EARLY CHANGES IN COAST REDWOOD (SEQUOIA SEMPERVIRENS) UNDERSTORY VEGETATION FOLLOWING FOREST HARVEST DISTURBANCES

Roy Andrew Woodward

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Early Changes In Coast Redwood (*Sequoia sempervirens*) Understory Vegetation Following Forest Harvest Disturbances

By

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Abstract

Seven 70-90 yr old redwood stands partially harvested since 1971 were sampled for understory vegetation species composition, frequency, and cover. Tractor-logged stands harvested 10 yr ago the had >50% conifer basal area removed now have understory cover four times greater than an adjacent unlogged stand. Cable-logged stands show larger amounts of understory cover, almost 50% greater than adjacent tractor-logged parcels harvested at the same time. Individual understory species were ranked according to Prevalent Species Numbers, with Whipplea modesta and Polystichum munitum being the most important in cover and frequency.

An attempt to relate understory vegetation properties in these stands with stand environmental factors revealed some significant correlations.

Tractor-logged sites with abundant soil disturbance begin to resemble less disturbed cable-logged sites about 7 yr after the disturbance episode in species composition and cover, indicating that overstory canopy removal is the most significant factor associated with timber harvesting in these stands. Measurements of forest soil moisture, evaporation, light, and temperature indicate these factors are sensitive to the amount of overstory canopy cover and effect species composition of the understory. The pattern of understory reformation in these stands will, in great part, be determined by the frequency and intensity of future harvests.

Natural regeneration by seed and stump sprouts of important conifer species (coast redwood, Douglas fir, grand fir, hemlock) was also assessed. Selective removal of grand fir and hemlock overstory trees repressed seedling establishment of these species. Douglas fir readily established from seed, but showed a preference for bare mineral soil such as created by heavily disturbed tractor-logged areas and skid roads. Coast redwood sprout clumps formed on about 100% of the cut trees. Coast redwood seedling establishment was relatively poor and was positively correlated with bare mineral soil. Native herbaceous vegetation and swordfern were not detrimental to Douglas fir seedling growth and may actually improve the site environment for young conifers. Introduced herbaceous vegetation did hinder coast redwood seedling growth, when compared with open grown seedlings. Douglas fir seedlings grown in an area cleared of surrounding understory vegetation showed probable osmotic adjustment to drought stress.

Thesis Advisor

Understory Reformation Following Partial Timber Harvesting In Second-Growth Coast Redwood Forests

by

R. A. Woodward*

Abstract

Seven 70-90 yr old coast redwood stands partially harvested since 1971 were sampled for understory species composition, frequency, and cover. Tractor-logged stands harvested 10 yr ago that had >50% of their conifer basal area removed now have understory cover four times greater than an adjacent unlogged stand. Cable-logged stands show even larger amounts of understory cover, almost 50% greater than adjacent tractor-logged parcels harvested at the same time. Individual understory species were ranked according to Prevalent Species Numbers, with Whipplea modesta and Polystichum munitum being the most important in cover and frequency.

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Introduction

Coast redwood (Sequoia sempervirens*) occupies some 647,000 ha near the Pacific Ocean of northern California and southern Oregon. The type is considered climax (Jacobs and McBride 1977, Veirs 1972), with pristine stands commonly containing magnificent trees over 91 m tall and 5.5 m diameter.

Coast redwood is a fast growing species excellent for lumber and specialized wood products. Harvesting has occurred for over 100 yr, and today fewer than 100,000 ha, mostly in parks, remain unlogged. The disappearance of the old-growth forest and the continued demand for redwood products in the past 25 yr have resulted in increased useage of second-growth stands.

Second-growth redwood stands currently being harvested are typically 70-90 yr old and have resulted from natural regeneration (sprouts and seedlings for redwood, seedlings for other conifer species) following intentional slash fires after the original clearcut harvests. These stands can be classified into two broad categories: those in river bottoms on alluvial flats, and those on upland sites (Becking 1967, Jacobs and McBride 1977, Stone and Vasey 1968).

The problem of how best to manage these second-growth stands was anticipated by researchers such as Fritz (1959), but controversy continues. Proponents of an uneven-aged (partial) management scheme state that clearcutting has no natural analogy, including fire (Fritz 1931, Simmons and Vale 1975, Veirs and Lennox 1981). Partial harvests have been touted as producing the greatest timber volume growth and as being the most satisfactory for multiple use of the forest (Twight 1973). The present study is confined to partial harvest stands.

The objectives of this study were to identify and describe, according to percent cover and frequency, the understory species that occupy recently harvested coast redwood stands. It was expected that changes in the flora due to intensity of harvest disturbance (as measured by percent of prelogging basal area of conifers removed and type of log removal system used), and amount of time that has elasped since the harvest took place would be found. The unknown effect of understory vegetation on small conifers (Cleary 1978) and the potential to use natural vegetation for erosion control (Reed and Hektner 1981), wildlife habitat, and watershed rehabilitation were additional factors of interest. Several excellent descriptions of coast redwood understory have previously been presented by Jacobs and McBride (1977), Lenihan et al. (1982), Muldavin et al. (1981), and Waring and Major

(1964). Unfortunately, these works have largely been confined to pristine forests, or stands recently clearcut and burned whereas this work is concerned with partially-cut second-growth stands.

The process of clearcutting in the coast redwood type and how such disturbed stands can be managed has concerned many authors (Boe 1970, Lenihan et al. 1982, Reed and Hektner 1981, Simmons and Vale 1975, Veirs and Lennox 1981). Some landowners, for various reasons, will insist upon partial harvests of their timber. Thus, it is important to understand the effects of the type of harvesting on forest understory and how these might best be manipulated.

Study Sites

The study sites are located in Mendocino County, California on Jackson Demonstration State Forest, a 20,000 ha experimental forest managed by the California Department of Forestry. Seven stands that had been harvested sequentially over the past 10 yr, plus one unlogged control stand, were sampled. These sites are 6-10 km inland from the Pacific ocean, with an average elevation of 150 m.

Precipitation averages 100 cm a year, falling almost exclusively as rain during the winter months of November to April. Coastal fog contributes a significant amount of moisture during the dry summer months (Azevedo and Morgan 1974). The climate falls well within Becking's (1967) Northern Coastal Maritime Redwood Zone, and more detailed climatic data for this area can be found in his work. In Koeppen's more widely known system, the climatic type is 'Csb', a middle latitude rainy climate with mild winters and dry but cool summers (Trewartha and Horn 1980). Soils are locally variable (Gardner 1960), but typically are very productive deep, sandy-loam ultisols or alfisols.

The pristine forest here was dominated by coast redwood, with some Douglas fir (Pseudotsuga menziesii), western hemlock (Tsuga heterophylla), grand fir (Abies grandis), and an occasional Bishop pine (Pinus muricata). The relative importance of these species changes over the range of coast redwood, depending on site, latitude, and elevation (Lennox et al. 1981). These stands were clearcut and logged with primitive equipment before the turn of the century, then burned shortly after harvest, clearing them of understory. Occasional old growth trees that had not been logged, remained as a secondary forest grew up. The secondary stands contained a minor hardwood component, tan oak (Lithocarpus densiflora). Prior to a second harvest, approximately 10 yr ago, these stands contained about 82

m^2 ha^{-1} of conifer basal area. This qualifies them as good, unmanaged Site II redwood type stands (Lindquist and Palley 1963).

Because of the proximity of these stands to the coast and their occurrence on slopes, some species commonly associated with the redwood type as a whole are conspicuously lacking in this study. Red alder (Alnus rubra), salmon berry (Rubus spectabilis), elderberry (Sambucus coerulea), and California bay (Umbellularia californica) are mostly confined to streambanks. Madrone (Arbutus menziesii) and giant chinquapin (Castanopsis chrysophylla) are also well-known redwood associates elsewhere, but they are less common in these second-growth stands.

Second-growth stands were harvested in the last several decades by two methods. Upper slopes were generally logged with rubber-wheeled or crawler tractors. This method requires considerable road building and creates further soil disturbance from tractors pulling logs through the forest to central landings for transport to the mill. Steeper lower slopes were usually logged with a cable system, utilizing a yarder with a running skyline. The cable permits logs to be lifted and brought to a central landing with a minimum of ground disturbance.

Seven stands which had been harvested sequentially in the past 10 yr were selected for sampling. Three of the stands were tractor-logged, three stands were tractor-logged in part and cable-logged in part, and one stand was cable-logged only. The stands are located in two adjacent drainages, three on Caspar Creek and four on Hare Creek (Figure 1). An unlogged control stand is situated between two logged portions along the North Fork of Caspar Creek. The stands have diverse topography, but are generally on north-facing slopes of 0-35°. Very little of the area is level, as all sites were upland and alluvial stands were not included.

The intensities of harvest over the past 10 yr for the seven stands varied considerably (Table 1). Earlier harvests were somewhat experimental, and higher volumes of timber were removed. In general, part of the management objective was to achieve greater redwood stocking, so Douglas fir was marked for cutting with a greater intensity than redwood. All other conifer species of merchantible size (>25 cm diameter breast height) were to be completely removed, if possible, without creating large gaps in the forest canopy. Since harvest these stands have not been further disturbed. Most roads in tractor-logged areas were closed and sealed immediately after completion of the harvest, to lessen soil erosion. No planting of conifers or of other species has occurred, nor has there been any herbicide of fertilizer application.

Methods

The stands were sampled in the 1982-1983. A random starting point was selected along the perimeter of each stand and a random direction for a transect into the area determined. A random number of paces (not to exceed 100) were then taken in the chosen direction to situate the first quadrat, a 16m^2 circle. About 30 subsequent quadrats were placed a random number (from 0 to 100) of paces apart along the original direction line until: 1) the edge of the harvest area was encountered, and the transect partial process began again; or 2) a maximum of six quadrats were sampled per direction, and a new direction was chosen. In this way any part of the entire harvest area could be included in the sampling. About 50 quadrats were placed in the unlogged control stand. More quadrats were used in the unlogged stand because of its greater area. Quadrats were resituated if they fell on former major access roads or places that had obviously been disturbed since the harvest.

All vascular plants growing on or over each quadrat were identified. Ocular estimates of percent ground cover were made, by species, to the nearest percent for plants occurring on or over the quadrat to a height of 1.8 m. Parts of plants over 1.8 m tall were counted as overstory canopy cover.

Frequency of species was calculated from the number of quadrats of occurence. Sampling took place from early spring through autumn.

During data analysis, species were grouped into shrub, fern, forb, grass, hardwood tree, vine, and conifer tree life form categories. Certain arbitrary decisions were made. Tan oak was always counted as a tree no matter how large it was. Wax myrtle (Myrica californica), which sometimes attains tree stature, was always counted as a shrub. Horsetail (Equisetum telmateia) was included with the forbs, but all herbaceous ferns were classed as ferns. Whipplea modesta was counted as a forb and not a vine, and salal (Gaultheria shallon) was considered a shrub. Sedges (Carex spp.) were lumped with forbs.

The species encountered on all harvests were assigned a Prevalent Species Number (Curtis 1959), calculated as (frequency) X (presence). Presence is the percent of all stands in which a species occurred, and frequency is the average frequency in 16 m^2 plots for all stands in which a species occurred. The Numbers are then normalized or relativized to a scale from 0 (no occurence) to 10 (present in every stand and every quadrat). Species with a Prevalent Species Number greater than 1 (and all shrub species encountered) are shown in Table 2.

Results and Discussion

A total of 58 species were encountered in the quadrats (Appendix A). Only about 5% of those were annuals. The total number of species encountered (conifers excluded) in a harvested stand varied from 16 in the 1977 cable-logged area to 28 in the 1973 tractor-logged stand. The unlogged control stand had 15 species. No obvious correlation exists between the intensity, type, or timing of harvesting and the total number of species found in a stand.

Earlier work in unharvested stands divided the coast redwood understory into two alliances: Redwood-Oxalis on mesic sites and Redwood-Swordfern on more xeric sites (Becking 1967, Lennox et al. 1981). The post-harvest sites, contained elements of both types. Timber harvesting increased the amount of sunlight reaching the forest floor, but because the stands are so near the ocean summer temperatures do not reach levels that would favor more xeric species. A few miles inland from these stands a better distinction can be made between the two types.

Other species associations have been reported following clearcutting of old growth in Redwood National Park. Muldavin et al. (1981) described residual species groups consisting of Polystichum/Oxalis, Lithocarpus/

Whipplea, Rhododendron/ Gaultheria, and Rhododendron/ Vaccinium ovatum.

An analysis of similarity of understory species was performed for all of the stands using Sorensen's Similarity Index (Mueller-Dombois and Ellenberg 1974). This scale ranges from SI=0 (complete dissimilarity) to SI=100 (complete overlap). The harvested stands averaged 75 SI among themselves, and they averaged 70 SI with the unlogged control stand. The high similarity between the logged and unlogged stands occurs because every species of the unlogged stand was also present in each harvest area. It is interesting that no matter what intensity of harvesting was performed, no species was completly removed from the forest. Other researchers have also found that pre-logging species in the coast redwood forest endure disturbance quite well and show a great amount of resilience (Fritz 1931).

The ten species with the highest Prevalent Species Numbers (Table 2) were used to assess the understory response to certain disturbance conditions. By this method, those species most likely to be encountered in any given stand are particularly considered. These species represent a mix of forbs, grasses, shrubs, and hardwoods. The greatest cover by the ten species on any one plot is Whipplea 85%, Viola 6%, Polystichum 80%, Oxalis 90%, Galium 7%, Hierochloe 40%, Lithocarpus 100%, Vaccinium ovatum

40%, Erechtites 40%, and Gaultheria 65%. Whipplea, though relatively rare in unlogged stands, has become the most common herb on the harvested sites. It is suspected that Whipplea arises from buried seed (Reed and Hektner 1982). This herb forms low growing mats and is considered valuable for erosion control in the area (Popenoe et al. 1982).

Viola, Oxalis, Galium, and the grass Hiercholoe are common but not major cover contributors. Polystichum is common in unharvested stands and is a major source of cover along with Vaccinium ovatum and Lithocarpus. Gaultheria is occasionally a significant cover contributor on logged and unlogged stands. Erechtites is strictly an exotic invader in the redwood type.

Table 3 presents the case of 3 tractor-logged areas harvested at different intensities but in nearly similar years. These harvests demonstrate the effect of harvest intensity on the ten understory species considered. Three species, Whipplea, Vaccinium, and Gaultheria all show an increase, while Oxalis shows a decrease, following disturbance. Other species appear to show mixed responses most attributable to intensity of harvest, with length of time since harvest a lesser factor.

These early partial harvests tended to have substantial volumes of timber removed. Such extensive overstory removals favored species such as Lithocarpus, an unfavorable result when conifer regeneration and growth is desired. Polystichum, on the other hand, decreased in cover with greater harvest intensities.

Table 4 examines the overall cover contributions for the different plant life forms. The life forms show no clear trends over time but seem to have responded to the intensity of disturbance. The total understory cover is essentially the same for all three harvests, and 70% cover is the maximum ground cover in these stands, no matter what the overstory canopy cover. One would expect to see a decline in cover as these stands progress to cover values like those present in the unlogged control stand. The "Other" category (Table 4) consists of the combined cover by vines and conifers. Conifer regeneration in these stands will not be considered in this paper. Fern species exhibited a marked decline in cover at the greater harvest intensity, and even now are below cover in the unlogged control.

Data from three harvests of similar intensity but of different years are presented in Table 5. These stands were cable-logged. All of the species except Erechtites showed an increase in cover over time, and all have exceeded the unlogged control. Whipplea demonstrated the greatest percentage increase. Polystichum is the only increaser species that has stabilized, while all of the others continue to expand.

Total cover in the oldest cable-logged stand is 81%, 10% higher than any tractor-logged stand (Table 6). This is probably the maximum ground cover value attainable for these stands, because the fern component has (apparently) reached a maximum and much of the hardwood cover will soon exceed 1.8 m in height, and pass out of the "ground cover" stratum as defined in this study. Forb and shrub cover have continued to increase with time, largely due to increases in the perennial species Whipplea, Oxalis, and Vaccinium. Note that grass cover never accounts for >5% relative cover in any stand. Some clearcut areas were maintained as pasture in the early days by frequent burning. These data suggest that most openings will quickly return to a forested type if left unmanaged.

Fireweed (Erechtites prenanthoides), an annual (sometimes perennial) forb, and blue blossom (Ceanothus thrysiflorus), an evergreen shrub, have been observed to invade clearcuts in this area and are suspected of excluding other more desirable perennial species that are useful for erosion control and less competitive with small conifers. The contribution to understory cover by invading species (those not occurring in the unlogged stand: manzanita (Arctostaphylos columbiana var. tracyi), thimbleberry (Rubus parviflorus), red huckleberry (Vaccinium parvifolium), coyote brush (Baccharis pilularis ssp. consanquinea), blue blossom, and fireweed) are presented in Table 7. Blue blossom has been noted to form dense thickets over 3 m tall that may persist for 20 yr. Table 7 shows that blue blossom is increasing to a small extent on the heavily tractor-logged older stands, though no dense thicket has formed. The species was usually restircted to larger canopy openings adjacent to old roads and landings. Total cover by all invader species is somewhat dependant on the degree of disturbance, but no clear statistical trend exists. Baccharis was very rare and never an important cover contributor. Fireweed was not an important component in the understory vegetation in any of these stands.

In cable-logged stands of similar logging intensity, blue blossom was of little importance (Table 8). Perhaps the species needs considerable light and soil disturbance to establish, factors not in its favor in these moderately harvested cable-logged sites. Total shrub cover has increased with length of time since harvesting. The contribution by invader species to total shrub cover has increased from 2% in the 1978 harvest to over 50% in the 1974 harvest. How long these invaders will persist remains to be seen. Fireweed is an early invader of cable-logged stands, but never accounted for much of the total cover present and it was quickly replaced by other species (mostly perennials).

Other authors have found that residual species present before timber harvesting regain dominance of a site within a few years of disturbance

(Dyrness 1965, 1973). Tables 7 and 8 do not show this phenomenon to occur for shrub species in our partially logged stands. Clearcut stands in the coast redwood type elsewhere have exhibited a herb/bursh phase dominated by invaders as well as residual species lasting up to 25 yr (Muldavin et al. 1981).

A comparison between cable and tractor-logged portions of the same stands is given in Table 9. Two separate years and harvesting intensities are shown. In every case, cable-logged portions have greater total understory cover than tractor-logged portions. The increase in sunlight to the forest floor following overstory removal is similar for the cable and tractor-logged portions, so differences in ground cover was not due to differences in overstory cover. Tractor-logging has two major effects on understory that cable systems do not: a greater amount of slow-to-recover perennial species (shrubs and ferns) are removed by tractor-logging and there is a greater disturbance to the soil seedbank and duff layer.

The cable-logged stand that experienced the earlier harvest (1974) showed greater cover in all life forms, except forbs, than tractor-logged stands. Forbs such as Whipplea may have more physical room to expand in tractor-logged areas as time passes, because cover by shrub and fern components is low.

Conclusion

Total percent cover values can be significant for a harvest area, but most of this cover is usually <1 m tall. Tractor-logged areas appear to have a peak understory cover of about 70% with cable-logged areas attaining values over 80%. The costs or benefits that this understory provides young conifer trees have yet to be determined.

Understory relative cover changes from stand to stand as a function of time since harvesting and of harvest intensity. Some species such as Whipplea modesta show an increase in cover with both intensity of harvest and time since harvest, and so would be most valuable for erosion control projects. Other species, such as Polystichum munitum, exhibit an increase in cover over time, but quickly reach an apparent maximum that is maintained for an undetermined length of time. All of the species present before harvest were also present after harvest and most increased in cover over time.

Overall, these stands reveal the effect of partial timber harvesting on coast redwood understory. The immediate disturbance is important in determining plant distribution for the first few years. The ultimate understory community organization will be determined by a multitude of factors. Further monitoring of experimental stands such as these will provide valuable information about secondary succession in the coast redwood type.

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Table 1. Stand characteristics from seven partially harvested coastal redwood stands and one unlogged control stand. Stands are identified by year of harvest. Type of log removal (T = tractor, C = cable) is also indicated.

Year Harvested	1971	1972	1973	1974	1976	1977	1978	UNLOGGED
Total ha	100	128	176	161	140	147	60	486
Volume Cut (m^3 ha^{-1})	241	251	193	213	230	164	218	0
% Basal Area Cut	59.2	68.6	64.5	40.3	43.5	31.1	41.3	0
Species Composition of Conifers Harvested (in % of volume removed)								
Redwood	50	53	70	28	44	40	40	68†
Douglas fir	33	39	29	52	46	40	41	25†
Others	17	8	1	20	10	20	19	7†
Log Removal Method	T	T	T	T&C	T&C	T&C	C	None

† Present species composition of the unlogged stand.

