

# Morphological response to competition in red alder: the role of water

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## Summary

Competition for resources often induces shifts in biomass allocation among plant parts resulting in long-term structural differences between neighbouring individuals in perennial communities. To study the morphological responses of red alder (*Alnus rubra*) to water availability, predawn plant water potential and stem and branch growth were measured every 2 weeks on 4-year-old trees planted at spacings ranging from 0.10 to 41.99 m<sup>2</sup> tree<sup>-1</sup>. Tree and branch samples were destructively analysed to determine biomass and leaf area, and regression equations were developed to predict biomass of tree components. These predictions were used to examine differences in growth and biomass allocation among trees at different levels of intraspecific competition. Decreased red alder spacing produced reductions in mean leaf area, height, basal diameter, above-ground biomass and above-ground biomass relative growth rate. A strong negative exponential relationship existed between mean total above-ground biomass relative growth rate and both the water stress integral ( $S\psi$ ) and periodic predawn water stress. Relative growth rate declined sharply at a water-stress level of between -0.3 and -0.4 MPa. The combination of sensitivity to water stress and high rates of biomass production in mesic environments suggests that red alder's water-stress avoidance syndrome is a major factor in its high growth rate.

*Key-words:* Growth analysis, Nelder density series, net assimilation rate, relative growth rate

*Functional Ecology* (1993) **7**, 462–468

## Introduction

Red Alder (*Alnus rubra* Bong.), an aggressive colonizer of disturbed sites in the Pacific Northwest (Hibbs & Cromack 1990), is becoming one of the more studied pioneer tree species in the temperate world. Interest in the high relative growth rates of young red alder (Newton, El Hassan & Zavitokovski 1968; Pezeski & Hinckley 1988; Shainsky 1988) has led to several studies of the patterns and processes of resource uptake and allocation, and its response to competition-induced limitations. Although relative growth rate of young red alder is higher than that of competing species, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and some shrub species, its sensitivity to water and light stress may significantly reduce its competitive ability relative to those species (Krueger & Ruth 1969; Shainsky 1988; S. Chan, in preparation). In a mixed plantation of red alder and Douglas-fir, Shainsky (1988) found that red alder possesses a greater competitive ability and exhibits greater growth potential, lower water stress, and consumes more resources than does Douglas-fir. Shainsky concluded that red alder's competitive advantage

stems from rapid early season height growth, which allows the leaves to capture light. Red alder roots tend to penetrate deeper than do those of Douglas-fir, resulting in greater exploitation of soil moisture and lower moisture stress. Despite red alder's ability to garner more resources, Shainsky found that its growth rates are more sensitive to water stress than are those of Douglas-fir and that red alder mortality due to low light levels is much higher. S. Chan (in preparation) found that red alder photosynthesis was not affected by water-stress levels over a broad range (-0.03 to -1.0 MPa), but the rate of photosynthesis declined sharply when water potential fell below -1.0 MPa. Chan also found that above-ground biomass production was more sensitive to light levels than to water potential. Studies such as Shainsky's and Chan's confirm the pioneer strategy of red alder as exhibited by high resource acquisition and stress avoidance, but still leave many questions unanswered about the effects of water stress and light on red alder growth.

Competition among individuals in a plant community is mediated by changes in resource availability (Barbour, Burk & Pitts 1980; Radosevich & Holt 1984). In order to understand how plant growth and

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community development are regulated by competition, the mechanistic links between growth and the relative availability, acquisition and the need for water and nutrients have to be identified. In perennial plant communities, this competition is reflected in shifts in biomass allocation among plant parts. These shifts can result in long-term morphological differences between neighbouring individuals (Harper 1977; Waring 1987). The way in which a plant distributes biomass within its structure can provide important information on resource limitations (Chapin *et al.* 1987; Waring 1987).

Although the current growth of a plant is a function of immediate growing conditions, its size and morphology are related to earlier conditions. The effects of current and past growing conditions on current growth can be distinguished by measuring individual plant dimensions over short time intervals and relating these measurements to resource levels. The growth measurements can then be integrated over longer periods of time. One method that is sensitive enough to identify short-term fluxes between the plant and its environment is the analysis of the pattern of biomass allocation to different areas of the tree coupled with frequent measurements of resources. The objective of this study was to use measurements of growth and biomass allocation in conjunction with concurrent measurements of water potential to assess the role of water availability in regulating the morphological response of red alder to competition.

