

MOISTURE, NUTRIENT, AND INSECT CONSTRAINTS ON PLANTATION GROWTH: THE "GARDEN OF EDEN" STUDY

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ABSTRACT

Factorial combinations of insect, nutrient, and weed control treatments were applied repetitively to eight *Pinus ponderosa* Dougl. ex Laws. var. *ponderosa* (ponderosa pine) plantations across a broad span of site qualities in California. Findings from the first 6 years showed that plantation growth potential was several times greater than previously realised. On the average, tree volumes from combined treatments were 4 times greater than for untreated controls. Sites of poor quality were limited primarily by soil drought, and fertiliser offered no further advantage over weed control alone. However, droughty sites often are infertile. Weeding not only improved moisture availability, but improved nutrient availability as well, and the joint effects were not easily separated. Controlling vegetation repeatedly with herbicides tripled volume growth and produced significant increases in foliar nutrient concentrations. Sites of medium quality also were limited by soil drought as well as by soil infertility. However, fertiliser application without vegetation control boosted weed growth which in turn blocked trees from a fertiliser response. Plantations on the best sites responded positively to both herbicides and fertilisers and effects were additive when treatments were combined. Despite an extreme range of site and plant stress conditions, insects had little influence on plantation development. Enhanced soil fertility and elevated foliar nutrient concentrations did not render trees more susceptible to insects. Thus, insecticides had no effect on tree growth. Findings suggest that weed control is essential for plantation development on poor sites under the Mediterranean climatic conditions, but not on better sites. Fertiliser responses are expected to continue for several years.

Keywords: plant competition; weed management; fertiliser; herbicides; insecticides; *Pinus ponderosa*.

INTRODUCTION

Pacific ponderosa pine is the most widely planted tree in California. Despite recent reductions in clearcutting on federal lands and trends toward more reliance on natural regeneration, ponderosa pine will continue to be planted extensively after wildfires, brushfield conversions, and in forest operations where natural regeneration is unreliable. On private lands it continues to be planted extensively. Thus, plantation silviculture will remain

an important aspect of ponderosa pine management in California. Because plantations will serve an increasingly important role in California's wood production, there is an acute need to understand how interacting factors affect plantation productivity and sustainability.

Woody shrubs adapted to California's summer-dry climate are regarded as pine's strongest competitor. Foremost are manzanita (*Arctostaphylos* sp. L.), an evergreen genus, and ceanothus (*Ceanothus* sp. L.), a genus that includes both evergreen and deciduous species. After disturbance, dense communities of manzanita and ceanothus form quickly from both seeds and sprouts. In time, they may reach heights of 2 m or more. Shainsky & Radosevich (1986) showed that tree growth was reduced substantially by as little as 25% ground cover of manzanita. Earlier, Oliver (1984) reached similar conclusions and found that this relationship was unrelated to site quality. Fiske (1982) concluded that pine plantations undergoing average competition from manzanita ultimately would fail.

Moisture availability clearly is the most common factor limiting plant growth in temperate regions of Mediterranean climate. Consequently, competition for soil moisture is considered the main mechanism of interaction between ponderosa pine and other vegetation. McDonald & Fiddler (1990) reported that predawn plant water potentials were 0.7 MPa higher in pine plots kept shrub-free with herbicides. Minimum potentials for pine in untreated plots occurred by midmorning, but this was delayed another 5 hours where vegetation was controlled. Ponderosa pine closes its stomates when plant water potentials fall below -1.2 MPa (Lopushinsky 1969), which can happen a few hours after sunrise during our dry summer. Thus, trees free of weed competition may extend their photosynthetic periods beyond the morning hours during summer months. In contrast, manzanita endures daily water potentials far lower than ponderosa pine because it seems to lack stomatal regulation (R.F. Powers and P.E. Reynolds unpubl. data), and is capable of drying the soil profile to considerable depth during the summer. Herbaceous species have not drawn as much research attention as woody shrubs because they are not as deeply rooted. However, White & Newton (1989) have shown that herbs can extract moisture as deeply as 0.9 m.

Many ponderosa pine plantations also are stressed nutritionally and respond well to fertiliser application (Powers *et al.* 1988). Throughout the region, a single application of nitrogen at 200 kg/ha increases 5-year volume growth by an average of nearly one-quarter where shrubs are not controlled, but response is doubled if shrub competition is low. As shown in droughty regions of Australia (Nambiar & Zed 1980; Nambiar & Sands 1993) and British Columbia (Messier 1993), weeds compete effectively with trees for nutrients on dry sites. On poor, droughty sites in California, shrub competition can preclude fertiliser response entirely, even when trees are severely deficient in nitrogen (Powers & Jackson 1978). When combined, weeding and fertiliser treatments seem to interact synergistically on poor sites and additively on better (Powers 1983). Research on nutrients other than nitrogen has been limited, but growth responses generally have been low (Cochran *et al.* 1981; Powers *et al.* 1988).

The identity and biology of many insects feeding on young ponderosa pine is well understood (Furniss & Carolin 1977). However, much of what is known is based on *ex post facto* observations of trees already under conditions of unusual stress where causes can only be surmised. Consequently, the attention focusing on severe but unusual cases may mistakenly be seen as the norm. We know much less about how insects affect the

performance of young plantations under varying degrees of management. Terminal feeders such as the ponderosa pine tip moth (*Rhyacionia zozana* (Kearfott) Stevens) and the western shoot borer (*Eucosma sonomana* Kearfott) often attack young plantations and, while they may not be lethal, suppress height growth to the point that trees are less able to compete with weeds (Stevens 1966; Stoszek 1973).

As plant competition increases, tree vigour may be reduced to the point that trees are less attractive to shoot-feeding insects. Zutter *et al.* (1986) found in the southern United States that pine tip moth infestations decreased with increasing levels of vegetative competition. Ross *et al.* (1990) noted that *Rhyacionia* infestation can be high in herbicide-treated plots, but that high growth rates allowed trees to recover quickly. Trees on moisture-stressed and nutrient-poor sites may have lower infestation rates than better sites, but weakened trees also are less tolerant of damage (Meeker & Kulhavy 1992). In California, Oliver (1984) found that top deformities in ponderosa pine plantations caused by the gouty pitch midge (*Cecidomyia piniinopsis* Osten Sacken (Eaton and Yuill)) were more than twice as common for trees growing in competition with manzanita as for trees in shrub-free plots. Bedard *et al.* (1989) showed that height growth can be reduced where both competition and midge injury are severe.

