Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder

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Abstract: We examined growth and biomass allocation of individual Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.) seedlings grown for 3 years under contrasting combinations of light and water. Alder growth was always greater than Douglas-fir. Full sunlight and soil moisture at field capacity caused large differences in size between the two species. With limited light and water, differences were smaller. Under full light and limited water, Douglas-fir allocated a high portion of its biomass to roots, whereas red alder allocated a high percentage to aboveground biomass components. Under light and water resource-limiting situations, red alder allocated more mass to stem, whereas Douglas-fir allocated more to roots. Red alder growth responded negatively to water limitation, whereas Douglas-fir did not. Red alder exhibited greater foliage plasticity to light. Species differences in size and allocation in response to resource availability may determine pathways by which Douglas-fir and red alder interact in a mixed community. Our findings support the hypothesis that the potential of species to use growth-limiting resources is an indicator of competitive ability. We suggest that red alder and Douglas-fir can co-exist under conditions of full light and limiting soil moisture availability. Furthermore, when contrasted with red alder, Douglas-fir's relatively greater tolerances to low light allow it to better persist in the understory. Red alder's rapid early growth and competitive ability will be superior under full light and nonlimiting soil moisture conditions.

Résumé : Nous avons examiné la croissance et l'allocation de la biomasse de semis de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et d'aulne rouge (*Alnus rubra* Bong.) soumis pendant trois années à des combinaisons contrastées de régimes lumineux et hydriques. La croissance de l'aulne était toujours supérieure à celle du douglas. La pleine lumière ainsi qu'une humidité du sol à la capacité au champ ont entraîné les différences de taille les plus fortes entre les deux espèces. Sous des régimes restrictifs de lumière et d'eau, les différences étaient plus faibles. Dans des conditions de pleine lumière et d'humidité restreinte, le douglas a alloué une proportion élevée de sa biomasse aux racines, alors que l'aulne rouge a alloué un pourcentage élevé à ses composantes aériennes. Dans des conditions de lumière et d'humidité restreintes, l'aulne rouge allouait plus à la tige tandis que le douglas allouait plus aux racines. La croissance de l'aulne rouge était ralentie par un stress hydrique alors que celle du douglas ne l'était pas. L'aulne rouge a également montré une plasticité plus forte de son feuillage aux conditions lumineuses. Les différences spécifiques en taille et en allocation en réponse à la disponibilité des ressources pourraient correspondre à des modes d'interaction entre le douglas et l'aulne rouge en communauté mixte. Nos observations supportent l'hypothèse que la capacité des espèces à utiliser les ressources qui limitent la croissance est un indicateur de compétitivité. De plus, comparativement à l'aulne rouge, la tolérance relativement plus grande du douglas à des conditions de faible luminosité lui permet de mieux persister sous le couvert. La croissance juvénile rapide de l'aulne rouge ainsi que sa compétitivité seront supérieures dans des conditions de pleine lumière et sans stress hydrique.

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Introduction

Competition among plants is a primary driver of differentiation in species composition, size, and survival. Competi-

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tion arises when adjacent plants share limited resources. Studies of competition between Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red alder (*Alnus rubra* Bong.) have focused primarily on Douglas-fir responses to alder density and the reduction of alder competition. Cole and Newton (1986, 1987) studied effects of inter- and intra-specific competition on tree growth and resource availability by varying the density of planted Douglas-fir and a 1:1 ratio of Douglas-fir and red alder (Nelder 1962). Shainsky and Radosevich (1991, 1992) employed an "addition series" (Spitters 1983) using Douglas-fir and red alder seedlings where the density and proportion of both species were simultaneously manipulated to create a range of competitive regimes. A key hypothesis in both studies was that gradients of resource availability can be created by gradients of spe-

cies densities, which contribute to both inter- and intra-specific competition. These studies suggest that resource assimilation and allocation by plants are in direct response to competition-induced limitations in resource availability (Tillman 1985).

The following two criteria are considered to be evidence for competition: (*i*) the depletion and assimilation of environmental resources associated with the abundance of neighbors and (*ii*) changes in morphology and physiology associated with the depletion of environmental resources (Goldberg 1990; Comeau et al. 1993; Radosevich et al. 1997). Thus, understanding how plants grow and species communities develop requires the elucidation of the mechanisms governing the interaction of growth, relative resource availability, and assimilation of resources at the individual plant level (Lambers et al. 1998). In this study, we directly vary resource availability (either light or water) to observe the interaction of those variables in relation to carbon assimilation, allocation, and morphology.

Availability of resources for growth is seldom optimal or continuous in natural environments. However, plants may adapt to changes in resource availability through adjustments in positioning and allocation of their absorptive organs (Grime 1979). Shifts in allocation to roots and leaves have been demonstrated in experiments when plants are exposed to gradients of light, moisture, and nutrients (Grime 1979; Reader et al. 1993; Newton and Cole 1991; Shainsky and Radosevich 1991, 1992). Light and soil moisture are key resources most highly correlated with density, competition, and growth. These resources often can be limiting on sites where alder and Douglas-fir occur (Curtis et al. 1998; Haeussler et al. 1990; Stein 1995), although information on the response of field-grown Douglas-fir and red alder to both light and soil water limitation is scarce.

Douglas-fir and red alder exhibit wide differences in genetic, morphological, physiological, and rhizosphere characteristics. Yet, the two species coexist on the same sites. Red alder is the predominant hardwood species in the Pacific Northwest. It is capable of nitrogen fixation and exhibits rapid establishment and juvenile growth following disturbance. Its life-span of 80–120 years is relatively short (Harrington 1990) compared with other major tree species in the region. Coastal Douglas-fir is a long-lived conifer that accounts for much of the plant biomass in the western portion of the Pacific Northwest. Conditions following disturbances (e.g., creation of canopy gaps, fire, mineral seed beds) favor the regeneration of Douglas-fir (Hermann and Lavender 1990). Similar requirements for red alder seedling establishment frequently result in competition between red alder and Douglas-fir during the seedling to sapling stages, if both species regenerate on the same site. Cole and Newton (1986, 1987) report that red alder inhibits growth of Douglas-fir through competition for light and water. Binkley (1983), however, suggests that red alder's nitrogen fixation may enhance the nitrogen status and growth of Douglas-fir, but such benefits are highest on sites with low soil fertility. Shainsky and Radosevich (1991, 1992) indicated that overstory red alder was a superior competitor that intercepted light and depleted soil moisture to the understory Douglas-fir trees. Yet, high densities of Douglas-fir in the understory reduced the

overstory alder canopy leaf area, which resulted in an increase of light available for the growth of the understory Douglas-fir trees (Shainsky and Radosevich 1991, 1992). Such feedbacks associated with competition, resource availability, and growth are difficult to separate when Douglas-fir and red alder occur as multiple individuals in separate populations or in mixture.