### Materials and methods

The study site was located in the Oregon Coast Range on Cascade Head Experimental Forest at an elevation of 330 m. Vegetation is transitional between the *Picea sitchensis* and *Tsuga heterophylla* (Raf.) Sarg. zones (Franklin & Dyrness 1973). The site was clearcut 5 years before the study and slash was burned. Prior to clearcutting, vegetation consisted of old-growth communities of *Picea*, *Tsuga*, devil's club (*Oplopanax horridum* (Smith) Mig.) and ladyfern (*Athyrium filix-femina* (L.) Roth) with abundant components of *Rubus* spp. and red alder. Current vegetation consists of herbaceous species, such as California figwort (*Scrophularia californica* Cham. & Schlecht.), bracken (*Pteridium aquilinum* (L.) Kuhn.), *Oregon oxalis* (*Oxalis oregana* Nutt.), and shrub species, such as *Rubus* spp. and Pacific red alder (*Sambucus calli-carpa* Greene). The growing season averages approximately 180 days. Average annual precipitation is 250 cm. The climate is characterized by high precipitation between October and May, often in the form of cloud condensation. From June until September, periodic rainfall events are separated by 3- to 4-week periods without precipitation.

Following clearcutting and slash burning, three Nelder type 1a density series (Nelder 1962) were established in the spring of 1985, with circular plant-

ings of red alder seedlings at spacings ranging from 0.1 to 41.99 m<sup>2</sup> tree<sup>-1</sup>. Four sample trees were chosen for measurement throughout the fourth growing season at six of the 15 spacings in each series, namely 41.99, 17.13, 3.57, 0.73, 0.26, and 0.10 m<sup>2</sup> tree<sup>-1</sup>. Based on preliminary measurements of basal diameters on all trees in the Nelder series, we selected two sample trees closest to the mean diameter at each sample spacing. In addition, one larger and one smaller tree were randomly selected from the remaining trees at each spacing. This provided a total sample of 72 trees (4 trees × 6 spacings × 3 series). The trees were divided into three vertical sections, each representing one-third of the initial height. One branch was randomly selected for repeated measurements from the total branch population in each section of each tree.

Sampling was conducted between 22 March and 9 October 1988. The three categories of growth measurements were (1) measurements at 2-week intervals for each sample tree, (2) 2-week measurements of each sample branch and (3) seasonal measurements of the total branch population. Every 2 weeks, basal diameter (3 cm above ground), diameter at breast height (DBH, 1.3 m above ground) and total height were measured on all sample trees. Branch basal diameter and total length were also measured at 2-week intervals on all sample branches. In addition, we measured basal diameter, total length and height above ground of all branches on each sample tree before and after the growing season. Concurrent with these growth measurements, we measured predawn plant water potential of each sample tree using a pressure chamber (Waring & Cleary 1967). All vegetation (except the planted red alder) was removed within a 2-m radius around each sample tree to minimize the competition for water.

In addition to these nondestructive measurements, branches were systematically harvested four times: before, twice during, and after the growing season. Three branches were collected at each spacing for each series, so that the total range of branch size was represented. An equal number of branches was sampled from each vertical section of the tree crowns. Branches were not taken from sample trees or their immediate neighbours. Fresh weight, total length and basal diameter were measured on branches harvested at the beginning and end of the growing season. Also, fresh leaf weight and leaf area (using a LI-COR Li3100 area meter) were measured for each branch collected during the growing season. Branches were then dried in an oven (at 70 °C) for at least 48 h and weighed.

To predict total above-ground biomass of sample trees, allometric equations were developed from data collected from on-site destructive harvests of 25 whole trees adjacent to the spacing series (Yoder, Harrington & Hibbs 1988). Multiple regression techniques were used to determine the best predictive

model for the data, relating basal diameter and height to total above-ground tree biomass. Allometric equations for predicting branch biomass and leaf area were developed from the destructive branch samples collected throughout the growing season.