Plant stresses stemming from competition for water and nutrients can be exacerbated by insect pests but much depends on physiological adaptations. Nambiar (1990) found that drought-adapted *Eucalyptus* species benefited much more from insect control than from weed control. The opposite was true for drought-sensitive species. However, findings often are contradictory because of small plot size and lack of understanding of moisture and nutritional relationships. Abundant soil moisture can produce new growth that is nutritionally rich and succulent and probably more palatable to insect pests. But fundamental changes in plant biochemistry resulting from fluctuations in available moisture may be important in the initiation and development of insect outbreaks (Mattson 1980). Nutritionally stressed plants contain higher proportions of terpene- and phenolic-based compounds as defense against herbivory by reducing digestibility, while plants on more fertile soils produce nitrogen-based defense compounds such as alkaloids which are toxins (Mattson 1980). But the significance of interactions between each of these factors on plantation performance in North America is unknown.

To our knowledge, only one other study combining weed, soil fertility, and insect control has been reported—that for *Eucalyptus grandis* Hill ex Maiden in New South Wales (Birk & Turner 1992). There, plantation biomass was more than doubled by herbicides, fertilisers, and insecticides applied repetitively for the first 6 years. However, the presence of an *Acacia* understorey severely reduced nitrogen uptake in *Eucalyptus* and largely blocked its response to fertiliser. Beyond this, interactions were not discussed in detail.

Study Objectives

We lack a comprehensive understanding of how plantation performance is constrained by natural limiting factors and what we can do about them silviculturally. Current knowledge rests on studies of single factors. Findings often are anecdotal and all are of limited scope. To address this, we began a multi-factor field experiment in 1985 that has come to be known popularly as the “Garden of Eden” study. Our long-range objectives were to:

- (1) Determine the growth potential of planted ponderosa pine in California as constrained or enhanced by (A) moisture availability, (B) nutrient availability, (C) insects, and (D) their interactions.
- (2) Investigate how these factors affect tree physiology, pest resistance, nutrient and water use, plant succession, and other site processes.
- (3) Develop a flexible model to estimate the effects of herbicides, fertiliser, and insecticide treatments over a broad array of forest sites.

This paper reports 6-year growth responses to repetitive “all-or-nothing” combinations of insect, vegetation, and nutrient control across a gradient of sites dominated by a Mediterranean climate. This is the first comprehensive report of a study expected to last another decade.

METHODS

Study Area

Our focus was that region of California known as the “westside ponderosa pine forest,” a temperate region of warm, dry summers and comparatively mild, wet winters. While part of the region is in the eastern rain shadow of the low Coast Ranges and Klamath mountains, that portion on the western flanks of the Sierra Nevada receives relatively high amounts of precipitation from winter Pacific storms with roughly a third to half falling as snow. The net effect is that the region encompasses a broad range of sites that includes the most productive ponderosa pine forests in North America (Oliver *et al.* 1983). We wished to examine the full range of site qualities typically under plantation management. Also, we wished to control vegetation with herbicides, which was administratively difficult to accomplish on federal lands. Therefore, we sought and obtained the full co-operation of forest industry for this experiment. Prospective sites available on industry lands were visited and ranked according to the following criteria:

- (1) The area must encompass at least 2 ha to provide an area with sufficient buffer;
- (2) Slope variability could not exceed 20% and aspects must be within 45°;
- (3) Soil variability could not exceed that at the Family level (Soil Survey Staff 1975) and had to be typical of soils of the region;
- (4) Insect pests common to ponderosa pine must be present in adjacent areas to provide a source of infestation;
- (5) Site index could not vary more than 20% about the mean for the area;
- (6) There should be no sign of soil diseases potentially affecting plantation growth.

Eight sites meeting all the criteria were found in three geomorphic provinces in northern California. Four were timbered, three were in brushfields which developed from wildfires, and one was in a brush-choked, sparsely-stocked pine plantation. Elevations were determined from topographic maps and annual precipitation was estimated from isohyetal maps of long-term averages for the state. Where possible, site index (Powers & Oliver 1978) was estimated from dominant trees on or bordering the site. Otherwise, it was estimated with less confidence from soil type and general climate. Soils were identified to the series level through reference to maps or through on-site profile descriptions. General characteristics of the eight sites appear in Table 1.

TABLE 1—Characteristics of eight Garden of Eden plantations in California.

Plantation (previous)*	Site index (m)	Elev. (m)	Annual precip. (mm)	Geomorphic province	Geologic material	Soil Great Group	Year planted
Elkhorn (P)	17	1490	1015	Klamath	Metasediment	Xerochrepts	1988
Pondosa (B)	20†	1175	760	Cascade	Volcanic	Palixeralfs	1988
Chester (B)	20	1465	890	Cascade	Volcanic	Xerochrepts	1987
Whitmore (B)	23	730	1140	Cascade	Volcanic	Haplohumults	1986
Jaws (N)	23†	1005	1035	Klamath	Metasediment	Haploxeralfs	1988
Erie (N)	24	1370	1700	Sierra	Metasediment	Xerochrepts	1987
Tickey (N)	28	1280	1525	Sierra	Volcanic	Haploxeralfs	1987
Feather (N)	30†	1220	1780	Sierra	Volcanic	Haploxeralfs	1988

*Previous vegetation was a plantation (P), brushfield (B), or natural stand (N).

†Site index (base age 50 years) estimated. No suitable site trees present.

Site Preparation and Plantation Establishment

Timbered sites were harvested and merchantable trees were skidded by tractor to landings beyond the study area. Logging residues and brushfields were cleared by tractor and brush rake using normal operational practices during summer when soils were dry and less likely to compact. Care was taken to remove as little topsoil as possible. With the exception of Jaws, residues were piled off the study site. At Jaws, the nature of landforms made off-site disposal impractical, so residues were concentrated into piles and burned.

