Residual roots from previous stand components are often cited as a major benefit to stump-sprouts of tanoak in southwest Oregon and northern California. Established patterns of belowground carbon allocation and root/shoot maintenance suggest that residual root systems of stumps will be reduced by carbohydrate depletion and root mortality and by shifts in allocation priority. A chronosequence approach was taken to relate changes in tanoak fine-root biomass to aboveground development during the first ten years after cutting of mature tanoak stands.

Tanoak stump sprouts did not maintain preexisting fine roots. Proportional to values in the mature forest, root surface area for 3-year sprouts was 15, 52, and 82 % in root diameter classes <.25, .25-1, and 1-2 mm respectively. A strong correlation between elevated soil temperature and dead root proportions suggests that increased respiratory depletion of carbohydrate supplies is the major cause of root mortality. Root dieback increased (in relative and absolute terms) with decreasing root size, which emphasizes the importance of high resolution in belowground studies.
As a result of increased root mortality and reduced root growth relative to shoot growth, the new sprout stands regained the root/shoot equilibrium found in mature forests within 4 years. This supports a general theory of functional equilibrium between root and shoot.

Rapid initial rates of leaf area growth declined to a lower, stable level of relative growth rate by age 4, coinciding with the time of minimum tanoak root density and root/shoot recovery. This may be the time of minimum dominance potential for tanoak stump-sprouts. The link between aboveground and belowground growth suggests that more extensive studies of tanoak dominance potential may be focused on aboveground characteristics.

In combination with the overall decrease in tanoak roots, a pattern of increased dieback in openings between sprout clumps (until age 4) suggests that competition from residual tanoak roots will not entirely preclude the benefits of increased light for other species in openings. However, invading herbs (primarily bracken fern) may account for substantial soil moisture depletion during tanoak sprout recovery. Compared to the fully occupied mature forest, soil moisture depletion in sprout stands was substantially reduced only in the first summer after burning.

To meet conifer management objectives, tanoak control treatments may be most effective if applied when sprout stands reach minimum root occupancy (age 4 in this study). In terms of competition, compensatory effects of invading herbs and shrubs are very important in moderating interactions between long-term dominants. Douglas-fir is the major potential crop tree on tanoak dominated sites. To effectively shift dominance to Douglas-fir in tanoak sprout stands, planting of large seedlings and herbaceous weed control are recommended in addition to tanoak control measures.
Tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.)
Root Dieback: Below- and Aboveground Site Occupancy by Stump-sprouts in Southwest Oregon

by

Glenn R. Ahrens

A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Completed December 14, 1989
Commencement June 1990
APPROVED:

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Dean of Graduate School

Date thesis is presented ____________________________

Typed by ____________________________
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ACKNOWLEDGEMENTS

I gratefully acknowledge the silviculturists on the Siskyou National Forest for their cooperation and assistance in location and protection of study sites. I also thank Michael Newton for his guidance, support, and patience during the preparation of this thesis. In addition, I thank the members of my committee and other staff at Oregon State University for the various forms of instruction I received. Also, I may never have finished this work without the continued encouragement of my good friends Cathy Rose, Lauri Shainsky, and Randy Molina.

Funding for this project came from the Fundamental Forestry Intensified Research Program (F.I.R.).
Tanoak (Lithocarpus densiflorus) is the most common sprouting hardwood on much of the commercial forest land in the Siskyou Mountains of southwest Oregon and northwest California (Franklin and Dyrness 1973). Douglas-fir (Pseudotsuga menziesii) production is often the dominant management objective on these lands. Comparisons of Douglas-fir growth on plantations with and without control of tanoak have shown substantial reductions in Douglas-fir growth where tanoak was not controlled (Roy 1955, 1981a, Radosevich et al. 1976, Harrington 1989). In the first ten years of stand establishment, Douglas-fir grows slowly relative to tanoak (Thornburgh 1981), and this initial dominance can result in dominant tanoak forests for 60 to 100 years (Sawyer 1980, Thornburgh 1981).

The ubiquity of tanoak is a result of both persistence and plasticity: individual tanoaks may live for hundreds of years in a variety of growth forms, including understory shrub, overstory tree, or vegetative sprout (Roy 1981b). As a result, immediate and well distributed tanoak sprout regeneration is common following disturbance on commercial forest lands. These sprouts may grow as much as 1.7 m tall in the first year (Roy 1981b); 1 m is common.

High residual root density from the previous hardwood component is often cited as an important factor contributing to the dominance of tanoak and other sprouting hardwoods after disturbance (Roy 1955, 1981b, McDonald...
Roy (1981b) compared Douglas-fir growth (over 28 growing seasons) in plantations with and without control of tanoak competition, and found growth reductions from competition that were uncorrelated with tanoak stem proximity or size. He concluded that maintenance of pre-harvest root systems by stump-sprouts results in severe moisture competition, even in large openings between sprout clumps. However, belowground site occupancy during hardwood sprout stand development has not been studied. During early development of sprout stands after clearing, root systems should be reduced by decreased photosynthate supplies, shifts in carbohydrate allocation to favor shoot growth, and increased respiratory depletion of carbohydrate reserves.

Belowground carbon allocation accounts for a large proportion of the total net primary production in forests (i.e. 25-75 percent, Edwards and Harris 1977, Santantonio 1977, Grier et al. 1981, Joslin and Henderson 1987). After clearing, the surviving stump and root systems of sprouting species will therefore experience a drastic reduction of photosynthate supplies. With soil surface exposure, elevated soil temperatures and respiratory depletion of carbohydrate reserves should cause increased root mortality (Redmond 1959, Marshall and Waring 1985). Studies of root/shoot relations in many species support the theory that plants maintain a characteristic root/shoot balance, and respond to changes by shifting allocation in order to recover this balance (Loomis 1953, Redmond 1959, Brouwer 1962, Zaerr and Brown 1976, Drew and Ledig 1980).

The objective of this paper is to relate changes in fine-root density and distribution to aboveground biomass and leaf area development during the first ten years after cutting in pure tanoak stands. Results are used to evaluate the role of tanoak root occupancy in post-disturbance vegetation dynamics and to characterize below-
ground attributes of sprout stand recovery after disturbance. Specific hypotheses of this study were:

1. Stump-sprouts do not maintain extensive pre-existing root systems; increased root mortality and decreased root growth result in net root dieback. The magnitude and rate of root dieback increases with decreasing root size.

2. Fine root/foliage ratios recover from initial effects of crown removal and return to an inherent balance for the species and site, which is approximated by root/foliage ratios in uncut forests.

3. Significant changes in spatial distribution of fine roots occur during sprout stand development.

**Assessing belowground site occupancy:**

To assess site occupancy, estimates of shoot or root quantities should represent resource use potential. Leaf area or crown cover are good relative measures of aboveground occupancy, if estimates of characteristic maximum leaf area index can be obtained. Analogous belowground characteristics are absorbing root surface area or biomass. Numerous studies suggest that "fine" roots (ranging from <1 to <5 mm diameter) are functional analogues to the short-lived leaves and twigs of the shoot system (McQueen 1968, Hermann 1977, Russel 1977, Kramer and Kozlowski 1979). The coarse root system acts as the permanent structural network giving support and soil-access to replaceable fine roots.

Differentiation of functional status within the fine
root category is difficult. Many authors categorize fine roots as either 1) "long" exploring roots that become part of the structural root system, or 2) "short" branching roots, (usually mycorrhizal) that are more important for absorption (summarized by Hermann, 1977). New, unsuberized roots have higher water and mineral absorption rates than older suberized roots (Kramer and Kozlowski 1979). However, in many forests most absorption may occur through suberized roots because unsuberized roots are absent or rare during much of the growing season (Kramer and Bullock 1966, McClaugherty et al. 1982).

The dynamic nature of fine-roots must also be considered in attempts to measure belowground site occupancy. Studies in a variety of forests demonstrate high rates of fine-root turnover (1-3+ times per year) and seasonal variation in standing crop estimates (Head 1973, Santantonio 1982, Perrson 1978, Harris et al. 1978). In addition to annual turnover, standing crop root densities have been found to fluctuate up to 6-fold from year to year (Fogel and Hunt 1983).

Even in well-stocked mature forests, there is much horizontal spatial variation in rooting density due to biotic and abiotic variation in the soil environment. Small scale cycles (1 cm) of fine-root exploration and dieback may be asynchronous with each other on a larger scale (100 cm), causing an increase in apparently random spatial variation (Reynolds 1970). Fine-roots are often more opportunistic than leaves, exploiting locally favorable conditions during any season.
METHODS

Approach:

Sprout stand development after cutting and burning was described using a chronosequence of different sites (ages) sampled during 1985 and 1986. Since standing crop fine-root densities may fluctuate up to 6-fold from year to year (Fogel and Hunt 1983), annual remeasurement may produce substantial confounding of year-to-year variation with the main effect of sprout stand age. With reasonable comparability of site characteristics between mature forest and adjacent sprouting stands, confounding of site variation with stand age effects should be less than confounding with the year-to-year variation noted above. Therefore, the chronosequence approach may be superior to annual remeasurement for the objectives of this study.

