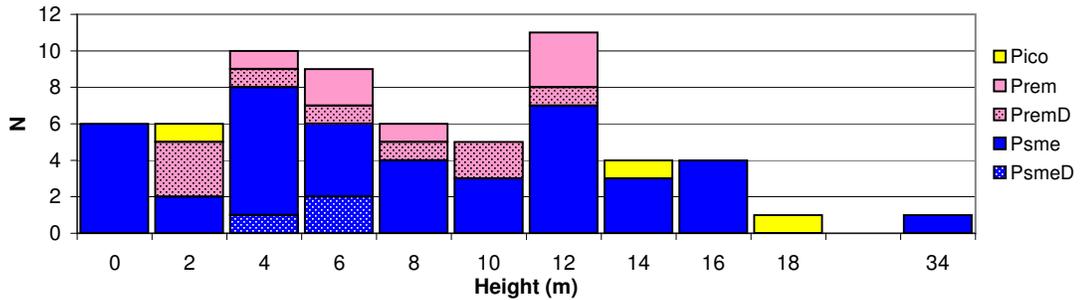
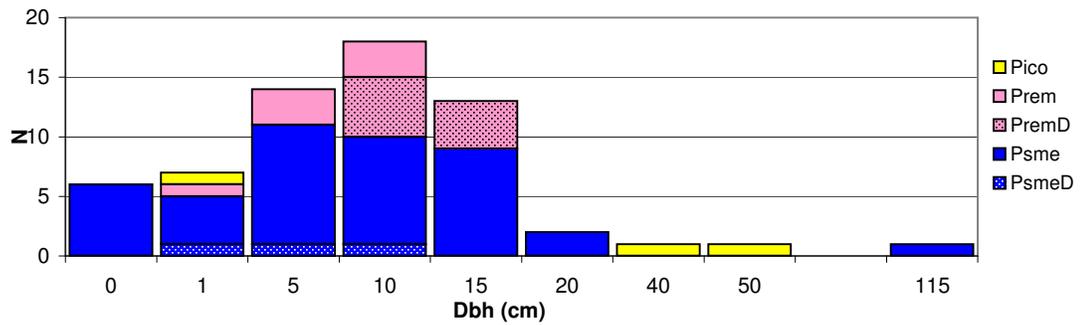
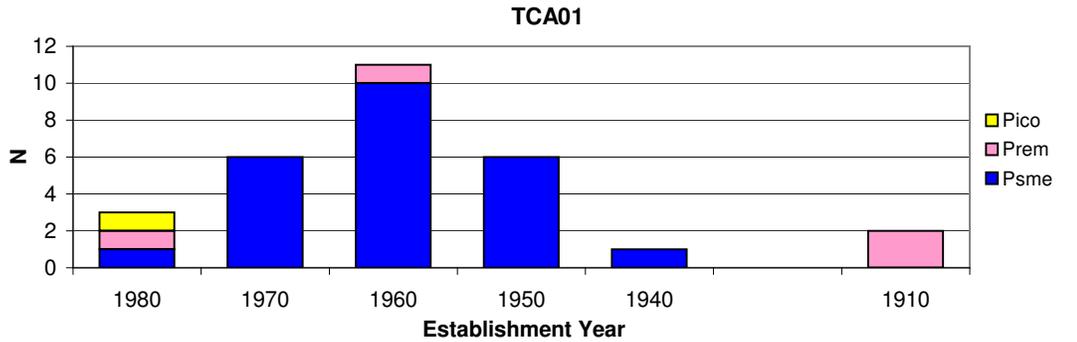
² Also used for bigleaf maple, grand fir, western white pine, bitter cherry, Pacific yew, western redcedar and mountain hemlock.

³ Also used for Pacific silver fir, Alaska yellow cedar, and Engelmann spruce.

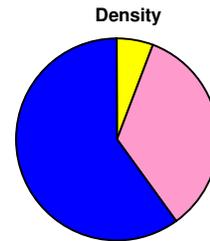
**APPENDIX B: SCIENTIFIC NAMES, CODES AND COMMON NAMES
OF TREE SPECIES**

| Common Name | Code | Scientific Name |
|---------------------|-------------|-----------------------------------|
| Pacific silver fir | PSF | <i>Abies amabilis</i> |
| grand fir | GF | <i>Abies grandis</i> |
| subalpine fir | SF | <i>Abies lasiocarpa</i> |
| bigleaf maple | BM | <i>Acer macrophyllum</i> |
| red alder | RA | <i>Alnus rubra</i> |
| paper birch | PB | <i>Betula papyrifera</i> |
| Alaska yellow cedar | AYC | <i>Chamaecyparis nootkatensis</i> |
| Pacific dogwood | PD | <i>Cornus nuttallii</i> |
| Engelmann spruce | ES | <i>Picea engelmannii</i> |
| lodgepole pine | LP | <i>Pinus contorta</i> |
| western white pine | WWP | <i>Pinus monticola</i> |
| bitter cherry | BC | <i>Prunus emarginata</i> |
| Douglas-fir | DF | <i>Pseudotsuga menziesii</i> |
| Pacific yew | PY | <i>Taxus brevifolia</i> |
| western redcedar | WRC | <i>C plicata</i> |
| western hemlock | WH | <i>Tsuga heterophylla</i> |
| mountain hemlock | MH | <i>Tsuga mertensiana</i> |

APPENDIX C: TREE AGE AND SIZE FREQUENCY DISTRIBUTIONS*



■ Pico
■ Prem
■ Psme



Age Class Frequency Distribution

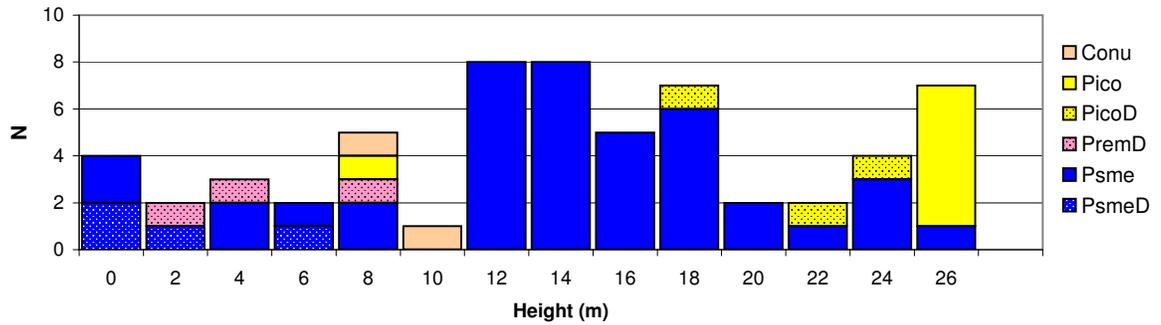
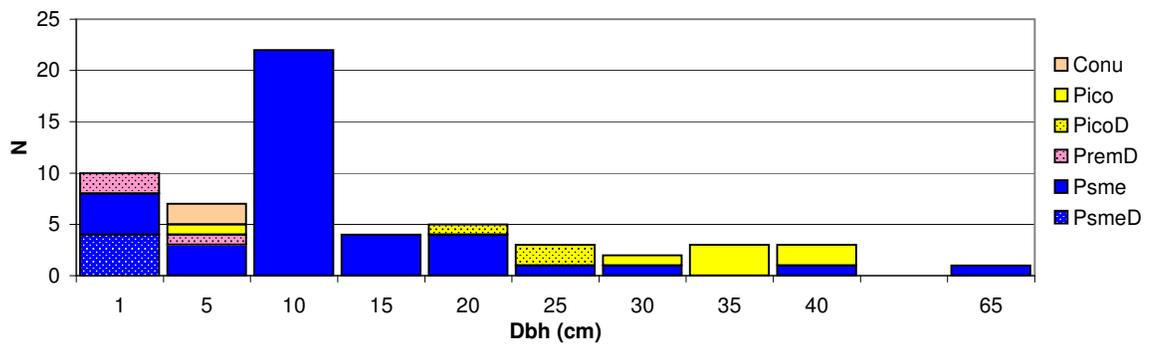
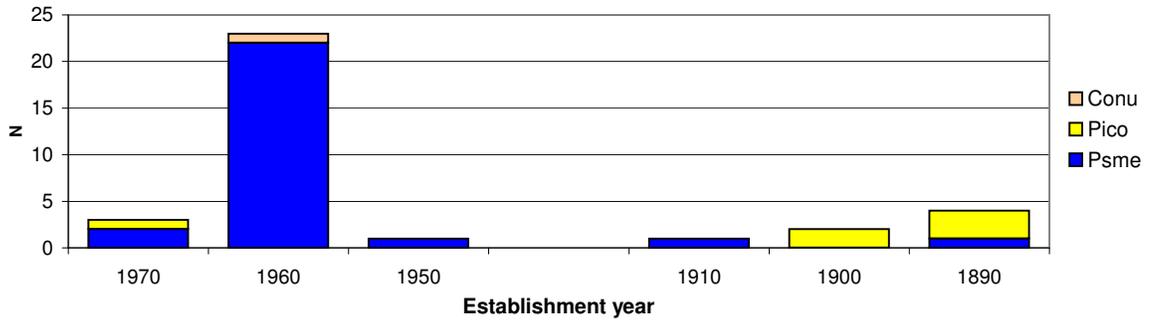
| Lifeform | # of Samples |
|----------|--------------|
| Sapling | 10 |
| Seedling | 0 |
| Tree | 19 |
| TOTAL | 29 |

Size Class Frequency Distributions

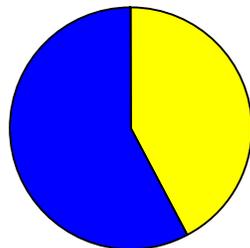
| Lifeform | # of Samples |
|----------|--------------|
| Sapling | 23 3 dead |
| Seedling | 5 |
| Tree | 35 5 dead |
| TOTAL | 63 |

* Pie charts include trees only. Species codes followed by a "d" indicate dead individuals.

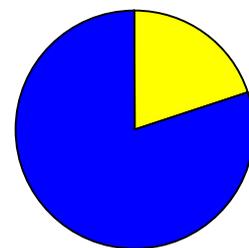
TCA02



Basal Area



Density

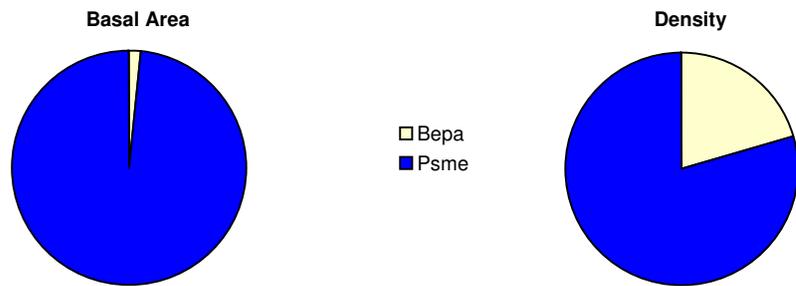
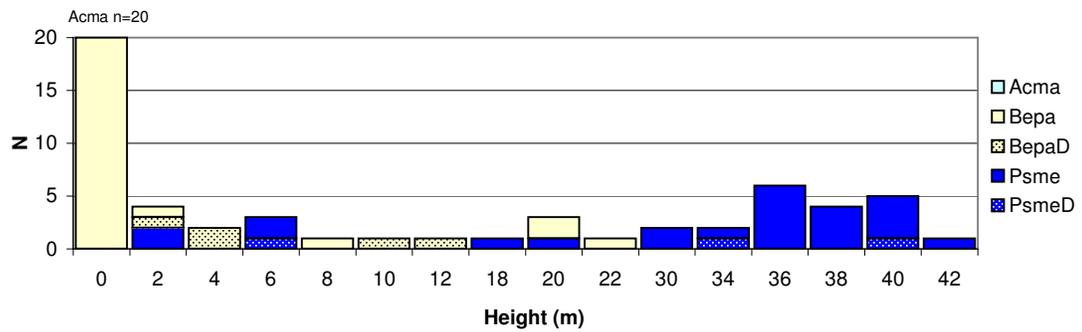
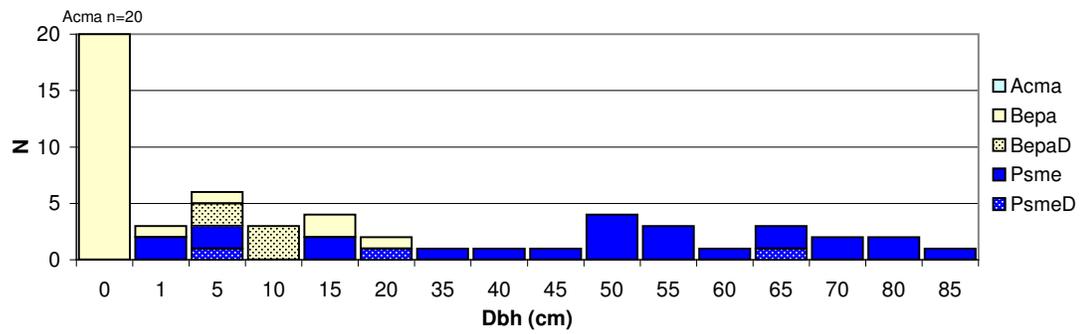
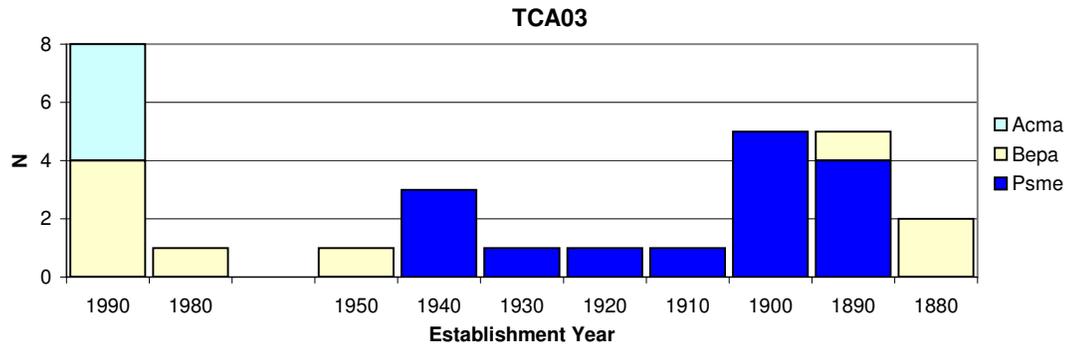


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sapling | 9 |
| Seedling | 0 |
| Tree | 25 |
| TOTAL | 34 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sapling | 15 (5 dead) |
| Seedling | 0 |
| Tree | 45 (5 dead) |
| TOTAL | 60 |

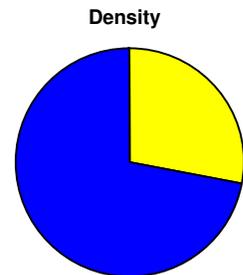
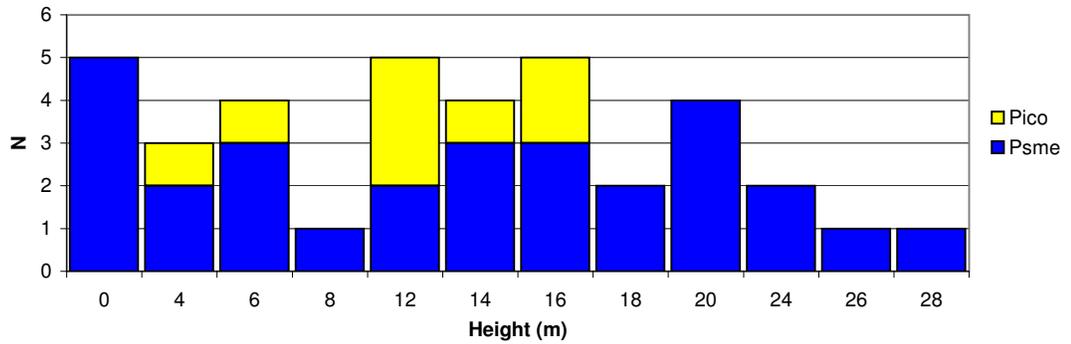
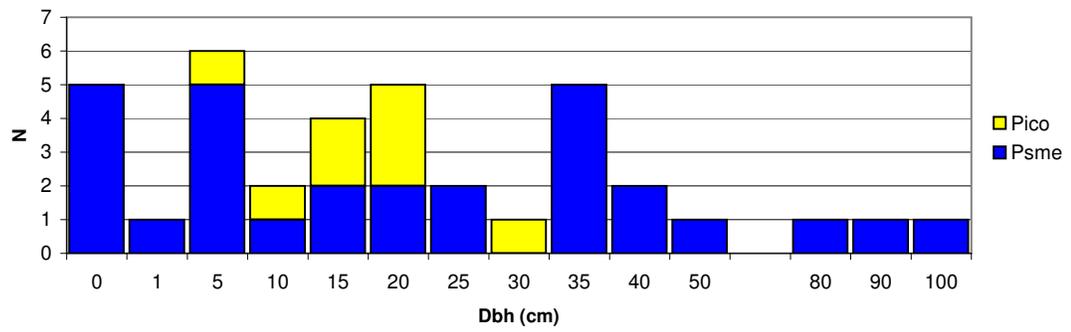
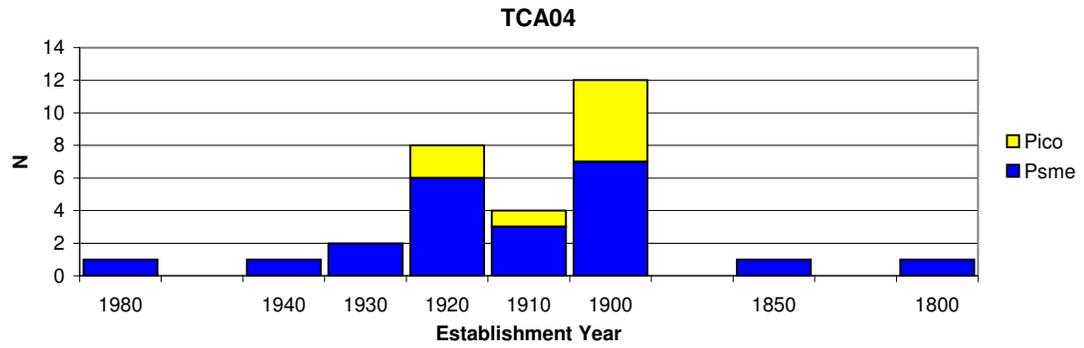


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 6 |
| Seed | 8 |
| Tree | 14 |
| TOTAL | 28 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 8 (2 dead) |
| Seed | 40 |
| Tree | 29 (6 dead) |
| TOTAL | 77 |

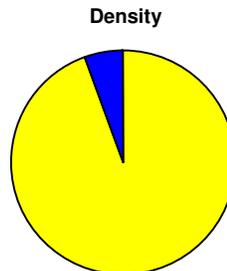
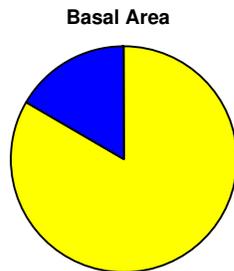
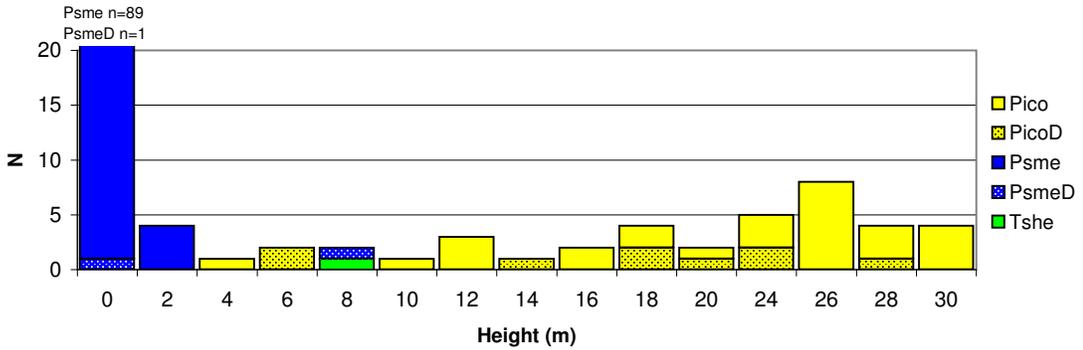
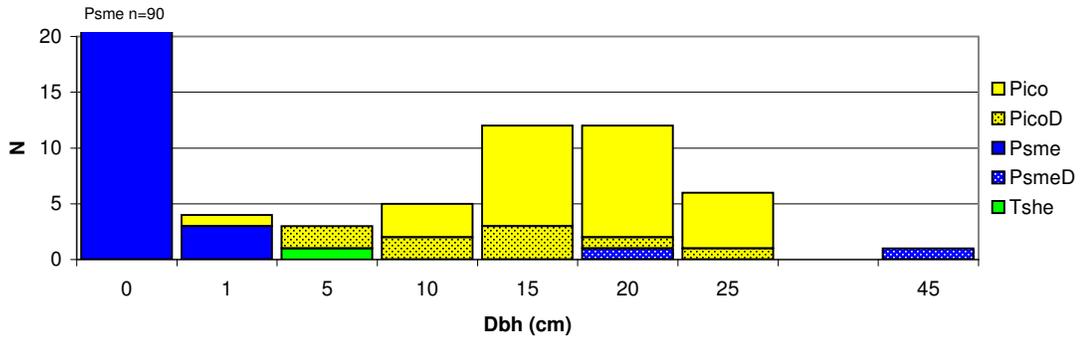
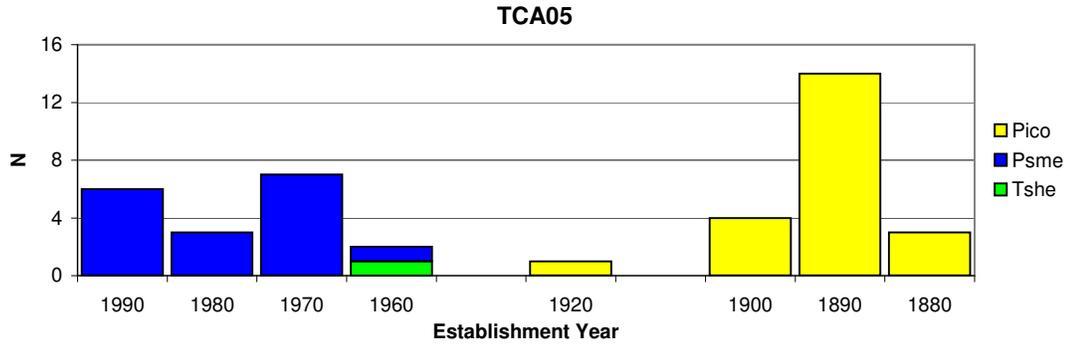


Age Class Frequency Distribution

| <u>Lifeform</u> | <u># of Samples</u> |
|-----------------|---------------------|
| Sap | 7 |
| Seed | 1 |
| Tree | 22 |
| TOTAL | 30 |

Size class Frequency Distributions

| <u>Lifeform</u> | <u># of Samples</u> |
|-----------------|---------------------|
| Sap | 7 |
| Seed | 5 |
| Tree | 25 |
| TOTAL | 37 |