After site preparation, 24 contiguous, rectangular plots measuring 19.5 by 21.9 m each were established by transit and tape in four columns and six rows. Planting spots were flagged at a square spacing of 2.4 m. In spring when soil temperatures had warmed to 6°C, bare root seedlings were planted in holes augered to enhance early survival. Seedlings were chosen from genetic stock judged by the Regional Forest Service Geneticist to be superior performers for the elevation and seed zone of each specific plantation. Except for the first plantation (Whitmore), seedlings were raised at the Institute of Forest Genetics at Placerville and lifted as 1-0 stock. Plantations were established between 1986 and 1988 (Table 1).

Treatments

Insecticide, herbicide, and fertiliser treatments, each at two levels, were assigned randomly to the 24 plots, producing three replications of eight factorial treatment combinations per plantation in a completely randomised design. Treatments were selected to create extreme "all-or-nothing" combinations of insect, weed, and soil fertility control applied repeatedly to at least the point of crown closure. Our aim was to create a series of growing conditions from minimal to maximal stress within the constraints of local climate. Main effect treatments and methods of application were:

- (1) Insect control using systemic insecticides (I): acephate or dimethoate applied directly to trees each spring when new needles had broken their bundle sheaths. Formulations were based on manufacturer's recommendations for the insects likely to be present and were applied by backpack sprayer to the point that crowns began to drip. Levels: annual application v. no application.
- (2) Vegetation control using herbicides (H): annual spring applications of glyphosate, hexazinone, or triclopyr based on manufacturer's recommendations for the soil type and

vegetation present. Herbicides were applied by backpack sprayer directly to all vegetation other than planted trees (which were shielded from spray through the first several years). Levels: annual application *v.* no application.

- (3) Nutrient control using fertilisers (F): dry, commercial salts of nitrogen, phosphorus, potassium, calcium, magnesium, sulphur, boron, copper, and zinc applied during the dormant season. Application followed a ramp schedule in which nutrient supply increases with demand (Axelsson 1983). Formulations and rates were based on estimated needs for optimal nutrition on an average site during the exponential phase of growth (Table 2). The first three applications (springs of years 1, 3, and 5) were poured from pre-weighed bags to holes at four positions around each seedling at a distance of about two-thirds seedling height. The last application was so massive that it was applied to the surface in parallel bands between rows of trees in the autumn of the sixth year in hope that it would solubilise and move into the soil by the start of growth year 7. Levels: biennial application *v.* no application.

TABLE 2—Quantity of nutrients applied as dry salts at 2-year intervals.

Nutrient	Amount applied (kg/ha)				
	At planting	End of year 2	End of year 4	End of year 6	Sum for 6 years
Nitrogen	15.6	46.6	213.7	798.7	1074.4
Phosphorus	7.9	23.2	103.4	395.2	529.7
Potassium	7.7	23.2	109.6	399.4	539.9
Calcium	10.1	23.6	118.6	264.0	416.3
Magnesium	5.5	16.8	61.7	137.2	221.2
Sulphur	5.2	28.3	16.0	62.4	111.9
Zinc	1.1	3.2	14.0	55.1	73.4
Copper	0.5	1.6	6.8	26.9	35.8
Boron	0.5	1.6	6.8	26.8	35.7

Measurements and Analysis

Measurement plots were established inward from the third row of trees of each treatment plot, creating a two-tree buffer surrounding 20 measurement trees. Plots were visited every year; mensurational data were collected after growth completion in years 2, 4, and 6 and foliar collections made in the autumns of years 1, 3, 5, and 7. Tree measurements included height, stem diameter at 20 cm above the ground, and live crown length and width as measured at two right angles. Competing vegetation was measured on four parallel strips, each 10 m long and centred between tree rows. Plot coverage was determined for each species by the proportion of the 40-m transects intercepted by plant crowns and measured by tape to the nearest centimetre. Heights also were recorded by species for each intercept. Tree volumes of stems and crowns were estimated from conic formula. Samples of fully expanded current- and 1-year-old needles were composited by age class from 8 to 10 trees per measurement plot. Collections came from two or three branches in the second or third branch whorl from the top. Foliage was oven-dried for 3 days at 65°C, weighed to determine average fascicle mass, ground, and analysed for total quantities of Kjeldahl nitrogen

(Bradstreet 1965); potassium, calcium, magnesium, sodium, manganese, and iron by atomic absorption (Johnson & Ulrich 1959); and sulphur, boron, copper, and aluminium by ICP (Zarcinas *et al.* 1987).

The nearness of the Whitmore plantation allowed more frequent measurements. From summer 1991 through summer 1992 (years 6 and 7), monthly readings were made of soil temperature and water potential using aluminium/fibreglass soil cells (SoilTest Inc., Lake Bluff, IL) buried at 20 and 50 cm, and of leaf water potential by pressure bomb (SoilMoisture Equipment Co., Santa Barbara, CA). Leaf water potentials were made at predawn and midday on five trees and five manzanita shrubs per plot. Stomatal conductance also was measured at midday on the same plants using diffusion porometry (Licor, Inc., Lincoln, NB). Trees and shrubs were chosen subjectively to span the range in height classes present. Understorey vegetation was harvested at Whitmore in autumn 1992 from four 1.0-m² subplots per treatment plot for biomass analysis before deciduous leaves had fallen. Manzanita, the dominant species, was separated into wood and leaf components. Leaf areas were determined on fresh subsamples of manzanita foliage by scanning photometer (Decagon Inc., Pullman, WA). All samples were oven-dried, weighed, and analysed chemically.

Treatment effects were analysed by analysis of variance. Percentage or binomial data were transformed by arcsin. Logarithmic transformations were used for data with variance proportional to the mean. Where treatment effects were judged significant at $\alpha = 0.10$ or less, pairwise comparisons were made using the ANOVA procedure and Fisher's least significant difference (LSD) if overall treatment effects were significant at $\alpha = 0.10$ or less, or t-test for simple comparisons of grouped data (SAS Institute Inc. 1988).