This paper focuses on the hypothesis that the effects of competition are controlled by the availability of environmental resources and the potential of species to respond through growth and carbon allocation. Thus, we study how contrasting availability of water and light affects the growth of Douglas-fir and red alder. Inherent growth and form characteristics suggest that differences in relative competitive ability and adaptive strategies exist between the two species (Harrington and Chan 1993; Haeussler et al. 1990). In this study we examine growth and biomass allocation of individual, free-growing Douglas-fir and red alder grown under contrasting combinations of light and water availability. Key aspects addressed are (*i*) the response of trees to two sharply contrasting environmental stresses and (*ii*) allocation and growth responses of key organs that influence the ability of the tree to capture and assimilate resources.

Materials and methods

Individual 1-year-old transplants of Douglas-fir and red alder were grown for 3 years in the central Willamette Valley of western Oregon (Oregon State University Horticulture Crops Research Farm near Corvallis, Oreg.) at two levels of light and water availability. The site was level with deep uniform Chehalis silty clay loam deposited by the nearby Willamette River. A total of 128 trees of each species were planted. Treatment conditions consisted of (*i*) unshaded, full light (L+); (*ii*) shaded, reduced to $12 \pm 2\%$ of full light (L–); (*iii*) normal patterns of soil moisture availability without irrigation (W–); and (*iv*) soil moisture augmented by periodic irrigation (W+). Tree responses to all pairwise combinations of light and water availability were studied; hereafter identified as L+W+, L+W–, L–W+, and L–W–. The two tree species were assigned to separate but adjacent blocks. Initial tree size varied slightly but, upon analysis, was not found to have a significant effect on the final tree size or allocation pattern. Similarly, the Douglas-fir seedlings originated from three different seed sources, but seed source was not found to affect either growth or allocation in this study.

To maintain a constant soil volume for root growth, trees were planted in 1 m deep × 0.5 m wide (0.2-m^3) holes lined with 2-ply, 8 mil thick polyethylene bags with drainage holes on the bottom. The lined holes were refilled with their original soil. Treatment light levels were achieved with wood teepee-shaped frames covered with shade cloth. The tent structures were 1.5 m in height during the first year and raised each year to accommodate the height of growing trees. Light availability was measured as photosynthetically active radiation (PAR) with a LI-COR LI-190S-1 quantum sensor (LI-COR Inc., Lincoln, Nebr.). The light conditions within each shade tent were calculated as a ratio of the sensor reading inside each tent to a reading at the same height outside the tent. Available PAR was not found to vary signif-

icantly among shade tents, and the mean amount of light transmittance through the shade tents was determined to be 12% of full sunlight.

Soil moisture availability during the growing season was determined by the amount of available water stored in the effective rooting volume of the lined planting hole, precipitation, and irrigation. However, the trees eventually established roots through the drainage holes in the container liner, which also increased soil water available to them.

All trees received irrigation during the first 2 months after planting. Soil moisture treatments were subsequently assigned randomly. One-half of the trees of both species received irrigation during the entire growing season. The other half was not irrigated. Irrigation was provided to the selected trees using a drip irrigation delivery system set at 20 psi (1 psi = 6.895 kPa) to deliver water at the rate of 7.6 L/h. Watering during the first growing season occurred once every 2 weeks to field capacity. Irrigation during the second and third growing season was modified to a weekly time interval and an index of soil moisture availability based upon measurements of soil moisture content using a neutron source depth moisture gauge (Troxler Inc., N.C.). This procedure minimized the exposure of irrigated trees to soil water potentials less than 0.1 MPa. Data for soil moisture depletion are presented for the third growing season only.

At the end of each growing season (beginning in early October), stem height to the nearest 0.5 cm and stem diameter to the nearest 0.1 cm were measured. Crown width was measured to the nearest centimetre and calculated as the mean of the widest crown diameter and the diameter perpendicular to it. During October of the third year, 72 randomly selected trees of each species, stratified across the four light and water treatments were harvested with the majority of the roots intact with a mechanical powered (Vemeer) tree spade with blades that extended 1.2 m into the ground. Small roots that had grown through the planting bag drainage holes were hand excavated with a shovel. Roots growing outside of the planting bags accounted for less than 5% of the total root dry mass. The soil surrounding the roots was carefully washed away with water and brushes. Harvested trees were stored in a cooler after being divided into the following components: stems, branches, roots, foliage, and buds. All components were dried at 70°C for 72 h and weighed to the nearest 0.1 g.

Prior to harvesting, approximately half the foliage from each red alder and Douglas-fir tree was collected to estimate leaf area and foliage mass. From this sample of foliage, approximately 30% were measured to determine leaf area. Projected leaf area (LA) for both species was measured with a LI-COR 3300 (LI-COR Inc., Lincoln, Nebr.) leaf area meter. Specific leaf area (SLA) was determined by dividing leaf area (LA) by leaf dry mass. Leaf area ratio (LAR) was determined by dividing leaf area by total plant dry mass. Instantaneous relative growth rates (RGR = $(1/W)(dW/dt)$, where W is the initial tree size, dW is the change in tree size, and dt is the change in time between measurements) of stem height and diameter were calculated based on Hunt (1990) for two consecutive 1-year periods, following the first full year of light and water treatments.

Statistical analysis of the data collected for each of the two species consisted of a multifactorial analysis of variance

Table 1. Soil water potential (–MPa) at 30 and 80 cm depths measured during July of the third growing season.