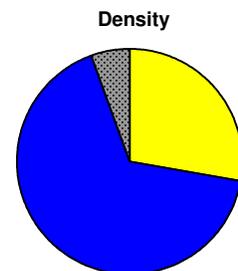
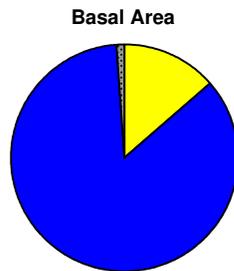
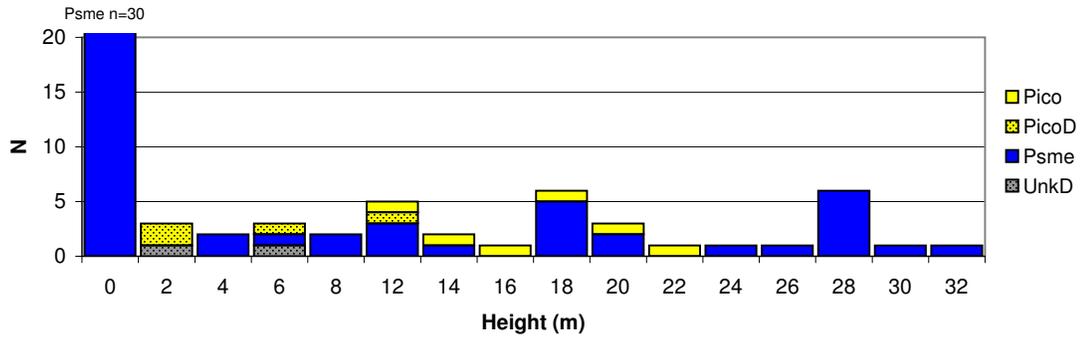
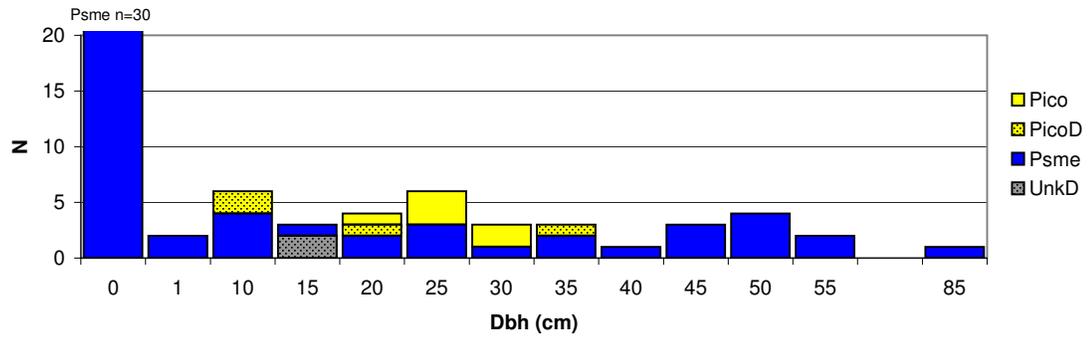
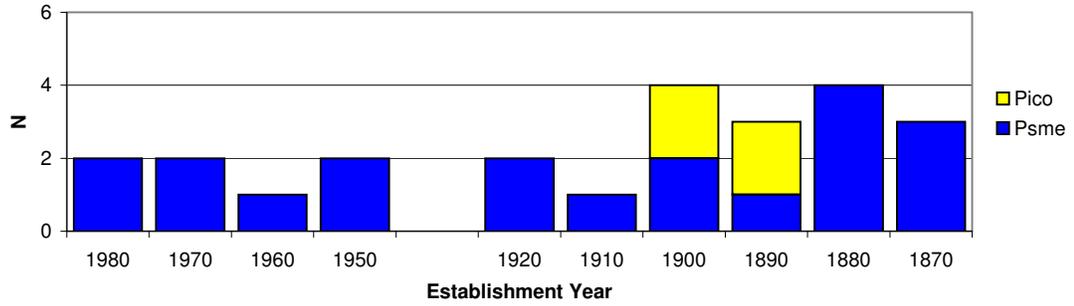
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 9 |
| Tree | 21 |
| TOTAL | 40 |

Size class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 13 (2 dead) |
| Seed | 84 |
| Tree | 36 (9 dead) |
| TOTAL | 133 |

TCA06



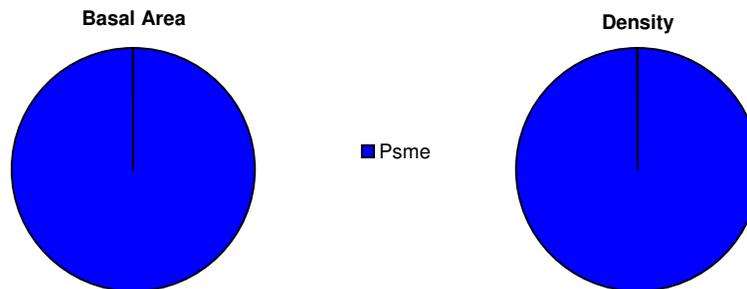
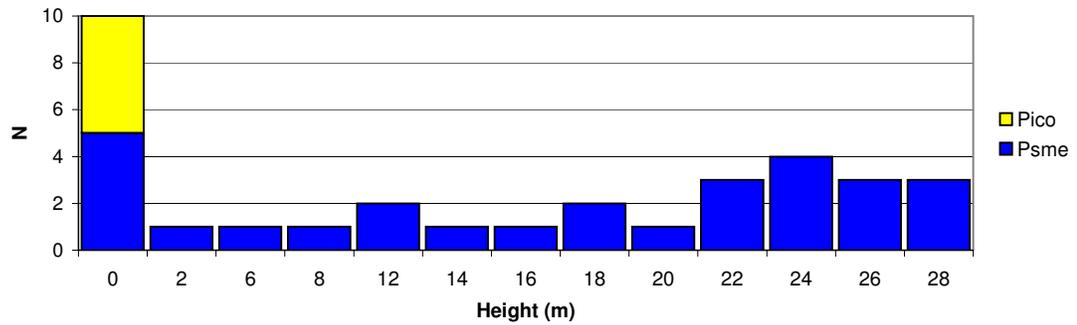
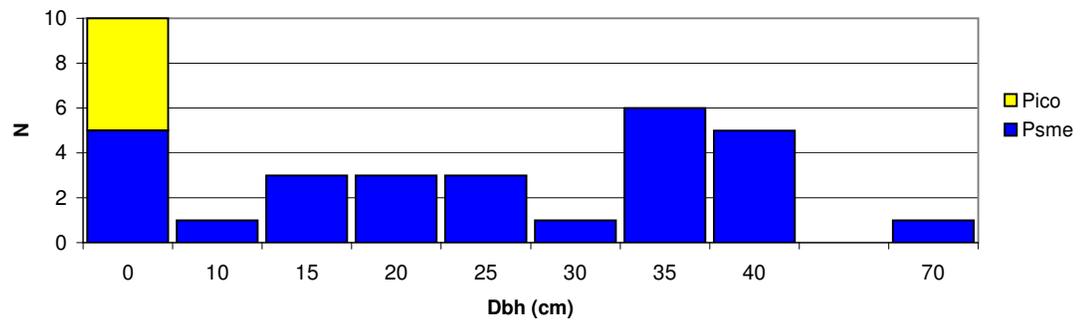
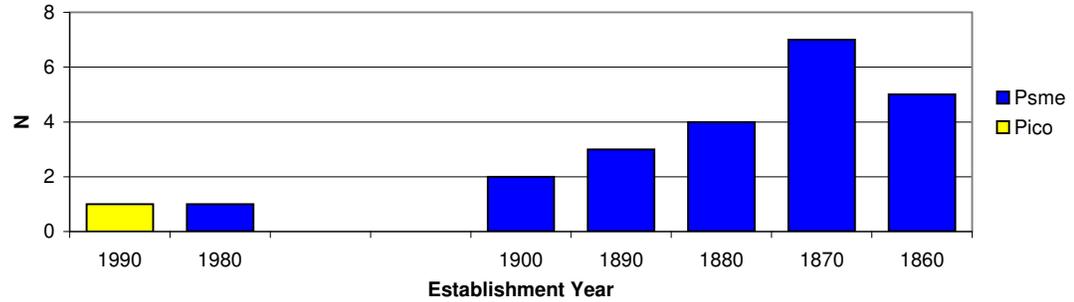
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 2 |
| Seed | 6 |
| Tree | 16 |
| TOTAL | 24 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 2 |
| Seed | 30 |
| Tree | 36 (6 dead) |
| TOTAL | 68 |

TCA07



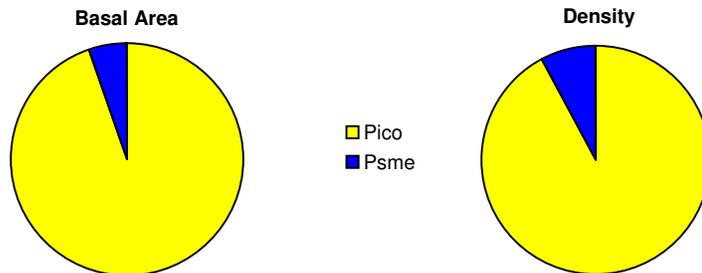
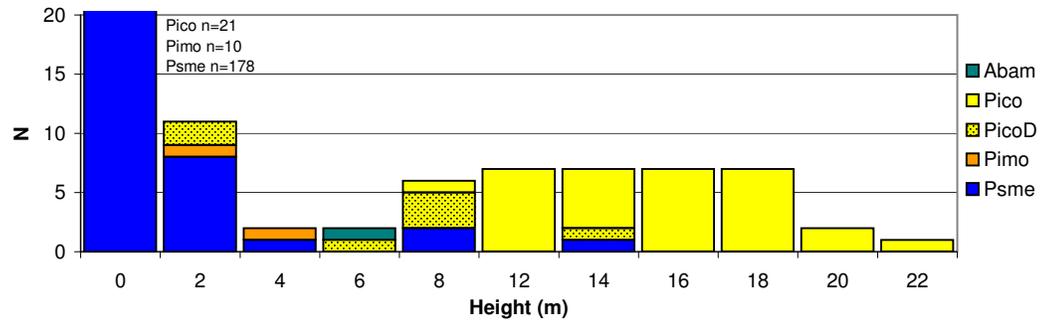
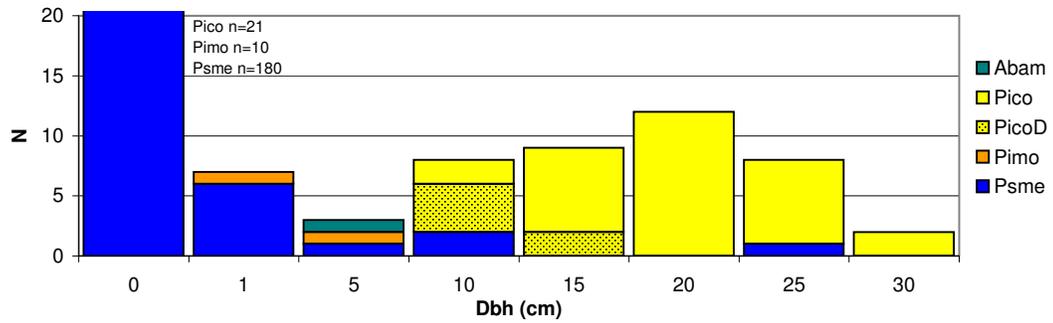
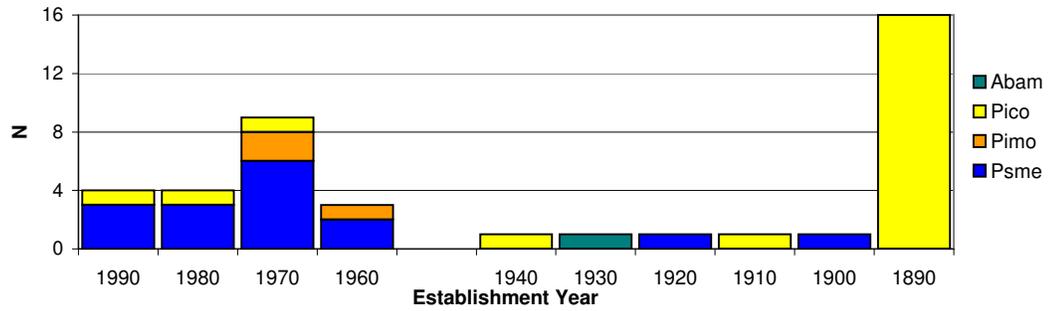
Age Class Frequency Distribution

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 0 |
| Seed | 2 |
| Tree | 21 |
| TOTAL | 23 |

Size class Frequency Distributions

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 0 |
| Seed | 10 |
| Tree | 23 |
| TOTAL | 33 |

TCA08



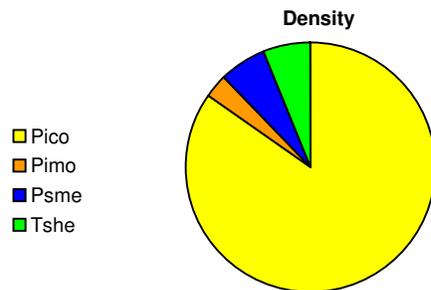
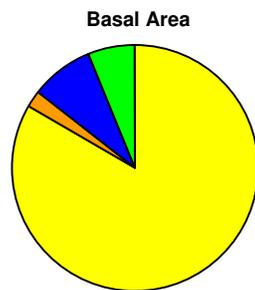
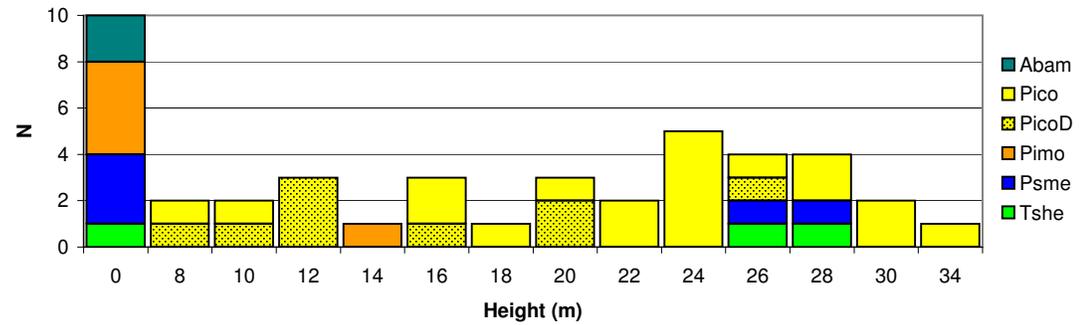
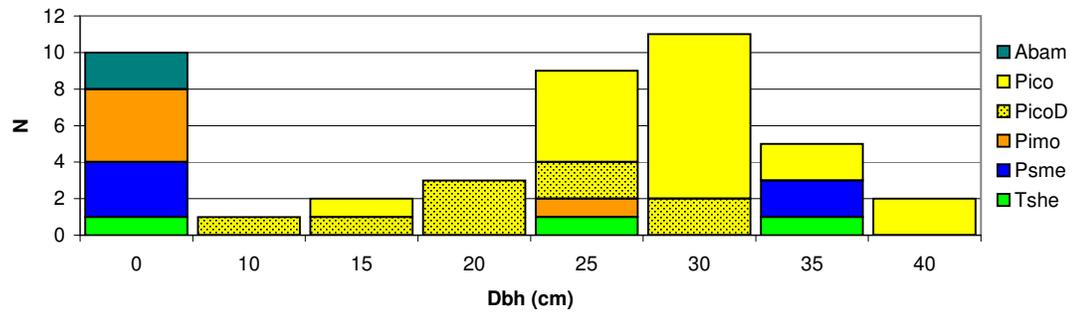
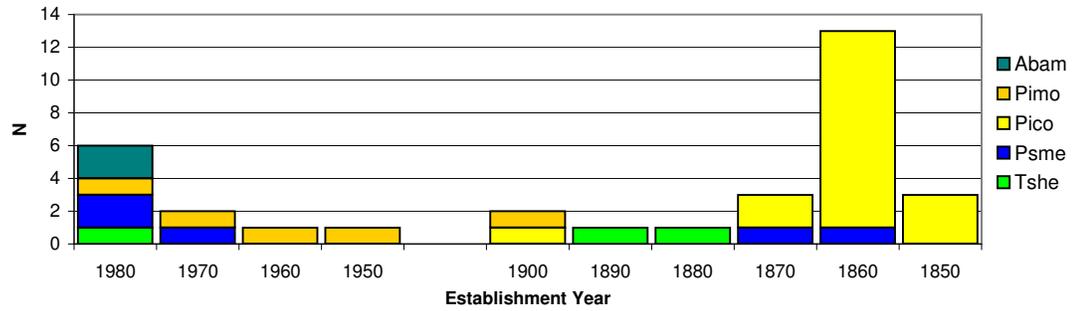
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 11 |
| Tree | 20 |
| TOTAL | 41 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 17 (1 dead) |
| Seed | 205 |
| Tree | 39 (6 dead) |
| TOTAL | 261 |

TCA09



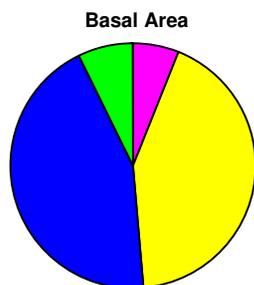
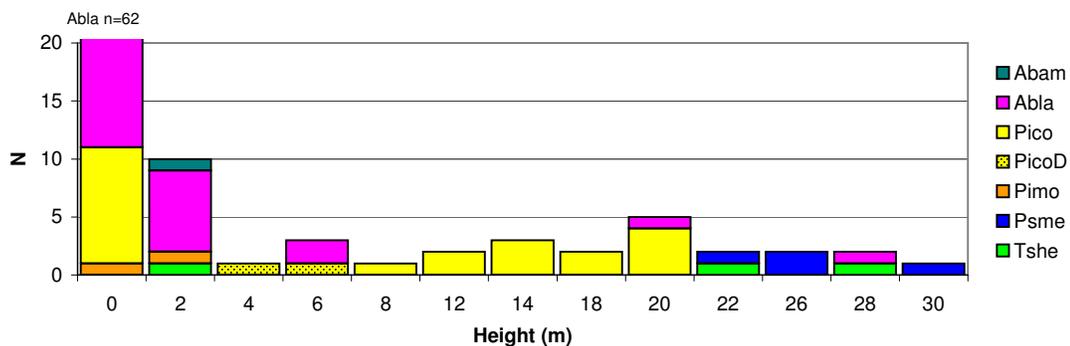
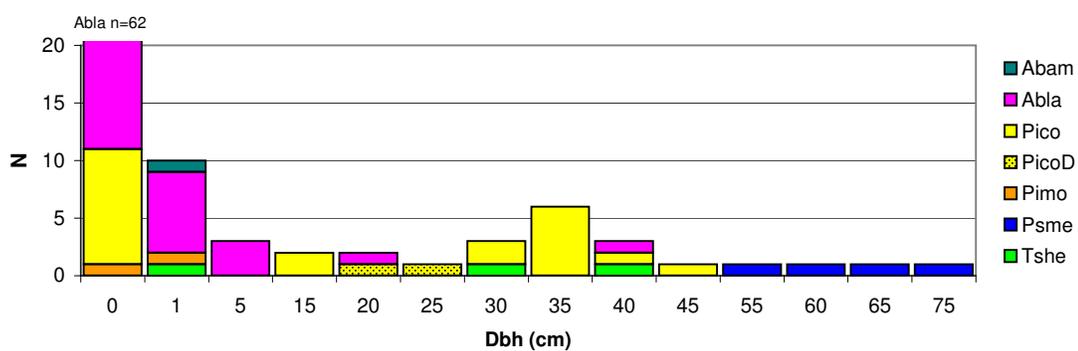
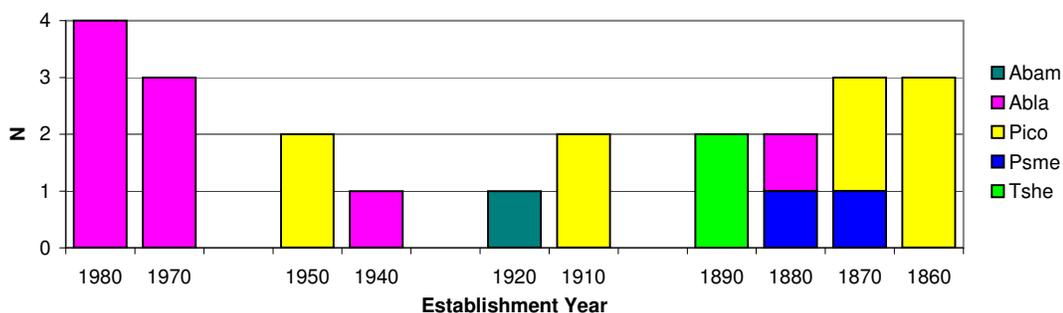
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 0 |
| Seed | 10 |
| Tree | 23 |
| TOTAL | 33 |

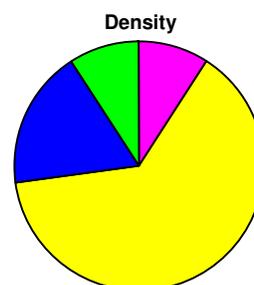
Size class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 0 |
| Seed | 10 |
| Tree | 33 (8 dead) |
| TOTAL | 43 |

TCA10



Abam
Abla
Pico
Psme
Tshe

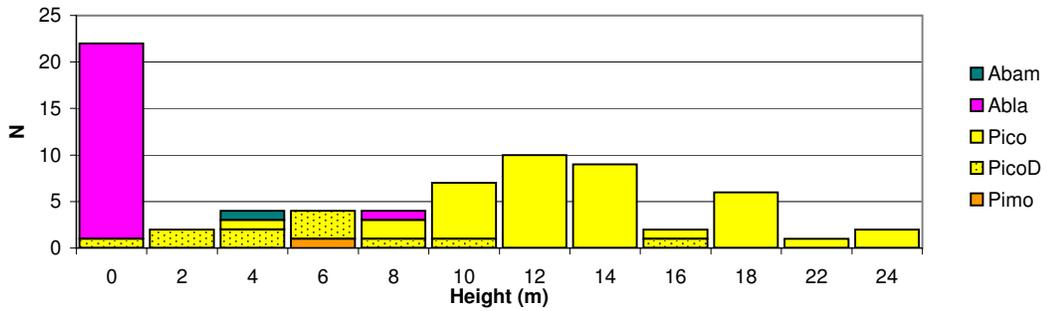
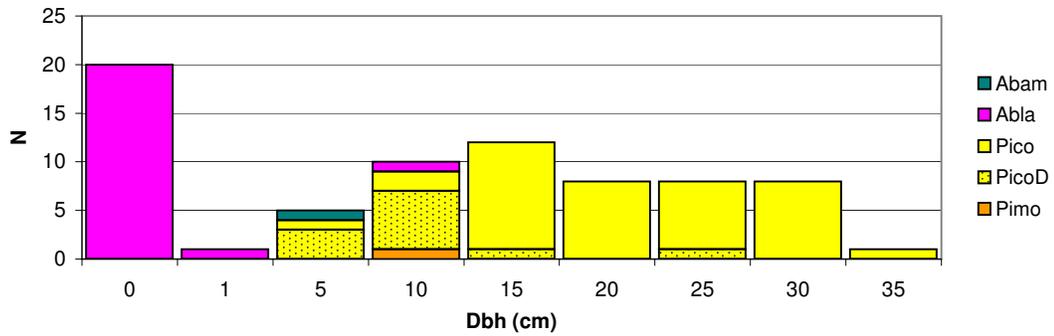
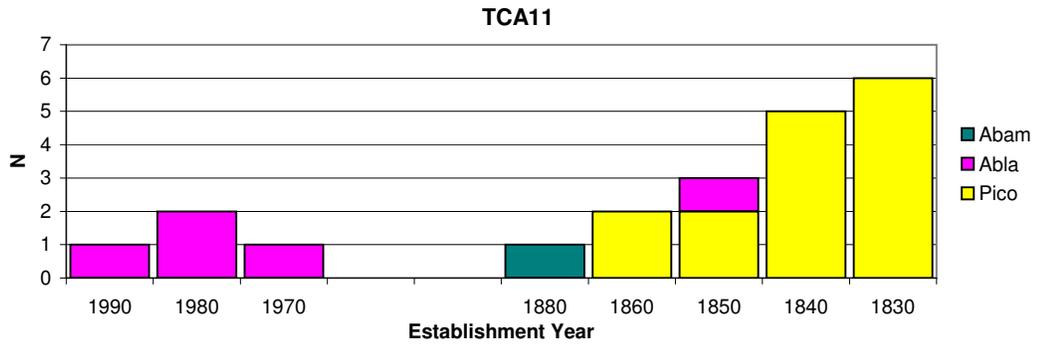


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 1 |
| Seed | 10 |
| Tree | 12 |
| TOTAL | 23 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 20 |
| Seed | 65 |
| Tree | 22 (2 dead) |
| TOTAL | 107 |