RESULTS AND DISCUSSION

General Effects

Climatically, the study period 1986 through 1993 was not unusual. Using Nevada City, a central location within the Sierra Nevada as an index, precipitation averaged 1375 mm, which is only 11 mm less than the 30-year average. As is typical for California, precipitation varied greatly from year to year, ranging from a high of 1843 mm in 1986 to a low of 1033 mm in 1990. The years 1987–92 marked a 6-year period of less than average precipitation, while 1986 and 1993 were unusually high.

Tree survival averaged 85% overall, with most of the mortality occurring in the first 2 years. Survival varied from a low of 64% at Elkhorn (the poorest site) to 100% at Feather (the most productive site). As a group, plantations on metasedimentary soils (Elkhorn, Jaws, and Erie) showed greater mortality than plantations on volcanics (71% survival *v.* 93%). Tree mortality on metasediments was associated mainly with fertiliser application at planting. Presumably, root systems already stressed by drought on dry, gravelly soils were injured further by fertiliser salts placed in the immediate rooting zone. Survival on volcanics was unrelated to treatment.

Six-year standing volumes for all plantations were examined for overall treatment effects and interactions by analysis of variance. We hypothesised that treatment responses varied by site quality. But because some of the site indices were only estimated (Table 1), we treated site quality as a class variable of low (SI < 23), medium (SI 23–24), and high (SI > 24). This

produced a 3-factor, 2-level, split plot ANOVA with 3-way interactions. Herbicide and fertiliser main effects were found to be highly significant statistically, as were site quality and its interactions with herbicide and with fertiliser treatments. This means that, while there was a general response to weed control and fertiliser, the response varied with site quality. Therefore, we proceeded to a more detailed examination of responses by individual plantation. A condensed ANOVA showing the significant effects is given in Table 3.

TABLE 3—Analysis of variance showing treatment effects significant at $p = 0.05$ or less. Residual model error (165 df) used to test all sources except site quality, which used split-plot error (5 df).

Source of variation	df	F	$p > F$
Site quality (S)	2	36.25	0.001
Herbicide (H)	1	108.84	0.0001
Fertiliser (F)	1	31.77	0.0001
S \times H	2	10.37	0.0001
S \times F	2	13.43	0.0001

Variance analysis of volume growth for individual plantations showed significant treatment effects at $\alpha = 0.05$ or less for all plantations except Erie, where survival was poorest. Poor initial survival at Erie made any interpretations of volume growth per unit area spurious and discussion will be confined to nutritional characteristics of surviving trees. Generally, insecticide and fertiliser treatments alone or combined had little effect on standing volumes after 6 years (Fig. 1). Insecticide seemed to have either no effect or one that was slightly negative (Table 4). Tree growth was not improved by fertiliser at most plantations unless accompanied by vegetation control. However, fertiliser without vegetation control increased volume growth by over 40% on the two best sites (Tickey and Feather) ($\alpha = 0.10$), which was similar to the gain from vegetation control alone. One should recognise that 6-year responses do not include those from the most recent and massive fertiliser application (Table 2) which occurred at the end of the sixth growing season.

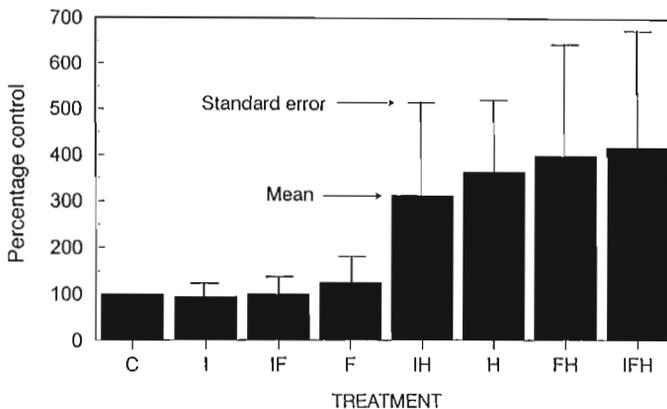


FIG. 1—Average volume at 6 years for all Garden of Eden plantations relative to volume in the control treatments. Means and standard errors for eight plantations. Treatments are control (C), and repetitive applications of insecticide (I), fertiliser (F), and herbicide (H).

TABLE 4—Average stem volume at 6 years for control (C), insecticide (I), fertiliser (F), and herbicide (H), treatments in each plantation.

Plantation	Volume at 6 years (m ³ /ha) when treatment was—								LSD* at—	
	C	I	F	H	IF	IH	FH	IFH	0.05	0.10
Elkhorn	0.07	0.07	0.06	0.26	0.04	0.31	0.31	0.21	0.22	0.18
Pondosa	0.07	0.09	0.14	0.47	0.09	0.29	0.63	0.53	0.31	0.25
Chester	0.46	0.58	0.53	1.03	0.51	1.03	1.09	1.12	0.22	0.18
Whitmore	0.27	0.28	0.28	0.95	0.34	0.92	1.22	1.42	0.37	0.31
Jaws	0.27	0.17	0.14	2.07	0.07	1.95	1.59	2.32	0.63	0.52
Erie	0.48	0.27	0.93	1.27	0.69	0.47	1.04	1.29	n.s.	n.s.
Tickey	1.77	1.29	2.37	2.12	2.14	1.93	2.80	2.81	0.80	0.66
Feather	2.05	2.07	2.59	3.12	3.75	3.15	4.14	4.86	1.22	1.01

* Least significant difference at $\alpha = 0.05$ and 0.10 by Fisher's LSD. No LSD shown for Erie Point because overall F test was judged not significant (n.s.).

Weeding and fertiliser were thought to interact synergistically on poor sites and additively on better (Powers 1983). Results here suggest that effects are additive, regardless of site quality. Plantations responded positively to herbicide treatment (volume was increased an average of 265%), but response on the best sites was very weak. Variability in herbicide response was high relative to insecticide and fertiliser treatments (Fig. 1). Overall, growth was greatest when insecticide, fertiliser, and herbicide treatments were combined. Average 6-year volumes for IFH treatments were 666% of controls. Overall, variability in response to individual treatments reflects differences in primary limiting factors at each plantation.