Table 2. Coast redwood forest understory species present following selective timber harvesting are reanked according to Prevalent Species Number (see text for details). Growth form (GF) abbreviations: 'f' denotes a forb, 's' a shrub, 'g' a grass, 'fe' a fern, 'h' a hardwood, and 'v' a vine. See Appendix A for common names. All shrub species are shown, but only the most common species of all other growth forms are listed.

		PREVALENT SPECIES NUMBER	
SPECIES	GF	ALL HARVESTS	UNLOGGED
Whipplea modesta	f	6.7	0.6
Viola sempervirens	f	6.2	1.0
Polystichum munitum	fe	4.5	5.9
Oxalis oregana	f	3.2	3.7
Galium spp.	f	3.1	0.6
Hierocholoe occidentalis	g	3.1	0.2
Lithocarpus densiflora	h	3.1	3.5
Vaccinium ovatum	s	2.8	1.2
Erechtites prenanthoides	f	2.3	---
Gaultheria shallon	s	1.4	0.2
Stachys bullata	f	1.2	---
Rubus ursinus	v	1.2	---
Arctostaphylos columbiana	s	1.0	---
Iris douglasiana	f	1.0	---
Rhododendron macrophyllum	s	0.9	---
Ceanothus thyrsiflorus	s	0.9	---
Rubus leucodermis	s	0.5	---
Myrica californica	s	0.5	---
Rubus parviflora	s	0.4	---
Vaccinium parvifolium	s	0.4	---
Berberis nervosa	s	0.2	---
Baccharis pilularis	s	0.1	---

Table 3. The percent cover of ten major (according to Prevalent Species Number) coast redwood forest understory species following partial timber harvesting. Growth form categories, after the slashes, are those defined in Table 2. Data are from three tractor-logged stands harvested at different intensities but in nearly similar years. An adjacent unlogged stand is shown for comparison.

	1971	1972	1973	UNLOGGED
Whipplea modesta/f	17.2	16.5	14.8	0.04
Viola sempervirens/f	0.7	0.3	0.7	0.04
Polystichum munitum/fe	9.2	6.0	8.7	9.3
Oxalis oregana/f	0.3	0.5	1.2	0.5
Galium spp./f	0.1	0.1	0.2	0.1
Hierochloe occidentalis/g	5.1	3.3	3.8	0.2
Lithocarpus densiflora/h	2.9	13.4	8.4	3.9
Vaccinium ovatum/s	3.0	3.0	0.5	1.2
Erechtites prenanthoides/f	0.4	0.2	0.7	None
Gaultheria shallon/s	4.7	3.2	1.1	0.02

Table 4. Understory percent cover (relative cover in parenthesis) by plant group for three coastal redwood stands partially harvested by tractor. The stands had different amounts of conifer basal area removed, but were harvested in nearly similar years. An adjacent unlogged area is shown for comparison. Means with like alphabetic coefficients are not statistically different (P<0.05).

	STANDS			
	1971	1972	1973	UNLOGGED
Hardwood	2.9 (4.1) a	13.9 (20.1)	8.5 (12.2)	3.8 (23.3) a
Grass	4.9 (6.9) b	3.3 (4.8) b	4.2 (6.1) b	0.2 (1.2)
Forb	18.9 (26.8) c	16.7 (24.1) c	1.1 (26.1) c	1.2 (7.4)
Fern	10.2 (14.4) d	6.6 (9.5)	11.1 (16.0) d	9.1 (55.9) d
Shrub	16.7 (23.7) e	17.1 (24.7) e	9.7 (14.0)	1.0 (6.1)
Other	17.1 (24.1) f	11.6 (16.8) f	17.8 (25.6) f	1.0 (6.1)
TOTAL	70.6 g	69.2 g	69.4 g	16.3

Table 5. The percent cover of ten major (according to Prevalent Species Number) coast redwood forest understory species following selective timber harvesting. Growth form categories (after the slash) are those defined in Table 2. Data are from three stands harvested at near similar intensities but in different years. All stands were cable-logged. An adjacent unlogged stand is shown for camparison.

	1974	1976	1978	UNLOGGED
Whipplea modesta/f	11.3	7.3	0.7	0.04
Viola sempervirens/f	1.2	0.2	0.2	0.04
Polystichum munitum/fe	20.9	20.7	14.0	9.3
Oxalis oregana/f	6.7	2.1	1.8	0.5
Galium spp./f	0.5	0.2	1.0	0.1
Hierochloe occidentalis/g	4.3	0.7	0.1	0.2
Lithocarpus densiflora/h	11.8	5.2	2.4	3.9
Vaccinium ovatum/s	5.8	3.5	1.2	1.2
Erechtites prenanthoides/f	0.1	0.4	1.7	None
Gaultheria shallon/s	2.2	0.1	0.1	0.02

Table 6. Understory percent cover (relative cover) by plant group for three cable-logged, selectively-harvested coast redwood stands. The stands had similar amounts of basal area removed, but were harvested in different years. An adjacent unlogged area is shown for comparison. Means with like alphabetic coefficients are not statistically different (P<0.05).

	1971	1972	1973	UNLOGGED
Hardwood	11.9 (14.7)	5.2 (11.0) a	2.5 (8.7) b	3.8 (23.3) ab
Grass	4.6 (5.7)	1.4 (3.0)	0.5 (1.7) c	0.2 (1.2) c
Forb	21.0 (25.9)	12.9 (27.2)	5.1 (17.8)	1.2 (7.4)
Fern	23.5 (29.0) d	21.8 (46.0) d	13.9 (48.4) e	9.1 (55.9) d
Shrub	18.7 (23.1)	5.1 (10.8)	2.2 (7.7)	1.0 (6.1)
Other	1.4 (1.7) f	1.0 (2.0) f	4.5 (15.7) f	1.0 (6.1)
TOTAL	81.1	47.4	28.7	16.3

Table 7. Contribution to shrub and forb cover from 'invader' species, i.e. those not present in the unlogged control stand. Data are from three stands of coast redwood, harvested partially by tractor at three different intensities in three nearly similar years. One species of shrub (blue blossom, *Ceanothus thrysiflorus*), and one forb (fireweed, *Erechtites prenanthoides*) are included separately.

	1971	1972	1973
All Species (% cover)	70.6	69.2	69.4
SHRUBS			
Total Number of Species	7	8	7
All Shrub Species (% cover)	16.7	17.1	9.7
All Shrub Invaders (% cover)	6.1	9.6	2.8
Blue Blossom (% cover)	5.4	2.5	2.7
Relative Cover by Invaders	36.2	56.2	28.4
Relative Cover by Blue blossom	32.3	14.6	27.8
FORBS			
All Species (% cover)	18.9	16.7	18.1
Fireweed (% cover)	0.4	0.2	0.6
Relative Cover by Fireweed	2.1	1.2	3.3

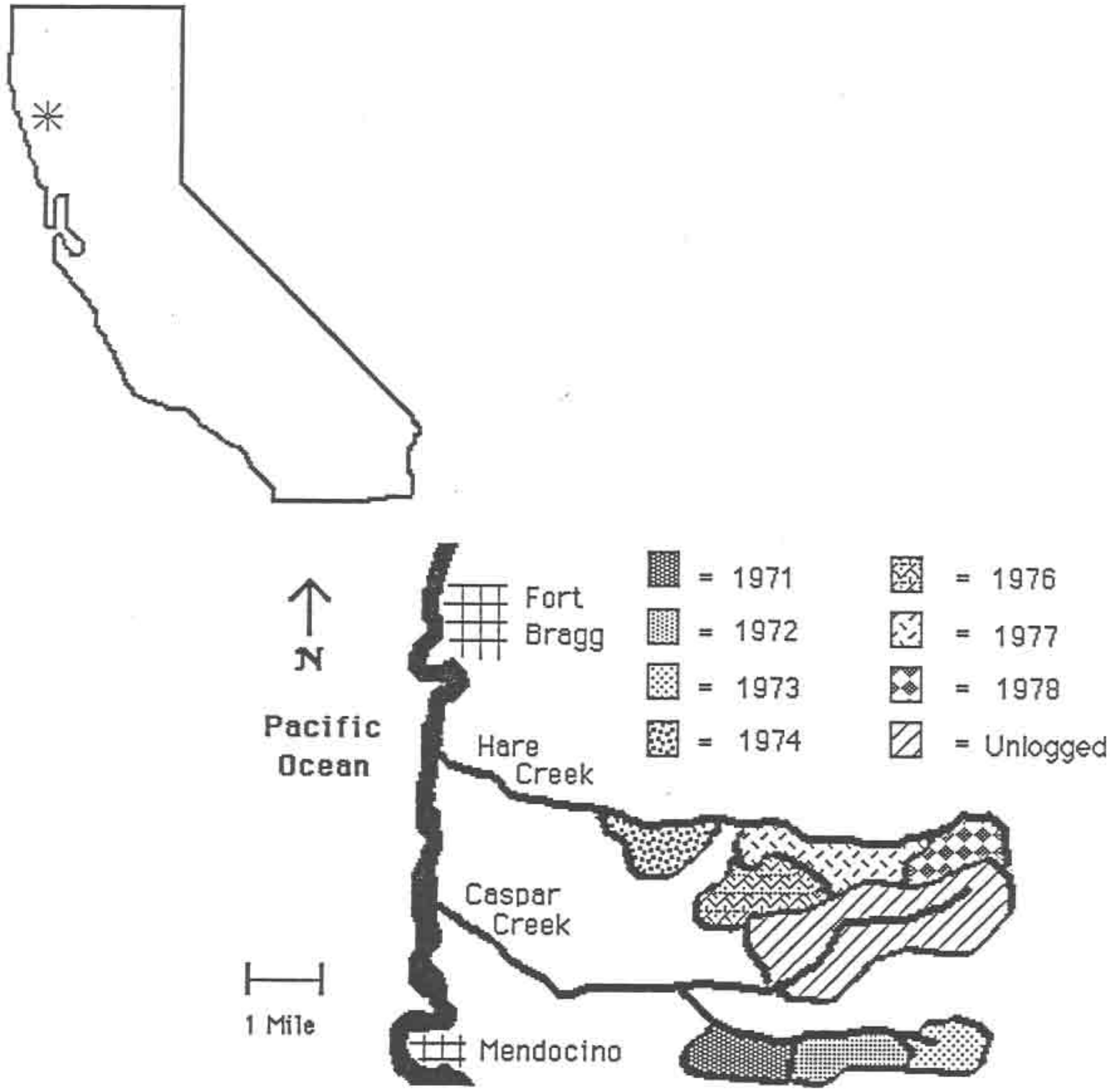
Table 8. Contribution to shrub and forb cover from 'invader' species. Data are from three stands of coast redwood, harvested partially by cable at three different intensities in three different years. One species of shrub (blue blossom, <u>Ceanothus thrysiflorus</u>), and one forb (fireweed, <u>Erechtites prenanthoides</u>) are included separately.

	1974	1976	1978
All Species (% cover)	81.1	47.4	28.7
SHRUBS			
Total Number of Species	8	6	5
All Shrub Species (% cover)	18.7	5.1	2.2
All Shrub Invaders (% cover)	9.6	1.4	0.04
Blue Blossom (% cover)	0	0.6	0
Relative Cover by Invaders	51.0	26.9	2.0
Relative Cover by Blue blossom	0	11.8	0
FORBS			
All Species (% cover)	21.0	12.9	5.1
Fireweed (% cover)	0.1	0.4	1.7
Relative Cover by Fireweed	0.3	3.1	32.9

Table 9. Comparison of percent understory cover (and relative cover) in two second-growth coastal redwood stands partially logged using two methods, tractor and cable. Means significantly different (P<0.05) are indicated with an *.

	1974 HARVEST (40.3% Basal Area Cut)			1977 HARVEST (31.1% Basal Area Cut)		
	CABLE		TRACTOR	CABLE		TRACTOR
Hardwood	11.9 (14.7)	*	1.0 (1.8)	4.7 (10.1)		5.6 (21.1)
Grass	4.6 (5.7)	*	0.8 (1.4)	1.0 (2.2)		3.3 (12.5)
Forb	21.0 (25.9)	*	31.9 (57.1)	26.1 (56.1)	*	7.5 (28.3)
Fern	23.5 (29.0)	*	7.7 (13.8)	6.3 (13.5)		5.0 (18.9)
Shrub	18.7 (23.1)	*	8.9 (15.9)	4.0 (8.6)		3.0 (11.3)
Other	1.4 (1.7)		5.6 (10.0)	4.4 (9.5)		2.1 (7.9)
TOTAL	81.1	*	55.9	46.5	*	26.5

Figure 1. Locations of seven coast redwood stands on Jackson Demonstration State Forest in Mendocino County, California. Dates indicate the year each site was partially harvested.



Fort
Bragg
N
Pacific
Ocean
Hare
Creek
Caspar
Creek
1 Mile
Mendocino
= 1971
= 1972
= 1973
= 1974
= 1976
= 1977
= 1978
= Unlogged

Appendix A. Species encountered on sampling plots in second-growth coast redwood following selective timber harvesting. For a more complete list of understory species collected (infrequent species) contact the author.

GRASSES

Bromus spp.	Brome grass
Cortaderia selloana	Pampas grass
Festuca spp.	Fescue
Hierochloe occidentalis	Vanilla grass
Poa spp.	Blue grass

CONIFERS

Abies grandis	Grand fir
Pseudotsuga menziesii	Douglas fir
Sequoia sempervirens	Coast redwood
Tsuga heterophylla	Hemlock

HARDWOODS

Lithocarpus densiflora	Tan oak

FERNS

Adiantum pedatum var. aleuticum	Five finger fern
Blechnum spicant	Deer fern
Dryopteris arguta	Coastal wood fern
Pityrogramma triangularis	Golden back fern
Polypodium scouleri	Leather leaf fern
Polystichum munitum	Swordfern
Pteridium aquilinum	Bracken fern

SHRUBS

Arctostaphylos columbiana var. tracyi	Manzanita
Baccharis pilularis ssp. consanguinea	Coyote brush
Berberis nervosa	Oregon grape
Ceanothus thyrsiflorus	Blue blossom
Gaultheria shallon	Salal
Myrica californica	Wax myrtle
Rhododendron macrophyllum	Rhododendron

Rubus leucodermis	Raspberry
Rubus parviflorus	Thimbleberry
Vaccinium ovatum	Blue huckleberry
Vaccinium parvifolium	Red huckleberry

VINES

Lonicera hispidula var. vacillans	Honeysuckle
Rubus ursinus	Blackberry

FORBS

Anaphilis margaritacea	Pearly everlasting
Asarum caudatum	Wild ginger
Carex spp.	Sedge
Circium vulgare	Bull thistle
Corallorhiza maculata	Spotted coral root
Cynoglossum grande	Western hound's tongue
Dentaria californica	Toothwort
Dicentra formos	Bleeding heart
Disporum smithii	Fairy bells
Epilobium adenocaulon	Northern willow herb
Equisetum telmateia	Horsetail
Erechtites prenanthoides	Fireweed
Fragaria caliornica	Strawberry
Galium spp.	Bedstraw
Iris douglasiana	Iris
Juncus spp.	Rush
Montia sibirica	Miner's lettuce
Oxalis oregana	Redwood sorrel
Smilacina racemosa var. amplexicaulis	Fat solomon's seal
Stachys bullata	Hedgenettle
Taraxacum officniale	Dandelion
Tiarella unifoliata	Sugar scoop
Trientalis latifolia	Pacific starflower
Trillium ovatum	Trillium
Vancouveria planipetala	Evergreen vancouveria
Vicia angustifolia	Vetch
Viola sempervirens	Redwood violet
Whipplea modesta	Yerba de Selva

Overstory Removal Effects on Understory Vegetation In the Coast Redwood Forest

by

Roy A. Woodward*

Abstract

An attempt to relate understory vegetation properties in partially harvested second-growth coast redwood stands with stand environmental factors revealed some significant correlations. Tractor-logged sites with abundant soil disturbance begin to resemble less disturbed cable-logged sites about 7 yr after the disturbance episode in species composition and cover, indicating that overstory canopy removal is the most significant factor associated with timber harvesting in these stands. Measurements of forest floor soil moisture, evaporation, light, and temperature indicate these factors are very sensitive to the amount of overstory canopy cover and effect species composition of the understory. The pattern of understory reformation in these stands will, in great part, be determined by the frequency and intensity of future harvests.

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Introduction

Harvesting of second-growth coast redwood (Sequoia sempervirens) (Plant nomenclature follows Munz and Keck (1968)) has taken place at an increasing rate for the past 20 yr, as pristine forests have become less available. The demand for redwood products has been great and will remain so in the future. Over 243,000 ha, 40% of the total coast redwood forest, are considered commercial timber lands and most will be harvested in the next 100 yrs.

Much thought and discussion has occurred on how to manage these second-growth stands (Fritz 1959, Twight 1973, Simmons and Vale 1975, and others). Most consideration has been given to maximizing timber yield at the time of harvest. The harvesting frequency in second-growth stands depends on the system of management. Stands managed on an even-aged scheme (clearcut) would be cut every 60-80 yr. Uneven-aged management (partial) would require reentry as often as every 15 yr, but having only a portion of the overstory trees would be removed.

Clearcutting even-aged stands is considered by most of the large corporate landowners to produce more merchantable timber and be more economically feasible than other practices. Clearcutting has significant effects on forest understory species, via widespread soil disturbance, increased solar radiation, and altered conditions for fog-drip and precipitation throughfall following overstory tree removal (Ahlstrom 1968, Dyrness 1965 and1973, Anderson et al. 1969, Minore et al. 1982). Rehabilitating clearcut lands in certain areas such as Redwood National Park has been of special concern (Veirs and Lennox 1981, Muldavin et al. 1981).

Partial (or intermediate) harvesting has a less pronounced but still significant effect on understory vegetation than clearcutting. Because uneven-aged stands will be logged every 10-20 yr, a disclimax or continually disturbed situation will be maintained on the forest floor. The consequences of disturbance, and in this case timber harvesting, to understory vegetation are complex. Major and Waring (1964) studied gradients of soil nutrients, soil moisture, temperature, and light on the forest floor in coast redwood and found a wide variety of responses by individual species to these factors.

The effects of logging on the forest soil are potentially numerous. Durgin (1980) reported that clearcutting in coast redwood-fir forests had a minor impact on soil organic matter which influences the physical and chemical properties of the soil. Sugihara and Cromack (1981) and Sugihara (1982) examined the role of nitrogen-fixing microorganisms in undisturbed forest systems and stated their importance in the reestablishment of disturbed vegetation. The redwood stands considered in the present study have few leguminous species, and known nitrogen-fixing plants such as red alder (Alnus oregana) and blue blossom (Ceanothus thrysiflorus) are relatively uncommon. Fertilizer and mulching treatments have been shown to increase species diversity and cover on naturally recovering clearcut redwood sites (Reed and Hektner 1982). Logging also changes the nutrient cycling pattern of the forest soil. Following harvesting nutrients are no longer returned to the soil from decaying foliage in a continuous process but a large flush occurs followed by a slower release that may be at a higher level than previously sustained. Repeated harvesting could lead to soil nutrient fluxs that favor exotic assemblages of understory species.

Slope and aspect had little effect on temperature and humidity in clearcut old-growth redwood on west and east facing slopes (Boe 1970), but was of major importance to regeneration of conifers in all of the partially cut stands studied by Graham et al. (1982) in Southwest Oregon (not coast redwood stands). The effect of overstory tree removal on the amount of fog drip reaching the forest floor is not well documented, but Azevedo and Morgan (1974) argued that this precipitation is of major importance in determining species composition and cover in redwood forest understories.

Anderson et al. (1969) stated that for pine forests in Wisconsin canopy openings influenced the amount of precipitation throughfall and thus soil moisture. They thought this effect of canopy removal more important than the canopy effect on light. Alaback (1982), on the other hand, says the most important effect of canopy closure after disturbance on understory species is the decrease of light in Alaskan spruce-hemlock forests. These differences are perhaps the result of studying different conifer species climatic regimes, and to differing lengths of time for forest canopies to reform following disturbance.

The majority of stands studied in this work are not on alluvial flats but are on hillsides thought by some authors (Becking 1967, Stone and Vassey 1968) to have been maintained somewhat in a climax condition by fire, although Veirs (1972) minimizes the role of fire in pristine redwood stands. It would be incorrect to try to fit the understory response in these stands to fire-succession models derived from intense fires that completely destroy the overstory and understory.

The present study was undertaken to describe the effect of partial timber harvesting on understory species in stands of coast redwood less than 15 km from the ocean. The vegetation of eight stands that were harvested over a period of several years was assessed and analyzed to determine relationships between understory development and identifiable site characteristics. Environmental and physical conditions at particular sites were measured to examine precisely what effect differing intensities of overstory removal had on understory species development. Final consideration is given to some of the consequences of these and other findings.

Methods

A complete description of the study sites and sampling methods is given in Woodward (1986). The understory of eight adjacent stands in Mendocino Co., California that had been partially harvested from 1971 to 1978 was sampled. Three stands were tractor-logged, four were partly tractor-logged and partly cable-logged, and one stand was cable-logged only. A contiguous unlogged stand also was sampled.