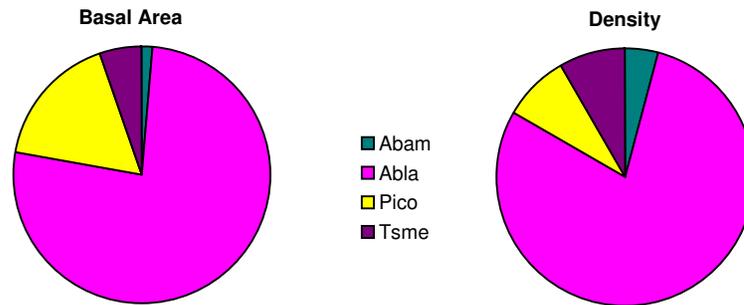
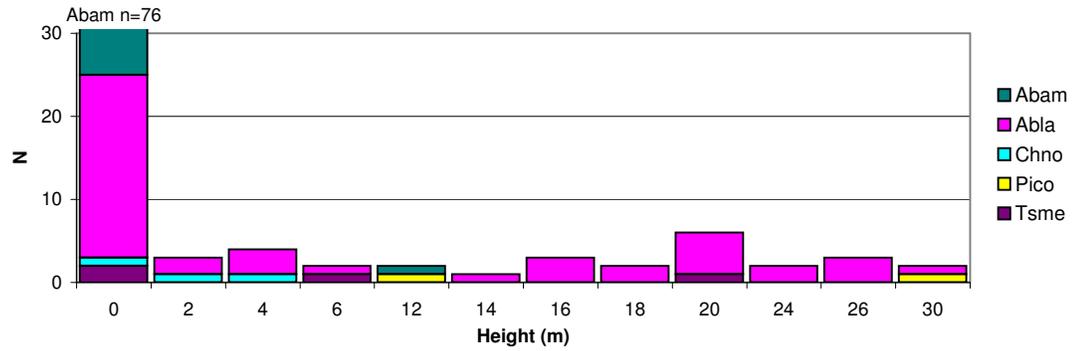
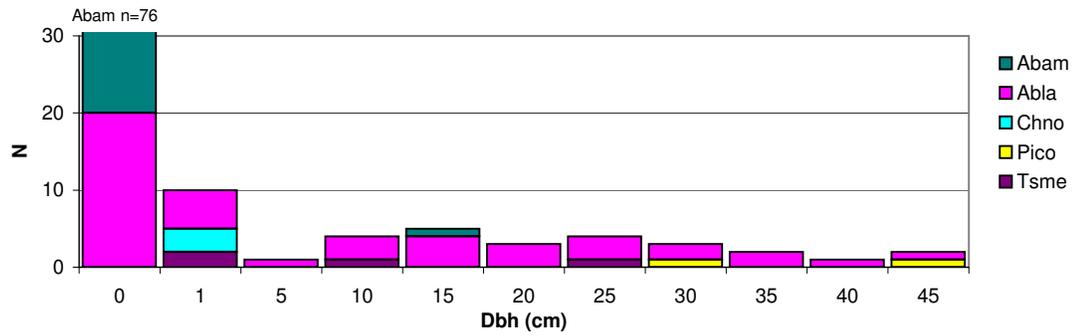
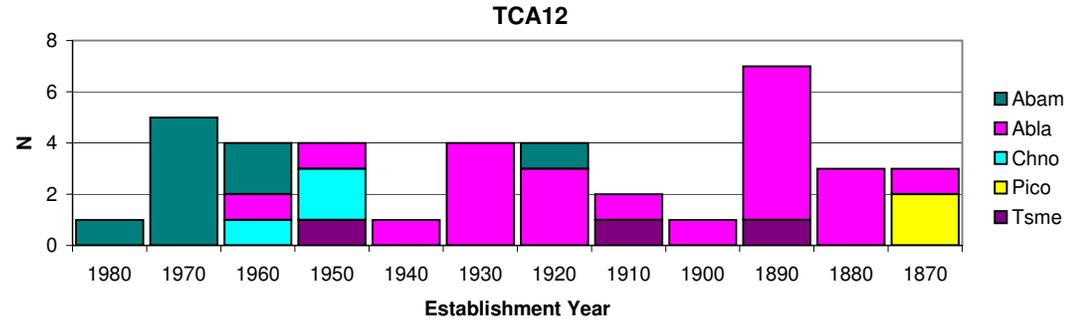


Age Class Frequency Distribution

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 3 |
| Seed | 4 |
| Tree | 14 |
| TOTAL | 21 |

Size class Frequency Distributions

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 5 (2 dead) |
| Seed | 20 |
| Tree | 48 (9 dead) |
| TOTAL | 73 |

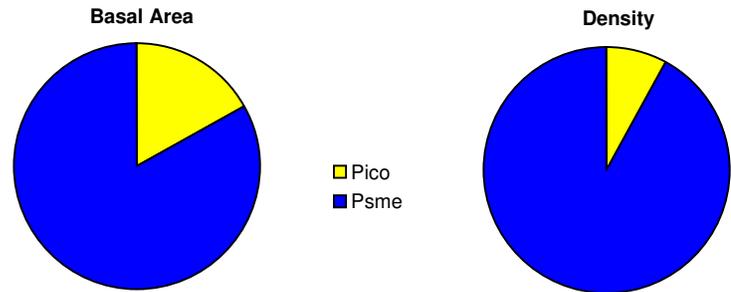
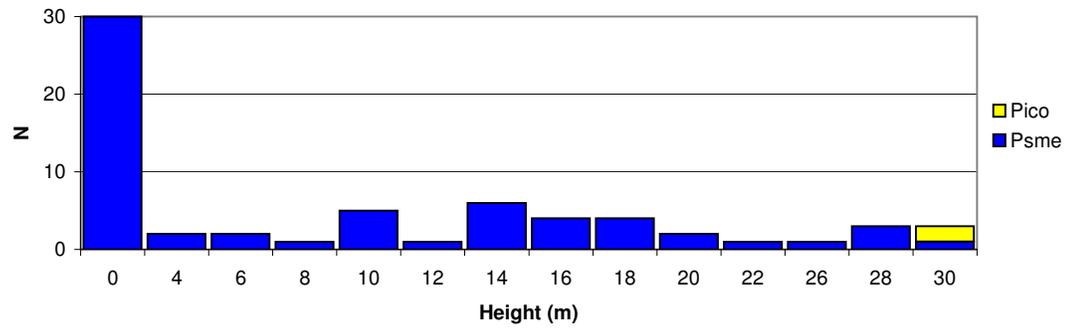
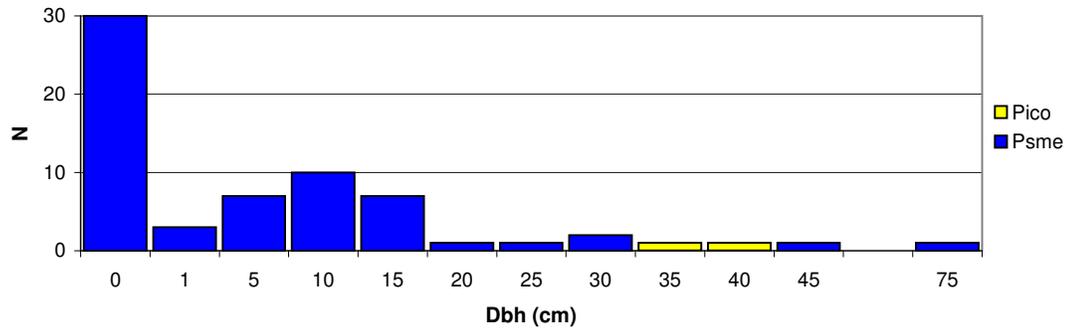
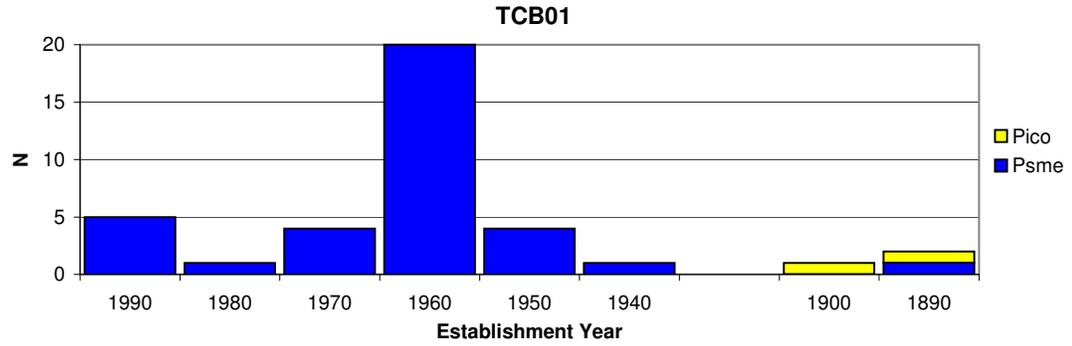


Age Class Frequency Distribution

| <u>Lifeform</u> | <u># of Samples</u> |
|-----------------|---------------------|
| Sap | 10 |
| Seed | 10 |
| Tree | 19 |
| TOTAL | 39 |

Size class Frequency Distributions

| <u>Lifeform</u> | <u># of Samples</u> |
|-----------------|---------------------|
| Sap | 11 |
| Seed | 96 |
| Tree | 24 (1 dead) |
| TOTAL | 131 |

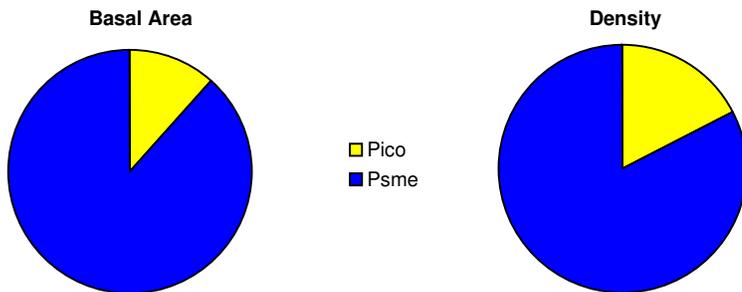
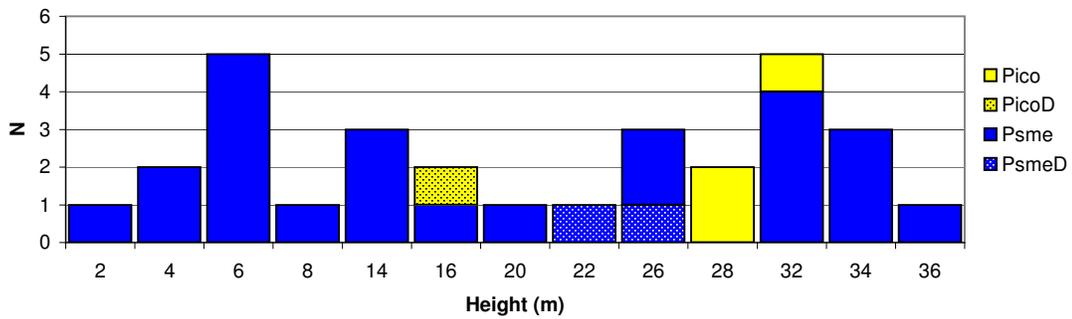
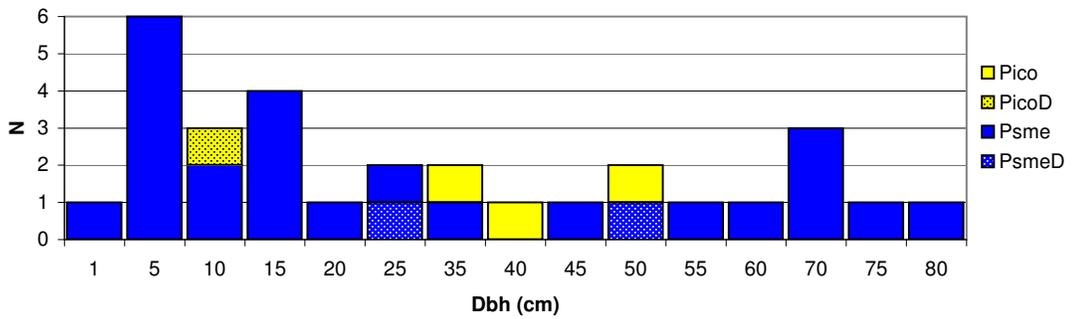
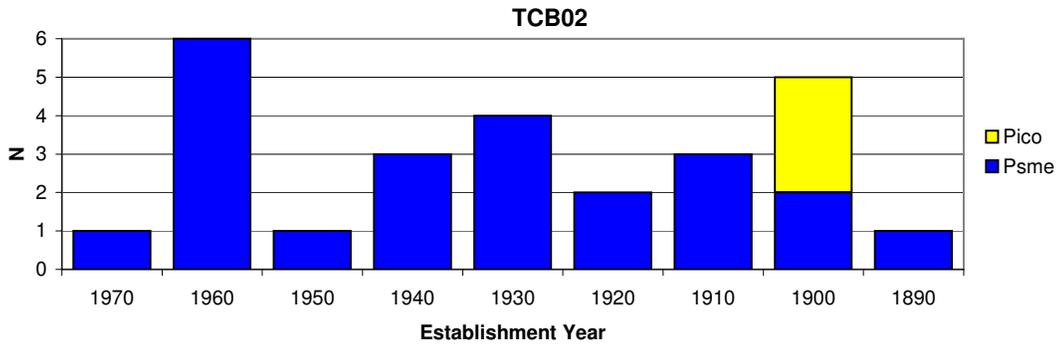


Age Class Frequency Distribution

| <u>Lifeform</u> | <u># of Samples</u> |
|-----------------|---------------------|
| Sap | 10 |
| Seed | 6 |
| Tree | 22 |
| TOTAL | 38 |

Size Class Frequency Distributions

| <u>Lifeform</u> | <u># of Samples</u> |
|-----------------|---------------------|
| Sap | 10 |
| Seed | 6 |
| Tree | 25 |
| TOTAL | 41 |



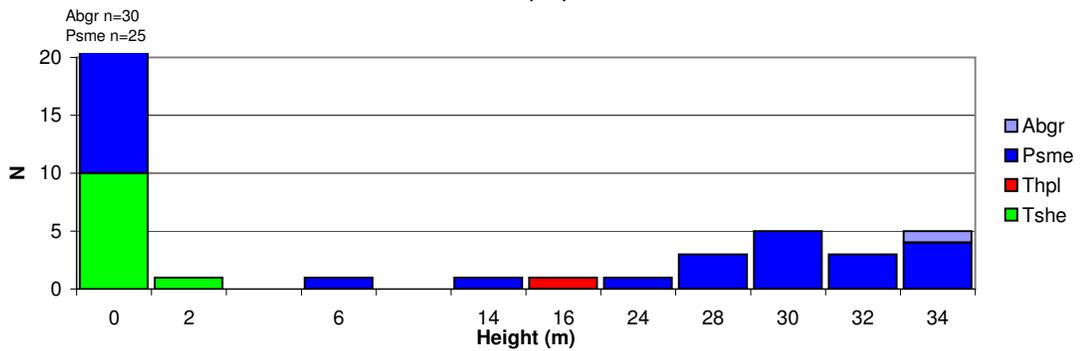
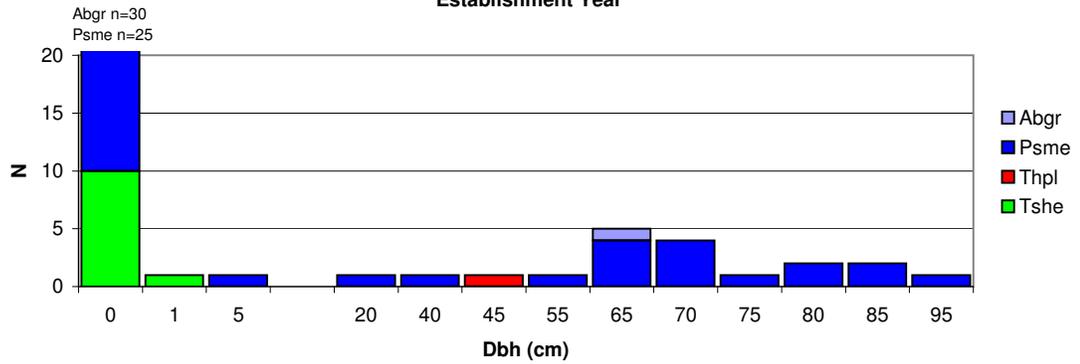
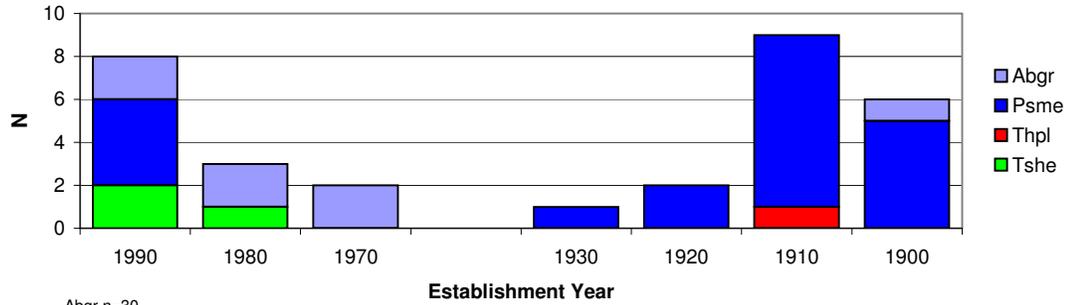
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 7 |
| Seed | 0 |
| Tree | 19 |
| TOTAL | 26 |

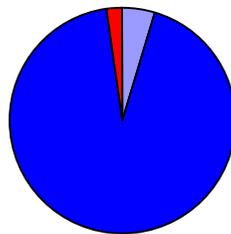
Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 7 |
| Seed | 0 |
| Tree | 23 (3 dead) |
| TOTAL | 30 |

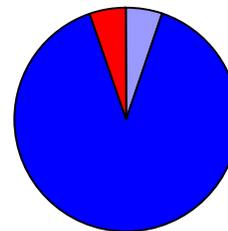
TCB03



Basal Area



Density



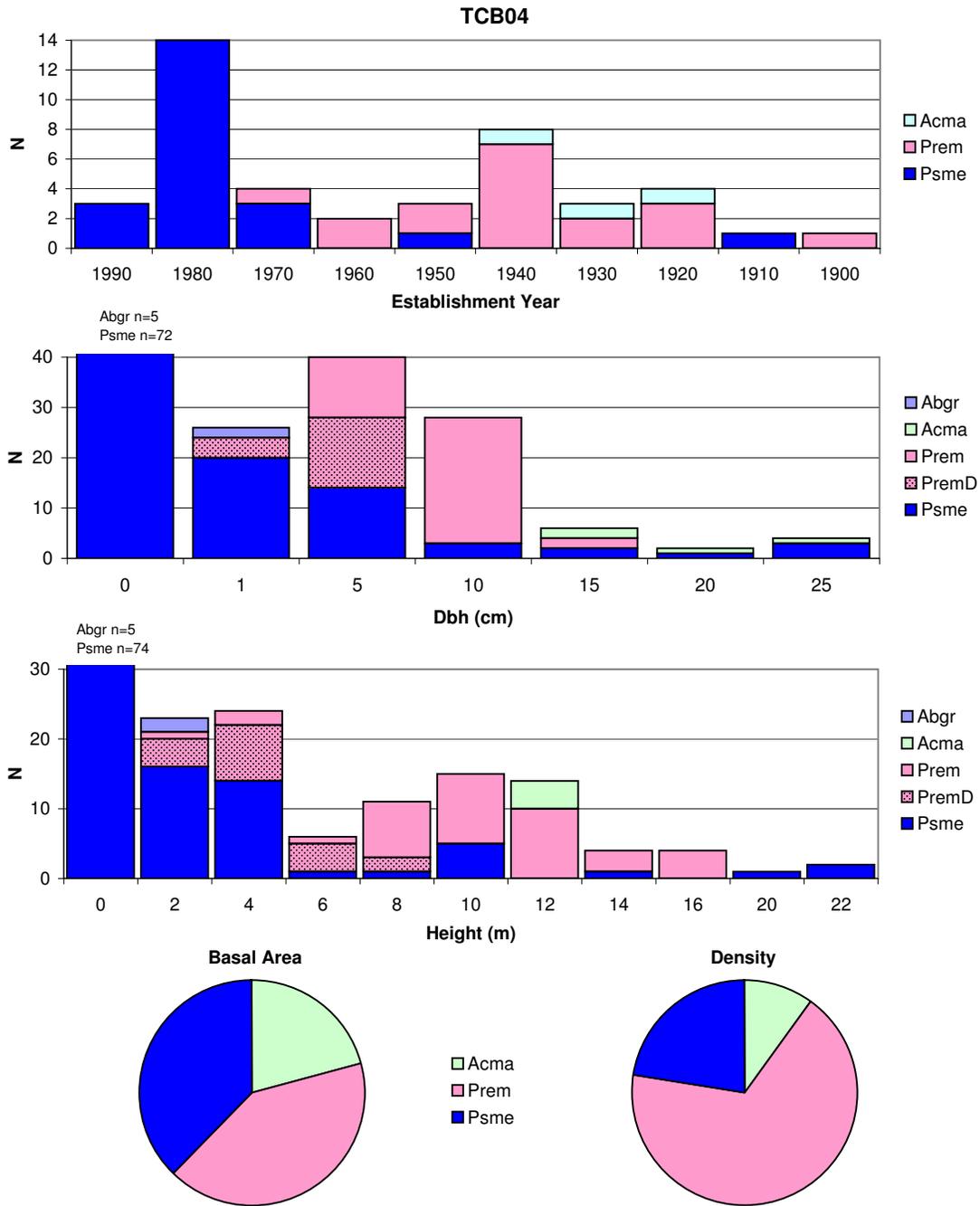
Abgr
Psme
Thpl

Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 2 |
| Seed | 12 |
| Tree | 17 |
| TOTAL | 31 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 2 |
| Seed | 65 |
| Tree | 19 |
| TOTAL | 86 |



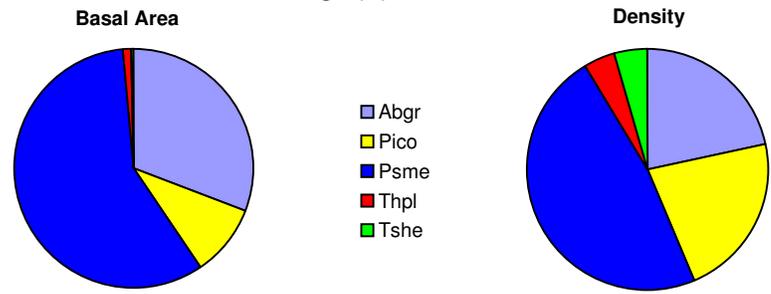
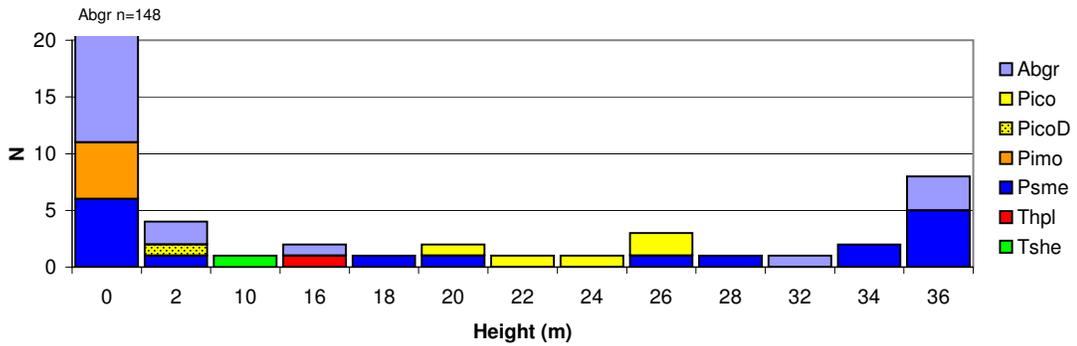
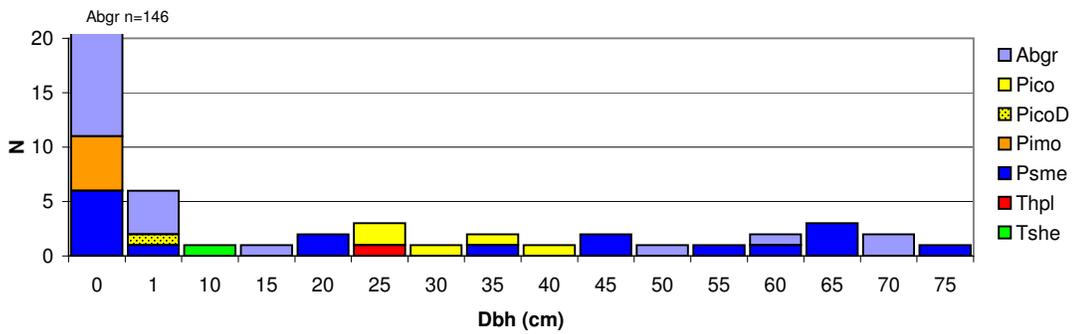
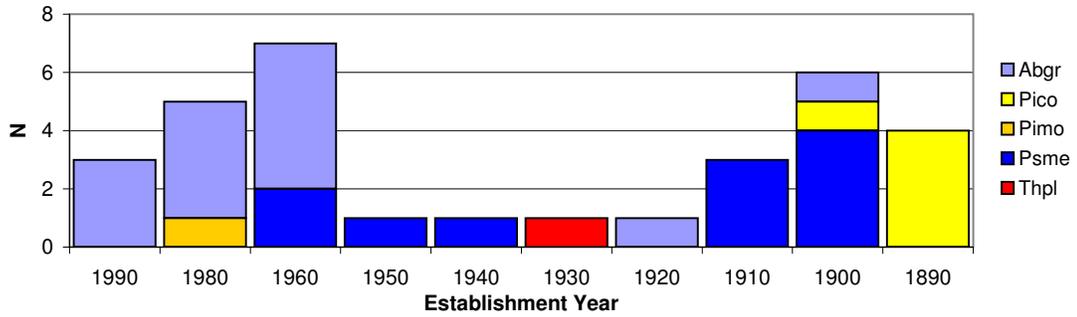
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 9 |
| Seed | 9 |
| Tree | 25 |
| TOTAL | 43 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 78 18 dead |
| Seed | 65 |
| Tree | 40 7 dead |
| TOTAL | 183 |

