Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient

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Abstract: Factorial combinations of vegetation, nutrient, and insect control treatments were applied repeatedly to three contrasting California plantations of *Pinus ponderosa* var. *ponderosa* Dougl. ex Laws. Ten-year findings show that potential productivity is far greater than previously believed. Stem volume gains were linked directly with increases in crown volume. Insect problems were negligible. Vegetation control increased tree growth profoundly on xeric sites but less so on the most mesic. Where soil was both droughty and infertile, growth responses traced primarily to improved soil moisture availability and secondarily to better nutrition. The most fertile site also was droughty, and trees responded only to improved moisture availability. Water was less limiting on the most productive site. There, both fertilizers and herbicides triggered similar, substantive growth increases. Drought from both plant competition and climate reduced stomatal conductance, xylem water potential, and net assimilation rates. Assimilation rates increased linearly with site index, but treatment differences were not apparent once drought had peaked. Fertilization improved water-use efficiency where water stress was not extreme. Advantages in water availability to pines from vegetation control will dissipate as tree crowns close and transpiration rises.

Résumé : Des traitements de contrôle de la végétation, des nutriments et des insectes ont été appliqués à plusieurs reprises selon un dispositif factoriel dans trois plantations différentes de *Pinus ponderosa* var. *ponderosa* Dougl. ex Laws. en Californie. Après 10 ans, les résultats montrent que la productivité potentielle est beaucoup plus élevée qu'on l'avait cru précédemment. Les gains en volume de la tige étaient directement reliés à l'augmentation du volume de la cime. Les problèmes dus aux insectes étaient négligeables. Le contrôle de la végétation a provoqué une forte augmentation de la croissance des arbres sur les sites xériques, cependant moindre sur les sites les plus mésiques. Lorsque le sol était sec et infertile, la croissance a d'abord réagi à une amélioration de la disponibilité en eau du sol et ensuite à une meilleure nutrition. Le site le plus fertile était également sec et les arbres ont réagi seulement à une amélioration de la disponibilité en eau. Sur le site le plus productif, c'est l'eau qui faisait le moins défaut. À cet endroit, les fertilisants ou les herbicides ont provoqué les mêmes fortes augmentations de croissance. La sécheresse due à la compétition végétale ou au climat a causé une réduction de la conductance stomatale, du potentiel hydrique du xylème et des taux d'assimilation nette. Le taux d'assimilation augmentait de façon linéaire en fonction de l'indice de site mais les différences entre les traitements s'estompaient lorsque la sécheresse devenait maximale. La fertilisation a amélioré l'efficacité d'utilisation de l'eau aux endroits où le stress hydrique n'était pas extrême. Les avantages que retirent les pins du point de vue de la disponibilité en eau grâce au contrôle de la végétation s'estomperont à mesure que le couvert se refermera et que le taux de transpiration augmentera.

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Introduction

Forests between the latitudes 32° and 40° north and south of the equator and growing near the sea are influenced by summer drought and cool, wet winters defining a Mediterranean climate. This important region includes extensive pine plantations of North and South America, Southern Europe, Africa, and Australia. In California and much of southwest-

ern Oregon, the chief plantation species is Pacific ponderosa pine (*Pinus ponderosa* var. *ponderosa* Dougl. ex Laws.), and its most aggressive competitors are the woody shrubs manzanita (*Arctostaphylos* sp. Adans.) and ceanothus (*Ceanothus* sp. L.), which can form dense thickets following disturbance (Oliver et al. 1983; Tappeiner et al. 1992). Even in pine plantations, shrub biomass can reach 20–30 Mg·ha^{-1} in 10 years, depending on site quality (Powers and Jackson 1978). Competitive effects can be severe when shrubs cover as little as 20% of the ground (Oliver 1984; Shainsky and Radosevich 1986; White and Newton 1989). The oldest study of continuous vegetation control in ponderosa pine plantations is on one of California's more productive sites (Oliver 1990). There, stand volumes at 20 years for trees spaced 3 m and wider were doubled where woody shrubs were excluded since planting. However, this study did not control herbaceous species, which can be strong competitors (White and Newton 1989). Therefore, it does not reflect the

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full potential of vegetation control, nor does it apply to droughtier sites. In his survey of plantation survival, Fiske (1982) concluded that many pine plantations undergoing average competition from manzanita ultimately would fail.

Many short-term studies have shown the consistent and important effect of vegetation control on reducing water stress to trees in dry regions (McDonald and Fiddler 1990; Nambiar and Sands 1993; Nambiar and Zed 1980; Petersen et al. 1988; Shainsky and Radosevich 1986). Therefore, soil moisture is assumed to be the main mechanism of shrub competition in summer-dry California and southwestern Oregon (Tappeiner et al. 1992). Shrubs growing densely in young plantations can reduce soil water potential (Ψ_s) below –1.5 MPa by late July (Petersen et al. 1988). Ericaceous plants such as manzanita seem more effective than pine in obtaining water held at very low Ψ_s. They can tap reserves in deep, fractured rocks, thereby remaining hydrated and further depleting the upper soil profile of water (Zwieniecki and Newton 1996). Physiological drought begins in pines when xylem water potential (Ψ_p) falls below –1.2 MPa and stomatal guard cells begin to close (Lopushinsky 1969). Consequently, gas exchange and growth are reduced.

However, few studies consider the competitive effects of understory vegetation on tree nutrition. Findings from such far-flung regions as Australia (Nambiar and Sands 1993), British Columbia (Messier 1993), and California (Powers and Ferrell 1996) demonstrate the favorable effects of vegetation control on soil nutrient availability. Gains are greater on poorer, droughtier sites and lessen as site quality improves (Powers and Ferrell 1996). Conversely, severe shrub densities can block tree response to fertilization either through induced water stress or direct competition for applied nutrients (Powers and Ferrell 1996; Powers and Jackson 1978). Australian studies on infertile, sandy soils have shown that under certain conditions, Ψ_p can be improved throughout the summer by nitrogen (N) fertilization despite substantive increases in weed biomass (Nambiar and Sands 1993). Improved nutrition, particularly N, can increase photosynthetic rates if stomates are not closed by drought (Mitchell and Hinckley 1993).

Fertilization generally involves a single nutrient applied as one large pulse. Yet, balanced nutrition should be a key to optimal plantation performance. Timmer's (1997) concept of "exponential nutrient loading" is more progressive. It seeks to produce a nursery seedling with balanced nutrition and an abundance of mycorrhizae (Quoreshi and Timmer 1998), imparting planted seedlings with an immediate advantage over competing vegetation. However, improved nutrition in the nursery may be short lived in the field. Eventually, plantations must rely on soil nutrient supply to sustain their growth. Needs for all nutrients are not static. Rather, they increase with stand development, peak near crown closure, then fall back to lower levels because of internal recycling (Switzer and Nelson 1972).