Treatment*	Douglas-fir		Red alder		No tree	
	30 cm	80 cm	30 cm	80 cm	30 cm	80 cm
L+W+	0.12	0.04	0.19	0.10	0.02	0.01
L+W–	1.45	0.70	1.21	0.54	0.19	0.05
L–W+	0.07	0.03	0.04	0.07	0.03	0.01
L–W–	1.05	0.43	0.98	0.44	0.11	0.63

*L+, unshaded, full light; L–, shaded, reduced to 12 ± 2% of full light; W–, normal patterns of soil moisture availability without irrigation; W+, soil moisture augmented by periodic irrigation.

where each observation was treated as independent and light and water treatments were designated as the main effects. The 95% confidence intervals of the treatment mean differences were calculated for each of the measured variables.

Results

Soil moisture depletion

Soil moisture depletion (v/v) ranged from 46 to 53% for Douglas-fir and from 40 to 48% for red alder. Planter bags without trees ranged between 59% and 60% depletion. Depletion values were converted to MPa from pressure–volume curves derived for the Chehalis soil series (Knezevich 1975). Depletions rarely led to soil water potentials that would cause permanent wilting (–1.5 MPa). The lowest soil water potential recorded (during the month of July, the summer month that year with the least amount of precipitation), –1.45 MPa (Table 1), equals 28% soil moisture content. Irrigated trees grew in soil that ranged from near field capacity (–0.03 Mpa) to –0.19 Mpa, whereas soil moisture availability in the unwatered treatments ranged from –1.00 MPa to –1.45 MPa in the upper 30 cm of soil and from –0.43 to 0.70 MPa at 80 cm depth. Both Douglas-fir and red alder depleted soil moisture in the upper 30 cm of the soil to a greater degree than at 80 cm. These results suggest there was available water for the trees to extract at soil depths below 30 cm.

Growth analysis: stem height, diameter, height/diameter ratio, and crown width

High levels of light and water caused large differences in size between the two species. However, when light and water were limited, these differences were smaller. Under conditions of limited resources, both species decreased growth; however, the relative response in red alder was more pronounced than in Douglas-fir.

Both red alder ($P = 0.05$) and Douglas-fir ($P = 0.04$) height responded to an interaction of light and water levels (Table 2). Whereas high levels of light and (or) water resulted in similar tree heights, trees were shortest when both light and water were limited. Red alder stem diameter also decreased with declining resources, as limitation of either light ($P < 0.01$) or water ($P < 0.01$) resulted in smaller-diameter trees (Table 2). However, Douglas-fir stem diameter decreased only with light limitation ($P < 0.01$) and not with water limitation ($P = 0.16$).

Table 2. Effects of light (L) and water availability (W) on size of Douglas-fir and red alder.

	L+	L–	P	W+	W–	P	L+W+	L+W–	L–W+	L–W–	P
Douglas-fir											
Height (cm)	126	119	0.29	127	118	0.16	124	128	131	108	0.04
	(9)	(9)		(9)	(9)		(13)	(13)	(13)	(13)	
Diameter (cm)	4.6	3.0	<0.01	3.9	3.6	0.08	4.6	4.5	3.2	2.7	0.16
	(0.3)	(0.3)		(0.3)	(0.3)		(0.4)	(0.4)	(0.4)	(0.4)	
Height/diameter ratio	28	40	<0.01	34	35	0.52	28	28	40	41	0.79
	(2)	(2)		(3)	(3)		(3)	(3)	(3)	(3)	
Crown width (cm)	84	89	0.31	84	89	0.31	78	91	91	87	0.07
	(6)	(6)		(6)	(6)		(9)	(9)	(9)	(9)	
Red alder											
Height (cm)	351	320	<0.01	357	316	0.01	362	341	352	277	0.05
	(19)	(19)		(19)	(19)		(27)	(27)	(27)	(27)	
Diameter (cm)	8.3	5.1	<0.01	7.6	6.1	0.01	9.8	7.1	5.3	4.6	0.08
	(0.8)	(0.8)		(0.8)	(0.8)		(1.2)	(1.2)	(1.2)	(1.2)	
Height/diameter ratio	44	67	<0.01	53	59	0.02	39	50	66	68	0.13
	(4)	(4)		(4)	(4)		(5)	(5)	(5)	(5)	
Crown width (cm)	258	209	0.01	245	227	0.04	273	245	218	198	0.74
	(17)	(17)		(18)	(18)		(25)	(25)	(25)	(25)	

Note: Values are means with one-half of the 95% confidence interval given in parentheses. See Table 1 for definitions of light and water parameters. The P values comparing light and water separately and the four treatment combinations are also given.

Stem height/diameter ratio increased with decreasing light in both red alder ($P < 0.01$) and Douglas-fir ($P < 0.01$). Additionally, limited water availability increased red alder height/diameter ratio ($P = 0.02$, Table 2).

Red alder mean crown width (mean maximum canopy width taken from two perpendicular cardinal directions) decreased with limited light ($P < 0.01$) or water ($P = 0.04$), but there were no differences in Douglas-fir crown widths among any of the four treatments (Table 2). Chen et al. (1996), on the other hand, found that Douglas-fir seedlings grown under low-light conditions decreased lateral branch lengths. The difference in our observations may be attributed to our low-light treatment providing more light (12 vs. 5% of full light) than some of the conditions reported in Chen et al. (1996). In addition, we characterized lateral crown growth as a summation of 4 years growth at the widest point of the tree, whereas Chen et al. (1996) measured lateral growth only on the uppermost whorl.