For each measurement period, we calculated relative growth rate (RGR), net assimilation rate, leaf area ratio, leaf weight ratio and specific leaf area (Hunt 1978). Of these parameters, RGR was primarily used to compare changes in growth with changes in water availability. Growth is related to both the magnitude and duration of water stress. In order to assess the effects of short-term, high-stress events on short-term growth, we selected three specific stress events (29 June, 9 August and 13 September) for analysis of growth. Using the mean instantaneous above-ground biomass RGR and predawn water potential for each sample spacing, the relationship between growth parameters (mean total above-ground biomass RGR, mean net assimilation rate and mean leaf-weight ratio) and water potential was determined by simple linear and non-linear regression techniques (STATGRAPHICS 1988). The influence of water stress on short-term growth was examined graphically at other time periods during the season. Long-term effect of water stress on seasonal mean above-ground biomass RGR was examined by calculating the water stress integral,  $S\psi$  (Myers 1988).

## Results

### EFFECTS OF SPACING

At the beginning of the fourth growing season, there was no linear relationship between above-ground biomass and spacing ( $P = 0.04$ ); tree biomass increased with spacing up to  $0.73 \text{ m}^2 \text{ tree}^{-1}$  and then decreased (Table 1). Biomass and height were smaller at spacings that had not achieved crown closure (from  $3.57$  to  $14.13 \text{ m}^2 \text{ tree}^{-1}$ ). By the end of the growing season, absolute above-ground biomass growth increased with increased spacing up to  $17.13 \text{ m}^2 \text{ tree}^{-1}$  and above-ground biomass RGR also increased as

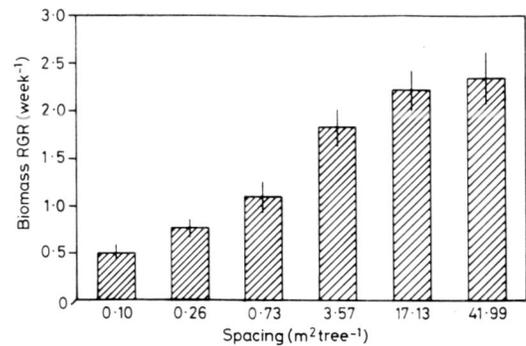


Fig. 1. Mean  $\pm$  SE above-ground biomass RGR of trees at six sample spacings.

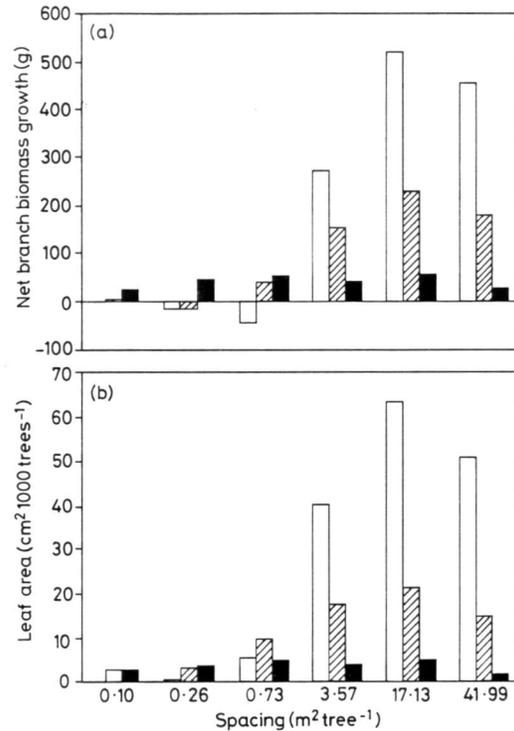
spacing increased (Fig. 1). A strong linear relationship existed between mean above-ground seasonal biomass RGR and the natural logarithm of spacing ( $r^2 = 0.97$ ,  $P < 0.001$ ).