For this study, I reasoned that a practical measure of functional root occupancy may be based on fine root density (root quantity per soil volume), categorized by diameter class (<.25, <1, 1-2, and 2-5 mm), suberization (new vs. old), and vitality (live vs. dead).

Estimates of absolute differences in dynamic attributes of fine-root turnover and seasonal fluctuation were beyond the scope of this study. The objective was to assess the relative levels of root density among stand ages. Standing crop samples were collected in mid-summer (July 7-24), late fall (Dec. 3-5) and early spring (March 27-31) to account for any seasonal changes in relative amounts of root between stand ages.

Root growth and mortality during sprout stand development were assessed by comparing proportions of live, dead, and new roots between stand ages. Root growth was also assessed by sampling root ingrowth in implanted, root-free soil (McClaugherty et al. 1982 and Persson 1981).
Study area:

The area chosen for study is approximately 20 miles east of the Pacific Ocean (Brookings, OR) in the Chetco Ranger District of the Siskyou National Forest (Figure 1). Annual precipitation averages 350 to 400 cm with growing season precipitation of 30 to 40 cm (May-September). In much of this region, stand replacement fires about 75 years ago have regenerated young seral stands that are often dominated by either tanoak or Douglas-fir. Over the last 10-15 years, slash-and-burn hardwood conversion treatments have been common in the areas dominated by tanoak. Thus the Chetco District has an array of both natural tanoak forest and post-treatment sprout stands. Sprout stands over a range of ages generally have similar treatment histories; the treatments were executed by private contractors to fairly consistent U.S. Forest Service specifications. My goal was to find suitable mature stands with adjacent sprout stands 2, 4, 6, and 8 years old. My criteria for stand selection were as follows:

1. Tanoak basal area was at least 90% of total basal area.

2. Coniferous species comprised less than 0.5 % of the total basal area within 30 m of study plots. Acceptable associate tree species were *Arbutus menziesii* and *Castanopsis chyrsophylla*.

3. Tanoak crowns all appeared healthy, with no apparent damage or mortality from herbicides or pathogens.

4. Post treatment sites were broadcast burned after cutting.
Figure 1. Study site location in southwest Oregon.
A total of 8 sites were chosen on 3 different ridges in the Chetco River drainage. The sites are named as follows:

Long Ridge sites
- LRO = Long ridge old forest
- LRY1 = Long ridge young sprout stand
- LRY2 = Long ridge young sprout stand

Pollywog Butte sites
- PWO = Pollywog Butte old forest
- PWY = Pollywog Butte young sprout stand

Snaketooh ridge sites
- SO = Snaketooh ridge old forest
- SY = Snaketooh ridge young sprout stand
- RY = Raccoon unit young sprout stand

Characteristics of vegetation, soils, environment and treatment history are shown for each site in Tables 1a and 1b.
Table 1a. Treatment history, location, and other physical characteristics of tanoak root study sites.

<table>
<thead>
<tr>
<th>SITE</th>
<th>AGE&lt;sup&gt;a&lt;/sup&gt;</th>
<th>TANOAK&lt;sup&gt;b&lt;/sup&gt;</th>
<th>SLOPE</th>
<th>ASPECT</th>
<th>ELEVATION (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Growing seas.</td>
<td>%BA (%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>since cut burn</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SY</td>
<td>3</td>
<td>93 (10)</td>
<td>W</td>
<td>630</td>
<td></td>
</tr>
<tr>
<td>LRY1</td>
<td>4</td>
<td>92 (30)</td>
<td>NW</td>
<td>550</td>
<td></td>
</tr>
<tr>
<td>PWY</td>
<td>4</td>
<td>100 (30)</td>
<td>WNW</td>
<td>762</td>
<td></td>
</tr>
<tr>
<td>RY</td>
<td>7</td>
<td>95 (40)</td>
<td>W</td>
<td>620</td>
<td></td>
</tr>
<tr>
<td>LRY2</td>
<td>9</td>
<td>100 (10)</td>
<td>WSW</td>
<td>670</td>
<td></td>
</tr>
<tr>
<td>SO</td>
<td>-</td>
<td>75 (10)</td>
<td>W</td>
<td>610</td>
<td></td>
</tr>
<tr>
<td>LRO</td>
<td>-</td>
<td>98 (10)</td>
<td>NW</td>
<td>550</td>
<td></td>
</tr>
<tr>
<td>PWO</td>
<td>-</td>
<td>100 (40)</td>
<td>WNW</td>
<td>765</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Time in growing seasons since cutting or burning referenced to October 1985.

<sup>b</sup> Tanoak stem or stump basal area as percent of total measured on plots.
Table 1b. Soil characteristics and plant associations for tanoak root study sites.

<table>
<thead>
<tr>
<th>SITE</th>
<th>PARENT</th>
<th>MATERIAL</th>
<th>DEPTH</th>
<th>SOIL(^{a})</th>
<th>TEXTURE</th>
<th>FRAG. UNIT</th>
<th>ASSOC. UNIT</th>
<th>ASSOC.</th>
<th>QUALITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>SY</td>
<td>Sandstone</td>
<td>70-90+</td>
<td>Sandstone</td>
<td>Silt 0-90+</td>
<td>Silt</td>
<td>16</td>
<td>51</td>
<td>lide3/ rhma-vaov2</td>
<td>III</td>
</tr>
<tr>
<td>LRY1</td>
<td>Sandstone</td>
<td>90+</td>
<td>Sandstone</td>
<td>Clay 0-90+</td>
<td>Clay</td>
<td>11</td>
<td>512</td>
<td>lide3/ vaov2</td>
<td>IV</td>
</tr>
<tr>
<td>PWY</td>
<td>Mudstone</td>
<td>60-90</td>
<td>Loam</td>
<td>Loam</td>
<td>Loam</td>
<td>13</td>
<td>51</td>
<td>lide3/ VI</td>
<td></td>
</tr>
<tr>
<td>RY</td>
<td>Mudstone</td>
<td>50-90+</td>
<td>Loam</td>
<td>Loam</td>
<td>Loam</td>
<td>23</td>
<td>51</td>
<td>lide3/ rhma-vaov2</td>
<td>III</td>
</tr>
<tr>
<td>LRY2</td>
<td>Sandstone</td>
<td>90+</td>
<td>Loam</td>
<td>Clay 0-90+</td>
<td>Clay</td>
<td>10</td>
<td>55</td>
<td>lide3/ rhma-vaov2</td>
<td>IV</td>
</tr>
<tr>
<td>LRO</td>
<td>Sandstone</td>
<td>90+</td>
<td>Loam</td>
<td>Clay 0-90+</td>
<td>Clay</td>
<td>13</td>
<td>512</td>
<td>lide3/ vaov2</td>
<td>IV</td>
</tr>
<tr>
<td>SO</td>
<td>Mudstone</td>
<td>50-90+</td>
<td>Loam</td>
<td>Loam</td>
<td>Loam</td>
<td>24</td>
<td>51</td>
<td>lide3/ rhma-vaov2</td>
<td>III</td>
</tr>
<tr>
<td>PWO</td>
<td>Mudstone</td>
<td>50-90</td>
<td>Loam</td>
<td>Loam</td>
<td>Loam</td>
<td>16</td>
<td>51</td>
<td>lide3/ rhma-vaov2</td>
<td>VI</td>
</tr>
</tbody>
</table>

\(^{a}\) Depth to bedrock or fractured bedrock.
\(^{b}\) Soil texture at 30 cm soil depth.
\(^{c}\) Rock fragment % by volume in cores to 60 cm depth.
\(^{d}\) Soil mapping units from Meyer and Amarranthus (1978).
\(^{f}\) Douglas-fir site quality from Forest Service records.
Study design:

This was an observational study. Plots were selected to represent the chronosequence using both subjective and objective criteria. With the chronosequence approach, differences in soils, environment, and stand history between sites (ages) may interact with (or confound) the apparent effects of time. To evaluate the importance of such interactions, replicate stands within an age were located on differing soil types and stand densities. Replicate tanoak stands could not be sampled for all ages. Sample size was limited by intensive soil core washing and root sorting procedures. Also, suitable young sprout stands were rare since sprouts were often controlled chemically or manually to meet conifer management objectives.

The chronosequence is represented by mature forest (sites LRO and SO), 1-year- (SY), 3-year- (LRY and PWY), 4-year- (RY), and 8-year-old (LRY2) sprout stands (see photographs, Figure 2a-h). Belowground sampling was done in three sample periods: July 1985, December 1985, and March 1986. Sites PWO and PWY were used in preliminary sampling in June 1985. PWY and LRY2 were sampled only in March 1986.

Below- and aboveground data for each site were collected within a representative 200 m² square plot permanently delineated on the site. Core-sampling points for belowground variables were located using randomly generated coordinates. Aboveground variables were sampled in circular plots (1 and 3 m radius as explained below) at each core point location for correspondence with belowground variables. Most aboveground variables were also completely inventoried within the 200 m² plot as explained in the Procedures.
Figure 2a. Interior of mature tanoak forest site, LRO.