Relative growth rates of stem height and diameter

Relative growth rates (RGR) of stem height and diameter for both species for period 1 (end of year 1 to end of year 2 of exposure to the light and water treatments) and period 2 (end of year 2 to end of year 3) are given in Table 3. Red alder RGR during period 1 were substantially larger than Douglas-fir RGR. However, large decreases in red alder RGR for both height and stem diameter occurred across all treatments between periods 1 and 2. During period 2, RGR for Douglas-fir increased or maintained similar levels relative to period 1, except for decreases in stem diameter RGR of trees under high light and under low water availability. Douglas-fir RGR for height and diameter under low light were greater than those of red alder during period 2. No significant interactions between light and water levels were observed in RGR for stem diameter during either growth period. During period 2, red alder height RGR was highest in the high-light, low-water (L+W–) treatment combination,

this was significantly different ($P = 0.02$) from either treatment with low light (L–W + or L–W–). Low light availability resulted in lower diameter RGR ($P < 0.01$) in both species during period 1 and in height and diameter RGR of Douglas-fir ($P = 0.04$, $P < 0.01$) and height RGR of red alder ($P < 0.01$) during period 2. Low water availability decreased the height RGR of red alder ($P < 0.01$) in period 1 and the stem diameter of RGR of Douglas-fir in period 2. Declines in red alder RGRs due to differences in light or water availability were small compared with the large declines in RGR between periods 1 and 2.

Tree biomass responses to resource addition and limitation

In red alder, the mass of each vegetative component was highest in the L+W+ treatment, and decreased consistently as resources decreased, with light limitation affecting growth more negatively than limitation for water (Table 4). The interaction of light and water availability had a significant effect ($P < 0.01$) on total component mass of red alder. Total component mass under L+W– ranged from 40 to 60% of that measured under L+W+ (Fig. 1). Under L–W+, the mass of the various components decreased to about 20% of the L+W+ mass (Table 4). When both resources were limited (L–W–), total mass (Table 4, Fig. 1) and the mass of each component (Table 4) was only about 10% that of L+W+.

Douglas-fir total mass and component mass also declined with declining resources, but less dramatically than red alder (Fig. 1, Table 4). Water availability had no effect ($P = 0.81$) on total mass of Douglas-fir. Light availability had a significant effect ($P < 0.01$) on total mass. Douglas-fir total biomass grown under low light levels averaged about 40% that of trees under full light. In every treatment, red alder exhibited more severe relative declines in growth of individual biomass components when light and water resources were limited than did Douglas-fir (Fig. 1, Table 4).

Table 3. Effects of light (L) and water availability (W) on annual relative growth rate (RGR) for two treatment growth periods based

	L+		L–		P		W+		W–	
	H	D	H	D	H	D	H	D	H	D
Douglas-fir										
Y_1 to Y_2 RGR	0.53	1.64	0.48	0.95	0.54	<0.01	0.43	1.20	0.57	1.39
	(0.12)	(0.15)	(0.12)	(0.15)			(0.12)	(0.15)	(0.12)	(0.15)
Y_2 to Y_3 RGR	1.05	1.12	1.22	0.96	0.04	0.04	1.19	1.22	1.08	0.85
	(0.11)	(0.11)	(0.11)	(0.11)			(0.11)	(0.11)	(0.11)	(0.11)
Red alder										
Y_1 to Y_2 RGR	6.61	5.71	6.42	4.04	0.61	<0.01	7.96	6.04	5.07	3.72
	(0.55)	(0.39)	(0.55)	(0.39)			(0.55)	(0.40)	(0.50)	(0.40)
Y_2 to Y_3 RGR	1.28	1.27	0.87	0.70	<0.01	0.09	1.04	1.01	1.11	0.96
	(0.11)	(0.09)	(0.11)	(0.09)			(0.11)	(0.09)	(0.11)	(0.09)

Note: Values are means with one-half of the 95% confidence interval given in parentheses. See Table 1 for definitions of light and water parameters. was calculated according to Hunt (1990, see text). The P values comparing the light and water conditions for height and diameter separately and the four

Table 4. Effects of light (L) and water availability (W) on tree component mass (g) and allocation (%) of Douglas-fir and red alder.

	L+		L–		P		W+		W–	
Component	g	%	g	%	g	%	g	%	g	%
Douglas-fir										
Stem	291	23	129	27	<0.01	<0.01	224	26	196	24
	(35)	(1)	(35)	(1)			(35)	(1)	(35)	(1)
Foliage	270	23	125	26	<0.01	<0.01	194	24	202	26
	(29)	(1)	(29)	(1)			(29)	(1)	(29)	(1)
Branch	270	22	96	20	<0.01	<0.01	197	22	170	19
	(33)	(1)	(33)	(1)			(34)	(1)	(32)	(1)
Bud	15	1.2	5	1.0	<0.01	<0.01	11	1.2	8	1.0
	(2)	(0.1)	(2)	(0.1)			(2)	(0.1)	(2)	(0.1)
Aboveground	826	69	360	74	<0.01	<0.01	610	73	576	70
	(90)	(1)	(90)	(1)			(90)	(1)	(90)	(1)
Root	357	31	117	26	<0.01	<0.01	230	26	244	30
	(31)	(1)	(31)	(1)			(31)	(1)	(31)	(1)
Total tree	1181		479		<0.01		840		819	
	(119)		(119)				(120)		(120)	
Stem/root	0.80		1.09		<0.01		1.07		0.82	
	(0.07)		(0.07)				(0.07)		(0.07)	
Red alder										
Stem	1962	28	540	31	0.01	<0.01	1662	29	1026	29
	(281)	(1)	(281)	(2)			(277)	(1)	(277)	(1)
Foliage	1344	18	359	20	0.01	0.05	1161	19	670	20
	(252)	(1)	(252)	(2)			(250)	(1)	(250)	(1)
Branch	1847	26	426	23	0.01	0.04	1533	25	925	24
	(307)	(2)	(307)	(2)			(305)	(1)	(305)	(1)
Bud	44	0.7	12	0.8	0.01	0.38	35	0.8	21	0.7
	(7)	(0.2)	(7)	(0.2)			(7)	(0.2)	(7)	(0.2)
Aboveground	5334	73	1278	75	0.01	0.08	4325	74	2287	74
	(792)	(2)	(792)	(2)			(792)	(2)	(792)	(2)
Root	1838	27	404	25	0.01	0.07	1595	26	831	26
	(244)	(2)	(244)	(2)			(244)	(2)	(244)	(2)
Total tree	7239		1673		0.01		5893		3019	
	(988)		(988)				(989)		(989)	
Stem/root	1.11		1.25		0.09		1.22		1.14	
	(0.12)		(0.12)				(0.12)		(0.12)	

Note: Values are means with one-half of the 95% confidence interval given in parentheses. See Table 1 for definitions of light and water parameters. for definitions of the light and water treatments.

on height (*H*) and stem diameter (*D*).