TCB05

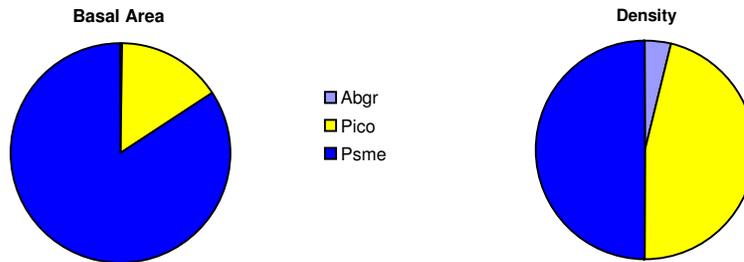
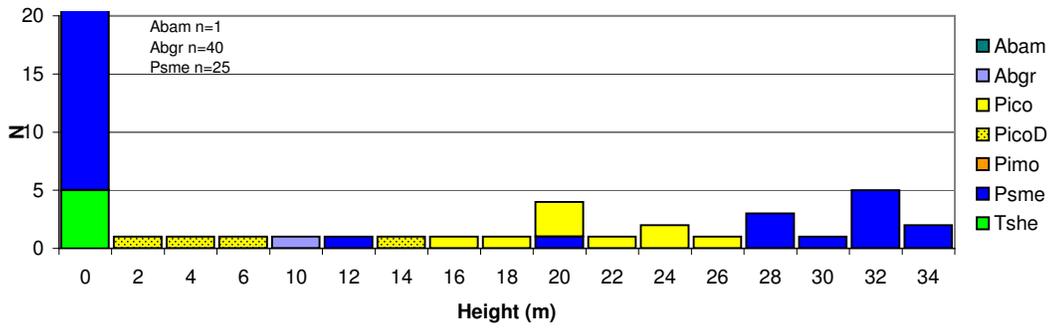
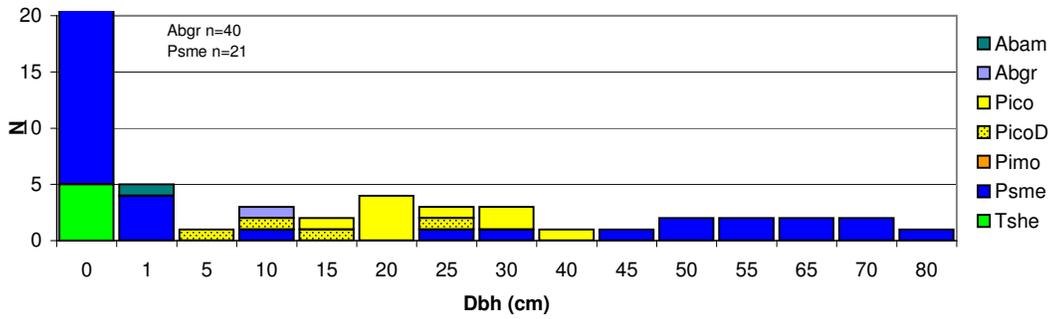
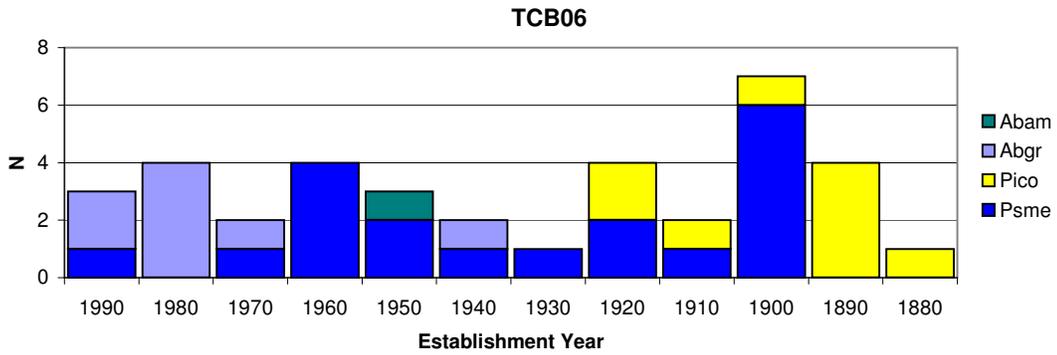


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 7 |
| Seed | 8 |
| Tree | 17 |
| TOTAL | 32 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 8 (1 dead) |
| Seed | 155 |
| Tree | 23 |
| TOTAL | 186 |



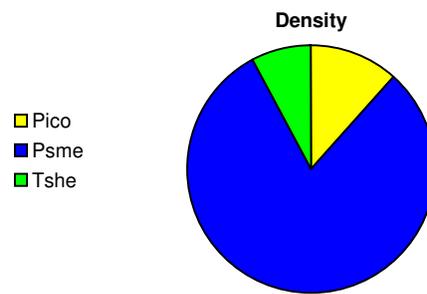
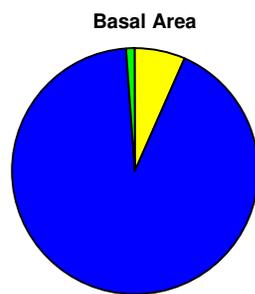
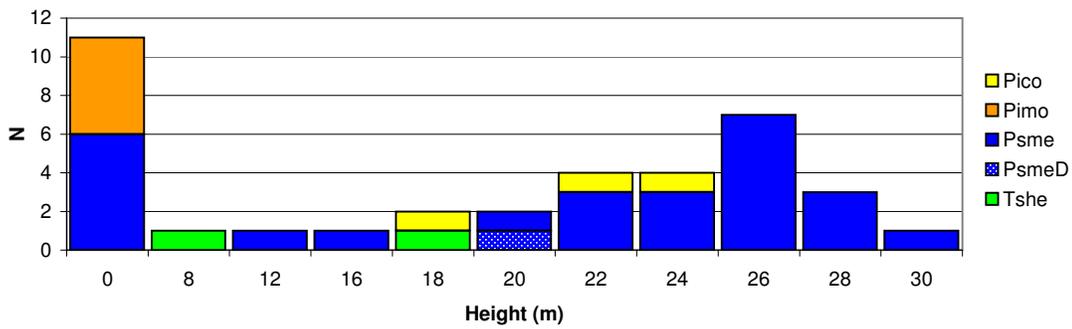
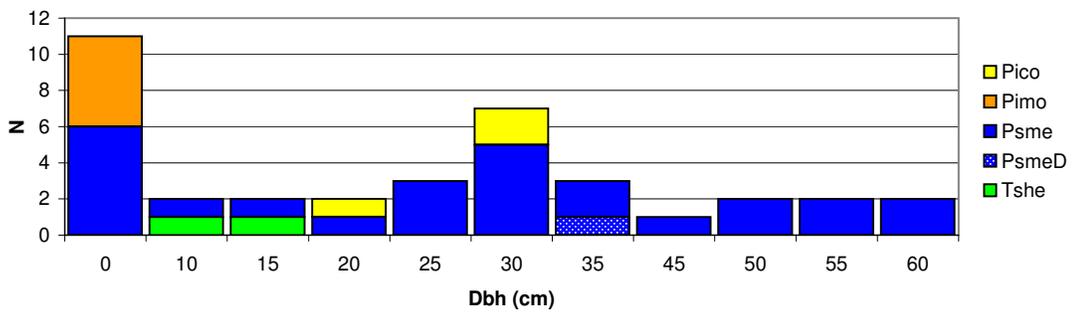
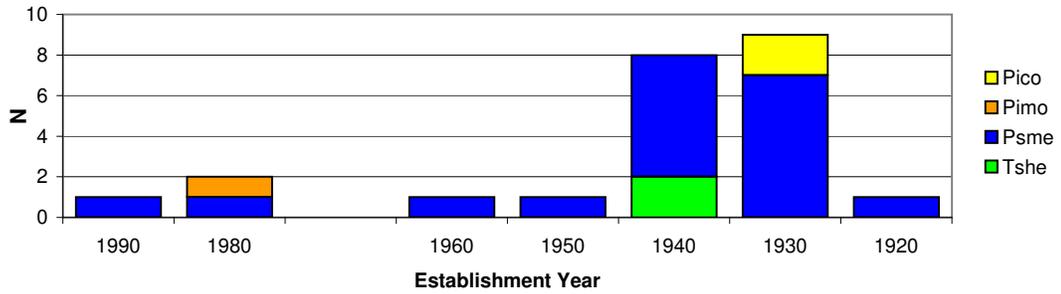
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 5 |
| Seed | 10 |
| Tree | 22 |
| TOTAL | 37 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 7 (1 dead) |
| Seed | 70 |
| Tree | 26 (3 dead) |
| TOTAL | 103 |

TCB07

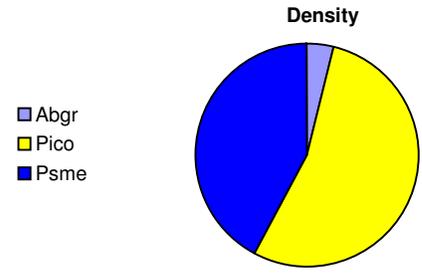
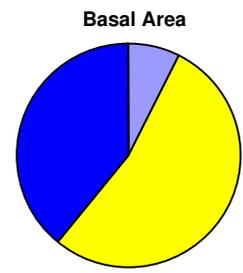
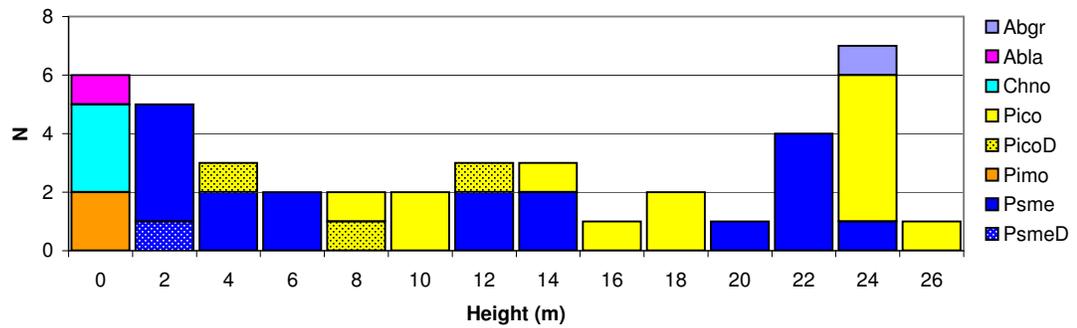
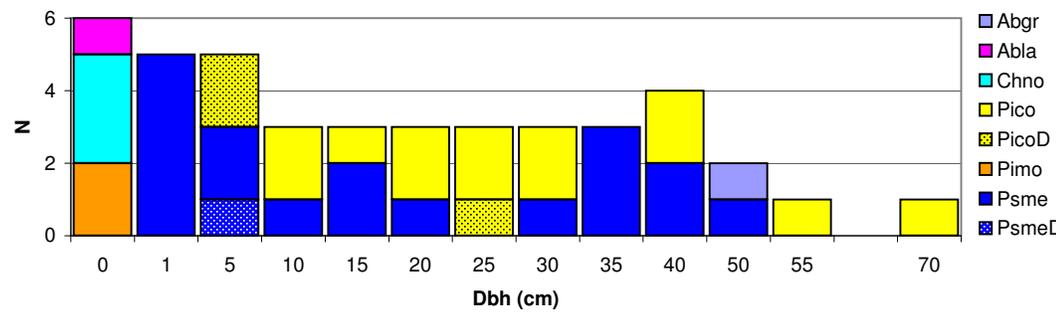
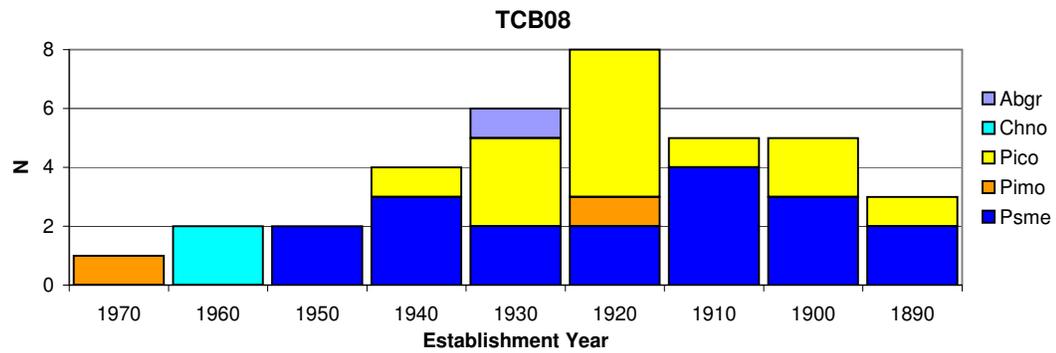


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 1 |
| Seed | 2 |
| Tree | 20 |
| TOTAL | 23 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 1 |
| Seed | 10 |
| Tree | 26 (1 dead) |
| TOTAL | 37 |



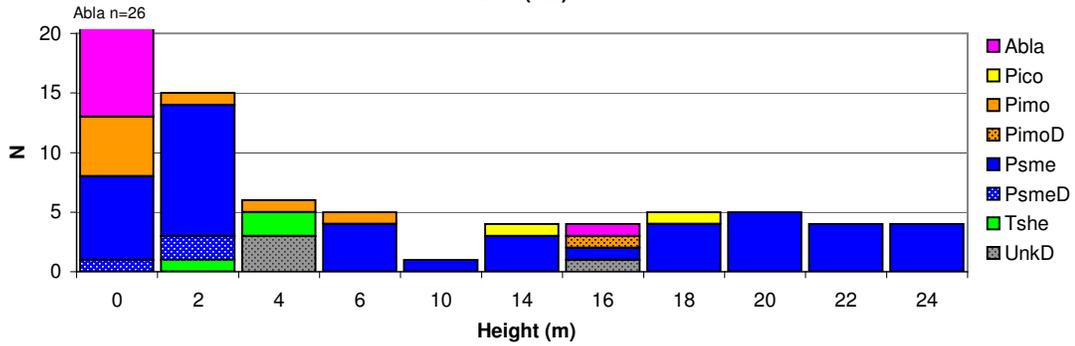
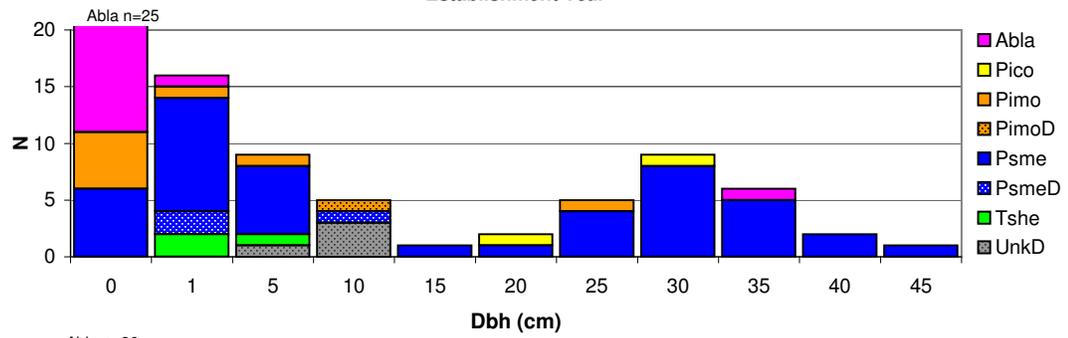
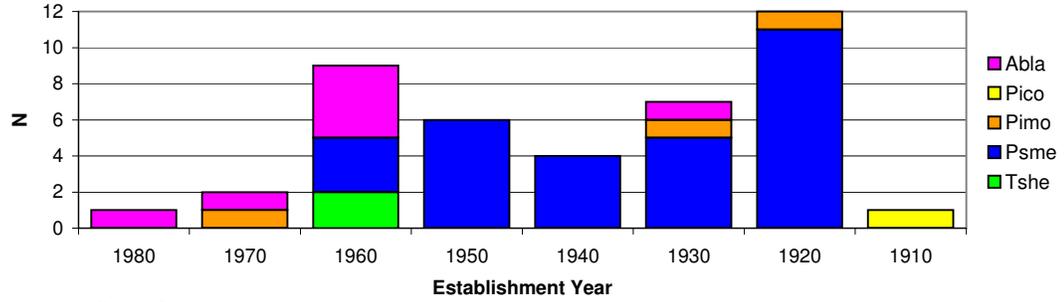
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 1 |
| Tree | 25 |
| TOTAL | 36 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 13 (3 dead) |
| Seed | 3 |
| Tree | 26 (1 dead) |
| TOTAL | 42 |

TCB09

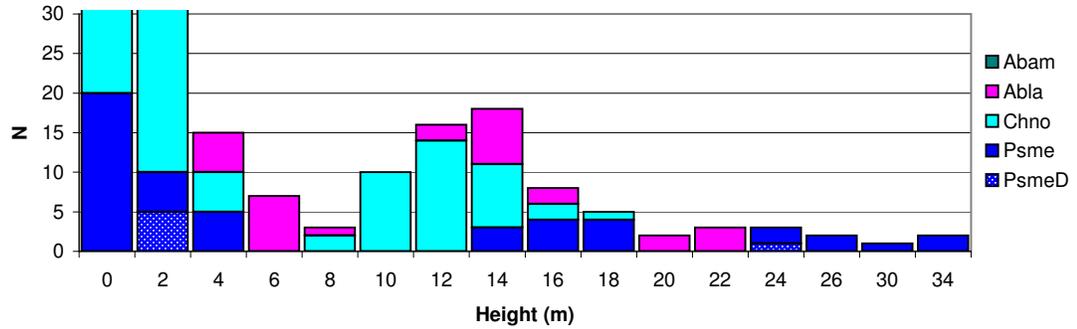
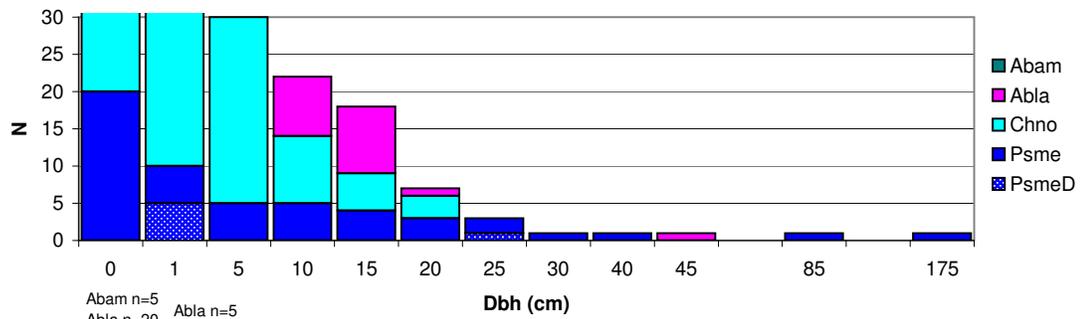
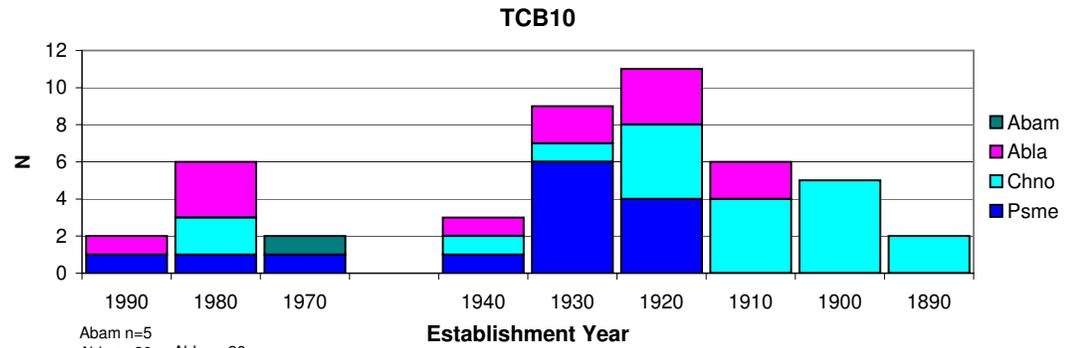


Age Class Frequency Distribution

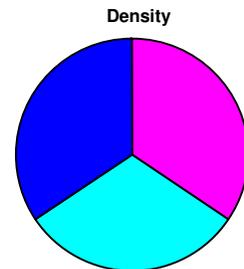
| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 7 |
| Tree | 25 |
| TOTAL | 42 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 26 (3 dead) |
| Seed | 35 |
| Tree | 31 |
| TOTAL | 92 |



■ Abam
■ Abla
■ Psme



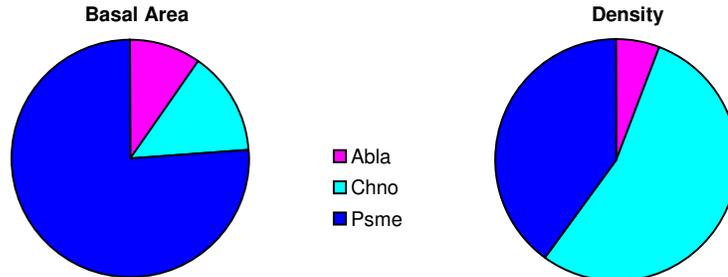
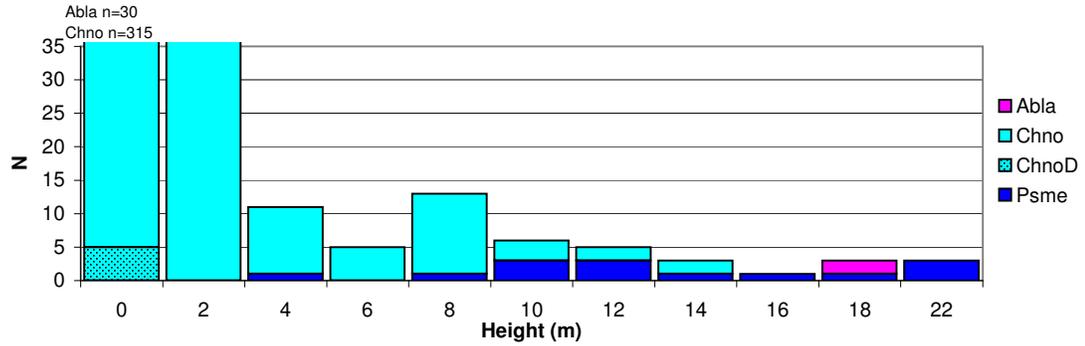
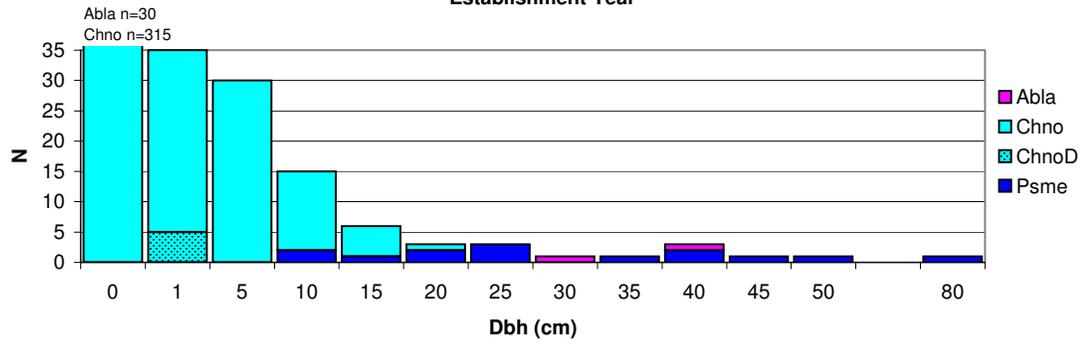
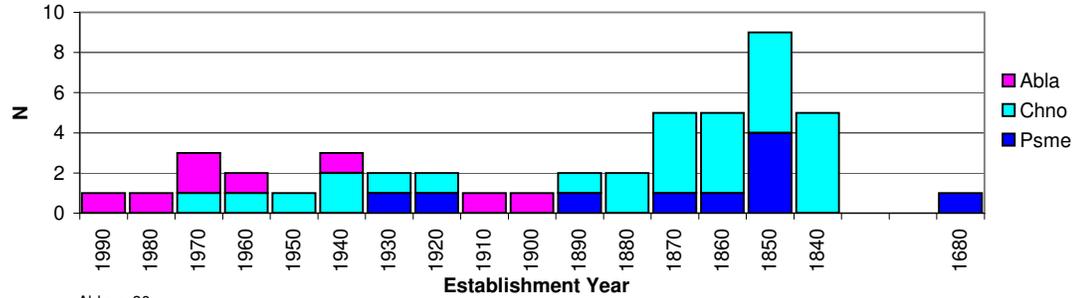
Age Class Frequency Distribution

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 10 |
| Seed | 10 |
| Tree | 26 |
| TOTAL | 46 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 90 (5 dead) |
| Seed | 100 |
| Tree | 55 (1 dead) |
| TOTAL | 245 |