Unlike total above-ground biomass RGR, mean branch biomass characteristics fell into distinct groupings of trees at wide and narrow spacing (Table 1). The average percentage increase of branch biomass for trees at narrow spacing ( $\leq 0.73 \text{ m}^2 \text{ tree}^{-1}$ ) was 25% compared to 368% for those at wide spacing ( $\geq 3.57 \text{ m}^2 \text{ tree}^{-1}$ ). Branch biomass growth also accounted for an increased proportion of total biomass growth as spacing increased (Table 1). The large increase in mean net branch growth at wider spacings is due in part to lower branch mortality under wide spacing conditions. As a percentage of gross growth, branch mortality averaged 60% for narrow spacings and only 2% for wide spacings. Differences in branch mortality were most apparent in the lower one-third of tree crowns (Fig. 2a), where the high branch mortality in closely planted trees resulted in negative net branch growth. Although branch mortality also occurred in the bottom third of widely spaced trees, it was offset by the vigorous growth in the upper third of these trees (Fig. 2a). There was also a decrease in leaf area in the lower third of the crown of trees at narrow spacing (Fig. 2b). Crown depth (top

Table 1. Initial size and growth characteristics of sample trees

Density ( $\text{m}^2$ $\text{tree}^{-1}$ )	Initial			Growth				
	Diameter (mm)	Height (cm)	Above-ground biomass (g)	Branch biomass (g)	Above-ground biomass (g)	Net branch biomass (g)	Branch/ tree (%)	Branch mortality (g)
0.10	22.7 $\pm$ 1.1	318.8 $\pm$ 12.2	191.6 $\pm$ 38.3	60.8 $\pm$ 13.0	158.0 $\pm$ 47.6	25.5 $\pm$ 5.2	16.1	13.3 $\pm$ 4.4
0.26	28.0 $\pm$ 1.2	325.4 $\pm$ 12.0	321.5 $\pm$ 38.2	113.8 $\pm$ 10.8	425.5 $\pm$ 63.1	13.4 $\pm$ 10.1	3.1	52.4 $\pm$ 10.1
0.73	33.6 $\pm$ 2.6	337.5 $\pm$ 17.9	571.1 $\pm$ 119.7	223.5 $\pm$ 32.9	1341.2 $\pm$ 300.6	47.0 $\pm$ 38.8	3.5	88.7 $\pm$ 20.1
3.57	36.9 $\pm$ 2.8	266.3 $\pm$ 14.4	521.9 $\pm$ 149.9	313.0 $\pm$ 106.2	2558.0 $\pm$ 400.0	464.2 $\pm$ 76.0	18.1	13.2 $\pm$ 4.9
17.13	30.8 $\pm$ 2.6	224.6 $\pm$ 17.9	293.7 $\pm$ 84.7	206.4 $\pm$ 48.8	2880.0 $\pm$ 775.1	802.5 $\pm$ 227.1	27.9	18.5 $\pm$ 11.2
41.99	30.6 $\pm$ 3.3	205.0 $\pm$ 20.7	301.4 $\pm$ 116.7	182.3 $\pm$ 57.5	2014.3 $\pm$ 589.2	654.3 $\pm$ 138.9	32.5	11.1 $\pm$ 8.5

\* Mean  $\pm$  SE.



**Fig. 2.** (a) Net branch biomass growth and (b) leaf area per tree in the lower (□) middle (▨) and upper thirds (■) of the sample tree crowns. Data are seasonal means for each sample spacing.

to bottom of crown) was positively correlated with RGR for trees at spacings that achieved crown closure ( $r^2 = 0.38$ ;  $P < 0.001$ ). Leaf area index increased from 0.16 to 2.7 until crown closure occurred, at which point it stabilized and was not affected by further decreases in spacing, except at the narrowest spacing.

#### EFFECTS OF WATER STRESS

Differences in predawn water potential between the treatments developed on 29 June, 9 August and 13 September (Fig. 3). The seasonal trend of above-ground RGR (Fig. 4b) generally corresponded to changes in predawn water potential (Fig. 4a). For trees at both wide and narrow spacing, RGR decreased following the first water-stress date (29 June). However, trees at wide spacing recovered slightly, while those at narrow spacing continued to decline as the growing season progressed, resulting in widely spaced trees having a higher maximum RGR and maintaining a higher average RGR throughout the growing season (Fig. 4b). A similar relationship was found between basal diameter RGR and predawn water potential. Trees at both wide and narrow spacing showed an initial decrease in basal diameter RGR following the first water-stress event (Fig. 4c). However, basal diameter RGR of widely spaced trees recovered, nearly reaching the maximum RGR exhibited before 29 June. Height growth RGR generally

decreased for trees at both wide and narrow spacings after the first water-stress event, and continued to decrease (Fig. 4d). Trends in leaf area RGR for trees at wide and narrow spacings were similar until 29 June (Fig. 4e). The widely spaced trees recovered to pre-stress RGR levels while narrowly spaced trees did not.