Figure 2b. Interior of mature tanoak forest, site SO.
Figure 2c. Edge of mature tanoak site LRO looking from site LRY.

Figure 2d. Soil/root core apparatus on site LRY.
Figure 2e. Site LRY 3 years after burning.

Figure 2f. Site LRY 3 years after burning.
Figure 2g. Site RY 4 years after burning.

Figure 2h. Site RY 4 years after burning.
Procedures:

**Belowground variables:**

Based on estimates of variation from preliminary samples, 10 or more sample points were randomly located in each plot for each sample period. Soil-root cores were removed with a 70 mm (inside diameter) stainless steel core tool driven with a 10 kg wooden hammer. Each core was taken approximately 10 cm at a time and separated by depth classes of 0-30, 30-60, and 60-90 cm. The 60-90 cm depth class was discontinued after the July sample. The top 5 cm were kept separate at points with intact litter layers.

For sampling root ingrowth, core holes from the July sample were refilled with sieved (3.2 mm mesh) soil from the 10-30 cm layer in nearby mature tanoak forest. During refilling the implanted soil was tamped to produce bulk densities as uniform as possible among the stands. The implanted soil was removed by re-coring with the same tool at the March 1986 sample period.

Soil moisture content and soil temperature were measured for each of the three periods, and also in September 1985 and August 1986. Moisture content was sampled at 3 to 5 core points in each plot (gravimetrically or with a Speedy Moisture Tester, Soil Test Inc.). Soil temperature was measured with a stainless steel probe thermometer at 5 or more locations in each plot. Initially, moisture and temperature measurements were made at the 30, and 60 cm depths. The 60 cm depth was discontinued after March 1986.

Gravimetric moisture content samples were collected in the following manner: The soil above the beginning of the depth intervals 25-30, 55-60, and 85-90 cm, was removed as part of the standard root density sample collection procedure. The core tool was then repositioned in the hole and driven 5 cm further. (Rotation of the tool using the
"T" handle usually sheared the end of the 5 cm segment cleanly.) The resulting sample was ejected directly from the tool into an 8 cm diameter can. Extraneous soil that fell into the hole during tool repositioning was scraped from the top of the sample and the can was then closed and sealed with electrician's tape.

After lifting, soil-root cores were stored at 2 °C (except during transit from Forest Service cooler in Brookings, OR to OSU, Corvallis) or, if processing was to be delayed beyond 2 months, at -20 °C to prevent significant changes in live/dead root ratios.

Each sample was soaked in water and wet-sieved through stacked 6.35, 3.2, 1.6, and 0.5 mm mesh sieves. Roots were sorted into < .25, .25-1, 1-2, and 2-5 mm diameter classes under a dissecting scope on .25 mm diameter wire mesh screen. Residual soil was washed from roots by soaking and brushing in detergent and sodium triphosphate.

Live roots were separated from dead roots by the following criteria:

1) Live roots are light brown to red-brown and flexible, with epidermis and periderm adhering to stele.

2) Dead roots often float with other debris; they are black to dark brown and brittle or crumbly, with epidermis and periderm readily parting from stele.

3) On live roots the stele is white and fibrous, whereas on dead roots the stele is discolored and tends to be crumbly.
New live roots were separated from old live roots using criteria formulated after examination of known samples of new and old tanoak root tissues. New live roots have intact cortex tissue that is light-brown in color, succulent in appearance and covers a bright, red-brown periderm. Old live roots had little remaining cortex tissue with red-brown periderm and white xylem tissue otherwise appearing similar to those tissues in new roots.

The above process retained all roots >.25 mm in diameter with reasonable certainty; roots <.25 mm were not consistently retained. Therefore most results of this study pertain to roots >.25 mm diameter. The additional effort was made to retain all <.25 mm roots for sites LRO, LRY1, and LRY2 in the March sample period. All organic material in the cores was retained in a process of repeated washing, sieving, and decanting to remove mineral material. Roots >.25 mm and more obvious <.25 mm roots were sorted as above. The remaining organic material consisted of a mixture of mycorrhizae, roots <.25 mm, and organic debris.

Marks et. al. (1965) developed a method for estimating length and biomass of mycorrhizae and roots in this type of debris mixture. The following adaptation of their method was used in this study:

The mixture of organic debris and fine roots was homogenized in a Waring blender for 10 s to produce more uniform root and mycorrhizae fragment sizes. The mixture was suspended in water and uniformly dispersed in a 25 x 25 cm gridded glass tray. Using a micrometer eyepiece on a boom-mounted dissecting scope, 20 systematically located fields were examined. Newman's (1965) length intersect method was used to estimate length of <.25 mm roots and mycorrhizae for each sample:
\[ R = \frac{(N \times A \times \pi)}{(2 \times L)} \]

\( R \) = length of root in the sample  
\( N \) = number of intersections of root and micrometer lines  
\( A \) = area of the glass tray  
\( L \) = total length of micrometer lines (number of fields * length of crosshairs in each field)

The ratio of length to dry weight was determined on subsamples of <.25 mm root material.

Sorted root samples were oven dried at 70 °C for 4 days and weighed to the nearest 0.1 mg. Surface area was measured on subsamples of the .25-1 and 1-2 mm diameter classes using a Licor leaf area meter (using the assumption that roots are cylindrical). Roots of other species were identified whenever possible and sorted into <2 and 2-5mm diameter classes. The same methods were used for standing crop and ingrowth samples.

Gravimetric moisture content samples were weighed, oven dried at 105 °C, and reweighed for determination of percent moisture content (MC) by weight. Bulk density and moisture content by volume were determined using sample volume calculated from core segment length and diameter. After drying and weighing, each MC sample was washed and sieved to separate the >2 mm fraction, which was then re-dried and weighed.

**Aboveground variables:**

All mature stems or stumps in each 200 m² plot were numbered and tagged, and their locations were mapped on a coordinate system to allow calculation of various sprout clump proximity indices for each core point location (stem maps shown in Appendix 1). Stem diameter at breast height
(dbh, 1.3 m) was measured for all stems in mature forest plots. In post-treatment (clearcut) plots, stump diameter (at 20 cm ht.) was measured for computation of previous stem basal area using regression of diameter-at-20 cm height on dbh in the mature plots.

Sprouts on all stumps were counted by diameter class (0.5 cm intervals) for calculation of basal area, live crown biomass, leaf weight, and leaf area using equations developed by Harrington (1984). Sprouts older than 6 years were beyond the scope of Harrington's equations. For the 9-year-old sprouts at LRY2, a sample of 20 stems was taken to develop equations predicting leaf area and biomass from basal stem diameter. The data were fit to a lognormal regression model as described in Baskerville (1972).

Complete aboveground measurements were made in September 1985. In sprout stands, a subsample of at least ten sprout clumps was remeasured in August 1986 for estimates of annual growth.

Live crown biomass, leaf weight, total biomass, and bole volume for older stems were calculated from regressions on dbh (Snell and Little 1983). All predictive equations for aboveground variables are shown in Appendix 2. Shrub and herb cover were estimated on 1-m radius circular plots centered at core sample points on each plot in August 1986.

**Calculations:**

Root biomass density estimates for a given soil depth zone were calculated as dry weight/soil volume using core segment length and cross sectional area (38.3 cm²). The result (g/cm³) was converted to kg/ha for the soil depth zone.

Root surface area estimates for roots .25-2 mm diameter were calculated using the ratio of surface area to
biomass within diameter and vitality classes. Estimates of <.25 mm root surface area were made assuming that roots are cylindrical, with an average diameter of .125 mm.

For relation to belowground data, most aboveground parameters (leaf area, biomass, live crown weight, bole volume etc.) were calculated using 3-m radius circular plots centered around each core. Tree crown cover was estimated using crown area measurements in the 200 m² plot and using the ratio of LAI to maximum LAI estimates (leaf area/crown area, an estimate of LAI at 100 % cover).

Root-to-foliage ratios were estimated for each plot using the ratio of means.

To test for any relation between root density and stem proximity, stem proximity indices for each core point were calculated using distances from core points to stems taken from stem location maps. In both mature and young plots, stems were clumped based on origin (single or multiple stem) of mature stems or stumps. Using tanoak size variables of mature stem basal area and current foliage weight, different size/proximity indices were calculated based on the N=1 to 6 nearest stem clumps within a 3 m radius of each soil core point as follows:

\[
\text{SPI1} = \frac{\text{Size of 1st nearest clump}}{\text{distance to first nearest clump}}
\]

\[
\text{SPI2} = \left(\frac{\text{Size of 1st clump}}{\text{distance first clump}} \right) + \left(\frac{\text{Size of 2nd clump}}{\text{distance second clump}} \right)
\]

e tc. to SPI6

or

\[
\text{SPI1} = \text{Size of the 1st clump}
\]

\[
\text{SPI2} = \text{Size of the 1st clump} + \text{Size of the 2nd clump}
\]

e tc. to SPI6
Analytical methods:

Data processing was done using SAS statistical software for microcomputers. Since this was an observational study, with subjective criteria for "representativeness", descriptive statistics are most appropriate. Statistical significance is not determined in the context of a replicated experimental design. Standard errors of the mean are shown for assessment of variability within sites and sample dates. The true significance of these results is dependent on the validity of the chronosequence and the representativeness of plots. Any statements of statistical significance are based on confidence intervals for simple pairwise comparisons of parameter estimates for each stand.