Cover and frequency of understory species was measured on approximately 300 randomly placed 16 m^2 quadrats in each study area. Bare soil, rock (>2.5 cm diameter), litter, and branch cover also were estimated. Overstory canopy cover was measured at each quadrat with a 'moose horn' device which projects a view directly overhead through a plexiglass covered with a grid of dots (Garrison 1949). Slope and aspect of each plot were measured with a clinometer and a compass and converted into potential solar beam irradiation. The potential solar radiation is computed from tables for 40° N Latitude prepared by Frank and Lee (1966). These tables use the slope and the aspect of each individual quadrat to calculate the inclination of the quadrat toward the sun and report the potential solar radiation as Langley's per year.

The depth of the litter/duff layer was measured at the center of each quadrat and an estimate made of its composition (percentage conifer, hardwood, grass, fern, shrub, and forb). Surrounding tree basal area and overstory species composition was made with a Spiegel Relaskop.

Relative soil depth/compaction was measured by pressing a 1.25 cm diameter, 1 m long pointed steel shaft into the ground as deep as possible at the center of each quadrat. Soil samples from the surface 15 cm were collected at a total of 44 quadrats from the different tractor, cable, and unlogged stands. Chemical and physical analyses were performed by the UC Davis Extension Soils Laboratory. Soil texture was determined by the hydrometer method; cation determinations were made by atomic absorption techniques.

An ordination of the plant cover and frequency values was performed using detrended correspondence analysis (Gauch 1982, Hill 1979, Beatty 1984). The ten most common understory species were selected for inclusion in this analysis, using the prevalent species concept of Curtis (1959). The eigen values obtained for individual species and harvested areas were then correlated with the above mentioned environmental factors to aid in predictions of disturbance effects.

Three sites that vary in extent of overstory canopy cover, each about 0.4 ha in size, that previously had been tractor-logged and are now dominated by three different types of understory species, were selected for special study. Whipplea modesta, (yerba de selva) a perennial herb that forms dense mats, dominated a level upland site (Whipplea Site). Polystichum munitum (swordfern), a fern common in the coast redwood forest that occurrs in clumps reaching 1 m in height, dominated a second level upland site (Polystichum Site). Annual and biennial forbs and grasses dominated a third site, which was situated on a narrow flat near a perennial stream (Ruderal Site).

The three study sites were visited once a month from June to October, 1983. Maximum and minimum monthly air temperatures at the soil surface were recorded with three Max-Min thermometers at each site.

Photosynthetic photon flux density (PPFD) was measured using the ozalid paper method (Friend 1961). Ten-sheet stacks of ozalid paper were placed in blackened plastic petri dishes and exposed to sunlight through a 1 cm^2 aperture. Light measurements were made by placing forty ozalid-dishes randomly on the soil surface at each site prior to sunrise, and then collecting the dishes at 6:00 p.m. the same day. The number of sheets exposed was counted and, after calibration, are reported as the sum of daily irradiance (μE cm^{-2} day^{-1}).

Soil moisture was measured once a month at each site at three different depths, 0-15 cm, 16-45 cm, and 46-75 cm. Soil samples were removed with a soil tube or auger and sealed in a plastic bag or metal soil can. The samples were then weighed, dried in an oven at 105° C for 24 hr, reweighed, and percent soil moisture by weight determined. Additional soil samples were collected and used to produce a soil water potential curve for each site using a pressure plate. For this technique, soil samples are wetted to saturation and placed in a pressurized chamber and allowed to completely drain. The moisture retained in the soil after this treatment reflects the moisture holding capacity of the soil at the chosen pressure. Subsequent soil samples are placed in the chamber at pressures that will reflect natural soil moisture potentials. The field-collected percent soil moisture measurements were thus converted to soil water potentials (-MPa).

Relative potential evaporation was assessed one day per month with Piche atmometer tubes (Muelder et al. 1963). These tubes resemble 30 ml graduated cylinders (mouths are 11 mm diam) with one end sealed and the other end having a spring held metal lid. The metal lid holds two sheets of Whatman #1 3 cm diameter filter paper pressed tightly in place against the mouth of the tube. The tubes are filled with distilled water and inverted so that the filter paper is at the bottom. As the filter paper wets, it seals the tube and acts as a wick exposing a constant wetted surface to the surrounding air. Evaporation occurs from the wet paper and is dependent on site temperature, sunlight, humidity, and wind. Ten such tubes were randomly placed so that the exposed filter paper was 30 cm above the soil surface. The tubes were put out before sunrise; water loss from the tube was measured at noon and 5:00 p.m..

Environmental measurements at the three sites were usually made during three consecutive days. Data for August 1983 were omitted because of rainy weather. Statistical methods follow Snedecor and Cochran (1980).

Results and Discussion

Correlations of understory species cover and quadrat environmental characterisitics revealed no exceptional results. Significant correlations existed but were self-evident, e.g. Polystichum cover was positively correlated with fern litter cover, and total hardwood basal area was positively correlated with hardwood litter cover. No species' performance was shown to be correlated with soil or litter depth, nor with the occurence of any other plant species. Species alliances as reported by other authors (Becking 1967, Lennox et al. 1981) for undisturbed coast redwood forests, such as swordfern-oxalis, were not demonstrated by the correlation analyses. The species tend toward a more unorganized stage of succession in these recently harvested stands.

Results of the soil chemical and physical analyses are shown in Table 1. The data for tractor-logged, cable-logged, and unlogged stands are presented separately to demonstrate that no significant differences exist between the three areas. Cation exchange capacity values are relatively large, which is certainly due to high amounts of soil organic matter. Average soil calcium is also substantial and shows alot of variation.

Correlations of understory species cover with soil chemical and physical features are presented in Table 2. In general, the species exhibiting a propensity to invade these disturbed sites (those species less common in the unlogged forest) have negative correlations or no significant association with the soil elements considered here. Whipplea, Viola, grass species, and Gaultheria, --rare in unlogged stands-- all decreased on quadrats with higher levels of potassium, calcium, and magnesium. Oxalis, common in unlogged stands, was the only species to increase as soil nutrients increased. These findings do not suggest the site is nutrient poor, but that the lower limits of necessary nutrients for some species may be attained in some localities in these stands.

The detrended correspondence analysis (DCA) (Gauch 1982) ordination performed on selected species cover and frequency data from all the sampled stands is presented in Figure 1. The harvest areas disjoin on the first DCA axis in a manner representative of the successional stage of the stands. Understory development in these stands is influenced by the time since disturbance and the intensity of the disturbance event and follows a pattern of increasing species numbers and cover for the time period considered. More recently harvested tractor-logged sites have the greatest disturbance impact and tend toward fewer occurences of most species and much less cover. Older tractor-logged sites and cable-logged sites have the greatest number of species and understory cover. The unlogged stand is not shown on this plot because its low cover and species composition skew the entire depiction.

Stands that were tractor-logged in 1971, 1972, and 1973 were harvested at a greater intensity than more recently tractor-logged stands (64.1% average basal area removed versus an average of 38.3% for the harvests since 1974). These older tractor-logged stands have shown resilience to the disturbance and now group with the later cable-logged stands on the ordination diagram, indicating that soil disturbance from the tractors has not been the major effect in determining understory dynamics in these stands. By 10 yr after harvesting the tractor areas are similar in structure to more recently logged cable areas; seems to indicate that the opening of the forest canopy (rather than soil disturbance) was the most significant effect of harvesting.

Ordination of individual species is plotted in Figure 2. Both Axis 1 and Axis 2 revealed trends that were ecologically relevant. Data for the tractor-logged and cable-logged stands are shown plotted on the same graph for comparison. Species showed the same general distributions in the tractor and the cable areas. Correlations of the potential solar radiation of each quadrat with the species' eigen value from the individual sites, suggested that species can be differentiated by their response to this factor. Lithocarpus (tan oak) is a common invader of logged stands in northern California and had its' greatest development on sites with high potential solar radiation.

Polystichum (swordfern) is the extreme of the ordination, being favored on sites with less potential solar radiation.

While the species varied on Axis 1 with potential solar radiation, correlations of the percentage overstory canopy cover with the individual species' eigen values for the second DCA axis denoted another relationship. Cover and occurrence of the species in the cable-logged area varied with conifer canopy cover. The species in the tractor-logged area responded in a similar manner, but to hardwood canopy cover.

Percentage canopy cover is an index of the available light on the forest floor. Overstory canopy not only affects total light but also the quality of the light and the manner in which it reaches the understory vegetation, whether as small temporary sunflecks or sustained full sunlight (Ustin et al. 1984). Understory species, such as Polystichum, which favored low-light sites on the first DCA axis but had an intermediate response to canopy cover on the second DCA axis, must be responding to these other factors in addition to total light. Other components of the forest floor environment affected by canopy cover are soil moisture, litter depth, humidity, and mineral nutrition.

Annual maximum and minimum temperatures for the three special Polystichum, Whipplea, and Ruderal sites are shown in Figure 3. The most recently logged site with the smallest total canopy cover, the Ruderal site, has the greatest fluctuations in seasonal temperatures. This site has the coldest temperatures in the winter and the warmest in the summer and is the only site to consistently receive freezing temperatures in the winter. The site may receive some shade in the winter from surrounding hills, but undoubtedly the deficiency of overstory canopy to insulate the forest floor produces lower winter temperatures.

The Polystichum site has the least temperature oscillations during the year, and is the warmest in the spring. The Whipplea site experiences less variation in temperature in the winter than the other sites having higher minimums and lower maximums.

Soil moisture potential for the three sites (Table 3) may have been anomalous for the 1983 growing season, because some precipitation occurred in each summer month, an event unusual in this region. The Whipplea site soil moisture never reached levels that would be considered deleterious for the grow of most plants. In the autumn, the soil had dried considerably but the onset of rains soon alleviated this situation. The drying pattern of the soil profile indicates the rooting zone of Whipplea, where moisture is withdrawn from the soil, seems to be >46 cm depth.

The Polystichum site already had low soil water potentials in June when this study began, possibly reflecting early spring growth of the fern and the relatively warm days in spring at this site. Rewetting of the soil in early July completely recharged the surface 75 cm. Polystichum did not cause serious depletions in the soil water for the remainder of the season.

The Ruderal site had little soil moisture available for sustained plant growth throughout the summer. Even with frequent rewetting episodes, the 100% vegetation cover quickly depleted soil moisture, leaving little opportunity for establishment of perennial species. The paucity of canopy cover also allowed for more rapid drying of the soil. By September the annual species had become dormant and the soil began to recharge with fall rains.

There was considerable variation in the quantity of radiant energy (PPFD) received at the three sites (Table 4). The variation corresponds well with the amount of overstory canopy, and demonstrate that a small change in the absolute amount of canopy can produce large changes in the amount of light that reaches the forest floor. The difference in total light received between the Ruderal and the Polystichum sites also indicates this may be a limiting factor to some species. The seasonal site differences in PPFD corresponds with differences in temperature at the three sites.

Figure 4 shows that evaporation at the Whipplea and the Polystichum sites was very similar. The absolute amounts of evaporation is not significantly different nor was the time of day (a.m. or p.m.) at which the evaporative loss peaked. The Ruderal site experienced as much as three times more evaporation during the summer than the other two sites. Exposure to more sunlight (less canopy cover) and resulting higher temperatures subjects the understory to extreme drying conditions. High evaporation rates continued into the Fall. The afternoon-to-morning evaporation ratio is 1.89 for the Ruderal site in June (as compared to 2.63 for the _Whipplea_ site and 1.49 for the _Polystichum_ site) and doubles in July and again in September (while the other sites remain about the same).

It is clear that understory species numbers and cover will decrease as overstory canopy increases (Larson and Wolters 1983). Partial harvests that remove less than 30% of the existing overstory canopy have a minor effect on the understory vegetation. However, such a small amount of overstory removal is not practical on most commercial forest land. Understory species compostion, cover, and the rate of succession on any site can be manipulated by varying the intensity of overstory removal. In many cases understory vegetation is advantageous to stop erosion and to conifer regeneration. Howard and Newton (1984) found that plants that formed ground covers or species that encroached from the side had no effect on Douglas fir height growth, and Cleary (1978) suggested that on dry, sunny sites the shading afforded by surrounding vegetation may actually benefit conifer seedlings.

The form that succession will take, or more importantly what climax (or disclimax) will be maintained, in these partially logged stands depends on the frequency of disturbance (how often the stands are reentered for subsequent timber harvests or silvicultural treatments) and the degree of disturbance (how many trees are removed during the next harvest and by what methods). All other factors being equal, it is thought (Miller 1982) that for a given rate of disturbance the species diversity and performance will depend on the size of the disturbance. Larger disturbances favor colonizing species while smaller disturbances favor residuals. The removal of canopy cover is as important as the size of the disturbance in the stands in this study. The redwood stands considered in the present study seem to present a compromise, with colonizing species occupying the site for a time but the development of the residual overstory conifers modifying the forest floor environment to reaccomodate the endemic species.

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Table 1. Soil chemical and physical properties from second-growth coast redwood stands. 'Tractor' and 'Cable' indicate the method of harvesting performed at each site. Means (± one standard deviation) are for 21 samples in the Tractor, 13 in the Cable, and 10 in the Unlogged.

		Mean	
Cation Exchange Capacity (µmol/g)			
	Tractor	14.76	±7.42
	Cable	17.56	±6.39
	Unlogged	16.66	±4.12
Sand (%)			
	Tractor	39.14	±11.60
	Cable	44.01	±12.27
	Unlogged	37.43	±11.81
Silt (%)			
	Tractor	35.51	±9.64
	Cable	29.12	±7.80
	Unlogged	33.07	±9.48
Clay (%)			
	Tractor	19.54	±4.94
	Cable	17.03	±3.48
	Unlogged	16.95	±4.21
Potassium (µmol/g)			
	Tractor	0.07	±0.03
	Cable	0.09	±0.02
	Unlogged	0.08	±0.01
Calcium (µmol/g)			
	Tractor	42.52	±28.47
	Cable	67.92	±35.87
	Unlogged	55.90	±16.52
Magnesium (µmol/g)			
	Tractor	12.90	±6.52
	Cable	14.27	±4.96
	Unlogged	10.90	±4.11

Table 2. Correlation coefficients for selected plant species' cover and soil chemical and physical characteristics at 44 sites in the coast redwood forest.

	CEC	K	Ca	Mg	Clay	Silt	Sand
Polystichum munitum	0.116	-0.056	0.242	-0.067	-0.219	-0.343	0.387
Whipplea modesta	-0.349	-0.137	-0.410	-0.152	0.084	0.136	-0.152
Viola sempervirens	-0.437	-0.446	-0.399	-0.399	-0.208	-0.018	0.120
Oxalis oregana	0.464	0.336	0.436	0.195	0.098	-0.182	0.097
Galium spp	-0.025	0.011	-0.067	0.105	-0.010	0.162	-0.125
Grass spp	-0.240	-0.304	-0.322	0.143	0.004	0.300	-0.243
Lithocarpus densiflora	-0.097	-0.083	-0.112	-0.107	0.071	-0.177	0.106
Vaccinium ovatum	0.110	-0.082	0.045	0.028	-0.064	0.167	-0.101
Erechtites prenanthoides	0.048	-0.017	0.065	0.100	0.137	0.030	-0.094
Gaultheria shallon	-0.364	-0.455	-0.314	-0.261	-0.276	0.139	0.029
Other spp	-0.174	-0.141	-0.219	-0.008	0.041	0.014	-0.032

Table 3. Seasonal soil moisture (in negative MPa) at three study sites with different understory species and overstory canopy cover in the coast redwood region.

	Depth (cm)	Polystichum	Whipplea	Ruderal
June 1983	0-15	0.16	0.0[1]	1.92
	16-45	1.10	0.0	>20.00[2]
	46-75	0.93	0.0	>20.00
July 1983	0-15	0.0	0.22	1.50
	16-45	0.0	0.0	>20.00
	46-75	0.06	0.0	>20.00
Sept. 1983	0-15	0.71	0.17	1.28
	16-45	0.66	0.0	1.87
	46-75	0.85	0.53	1.48
Oct. 1983	0-15	0.55	0.83	1.00
	16-45	0.94	0.55	1.68
	46-75	1.10	0.52	1.05

1 = ≥0.03 MPa; moisture above the field capacity.

2 = soil moisture in this range is considered to be unavailable for plant uptake.

Table 4. Daytime photosynthetic photon flux density (Σ Daily $\mu E\ cm^{-2}$) by month for three sites with different dominant understory species and different amounts of overstory canopy in the coast redwood forest. Each monthly total is based on > 40 readings.

	Photosynthetic Photon Flux Density (Σ Daily $\mu E\ cm^{-2}$)		
	Polystichum	Whipplea	Ruderal
Canopy Cover (%)	82.4	63.2	56.9
June 1983	1334.3	2415.0	9070.6
July 1983	952.0	1704.8	6056.1
September 1983	177.7	---	803.5
October 1983	101.3	155.3	242.5

Figure 1. Ordination of 12 partially harvested second-growth coast redwood stands. The year of each harvest is shown and the method of harvesting: tractor (T) and cable (C). A complete explanation of the figure is given in the text.

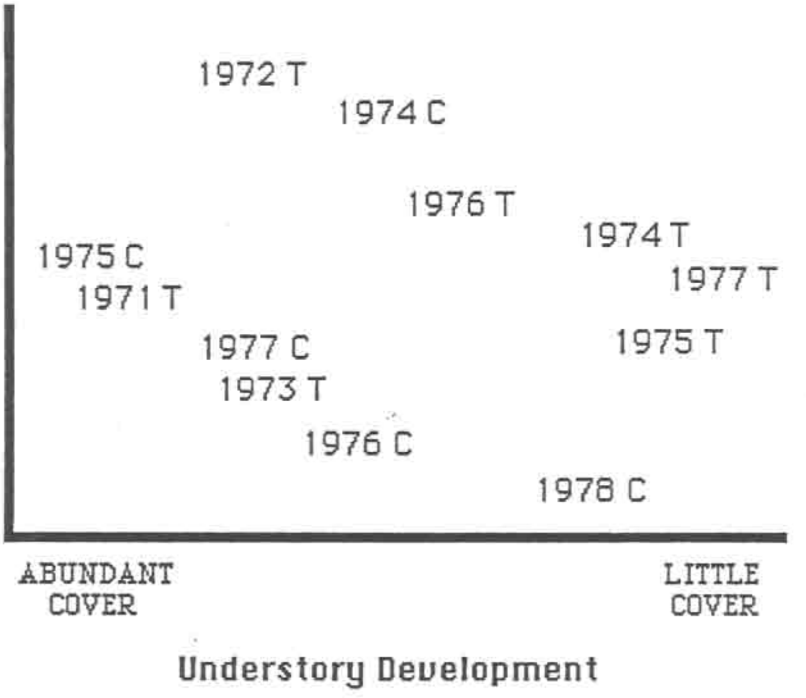

1972 T
1974 C
1976 T
1974 T
1975 C
1977 T
1971 T
1977 C
1975 T
1973 T
1976 C
1978 C
ABUNDANT COVER
LITTLE COVER
Understory Development

Figure 2. Ordination of the most common understory species (generic names shown) from 12 partially harvested second-growth coast redwood stands. Stands were harvested by two methods; tractor (bold generic names) and cable (underlined, normal type generic names).