Where soil moisture is not strongly limiting, nutrient supply will determine the site's carrying capacity for leaf area and growth. Leaf area is critical because light interception is related linearly to growth, a relationship that seems unaffected by water and nutrient stress (Linder 1987). However, increased leaf area may be a mixed blessing in a Mediterranean climate. Greater leaf area means a greater transpiring surface that depletes soil water faster and leads to stress during drought. Methods are needed to improve the efficiency of water use in plantations of drier climates.

In his keynote to a symposium on sustainable forest productivity, Nambiar (1996) underscored the importance of intensively managed, high-yielding plantations in meeting social needs for fiber and in reducing pressures on natural forests for timber production. The key to sustainable plantation management lies in a fundamental understanding of how water and nutrient supplies affect tree growth, how this varies across sites and time, and how it can be influenced positively by management. The best approach lies in well-replicated experiments involving multiple treatments in factorial combinations that minimize confounding, applied to a variety of sites, and carried for long periods (Powers et al. 1994). Unfortunately, most studies are brief. Few involve more than a single factor or extend to multiple sites.

The "Garden of Eden" experiment (Powers and Ferrell 1996) was chartered in 1985 to investigate basic tree × soil interactions and to address fundamental questions about the factors governing plantation growth in a Mediterranean climate. It was designed to overcome many of the problems of conventional studies. Treatments involve full factorial combinations of vegetation, nutrient, and insect control applied repeatedly and regularly on an extreme gradient of site qualities. This experiment centers specifically on pine plantation performance under the strong constraints of a Mediterranean climate. Plantation studies of great scale and scope do exist through research cooperatives in the southern pine region of the United States (Allen 1990; Glover and Lauer 1996). However, we believe that the Garden of Eden network is unrivaled in research intensity, extent, and duration in western North America. To our knowledge, the only similar three-factor experiment involves *Eucalyptus grandis* Hill ex Maiden in New South Wales (Birk and Turner 1992).

Six-year findings were reported at the last International Vegetation Management Conference (Powers and Ferrell 1996), but they were preliminary. One important event since then is that canopy closure (the first major turning point in stand development; Switzer and Nelson 1972) has been reached in at least some treatments at all stands. Another is that the final and most massive fertilization pulse (a load nearly three times that of the cumulative total to that point) has since been added and responses have now emerged. What is the long-term impact of extreme control measures, alone and in combination, on young stand response? Is what's true for one site true for all? Here we report 10-year responses to sustained vegetation, nutrient, and insect-control treatments in plantations that contrast in their principal limiting factors. Further, we discuss mechanisms controlling plantation response and water-use efficiency in a region of summer drought.

Materials and methods

Field sites

As detailed by Powers and Ferrell (1996), ponderosa pine plantations were established at eight locations covering an extreme range of site conditions in the Klamath, Cascade, and Sierra Nevada geomorphic provinces of California. Plantations were established on industrial forest lands between 1986 and 1988, following

either timber harvest or conversion from brushfields. Regardless, care was taken to minimize soil disturbance. Each plantation has 24 contiguous, rectangular plots, each measuring 20×22 m (0.04 ha). Plots were planted in spring with 1–0 bare-root stock of superior families of ponderosa pine at a square spacing of 2.5 m (1647 trees/ha). Seedlings were reared at the Institute of Forest Genetics in Placerville, Calif. Site indices (50-year base) were estimated from heights and ages of dominant trees in the bordering stands (Powers and Oliver 1978).

Experimental design and treatments

Treatments applied at the time of planting and at regular intervals thereafter were a control (C); insecticide (I) as acephate or dimethoate; herbicide (H) as glyphosate or hexazinone; and fertilizer (a mix of N, phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), copper (Cu), boron (B), and zinc (Zn)) in all possible combinations for a total of eight treatments replicated three times at each plantation. Both insecticides and herbicides were applied annually according to manufacturers' recommended rates using directed sprays. Fertilizers were applied every 2 years at an exponential rate, starting at the time of planting and extending through year 6. A total of 1074 kg N·ha^{-1} was applied over the first 6 years of growth. Cumulative totals for other elements (in kg·ha^{-1}) were P, 530; K, 540; Ca, 416; Mg, 221; S, 112; Zn, 73; Cu, 36; and B, 36.

Sampling and measurements

Soil samples were collected from the upper 20 cm of unfertilized plots following establishment, each sample being a composite of 10 (an intensity of 840 samples/ha). These were analyzed for standard chemical properties, including organic carbon (C), total Kjeldahl N (TKN) and bicarbonate-soluble P (Page et al. 1982). Tree measurement plots were established from the third row inward of treatment plot boundaries and encompassed 20 trees. In even-numbered years (years 2, 4, 6, 8, and 10) measurements were taken of basal or breast-height diameter, total height, crown width and length, and understory cover and height by species. Diameters and heights were used to estimate tree volumes as described by Oliver and Powers (1978). In odd-numbered years (years 1, 3, 5, 7, and 9) samples were taken in late summer of both current-year and 1-year-old needles from the upper crowns of at least 10 trees per measurement plot (840/ha). Late summer is the best period for separating both treatment and site-quality effects (Powers 1984). Needles were dried, counted, weighed, and analyzed for their nutrient content by standard laboratory procedures as described by Powers and Ferrell (1996).

Three plantations received more intensive study. They grow within 130 km of each other on volcanic parent materials in the southern Cascade – northern Sierra Nevada geomorphic province. However, beyond that they differ substantially in climate, elevation, soil development, and site quality. Chester, at the highest elevation, has a cool, dry climate with precipitation mainly as snow, and a weakly developed soil tentatively classified as the Windy series (skeletal, frigid Humic Vitrixerands). It was planted in spring 1987 following the clearing of a dense brushfield of *Arctostaphylos patula* Greene and *Ceanothus velutinus* Dougl. ex Hook. Feather, at midelevation, has a moderate climate with precipitation balanced between snow and rain. The soil series at Feather is Cohasset (loamy, mesic Ultic Haploxeralfs). It was planted in 1988 following the harvesting of a mixed, natural stand of conifers and hardwoods. And at the lowest elevation is Whitmore (warm, dry climate, precipitation almost entirely as rain). The soil series there is Aiken (clayey, mesic Xeric Haplohumults). Whitmore was planted in 1986 following clearing of a dense brushfield of

Arcostaphylos viscida Parry and *Arctostaphylos manzanita* Parry). Climatological monitoring of each of these sites over 2 years shows them to differ significantly in every measured attribute (Reynolds and Powers 2000).

Intensive measurements were made at midseason intervals beginning in spring when Chester, Feather, and Whitmore plantations were 8, 7, and 9 years old, respectively. Five trees spanning the size range in each plot were sampled repeatedly in all replicates of four treatments (C, H, F, and HF). Measurements included stomatal conductance (G_s), transpiration (E), and net assimilation (NA) for upper-crown foliage using a LI-COR 6200 portable CO_2 analyzer.[2] Xylem Ψ_p was measured at the same intervals on twigs using a Soilmoisture Equipment Corp. pressure bomb. Measurements were taken throughout daylight hours with both units. Plot sequences were randomized to avoid bias due to time of day and sun angle. Individual tree data were averaged for each replicate treatment plot. Recording meteorological stations operated continuously at all plantations. Work concluded the following spring.