Variance calculations for estimates obtained using regression models from varied sources do not incorporate the error due to regression. Regression parameter estimates and correlation coefficients for all predictive equations are shown in Appendix 2.

To evaluate changes during stand development in horizontal distributions and variability in root density, frequency distributions for root density variables were generated by converting from continuous to interval data. Multiple linear regression was used to determine the amount of variability in root estimates explained by combinations of size/proximity indices, roots of other species, and rock fragment content.

Correlations between soil temperature and root mortality were assessed using simple linear regression of mean soil temperatures and the mean proportions of dead-to-total root biomass.

Rock fragment content increased variability in gravimetric moisture content samples. Also, moisture content estimates from the Speedy Moisture meter
(Snaketooth Butte sites only) were made on the < 2mm fraction only. Differences in moisture depletion were therefore evaluated by comparing least-squares-means calculated using rock fragment content as a covariate.
RESULTS

**Aboveground site occupancy**

Mature stem basal area (from dbh in mature stands; from calculated dbh in sprout stands), did not differ substantially among the sites (Table 2), with an overall average of 63.0 m$^2$/ha (274.4 ft$^2$/ac). After one growing season crown biomass estimates in sprout stands were about 3% of that in uncut mature forests. This figure grew to 55% after eight growing seasons.

Very similar estimates of maximum tanoak leaf area index (LAI) were obtained using three different methods:

1) 9.45 m$^2$/m$^2$; the average leaf area index for individual 5-year old tanoak clumps calculated as leaf area/crown area using leaf area prediction equations from Harrington (1989).

2) 9.42 m$^2$/m$^2$; the average leaf area index for 200 m$^2$ plots in the closed canopy mature tanoak forest (Snell and Little (1983) leaf weight equations, Harrington (1984) specific leaf weight value).

3) 9.3 m$^2$/m$^2$; the leaf area index of a 3-m-radius plot in the 9-year-old sprout stand with a closed canopy (leaf area from equations developed in this study).

Tanoak leaf area development (Figure 3) shows a generally linear trend during the first eight years after burning. Comparable estimates of leaf area development for interior tanoak sprout stands (Harrington 1989) show a similar trend.
Table 2. Stem basal area (mature stems in uncut forest or previous mature stem from stumps in sprout stands), live crown biomass, and foliage biomass for mature and resprouting tanoak stands. Age refers to the number of growing seasons since burning.

<table>
<thead>
<tr>
<th>SITE</th>
<th>AGE</th>
<th>MATURE STEM BASAL AREA (m²/ha)</th>
<th>LIVE CROWN BIOMASS * (kg/ha)</th>
<th>FOLIAGE BIOMASS (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>C</td>
<td>R</td>
</tr>
<tr>
<td>LRO</td>
<td>75</td>
<td>76.2</td>
<td>73.3a</td>
<td>84,386</td>
</tr>
<tr>
<td>SO</td>
<td>75</td>
<td>62.1</td>
<td>63.4a</td>
<td>78,000</td>
</tr>
<tr>
<td>SY</td>
<td>1</td>
<td>73.4</td>
<td>66.7a</td>
<td>3,075</td>
</tr>
<tr>
<td>LRY</td>
<td>3</td>
<td>56.1</td>
<td>56.7a</td>
<td>11,393</td>
</tr>
<tr>
<td>PWY</td>
<td>3</td>
<td>--</td>
<td>56.1a</td>
<td>---</td>
</tr>
<tr>
<td>RY</td>
<td>4</td>
<td>60.8</td>
<td>62.1a</td>
<td>15,208</td>
</tr>
<tr>
<td>LRY2</td>
<td>8</td>
<td>--</td>
<td>55.0a</td>
<td>---</td>
</tr>
</tbody>
</table>

* Sources for equations used to estimate crown and foliage biomass: Mature stands, Snell and Little 1983; 1-6 year-old sprout stands, Harrington 1984; >6 years (LRY2), this study.

** R - values from rectangular 200 m² plots. C - values from 3-m-radius circular plots centered on core points. Significance tests are based on values from 3-m-radius plots: Column means followed by the same letter are not significantly different (P=.05).
Figure 3. Tanoak leaf area index in developing sprout stands. Single sided leaf area estimated from inventory of all stems on circular 3-m-radius plots on Chetco sites. Annual remeasurement data from interior Siskyou sites are shown for comparison (Data from Harrington 1989, LAI estimated from crown area).

As a measure of relative site occupancy, percent cover for tanoak was calculated as the ratio of current LAI to the average maximum LAI estimate. Aboveground site occupancy for tanoak and other species (herbs + shrubs) is shown in Figure 4. Herb and shrub cover increase rapidly and comprise 43% of the total cover after year four. Nine years after burning, herb and shrub cover decrease to only 7% of the total cover. Bracken fern is the dominant species after tanoak, comprising an average of 80% of the total cover of "other species" (see Appendix 3 for species list).
Figure 4. Changes in foliar cover of tanoak and madrone along with other species during sprout stand development. Age 0 refers to mature tanoak forest. Hardwood cover was estimated for each 3-m-radius plot as current LAI / maximum LAI. Herb and shrub cover was ocularly estimated on 1-m-radius plots centered on root-core points.

**Belowground site occupancy**

**Live+dead root biomass:**

Averaged over all sample dates, total root weight (live+dead) to 60 cm soil depth, was substantially lower in all sprout stands relative to mature forests for all root size classes (Figure 5).
In sprout stands, root biomass in the 2–5 mm diameter class was about 65 percent of that in mature forests. Among the sprout stands, there was a slight decrease in 2–5 mm root biomass with increasing sprout age. Biomass of roots less than 2 mm diameter decreased with time during sprout stand development. Root biomass in the .25–1 mm class decreased with sprout age until age 4. A recovery trend was apparent for .25–1 mm roots by the 8th year after burning.

Relative levels of fine root biomass among stand ages were similar for all sampling dates (Figure 6). In general, the highest values of .25–1 mm root biomass occurred in March, though these were significantly higher only in sites LRO and RY. Within age classes, replicate stands (LRO vs. SO and LRY vs. PWY) showed very similar levels of fine root biomass in the March sample.
Figure 6. Live+dead tanoak root weight (.25-1 mm dia.) by site and sample period.

Roots larger than 1 mm showed more variation, and there were no significant seasonal differences for live+dead root weight within a stand.

Root biomass decreased with increasing soil depth in all stands. The root density profile for undisturbed mature forests (Figure 7) shows 65% of the roots to 90 cm depth are in the 0 to 30 cm depth zone and 85% are in the 0 to 60 cm zone. The 0 to 5 cm layer (which included forest floor) contained 28% of the total .25-1 mm root mass in the mature forest.

Decreases in root biomass during sprout stand regeneration and development were greatest in the top 30 cm (Figure 8). Minimum .25-1 mm root biomass occurred in the 4-year sprout stand, where estimates were 18, 33, and 50 percent of mature forest values for 0-30, 30-60, and 60-90 cm depth zones respectively.
Figure 7. Distribution of .25-1 mm root biomass by soil depth zone in mature tanoak forest to maximum soil depth of 90 cm.

**Roots of other species:**

Pacific madrone (*Arbutus menziesii* Pursh) was a minor component of most stands. Over all sites combined, madrone roots comprised an average of 2.6% of the hardwood root biomass; generally consistent with aboveground proportions of the madrone component (average 3.3% by basal area).

Trends in .25-2 mm root weight for tanoak and other species (Figure 9) are very similar to those for aboveground site occupancy. From minimum values of 100 kg/ha in mature forests, roots of other species increase to maximum values of 2,078 kg/ha in the 4-year sprout stand. Eight years after burning, roots of other species were reduced to 248 kg/ha. Bracken fern was the most abundant species after tanoak, on average comprising 80% of the root mass of other species.
Figure 8. Changes in root weight by soil depth zone for live+dead roots a) .25-1 mm diameter and b) 1-2 mm diameter. Bars are standard error of the mean.
Figure 9. Root density of tanoak, madrone, and other species. Live+dead roots, .25-2 mm diameter averaged over all sample periods for each age. Bars are standard errors of the mean.
**Root mortality:**

Through age four the proportion of dead roots to the total live+dead root mass was significantly higher in sprout stands compared to the mature forest (Figure 10a). By age 8 the proportion of dead roots had returned to an equal or lower level compared to the mature forest.

The highest dead root proportions occurred in the 1-year old sprout stand: dead roots comprised 65, 67, and 57 percent of the total in .25-1, 1-2, and 2-5 mm diameter classes respectively. These proportions were about three times as high as those in mature forests.