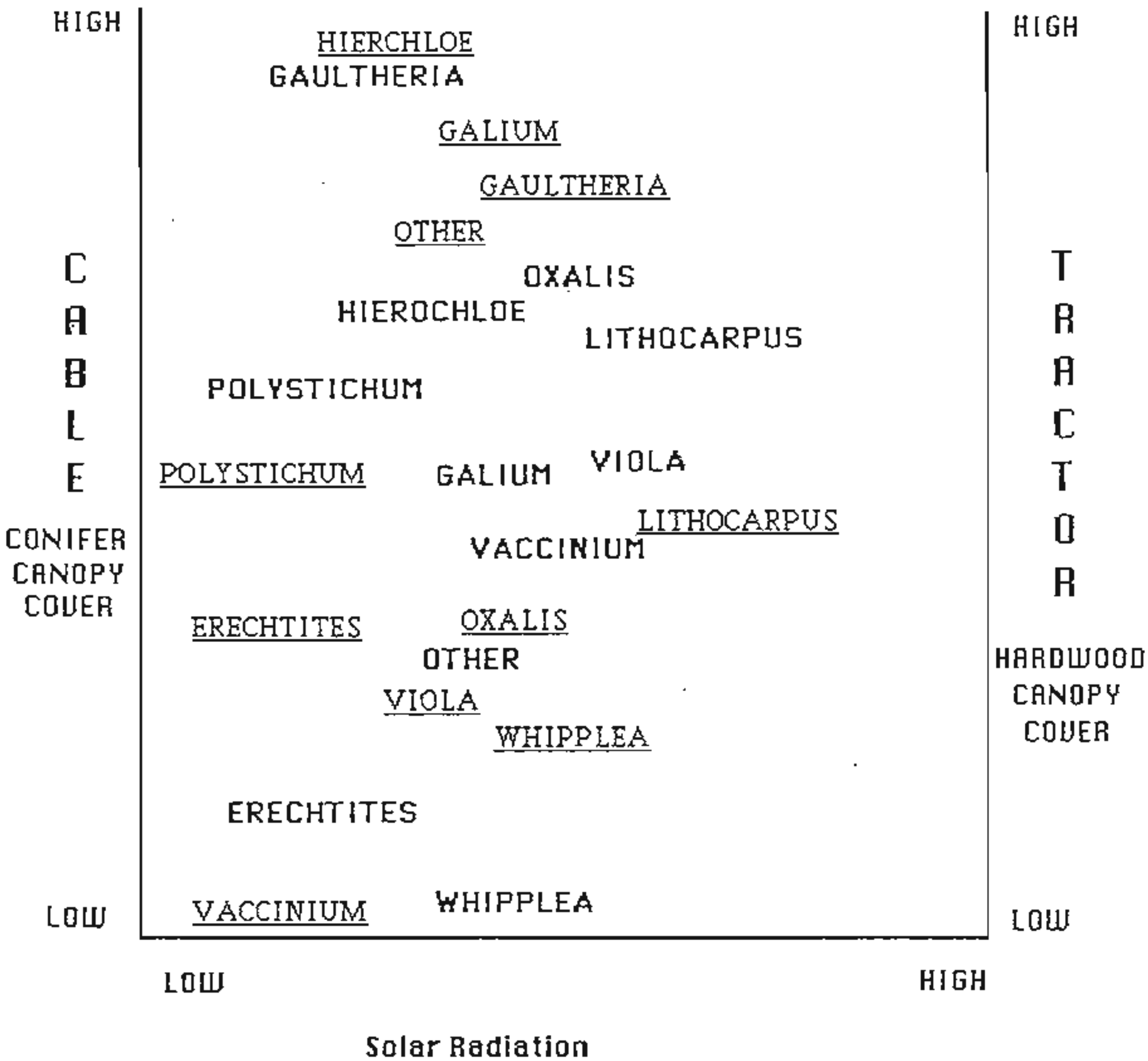
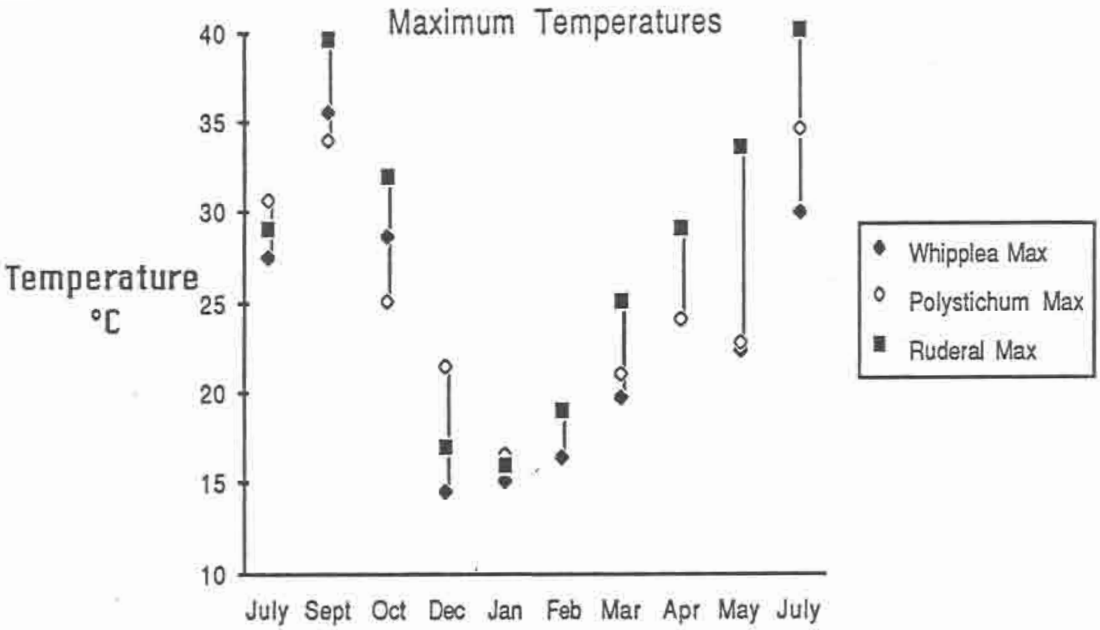

HIGH
HIERCHLOE
GAULTHERIA
GALIUM
GAULTHERIA
OTHER
OXALIS
HIEROCHLOE
LITHOCARPUS
POLYSTICHUM
POLYSTICHUM
GALIUM
VIOLA
LITHOCARPUS
VACCINIUM
ERECHTITES
OXALIS
OTHER
VIOLA
WHIPPLEA
ERECHTITES
VACCINIUM
WHIPPLEA
LOW
CABLE
CONIFER CANOPY COVER
HIGH
TRACTOR
HARDWOOD CANOPY COVER
LOW
LOW
HIGH
Solar Radiation

Figure 3. Maximum and minimum temperatures for three sites in the coast redwood forest. The sites are dominated by three different understory types (Whipplea, Polystichum, and Ruderals) and have different amounts of overstory canopy cover (Polystichum = 82.4%, Whipplea = 63.2%, and Ruderals = 56.9%).


Maximum Temperatures
Temperature °C
40
35
30
25
20
15
10
July
Sept
Oct
Dec
Jan
Feb
Mar
Apr
May
July
Whipplea Max
Polystichum Max
Ruderal Max

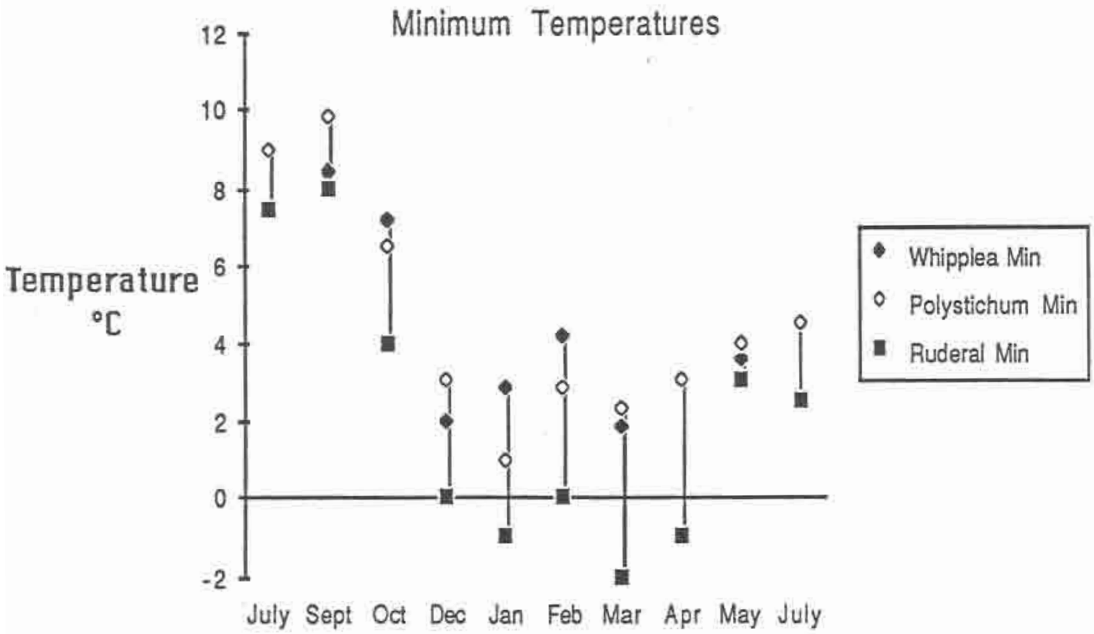
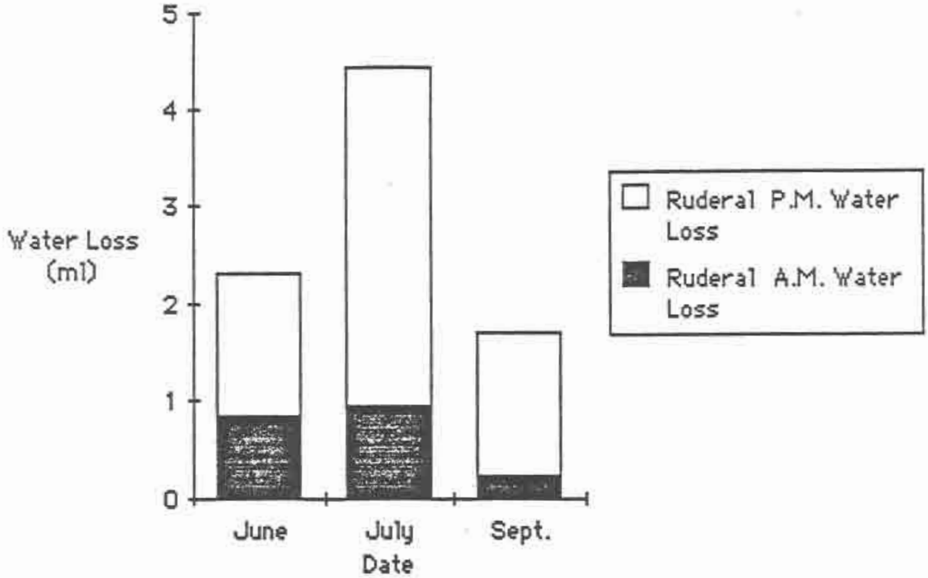
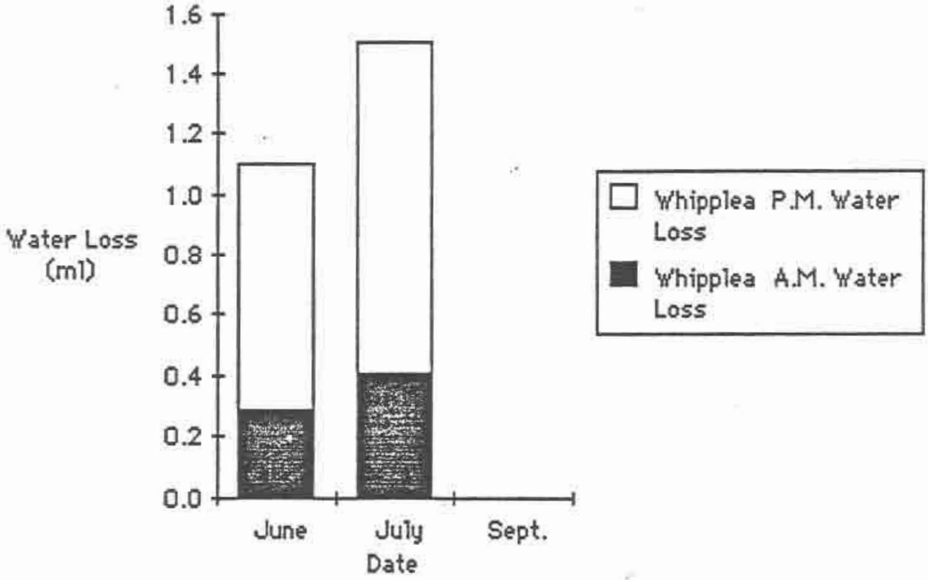
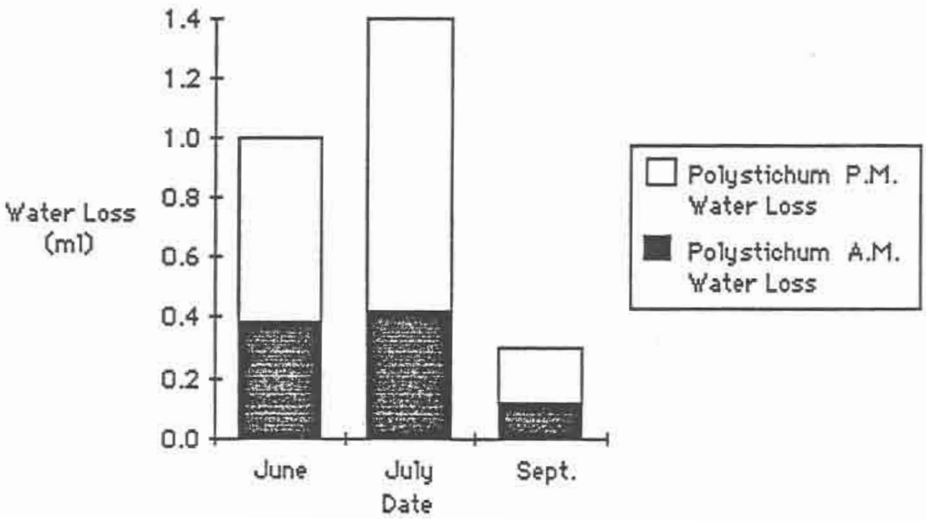

Minimum Temperatures
Temperature °C
12
10
8
6
4
2
0
-2
July
Sept
Oct
Dec
Jan
Feb
Mar
Apr
May
July
Whipplea Min
Polystichum Min
Ruderal Min

Figure 4. Evaporation from Piche atmometer tubes at three sites in the coast redwood forest. Each site is dominated by different understory types and has different amounts of overstory canopy cover.





Polystichum A.M. Water Loss



Natural Regeneration of Coast Redwood (*Sequoia sempervirens*) Stands Following Partial Harvesting

by

Roy A. Woodward*

Abstract

Natural regeneration by seed and stump sprouts of important conifer species (coast redwood, Douglas fir, grand fir, hemlock) was assessed in eight partially harvested second-growth stands near the Pacific Ocean in northern California. Two methods of log removal, tractor skidding and skyline cable logging, were employed. Selective removal of grand fir and hemlock overstory trees repressed seedling establishment of these species. Douglas fir readily established from seed, but showed a preference for bare mineral soil such as created by heavily disturbed tractor-logged areas and skid roads. Coast redwood sprout clumps formed on about 100% of the cut trees. Coast redwood seedling establishment was relatively poor and was positively correlated with bare mineral soil. Native herbaceous vegetation and swordfern were not detrimental to Douglas fir seedling growth and may actually improve the site environment for young conifers. Introduced herbaceous vegetation did hinder coast redwood seedling growth, when compared with open grown seedlings. Douglas fir seedlings grown in an area cleared of surrounding understory vegetation showed probable osmotic adjustment to drought stress.

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Introduction

The coast redwood (*Sequoia sempervirens* (D. Don) Endl.) forest of California contains some of the most valuable commercial forest land in the world (Zinke 1977). This forest is capable of exceptional timber production and has a long history of use. In the early part of the twentieth century, clearcutting of old growth stands was progressing at a rapid rate and forest managers recognized the need to plant new conifers to insure future production (Metcalf 1924). This 'artificial reproduction', as it was termed, actually took place on hundreds of acres of cutover land prior to the Depression of 1929.

However, most of the coast redwood forest presently being logged is second-growth that naturally established following clearcutting of the old growth forest over the past 100 yr. Much of this land has only become 'managed' (brush and hardwood control, fire suppression, selective removal of damaged or diseased trees) in the past two decades, with some thought being given as to what type of forest will exist 20, 50, and 100 yr in the future. Given that harvesting of public and private forest land will continue, some silviculturalists (Twight 1973, Namkoong and Roberds 1974) have stated that only partial harvests (as opposed to clearcutting) can insure future yields and survival of the coast redwood forest. Others (Lindquist 1986) have found that partial cutting has led to stand conditions where redwood regeneration is scarce and unable to grow in an acceptable manner for creation of an unevenaged system.

The type of silvicultural system used depends much on the location of the site and the current market demands for Douglas fir-redwood stumpage. Regeneration considerations have been secondary but are becoming more important in choice of systems. Clearcut sites are increasingly planted with coast redwood the winter following the harvest, and this, with natural redwood sprouting, has been found sufficient to meet the legal requirements of stocking. Natural seedling establishment also occurs on clearcut blocks and some investigators have found that Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) is favored over coast redwood in some parts of the coast redwood range (Veirs and Lennox 1981, Veirs 1972).

There are many differences between clearcut and partial-cut stands when considering small conifer establishment (Boe 1970, Person and Hallin 1942, Graham et al. 1982). It is easier to prepare the clearcut site for replanting and the distrubance of the soil and overstory canopy caused by clearcutting are often beneficial to seedling growth (Strothman and Roy

1984). The environment of partially harvested stands is more like unlogged stands (Ahlstrom 1968) than clearcut stands, but important changes do take place on the forest floor that affect conifer establishment and subsequent growth.

There is a significant increase in understory vegetation following partial harvesting (Woodward 1986a). Grass competition has been found to slow ponderosa pine growth (Larson and Schubert 1969) and other common understory species inhibited germination, radicle extention, and shoot growth in the southern pine forest (Hollis et al. 1982). Encroaching vegetation has been shown to have no effect on Douglas fir seedlings until they are overtopped (Howard and Newton 1984). Fog drip (Azevedo and Morgan 1974) reaching the forest floor decreases following partial harvests, resulting in less water being available for tree growth (Ahlstrom 1968). Soil temperatures and air temperatures also become more diverse, which can have a detrimental effect on redwood seedling growth (Hellmers 1963 and 1966).

In order to examine the condition of natural regeneration of conifers following partial harvesting, I surveyed eight stands in the coast redwood forest of northern California. The numbers and species of conifer seedlings (and coast redwood stump sprouts) were determined for each stand, and environmental data were collected from selected sites. Competition from neighboring vegetation was assessed by measurement of the growth rates of small Douglas fir and coast redwood seedlings. Conclusions are made as to the present situation of conifer seedlings in these stands.

Methods

Regeneration Transects - Conifer Density and Growth

The study was conducted at Jackson Demonstration State Forest in Mendocino County, California. Eight adjacent stands in the coast redwood forest that had been clearcut prior to 1910 and subsequently left for conifers to regenerate naturally, were selected for study. These stands were sequentially relogged from 1971 to 1978 with a partial removal of overstory trees taking place. Three of the stands were logged with rubber wheeled or crawler tractors, one was logged with a running skyline cable system, and four were logged partly by tractor and partly by cable systems. An adjacent stand that had been originally clearcut at the same time as the eight study sites (prior to 1910), but had not been relogged, also was sampled as a control site. For a more complete description and map of the study sites see Woodward (1986b). The volume, percentage of basal area, and species composition of conifer trees removed from each stand were determined by the California Department of Forestry at the time each stand was harvested by examining each loaded logging truck as it left the site and comparing the data with preharvest stand measurements.

Ten transects were placed in each study area in order to determine the density of young conifers. The starting point for each transect was selected randomly along the perimeter road on the uphill side of each harvest area. The direction of the transect was determined from a randomly chosen compass setting that included all possible directions that led into the harvest site. I followed each transect line starting at one edge of the harvest area until I arrived at the other edge of the harvest area. The same selection process was followed until ten transects were placed in each harvest area. The transects varied in length from 150 m to 730 m, and the intensity of sampling was equal for each harvest area. The number of young conifer trees (defined as trees <10.0 cm diameter breast height) that had naturally established in each stand were counted on each transect in 1982. Each tree encountered within 1 m to each side of the transect line was identified to species and the height to the nearest centimeter was measured. Coast redwood seedlings were counted separately from sprouts when they could be distinguished. (An occasional broken piece of coast redwood or a stump will become buried during logging and will send up only one sprout which is difficult to differentiate from a seedling tree.) In addition to coast redwood, other conifer species encountered were Douglas fir, grand fir (Abies grandis (Dougl.) Lindl.), hemlock (Tsuga heterophylla (Raf.) Sarg.), and Bishop pine (Pinus muricata D. Don).

The fallen and bucked logs are removed from cable-logged areas along narrow corridors, and are often completely lifted into the air to avoid contact with the ground. The logs in the tractor-logged areas are necessarily skidded on the ground creating a plowing effect, and the ground is additionally churned by the manuverings of the tractors. In the tractor logged areas more sites are potentially left bare for seedling establishment. Comparisons of transect data of young conifer density from tractor-logged and cable-logged sites will test the hypothesis that redwood seedling establishment requires bare mineral soil.

Regeneration On Skid Roads

Soil compaction by tractors skidding logs, the plowing effect of the tractors exposing bare mineral soil, and the greater removal of overstory canopy along roads may affect the ability of such areas to support small tree growth. In order to analyze these effects, the regeneration and growth of conifers along skid roads that had been abandoned since the harvest in one timber stand was studied. The number of seedling conifers situated on skid roads was sampled by randomly placing 75 3 m wide by 6 m long quadrats along roads. The number of small trees of each species were counted on each of these quadrats and the height measured to the nearest centimeter.

Regeneration-Understory Experiments

To assess the interactions between understory vegetation and small conifer trees, three experimental sites were established. One site was in a stand that was partially harvested by tractors in 1966, located in the headwaters of the Jughandle Creek drainage. The site was on level ground and had a Douglas fir/coast redwood overstory (canopy cover averaged 63% ±27) and a predominately Whipplea modesta Torr. (yerba de selva) understory.