Repeated Insect Control

Annual fall surveys indicated that overall incidence of injury from pine-feeding insects was very low in all plantations and unrelated to treatment. Occasionally, terminal or lateral shoots were killed or stunted by the western shoot borer (*Eucosma sonomana*) or the ponderosa pine tip moth (*Rhyacionia zozana*) but incidence was low, rarely exceeding one or two shoots in 10% of trees. Injured terminals sometimes caused forking but, with the usual resumption of dominance by a single terminal shoot, long-term effects on tree growth are expected to be minimal. Thus, tree volumes through the sixth year of growth were not noticeably affected. Perhaps plant competition had not yet reached the point of rendering trees susceptible to insects. However, trees in control plots were definitely under competitive stress by year 6. Insect problems reported in young pine stands in California (Oliver 1984; Bedard *et al.* 1989) and in the southern United States (Zutter *et al.* 1986; Ross *et al.* 1990; Meeker & Kulhavy 1992) were simply not found here. Statewide forest pest surveys published for the 1986–93 period suggested that this period was typical, relative to plantation insect outbreaks (Anon. 1986–93). Because repeated insecticide treatment had no discernible effect on plantation performance or foliar chemistry, we have combined results from these plots with those for control, herbicide, fertiliser, and herbicide + fertiliser treatments for the remaining discussion.

Repeated Vegetation Control

Response to herbicide treatment was related inversely to site quality (Table 4). On the five poorest sites, all plantations responded positively and significantly to herbicide treatment (α

= 0.10) and 6-year volume growth was triple that of controls. These five sites also were the driest. Precipitation averaged less than 1150 mm annually (Table 1). Three plantations in this group (Elkhorn, Chester, and Jaws) have high gravel contents in their soils, and the Ponderosa plantation is underlain at less than a metre by a duripan of pyroclastic material. Whitmore receives the most precipitation and has the deepest soil of this group, but it also is lowest in elevation (730 m) and undoubtedly is the warmest (summer air temperature maxima routinely exceed 40°C and humidity is low). The soil is a deeply weathered Aiken clay with low available water retention. Soil water potential in the upper 50 cm exceeded -1.5 MPa only 150 days during the sixth and seventh year in control plots but low tension moisture was extended another month where herbicides were used. With herbicides, summer leaf water potentials were 0.13 and 0.10 MPa greater than in control plots at predawn and midday respectively ($\alpha = 0.10$).

In contrast, the three plantations receiving more than 1500 mm of precipitation annually showed lesser response to herbicides. Two of these (Tickey and Feather) grow on deep Cohasset loams with relatively high available water holding capacities. Soil of the Erie plantation is a gravelly loam of the Hurlbut series. However, soil moisture supply probably is greater than expected for a gravelly soil. The Hurlbut series is formed from vertically tipped, fractured, weathered schist which permits fairly deep water and root penetration.

While increased soil moisture availability generally is thought to be the primary effect of vegetation control on drier sites, a companion effect of at least equal significance is improved nutrition (Nambiar & Sands 1993; Messier 1993). In our study, vegetation control generally led to higher nitrogen and phosphorus concentrations from age 3 onward. On the poorest site (Elkhorn), fifth-year foliar concentrations of nitrogen, phosphorus, and sulphur were increased significantly by weed control (Table 5). On a medium-quality site (Whitmore), nitrogen, potassium, and sulphur concentrations were increased, but phosphorus was not. Although mean mass of individual fascicles was relatively unaffected, crown volume more than tripled on both sites. Greater crown volumes composed of fascicles of higher nutrient content indicate that vegetation control caused a substantial increase in soil nutrient availability and nutrient uptake by trees. However, on the most productive site (Feather), vegetation control only affected nitrogen concentration. Greater crown volume at Feather

TABLE 5—Effect of competing vegetation on crown volume per tree, fascicle mass, and elemental concentration in ponderosa pine needles at age 5 years. Average crown volume and fascicle mass determined at 6 years.

Plantation (and site index)	Competing vegetation	Crown volume per tree (m ³)	Mass per fascicle (mg)	Foliar concentration of—				
				N	P (g/kg)	K	S (mg/kg)	Al
Elkhorn (SI 17)	Present	0.07a*	172a	9.63a	1.12a	6.60a	689a	208a
	Absent	0.33b	189a	12.19b	1.29b	6.78a	825b	201a
Whitmore (SI 23)	Present	0.29a	212a	10.30a	0.68a	5.27a	623a	136a
	Absent	0.96b	263a†	12.09b	0.71a	6.66b	724b	108b
Feather (SI 30)	Present	2.02a	240a	13.63a	1.08a	5.46a	867a	275a
	Absent	3.26b	247a	16.12b	1.10a	5.37a	972a	278a

* Column means for a site quality class followed by the same letter do not differ significantly at $\alpha = 0.05$.

† Significant at $\alpha = 0.10$.

accompanied by stable or slightly increased nutrient concentrations means that nutrient uptake was increased but not to the proportion seen on poorer sites.

Because vegetation control improves nutrient availability, it follows that trees under nutrient stress benefit most from reduced competition. Conversely, trees with adequate nutrition may be less affected. Such was the case at Elkhorn and Whitmore, where foliar nitrogen concentrations in control treatments by year 5 (Fig. 2) were at or below the critical level of about 10 g/kg (Powers 1983; Powers *et al.* 1988). Through year 5, herbicide treatment kept foliar nitrogen concentrations well above critical level. And by year 7, foliar nitrogen concentrations remained higher on weed-free plots ($\alpha = 0.05$), although concentrations had dropped to critical level at Elkhorn (Table 5).