P		L+W+		L+W−		L−W+		L−W−		P	
H	*D*	*H*	*D*	*H*	*D*	*H*	*D*	*H*	*D*	*H*	*D*
0.10	0.06	0.46	1.49	0.59	1.79	0.41	0.90	0.54	1.00	0.98	0.33
		(0.16)	(0.21)	(0.16)	(0.21)	(0.16)	(0.21)	(0.16)	(0.22)		
0.17	<0.01	1.10	1.35	1.00	0.88	1.28	1.08	1.16	0.83	0.96	0.16
		(0.16)	(0.15)	(0.16)	(0.15)	(0.16)	(0.15)	(0.16)	(0.15)		
0.00	0.48	8.14	7.09	5.09	4.33	7.79	4.99	5.04	3.10	0.69	0.51
		(0.77)	(0.55)	(0.77)	(0.55)	(0.77)	(0.55)	(0.77)	(0.55)		
0.36	0.11	1.16	1.32	1.41	1.22	0.92	0.71	0.81	0.70	0.02	0.06
		(0.16)	(0.14)	(0.15)	(0.14)	(0.15)	(0.14)	(0.15)	(0.14)		

Growth period 1 is from the end of year 1 (Y_1) to the end of year 2 (Y_2) of treatment application, while growth period 2 is from year 2 to 3 (Y_3). RGR treatment combinations are also given. See Table 1 for definitions of the light and water treatments.

P		L+W+		L+W−		L−W+		L−W−		P	
g	%	g	%	g	%	g	%	g	%	g	%
0.26	<0.01	291	24	290	23	156	28	101	25	0.28	0.23
		(53)	(2)	(53)	(2)	(53)	(2)	(53)	(2)		
0.64	0.04	240	22	299	24	147	26	104	27	<0.01	0.25
		(40)	(2)	(40)	(2)	(40)	(2)	(40)	(2)		
0.28	<0.01	271	23	269	20	121	21	71	18	0.38	0.57
		(47)	(2)	(47)	(2)	(47)	(2)	(47)	(2)		
0.05	<0.01	17	1.3	13	1.0	6	1.0	3	0.9	0.69	0.30
		(3)	(0.2)	(3)	(0.2)	(3)	(0.2)	(3)	(0.2)		
0.59	<0.01	782	70	869	69	438	77	282	71	0.06	0.02
		(128)	(2)	(128)	(2)	(128)	(2)	(128)	(2)		
0.40	<0.01	335	30	378	32	125	23	109	29	0.12	0.03
		(43)	(2)	(43)	(2)	(43)	(2)	(43)	(2)		
0.81		1114		1247		566		392		0.07	
		(168)		(168)		(168)		(168)			
<0.01		0.86		0.74		1.28		0.90		<0.01	
		(0.10)		(0.10)		(0.10)		(0.10)			
<0.01	0.80	2600	27	1426	29	677	32	358	29	0.04	0.03
		(398)	(2)	(398)	(2)	(398)	(2)	(398)	(2)		
<0.01	0.37	1841	17	927	19	447	21	242	20	0.05	0.26
		(357)	(2)	(357)	(2)	(357)	(2)	(357)	(2)		
<0.01	0.44	2470	25	1324	27	549	25	261	21	0.06	0.03
		(438)	(2)	(438)	(2)	(438)	(2)	(438)	(2)		
<0.01	0.61	54	0.7	33	0.7	16	0.9	8	0.7	0.15	0.44
		(9)	(0.3)	(9)	(0.3)	(9)	(0.3)	(9)	(0.3)		
<0.01	0.94	6962	70	3706	75	1688	78	868	71	0.03	<0.01
		(1115)	(3)	(1115)	(3)	(1115)	(3)	(1115)	(3)		
<0.01	0.94	2681	30	1130	25	455	22	334	29	<0.01	<0.01
		(348)	(3)	(348)	(3)	(348)	(3)	(348)	(3)		
<0.01		9643		4836		2143		1202		<0.01	
		(1395)		(1395)		(1395)		(1395)			
0.33		0.97		1.24		1.46		1.03		<0.01	
		(0.16)		(0.16)		(0.16)		(0.16)			

The *P* values comparing the light and water conditions for height and diameter separately and the four treatment combinations are also given. See Table 1

Fig. 1. Total tree mass with varying levels of light and water availability expressed as a percentage of tree mass with full light and irrigation for red alder and Douglas-fir. Error bars are 95% confidence intervals.
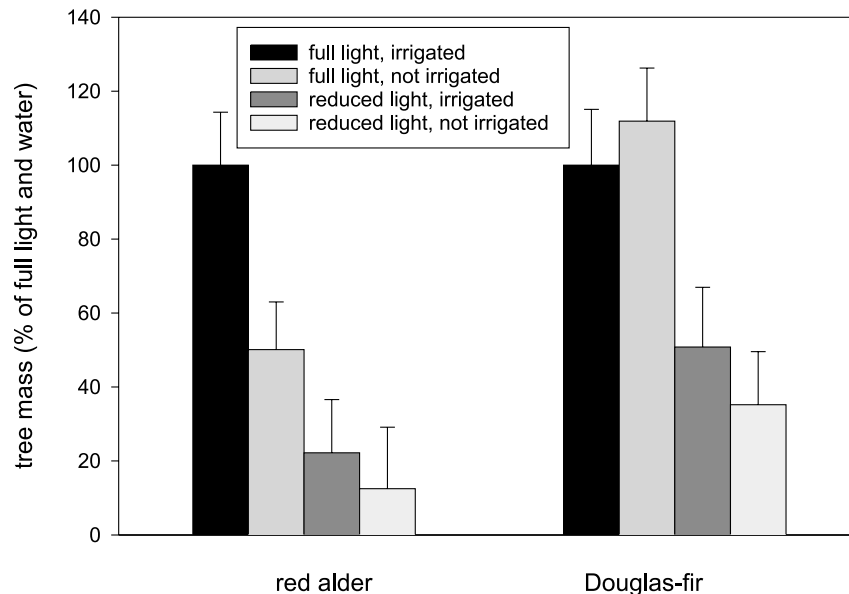
The total mass accumulated by red alder was affected by the interaction of light and water availability. Low light levels reduced mass accumulation more than low moisture levels. Douglas-fir total biomass production was affected only by light.