Twenty Douglas fir trees <1.5 m tall that had naturally established on the site, were selectively chosen. A 1 m^2 area was delineated around each tree and the species composition and cover of the vegetation surrounding each tree was visually estimated. The following treatment was applied to randomly selected trees: the area around 10 of the trees was completely cleared (using a hoe) of all understory vegetation and the vegetation around 10 other trees was left undisturbed. The trees were numbered with metal tags and the height was measured to the nearest centimeter. Each tree was fenced (0.5 m^2 area enclosed) with two inch mesh poultry wire to protect them from black-tailed deer (Odocoileus hemionus). Redwood lath was used to support the wire and situated on the east and west sides of each tree to decrease shading. This was known as the Whipplea site.

A second experimental site was located on a level portion of one of the previously mentioned eight logged stands. This stand was logged by tractors in 1975 and is on the south side of the Hare Creek drainage. 20 naturally seeded Douglas fir trees <1.5 m tall growing in close proximity were individually fenced as described above. The overstory at this site is mostly coast redwood and the canopy cover averages 82% ±9. The understory is relatively sparse (less than 20% cover) and is dominated by Polystichum munitum (Kaulf.) Presl. (swordfern), a fern common in the coast redwood forest that forms individual clumps often 1 m in diameter and 1 m tall. The swordfern at this site did not exist as a continuous closed stand, as is common in some areas of the forest, but as dispersed clumps.

The 20 Douglas fir were randomly selected depending on their proximity to swordfern clumps. 10 trees with their central trunks within 1 m of 2 clumps of swordfern were selected and 10 trees that had no swordfern within 1 m were selected. All other vegetation (mostly scattered plants of Galium, Viola, and Trillium) was cleared by hand from around each tree. The trees were numbered with metal tags and their heights measured. This was known as the Polystichum site.

The third experimental plot was located in the Pudding Creek drainage on land owned by Georgia-Pacific Corporation. This area was partially logged by tractors in 1982 and has a coast redwood overstory that averages 56% ±28 canopy cover. The study site is on a flat area in the bottom of a canyon about 100 m from Pudding Creek. The site was planted with containerized 2-0 coast redwood in December of 1982 immediately after logging. The only site preparation was brush raking to remove limbs and tree tops. This site had been heavily disturbed from the late 1800's until the 1930's because of a close proximity to a logging settlement. Annual exotic herbs were common over much of the area prior to logging. A mixed understory vegetation of exotic annual and native perennial herbs (i.e. Cirsium, Taraxacum, Anagallis, Plantago, Juncus, Bromus, Carex, Erodium, Melilotus, etc.) formed almost an 80% groundcover around the small trees by the spring of 1983.

20 of the small redwood trees (all were ≈20 cm tall) were randomly selected and fenced as described above. The following treatments were then applied to the trees: a 1 m^2 area around 10 of the trees was completely cleared of all vegetation with a hoe. The area around 10 other trees was left completely undisturbed. The trees were numbered with metal tags and their heights measured. This is known as the Redwood site.

Beginning in May, 1983 until July, 1984 the following measurements were made monthly at each of the three experimental sites (not every measurement was made each month because of rain or cessation of growth of the small trees).

The water content of the soil was measured as often as once a month at three depths, 0-15 cm, 16-45 cm, and 46-75 cm. Soil samples were removed with an auger or Veihmeyer soil tube and sealed in metal soil cans or ziplock type plastic bags. The soil samples were weighed, dried in an oven at 105° C for 24 hr, reweighed, and the percent soil moisture by weight determined. Additional soil samples were collected and placed on a pressure plate to produce a soil water potential curve for each site. For this technique, soil samples are wetted to saturation, placed in a pressurized chamber, and allowed to drain to an equilibrium point. The moisture retained in the soil after this treatment reflects the moisture holding capacity of the soil at the chosen pressure (water potential). Subsequent soil samples are placed in the chamber at pressures that will reflect natural soil moisture potentials. The field-collected soil moisture measurements were thus converted from percentage water content to soil water potentials (-MPa).

Maximum and minimum monthly air temperatures at the soil surface were recorded with 3 shaded maximum-minimum thermometers placed next to randomly selected trees at each site. Relative potential evaporation was assessed one day per month with Piche atmometer tubes (Muelder et al. 1963). 10 tubes, 5 for each treatment at each experimental site, were placed on the wire cages around selected trees so the bottoms (the evaporative surface) were 30 cm above the soil surface. The tubes were put out before sunrise, and water loss from the tube was measured at noon and sunset.

Photosynthetic photon flux density (PPFD) was measured using the ozalid paper method (Friend 1961). Ten-sheet stacks of ozalid paper were placed in blackened plastic petri dishes and exposed to sunlight through a 1 cm^2 aperture. Light measurements were made by placing 2 ozalid dishes on the soil surface beneath the edge of the canopy of each small tree, and two dishes 1 m in the air suspended on the redwood lath supporting the poultry wire, prior to sunrise, and then collecting them at 6 pm (local time) the same day. The number of sheets exposed was counted and, after calibration, are reported as the sum of daily irradiance ($\Sigma\mu E\ m^{-2} day^{-1}$). Calibration is achieved by placing stacks of ozalid paper under a constant light source (as measured with a quantum sensor) for different lengths of time and counting the number of exposed sheets. This is performed with an intense light source to simulate bright direct sunlight, and a low-level light source to simulate shaded, forest floor conditions. Regression equations are derived relating amount of light absorbed ($\Sigma\mu E\ m^{-2} day^{-1}$) to the number of ozalid paper sheets exposed.

To measure growth, the height of each experimental tree was measured to the nearest millimeter monthly during the period the trees were actively growing (March until November).

Pre-dawn xylem water potential measurements were made monthly during the active growing period using a Scholander pressure chamber with compressed nitrogen gas. One twig sample each was removed from three randomly chosen trees from each treatment at each experimental site. Each twig was placed in the pressure chamber chamber and pressure applied slowly until xylem sap wetted the cut end. The pressure required to retrieve the xylem sap was recorded and is reported as plant water potential (-MPa).

At the end of the experiment in July, 1984 pressure-volume (PV) curves were developed using the methods discussed in Tyree and Hammel (1972) (see also Robichaux and Holsinger 1984, Cleary and Zaerr 1984). These curves determine if osmotic adjustment has occured in the study trees as a result of changing water relations due to the experimental treatment. Large twigs of trees from each experimental site and each treatment were cut and immediately immersed in bottles of deionized water and sealed. The twigs were allowed to stand for 24 hr, blotted dry, and then weighed to the nearest milligram. The twigs were then placed in a Scholander pressure chamber at -0.5 MPa and the exuded xylem sap carefully blotted away until it stopped forming at the cut end. The twigs were then reweighed and put back in the pressure chamber at -1.0 MPa. This procedure was repeated, increasing the pressure by -0.5 MPa increments, until -4.0 MPa was acheived.

The tree and environmental measurements at the three experimental sites were usually made over three consecutive days, as the weather permitted. I should point out that there is pseudo-replication of the experimental plots because there are not replicate treatments, but only replicate plots in one treatment. In general, the results are very conclusive, but some statistical tests are not as robust as they could be. Laboratory analyses were conducted at UC Davis and at the California Department of Forestry Hydrology Laboratory in Fort Bragg, California. Statistical methods follow Snedecor and Cochran (1980).

Results and Discussion

Regeneration Transects - Conifer Density

The intensity of partial harvesting for the eight stands sampled with transects is shown in Table 1. Harvests conducted in the early 1970's removed more trees than later harvests and tended to remove a greater proportion of coast redwood.

The natural regeneration of conifers from seeds on the tractor-logged areas was variable among species on the same harvest site (Table 2). Douglas fir quickly established following the disturbance and maintained a fairly constant density for the first few years. Coast redwood, on the other hand, established more slowly and increased in number over the first few years.

It is a general practice to try to remove all mature grand fir and hemlock during a partial harvest, so that the total density of seedlings for these two species only reflects, to some extent, the number of seed trees remaining after the harvest. This was particularly true in the early 1970's harvests. Otherwise, grand fir and hemlock regeneration was similar to Douglas fir, indicating establishment is generally favored by similar conditions. The species composition of conifers and total numbers present for the tractor-logged and cable-logged sites are shown in Table 2.

The 1971, 1972, and 1973 tractor-logged harvests have yielded relatively many redwood seedlings because establishment has continued since the time of harvest and these sites had the most soil disturbance (judging from the greater intensity of harvest) at the time of logging. One can correlate the density of coast redwood seedlings with the amount of soil disturbance by using volume and basal area of overstory trees removed as predictors: the more trees removed, the more tractor activity and greater soil disturbance. This correlation was significant ($p<0.05$) for all of these harvests.

Further evidence of the beneficial nature of soil disturbance on establishment of coast redwood and associated conifer species is seen in the cable-logged stands. These stands were generally thinned to the same degree as the adjacent tractor-logged stands, and the initial species composition was similar to the tractor logged areas, but the total number of small trees present is much smaller. The total number of seedlings on the cable- logged stands is usually less than half the number in the adjacent tractor-logged stand. The exception to this trend is the 1977 harvest, in which there is an unusually large number of grand fir seedlings in the cable-logged area. The density of coast redwood continues to increase year-to-year (as evidenced by the sequence of sites logged in different years) on the cable-logged sites, but in the cable-logged stand that was harvested 8 yr prior to sampling (1974) there were only 88 ha^{-1} coast redwood seedlings. The corresponding tractor-logged site had 103 ha^{-1} seedlings which was significantly different ($p<0.05$).

It has been stated for many years by local foresters and in the published literature that coast redwood seedlings establish best on bare mineral soil (Becking 1967, Stone and Vasey 1968, Roy 1966, and others). The reasons for this are not completely understood. Coast redwood produces abundant cones; even though seed viability is typically low (often less than 10%), enough good seed remains to produce a large annual crop of seedlings (Muelder and Hansen 1961). Jacobs and Mcbride (1977) report the maximum seed production is from trees 60-100 yr old and maximum viability from trees about 250 yr old. Yet, in undistrubed (unlogged or unburned) stands few, if any, small seedlings of coast redwood can be found. On disturbed sites, most seedlings can be found where bare mineral soil has been exposed.

Small seedlings are attacked by insects, deer, nematodes, and to a lesser extent cold winter temperatures (Roy 1966, Muelder and Hansen 1961, Cid Del Prado Vera and Lownsbery 1984), but seldom is >50% mortality due to these factors. A more likely reason for seedling death is dessication caused by several interacting factors. Coast redwood has no root hairs and relies on endomycorrhizae (Sugihara and Cromack 1981), which may result in a poor ability to obtain soil moisture. It also has a high transpiration rate and poor stomatal control (Roy 1966). Florence (1965) found few coast redwood seedlings surviving in pristine stands, and he attributed this to poor microbial digestion of organic matter which results in little mineralization of nitrogen and thus little available nitrogen for seedling growth. Nitrogen deficiency may predispose seedlings for attack by pathogens. Fritz and Rydelius (1966) obtained improved survival of coast redwood seedlings following fumigation of the soil to kill weeds and pathogens. Muelder and Hansen (1961) state that deep soil pathogens destroy roots and leave trees unable to extract sufficient moisture during the dry season.

Apparently, coast redwood is better able to germinate and establish on bare mineral soil because: 1) there is a great reduction in soil pathogens in the organic matter layer that cause damping off and of other soil pathogens that kill growing roots, 2) there is less competition from existing vegetation for soil moisture on bare sites, and 3) bare mineral soil retains moisture that is more available for seedling growth than does forest litter.

It is difficult to maintain a condition of bare mineral soil and no understory vegetation. Burning of the forest floor will remove existing vegetation and hot fires may kill soil pathogens (Muelder and Hansen 1961), but burning may also encourage germination of shrub seeds in the seed bank that will enventually overtop and shade small conifers (McDonald 1976). Shade may be beneficial to small trees, particularly those with pathogen-damaged root systems and decreased abilities to acquire water (Fritz and Rydelius 1966), but lack of summer moisture is considered the most significant killer of young conifers (Cleary 1978, Fritz 1959, Ustin et al. 1984). Many understory species will effectively use most of the soil moisture by the end of spring.

An additional effect of tractor logging is an increase in the number of coast redwood sprout clumps. The number of coast redwood trees removed is similar for adjacent tractor and cable-logged sites (almost 100% of these second-growth cut stumps form sprout clumps), yet there is a consistent difference in the number of sprout clumps between the two areas (Table 3). Apparently two things happen in the tractor area that create more sprout clumps. First, a greater number of not-fallen coast redwood trees are damaged by the tractors (wounded in passing or small trees are run over), and these form sprout clumps when damaged. Secondly, many pieces of coast redwood (tops, broken logs, displaced root masses) become buried by the action of the tractors and develop sprout clumps which will result in young trees.

Regeneration of conifers from seed and sprouts appears adequate in these stands to perpetuate each species. There will be a decrease in hemlock, grand fir, and pine in most stands, but this was the intention of removing most of the overstory trees of these species. Presently, there is less coast redwood than Douglas fir and grand fir in the cable logged stands, but future harvest reentries are planned before these trees mature, so the long term effect of present species composition is undetermined.

Regeneration Transects - Conifer Growth

The heights of conifer saplings are shown in Table 4. The coast redwood are consistently taller than associated species of similar ages except for the 1971 harvest, where grand fir has surpassed it. Even though coast redwood has an exceptional growth rate for the first few years, Douglas fir and grand fir will often be the same height and diameter by the time the trees are 60 yr old (Fritz 1959). There were statistically significant differences between the heights of Douglas fir saplings on the tractor- and cable-logged sites for the 1975 and 1977 harvests. This might be explained by the greater cover of associated understory species on the tractor-logged sites which has shaded and surpressed the small trees, but the height of grand fir was also statistically different for these same sites and it was taller on the 1975 tractor-logged site than on the cable site. There may be a difference in the age of the trees measured, or else the lower slopes of the 1975 harvest that was cable-logged are a better site for grand fir growth.

Regeneration Transects - The Control Site

Regeneration was uncommon in the unlogged control stand adjacent to the harvested stands. I found 77 coast redwood seedlings (some of them probably individual sprouts) and 44 Douglas fir per hectare. I discovered no grand fir, hemlock, or Bishop pine seedlings. There were 17 sprout clumps per hectare, most originating from trees that were not obviously damaged and had begun to grow one or two sprouts at their base. There was little significant regeneration in these stands at the time they were harvested, (as evidenced by the lack of advance regeneration in the unlogged control stand, see Table 2) and it is doubtful if any of these trees survive the harvesting operation.

Regeneration On Skid Roads

Regeneration of conifer seedlings on and off skid roads was studied on the 1975 tractor-logged site. Coast redwood seedling density was 1.5 times, and Douglas fir was 4.0 times, greater on skid roads than off skid roads. Grand fir, hemlock, and Bishop pine were not as common on skid roads. This observation again points out the importance of bare mineral soil for the establishment of coast redwood. Douglas fir may be responding to the increased light along the roads as well as the bare soil (Cleary 1978). In total, skid roads cover about 9% of the area of the 1975 harvest and contain about 21% of the conifer regeneration.

The height of coast redwood seedlings on skid roads averaged 23 cm (± 22) compared with 113 cm (± 91) for trees off skid roads a difference which was statistically significant ($p<.001$). It is likely that most of the trees measured on skid roads were seedlings and not sprouts because the tractors had scraped away the surface; further pieces of trees that may sprout were likely buried beside the road and not in it, so the height differences in part are due to comparing seedlings on roads with seedlings and some sprouts from off roads. On the other hand, the soil on the skid roads is relatively compressed and is not as favorable a site for coast redwood growth. Zinke (1962) discovered damage to redwood root systems by trampling and attributed this in part to soil compaction. The grand fir on skid roads was also significantly shorter (29 cm ± 17) than off skid roads (57 cm ± 60), but the Douglas fir had no significant difference in height (34 cm in both cases).

Experimental Sites - General

For convienence, the temperature data for the three experimental sites are shown together in Figure 1a (maximums) and 1b (minimums). The Polystichum site has the least extremes in yearly temperature, while the Redwood site (located in a canyon bottom) has the greatest. The Redwood site had summer high temperatures of 44° C; the Polystichum site maximum was 35° C and the Whipplea site 32° C. Only the Redwood site experienced freezing winter temperatures, which first occurred in December and reoccurred until April, reaching a minimum of -2° C in March. Yearly temperatures are relatively mild, with prolonged freezing conditions restricted to low-lying, shaded spots such as the Redwood site.

There was no significant difference in evaporation among any of the treatments at any site as measured with the Piche atmometer tubes. Apparently, small cleared patches or the close proximity of Polystichum clumps do not effect atmospheric evaporation measured at this scale. The averages for all tubes at each of the three sites are presented in Figure 6. Evaporation is closely correlated with monthly temperatures with the Redwood site having the greatest daily water loss (4.8 ml) and the Whipplea site second (2.1 ml), and the Polystichum site third (1.9 ml). Evaporation is relatively low at these sites compared with other forest types. Lanini and Radosevich (1986) measured evaporation losses with Piche tubes as high as 1.4 ml per hr in young mixed conifer forest at 1540 m elevation in the Sierra Nevada mountains. The Whipplea and Polystichum sites lose about twice as much water to evaporation in the afternoon as in the morning, while the Redwood site loses about four times as much. The vegetation of the Redwood site will continue to be dominated by invading ruderals until the extremes in temperature and evaporation are modified by future overstory canopy growth (Woodward 1986b).

Experimental Sites - Whipplea Site

The understory vegetation establishment and succession at each site were examined in earlier works (Woodward 1986a and 1986b). I will confine the present discussion to the response of the small conifer trees to site characteristics. I will not attempt statistical comparisons between sites because of differences in the age of the small trees and the different modes of regeneration.

The photosynthetic photon flux density (PPFD) on the ground was significantly different ($p<.01$) between the cleared (0% Cover) and the uncleared (100% Cover) treatment plots for the June and July sampling periods (Figure 3). The PPFD one meter above the soil surface was similar for both treatments and averaged 30% greater than measurements taken at the 0% cover plots on the ground (certainly due to a decrease in the amount of shading from the sides; all of the study trees were less than 1.5 m tall). Height growth was not correlated with the increase in light during summer (Figure 4), because trees in the 100% Cover treatment actually had greater growth in the spring and were able to continue growing throughout the summer (though at a reduced rate), whereas the trees in the 0% Cover treatment almost ceased growing by July. Trees in both treatments had greatest growth early in the season when light levels were very similar. An explanation for the greater growth of trees in the 100% Cover treatment is suggested by examining the monthly xylem water potential of trees in each treatment (Figure 5). The water potentials remain relatively high throughout the growing season, but there are significant differences between the treatments in spring and late summer. The trees growing surrounded by 100% Cover maintain a higher growth rate and a less negative xylem water potential than open-grown trees. Water is removed from the soil by the surrounding vegetation (mostly Whipplea and Viola sempervirens Greene; I could find no data on water use by these species), but the vegetation also shades the soil and the soil drying caused by these species is not as significant as the drying caused by evaporation in their absence. The Douglas fir tree in each 0% Cover area also must have greater evapotranspiration because of exposure to the sun, which results in more moisture removal from the soil. The seasonal soil water potentials for each treatment at the 0-15 cm depth are presented in Figure 6. (I am presenting only the 0-15 cm depth results, because the data for other depths were similar.) The soil at the 100% Cover treatment had more available moisture during the warm summer months and the trees on this treatment were able to continue growing during this period.

Cumulative total height growth was almost twice as much on the 100% Cover treatment (4.9 cm) as on the 0% Cover treatment (2.9 cm). Such differences are very significant for these small trees. Certain hardwood or shrubby invaders (i.e. Lithocarpus densiflora (H. & A.) Rehd. (tan oak) and Ceanothus thrysiflorus Esch. (blue blossom)) are the usual targets for herbicide treatments in these timber stands because they will shade the small conifers for many years. It is not justified, however to attempt control of the native herbaceous understory species to increase the establishment or growth of conifers. These understory species appear to provide an environment favorable to young tree growth, without producing serious competition. Secondary benefits such as improved soil stabilization, water quality, and wildlife habitat may also be realized by leaving the natural understory alone.

Experimental Sites - Polystichum Site

The average PPFD on the ground for the Polystichum treatments is shown in Figure 7. There is a significant difference ($p<.01$) between 2 swordfern clumps and 0 ferns, with 0 ferns receiving twice as much light during the summer. PPFD measurements taken at 1 m above the ground level for the two sites showed that the 0 fern treatment received only 19% more light at this height while the 2 fern treatment received 57% more light. The total PPFD and Douglas fir water potentials were consistently lower at the Polystichum site than at the Whipplea site.