At Whitmore, foliar phosphorus concentration on control plots was below the critical level of 0.8 g/kg (Powers 1983) by year 3 (Fig. 2). Concentrations were slightly higher on weed-free plots by year 3 ($\alpha = 0.05$), but did not differ from controls thereafter. Differences in phosphorus availability between Elkhorn and Whitmore can be explained by the capacity of each soil to fix phosphate. The red Aiken soil series at Whitmore reflects the presence of ferric oxides and a notorious capacity to sorb phosphorus (Ulrich *et al.* 1947). Small amounts of phosphate made available through reduced competition would be fixed quickly into unavailable forms by oxides of polyvalent cations. In contrast, the gray Sheetiron soil series at Elkhorn has a much lower capacity to fix phosphate (Powers *et al.* 1975). Therefore, reduced weed competition for soil phosphorus at Elkhorn increases soil phosphorus availability. Foliar concentrations of aluminium were not increased by vegetation control on any site. In fact, aluminium concentrations were significantly decreased at Whitmore

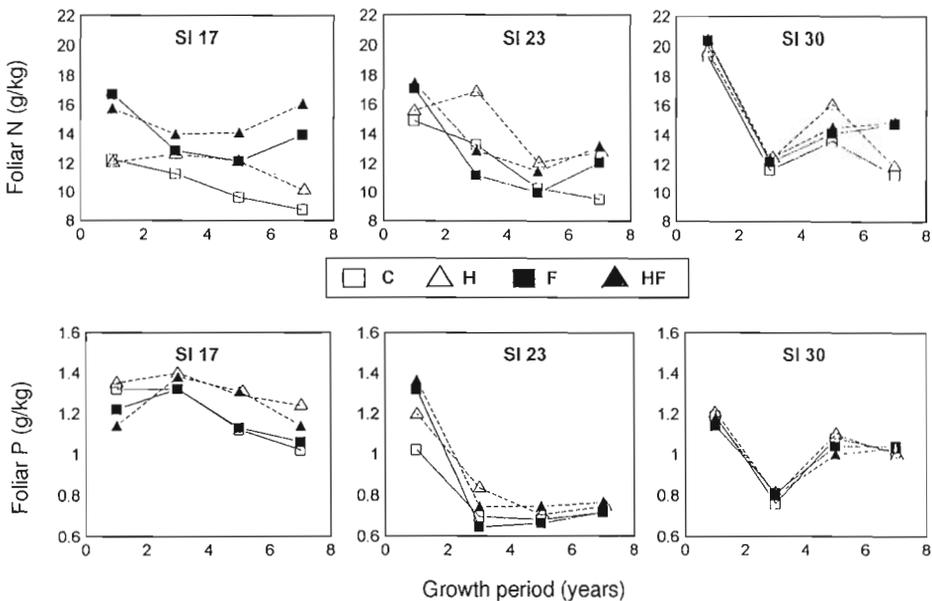


FIG. 2—Concentrations of nitrogen and phosphorus in current-year needles of ponderosa pine in three plantations of site index 17 (Elkhorn), 23 (Whitmore), and 30 (Feather). Treatments are control (C), herbicide (H), fertiliser (F), and herbicide + fertiliser (HF). Dark symbols denote fertiliser applied, light symbols denote no fertiliser. Each mean is the average of six treatment plots.

(Table 5). This is a notable finding because it indicates that ponderosa pine discriminates between nutrients and non-nutrients, even if availability is increased by reduced competition.

Repeated Fertiliser Application

Contrary to conventional wisdom, growth responses to fertiliser generally improved with site quality (Table 4). However, foliar analyses showed that trees responded very quickly to fertilisers placed in the soil at planting (Fig. 2), and the poorer the site, the greater the rise in foliar nutrient concentration. Despite some initial mortality on gravelly soils, fertiliser generally did not depress growth (Table 4). This suggests that early increases in foliar nutrient concentrations reflected increases in uptake, rather than a concentration effect in seedlings stunted from chemical toxicity. The uptake effect depended on the degree of deficiency and the solubility of the fertiliser in the soil. At Elkhorn where foliar nitrogen concentrations in control trees were relatively low by the end of the first growing season, nitrogen concentrations in fertiliser-treated trees averaged one-third greater ($\alpha = 0.01$) than in controls. In contrast, first-year foliar phosphorus concentrations at Elkhorn were lower on plots treated with both herbicide and fertiliser ($\alpha = 0.01$) and with fertiliser alone ($\alpha = 0.10$).

Contrasting patterns for foliar nitrogen and phosphorus probably reflect both the relative dissolution rates of the fertiliser salts ammonium nitrate (highly soluble) and diammonium phosphate and triple super phosphate (weakly soluble). Reduced first-year foliar phosphorus concentration at Elkhorn could trace to (1) dilution when phosphorus is already at luxury levels; (2) less availability because of solubility reactions between phosphate and both applied calcium and native iron, manganese, and aluminium in the soil; (3) root tip injury from fertiliser salts in a limited soil volume; and possibly (4) to seedling damage due to drifting herbicide spray. The facts that this reaction did not occur at other sites, that first-year tree growth at Elkhorn was not increased by any treatment (Fig. 3), and that fertiliser

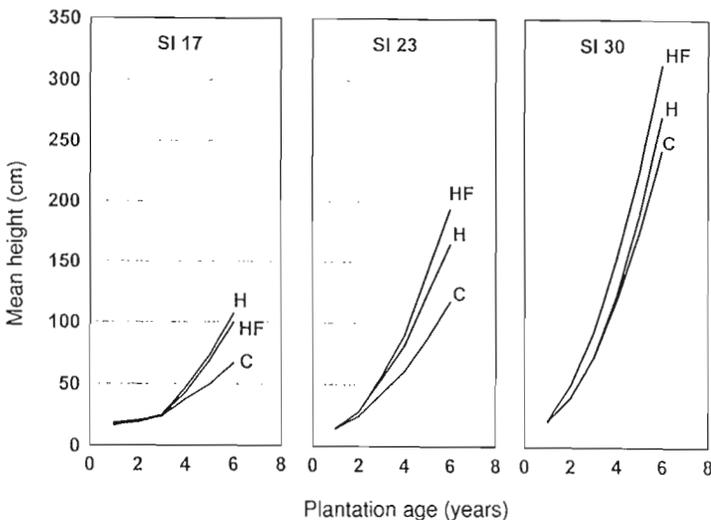


FIG. 3—Cumulative height growth for control (C), herbicide (H), and herbicide + fertiliser treatments (HF) through the first 6 years at three plantations of site index 17 (Elkhorn), 23 (Whitmore), and 30 (Feather).

treatment led to seedling mortality point to root damage as the most likely explanation. However, another possibility is that low dissolution of fertiliser phosphorus during droughty soil conditions limited the diffusion of phosphate to the rhizosphere.