Here, we report results from intensive physiological measurements made in the month of August when growth usually ceases because of summer drought (Oliver et al. 1983; Powers 1984). Reynolds and Powers (2000) recently have shown that August coincides with minimal Ψ_p and maximal vapor pressure deficit (VPD). Therefore, August is a logical month for comparing treatment differences on physiological properties reflecting water use.

Statistical analyses

Treatment differences were examined by randomized block (location) analysis of variance (ANOVA) and repeated measures procedures for time series data. Where effects were significant at least at $P = 0.10$, treatments means were compared using Tukey's test and the probability of type I errors indicated by α. Where it was meaningful, adjusted coefficients of determination were calculated from regression if simple linear trends were significant at $P = 0.10$ or less.

Results

Location differences

Characteristics of the three sites differed fundamentally in ways that govern their productivity and affect their responses to treatment (Table 1). One major distinction is mean air temperature in August, which declined linearly with elevation ($r^2 = 0.99$, $P = 0.04$). Chester, at twice the elevation of Whitmore, averaged one-third cooler in August and nearly one-fifth higher in relative humidity (RH). Although annual precipitation was greater at Whitmore than at Chester, Whitmore's high summer temperatures, low RH, clayey soil texture, and very low soil organic C concentration marks it as the droughtiest site of all. Soil organic C concentrations (an index of available water-holding capacity) were nearly identical at Chester and Feather and three times greater than at Whitmore. This, coupled with the highest annual precipitation, highest summer RH, loamy soil texture, and intermediate temperature suggests that summer drought would affect Feather the least. Soil fertility, indexed both by TKN and C:N ratio, which correlate with available N (Powers 1980, 1984), and by available P, was greatest at Chester. By any measure, soil fertility was least at Whitmore, but the high soil C:N ratio (29:1) and low available P at Feather suggests that both N and P are potentially limiting there. Feather's site index was half again greater than

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[2]Mention of any trade name or product does not constitute endorsement by either the United States or Canadian Forest Services.

Table 1. Physical and chemical site conditions for three Garden of Eden plantations.

Location	Site index (m)	Elevation (m)	Annual precipitation (mm)	Soil texture	Organic soil C (g·kg⁻¹)	Total soil N (mg·kg⁻¹)	Available soil P (mg·kg⁻¹)	August air temperature (°C)	August RH (%)	August soil temperature (°C)
Chester	20	1465	890	Cindery	60.4	2948	10.00	16.9	46.6	19.6
Feather	30	1220	1780	Loam	60.3	2090	1.88	19.2	49.2	20.6
Whitmore	23	730	1140	Clay	22.8	938	1.12	25.4	39.4	24.0

Note: Air temperatures and relative humidity (RH) are 24-h averages measured at canopy height. Soil chemical values are averages for the upper 20 cm of mineral soil. Soil temperature is at 20 cm depth.

Table 2. Understory and overstory ground cover (%) at 10 years by life form for control and fertilized treatments.

Life form	Chester Control	Chester Fertilized	Feather Control	Feather Fertilized	Whitmore Control	Whitmore Fertilized
Understory vegetation						
Trees	1.3a	0.4a	9.7a	8.1a	0.3a	2.7a
Shrubs	37.4a	18.7b	78.6a	35.2b	71.5a	84.4a
Herbs	$0.1a_a$	$1.7a_b$	22.4a	15.5a	20.8a	13.3a
Grasses	25.5a	67.0b	0.0a	0.0a	1.3a	2.5a
Total understory	64.3a	87.8b	110.7a	58.8b	93.9a	102.9a
Overstory pines	$50.3a_a$	$74.6a_b$	108.5a	345.6b	$31.6a_a$	$60.9a_b$

Note: Means not sharing a common letter for each plantation and life form differ at $\alpha = 0.05$ (subscripts show differences at $\alpha = 0.10$).

Chester's, translating to nearly a threefold difference in potential yield without further treatment (Oliver and Powers 1978).

Competing vegetation

Ground cover of understory vegetation at 10 years on control plots ranged between 64 and 111% (Table 2). Coverage differed significantly among plantations ($P < 0.001$) and increased with site index. Woody shrubs, almost entirely *Arctostaphylos* and *Ceanothus* species, were the predominant understory life forms, accounting for 57, 71, and 76% of the ground cover at Chester, Feather, and Whitmore, respectively. Shade-tolerant understory trees such as *Libocedrus decurrens* Torr. and *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. were fairly common at Feather but were rare elsewhere. Grasses were abundant only at Chester, probably because of the lower crown coverage of both pines and shrubs (Table 2). Fertilization promoted understory development at Chester, mainly by increasing the coverage of grasses that excluded woody shrubs. At Whitmore, fertilization effects that had strongly promoted shrub development through 7 years (Powers and Ferrell 1996) were subsiding. At Feather, shrub coverage was 55% lower on fertilized plots, largely because of a threefold increase in overstory pine cover.

Tree growth

Survival stabilized by the third year and was high in all treatment plots at all three plantations, varying from 86% at Chester to 100% at Feather. Randomized block ANOVA of 10-year tree volumes revealed strong block (location), treatment, and block × treatment interactions ($P < 0.001$), indicating that treatment responses differed among plantations. Volume growth responses are shown in Fig. 1. Systemic insecticide treatment alone or combined with other treatments had no influence on tree growth at Chester or Whitmore, although growth was improved at Feather when I was combined with HF. All plot trees in each plantation were examined at least once annually for signs of insect activity and overall injury from pine-feeding insects was very low throughout and unrelated to treatment, even for *Ecosma sonomana* Kearfott, a shoot borer that is unaffected by these systemics (G.T. Ferrell, Pacific Southwest Research Station, Redding, Calif, unpublished data). We conclude that the apparent effect of I in combination with HF at Feather merely is an example of type II error. Consequently, insecticide treatments are ignored as an individual effect for the remainder of this paper.

Stand volumes on control plots were similar for Chester and Whitmore, as would be expected by their similar site indices estimated from trees in the surrounding stands, and were comparable with those expected for planted trees of such spacing and site qualities (Oliver and Powers 1978). At Feather however, control plot volumes were twice those predicted from yield tables. The primary treatment affecting growth at each plantation was herbicide control of competing vegetation, easily doubling volume growth at Chester and Whitmore. Although Feather had the highest ground cover of any plantation (111%), tree volumes were a relatively modest 56% greater for the H treatment. Fertilization, which had no noticeable effect in any plantation at 6 years (Powers and Ferrell 1996), now produced significantly higher standing volume at Feather, where responses were similar but slightly greater than those from herbicides.