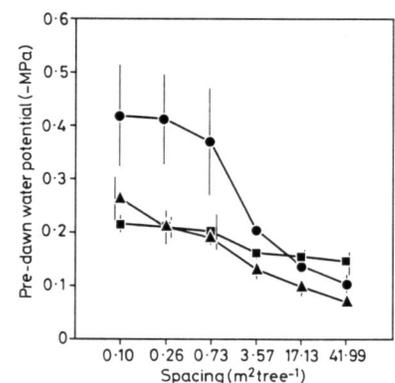
A negative exponential relationship ( $r^2 = 0.76$ ,  $P < 0.001$ ) existed between mean total above-ground biomass RGR and predawn water potential for the three peak water-stress dates when data from these three dates were pooled. Regression models were developed to test if spacing could be substituted for predawn water potential to predict RGR. Tests indicated that spacing and water potential were not substitutable; water potential contributed important information for predicting RGR that was independent of that predicted by spacing.

Net assimilation rate and leaf-weight ratio were used to assess the physiological response of trees to water stress. Net assimilation rate is a measure of the efficiency of biomass production; leaf-weight ratio is indicative of the photosynthetic potential of the tree and is a function of specific leaf area and leaf-area ratio. For the three dates identified as stress events, mean net assimilation rate for each spacing showed a negative exponential relationship with mean predawn water potential ( $P < 0.001$ ). Mean leaf-weight ratio showed no significant relationship to mean predawn water stress for similar dates (Table 2).

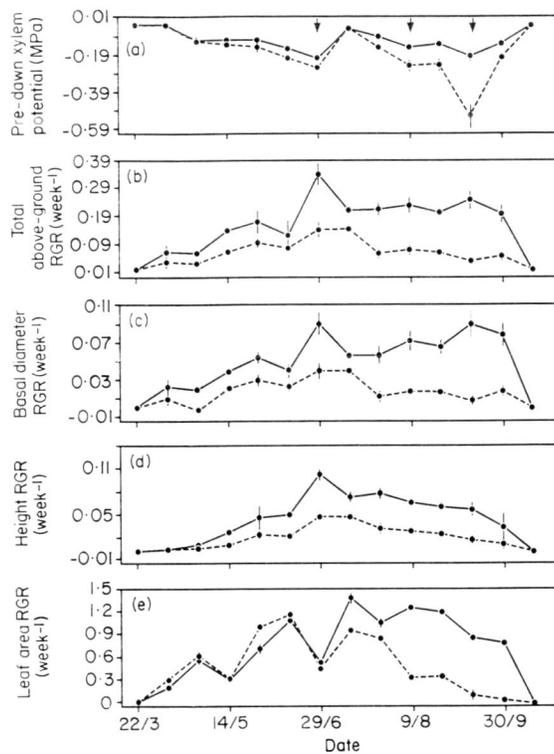
A negative exponential relationship ( $r^2 = 0.68$ ,  $P < 0.001$ ) existed between seasonal mean total above-ground biomass RGR and water-stress integral. The relationship between seasonal mean net assimilation rate, seasonal mean leaf-weight ratio and water-stress integral was also examined. Neither net assimilation rate nor leaf-weight ratio was significantly related to the water-stress integral.

#### Discussion

The Nelder design creates a strong gradient of competitive environments that persist for several years,



**Fig. 3.** Predawn water potential gradients for 29 June (■), 9 August (▲) and 13 September (●).



**Fig. 4.** Seasonal measurements of (a) predawn water potential and seasonal carbon allocation trends as shown in (b) above-ground RGR, (c) basal diameter RGR, (d) height RGR and (e) leaf area RGR for low (—) and high (---) plantings. Arrows show dates when a predawn water potential gradient developed. Bars represent  $\pm 1$  SE.