TCB11

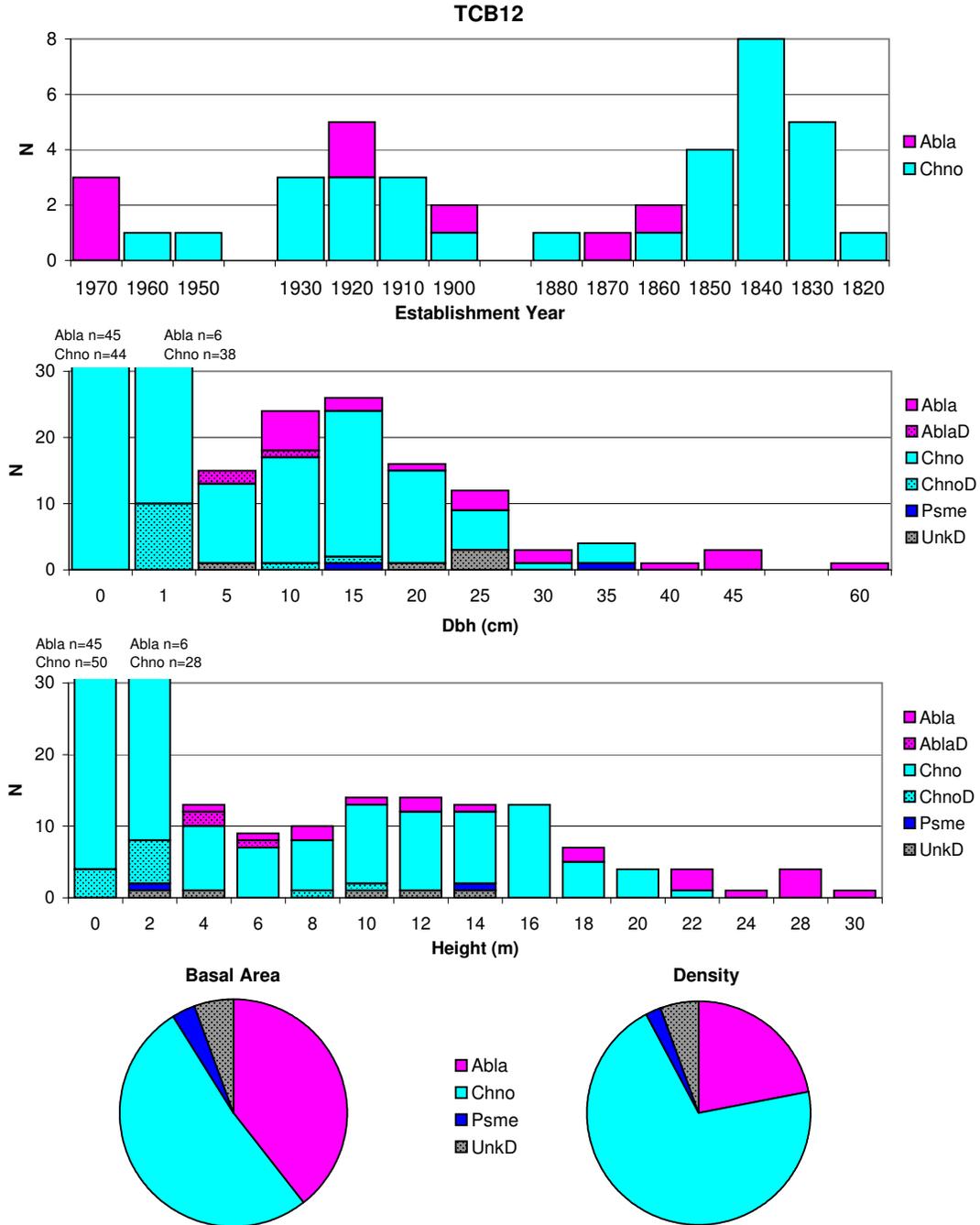


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 10 |
| Tree | 26 |
| TOTAL | 46 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 85 (5 dead) |
| Seed | 335 |
| Tree | 35 |
| TOTAL | 455 |

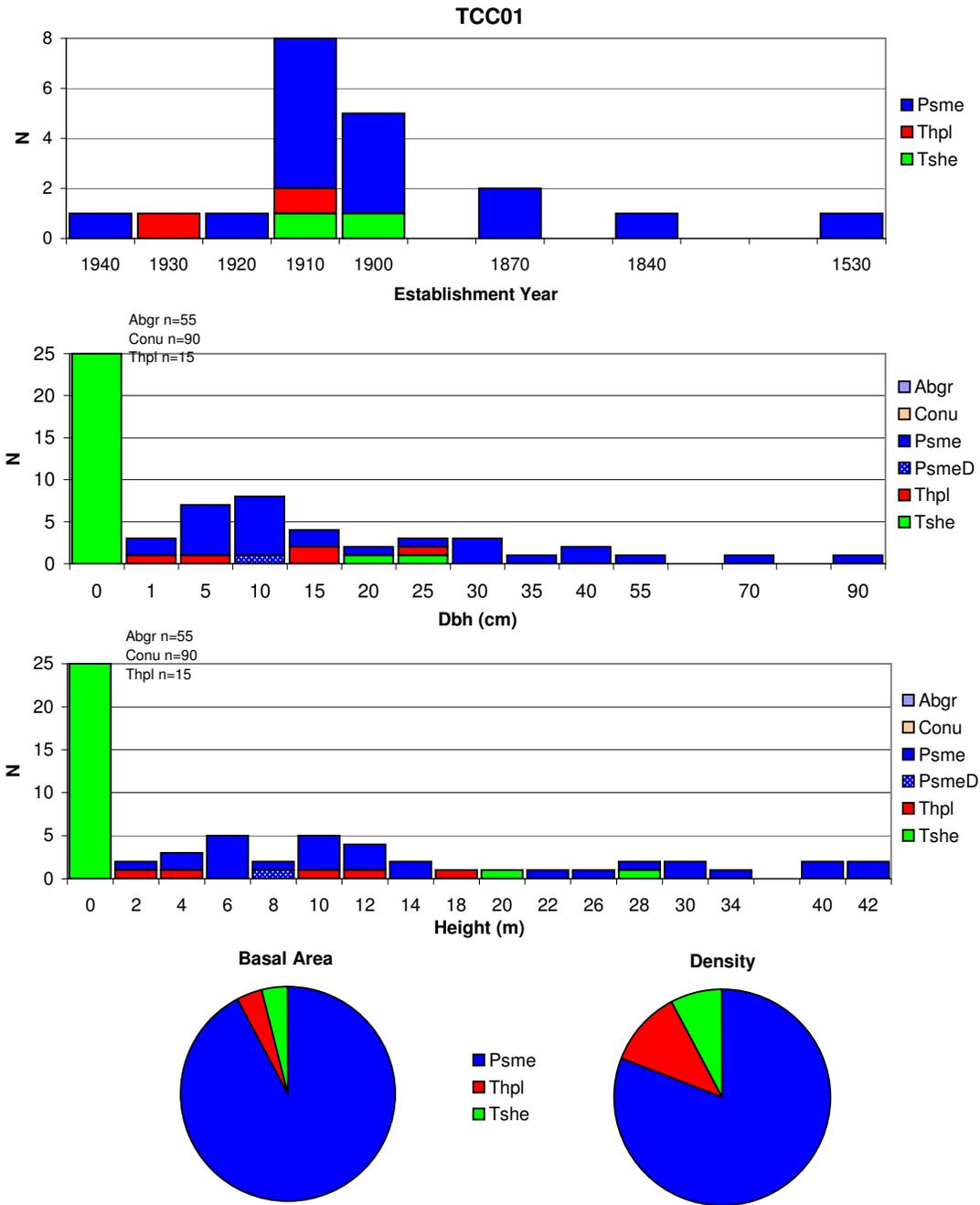


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 9 |
| Tree | 21 |
| TOTAL | 40 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 72 (12 dead) |
| Seed | 85 |
| Tree | 91 |
| TOTAL | 248 |

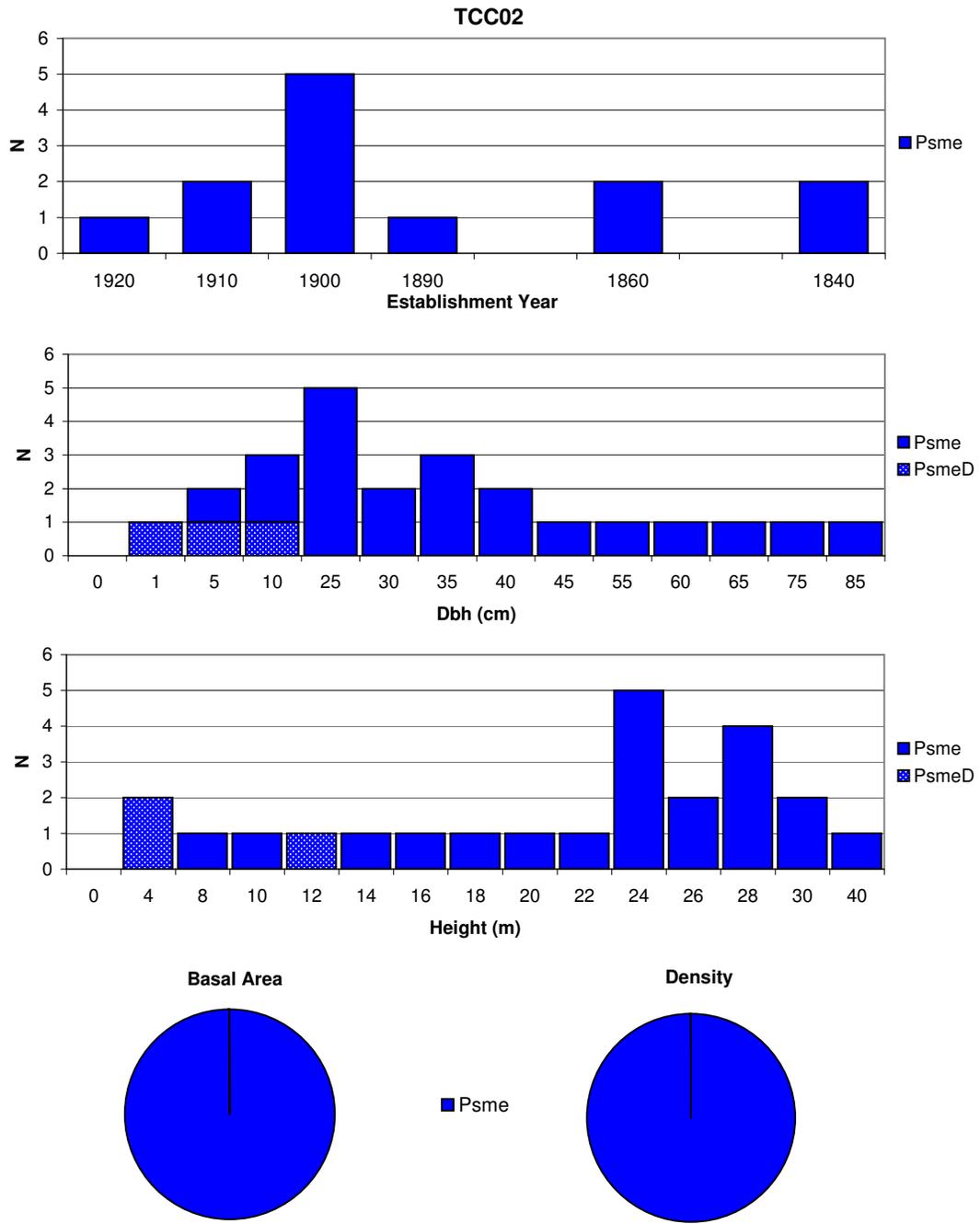


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 1 |
| Seed | 0 |
| Tree | 19 |
| TOTAL | 20 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 37 |
| Tree | 26 |
| TOTAL | 73 |

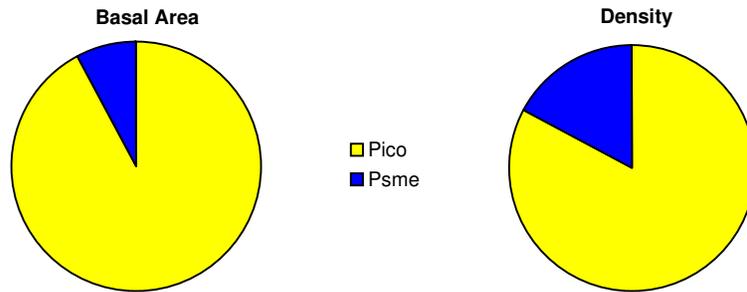
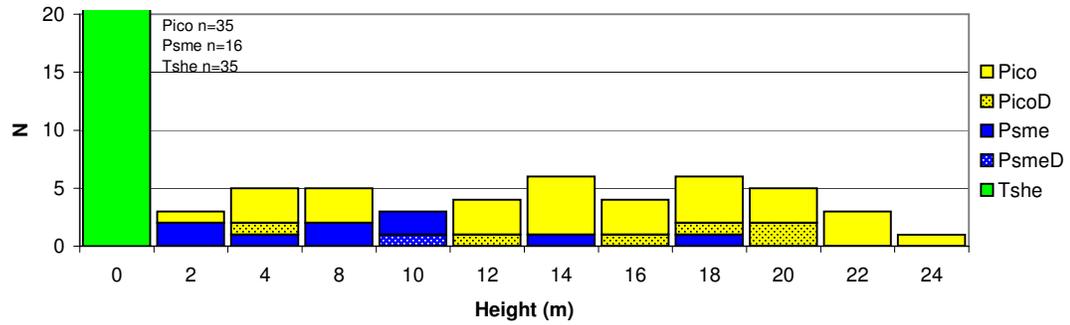
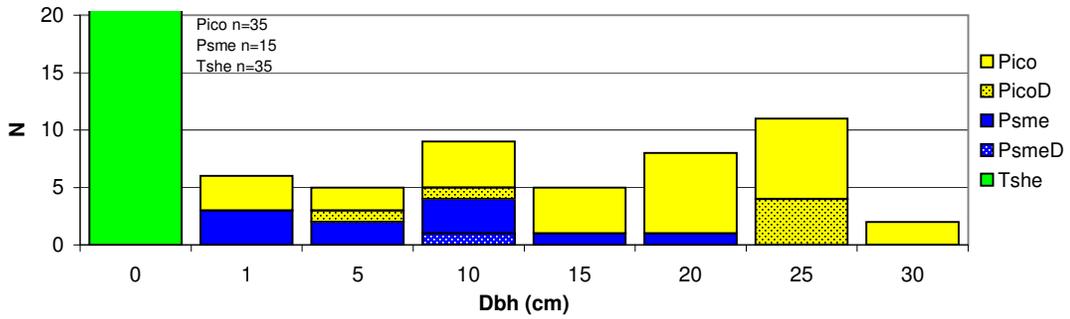
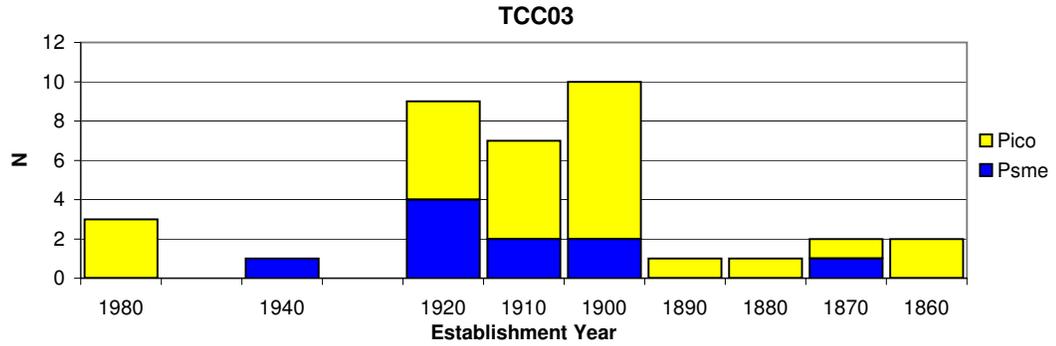


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 0 |
| Seed | 0 |
| Tree | 13 |
| TOTAL | 13 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 3 |
| Seed | 0 |
| Tree | 21 (1 dead) |
| TOTAL | 25 |



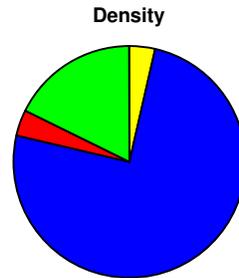
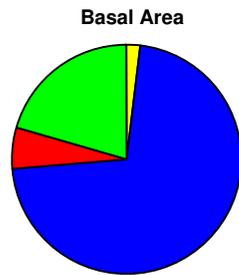
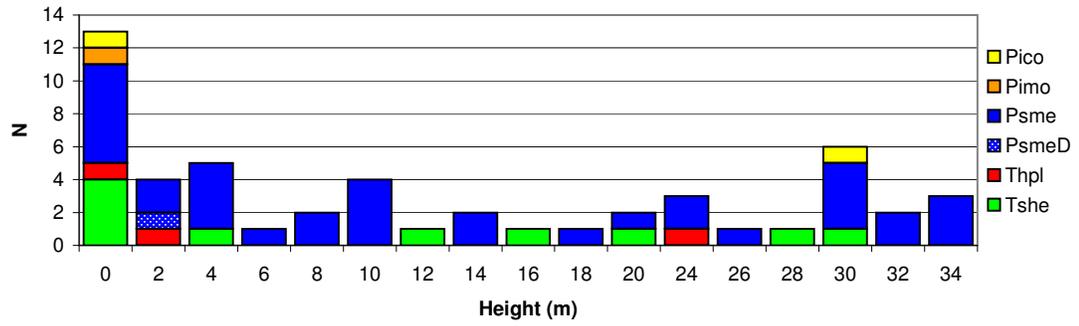
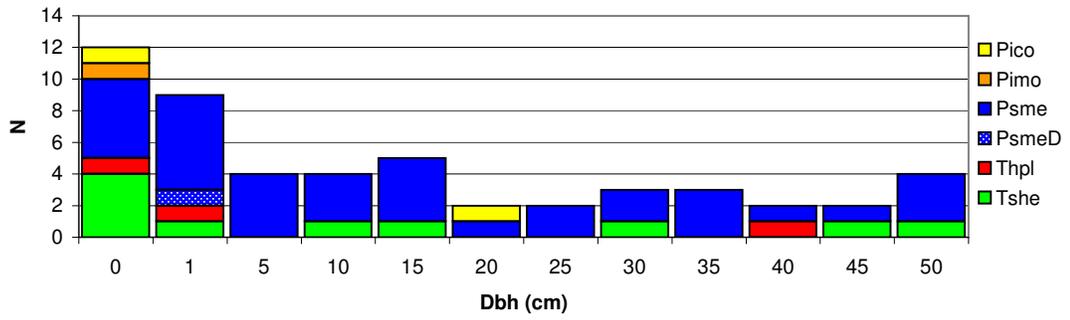
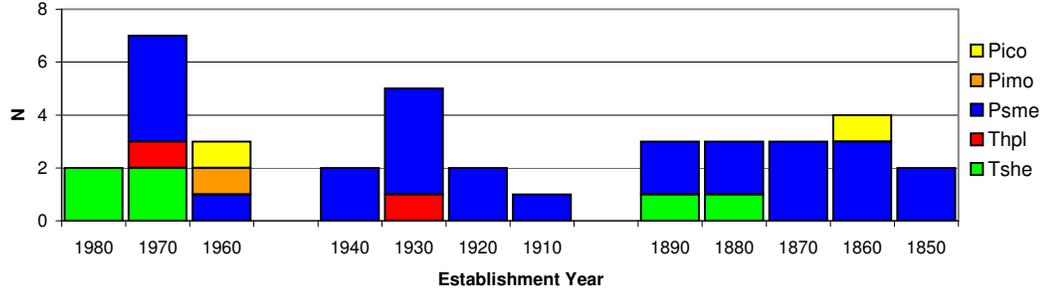
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 4 |
| Tree | 22 |
| TOTAL | 36 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 11 (1 dead) |
| Seed | 85 |
| Tree | 35 (6 dead) |
| TOTAL | 63 |

TCC04

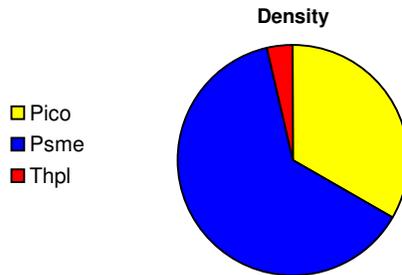
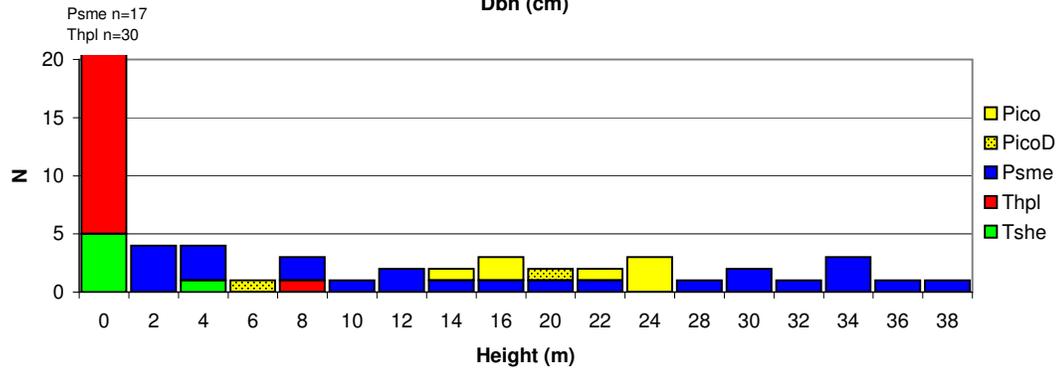
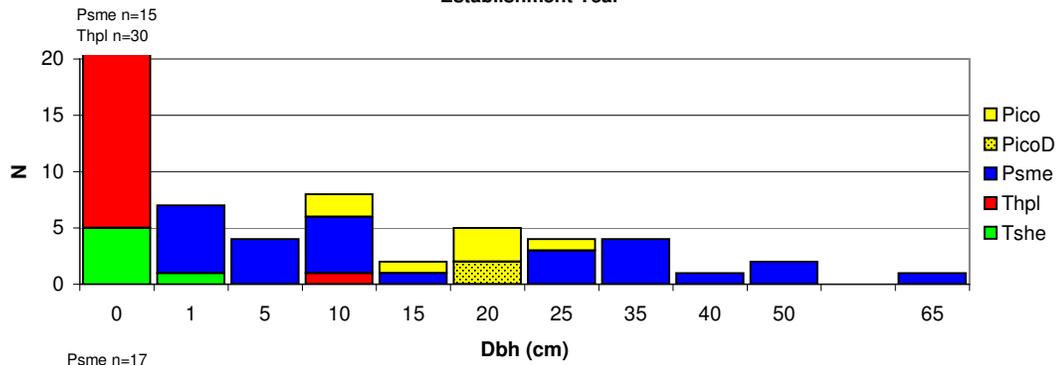
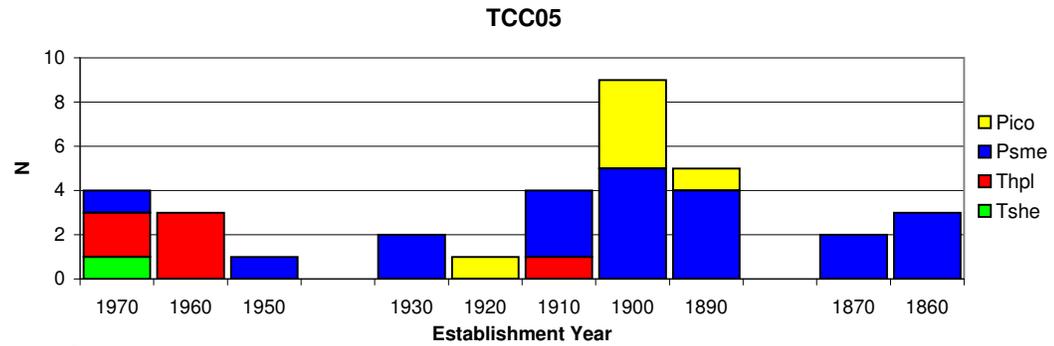


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 9 |
| Seed | 10 |
| Tree | 18 |
| TOTAL | 37 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 14 (1 dead) |
| Seed | 10 |
| Tree | 28 |
| TOTAL | 52 |