In the 3-year sprout stands, dead root proportions were about twice as high as mature forest values. In the 4-year sprout stand, dead root proportions in the .25-1 mm diameter class were similar to the 3-year stand whereas proportions in the 1-2 and 2-5 mm classes were almost identical to the 1-year sprout stand. Dead root proportions did not change significantly with sampling date (Figure 10b).

Mean dead root proportions for each site increased with increasing summer soil temperature. Mean August soil temperature at 30 cm explained 96% of the between-site variation in mean dead root (.25-2 mm roots) proportion (Figure 11).
Figure 10. Dead root proportions (dead root weight / total live+dead root weight) during sprout stand development by a) root size class and b) sample period. Bars are standard error of the mean proportion.
Figure 11. Mean August soil temperature at 30 cm depth versus mean dead root proportion (dead root weight / total live+dead root weight, .25-2 mm dia. roots). Closed circles = mature forest, open circles = young sprout stands.
New root growth:

In mature forests, new root ingrowth (0.25-2 mm diameter), into implanted soil during eight months was about 12% of the live root standing crop (Table 3). In the 1-year sprout stand this value dropped to 3%. Ingrowth as a proportion of live standing crop was highest in the 3- and 4-year sprout stands, with values of 34 and 46% respectively.

Another relative measure of new root growth was the proportion of new live roots out of the total live root mass. Very few new live roots were found in July and December, therefore, biomass in this category was only estimated for the March sample. This measure also showed less new root growth in mature forests and in the 1-year sprout stand compared to the older sprout stands. However, new root proportions were similar for all sprout stands older than 1 year.

Root size vs. dieback:

Both the rate and magnitude of root dieback increased with decreasing root size (Figure 12). Mycorrhizal roots (any root fragment 0-2 mm diameter with an ectomycorrhizal sheath) showed a trend similar to < 0.25 mm roots, with an indication of greater recovery by age eight.

In the mature forest, 63% of the total fine root (<2.0 mm) surface area was in the finest size class (Table 4). In this subsample, accounting for roots <.25 mm nearly doubled the magnitude of root dieback compared to estimates that exclude these very fine roots: 0-2 mm root surface area in the 3-year stand is only 32% of that in the mature forest, whereas .25-2 mm surface is 61% of that in mature forest.
Table 3. Relative measures of new root growth expressed in proportion to the total live root mass (.25-2.0 mm diameter). Ingrowth was taken from core holes refilled in July 1985 and sampled in March 1986. New root proportions are from the March sample. Age is the number of growing seasons since burning. Standard error of the ratio of means in parentheses.

<table>
<thead>
<tr>
<th>Age (grw. seas.)</th>
<th>Ingrowth proportion</th>
<th>New root proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>LRO 75</td>
<td>0.11 (.024)</td>
<td>0.064 (.010)</td>
</tr>
<tr>
<td>SO 75</td>
<td>0.14 (.019)</td>
<td>0.047 (.009)</td>
</tr>
<tr>
<td>SY 1</td>
<td>0.03 (.014)</td>
<td>0.074 (.018)</td>
</tr>
<tr>
<td>LRY 3</td>
<td>0.34 (.055)</td>
<td>0.122 (.018)</td>
</tr>
<tr>
<td>PWY 3</td>
<td>-</td>
<td>0.109 (.020)</td>
</tr>
<tr>
<td>RY 4</td>
<td>0.46 (.203)</td>
<td>0.094 (.032)</td>
</tr>
<tr>
<td>LRY2 8</td>
<td>-</td>
<td>0.101 (.020)</td>
</tr>
</tbody>
</table>
Figure 12. Root dieback and root size at Long Ridge sites: Root density in 3-year and 8-year sprout stands expressed as a proportion of the adjacent mature forest value for each root size class. Mycorrhizal roots were defined as any root, 0–2 mm with a fungal sheath.
Table 4. Root surface area of live+dead roots by size class, including <.25 mm dia. roots for Long Ridge sites, estimated from March samples. Equations and conversion factors used to estimate root surface area are shown in Appendix 2.

<table>
<thead>
<tr>
<th>Age (grw. seas.)</th>
<th>Root surface area (cm² cm⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dia. class: &lt;.25mm .25-1mm 1-2mm Total</td>
</tr>
<tr>
<td>LRO 75</td>
<td>12.0 5.0 2.2 19.2</td>
</tr>
<tr>
<td>LRY 3</td>
<td>1.8 2.6 1.8 6.2</td>
</tr>
<tr>
<td>LRY2 8</td>
<td>2.2 2.5 1.3 6.0</td>
</tr>
</tbody>
</table>

Root shoot ratios:

During shoot recovery, standing crop fine-root/leaf weight ratios rapidly declined, reaching a level similar to that in mature forests four years after burning (Figure 13a). Initially, new root growth (new fine root proportion from Table 3) was reduced relative to new leaf growth (Figure 13b). Root/shoot growth ratios then recovered from low initial levels until year four, after which there was little change.
Spatial distribution:

Relative frequency distributions for core-point estimates of root weight grouped in 300 kg/ha intervals are shown in Figure 14. The distribution of live root density in mature forests shows a broad range (CV=254%), which demonstrates a high degree of horizontal spatial heterogeneity. The stand with the lowest live root estimates (four years since burning, site RY) had similarly high variability in live root density (CV=221%). The other sprout stands showed lower variability in live root estimates (CV=92-98%). Variability in dead root estimates increased greatly in the 1-year sprout stand.

Relative frequencies of point estimates of dead-to-total root biomass ratios are also plotted (Figure 15). Spatial heterogeneity in dead root proportions is more pronounced in young sprout stands. The distributions are shifted toward higher ratios at 30-60 cm soil depth. With increasing sprout stand age, the dead root ratio distributions recover position and shape attributes of the mature forest distributions. The 4-year sprout stand shows the greatest spatial variability in dead root ratio.
Figure 13. a) Standing crop fine-root / foliage weight ratios for .25-2 mm diameter live roots. Bars are standard error of the ratio of means. b) Root/foliage growth ratios (new root/total live root)/(new leaf/total leaf) for .25-2 mm diameter live roots.
Figure 14. Relative frequency (%) distributions for values of .25-1 mm tanoak root weight for live and dead roots in sprout stands. Data from point estimates of root weight were grouped in 300 kg/ha intervals.
DEAD ROOT PROPORTION

Figure 15. Relative frequency (%) distributions for values of dead root proportion (dead roots / live+dead roots) for .25-1 mm tanoak roots in sprout stands.
Tanoak size/proximity indices, along with rock fragment content and other species' root biomass were tested for their ability to explain variation in point estimates of tanoak root weight. Leaf weight and leaf weight/proximity for the nearest tanoak sprout clump(s) within 3 m of core points explained 39 to 53% of the variation in .25-2 mm root biomass in young sprout stands (Table 5). However, relationships between specific size/proximity indices and root biomass were not consistent between sites.

Among sprout stands, the 4-year old stand, which showed the highest variability of root biomass, also had the greatest amount of variation explained by size/proximity indices, roots of other species, or soil rock fragment content.

Size/proximity indices were not correlated with root biomass in mature forest sites. In mature tanoak forests, the best relationships were negative correlations between rock fragment content and root biomass

**Soil temperature and moisture content:**

Summer soil temperatures increased by as much as 6.8 °C in the youngest (most exposed) sprout stand relative to the closed canopy tanoak forest (Table 6). The difference in temperature between sprout stands and mature forests diminished with increasing sprout stand age (leaf area). Soil temperatures in the 8-year sprout stand were no different from those in the mature forest at any date. December soil temperatures were similar for all the sites.
Table 5. Summary of regression parameters and coefficients of variation for multiple regression analyses of point estimates of fine root weight versus tanoak proximity index and soil rock fragment content. Values in parentheses are partial correlation coefficients for the independent variable.

Dependent variable:
live+dead tanoak root biomass (kg/ha) .25-2mm diameter

<table>
<thead>
<tr>
<th>Age (grw. seas.)</th>
<th>Regression coefficients</th>
<th>R²</th>
<th>Prob.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Interc.</td>
<td>SPI3</td>
<td>SPI5</td>
</tr>
<tr>
<td>LRO 75</td>
<td>16.56</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SO 75</td>
<td>19.61</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SY 1</td>
<td>10.24</td>
<td>1.43</td>
<td>-1.52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(.17) (.22)</td>
<td></td>
</tr>
<tr>
<td>LRY 3</td>
<td>5.71</td>
<td>0.77</td>
<td>-</td>
</tr>
<tr>
<td>PWY 3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>RY 4</td>
<td>9.72</td>
<td>-0.17</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(.15) (.38)</td>
<td>(.11)</td>
</tr>
<tr>
<td>LRY2 8</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

SPI3 = Size/proximity index based on the 3 nearest sprout clumps. SPI5 = index based on 5 or more nearest clumps. RF = % rock fragment content by volume.
Table 6. Soil temperature at 30 cm soil depth at different times of year.