Fig. 1. Standing bole volume at 10 years for Chester, Feather, and Whitmore in relation to treatment. C, Control; I, insecticide; F, fertilization; H, herbicide treatments applied regularly through year 6. Treatment bars with the same letter do not differ at $\alpha = 0.05$.
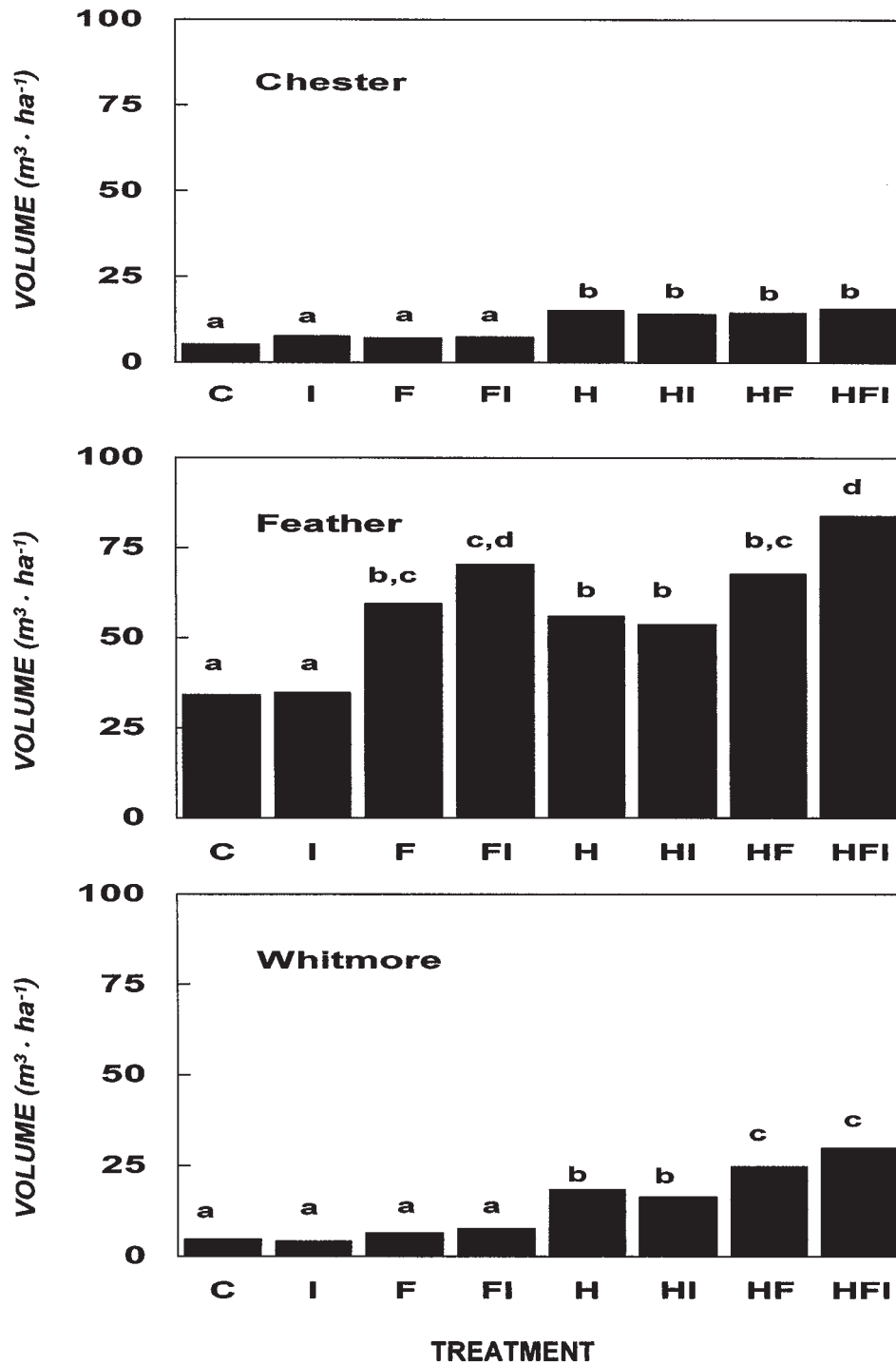
Combined H and F treatments had no obvious benefit at Chester, but volume increment was improved significantly at Whitmore. At Feather, pooling volumes from insecticide treatments with C, H, and F showed that F and H treatments were comparable but that HF produced a third more volume increment than F ($\alpha = 0.10$) and twice the volume increment as H ($\alpha = 0.05$). Standing volumes at 10 years in HF treatments were 14 and 11 times greater at Feather and Whit-

more, respectively, than 10-year volumes reported for those site qualities and spacings in yield tables (Oliver and Powers 1978). In fact, standing volumes for the HF treatment at Feather were six times greater than for the highest site index reported by Oliver and Powers (1978). Literally, they were "off the chart." For all sites, HF volumes at 10 years approached those for plantations nearly twice that age.

Trends in tree height growth over time are shown in

Fig. 2. Cumulative stand heights by treatment for the first 10 years of plantation development. Herbicide treatment dominated growth trends at Chester and Whitmore. Fertilization had the strongest effect at Feather.
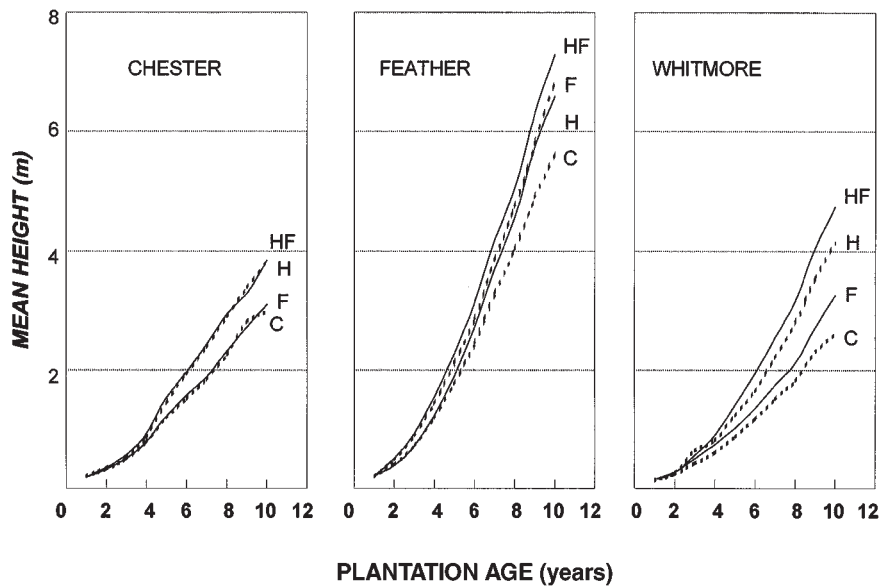