providing an opportunity to examine changes in growth and resource limitations of perennial plants with competition. Our measurements revealed two temporal patterns of growth: (1) a change in overall growth with spacing and (2) a seasonal change in the allocation of growth within the tree with spacing. Both these changes are driven by changes in resource availability associated with spacing, and thus provide information on the response of red alder to competition. At the beginning of the season, trees growing at

a spacing of  $0.73 \text{ m}^2 \text{ tree}^{-1}$  had the largest mean above-ground biomass, but by the end of the growing season, the largest trees were found at the  $17.13 \text{ m}^2 \text{ tree}^{-1}$  spacing, indicating a change with time in the relationship between RGR and spacing. At the beginning of the study, the highest RGR were found at relatively narrow spacings (e.g.  $0.73 \text{ m}^2 \text{ tree}^{-1}$ ). As trees grew larger, the interaction between them increased, causing RGR at very narrow spacings to decrease. This was accompanied by an increase in growth at wider spacings, resulting in a shift in maximum RGR from narrow to wide spacings with time. This shift indicated that an optimum level of interaction among red alder trees exists, which produces maximum relative growth. Growth at this optimum level of interaction might be enhanced by increased humidity and decreased temperature extremes, wind and/or animal damage.

#### SEASONAL PATTERNS

Biomass allocation among plant parts shifted through the growing season. Relative growth rate of stem diameter, plant height and leaf area all increased rapidly in the early weeks of the growing season (Fig. 4). Diameter growth persisted at high levels throughout the growing season, but height and leaf area RGR peaked by the middle of the season. Red alder has an indeterminate growth habit (Harrington 1990) so these patterns result from biomass allocation rather than from being regulated by a preset limit of preformed leaves and internodes. A larger percentage of later season photosynthate was allocated to diameter growth. This pattern has been observed in other species and could be a response to dry soil conditions late in the season.

#### LIGHT AND WATER

The observed relationships between spacing and growth can probably be attributed to the effect of light and water. Mineral nutrients were not considered to

**Table 2.** Physiological growth parameters

Spacing	RGR* (week <sup>-1</sup> )	NAR† (g cm <sup>-2</sup> week <sup>-1</sup> )	LWR‡	LAR§ (cm g <sup>-1</sup> )	SLA¶ (cm g <sup>-1</sup> )
0.10	0.021 $\pm$ 0.0055	0.0015 $\pm$ 0.0005	0.075 $\pm$ 0.003	15.6 $\pm$ 0.7	208.0
0.26	0.040 $\pm$ 0.0055	0.003 $\pm$ 0.0005	0.115 $\pm$ 0.009	16.9 $\pm$ 1.3	147.5
0.73	0.0595 $\pm$ 0.008	0.006 $\pm$ 0.0005	0.077 $\pm$ 0.007	12.0 $\pm$ 1.1	155.4
3.57	0.1145 $\pm$ 0.0085	0.014 $\pm$ 0.0015	0.053 $\pm$ 0.004	9.1 $\pm$ 0.7	171.0
17.13	0.146 $\pm$ 0.013	0.015 $\pm$ 0.002	0.113 $\pm$ 0.011	13.0 $\pm$ 1.3	115.1
41.99	0.151 $\pm$ 0.0125	0.003 $\pm$ 0.0005	0.348 $\pm$ 0.036	63.8 $\pm$ 6.6	183.2

\* RGR is  $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ .

† NAR (net assimilation rate) is  $(W_2 - W_1)(\ln LA_2 - \ln LA_1)/(LA_2 - LA_1)(t_2 - t_1)$ .

‡ LWR (leaf weight ratio) is  $LW_2/W_2$ .

§ LAR (leaf area ratio) is  $LA_2/W_2$ .

¶ SLA (specific leaf area) is  $LA/LW$  where  $W$  is total above-ground biomass,  $LA$  is leaf area,  $LW$  is leaf weight, and  $t$  is time.

be limiting factors for plant growth because all major nutrients were present in the soil at adequate to high levels (unpublished data). The availability of light and water varied along the spacing gradient, so it was not possible to separate their effects completely. However, an examination of the biomass-allocation patterns and regression results provided some insight into the roles of light and water in mediating the effects of competition in red alder.