<table>
<thead>
<tr>
<th>Shoot Age</th>
<th>Soil temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>Dec.</td>
</tr>
<tr>
<td>LRO</td>
<td>75</td>
</tr>
<tr>
<td>SO</td>
<td>75</td>
</tr>
<tr>
<td>SY</td>
<td>1</td>
</tr>
<tr>
<td>LRY</td>
<td>3</td>
</tr>
<tr>
<td>PWY</td>
<td>3</td>
</tr>
<tr>
<td>RY</td>
<td>4</td>
</tr>
<tr>
<td>LRY2</td>
<td>8</td>
</tr>
</tbody>
</table>

Differences in soil moisture depletion (Figure 16) between sprout stands and mature forest were apparent only in the youngest sprout stand at the earliest sample date. In July (26 days after the last significant rainfall) the 1-year-old stand showed no soil moisture depletion at 60 cm; at 30 cm soil depth, moisture depletion was about 30% of that in the mature forest.
Figure 16. Soil moisture depletion (difference between dry season moisture estimate and average December and March estimate) at 30 and 60 cm soil depth for Long Ridge and Snaketooth Butte sites. Bars are the standard error of the difference.
DISCUSSION

The significant trends for fine root density, dead root proportion, and root/leaf ratios support the hypothesis that net root dieback and root/shoot adjustment occur during early development of tanoak sprout stands. These trends result from two probable mechanisms: 1) increased root mortality with elevated soil temperature and respiration rate; and 2) endogenous mechanisms that reduce root growth relative to shoot growth to restore root/shoot equilibrium.

The high correlation \( R^2 = 0.96 \) between dead root proportion and soil temperature agrees with results of previous work, showing that fine-root mortality is primarily a function of carbohydrate supply and maintenance respiration rates (Marshall and Waring 1985). In general, root respiration rates of woody plants may be expected to double with a 10 °C temperature increase \( (Q_{10} 1.98-2.01, \) Jarvis and Leverenz 1983, Marshall 1985). The difference between two soils, in annual respiration, should then be a function of the integrated difference between their respective annual temperature cycles (Figure 17). Temperature maxima in late summer, the peak of the annual cycle, are probably a good index of the integrated annual difference in soil warming. Thus, mean dead root proportions in pooled samples from all seasons were highly correlated with August soil temperatures.

Soil exposure after overstory removal increased soil temperatures, and subsequent leaf area development in sprout stands reduced soil exposure (until age eight years when soil exposure, soil temperatures, and dead root proportions were similar to mature forest values). Thus both leaf area and soil temperature are correlated with root mortality.
Figure 17. Hypothetical annual soil temperature cycles for closed canopy and exposed soil sites. Curves were plotted using regression equations of soil temperature versus sin and cos transformations of Julian date.

However, a deviation from the inverse relation between leaf area and soil temperature occurred in the 4-year-old stand. In this case the close relation between dead roots and temperature was maintained, suggesting that increased temperature rather than leaf area was the main effect on root mortality. The 4-year-old sprout stand had a relatively steep WSW aspect with larger openings than either of the 3-year old sites. Leaf area was higher in the 4-year old stand, but both soil temperatures and dead root proportions were greater than in the younger but less exposed stands.

Maintenance of excess living roots would require allocation of carbohydrate from current photosynthate or from mobilized reserves. In this case, increasing foliage could reduce root mortality via an increase in photosynthate supply. Carbohydrate supplies were not measured in this study. However, the dead root/soil...
temperature relationship suggests that increased carbohydrate supplies (photosynthate or reserve) are not allocated to pay the higher maintenance costs of residual roots in warmer soils of sprout stands. Marshall and Waring (1986) demonstrated that after initial accumulation of starch reserves during growth, current carbon supplies were not allocated to maintenance of fine roots.

Dead roots were most abundant on the site with the highest soil moisture conditions. Some authors have shown increases in root mortality associated with soil drought (Deans 1979, Perrsson 1980). Prolonged soil drought had not occurred on any site at the July sampling (the only dry season sample) due to the relatively short period since the last heavy rains (19 days) and an adequate available soil water holding capacity. Any effects of drought were probably overshadowed by the greater effect of increased respiration and carbohydrate depletion. Increases in the amount of dead roots during drought may also result from decreased decomposition rates in dry soils (Kummerrow et. al. 1977). Controlled experiments with Douglas-fir (Marshall and Waring 1985) showed that drought did not increase fine-root mortality until carbohydrate limitations were induced by shading or high soil temperatures.

Though there was substantial spatial (horizontal) variation in root mortality, this variation was not explained by spatial variations in temperature or moisture content. Also, dead root proportions did not change with seasonal changes in temperature or moisture content within a site. Most other fine-root studies show a high degree of spatial variation within a stand at any time. Reynolds (1970) indicated that small scale (1-10 cm) cycles of fine root exploration and dieback may be asynchronous with each other on a large scale (100 cm), causing an increase in apparently random variation.
Horizontal variation in soil chemistry and biotic influences such as hyphal mats should also produce spatial variation in rooting density that is independent of temperature effects. Thus, in this study the most visible relationship is between annual temperature regimes and average root mortality, differing between sites.

The trend of increasing root dieback with decreasing root size (Figure 12) is consistent with results of other fine root studies, which demonstrate increasing rates of production and turnover with decreasing size within the fine-root category (<5 mm dia., Keyes and Grier 1981, Srivastava et al. 1986, Joslin and Henderson 1987). Joslin and Henderson (1987) found turnover rates for <1 mm white oak (Quercus alba L.) roots that were 4 times greater than for roots 1-5 mm in diameter. Mycorrhizal fungal hyphae represent a still finer level in the belowground system, directly supported by the tree. Fogel and Hunt (1983) found that accounting for both root and fungal components greatly increases the proportion of total organic matter and nitrogen turnover that may be attributed to the belowground system.

Therefore, it is logical that the very-fine belowground components in this study are the most sensitive to perturbation in carbohydrate status. Since these smallest roots also account for a majority of the total fine root surface area, they appear to be most important in terms of functional attributes such as absorption. The trends in Figure 12 suggest a logical differentiation (perhaps functional) between roots larger than 1 mm and those smaller than 1 mm. Allocation of current photosynthate and/or carbohydrate storage capacity may be greater for structural roots, whereas finer, absorbing roots may be dependent on smaller initial photosynthate allocation and storage capacity (Marshall and Waring 1985).

Excluding the <.25 mm roots, maximum estimates of <2mm
tanoak root biomass (6,000-7,000 kg ha⁻¹) are equal or
greater in magnitude than comparable figures reported for
all roots <2 mm (white oak 3,500-4,500 kg ha⁻¹, Joslin and
Henderson 1987; Douglas-fir 2,800-8,300 kg ha⁻¹, Keyes and
Grier 1981). These results emphasize the importance of
high resolution for examining changes in the belowground
system.

I found only one other study of root biomass in re-
sprouting hardwood stands: Edwards and Ross-Todd (1979)
estimated changes in root biomass in Liriodendron
tulipifera L. stands for two years after stem girdling.
Their fine-root category included all roots less than 5 mm
in diameter with no distinction between species. They
found no significant differences in root mass compared to
the undisturbed forest 20 months after girdling. My
results suggest that greater resolution between size class,
vitality, and species would have revealed more significant
changes after stem girdling.

The relatively small fluctuation in tanoak fine-root
biomass between seasons may seem surprising in contrast to
the substantial seasonal change reported by some other root
studies. However, if the same 4-month sample period
employed here is applied to studies with more frequent
sampling, there is often a similar lack of fluctuation
(Keyes & Grier 1981, McClaugherty et. al. 1982, Fogel &
Hunt 1983, Srivastava et. al. 1986). Joslin and Henderson
(1987) demonstrated substantial annual turnover, although
they found very little seasonal fluctuation (monthly
sampling interval) in fine root standing crop under mature
white oak.

Along with root mortality, root growth is also a
dynamic factor determining net changes in fine-root
biomass. Reduced carbon allocation to root growth and
maintenance may be a major avenue of root/shoot adjustment.
Relative root growth (new root/total live root, Table 3)
should be an indicator of relative carbon allocation to root growth and maintenance. If this is true, relative carbon allocation to roots is reduced during early sprout-stand development, but after age three carbon allocation to roots is even greater than that found in mature forests. This is discussed below in the context of root/shoot adjustment.

There are two components to the balance between root and shoot: a standing crop ratio and a growth or activity ratio. Drew and Ledig (1980) propose a functional equilibrium model for maintenance of root/shoot ratios:

\[(\text{Root wt.}) \times (\text{specific absorption rate}) = k \]
\[(\text{Shoot wt.}) \times (\text{specific photosynthetic rate})\]

absorption rate = water or nutrient absorption per unit of root wt

photosynthetic rate = carbon fixation per unit shoot wt

They suggest that this function is the empirical result of homeostatic mechanisms that maintain a characteristic root/shoot ratio over the long term with cyclic short term oscillations. Another interpretation is that annual primary production is balanced by annual water and nutrient absorption at a level (k) that is characteristic for the species and environment. Net leaf area expansion (growth in LAI) should be balanced by an expansion of the absorbing root system.