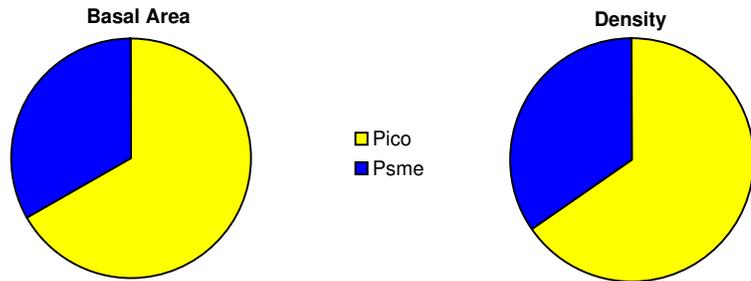
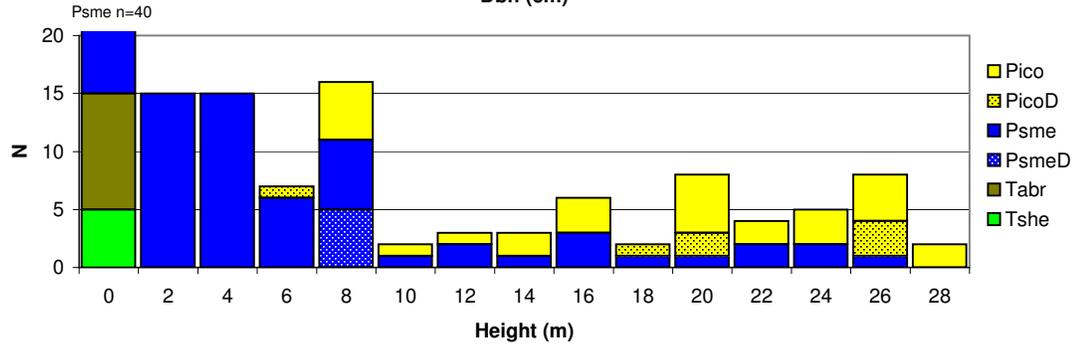
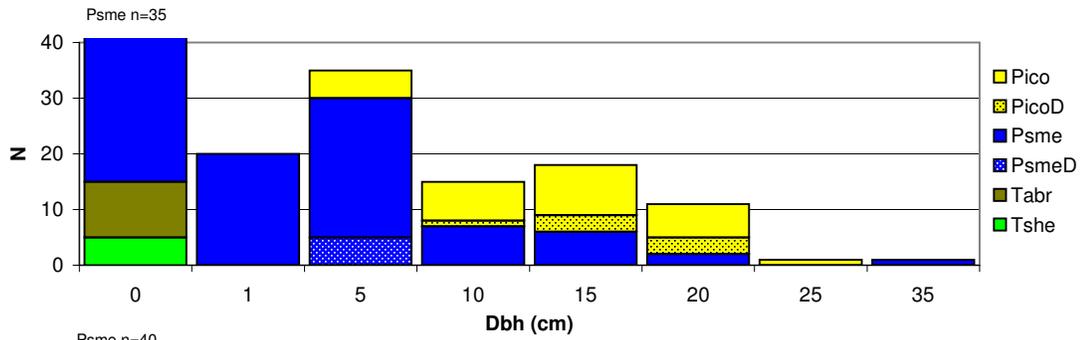
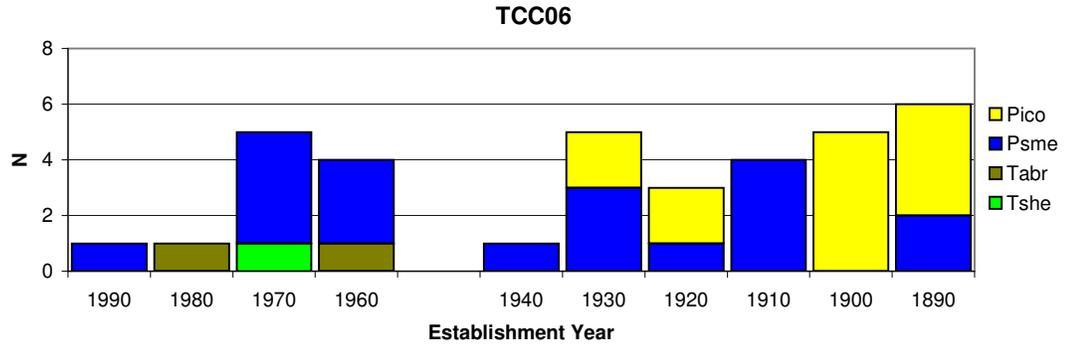


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 6 |
| Seed | 7 |
| Tree | 21 |
| TOTAL | 34 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 11 |
| Seed | 50 |
| Tree | 27 (2 dead) |
| TOTAL | 88 |

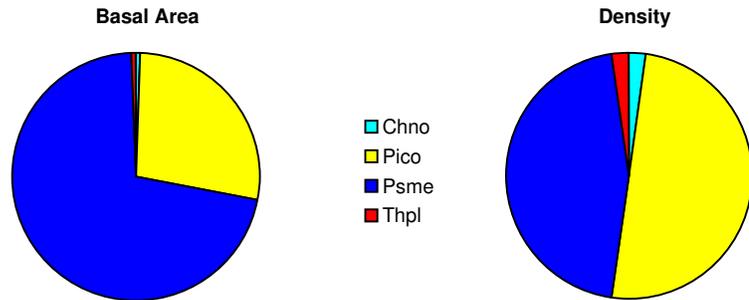
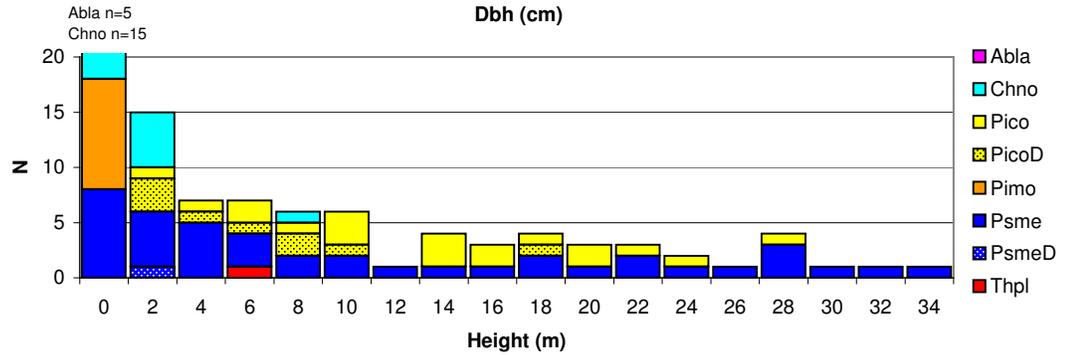
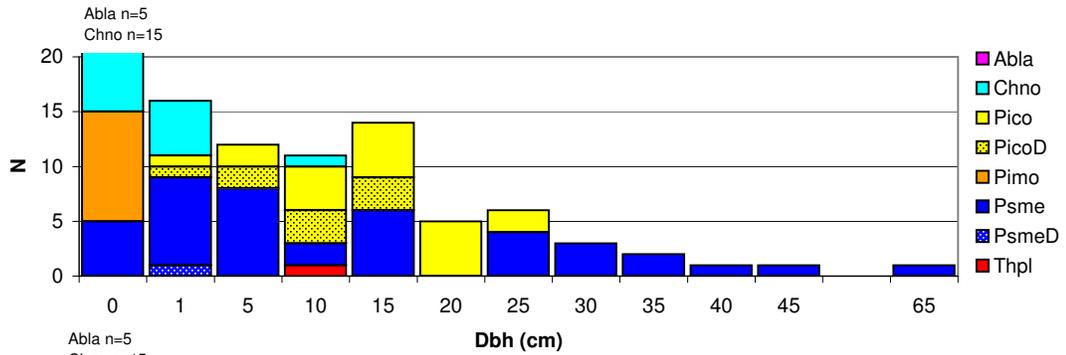
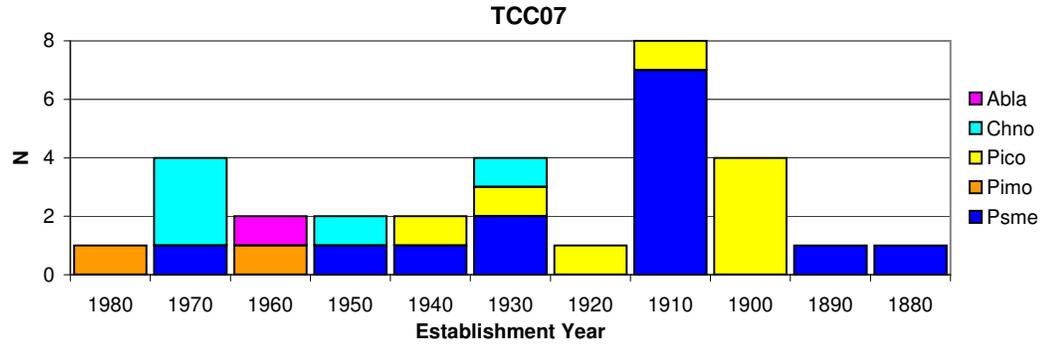


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 2 |
| Seed | 10 |
| Tree | 23 |
| TOTAL | 35 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 55 (5 dead) |
| Seed | 50 |
| Tree | 46 (7 dead) |
| TOTAL | 151 |



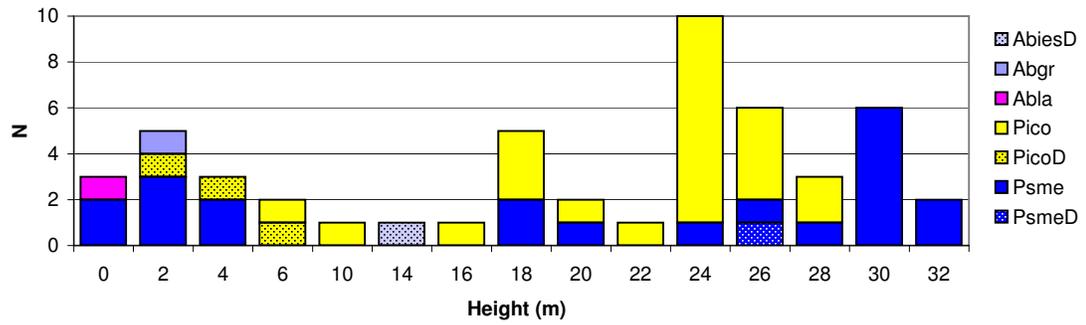
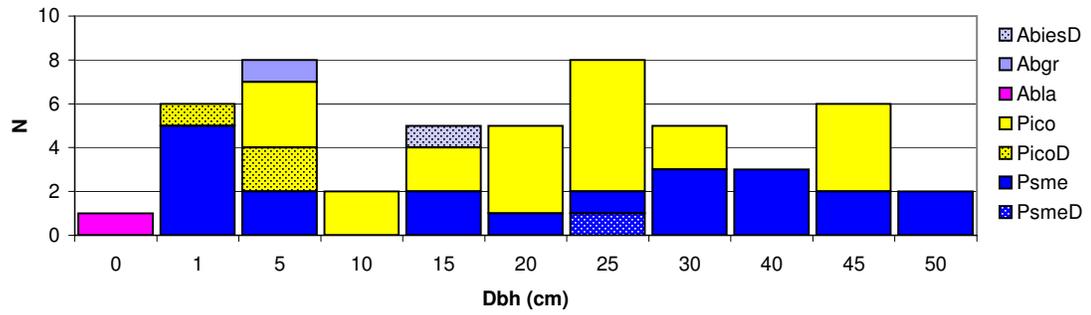
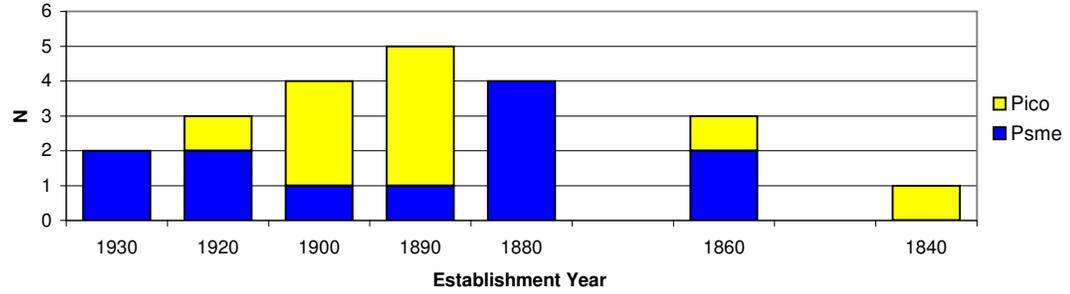
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 6 |
| Seed | 7 |
| Tree | 17 |
| TOTAL | 30 |

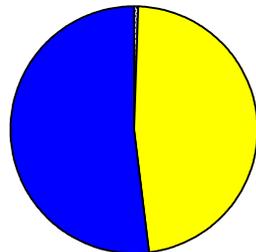
Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 28 (4 dead) |
| Seed | 35 |
| Tree | 44 (6 dead) |
| TOTAL | 107 |

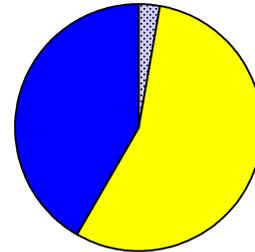
TCC08



Basal Area



Density



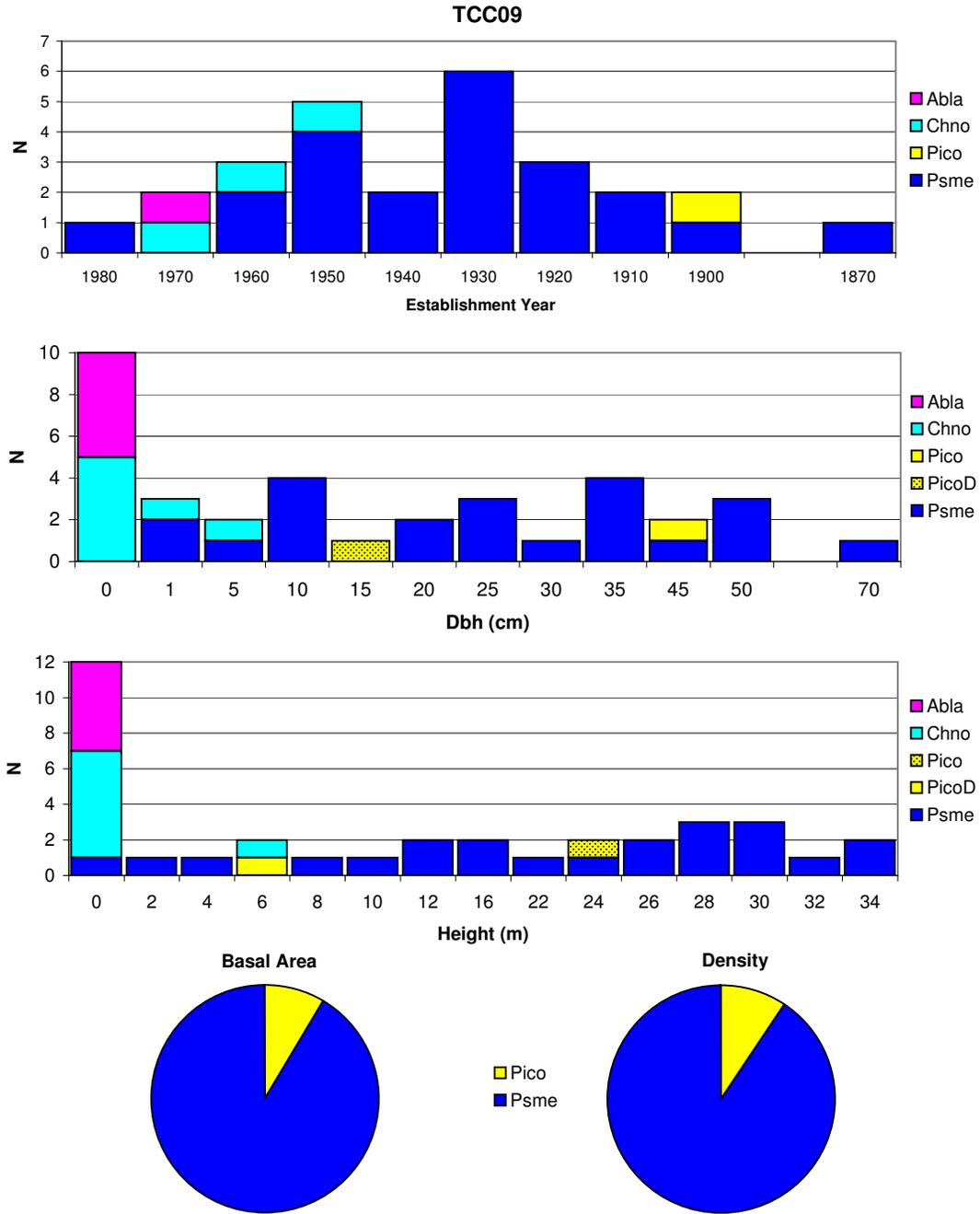
AbiesD
Pico
Psme

Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 6 |
| Seed | 0 |
| Tree | 16 |
| TOTAL | 22 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 14 (3 dead) |
| Seed | 5 |
| Tree | 36 (1 dead) |
| TOTAL | 55 |

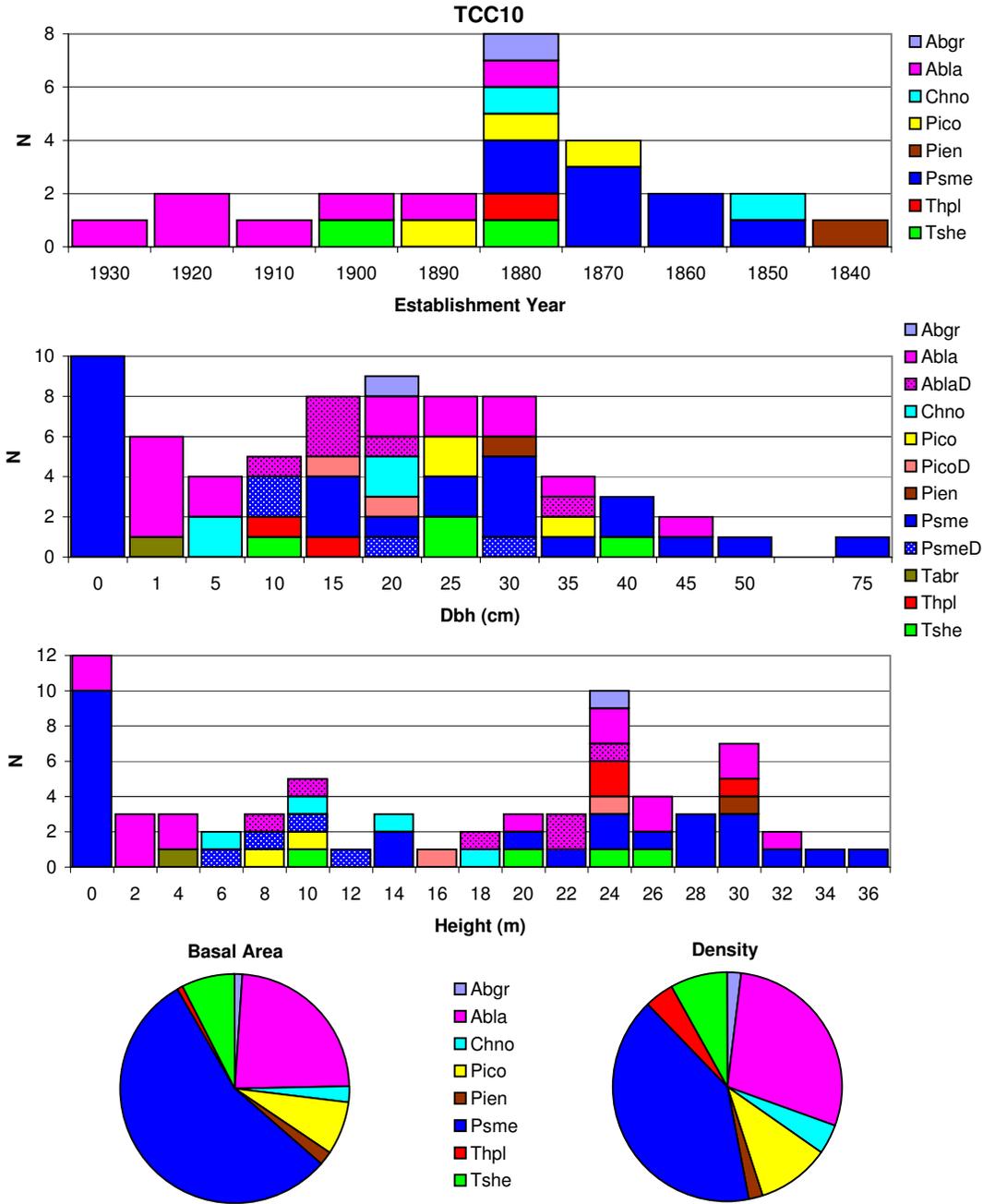


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 5 |
| Seed | 2 |
| Tree | 20 |
| TOTAL | 27 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 5 |
| Seed | 10 |
| Tree | 21 (1 dead) |
| TOTAL | 36 |

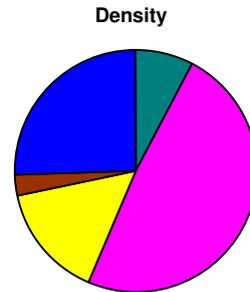
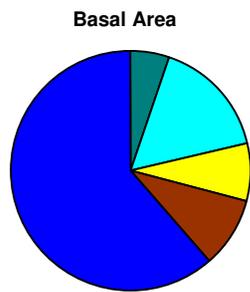
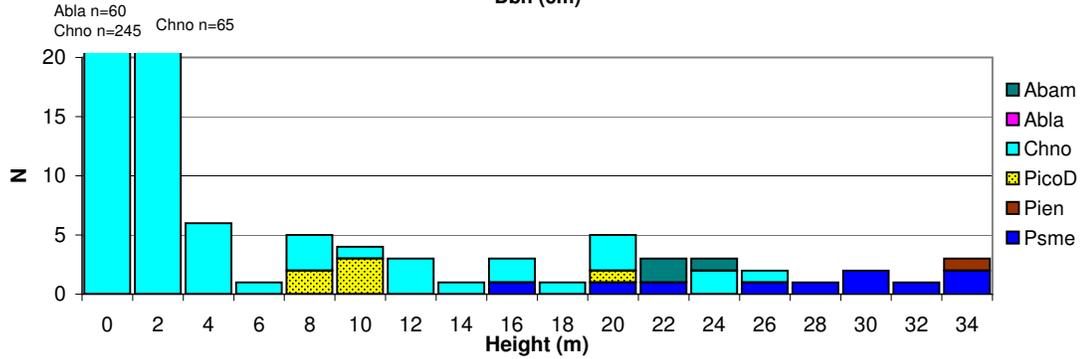
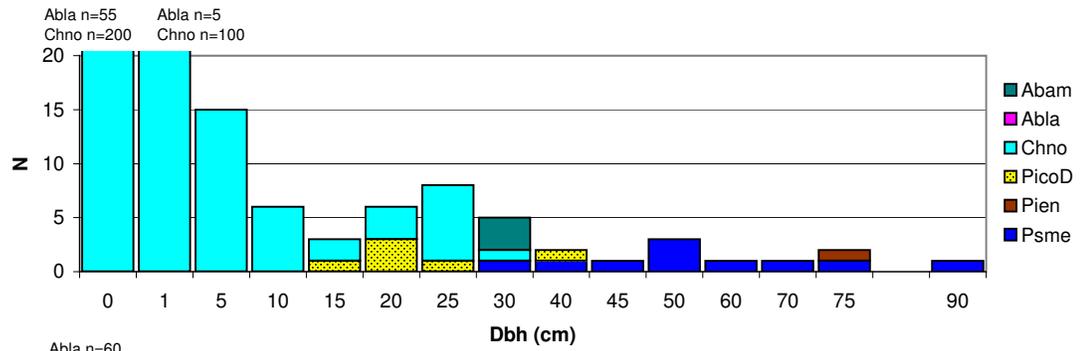
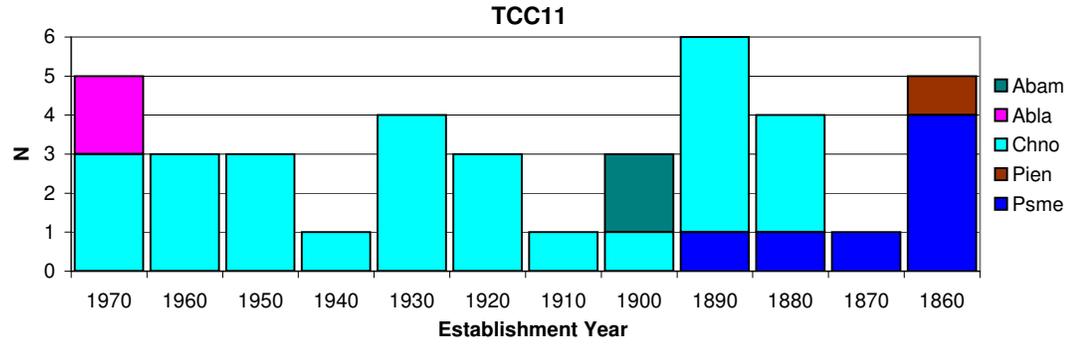


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 4 |
| Seed | 0 |
| Tree | 21 |
| TOTAL | 25 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 10 |
| Tree | 49 (12 dead) |
| TOTAL | 69 |