Fig. 3. Relationship of crown and stem volumes at 10 years. Treatments are indicated by letters C, F, H, and HF. The curve appears to depart from linearity.
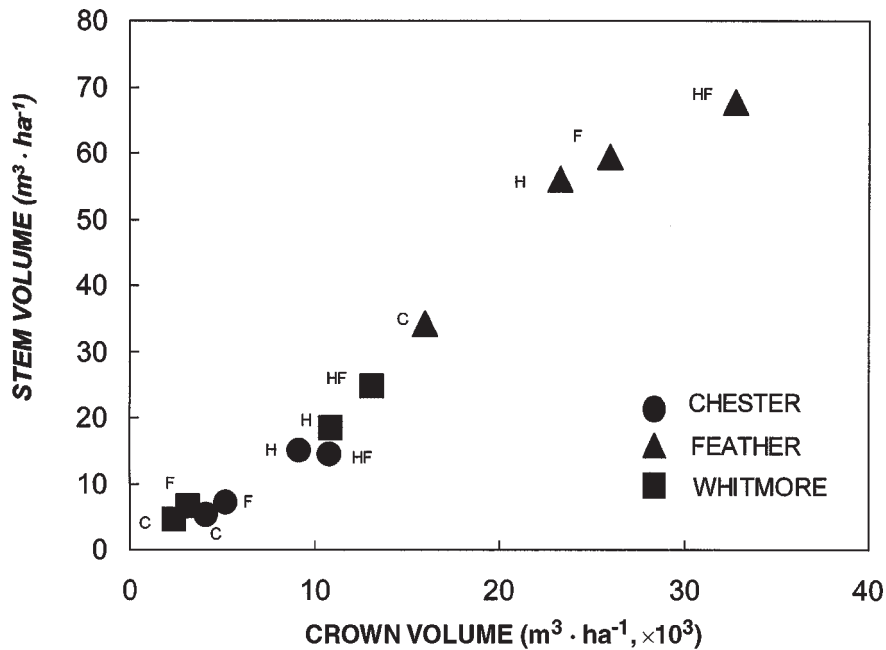

Fig. 2. Growth separations due to herbicide treatment were evident at all plantations by year 4. No fertilizer effect was seen at Chester, but increases were apparent by year 6 at Feather and Whitmore. At Whitmore, combined treatments (HF) produced trees that were twice as tall as those for controls by year 10, and differences are increasing. Crown volumes of individual trees at 10 years were estimated as simple geometric solids by conic formula. While we recognize that this does not account for changes in crown geometry following crown closure, it does provide a surrogate for crown biomass or leaf area. Crown volumes were summed per plot and treatment and expanded to cubic metres per

hectare. These ranged over an order of magnitude, from a low of 2.4×10^3 m^3·ha^{-1} for the Whitmore C treatment, to 32.7×10^3 m^3·ha^{-1} for Feather HF. Stand crown and stem volumes at 10 years are highly correlated ($r^2 = 0.98$, $P < 0.001$), comparing favorably with the tight linear trend found for tree averages at age 6 before crowns had closed (Powers and Ferrell 1996). But there is one important exception: the trend now seems sigmoidal (Fig. 3).

Nutrition

At Whitmore, the least fertile and droughtiest site, soil N availability was improved significantly through the ninth

Fig. 4. Changes in foliar N concentration with time, relative to treatment. Deficiencies are apparent at Whitmore by the seventh year in both current and 1-year-old foliage on unfertilized plots. Chester is well supplied with N (>10.5 g N/kg foliage). Nutrition generally was improved temporarily by herbicide treatment. See Table 3 for statistical significance.
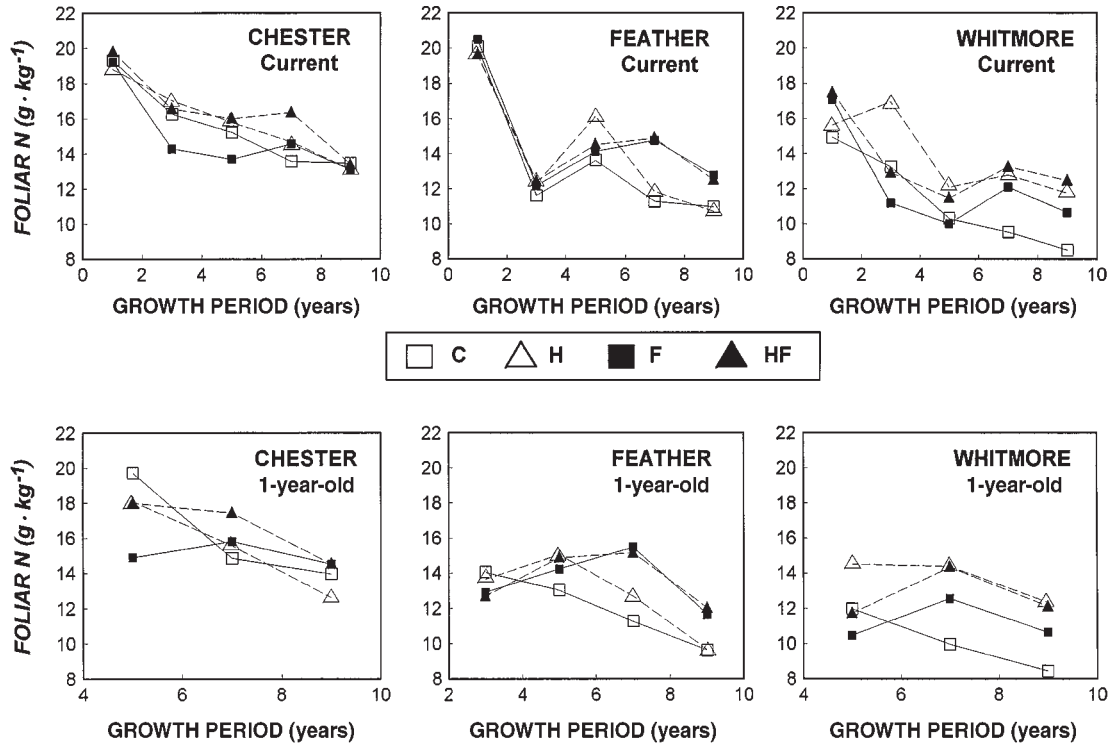
year simply by vegetation control (Fig. 4, Table 3). Phosphorus availability (Fig. 5) was enhanced only through year 3. Lacking vegetation control, foliar N concentrations in both current- and previous-year foliage declined steadily on all sites, falling below the critical level of 10.5 g N·kg^{-1} for current- and previous-year foliage (Powers 1983) by year 9 at Feather and year 7 at Whitmore. By year 7, following the final and most massive installment the previous fall (800 kg N·ha^{-1}), fertilization significantly increased N uptake and foliar N concentration in both current- and previous-year needles at Whitmore and Feather but not at Chester. This foliar N improvement from fertilization coincides with the emergence of height growth response to this treatment (Fig. 2). Where foliar N concentrations in year-old needles fell below critical level (Feather and Whitmore), concentrations were significantly increased by fertilization (Fig. 4, Table 3). At Chester, where foliar N concentrations remained adequate, fertilization had no promotive effect.