This equilibrium is demonstrated by the trends in tanoak root/shoot recovery (Figure 13, Table 3). In recovering sprout stands, root growth does not appear to balance leaf area expansion until the standing crop root/shoot balance is reached. Root growth is low during
the initial period of rapid sprout growth, perhaps due to a high shoot allocation priority. As the standing crop root/shoot ratio recovers, root growth increases to balance leaf growth. Relative to the stable mature forest (in which there is little net expansion of the shoot or root systems) root growth is higher in older sprout stands to balance the net expansion in leaf area.

No direct estimates were made for the root growth/leaf growth balance in mature forests. If I assume a stable state, in which new root and leaf growth balance root and leaf mortality, an estimate of leaf retention time may be used to estimate the ratio of root/leaf growth. Assuming an average leaf retention of 4 years (Harrington, personal communication), and estimating gross foliage growth rates (leaf area expansion + assumed leaf fall), the root/leaf growth balance in mature forests does appear to represent an "inherent" balance, which is recovered in sprout stands by age 4.

Although some correlation between fine-root densities and stem proximity has been demonstrated in young plantation forests, root density in mature forest stands is often uncorrelated with stem proximity (Reynolds 1970, Roberts 1976, Santantonio et al. 1977, Bowen 1984). This was the case for <2 mm roots in mature tanoak forest. However, the stronger positive correlation between fine root density and stem proximity in young sprout stands forests suggests a spatial pattern of root dieback, creating lower root density in openings.

The three-fold decrease in overall root density, along with a pattern of reduced density in openings should considerably reduce the resource exclusion encountered by spreading root systems of young Douglas-fir in between tanoak clumps. The size of evenaged Douglas-fir trees grown with tanoak sprouts should integrate competitive
environment with respect to neighboring tanoak.

Roy (1981) assessed the influence of tanoak stem proximity on Douglas-fir size, using the single nearest tanoak's proximity or size. I would expect any influence of nearby sprouts to be a function of their size and distance simultaneously, with all neighboring sprout clumps contributing to the effect. Further analysis of Roy's data, using multiple regression on both the diameter and distance of the nearest tanoak, explains a significant amount of the variation in Douglas-fir diameter and height (40 and 28% respectively, data courtesy of U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Redding, CA). This is similar to the amount of spatial variation in root density explained by indices of size/proximity (39-53%) in young sprout stands here. This does not support the conclusion that tanoak root competition in openings between sprout clumps precludes the benefits of increased light availability.

The reduction in tanoak root density is compensated by an increase in bracken fern root density. Differences in soil moisture depletion were found only in the first year after burning, when both bracken and tanoak leaf area were very low. Bracken fern, has been shown to account for 25-50% of the soil moisture depletion in understories of Scotch pine plantations (Roberts et. al. 1980). Water use in closed pine forests was equal to that in open pine forest that had an understory bracken LAI of about 1.0 m² m⁻². Comparable levels of bracken fern leaf area occurred in 3- and 4-year-old tanoak stands, which may explain the similarity of moisture depletion compared to the closed canopy tanoak forest. In general, post-disturbance vegetation often attains full soil moisture depletion capacity after two to three years of recovery (Newton and Preest 1988, Hobbs and Wearstler 1985).

The relation between root density and resource use is
not clear, especially in the case of tanoak sprouts, which have an initial surplus of root for the sprouting shoot. In a study of soil moisture depletion in the Oregon coast range, Drew (1968) found the highest moisture depletion under vine maple (*Acer circinatum*), even though root densities were low relative to the other species he studied. Water absorption is closely related to rooting density in moist soil, but as soils become drier, root growth, root hairs, and mycorrhizae become more important (Drew 1968, Whitehead and Jarvis 1981, Bowen 1984). The total length of root exploring the soil over the year depends on root turnover rate, and thus resource use is a function of both root dynamics and standing crop.

Transpiration is a function of leaf area and vapor pressure deficit. Maximum water use by tanoak in young sprout stands should then be relatively low due to low leaf area. Transpiration rates are generally higher for new versus old foliage. Vapor pressure deficits experienced by young sprouts may also be increased in the blackened clearcut environment. Thus, effects of reduced leaf area may be partially compensated by higher water use per unit leaf area in younger sprout stands.

Sawyer (1980) argues that species composition in tanoak/Douglas-fir communities is not environmentally controlled (i.e., tanoak forests are not necessarily on "tanoak sites"). He describes a typical pattern in which nearly pure stands of tanoak or Douglas-fir dominate younger phases, with eventual mixture of the other species. Succession generally leads to the same composition at maturity: an open Douglas-fir overstory with a fairly continuous tanoak understory up to 30 meters tall. However, dominant sprout-origin tanoak forests may persist for over 100 years (Thornburgh 1981 and Sawyer 1980).

Given the observation that pure stands of either
tanoak or Douglas-fir occur in the mixed evergreen Zone, it appears that both species are well adapted to the fire-disturbance regime, and that competitive exclusion can take place in young stands. The tendency toward competitive exclusion seems to be more pronounced on better sites; early dominance establishes a stronger trend toward continued dominance. This increases the severity of competition, but it also increases the potential for vegetation management treatments to effectively and permanently shift dominance to desired species.

In post-disturbance vegetation, the temporary flush of herbaceous invaders, exemplified here by bracken fern, will moderate interactions between long-term dominants. Compared to Douglas-fir seedlings, tanoak sprouts are much less affected by invading plants. Although most tanoak roots were found in the 0-60 cm layer, stump sprouts undoubtedly have some roots that go much deeper (field observations of road cuts, windthrow, and stump excavations by Newton, Ahrens, and others). The soil environment for small Douglas-fir seedlings is primarily in the 0-60 cm soil zone, generally well occupied by tanoak and bracken.

After soil moisture depletion in upper soil layers, water absorption by sparse roots deeper in the profile becomes important. The ability of plants to meet the majority of their absorption needs from a small portion of their root system exploiting favorable soil zones is well documented (Russell 1977, Kramer and Kozlowski 1979). Tanoak sprouts show relatively low plant moisture stress (predawn xylem pressure potential) during summer drought conditions (Harrington 1989).

With compensatory increases in bracken and others, resource availability does not depend solely on tanoak root and foliage density. However in the presence of the long-term dominant Douglas-fir, treatments that reduce tanoak will shift dominance in favor of Douglas-fir and bracken.
The extent and balance of this shift in dominance depends on the effectiveness of tanoak control and the ability of the Douglas-fir to exploit resources released under the influence of herbaceous vegetation. In the context of vegetation management, early establishment of large Douglas-fir seedlings will help shift the balance between bracken and Douglas-fir after tanoak control treatments.

During site occupancy expansion, LAI of woody plants may be expected to increase exponentially for free-growing populations of seedling-origin, while relative growth rate (RGR) in LAI remains constant. This type of growth was demonstrated for Douglas-fir growing with and without tanoak in the Siskyous (Harrington 1989). Initially, dominant tanoak sprouts show a constant leaf area increment (Figures 3 and 18) and a declining relative growth rate. After the initial decline, the relative growth rate of LAI seems to stabilize at a constant rate, behaving more like an expanding population of seedling-origin. Maximum tanoak site occupancy (represented by the pure stands in this study) occurs at a LAI of 9.4 which is comparable to values found in similar temperate broad-leaved evergreen forests (8.8 and 8.9) and in dry evergreen tropical forests (8.6) (Schulze 1983).

For tanoak stump sprouts, recovery of a lower, stable leaf area growth rate may indicate the exhaustion of the excess reserves from old stumps and roots. Sprout vigor has been shown to be a function of parent tree diameter (Harrington et al. 1984), presumably stemming from a relation between total productive capacity (current leaf area) and carbohydrate reserve capacity. The time at which sprouts first reach the lower, stable leaf RGR may represent the lowest current leaf area at which carbon reserve capacity from the parent trees is also exhausted. Minimum root density, stable leaf area index RGR, and the
overall recovery of root/shoot balance all coincide at age four. This point may be the time of minimum tanoak dominance potential in terms of belowground occupancy and aboveground growth potential. Manual or chemical tanoak control treatments may be most effective at this stage.

Figure 18. Relative growth rates (annual increase in LAI/previous year's LAI) for tanoak leaf area index in southwest Oregon.
Cutting, burning, and any subsequent conifer release treatments that kill or remove tanoak crowns (but not roots) will initiate a new root dieback root/shoot recovery cycle. Each successive crown removal starts the cycle at a new level of root density. Sprout vigor and leaf area development are reduced by successive slashing (Hobbs 1989 personal communication). The coincidence of root/shoot balance recovery, minimum root density, and stable shoot RGR suggests that further study of tanoak sprouts could be focused aboveground. Site specific assessment of the timing of minimum tanoak dominance potential below- and aboveground, may be facilitated by more extensive examination of aboveground sprout vigor as a function of successive disturbance, under a range of environmental conditions.
CONCLUSIONS

Tanoak stump sprouts do not maintain preexisting fine roots: net root dieback results from increased mortality and decreased new root growth. The strong correlation between elevated soil temperature and dead root proportions suggests that increased respiratory depletion of limited carbohydrate supplies is the major cause of root mortality. Root dieback was greatest (in both relative and absolute terms) for the finest root size class (<.25 mm), which emphasizes the importance of high resolution in studies of belowground systems.