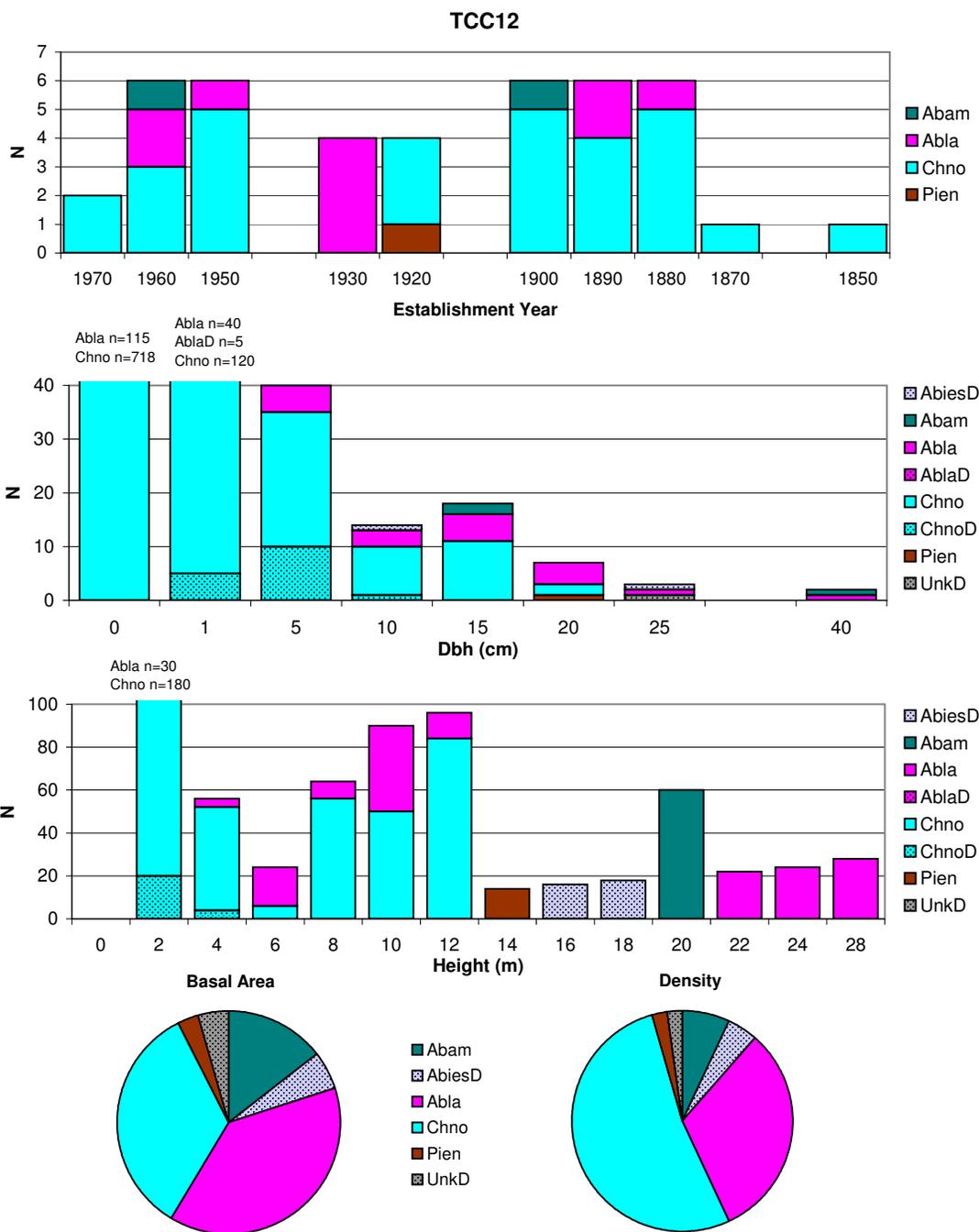


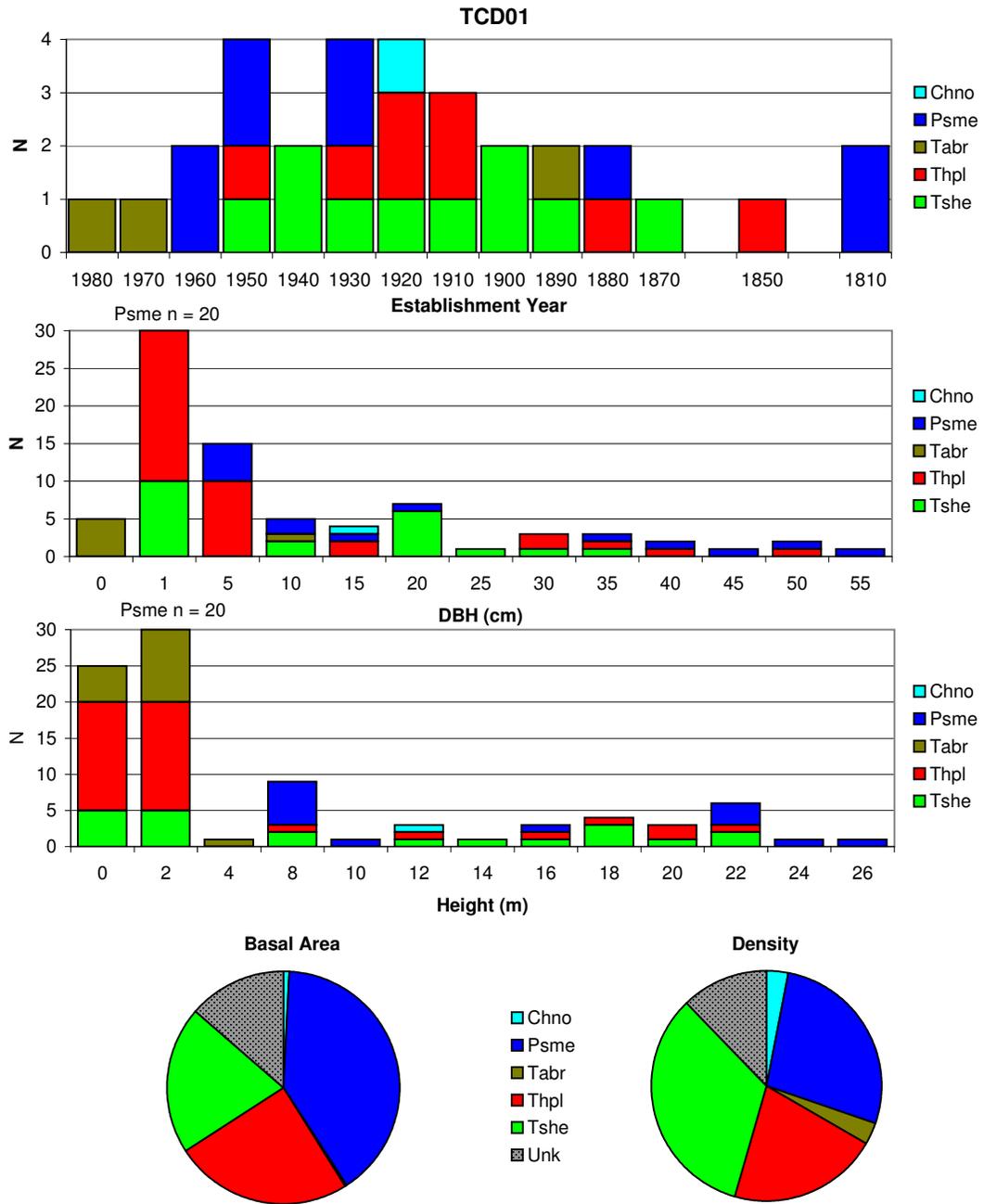
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 9 |
| Seed | 9 |
| Tree | 21 |
| TOTAL | 39 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 165 |
| Seed | 210 |
| Tree | 39 (7 dead) |
| TOTAL | 414 |





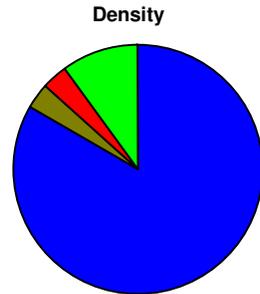
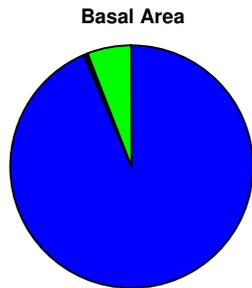
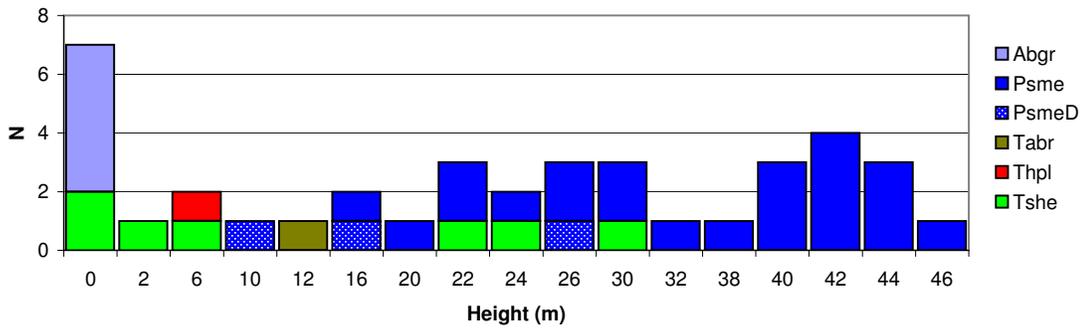
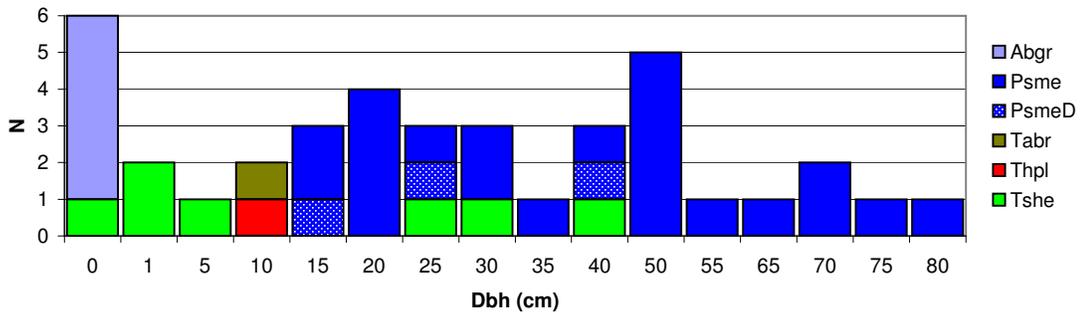
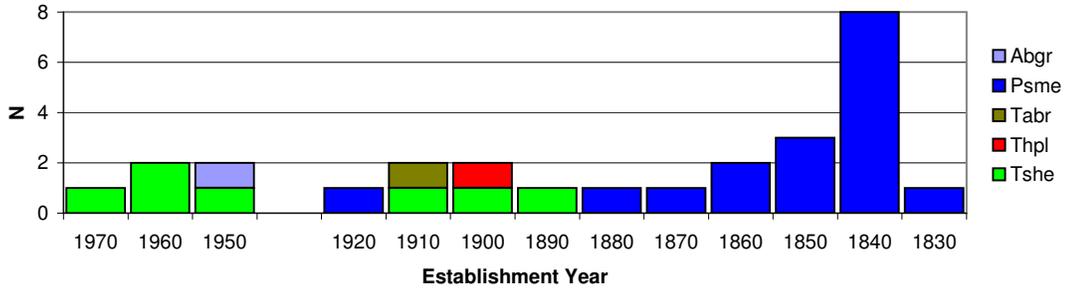
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 0 |
| Tree | 21 |
| TOTAL | 31 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 16 |
| Seed | 1 |
| Tree | 33 |
| TOTAL | 50 |

TCD02

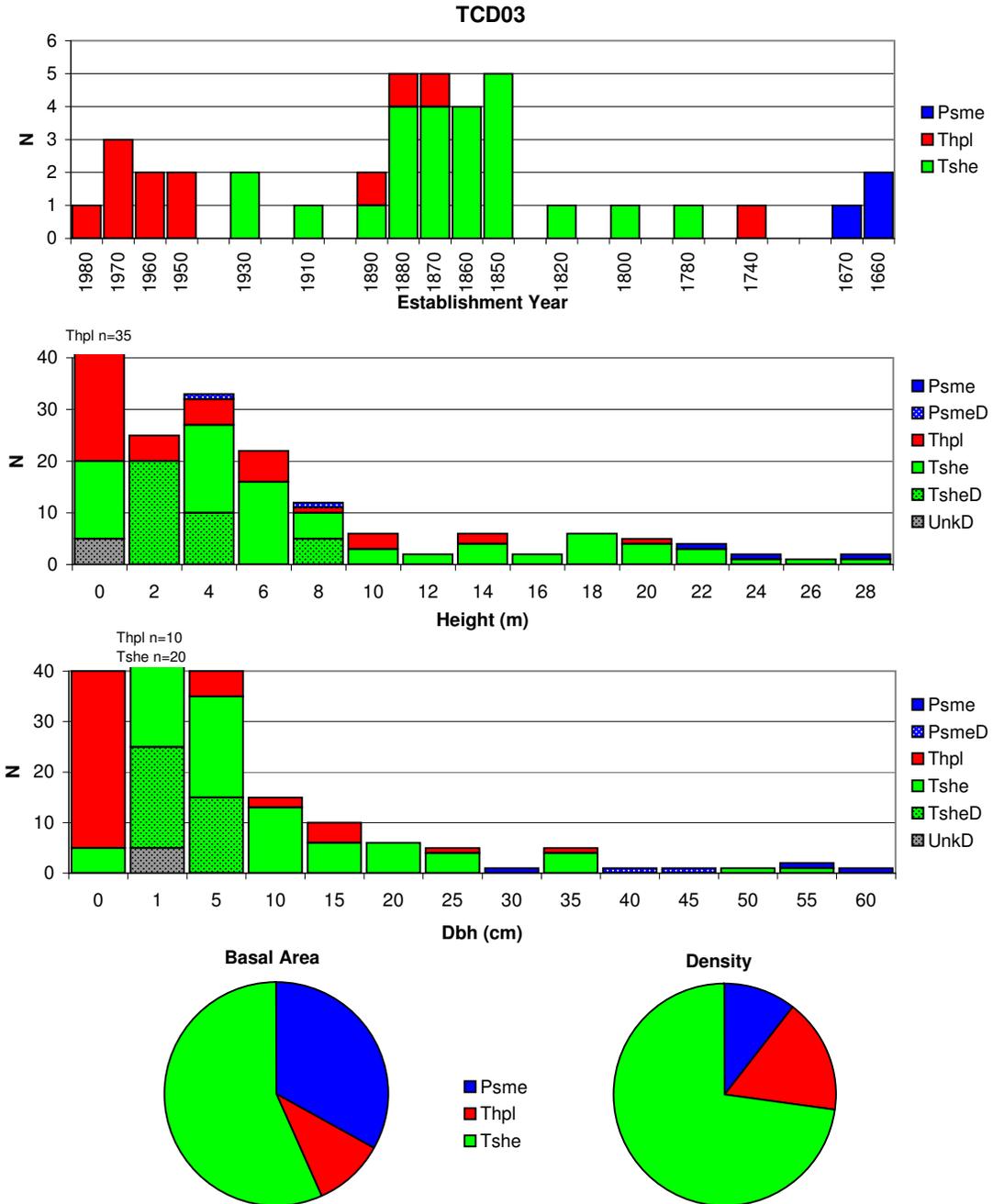


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 4 |
| Seed | 1 |
| Tree | 22 |
| TOTAL | 27 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 4 |
| Seed | 5 |
| Tree | 30 (3 dead) |
| TOTAL | 39 |

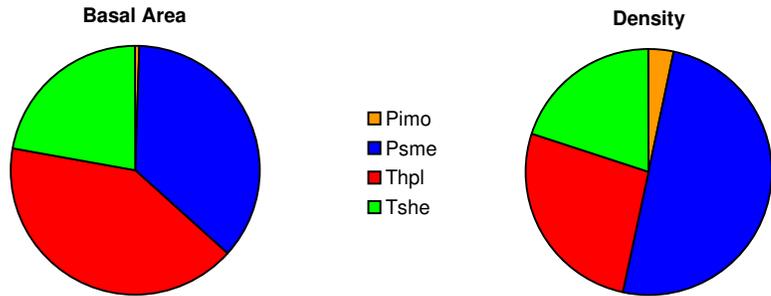
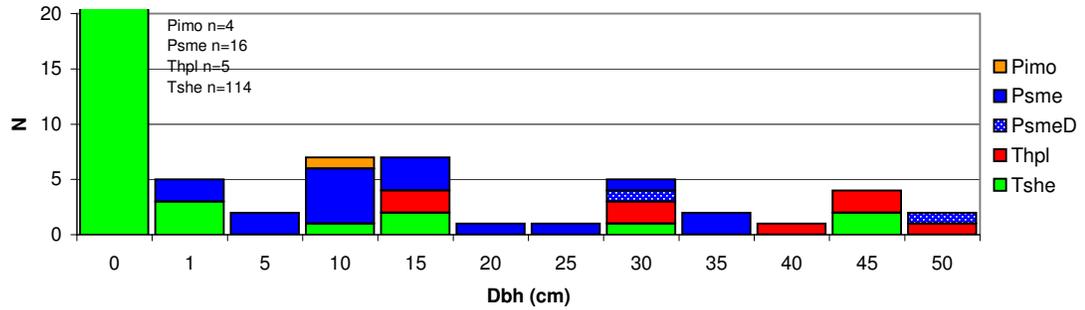
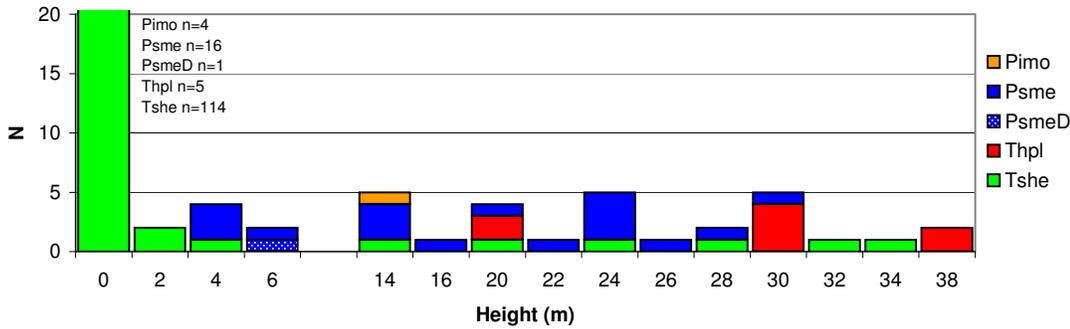
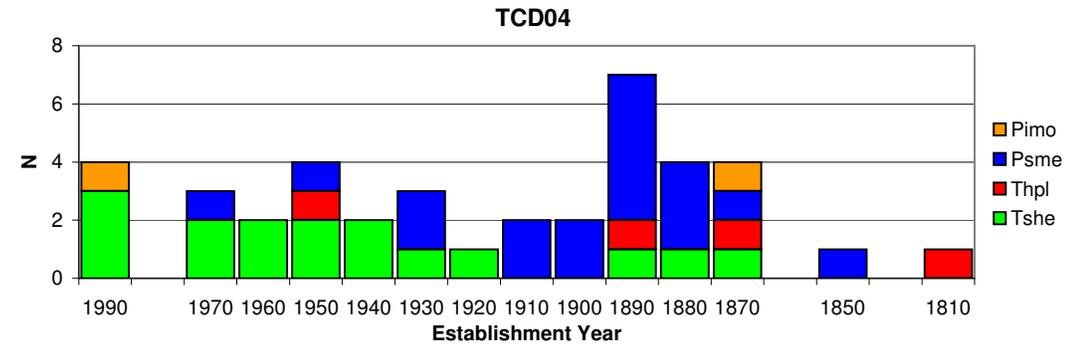


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 6 |
| Seed | 8 |
| Tree | 25 |
| TOTAL | 39 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 95 (40 dead) |
| Seed | 40 |
| Tree | 48 (2 dead) |
| TOTAL | 75 |



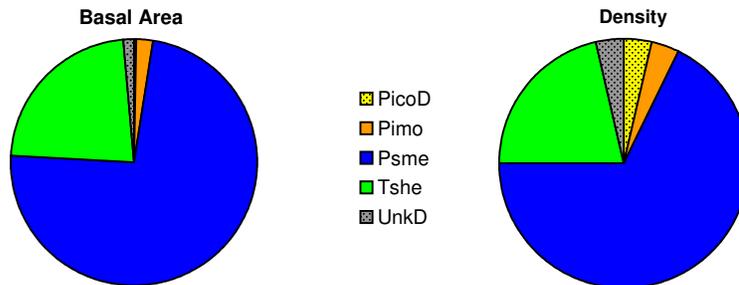
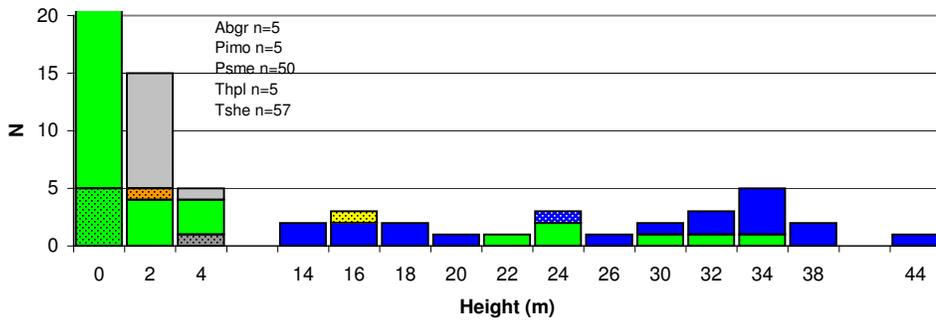
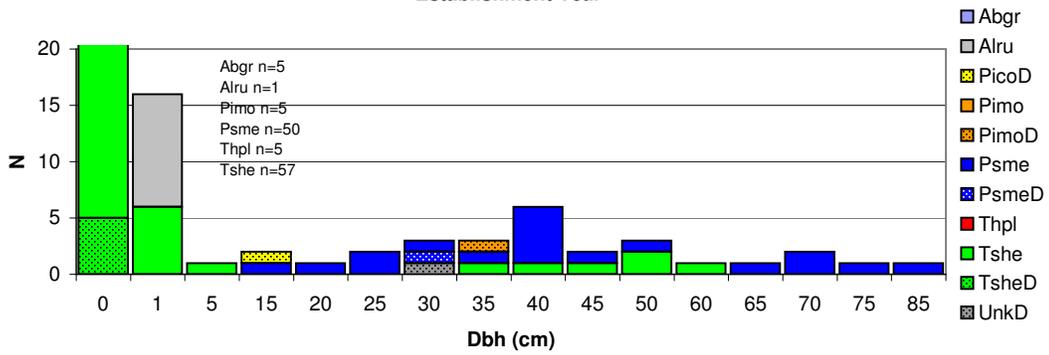
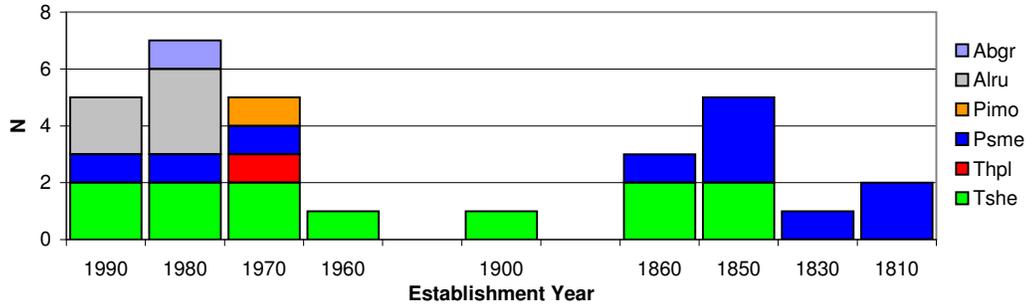
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 9 |
| Tree | 21 |
| TOTAL | 40 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 136 |
| Tree | 30 (2 dead) |
| TOTAL | 74 |