The higher PPFD in the 0 fern treatment causes greater evapotranspiration and produces lower soil water potentials in the spring when compared with 2 fern treatment (Figure 8). Only with a decrease in the PPFD in the fall, and periods of precipitation, does the soil rewet. Figure 8 shows the relationship of PPFD to 0-15 cm depth soil water potential at the 0 fern treatment. (The 0-15 depth is used because it appears to be a good indicator of soil water conditions deeper in the profile. The soil water potentials (-MPa) for 0-15 cm, 16-45 cm, and 46-75 cm depths at the 0 fern treatment in July were .64, .97, and 1.69, respectively. A similar trend was shown for both treatments for the entire season.)

The overall effect of this drying of the soil seems to be an absence of swordfern from the microsite that receives the most light. Douglas fir seedling height growth for the entire period April-October does not appear to be adversly effected by the drying of the sun or by the presence of swordfern clumps (Figure 9), but there is a slight apparent difference in the period of growth between the two treatments. The 0 fern treatment trees appear to have a greater percentage of their seasonal growth in the spring while the 2 fern treatment trees have a greater percentage in the fall. The seasonal xylem water potentials of trees in the two treatments (Figure 10) show that the 0 fern treatment trees have less negative water potentials in the spring than the 2 fern treatment trees, but the difference is very slight and in any case values are quite low.

The height growth of the Douglas fir trees near fern clumps was similar to open grown trees (12.5 cm per yr and 10.2 cm per yr respectively). However, there appears to be a slight difference in sites between the 0 fern and 2 fern treatment areas. There could have been a better control on this experiment to determine the effect of swordfern clumps on tree height growth by first locating trees near 2 fern clumps and then randomly choosing certain trees and removing the ferns from around them and following their growth rate. Nevertheless, the height growth exhibited by the 2 fern treatments trees was significant (>10 cm yr) and does not indicate that swordfern was providing serious competition to the young trees once they were established.

Experimental Sites - Redwood Site

The PPFD at the Redwood site reached levels during the summer about three times that of the other experimental sites. There were significant differences ($p<.01$) of PPFD in June and July between the 0% cover treatment and the 100% cover treatment, and the 0% cover treatment showed a trend of receiving more light than the 100% cover treatment for each month of the year (Figure 11). The PPFD at 1 m height was the same for both treatments and averaged 28% more light than on the ground. In both treatments adequate light reaches the small trees as shown by the sustained height growth (described later).

The high radiation levels had a major effect on soil moisture. The two treatments were basically similar at the 0-15 cm throughout most of the growng season (Figure 12). The soil became steadily drier over the growing season and tree water potentials for each treatment also decreased though a recovery occurred by September when rains occurred (Figure 13). This effect was most pronounced at the Redwood site because the study trees (coast redwood) had been planted from containers less than a year before and were still shallowly rooted (as evidenced by digging up a few trees and examining the root systems).

Diurnal water potential measurements were made on July 24, 1983 for a sample of trees from the 0% cover treatment, 100% cover treatment, and of a coast redwood sprout clump that was near the planted seedlings (Figure 14). This was a warm summer day (maximum temperature on the ground in direct sunlight was 39°) with no coastal fog in either the morning or afternoon. There was a significant difference ($p<.01$) at all time periods between the three sampling groups. Redwood sprouts had the least negative water potential throughout the day, but exhibited a larger decrease in the afternoon than the seedlings. The 0% cover treatment had a decreased water potential of -0.4 MPa by 1000 hrs, but had some recovery during the afternoon. The 100% cover treatment started with the lowest water potential (-2.35 MPa) and only slightly decreased to -2.48 MPa at 1200 hrs, when perhaps stomatal closure brought about an increase in water potential by the late afternoon.

The higher water potential of the sprout clump is easily explained by the larger root system the sprouts inherited from the cut mother tree. The diurnal differences are not very great for any of the samples chosen and indicate that stomatal control and/or plant water uptake processes are able to supply the tree's water requirements during these warm and dry periods. The absolute differences in water potential between the 0% cover treatment and the 100% cover treatment, averaging -1.0 MPa cannot be explained. The soil water potential is similar at each treatment, so competition by surrounding vegetation on the 100% cover treatment is only an indirect cause. It is possible that root competition by encircling vegetation has retarded root system development of the trees in the 100% cover treatment and the roots cannot take up water as fast as the trees in the 0% cover treatment.

The decreasing water potentials of the 100% cover treatment trees appear to slow seasonal height growth. The 0% cover treatment trees maintain a higher growth rate longer into the dry season (June-September) than the 100% cover treatment trees (Figure 15), though all of the trees had some growth during the summer and as late as November. (In contrast, all of the Douglas fir trees at the other experimental sites ceased growing by late September). The yearly average total growth for the trees was 11.9 cm for the 0% cover treatment and 7.6 cm for the 100% cover treatment. There was complete survival of all of the trees throughout the experiment.

Experimental Sites - Adjustments To Drought Stress

To assess the ability of small conifers to adjust to relative drought stress (or removal of drought stress) measurements of the relative water content in relation to the inverse balance potential were made for trees from each treatment at the end of the experiment (Figures 16, 17, and 18). The extrapolated Y-intercept of each curve reflects differences in tissue osmotic properties. The slope of the curve reflects differences in tissue elastic properties. In order to grow, the tree must maintain positive cell turgor pressure. As water becomes less available to the tree due to competition, decreased precipitation, or increased transpiration (or all of these), some internal adjustment must eventually be made or the tree will cease growing.

The 0% cover treatment and 100% cover treatment trees from the Redwood site show surprisingly similar curves (Figure 16). The 100% cover treatment trees show no ability to osmotically adjust in the dry summer months. The xylem water potential of these trees decreased (Figure 13) and there was a resulting decline in growth rate. The Douglas fir trees in both treatments of the Polystichum site show the same trend (Figure 17) of no osmotic adjustment among the treatments. This is not unexpected, since there was no large difference in the xylem water potential of these trees over the course of the experiment.

A significant difference does appear between the Douglas fir trees of the 0% cover treatment and the 100% cover treatment of the Whipplea site. The curves have similar slopes but there is an offset in the Y-intercept. The trees from the 0% cover treatment have a lower relative water content at the same inverse balance potential as the trees of the 100% cover treatment. The 0% cover treatment trees had lower xylem water potentials during the dry months of the experiment and apparently made osmotic adjustment to maintain cell turgor. These trees did have a decline in growth rate for this period when compared with the 100% cover trees.

Natural regeneration of conifers in partially harvested stands can be sufficient to provide adequate stocking for maintenance of conifers on the site. Certain harvesting procedures enhance the establishment of certain conifer species. Removal of potential overstory seed trees of grand fir and hemlock will greatly reduce the number and extent of these species in the stand. Douglas fir readily establishes from seed, particularly on skid roads with heavily churned soil; following a series of partial harvests it could remain as the sole co-dominant with coast redwood in these stands. Coast redwood has poor initial establishment from seed, but stump sprouts arise from almost 100% of the cut second-growth trees so there is no chance of the species disappearing from these managed stands. In general, harvesting operations that expose top soil (tractor skidding) favor coast redwood seedling establishment. The development of natural conifer regeneration under partial cut overstory to permit continuance of partial cutting with the intent to develop an unevenaged stand has been less than desirable on some test plots in this area (Lindquist 1986). Rather, the next harvest may be a regeneration cut (clearcut), leading to development of an evenaged structure. Continued monitoring of the fate of small trees in partial harvests will help determine the effect of each system.

It is evident that native herbaceous vegetation surrounding the young trees does not adversely effect their water status. The native herbaceous species grow concurrently with the conifer seedlings (Douglas fir in this study) during the spring when adequate soil moisture exists, so little competition occurs. The study sites had exceptionally high precipitation during the period of this study, therefore competition could be more serious during drought situations. Soil moisture is actually more plentiful later in the growing season at plots having native herbaceous understory vegetation that shades the soil than on cleared plots. Most of the native herbaceous vegetation that establishes following timber harvesting does not inhibit the growth of conifer seedlings by diminishing sunlight. Introduced weedy herbaceous species, however, did slow height growth of planted coast redwood and some control measures would be advisable to maximize conifer production.

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Table 1. The harvest intensities of eight partially logged stands in northern California (average size about 150 ha). Catagories shown are: Year of harvest; volume cut, represented as cubic meters per hectare (m^{-3} ha^{-1}); basal area cut is a percentage of the original stand basal area (% BA); and the relative amount cut of coast redwood (% RW), Douglas fir (% DF), and other conifers (% Other, viz. grand fir, hemlock, and Bishop pine). Data from harvest records provided by the California Department of Forestry and data for both tractor- and cable-logged areas were similar and are shown combined in this table.

Year Cut	m^{-3} ha^{-1}	% BA	% RW	% DF	% Other
1971	82.90	59.2	50.0	33.0	17.0
1972	86.11	68.6	53.0	39.0	8.0
1973	66.28	64.5	70.0	29.0	1.0
1974	73.29	40.3	28.0	52.0	20.0
1975	69.28	38.1	44.0	52.0	4.0
1976	79.10	43.5	44.0	46.0	10.0
1977	56.47	31.1	40.0	40.0	20.0
1978	74.89	41.3	40.0	41.0	19.0

Table 2. Conifer seedling regeneration (number per hectare) from eight partially harvested coast redwood stands in northern California. Three stands were tractor-logged, four were partly tractor- and partly cable-logged, and one stand was cable-logged only. The intensities of harvest (Table 1) were equal for each given year, so corresponding tractor and cable sites had similar amounts of overstory trees removed.

Year	Method	Redwood	Douglas fir	Grand Fir	Hemlock	Other	TOTAL
1971	Tractor	558	1238	1524	1109	0	4429
1972	Tractor	832	2764	338	366	0	4300
1973	Tractor	439	2574	308	12	0	3333
1974	Tractor	103	1039	6516	936	26	8594
	Cable	88	990	1028	276	0	2382
1975	Tractor	171	1356	922	26	26	2475
	Cable	41	716	143	0	0	900
1976	Tractor	67	2579	124	0	0	2770
	Cable	18	109	36	0	9	163
1977	Tractor	15	1284	92	15	0	1406
	Cable	0	617	569	0	0	1186
1978	Cable	55	558	21	0	0	634
Unlogged		77	44	-	-	-	121

Table 3. The number of clumps of coast redwood sprouts formed (per hectare) after partial harvesting in a series of stands in northern California. Year of harvest is shown. Three stands were tractor-logged, four tractor- and cable-logged, and one stand cable logged.

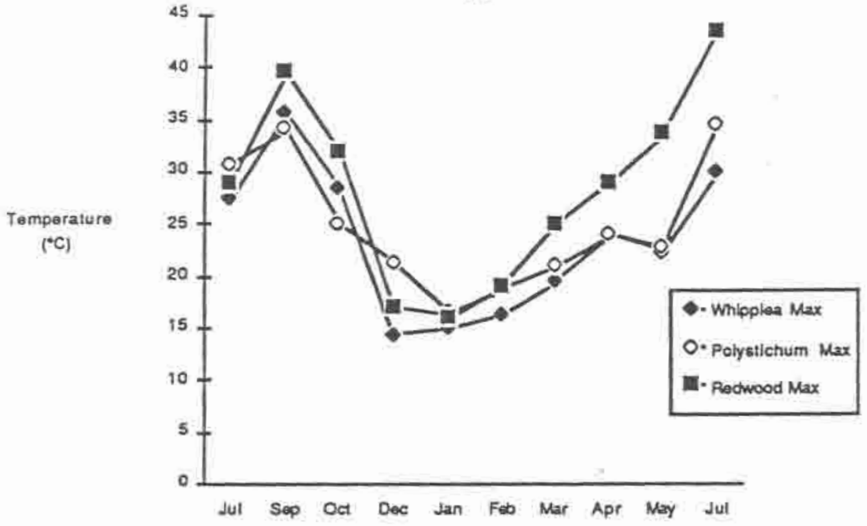
Year	Method	Sprout Clumps
1971		
	Tractor	255
1972		
	Tractor	410
1973		
	Tractor	616
1974		
	Tractor	347
	Cable	213
1975		
	Tractor	540
	Cable	471
1976		
	Tractor	279
	Cable	110
1977		
	Tractor	413
	Cable	237
1978		
	Cable	221
Unlogged		17

Table 4. Average heights (cm) of conifers that have naturally reseeded partially harvested stands in the coast redwood forest. Heights of tractor-logged and cable-logged areas that were logged in the same year that are significantly different ($P < .001$) are indicated by ***. The year of each harvest is shown in the left column. Three stands were tractor logged, four stands were partly tractor- and partly cable-logged, and one stand was cable logged only. The coast redwood heights are somewhat inflated because some tall sprouts were probably erroneously included with seedling measurements.

Year	Method	Redwood	Douglas fir	Grand fir
1971				
	Tractor	127.9	83.7	139.5
1972				
	Tractor	92.7	51.5	83.4
1973				
	Tractor	126.9	55.8	81.8
1974				
	Tractor	163.1	61.0	51.1
	Cable	120.9	59.7	46.8
1975				
	Tractor	113.8	33.5	56.9
	Cable	165.0	69.8***	34.0***
1976				
	Tractor	39.3	32.5	26.5
	Cable	15.0	23.9	23.3
1977				
	Tractor	28.0	12.3	13.6
	Cable	-	20.4 ***	25.3***
1978				
	Cable	59.9	8.7	15.3

Figure 1. Maximum (A) and minimum (B) monthly temperatures from three experimental sites in the coast redwood forest.

A


45
40
35
30
25
20
15
10
5
0
Temperature
(°C)
Jul
Sep
Oct
Dec
Jan
Feb
Mar
Apr
May
Jul
Whipplea Max
Polystichum Max
Redwood Max

B

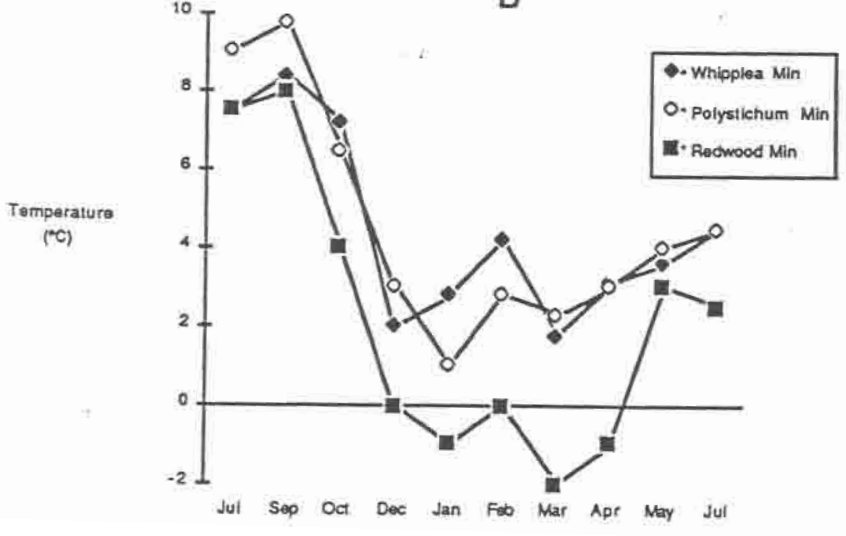
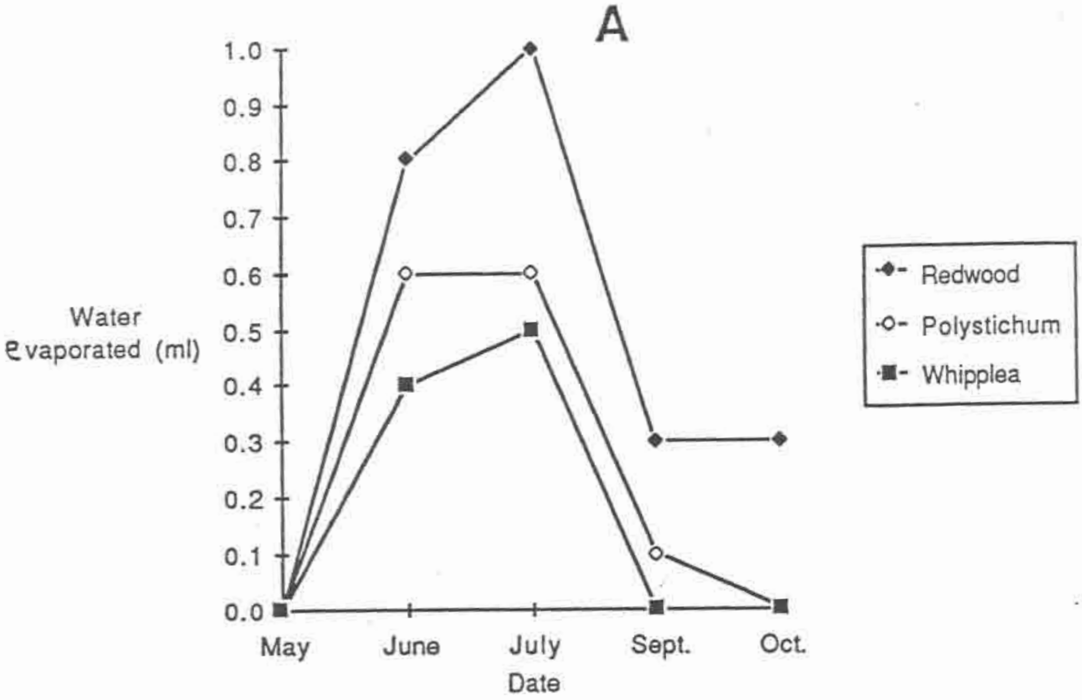

10
8
6
4
2
0
-2
Temperature
(°C)
Jul
Sep
Oct
Dec
Jan
Feb
Mar
Apr
May
Jul
Whipplea Min
Polystichum Min
Redwood Min

Figure 2. Relative potential evaporation was measured at three experimental sites in the coast redwood forest with Piche atmometer tubes. Data are shown for two daily periods: (A) sunrise (approx. 600 hrs local time) to noon (1200 hrs local time), and (B) noon to sunset (approx. 1700 hrs local time).


A
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Water
evaporated (ml)
May
June
July
Sept.
Oct.
Date
Redwood
Polystichum
Whipplea

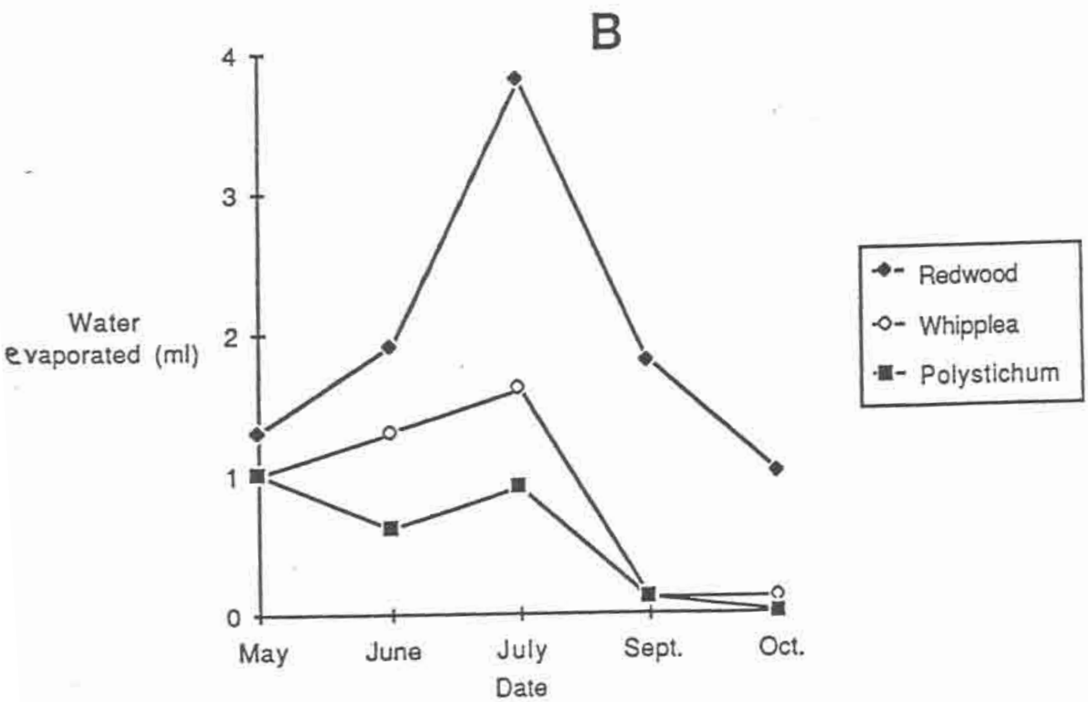

B
4
3
2
1
0
Water
evaporated (ml)
May
June
July
Sept.
Oct.
Date
Redwood
Whipplea
Polystichum

Figure 3. The average daily photosynthetic photon flux density on the ground for the Whipplea experimental site. The 0% cover area was cleared of all understory vegetation and the 100% cover area was undisturbed.