Foliar P concentration was unaffected by herbicide treatment at Feather (Fig. 5, Table 3) and improved only briefly (year 3) at Whitmore, where soil available P is very low (Table 1). Herbicide treatments also improved foliar P concentrations briefly at Chester ($\alpha = 0.10$), but the soil at Chester tested high in P (Table 1), and trees generally were well supplied anyway (Fig. 5). Borderline deficiencies of P were apparent in 1-year-old foliage at both Chester and Feather. However at Whitmore, P concentrations in 1-year-old needles were well below the critical level of 0.8 g P/kg foliage (Powers 1983), indicating a severe and acute deficiency on this notoriously P-sorbing Aiken soil series (Ulrich et al. 1947). Despite the massive addition of fertilizer P (530 kg·ha^{-1}), con-

centrations of P in current-year foliage were raised only slightly by year 9 and only when fertilization and herbicide treatments were combined (Fig. 5).

August physiology

Xylem Ψ_p clearly was lowest (water stress was greatest) at Whitmore, regardless of treatment (Table 4). It tended to decline with growth rate at Whitmore ($r^2 = 0.74$, $P = 0.09$), but correlations were weak elsewhere. At Whitmore, only the HF treatment differed significantly from the control (Ψ_p was lower by an average of 0.17 MPa). This contrasts with Feather, where Ψ_p was greatest in trees on HF plots and significantly greater than for H alone. No treatment effects were evident at Chester, although higher growth rates were associated with higher Ψ_p. Water potentials were correlated inversely with VPD at Chester ($r^2 = 0.73$, $P = 0.09$) and Feather ($r^2 = 0.80$, $P = 0.07$). The highest VPDs were at Whitmore and Chester at the elevational extremes. The lowest VPD was at Feather, which also has the highest relative humidity and precipitation (Table 1). There, VPDs were lowest for HF trees ($\alpha = 0.05$), but the opposite was true at Whitmore. Transpiration rates (E) were greatest at Feather and least at Whitmore (Table 4). Rates were affected by treatment only at Feather (higher in H treatments, lower in HF). Rates at Feather increased directly with VPD ($r^2 = 0.86$, $P = 0.05$).

August stomatal conductance rates increased with E ($r^2 = 0.79$, $P < 0.01$). They were greatest at Feather (the more mesic site) and least at Chester (Table 4). At Feather and Whitmore, rates tended to be lower in treatments promoting the greatest growth, but the opposite was true at Chester. Net

Table 3. Statistical comparisons among treatments for nitrogen and phosphorus concentrations in (A) current- and (B) previous-year needles.

(A) Current-year needles.

	Nitrogen concentration				Phosphorus concentration			
Year	Control	Fertilizer	Herbicide	Fertilizer + herbicide	Control	Fertilizer	Herbicide	Fertilizer + herbicide
Chester								
3	ab	b	a	a	ab_{ab}	a_a	b_c	b_{bc}
5	a_{ab}	a_b	a_a	a_a	ab	a	b	ab
7	a	a	a	b	a	a	a	a
9	a	a	a	a	a	a	a	a
Feather								
7	a	b	a	b	a	a	a	a
9	a	b	a	b	a	a	a	a
Whitmore								
1	a	ab	ab	b	a	b	ab	b
3	a	a	b	a	ab	a	c	b
5	a	a	b	b	ab_a	a_a	ab_{ab}	b_b
7	a	b	b	b	ab	a	ab	b
9	a	b	c	c	a	ab	a	b

(B) Previous-year needles.

	Nitrogen concentration				Phosphorus concentration			
Year	Control	Fertilizer	Herbicide	Fertilizer + herbicide	Control	Fertilizer	Herbicide	Fertilizer + herbicide
Chester								
7	a_a	ab_{ab}	ab_a	b_b	a	a	a	a
9	ab	b	a	b	a	a	a	a
Feather								
7	a	b	a	b	a	a	a	a
9	a	b	a	b	a	a	a	a
Whitmore								
5	a	b	c	a	a	a	a	a
7	a	b	c	c	a	a	a	a
9	a	b	c	c	a	a	a	a

Note: Only years with significant differences are shown. Within a year, treatments not sharing a common letter differ at $\alpha = 0.05$ (subscripts show differences at $\alpha = 0.10$).

assimilation rates increased directly with site index when vegetation was controlled ($r^2 = 0.99$, $P = 0.04$). Otherwise, NA was not affected by treatment. Actual water-use efficiency (WUE = NA/E) was insensitive to site index and to treatment except at Feather, the most mesic site. There, WUE was nearly 60% greater for the HF treatment than for H ($\alpha = 0.10$; Table 4).

Discussion

This elevational sequence encompasses a remarkable array of factors governing plantation growth and response to treatment. Although all plantations are under the overriding influence of a Mediterranean climate, the significance of summer drought varies by site. Chester at the highest elevation has the shortest growing season. The area remains beneath snow until late spring, well after growth has commenced at lower elevations. Although annual precipitation at Chester is appreciably lower than at the other two sites, the sandy texture of the volcanic ash in the cindery soil means that water infiltration rates will be very high, as will water retention because of high soil organic C content. Furthermore, low summer air temperature and high RH suggest that water stress would not be as severe as at Whitmore, the warmest site. This is verified by higher Ψ_p and E at Chester during the peak of the dry season (Table 4). However,