The new sprout stand rapidly (within four years after burning) regains the functional root/shoot equilibrium found in uncut tanoak forests. This adjustment trend resulted from reduced root growth relative to shoot growth and increased root mortality during the first four years.

There is a pattern of increased root dieback in openings during the first 4 years of sprout development. In combination with the overall root dieback, this suggests that soil resource competition from residual tanoak roots will not entirely preclude the benefits of increased light for other species in openings between sprout clumps.

To meet conifer management objectives, top-kill methods of tanoak control may be most effective if applied when sprout stands have reached their minimum root occupancy (age four years in this study). The compensatory increase in other species (primarily bracken fern in this case) is very important, and crop tree dominance ratios at the time of tanoak control can be maximized by planting large transplant trees immediately after disturbance. Herbaceous weed control may also be necessary to ensure a
shift in dominance from tanoak to crop trees.

For a dominant stand of sprout regenerating tanoaks, cutting and burning is a perturbation which causes temporary changes in soil environment, root respiration and absorption rates, and root/shoot balance, along with a temporary increase of other plant species. The results of this study demonstrate a fairly rapid, interactive recovery from disturbance, with all of the above factors approaching levels characteristic of the previous tanoak forest within nine years. Tanoak forests appear to be an exceptionally stable, longlived vegetation type, with tanoak maintaining high levels of dominance throughout all stages of succession.
LITERATURE CITED


APPENDICES
APPENDIX 1
Stem maps
Stem map: site LRO
Stem map: site LRY
Stem map: site SO
Stem map: site SY
Stem map: site RY
APPENDIX 2

Prediction equations and conversion ratios.

a) Regression equations used for estimating biomass and leaf area of tanoak and madrone.

<table>
<thead>
<tr>
<th>Range in stem dia. (cm)</th>
<th>Equation</th>
<th>$R^2$</th>
<th>Sy.x</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TOAK</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.3-4.5</td>
<td>$(\ln)y = -1.720 + 2.24(\ln)x$</td>
<td>0.91</td>
<td>0.41</td>
<td>4</td>
</tr>
<tr>
<td>0.5-7.5</td>
<td>$(\ln)y = -1.941 + 1.87(\ln)x$</td>
<td>0.95</td>
<td>0.21</td>
<td>2</td>
</tr>
<tr>
<td><strong>MADRONE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5-5.5</td>
<td>$(\ln)y = -1.779 + 1.885(\ln)x$</td>
<td>0.93</td>
<td>0.30</td>
<td>4</td>
</tr>
<tr>
<td><strong>TANOAK</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.3-4.5</td>
<td>$y = -.007 + .128(x),$</td>
<td>0.98</td>
<td>0.06</td>
<td>1</td>
</tr>
<tr>
<td>0.5-7.5</td>
<td>$y = .042 + .100(x),$</td>
<td>0.97</td>
<td>0.22</td>
<td>2</td>
</tr>
<tr>
<td><strong>MADRONE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5-5.5</td>
<td>$y = -.108 + 0.117(x),$</td>
<td>0.97</td>
<td>0.13</td>
<td>1</td>
</tr>
<tr>
<td><strong>TANOAK</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.3-4.5</td>
<td>$(\ln)y = 4.41 + 2.234(\ln)x,$</td>
<td>0.97</td>
<td>0.19</td>
<td>4</td>
</tr>
<tr>
<td>0.5-7.5</td>
<td>$(\ln)y = 4.05 + 2.282(\ln)x,$</td>
<td>0.98</td>
<td>0.21</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>$x = \text{diameter breast high (cm)},$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5-52.0</td>
<td>$(\ln)y = 3.20 + 2.277(\ln)x,$</td>
<td>0.94</td>
<td>0.46</td>
<td>3</td>
</tr>
<tr>
<td>Range in stem dia.</td>
<td>Equation</td>
<td>$R^2$</td>
<td>$S_y.x$</td>
<td>Source</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------------------------------</td>
<td>-------</td>
<td>---------</td>
<td>--------</td>
</tr>
<tr>
<td><strong>MADRONE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.5-5.5</td>
<td>$(\ln)y = 3.854 + 2.335(\ln)x$</td>
<td>.98</td>
<td>.20</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>$x = $ diameter breast high (cm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5-52.0</td>
<td>$(\ln)y = 3.89 + 2.484(\ln)x$</td>
<td>.89</td>
<td>.73</td>
<td>3</td>
</tr>
<tr>
<td><strong>TANOAK</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.5-52.0</td>
<td>$y = 1/(1.7936 + .3031(x)^{.7239})$</td>
<td>.0013</td>
<td></td>
<td>3</td>
</tr>
</tbody>
</table>

$y =$ leaf wt. fraction of live crown biomass  
$x =$ stem diameter breast high

**MADRONE**

2.5-52.0  
$y = 1/(1.6013 + .1060(x)^{1.309})$  
$0.0045$  
$3$
APPENDIX 2 (cont)

b) Root surface area, length, and dry weight conversions.

<table>
<thead>
<tr>
<th>Root category</th>
<th>Conversion ratio</th>
<th>$S_X$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>surface area/dry weight cm$^2$/g</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>.25-1mm dia. old live roots</td>
<td>145.5</td>
<td>3.08</td>
<td>130</td>
</tr>
<tr>
<td>.25-1mm dia. new live roots</td>
<td>449.8</td>
<td>32.75</td>
<td>30</td>
</tr>
<tr>
<td>.25-1mm dia. dead roots</td>
<td>237.1</td>
<td>11.14</td>
<td>16</td>
</tr>
<tr>
<td>1-2mm dia. old live roots</td>
<td>69.6</td>
<td>1.25</td>
<td>124</td>
</tr>
<tr>
<td>1-2mm dia. new live roots</td>
<td>259.9</td>
<td>9.74</td>
<td>42</td>
</tr>
<tr>
<td>1-2mm dia. dead roots</td>
<td>111.3</td>
<td>4.83</td>
<td>19</td>
</tr>
</tbody>
</table>

length/dry weight (cm/g)
| <.25 mm dia. live+dead        | 7008.5           | 233.92| 11  |

surface area/length (cm$^2$/cm)
| <.25 mm dia. live+dead        | 0.03927          | -     | -   |

(assumed average root diameter = 0.125mm, midpoint of diameter class)

c) Specific leaf area

<table>
<thead>
<tr>
<th>Species</th>
<th>Specific leaf area</th>
<th>$S_X$</th>
<th>n</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(cm$^2$/g)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tanoak</td>
<td>57.8</td>
<td>0.65</td>
<td>75</td>
<td>1</td>
</tr>
<tr>
<td>Tanoak</td>
<td>64.9</td>
<td>0.92</td>
<td>30</td>
<td>2</td>
</tr>
<tr>
<td>Madrone</td>
<td>83.6</td>
<td>1.01</td>
<td>36</td>
<td>1</td>
</tr>
</tbody>
</table>

Sources: 1) Harrington et al. 1984, 2) This study 3) Snell and Little 1983 4) Harrington 1989
APPENDIX 3

Aboveground cover of herbs and shrubs.

<table>
<thead>
<tr>
<th>Species</th>
<th>Site: LRO</th>
<th>SO</th>
<th>SY</th>
<th>LRY</th>
<th>PWY</th>
<th>RY</th>
<th>LRY2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pteridium aquilinum</strong></td>
<td>0.8</td>
<td>0.4</td>
<td>-</td>
<td>14.8</td>
<td>12.2</td>
<td>26.9</td>
<td>5.8</td>
</tr>
<tr>
<td><strong>L.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Xerophyllum tenax</strong></td>
<td>0.4</td>
<td>1.7</td>
<td>0.3</td>
<td>-</td>
<td>0.6</td>
<td>0.8</td>
<td>-</td>
</tr>
<tr>
<td><em>(Pursh)</em> Nutt.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Berberis nervosa</strong></td>
<td></td>
<td>0.4</td>
<td>0.5</td>
<td>-</td>
<td>-</td>
<td>3.8</td>
<td>-</td>
</tr>
<tr>
<td><strong>Pursh</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Arctostaphylos patula</strong></td>
<td></td>
<td></td>
<td>1.2</td>
<td>0.7</td>
<td>0.9</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Greene</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Grasses</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Vaccinium ovatum</strong></td>
<td></td>
<td>-</td>
<td>0.6</td>
<td>2.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td><strong>Vicia spp.</strong></td>
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<td><em>(Torr.) Nicholson</em></td>
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