Concentrations increased by the third year at Elkhorn so that fertiliser-treated trees did not differ significantly from untreated. At Whitmore, first-year foliar concentrations of both nitrogen and phosphorus were greater on fertiliser-treated plots ($\alpha = 0.01$), but differences were negligible at Feather (Fig. 2). In all cases, foliar nutrient concentrations were above critical level for all treatments in all plantations in the first year, reflecting the carry-over effect of seedlings raised in a rich nursery environment. Except possibly for phosphorus at Whitmore with its exceptionally high phosphorus sorption capacity (Ulrich *et al.* 1947), this effect probably carried into year 2 (Fig. 2). Consequently, tree growth generally was not improved through year 2 by fertiliser (Fig. 3).

Interactions

Ponderosa pine is known for its adaptation to drought (Lopushinsky 1969; Oliver *et al.* 1983). Based on experiments with *Eucalyptus* species with contrasting drought tolerances (Nambiar 1990), one might predict that ponderosa pine would respond well to insect control, but that was not the case. One reason for this is that foliovores are not a major pest of ponderosa pine (Furniss & Carolin 1977) as they are of *Eucalyptus* species or broadleaves in general. Weevils, shoot or twig borers, and bark beetles pose much greater threats.

Despite a steep site gradient and our extreme range of growing conditions, interactions noted in the southern United States between insect pests of pine plantations and degree of moisture or nutrient stress (Ross *et al.* 1990; Meeker & Kulhavy 1992) were not found through 6 years of plantation development encompassing considerable climatic flux. At least half of our study period coincided with several years of consecutive drought which might have influenced insect-host relationships. However, this seemed a normal period relative to insect activity in plantations throughout the region (Anon. 1986–93). Perhaps early control of competition through effective site preparation reduced problems to the point of insignificance.

Foliar nitrogen concentrations declined between years 1 and 3 for treatments without fertiliser at all plantations (Fig. 2). Nutrients brought from the nursery were diluted in new growth as planted trees adjusted to their field conditions. The effect was particularly strong on control plots because of weed competition for soil nutrients. Even with fertiliser, foliar nitrogen concentrations declined if weeds were present, reaching critical levels by year 5 on both fertiliser-treated and control plots lacking weed control at Whitmore. Through year 6, fertiliser-treated trees at Whitmore were not significantly larger than controls (Table 4, Fig. 3). By year 3, foliar phosphorus concentration had dropped to or below critical level at Whitmore, reflecting the particularly high sorption capacities of the Aiken soil series. Fertiliser application did not overcome this capacity.

The cause of the decline in both foliar nitrogen and phosphorus by year 3 at Feather is not clear. It did not occur at Elkhorn or Whitmore, and is not attributable to analytic error. Possibly, low values trace to very rapid growth rates at Feather, relative to the other sites (Fig. 3), and to the fact that 1990—year 3 at Feather—was the driest year of the study. As soils dry, ion diffusion follows an increasingly tortuous pathway along water films lining soil

pores and uptake declines (Barber 1974). Another factor may be the phosphorus sorption capacity of the Cohasset soil series which, although not as severe as for the Aiken series at Whitmore, still is very high (Powers *et al.* 1975). This is supported by foliar phosphorus concentrations dropping in all treatments to critical level by year 3 (Fig. 2). Phosphorus stress may have lessened uptake of other nutrients as well.

On the five poorest and driest sites, weed competition was severe enough to preclude response to any treatment lacking herbicides. In some cases, growth on fertiliser-treated plots averaged less than on the controls (Table 4). Two factors account for this. Firstly, weed species responded strongly to fertiliser. Secondly, fertiliser increased seedling mortality on gravelly soils. By the end of the seventh year, woody shrubs on fertiliser-treated plots at Whitmore had more than doubled in mass and leaf area compared with shrubs on controls (Table 6). Total vegetative cover was increased slightly by fertiliser on all but the poorest sites where low soil moisture restricted response to improved nutrition. However, small increases in percentage vegetative cover can understate the increases occurring in understorey biomass and area of transpiring leaf surface (Table 6). Such increases of understorey species spell large increases in water use, nutrient uptake, and nutrient immobilisation. At Whitmore, assuming a mean concentration of 4 g N/kg wood, nitrogen immobilisation in woody shrubs alone could account for one-third (70 kg/ha) of the nitrogen applied in fertiliser through the sixth growing season (214 kg N/ha, Table 2).

TABLE 6—Characteristics of competing vegetation after 7 years at Whitmore as affected by fertiliser application. Mass, leaf nitrogen, and leaf area are for manzanita, only.

Characteristic	Treatment				LSD
	C	F	H	HF	
Coverage (%)	55 a*	65 a	4 b	4 b	27
Volume (m ³ /m ²)	0.19a	0.24a	0.01b	0.01b	0.15
Total mass (Mg/ha)	6.29a	16.40b	n.d.	n.d.	9.57
Leaf mass (Mg/ha)	3.23a	7.84b	n.d.	n.d.	3.70
Leaf nitrogen (kg/Mg)	7.86a	9.37b	n.d.	n.d.	0.37
LAI (m ² /m ²)	1.07a	2.44b	n.d.	n.d.	1.34

* Means within a row followed by the same letter do not differ significantly at $\alpha = 0.10$. Fisher's LSD for control (C) and fertiliser (F) contrasts, only. Analyses for coverage based on arcsin transformations.

Growth rates were improved by fertiliser on the better sites, particularly when combined with herbicide treatment (Table 4, Fig. 3). However, nitrogen and phosphorus in current-year needles at Feather were adequate in all treatments by year 5 (Fig. 2). On the three best sites, current-year concentrations of other nutrients supplied in fertiliser did not fall below known critical levels at the end of the fifth year (Table 7).