Fig. 5. Changes in foliar P concentration with time, relative to treatment. Deficiency is apparent in 1-year-old foliage of all plantations, regardless of treatment. The problem is most acute at Whitmore, where current foliage of unfertilized trees are below critical level of 0.8 g P/kg foliage. See Table 3 for statistical significance.
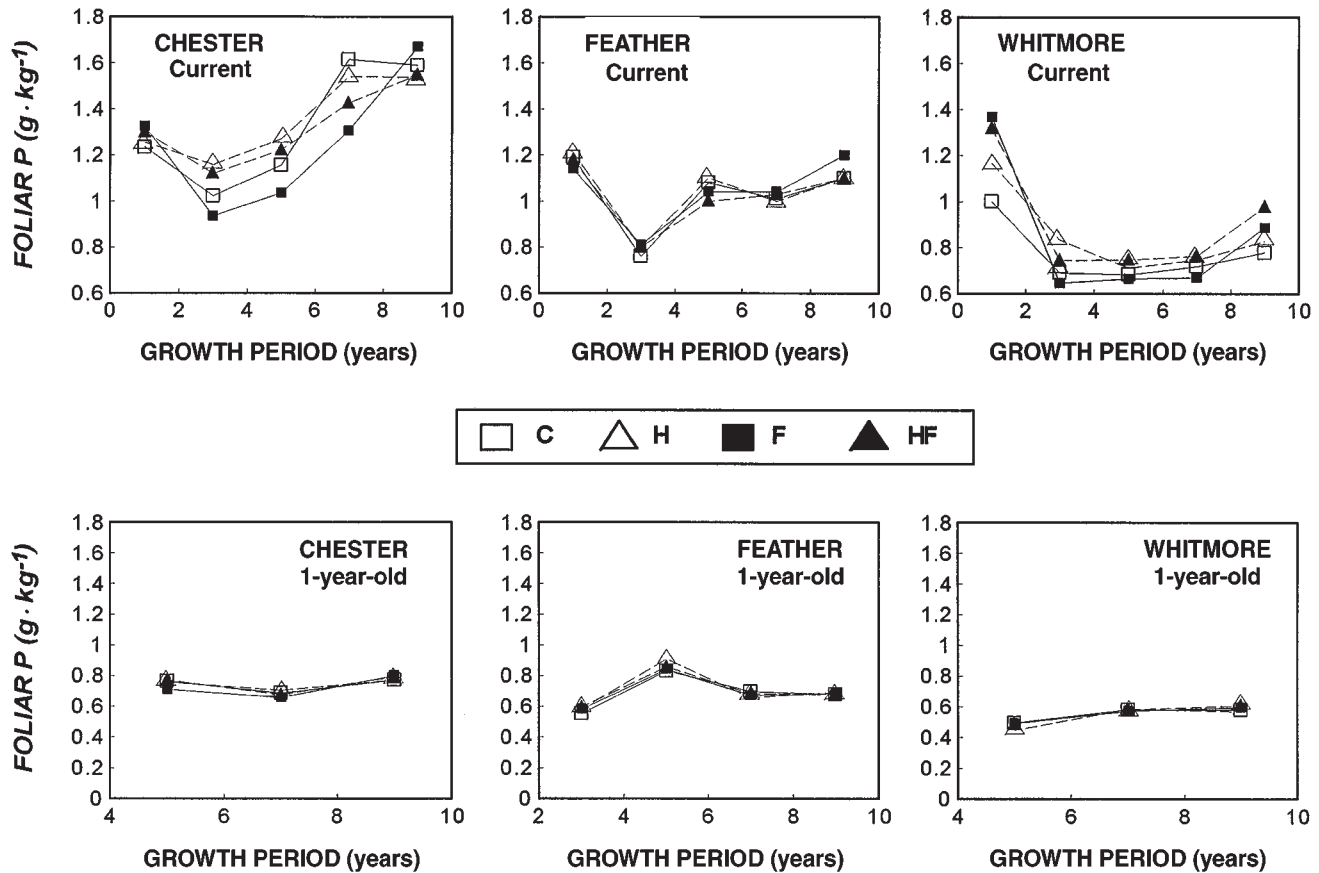
Chester's cindery soil and low precipitation mean that soil water supply does become limiting, as verified by the consistent response of tree growth to vegetation control (Fig. 1).

Soil fertility at Chester is high. The organic C concentration of its topsoil matches that for the more productive Feather site and is more that twice that at Whitmore. Chester's soil TKN concentration exceeds Feather's by 41% and is three times greater than at Whitmore. This, and its favorable 20:1 C:N ratio, reflects the legacy of its previous plant community dominated by the N-fixing *Ceanothus velutinus.* Although the soil at Chester is immature, P availability is high because its volcanic ash mixed among cinders has not weathered to a high sorption capacity. Consequently, the solubility of soil P is much greater there than at the other sites (Table 1). High availability of soil N and P is reflected in high concentrations of these nutrients in both ages of foliage (Figs. 3 and 4), and it isn't surprising that trees at Chester showed no response to fertilization. Perhaps nutritional stresses will emerge as plots reach leaf area carrying capacity. However, as tree crowns have not yet closed (Table 2) and crown volumes are very low (Fig. 3), that seems several years away.

Whitmore at the lowest elevation is a plantation stressed both hydrologically and nutritionally. Although the site ranks intermediate in precipitation, the fine texture of its Aiken clay means that infiltration rates of winter rainfall would be the lowest, and runoff the highest, of any of the sites. Very low soil organic C concentration, coupled with fine soil porosity, suggests that Whitmore ranks lowest in soil storage capacity for plant-available water. High summer air and soil temperatures and low RH further indicate that Whitmore is the droughtiest of the three sites. This is supported by Whitmore's physiological data for August, showing the lowest Ψ_p and E of any plantation (Table 4). Thus, it is clear why Whitmore responded so strongly and positively to vegetation control (Fig. 1).

The soil at Whitmore is nutritionally impoverished. Soil TKN and available P concentrations rank lowest of all the sites. Vegetation control at Whitmore also improved soil N availability through the first 10 years, but the effect was short lived for soil P (Figs. 3 and 4). While growth response to vegetation control was due largely to improved water availability, it was due partly to improved nutrition (particularly, N). However, despite continuous vegetation control, foliar P concentrations have fallen below critical level without fertilization. Phosphorus stress will become increasingly severe because of the notorious P sorption capacity of this iron-rich soil (Ulrich et al. 1947).

The overriding effect of drought at Whitmore and the aggressive nature of its understory shrubs explain why tree growth was not improved by fertilization unless vegetation was controlled or until trees finally began to dominate the understory (Figs. 1 and 2). Measurements of the understory after year 7 (Powers and Ferrell 1996) show that the main

Table 4. Treatment-related differences for midday physiological measurements at canopy level in August 1995.

Variable	Plantation	Treatment			
		Control	Fertilizer	Herbicide	Herbicide + fertilizer
Xylem water potential (MPa)	Chester	−1.62a	−1.55a	−1.54a	−1.58a
	Feather	−1.59ab	−1.60ab	−1.69b	−1.48a
	Whitmore	−1.70a	−1.62a	−1.77ab	−1.87b
Vapor pressure deficit (kPa)	Chester	3.73a	3.39b	3.01c	3.44b
	Feather	2.68a	2.57ab	2.76a	2.43b
	Whitmore	$3.15ab_a$	$3.35bc_b$	$3.11a_a$	$3.56c_c$
Transpiration rate ($mmol·m^{-2}·s^{-1}$)	Chester	1.41a	1.34a	1.38a	1.38a
	Feather	$1.76ab_{ab}$	$1.54a_b$	$2.08b_a$	$1.41a_c$
	Whitmore	1.17a	1.24a	1.05a	1.16a
Stomatal conductance ($mol·m^{-2}·s^{-1}$)	Chester	$0.033a_a$	$0.034a_a$	$0.042b_b$	$0.035ab_a$
	Feather	$0.065a_a$	$0.053ab_b$	$0.067a_a$	$0.051b_b$
	Whitmore	0.040a	0.036ab	0.033b	0.031b
Net assimilation ($\mu mol·m^{-2}·s^{-1}$)	Chester	3.52a	3.09a	2.89a	2.75a
	Feather	4.11a	4.54a	4.48a	4.67a
	Whitmore	2.54a	2.50a	3.08a	3.21a
Actual water use efficiency ($\mu mol\ CO_2/mmol\ H_2O$)	Chester	2.52a	2.28a	2.09a	1.99a
	Feather	$2.37a_{ab}$	$3.09a_{ab}$	$2.19a_b$	$3.46a_a$
	Whitmore	2.14a	2.04a	2.95a	2.99a