Aboveground versus belowground component mass and allocation

Aboveground biomass was defined as the sum of stem, branch, foliage, and bud mass. Allocation was defined as the mass of a given component (or group of components) divided by total tree mass. Significant interactive effects of light and water treatments on aboveground allocation are evident for both Douglas-fir ($P = 0.02$) and red alder ($P < 0.01$) (Table 4). Aboveground allocation was highest under L–W+ (78 and 77% for red alder and Douglas-fir, respectively). For red alder, aboveground allocation was also high under L+W– (75%). However, for Douglas-fir, aboveground allocation was lowest under this regime (69%) and did not differ significantly from that measured under L+W+. A corresponding difference between the responses of the two species to the L+W– treatment was detected in root allocation (Table 4). Douglas-fir root allocation was highest (32%) under this treatment, whereas red alder root allocation (25%) was lower than that under L+W+ and L–W–.

Mean Douglas-fir stem/root ratio was highest in the L–W+ treatment (1.28) and lowest in the L+W– treatment (0.74). Stem/root ratios among the remaining treatments, L+W+ and L–W– were similar and intermediate between these extremes (Table 4). Mean stem/root ratio in red alder was also highest in the L–W+ treatment (1.46). Unlike Douglas-fir, red alder in the L+W– treatment exhibited a high (1.24 vs. 0.74) mean stem/root ratio similar to the L–W+ treatment. Red alder allocated a greater proportion of mass to shoots versus roots under conditions of partial stress associated with light or water limitations, whereas the lowest shoot/root ratios for red alder occurred in the L+W+ and L–

W– treatments. However, under these same conditions of partial stress (L–W+ and L+W–), the stem/root ratios for Douglas-fir were dissimilar (Table 4).

Branches

Under high-light conditions, branches accounted for nearly as much mass as the stem for both species. Decreases in red alder branch mass were evident under either low light or water levels ($P < 0.01$). Allocation of mass to branches was lowest ($P = 0.03$) in red alder grown under L–W–. Limited water decreased the percent allocation but not the total branch mass of Douglas-fir. Low light reduced both the mass of Douglas-fir branches and the percent allocation of total mass to branches. Douglas-fir allocated a smaller percentage of total mass to branches than did red alder (Table 4).

Buds

Neither bud mass nor the allocation of mass to buds was affected by the interactions of light and water availability for either species (Table 4). The reduction of either light or water resulted in lower bud mass for red alder and Douglas-fir ($P < 0.01$). However, light limitation resulted in a sharper decline in bud mass than water limitation. Neither light availability nor water availability affected the partitioning of mass to buds in red alder; however, decreases in either of these resources also decreased bud allocation in Douglas-fir. Relative to red alder, Douglas-fir allocated a higher percentage of its total mass to buds.

Foliage

The interaction of light and water availability significantly influenced the foliage mass of Douglas-fir ($P < 0.01$) and red alder ($P = 0.05$) but did not affect the percentage of total mass allocated to foliage (Table 4). Significant increases in percent allocation to foliage occurred under low light or low water availability in Douglas-fir, whereas for red alder, an

Table 5. Effects of light (L) and water availability (W) on foliage characteristics of red alder and Douglas-fir.

	L+	L−	P	L+	L−	P	L+W+	L+W−	L−W+	L−W−	P
Douglas-fir											
LA	1.7	0.9	<0.01	1.4	1.4	0.99	1.6	1.9	1.1	0.8	<0.01
	(0.2)	(0.2)		(0.2)	(0.2)		(0.3)	(0.3)	(0.3)	(0.3)	
LAR	15.1	20.0	<0.01	17.3	17.8	0.48	14.4	15.7	20.2	19.8	0.22
	(1.0)	(1.0)		(1.0)	(1.0)		(1.4)	(1.4)	(1.4)	(1.4)	
SLA	65.7	76.0	<0.01	72.2	69.5	0.13	66.6	64.7	77.7	74.3	0.66
	(2.4)	(2.4)		(2.5)	(2.5)		(3.4)	(3.4)	(3.4)	(3.4)	
Red alder											
LA	11.5	5.8	<0.01	11.2	6.8	<0.01	15.0	8.6	7.2	3.9	0.28
	(2.0)	(2.0)		(1.9)	(1.9)		(2.8)	(2.8)	(2.8)	(2.8)	
LAR	16.2	32.9	<0.01	23.8	25.3	0.29	14.2	18.1	33.3	32.5	0.11
	(2.0)	(2.0)		(2.0)	(2.0)		(2.8)	(2.8)	(2.8)	(2.8)	
SLA	87.9	163.8	<0.01	122.7	129.0	0.29	82.2	93.6	163.3	164.4	0.39
	(8.3)	(8.3)		(8.3)	(8.3)		(11.8)	(11.8)	(11.8)	(11.8)	

Note: Values are means with one-half of the 95% confidence interval given in parentheses. The P values comparing the light and water conditions for height and diameter separately and the four treatment combinations are also given. See Table 1 for definitions of the light and water treatments. LA, leaf area (m^2); LAR, leaf area ratio (cm^2 leaf area/g tree mass); SLA, specific leaf area (cm^2 leaf area/g leaf mass).

increase was evident only under low-light conditions. In each of these cases, foliage allocation increased by 2–3% as a result of resource reduction.

Interactions ($P < 0.01$) between light and water availability on total leaf area were evident for Douglas-fir but not for red alder (Table 5). Douglas-fir leaf area in the L–W– and L–W+ were 40–60% lower than trees growing under full light. Red alder leaf area was also approximately 40% less with reduced soil moisture, whereas Douglas-fir leaf area showed a small response to reduced soil moisture only when grown under low light. Both species exhibited higher LAR and SLA when grown under reduced light (Table 5), but neither LAR nor SLA was impacted by soil water availability.