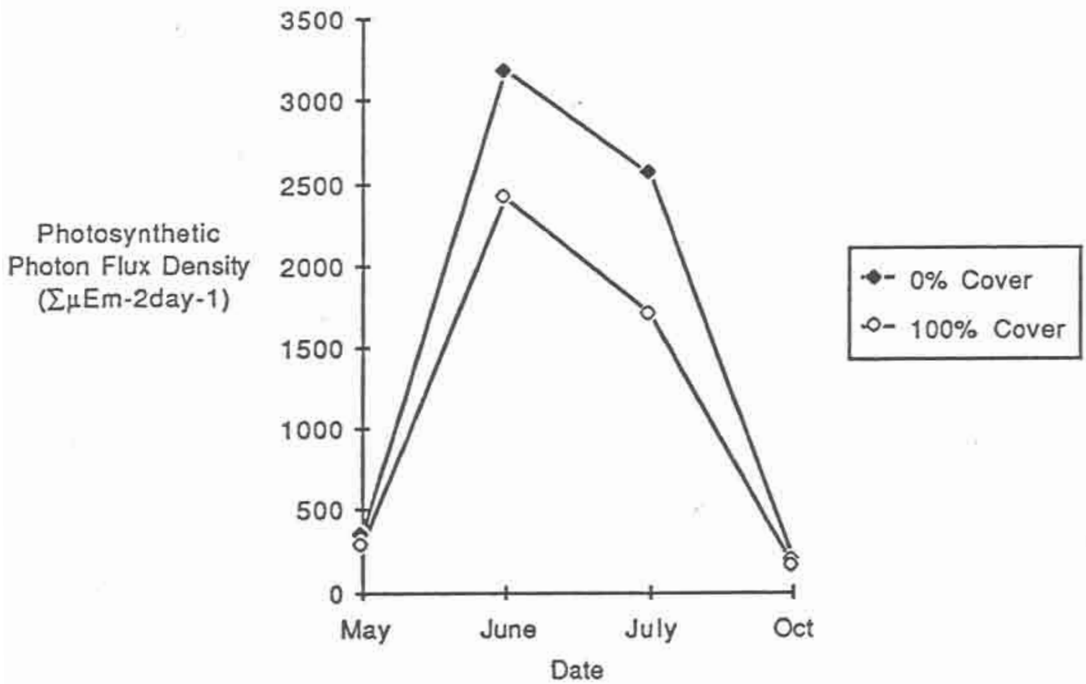
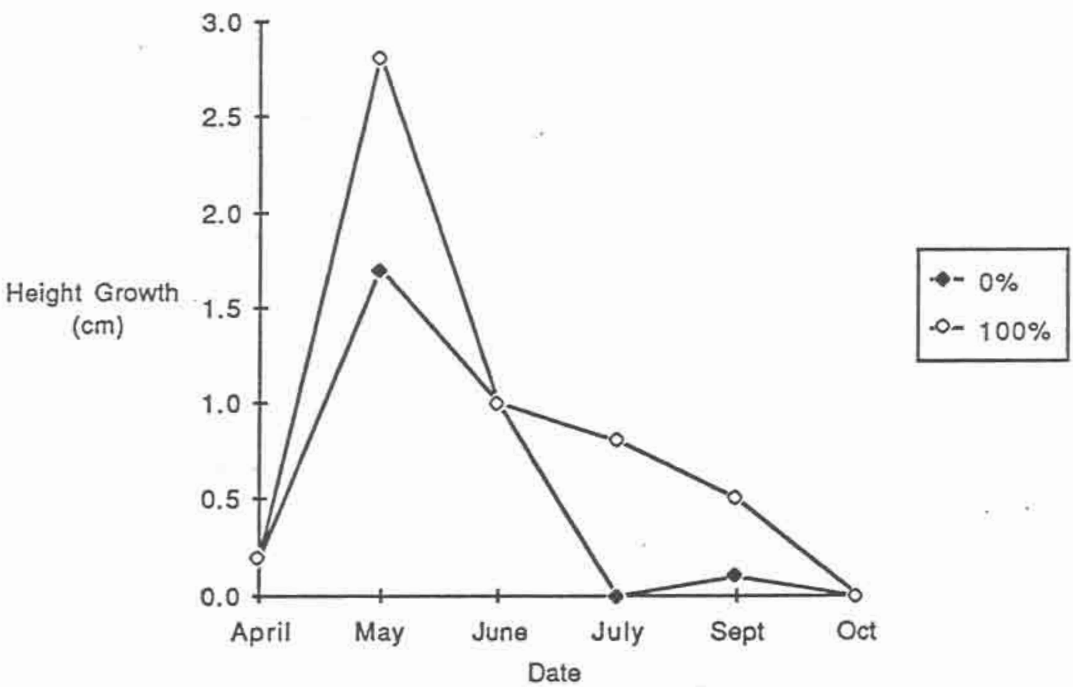
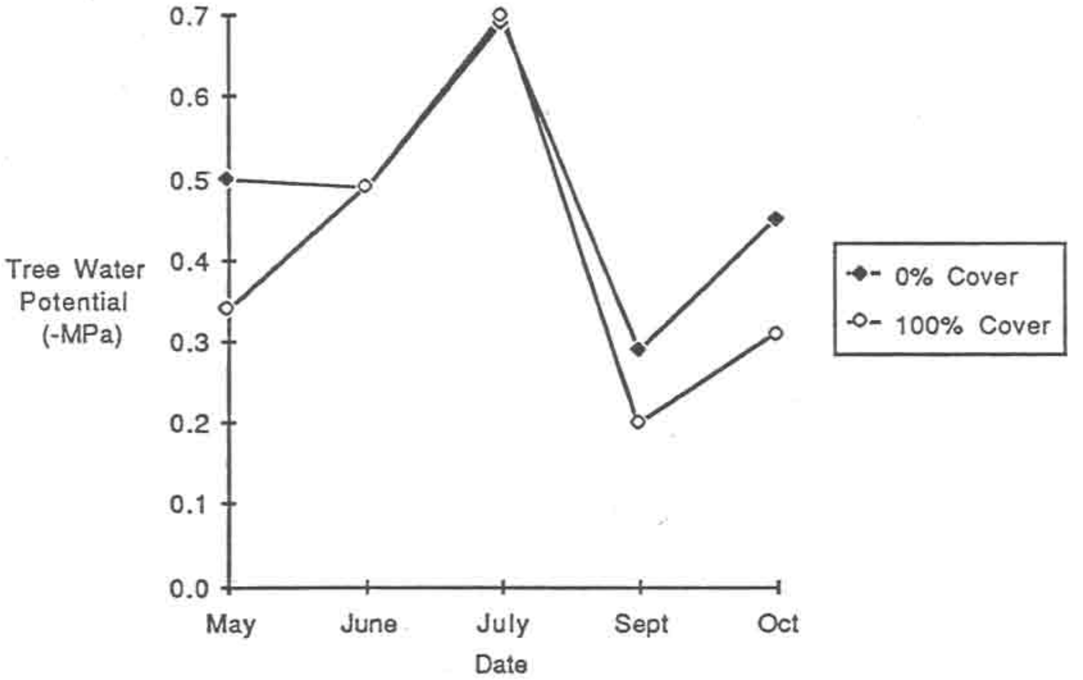

3500
3000
2500
2000
1500
1000
500
0
Photosynthetic
Photon Flux Density
(ΣμEm-2day-1)
May
June
July
Oct
Date
0% Cover
100% Cover

Figure 4. The average monthly increase in height growth of Douglas fir seedlings at the Whipplea experimental site. The 0% cover area was cleared of all understory vegetation and the 100% cover area was undisturbed.



3.0
2.5
2.0
1.5
1.0
0.5
0.0
Height Growth (cm)
April
May
June
July
Sept
Oct
Date
0%
100%

Figure 5. Average seasonal pre-dawn xylem water potentials for Douglas fir seedlings at the Whipplea experimental site. The 0% cover area was cleared of all understory vegetation and the 100% cover area was undisturbed.



0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Tree Water Potential (-MPa)
May
June
July
Sept
Oct
Date
0% Cover
100% Cover

Figure 6. The average seasonal soil water potential of a composite soil sample from 0-15 cm depth. The 0% cover area was cleared of all understory vegetation and the 100% cover area was undisturbed.

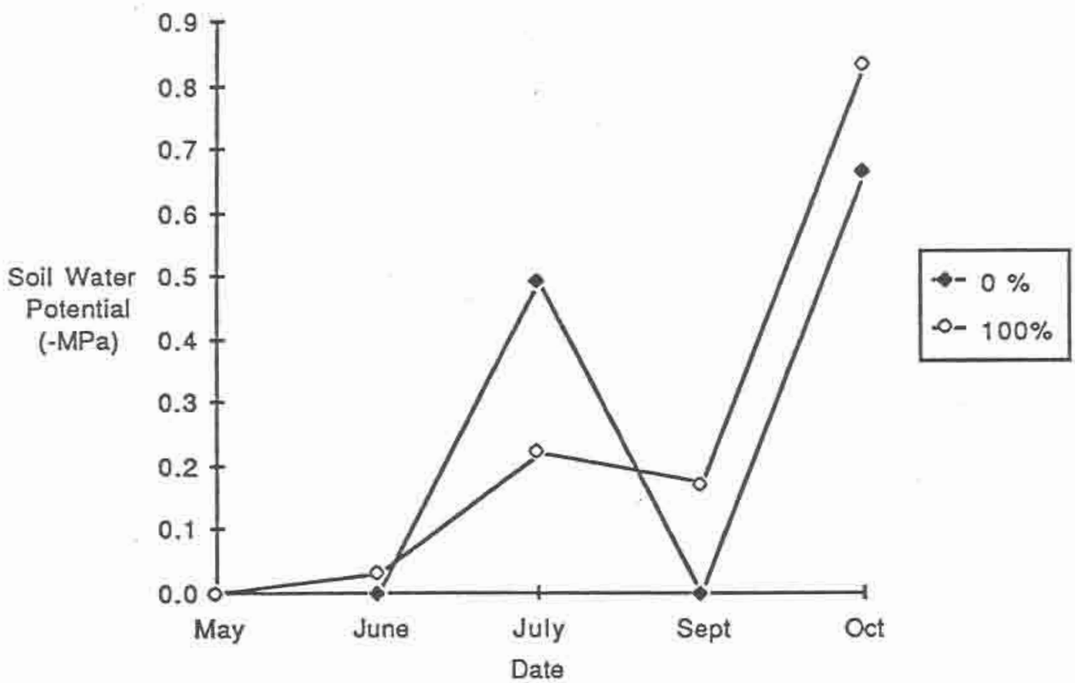
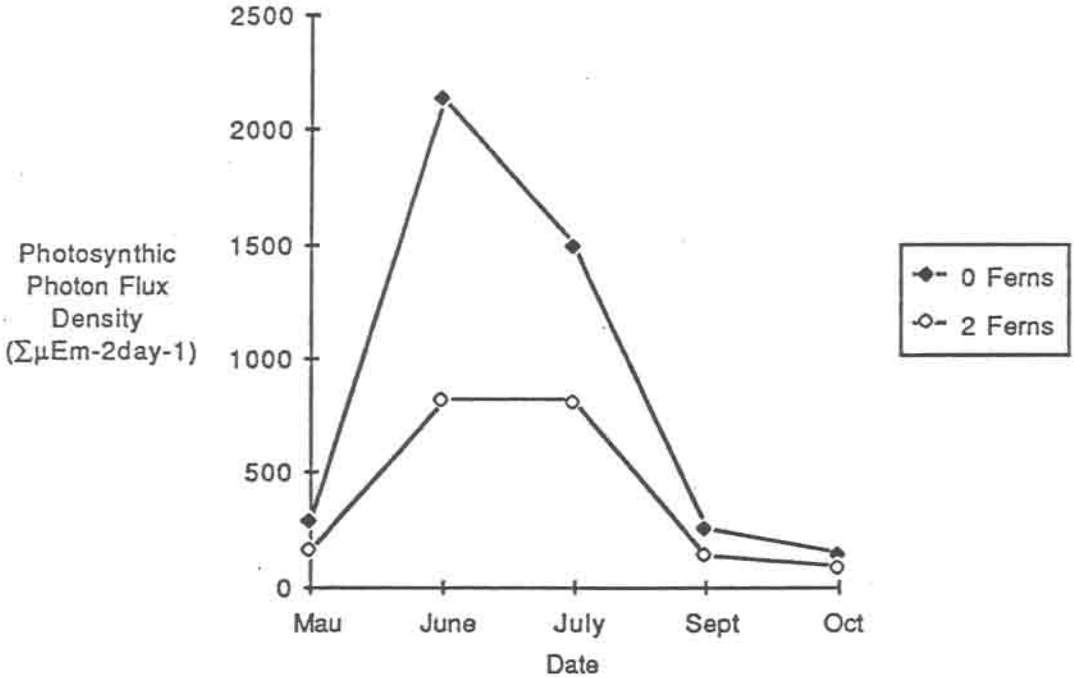

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Soil Water Potential (-MPa)
May
June
July
Sept
Oct
Date
0 %
100%

Figure 7. The average daily photosynthetic photon flux density on the ground for the Polystichum experimental site. The '0 Ferns' locations had no Polystichum munitum within one meter, the '2 Ferns' locations had two clumps of Polystichum munitum within 1 m of the sampling point.



2500
2000
1500
1000
500
0
Photosynthic
Photon Flux
Density
(ΣμEm-2day-1)
Mau
June
July
Sept
Oct
Date
0 Ferns
2 Ferns

Figure 8. The seasonal soil water potential of a composite sample from a depth of 0-15 cm for the Polystichum experimental site. The '0 Ferns' locations had no _Polystichum munitum_ within one meter, the '2 Ferns' locations had two clumps of _Polystichum munitum_ within one meter of the sampling point. The average photosynthetic photon flux density for areas having '0 Ferns' from the Polystichum experimental site is also shown.

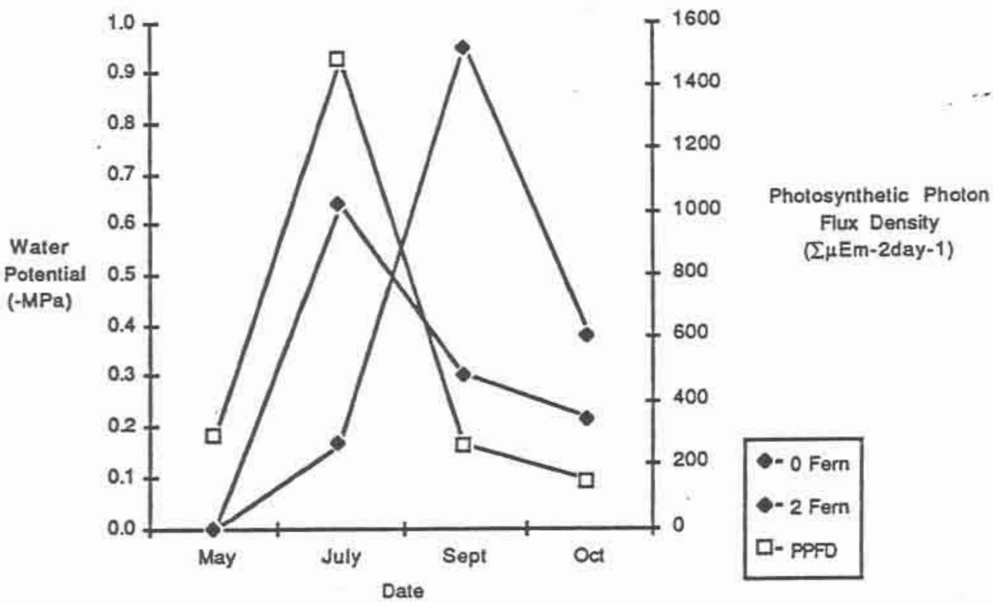

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Water
Potential
(-MPa)
1600
1400
1200
1000
800
600
400
200
0
Photosynthetic Photon
Flux Density
(ΣμEm-2day-1)
May
July
Sept
Oct
Date
0 Fern
2 Fern
PPFD

Figure 9. Average monthly height growth of Douglas fir trees from the Polystichum experimental site. The '0 Ferns' locations had no Polystichum munitum within 1 m, the '2 Ferns' locations had two clumps of Polystichum munitum within 1 m of the sampling point.

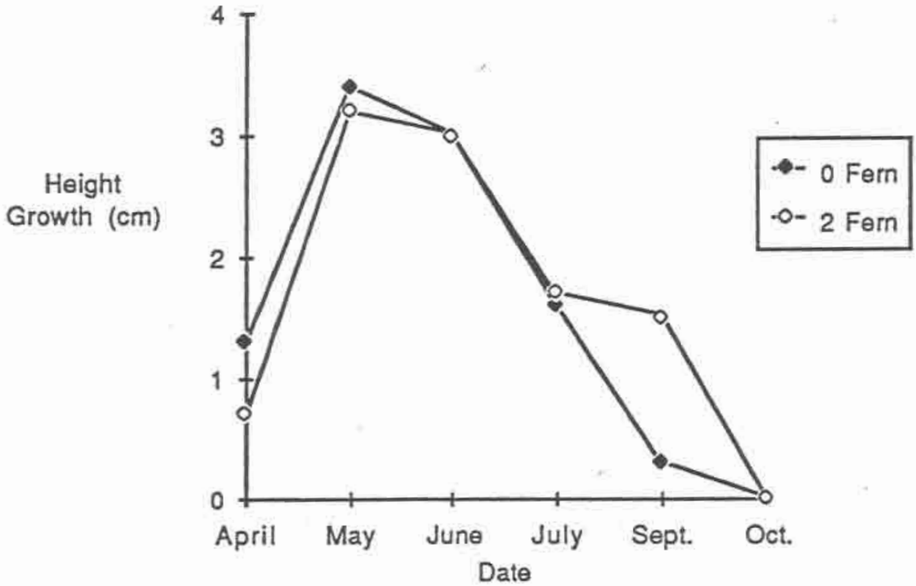
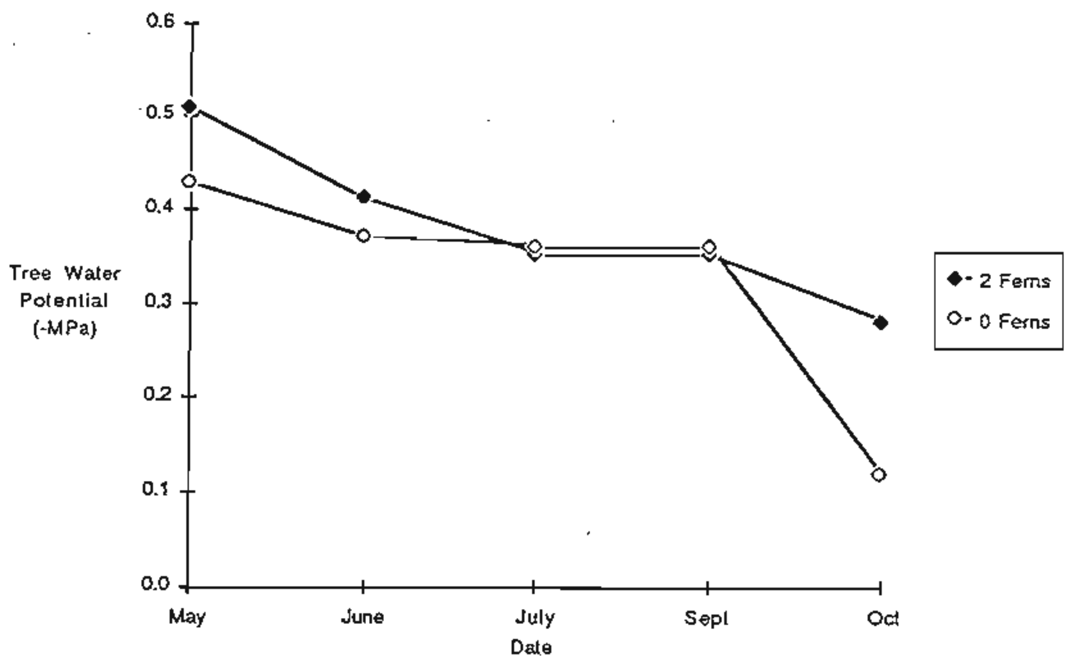
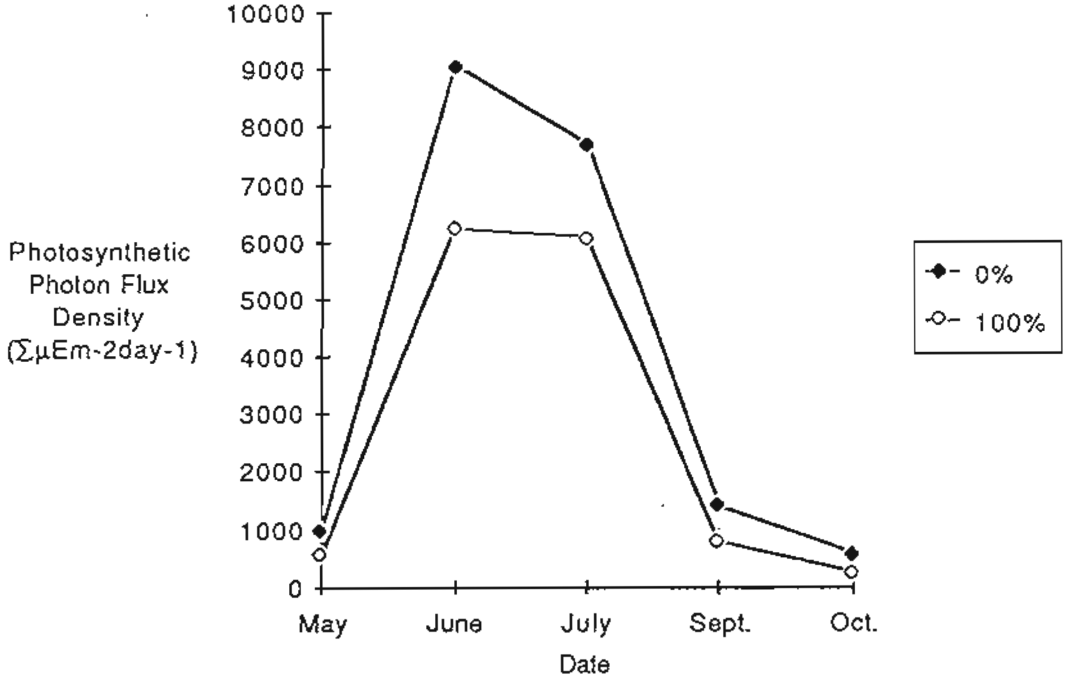

4
3
2
1
0
Height
Growth (cm)
April
May
June
July
Sept.
Oct.
Date
0 Fern
2 Fern

Figure 10. The seasonal average pre-dawn xylem water potential for Douglas fir trees from the Polystichum experimental site. The '0 Ferns' locations had no Polystichum munitum within 1 m, the '2 Ferns' locations had two clumps of Polystichum munitum within 1 m of the sampling point.