Note: For each plantation, row means not sharing a common letter differ at $\alpha = 0.05$ (subscripts show differences at $\alpha = 0.10$).

effect of fertilization was to double the leaf area and biomass of *Arctostaphylos*. However, the effect seems to be dissipating by year 10. Judging from foliar analyses in year 9 (Fig. 5), the massive additions of fertilizer P have overcome the P sorption capacity of Whitmore's soil. However, the strong synergism between vegetation control and fertilization on such a site points to the immense advantage of combined treatments (Fig. 1). Accelerated growth is a two-edged sword in a Mediterranean climate because it also spells greater water use. Combined treatments at Whitmore produced five times the crown volume as control plots (Fig. 3), translating to a greater transpiring surface and higher water stress in summer (Table 4). Therefore, drought will always cap the growth ceiling on such sites.

Conditions at Feather (high precipitation, moderate temperature, and a rich soil with high water-holding capacity) support high growth rates on control plots (Fig. 1). However, high growth rates also spell high demand for soil moisture and nutrients. For example, tree canopy in the control treatment at Feather had closed to 108% by 10 years, equivalent to a crown volume of 16×10^3 m^3·ha^{-1} (Fig. 3). Coverage there was twice that of Chester and three times that of Whitmore (Table 2), and crown volume differences were even greater (Fig. 3). This equates to a greater transpiring surface and more nutrient immobilization. While August *E* rates at Feather were the highest of any plantation, midday Ψ_p still reached levels triggering stomatal closure (Table 4). Accordingly, trees responded positively, if relatively modestly, to vegetation control. Accelerated tree growth from vegetation control increases crown cover and volume, thereby shifting moisture competition from between trees and understory to intertree demands. By year 7, no significant differences were found for any measures of plant water status between C and H treatments (Table 4).

Feather's Cohasset soil is relatively fertile. Moderate climate and favorable soil conditions there mean that growing seasons are potentially longer than for sites at higher or lower elevations. High rates of annual growth spell high rates of nutrient uptake and immobilization in stem and crown biomass, and this translates to a nutrient demand that gradually reaches or exceeds the nutrient supplying capacity of the untreated soil as crowns begin to close. Although foliar N concentrations in current-year needles remained high throughout the study period in C and H plots, concentrations declined steadily in 1-year-old foliage and dropped below critical level by year 9 (Fig. 4).

Because water availability is not as strong a limiting factor at Feather, trees were able to respond strongly and positively to fertilization without vegetation control. Small, temporary gains in water availability from vegetation control, compared with more lasting nutritional gains from fertilization, explain the absence of the strong synergism found at Whitmore when treatments were combined. This supports similar findings from a short-term study of this same soil type in the Sierra Nevada but 85 km further south (Powers 1984; Powers and Jackson 1978). Foliar P concentrations remained adequate in current-year needles but were slightly below critical level in older foliage (Fig. 5).

Although P concentrations in older needles were not affected by fertilization, higher growth rates mean more P

uptake. Constant concentration in more crown biomass suggests that fertilization did indeed affect P availability. However, it also underscores the difficulty of raising P solubility very much on soils with such high sorption capacity. The key to fertilization response seems to be when concentrations of phloem-mobile nutrients fall below critical level in older needles. Older foliage is a translocation source for amino N to younger foliage and is the first to show N deficiencies (Nambiar and Fife 1991; Powers 1984).

Water-use efficiency is a singularly important matter for sites dominated by a Mediterranean climate. Physiological measurements taken in August provide some clues to late growing season effects of silvicultural treatment, but August may not be a particularly useful time for addressing questions of WUE. More likely, treatment effects on WUE would be noted earlier when water stress is occurring but has not yet reached an extreme. Therefore, it is particularly meaningful that Feather (the site least limited by summer drought) was the only site showing a treatment effect on WUE in August (Table 4). There, the combined HF treatment showed an improvement over H. Average WUE also was higher on F than on C treatments, but differences were not quite significant at $\alpha = 0.10$. From this we infer that better nutrition leads to higher assimilation rates per unit of transpired water, provided that drought is not severe. This supports Mitchell and Hinkley's (1993) findings on better watered sites. It accounts for the strong linear relationship we found among sites in NA and site index but no significant correlation among treatments within sites during the peak of drought. Measurements taken earlier in the growing season when water stress was lower might have revealed stronger differences here and perhaps at Whitmore.

Arraying all stand data for crown and stem volumes at 10 years (Fig. 3) shows strong effects of both site quality and treatment on crown development, which drives wood growth. The apparent departure of the trend from linear at earlier stages of stand development (Powers and Ferrell 1996) to sigmoid by age 10 merely may trace to our failure to account for changes in crown architecture following crown closure. If so, we would have underestimated crown volumes at higher crown densities. However, if this underestimation is minor and the trend truly is sigmoid, we may be approaching an asymptotic plateau analogous to the lowest threshold for leaf area that maximizes dry matter production (Switzer and Nelson 1972).

Conclusions

Our findings illustrate Nambiar and Sands' (1993) principle that such treatments as vegetation control that alter moisture availability to trees must alter nutrient availability, too. We add that soil moisture and nutritional improvements from early vegetation control may dissipate as crowns close and transpiration rates reflect tree-to-tree competition. On the droughtiest sites, early vegetation control may tip the productivity scales from failure to success, but the importance of this declines as site quality improves. Where drought is not as great, fertilization leads to major gains in growth. Our combined HF treatments on average and better sites produced stand volumes greatly exceeding those projected for plantations of similar site quality and spacing but

managed with less intensity (Oliver and Powers 1978). As well, at Feather, growth rates for the most productive treatments exceed any reported previously. The massive quantities of N, P, and other nutrients applied exponentially in this experiment surpass rates reported previously in the literature, and we have no doubt that site quality has been fundamentally improved. Implications are that improved nutrition on better sites leads to greater WUE, a particularly important factor in plantation management within the constraints of a Mediterranean climate. With full site occupancy, water availability will again limit growth. The remedy for this is timely thinning. Accordingly, we have developed and are applying a thinning regime for each plantation according to the specific growth rate of individual treatments. Our findings show the great potential of ponderosa pine plantations to respond to innovative, repeated silvicultural treatment. The key to effective silvicultural investments and increased, sustainable wood supply rests not on broad-brush treatments but on recognizing the principal limiting factors for each site and correcting them.

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