LAR and SLA were almost twice as high for red alder than Douglas-fir growing under reduced light. Figure 2 shows examples of the potential plasticity of red alder leaves that developed in this study under low light conditions (~12% of full light). The shade leaves shown in the photograph are nearly 5.6 times greater than the open-grown leaves. These largest shade-adapted leaves were usually found in the middle to lower crown of the tree where self-shading from overhead foliage occurred. Figure 3 synthesizes some of the contrasts in morphology and allocation patterns of Douglas-fir seedlings 3 years after growing under the four different levels of light and water availability. Heights of all trees are similar. Roots of Douglas-fir under limiting soil moisture have large diameter, deep, coarse taproots, in contrast to well-watered trees with a more fibrous root system. Foliage mass and leaf area are approximately half as abundant when grown under shade.

Discussion

In this study, we elucidate the mechanisms by which two taxonomically distinct tree species, red alder and Douglas-fir, share a similar ecological niche. In the Pacific Northwest, these two species are major colonizers of areas disturbed by logging or fire (Harrington 1990; Hermann and

Lavender 1990). However, Douglas-fir persists over a much longer successional time span and is a dominant of middle to late seral forests (Oliver and Larson 1996). Although there are differences in the times that the two species peak and decline following a disturbance, both species grow on the same sites for many years. We hypothesized that the species demonstrate a unique set of morphological and allocation characteristics (e.g., stem height and diameter, crown width, aboveground to root allocation) in response to environmental resources, which may provide the species with differing means to grow under competition. To test our hypothesis, we observed growth and allometric responses of open-grown individuals subjected to differing levels of two resources. Our study design yielded results that validate the utility of a resource availability approach to evaluate the competitive ability of tree species growing in similar ecotones based on resource availability, assimilation, allocation and morphology.

Species differences in growth and allocation

Increasing light availability had a positive effect on the size and mass of both species: red alder trees growing under full light conditions were generally two to five times greater in size than those under shaded conditions, and Douglas-fir trees grown in full light were generally twice the size as those grown in shade. There were, however, differences between the two species in the relative priority for allocation of mass to roots, stems, branches, leaves, and buds under the varying levels of light and water availability, suggesting that different strategies for growth under resource limitations exist for both species. Under high light but water-limited situations we observed that red alder had a higher allocation of mass to stems and branches than to roots (Table 4) than did Douglas-fir. Greater allocation to stems results in greater height and, thus, a competitive advantage for red alder to intercept light. Douglas-fir's higher allocation to roots suggests its ability to tolerate water limitation. Unlike red alder,

Fig. 2. Contrasting size and potential plasticity of red alder leaves from trees grown under open-sky light (left) and shaded low light (right) conditions. The leaf areas of shaded leaves are nearly 5.6 times greater than the open-grown leaves.

height of Douglas-fir was not affected by shaded conditions over the duration of this study.

Light limitation increased the *H/D* ratio of both species. However, when compared to trees in the literature that were grown under very low light conditions, the *H/D* ratios we found for red alder and Douglas-fir growing in low light (68 and 40, respectively) are not extreme: *H/D* ratios of ≥100 have previously been reported for light-stressed trees (Chen and Klinka 1998). It is possible that the minimum light level tested in this study, 12% of full light, did not represent the extreme light stress that either species may encounter in natural stands. For example, Chen (1997) found that Douglas-fir seedlings in a forest understory grew measurably in height with light levels as low as 5% full sun.

The availability of soil moisture affected the size of red alder but, except for bud mass, did not have a significant effect on Douglas-fir. Drever and Lertzman (2001) reported that at low light levels, soil moisture had little effect on the radial and height growth of Douglas-fir. Giordano and Hibbs (1993) and Hibbs et al. (1995) reported that red alder's sensitivity to water stress and high rates of biomass production suggests that water stress avoidance is a major factor in its high growth rate. Our findings suggest that red alder has a higher ability to avoid water stress by capturing light and water through high initial relative growth rates, resulting in rapid absolute growth and high allocation towards aboveground mass. Douglas-fir's ability to avoid water stress through higher allocation to roots may partially explain the

ability of the two species to occupy similar niches and overlap in species succession. Red alder's higher initial growth rates and relative size allows it to occupy more space and resources. However, Douglas-fir is more shade tolerant than red alder, as evidenced by smaller relative decreases in growth and mass under low light.

Several studies have shown that as light availability decreases, plants allocate more biomass to aboveground components relative to belowground components (Chen 1997; Drew and Ferrell 1977; Landhausser and Lieffers 2001). This response has been interpreted as a mechanism for increasing photosynthetic surface, particularly if coupled with an increase in specific leaf area and (or) leaf biomass allocation. In this study, both Douglas-fir and red alder had higher stem/root ratios under shaded, well-watered conditions compared to unshaded, well-watered conditions, suggesting a mechanism for adapting to low light in combination with high water availability by emphasizing aboveground growth as a mechanism to capture light. However, both species allocated a similar percentage to roots under high light and moisture (L+W+) and low light and low moisture (L–W–), suggesting that the when both resources are limiting, the opposing effects of increasing aboveground allocation in response to low light and increasing belowground allocation in response to water stress are negated.

Stem to root allocation in the two species were also similar with respect to water under low light. In low-light environments, both red alder and Douglas-fir increased root

Fig. 3. Contrasting morphology of Douglas-fir seedlings 3 years after growing under different levels of light and water availability. From left to right, light and water treatments are L+W+, L+W–, L–W+, and L–W–. See Table 1 for definitions of the treatments. Roots of Douglas-fir under limiting soil moisture have deep, coarse taproots, in contrast to well-watered trees with a more fibrous root system. Heights of all trees are similar. Foliage mass and leaf area are approximately half as abundant when grown under shade.

allocation with water stress. Drew and Ferrell (1977) found that shoot growth was favored over root growth in Douglas-fir seedlings exposed to shady yet otherwise optimal growing conditions. However, when warmer temperatures caused moisture limitation, the seedlings in their study increased root allocation, especially when shaded. Our results support their observations with Douglas-fir, and here we present data that show similar trends in red alder.