0.6
0.5
0.4
0.3
0.2
0.1
0.0
Tree Water
Potential
(-MPa)
May
June
July
Sept
Oct
Date
2 Ferns
0 Ferns

Figure 11. The average photosynthetic photon flux density on the ground for the Redwood experimental site. The 0% cover site was cleared of all understory vegetation and the 100% cover site was undisturbed.



10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
Photosynthetic Photon Flux Density (ΣμEm-2day-1)
May
June
July
Sept.
Oct.
Date
0%
100%

Figure 12. The average seasonal soil water potential (0-15 cm depth) for the Redwood experimental site. The 0% cover site was cleared of all understory vegetation and the 100% cover site was undisturbed.

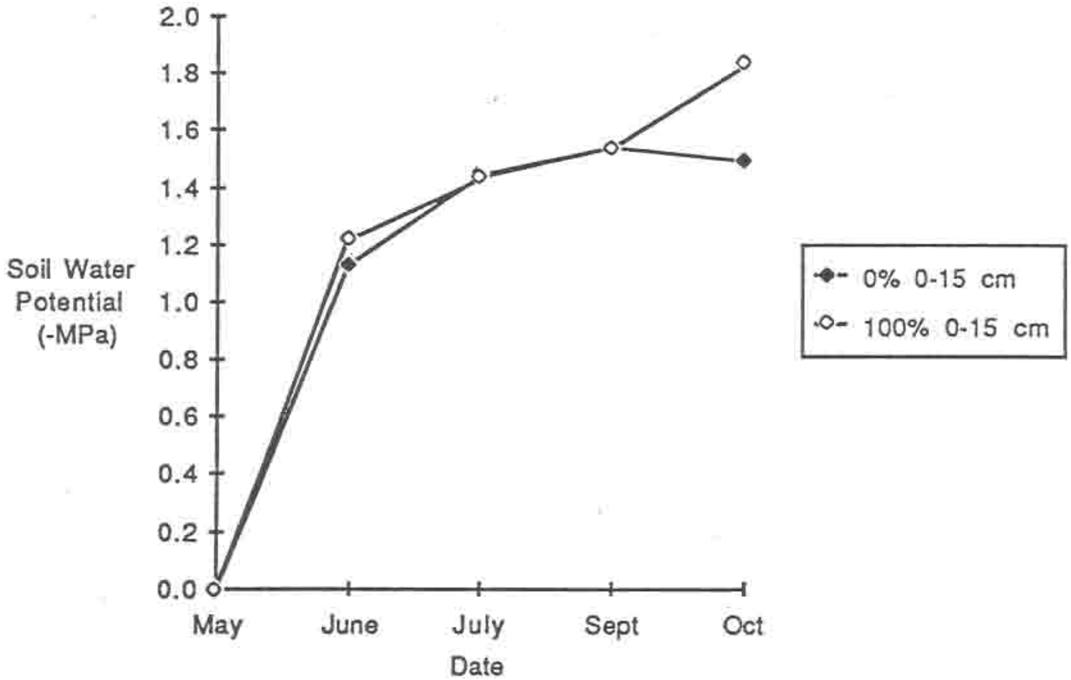
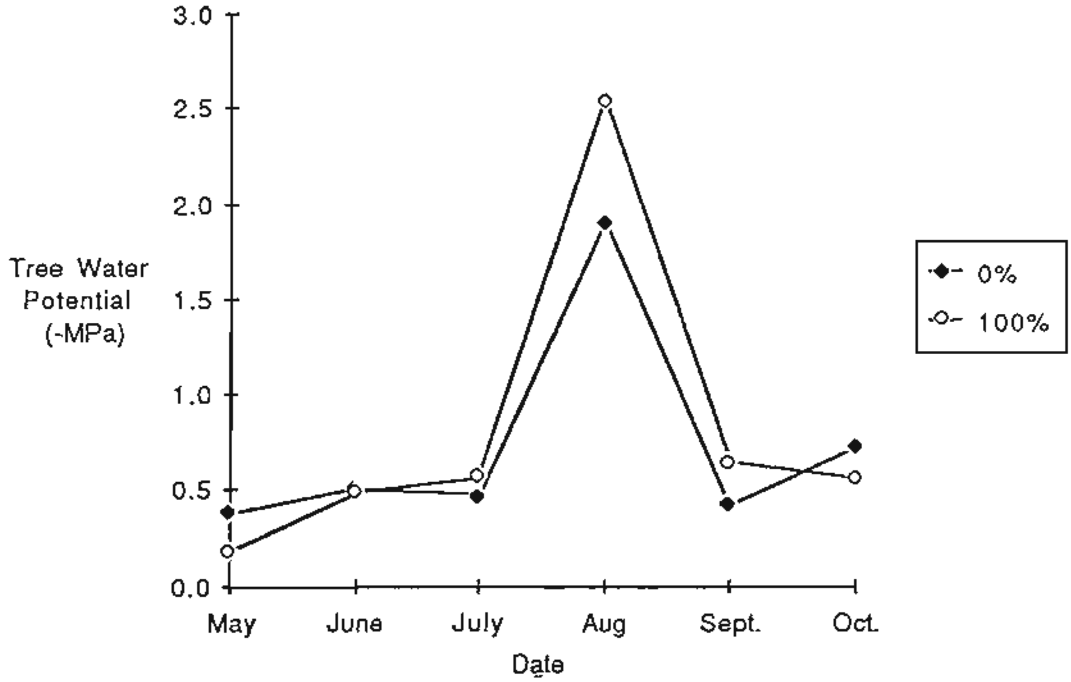
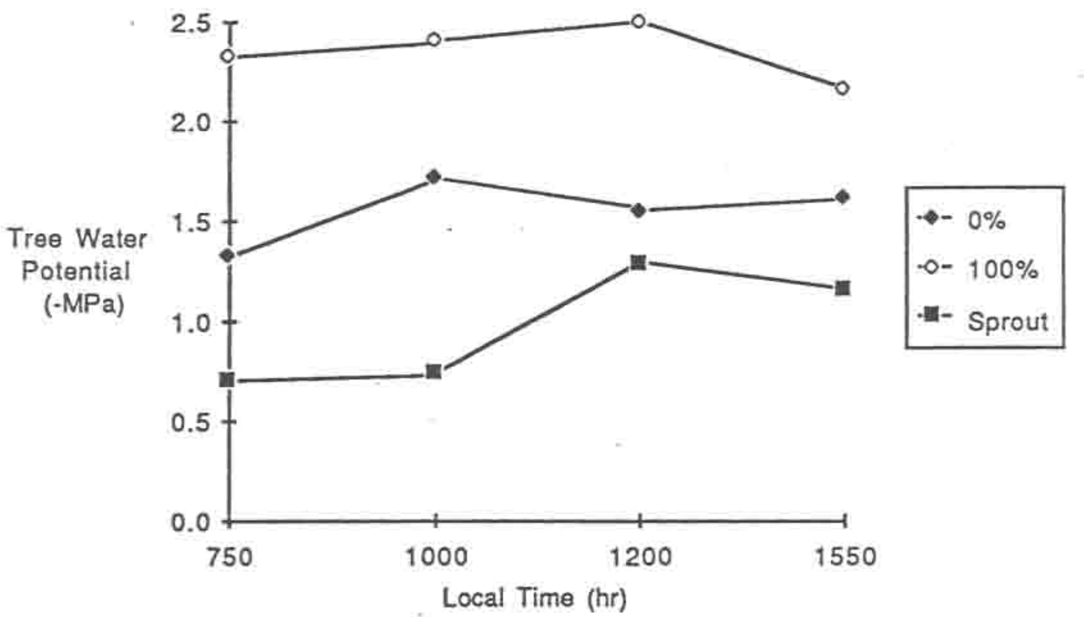

2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Soil Water Potential (-MPa)
May
June
July
Sept
Oct
Date
0% 0-15 cm
100% 0-15 cm

Figure 13. Average seasonal pre-dawn xylem water potential for coast redwood seedlings at the Redwood experimental site. The 0% cover site was cleared of all understory vegetation and the 100% cover site was undisturbed.



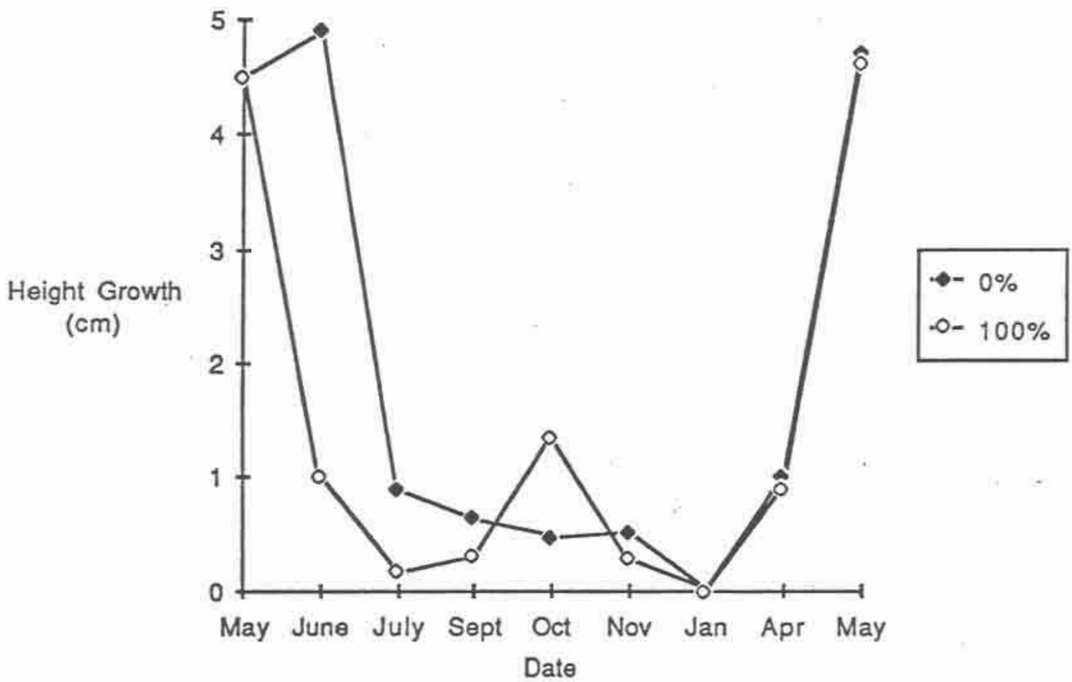
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Tree Water
Potential
(-MPa)
May
June
July
Aug
Sept.
Oct.
Date
0%
100%

Figure 14. Average diurnal xylem water potential curves for three types of samples (two coast redwood seedling groups and one sprout clump) from the Redwood experimental site. The 0% cover site was cleared of all understory vegetation and the 100% cover site was undisturbed. A nearby undisturbed coast redwood sprout clump of approximately the same age as the seedlings was also sampled.



Tree Water Potential (-MPa)
2.5
2.0
1.5
1.0
0.5
0.0
750
1000
1200
1550
Local Time (hr)
0%
100%
Sprout

Figure 15. Average seasonal height growth of coast redwood seedlings from the Redwood experimental site. The 0% cover site was cleared of all understory vegetation and the 100% cover site was undisturbed.



5
4
3
2
1
0
Height Growth
(cm)
May
June
July
Sept
Oct
Nov
Jan
Apr
May
Date
0%
100%

Figure 16. Pressure-volume curves for coast redwood seedlings grown for one year under the following treatments. One set of trees (0% Cover) had all surrounding understory vegetation removed to a distance of one half meter. The other set of trees (100% Cover) had undisturbed surrounding vegetation.

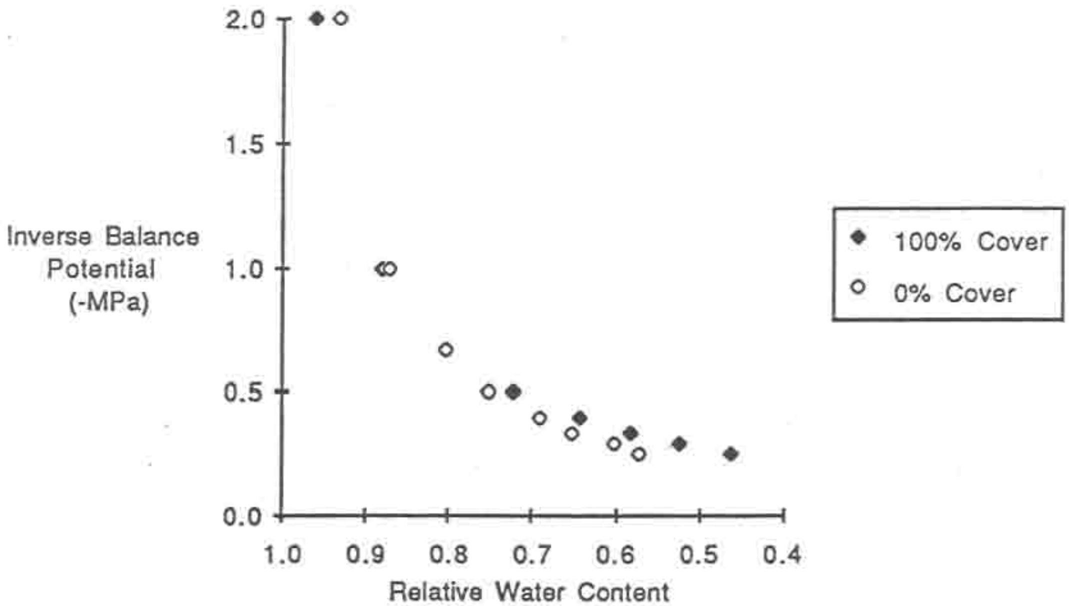
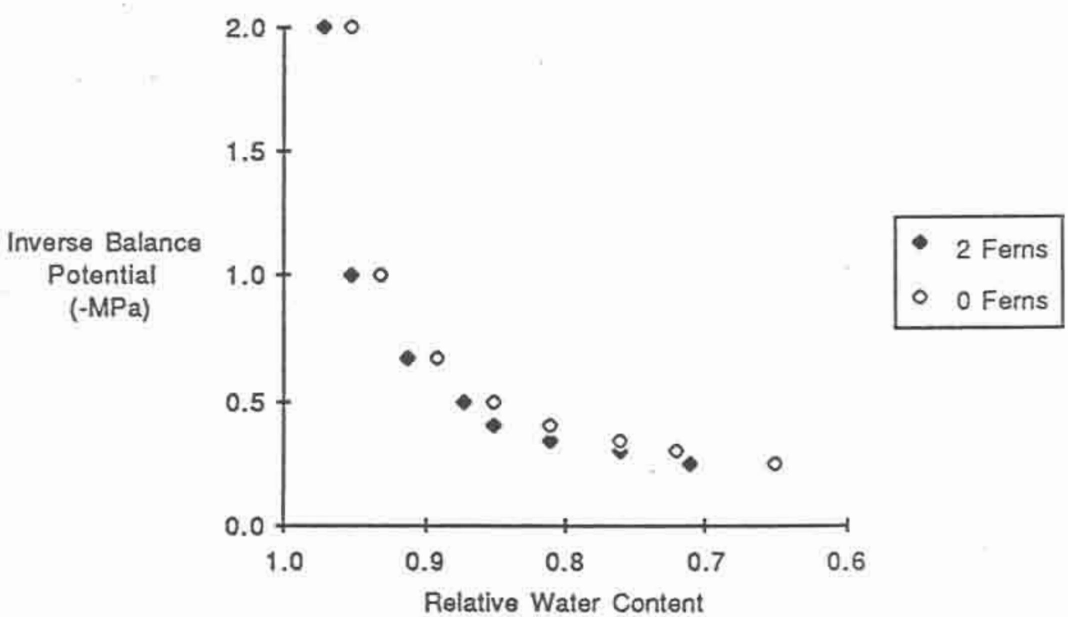
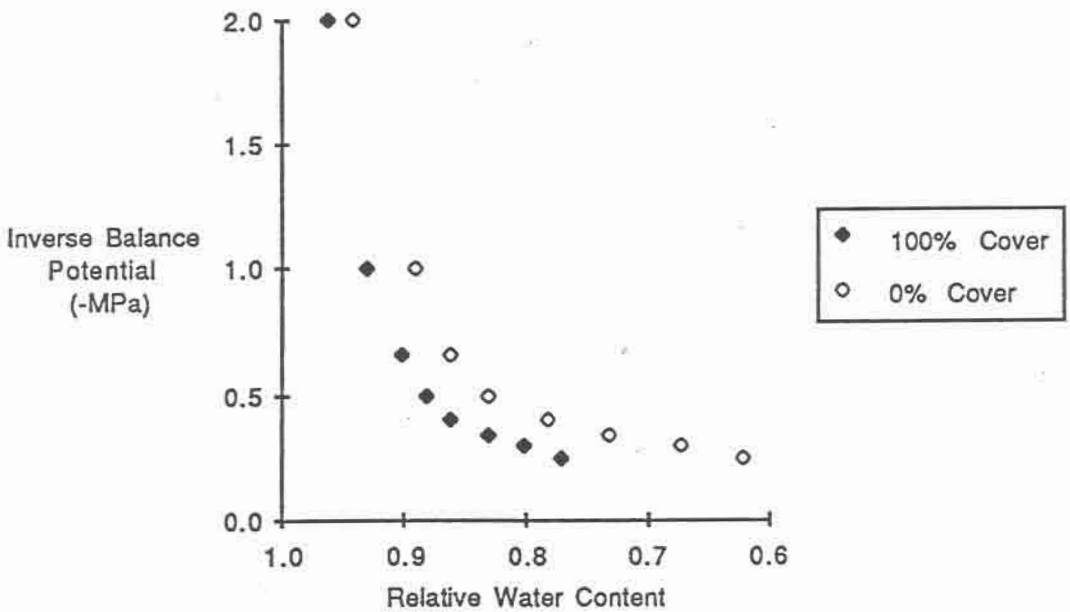

2.0
1.5
1.0
0.5
0.0
Inverse Balance
Potential
(-MPa)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Relative Water Content
100% Cover
0% Cover

Figure 17. Pressure-volume curves for Douglas fir seedlings grown for one year under the following treatments. One set of trees (0 Ferns) had no surrounding vegetation or swordfern clumps within 1 m. The other set of trees (2 Ferns) was growing within 1 m of two clumps of swordfern.



Inverse Balance
Potential
(-MPa)
2.0
1.5
1.0
0.5
0.0
1.0
0.9
0.8
0.7
0.6
Relative Water Content
2 Ferns
0 Ferns

Figure 18. Pressure-volume curves for Douglas fir seedlings grown for one year under the following treatments. One set of trees (0% Cover) had all surrounding understory vegetation removed to a distance of one half meter. The other set of trees (100% Cover) had undisturbed surrounding vegetation.


2.0
1.5
1.0
0.5
0.0
Inverse Balance
Potential
(-MPa)
1.0
0.9
0.8
0.7
0.6
Relative Water Content
100% Cover
0% Cover