When sufficient water is present to maintain turgor pressure and mineral nutrition, leaf area is determined primarily by the amount of available light. Leaves are distributed down through the canopy to the depth at which light intensity is less than the level required for net positive photosynthesis. In this way, light regulates the pattern of biomass allocation by causing trees to produce leaves where they are best able to intercept light. Crown depth varied strongly with spacing, indicating changes in the light environment within the canopy over the spacing gradient (Fig. 2b). Differences among spacings in leaf area were driven largely by differences in the lowest portion of the canopy (Fig. 2b). Shainsky (1988) measured light in the understorey in a red alder spacing series and found levels about 10% of those in the open. Once crown closure was achieved, the low light level in the understorey was constant for all spacings. In our study, leaf area per tree dropped gradually through a range of spacings, reaching a minimum at  $0.1 \text{ m}^2 \text{ tree}^{-1}$ . Leaf area index, however, remained fairly stable once crown closure was achieved. As understorey light level is determined largely by leaf area index (Kira, Shinozaki & Hozumi 1969), we appear to be observing a pattern similar to that found by Shainsky (1988), even though leaf area per tree increased with tree spacing.

The strong relationship between above-ground biomass RGR and predawn plant water potential (Fig. 4a,b) indicates that growth in this environment is highly dependent on water availability. The site receives about 250 cm of annual precipitation and the mean July temperature is  $15.3^\circ\text{C}$ . Yet in the summer, periods as short as 3 weeks without rain result in large changes in growth.

Mean predawn plant water potentials less than  $-0.5 \text{ MPa}$  were rarely observed in this study, but these low water potentials were associated with significant short-term growth reductions. Long-term water stress, as measured by the water-stress integral, was generally below 30 MPa-days. Stress was mild compared with levels observed for other species (*Pinus radiata*, Meyers 1988; *Pseudotsuga menziesii*, Shainsky 1988). In a related study during the same growing season, Lu (1989) measured both predawn and midday plant water potential values at this site and found that they correspond with midday readings near  $-1.5 \text{ MPa}$ . The results of this study showed that short-term water stress causes red alder to modify short-term growth rates. The relationship between

long-term growth rate and patterns of biomass allocation and the water stress integral indicate the importance of long-term, low-level water stress to red alder growth.

#### EFFECTS OF WIDE SPACING

Individual tree growth generally increased with spacing, but trees at the widest spacing usually deviated from this trend, showing less growth than expected. For example, net branch biomass growth and total above-ground biomass growth of trees at the widest spacings decreased by 18 and 30%, respectively, compared to the next widest spacing. It is not clear why growth during the measurement growing season dropped at the widest spacings. While some of these trees experienced more deer and elk damage in previous years than did closely planted trees, micro-environmental factors including temperature, wind and humidity also may have varied across the series.

#### PHYSIOLOGICAL RESPONSE TO WATER STRESS

Relative growth rate is regulated by two primary factors: the efficiency of the leaves and the ratio of leaf biomass to whole plant biomass (Causton & Venus 1981). If RGR were regulated by changes in leaf area, there would be a strong relationship between leaf-weight ratio and RGR. The absence of this relationship and the strong relationship between net assimilation rate and RGR indicates that, in this study, RGR is being driven primarily by reductions in net assimilation rate (photosynthetic efficiency). Both light availability and water stress can reduce photosynthetic efficiency. Although it is hard to assess how much low light associated with decreased spacing affected the net assimilation rate, the strong negative exponential relationship between mean net assimilation rate and mean predawn water potential on dates when water stress occurred supports the idea that short-term changes in water stress levels contributed strongly to differences in net assimilation rate over the spacing gradient.

#### ECOLOGICAL IMPLICATIONS

The cessation of red alder growth in response to water stress has important ecological consequences. This study indicated that the ecological habit of red alder is characterized by early growth initiation, indeterminate growth and the rapid development and continual production of leaf area. Evidence of these characteristics is found in red alder's colonization of disturbed sites, in its rapid growth and full site occupation and in the development of dense stands of trees (Hibbs & Cromack 1990). However, red alder's sensitivity to water stress reduces its competitive ability on sites that are subject to prolonged periods of water stress, resulting in reduced ability to colonize new sites.

reduced growth and reduced stand development. Cessation of growth of red alder in environments that are characterized by only moderate and periodic levels of moisture stress is less common, and short-lived when it does occur. Such environments allow red alder to maintain an efficient carbon capture system that would result in maximum production rates.

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Received 15 October 1991; revised 9 July 1992; accepted 29 July 1992