Powers (1984) proposed that current-year foliage may not be the best indicator of nutritional status except on the poorest sites. Phloem-mobile nutrients such as nitrogen, phosphorus, and potassium will be depleted from older foliage before deficiencies are evident in younger. Analysis of foliage collected in autumn from the best sites at year 5 showed that nutrient concentrations in current-year needles exceeded critical levels for every element (Table 7). However, 1-year-old needles showed a hidden deficiency in that they were at or below critical level for phosphorus and potassium in each plantation. Apparently,

TABLE 7—Nutrient concentrations in current and 1-year-old needles on the three best sites in the autumn of the fifth growing season.

Plantation (and site index)	Treatment	Foliar concentration of—								
		N	P	K	Ca	Mg	S	Zn	B	Cu
		(g/kg)					(mg/kg)			
Current-year needles										
Erie (24)	Control	12.38	1.07	6.44	1.38	0.82	790	32	14	2
	Fertiliser	14.74	1.14	6.86	1.20	0.78	872	29	42	3
Tickey (28)	Control	15.62	0.98	6.84	0.96	0.71	840	22	23	3
	Fertiliser	15.13	1.00	7.52	1.01	0.64	886	23	36	3
Feather (30)	Control	13.63	1.08	5.46	1.63	1.09	867	35	19	3
	Fertiliser	14.13	1.04	5.45	1.56	1.07	882	28	31	2
1-year-old needles										
Erie (24)	Control	11.12	0.71	3.84	2.94	1.02	798	39	11	2
	Fertiliser	12.06	0.76	4.34	2.60	0.96	886	42	64	3
Tickey (28)	Control	17.09	0.70	4.10	3.30	1.19	1009	33	29	3
	Fertiliser	14.14	0.69	3.88	3.38	1.13	937	30	49	3
Feather (30)	Control	13.04	0.83	4.43	3.90	1.31	893	38	23	2
	Fertiliser	14.24	0.84	4.16	4.06	1.30	956	36	34	2
Critical level*		10.5	0.8	4.8	0.5	0.5	—	10	8	2

* Critical levels for nitrogen, phosphorus, potassium, calcium, and magnesium in *Pinus ponderosa* from Powers (1983); zinc, boron, and copper for *P. radiata* from Will (1978).

the 103 kg P/ha and 110 kg K/ha applied through year 5 (Table 2) had not achieved optimal nutrition. Interestingly, of the nine nutrients supplied through fertiliser, only boron was consistently higher in current- and 1-year-old needles ($\alpha = 0.05$) (Table 7). Although boron critical levels have not been established for ponderosa pine, concentrations were low in control treatments and were near the marginal deficiency level of 8 to 12 mg/kg established for *Pinus radiata* D. Don (Will 1978). Furthermore, boron is entirely soluble in the soil solution, meaning that its availability is lessened during drought and when weeds are present (Attiwill & Leeper 1987). Improved boron nutrition during drought may account for some of the fertilisation response on the better sites.

Nutrient concentrations measured at any given time are just a snapshot of what is a dynamic process. Although foliar concentrations of phosphorus and potassium were below critical level in 1-year-old needles of fertiliser-treated trees by autumn, concentrations may have been satisfactory through much of the growing season. If growth demand is great and if reserves in older foliage are adequate, nutrients will translocate to newer, more active foliage throughout the year according to their phloem mobility and degree of demand (Powers 1984; Nambiar & Fife 1991). On the best sites, deficiencies may appear only late in the year when water potential and mobility rates are low.

Average crown volumes at Erie, Tickey, and Feather were 107, 24, and 50% greater on fertiliser-treated trees at 6 years than on controls ($\alpha = 0.05$). Thus, trees with fertiliser had ample reservoirs of nutrients stored in their crowns. We believe that sustained retranslocation of nutrients from older foliage to younger helps explain high growth response to fertiliser on sites with better moisture regimes. Because moisture regimes are better, the fertiliser effect

should be sustained for many years. On poorer and droughtier sites, retranslocation would diminish unless moisture availability was improved by weeding. Because such sites remain droughty, the effect should disappear by the time the plantation achieves leaf area carrying capacity.

Fertiliser application rates were exponential, meaning that the final treatment in the autumn of year 6 was massive—roughly 3-times the amounts in years 0, 2, and 4 combined. This produced sizable increases in foliar nitrogen concentration on all sites by year 7, regardless of weed treatment. In contrast, foliar nitrogen concentrations in plots without fertiliser declined or increased only slightly. On average and better sites, growth clearly was improved when fertilisers were combined with weed control, and differences seem to be widening (Fig. 3). Therefore, we expect that differences in both growth and foliar nutrient concentrations will increase in the years ahead on average and better sites as crowns close and trees rely increasingly on internal nutrient cycling.

CONCLUSIONS

On average, growth rates in ponderosa pine plantations are quadrupled through 6 years by appropriate combinations of weed and nutrient control treatments applied repetitively.

Insects, sometimes seen as pest problems in young plantations, had no influence on tree growth across the extreme range of physiological stresses and enhancements encompassed by the Garden of Eden experiment. Thus, assumptions about pest problems in young, westside plantations must be reassessed.

Weed control seems essential for satisfactory plantation performance on poor, droughty sites. Soil moisture is such an overriding factor that weed control plus fertiliser offers no further advantage beyond weed control alone. Furthermore, the presence of weeds essentially blocks uptake of fertiliser nutrients by pine.

Positive effects from weeding are not due simply to improved soil moisture. Droughty sites often are nutrient deficient, and effective weeding enhances soil nutrient availability as well as soil moisture supply. Uptake rates increase for nutrients but not for non-nutrient cations such as aluminium. Because weeding affects both soil moisture and nutrients, the relative importance of soil moisture and nutrition cannot be isolated easily in conventional field experiments of vegetation control and fertiliser application.

Pine on sites averaging more than 1500 mm of precipitation annually responded positively to weeding and fertiliser alone or in combination. Weed control had relatively less effect on growth response or nutrient uptake than for poorer, drier sites. Put simply, drought is less of a limiting factor on better sites.

Contrary to popular belief, fertiliser response was roughly proportional to site quality. Survival was decreased by fertiliser on the poorest sites, but not on better.

In general, growth responses to fertiliser and herbicide were additive. Growth and foliar nutrient trends indicated that fertiliser application will have a long-lasting effect on sites of better quality.

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