TCD05

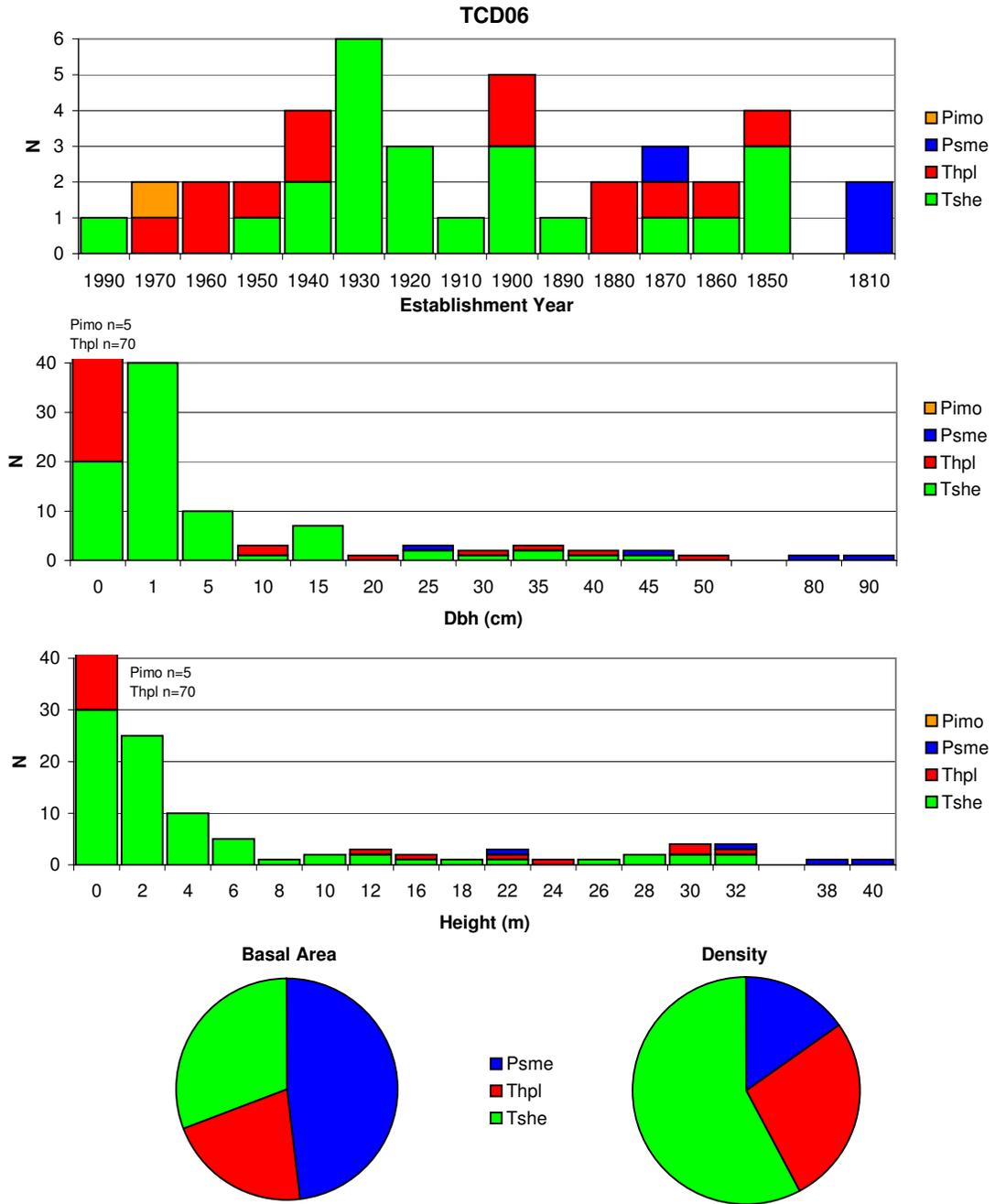


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 8 |
| Seed | 10 |
| Tree | 12 |
| TOTAL | 30 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 20 |
| Seed | 125 |
| Tree | 28 (4 dead) |
| TOTAL | 173 |



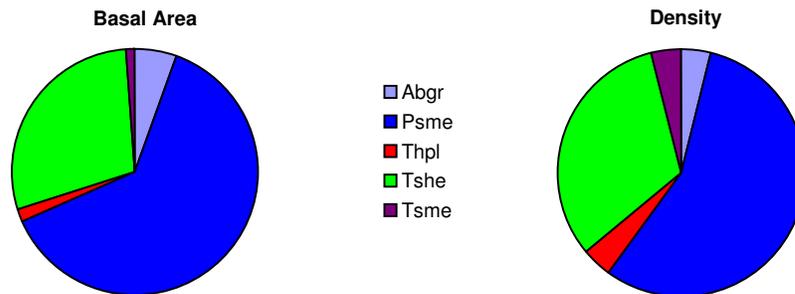
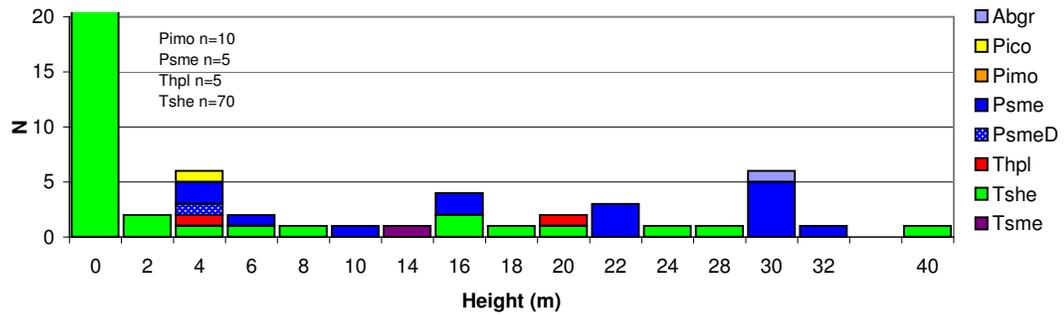
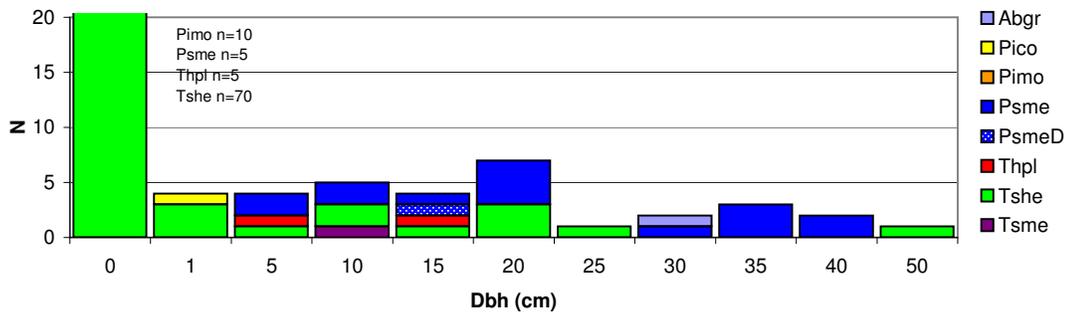
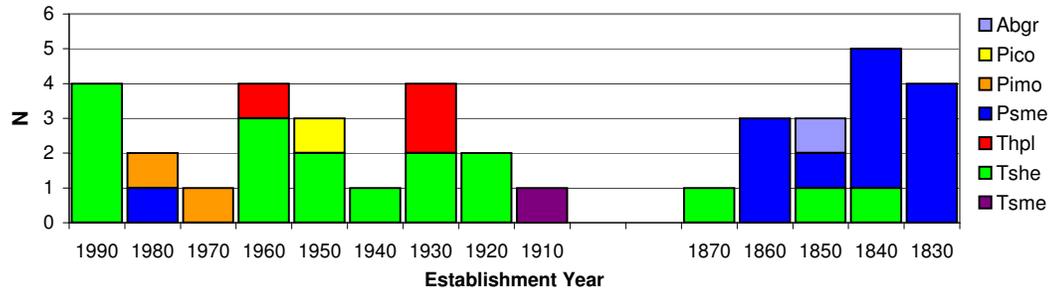
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 10 |
| Seed | 9 |
| Tree | 21 |
| TOTAL | 40 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 50 |
| Seed | 95 |
| Tree | 26 (1 dead) |
| TOTAL | 171 |

TCD07



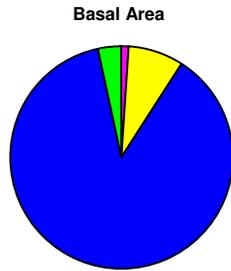
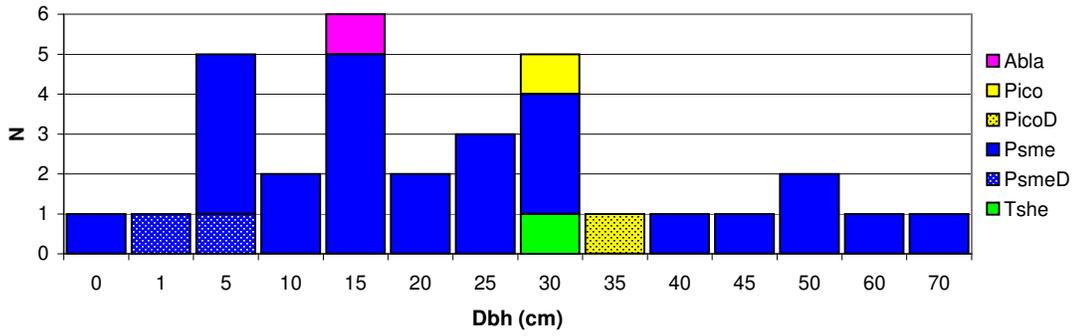
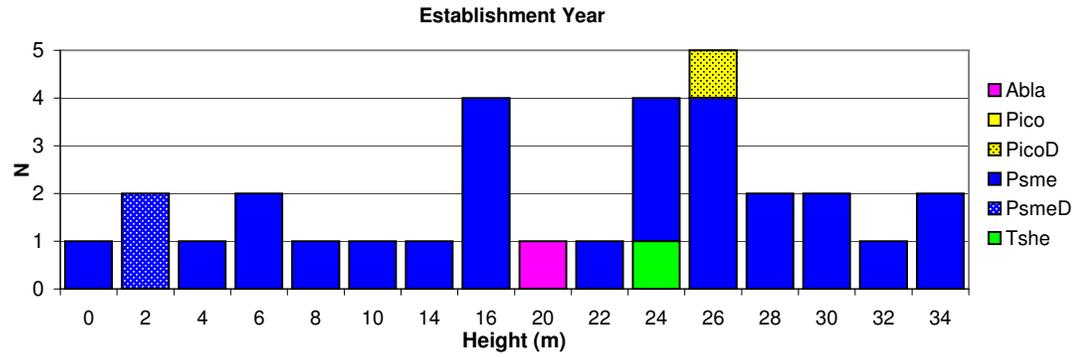
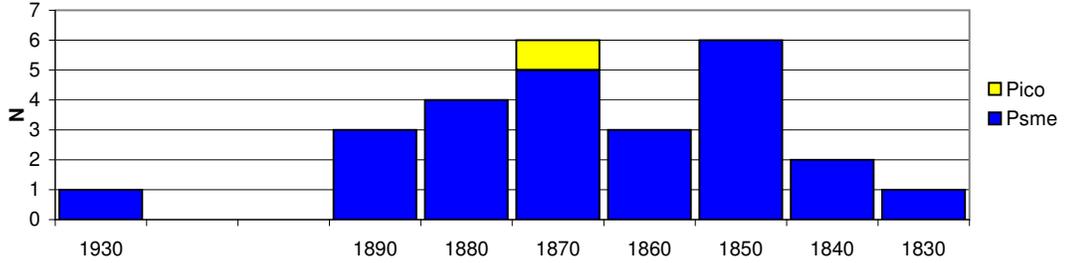
Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 5 |
| Seed | 10 |
| Tree | 23 |
| TOTAL | 38 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 8 |
| Seed | 90 |
| Tree | 25 (1 dead) |
| TOTAL | 123 |

TCD08

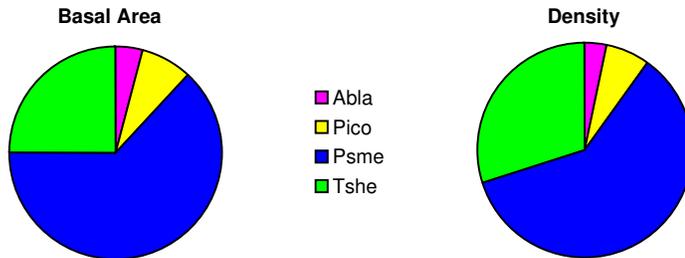
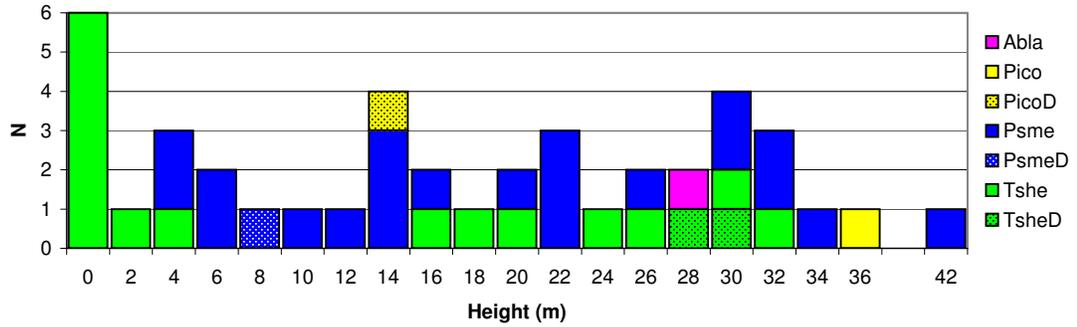
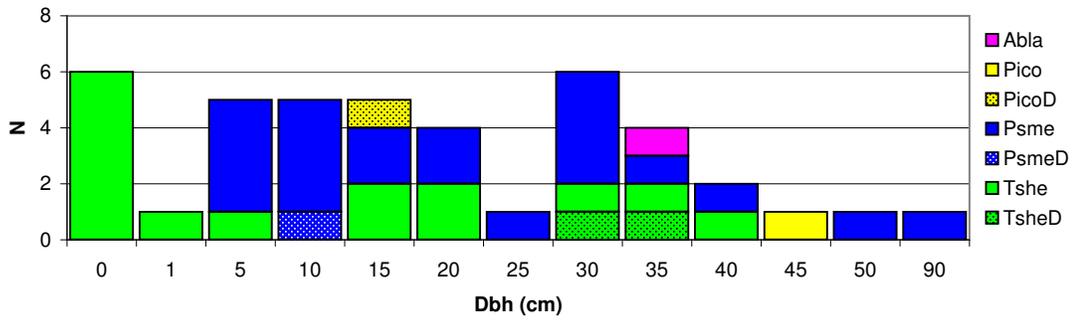
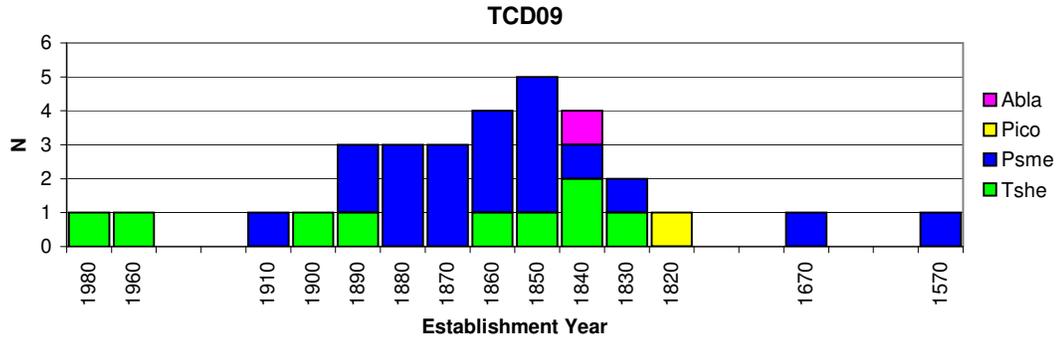


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 5 |
| Seed | 0 |
| Tree | 21 |
| TOTAL | 26 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 7 (2 dead) |
| Seed | 5 |
| Tree | 25 (1 dead) |
| TOTAL | 37 |

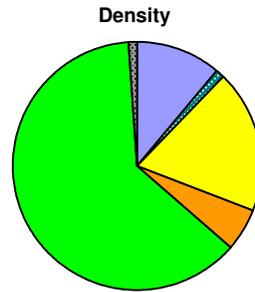
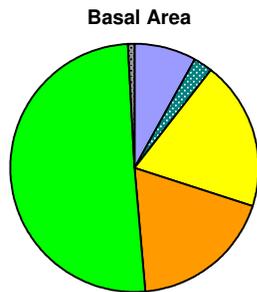
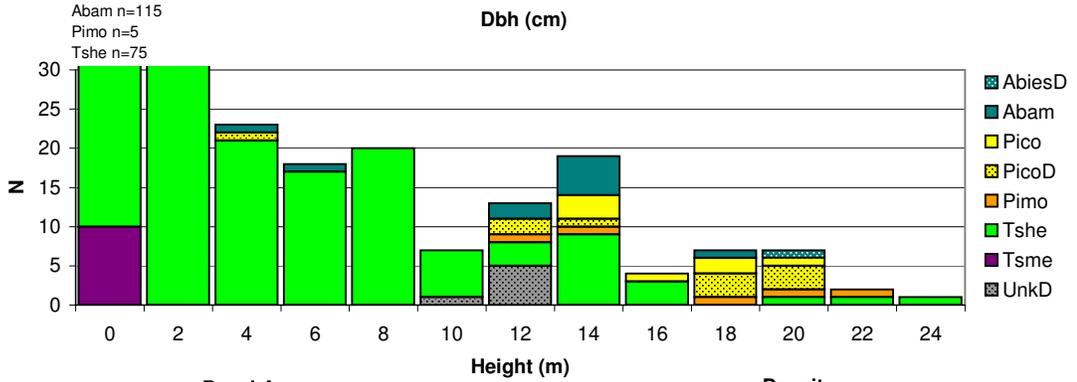
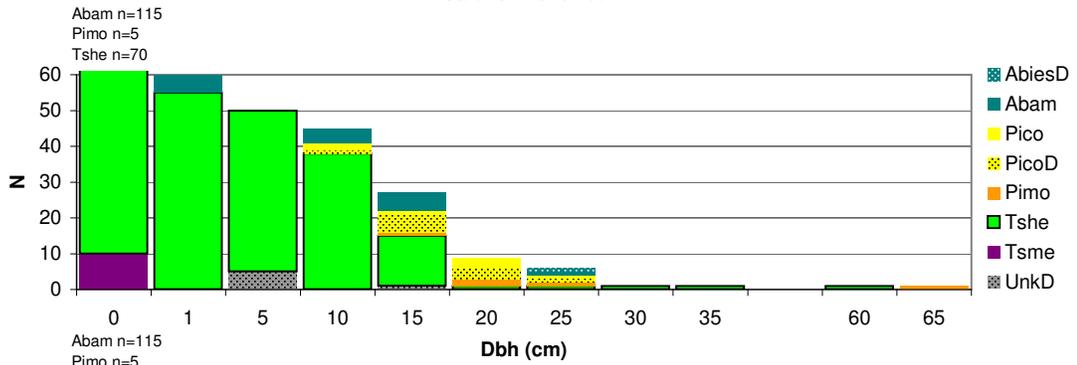
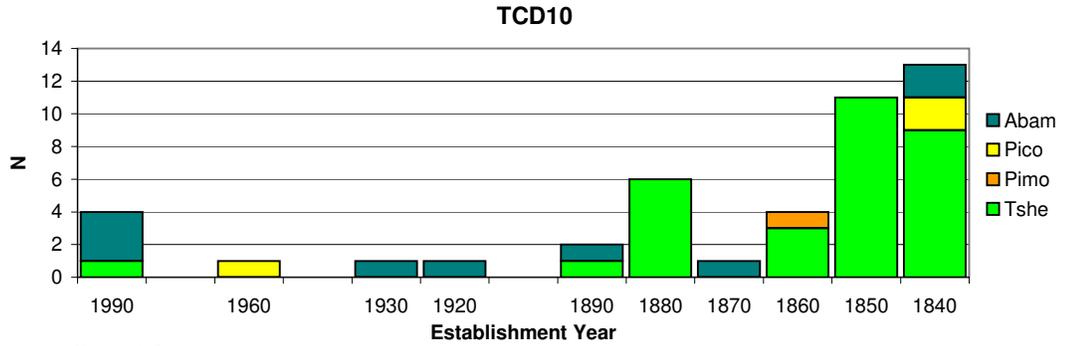


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 6 |
| Seed | 1 |
| Tree | 24 |
| TOTAL | 31 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 7 |
| Seed | 5 |
| Tree | 30 (4 dead) |
| TOTAL | 42 |

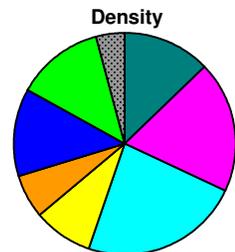
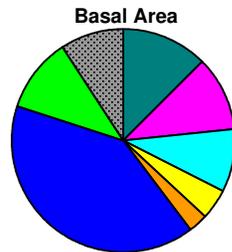
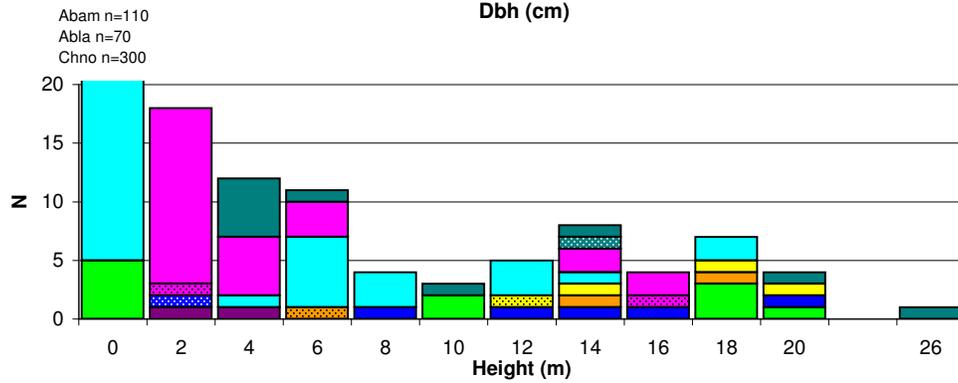
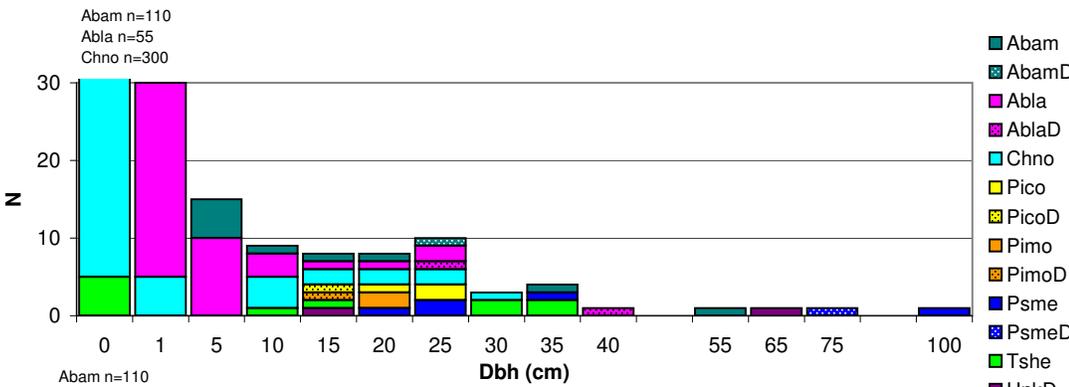
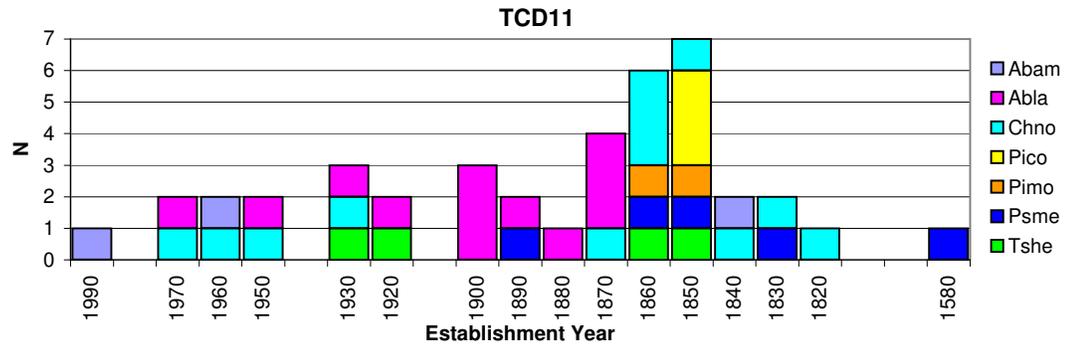


Age Class Frequency Distribution

| Lifeform | # of Samples |
|----------|--------------|
| Sap | 9 |
| Seed | 8 |
| Tree | 27 |
| TOTAL | 44 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|----------|---------------|
| Sap | 100 (15 dead) |
| Seed | 195 |
| Tree | 91 (16 dead) |
| TOTAL | 386 |



Age Class Frequency Distribution

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 6 |
| Seed | 9 |
| Tree | 26 |
| TOTAL | 41 |

Size Class Frequency Distributions

| Lifeform | # of Samples |
|--------------|--------------|
| Sap | 55 |
| Seed | 460 |
| Tree | 47 (8 dead) |
| TOTAL | 562 |