The high allocation to shoots versus roots of red alders grown under full light and unwatered conditions suggests a mechanism whereby red alder exhibits a drought avoidance strategy that emphasizes growth to facilitate resource capture. On the other hand, prioritizing allocation to roots, as evidenced by the lower stem/root ratio (Table 4), under this same set of conditions provides Douglas-fir with a mechanism to tolerate low moisture conditions by increasing its ability to capture soil moisture and, thus, minimize the effects of drought (Reader et al. 1993).

The differences noted above may explain some different ecological roles of the two species. Red alder, characterized as a pioneer species and by high growth rates, exhibits a strategy enabling it to capitalize on available resources for rapid growth. Thus, in a high-light environment, it produces a large amount of foliage and consequently more aboveground woody biomass to support it. Biomass investment in

root growth, on the other hand, is considered a conservative mechanism providing infrastructure for more sustained growth over the longer term; late successional species often are characterized by high root allocation (Gleeson and Tillman 1994; Tillman 1985). Douglas-fir, a longer lived species than red alder, produces more roots that can sustain foliage, perhaps as a competitive mechanism to persist over time despite limited water availability.

The structure of aboveground biomass, characterized by crown architecture, allocation and form of foliage, and vertical and lateral growth all influence a plant's ability to capture light resources (Messier et al. 1999) and shade competitors. In our study, light limitation induced different patterns of aboveground architecture in the two species. Under limited light, red alder reduced both height and crown diameter. Douglas-fir, on the other hand, maintained the same levels of height and crown diameter growth as under full-light conditions. Examining the relative responses of vertical and lateral growth reveals further subtleties between the species. Under limited light, the ratio of height to crown width in red alder increased, whereas in Douglas-fir there was no detectable effect. Messier et al. (1999) suggest that favoring vertical growth over lateral growth is a desirable trait in early successional forest species, where a slight increase in height results in much greater light availability.

Thus, red alder shows yet another adaptation to light capture in early forest succession by plasticity in aboveground architecture, whereas Douglas-fir does not respond in this way.

Foliage modification is another mechanism by which a species exhibits plasticity with respect to photosynthetic potential (Chen et al. 1996). Red alder exhibited such morphological plasticity under light limitation in the following ways: by increasing leaf size, leaf-area ratio and specific leaf area, by increasing its stem/root ratio, and by slightly increasing foliage biomass allocation. Red alder SLA and LAR under limited light were nearly double that under normal light, despite total leaf area being reduced by approximately half (Table 5). Some red alder trees growing under low light produced leaves five to six times larger than under full sun (Fig. 2). The percent allocation to foliage biomass also increased under low light but was less pronounced than leaf size or relative thinness of the foliage as described by the high SLA (Table 5). Foliage mass under high light was about 400% greater in relative terms than that under low light (Table 4), yet the percent allocation to foliage still ranked lower than that of roots, stems, or branches (Table 4). Red alder apparently acclimates to limited light not only by allocating more of its resources to aboveground organs but, more importantly, through greater foliage plasticity with larger and thinner leaves. Other reported leaf adaptations to light capture under shade include reduction in the number of stomata, less parenchyma tissue, and scaled-back photosynthetic compensation point and saturation rate (Messier et al. 1999); however, these parameters were not examined in our study.

In our study, Douglas-fir showed much less plasticity to foliage production than red alder with respect to light. Similarly to red alder, Douglas-fir foliage biomass allocation also increased with limited light. However, the LAR increased by a smaller margin than in red alder and SLA change was not significant. Unlike red alder, Douglas-fir allocated a higher percentage of its biomass to foliage than branches when either resource was limiting. Thus, Douglas-fir apparently adapted to reduced light and (or) water mainly by producing more needles per unit branch and stem, and a lower relative increase in foliage area to total tree mass (LAR) versus a large change in leaf morphology and taller stem as observed in red alder. These different responses to light availability may be related to the different growth habits of the two species. Leaf architecture, one major component of which is SLA, is commonly connected with leaf life-span (Cornelissen et al. 1998). Because alder is deciduous, its leaves do not need to be built for longevity. Larger, thinner leaves with less protective tissue, yet which increase the probability of light interception, are, therefore, appropriate under low light for this species (Fig. 2). Douglas-fir, on the other hand, must produce durable leaves that can withstand extremes of temperature and moisture stress over the course of several years. Therefore, the plasticity of Douglas-fir's foliage form can be expected to be more limited.

Potential effects on competitive interactions

We suggest that the species differences in size and allocation in response to resource availability may determine pathways by which Douglas-fir and red alder interact in a mixed community. In the first years of establishment, red alder outgrows Douglas-fir (Bernsten 1961) mainly because of alder's superior ability to capture light. We see this in the prioritization of allocation toward stem mass in red alder. In this early successional stage, red alder favors shoot growth over root growth and vertical growth over lateral growth. However, if moisture is limited due to climate, site effects, or competition, Douglas-fir can persist in the alder understory, because it is less sensitive to moisture limitation than red alder (Shainsky and Radosevich 1992). In our study, after only three annual growth periods, red alder showed great reductions in relative growth rate, while Douglas-fir did not.

In our experiment, we simulated the environment that red alder is experiencing in this situation with the L+W– treatment. Douglas-fir, which is shaded by the taller alder, is simultaneously growing in conditions we simulated by the L–W– treatment. The high relative growth rate (Table 3) observed in red alder stem height and diameter between the first and second years of light and water treatments resulted in a large initial size and mass advantage as compared with Douglas-fir. Declines in RGR are expected as plants get larger. However, the large declines in red alder RGR between years 2 and 3 suggest that the rapid initial exponential growth of red alder may confer only a relatively short competitive advantage when compared with a longer lived species such as Douglas-fir. Douglas-fir increased or at least maintained its relative growth rate during this same period, a mechanism that may allow it to persist in the understory and eventually outgrow red alder as the trees become larger and use more of the available soil moisture. Our findings suggest that in a high-light environment, red alder stem/root ratio does not change with moisture limitation; however, in a low-light environment, Douglas-fir root allocation increases with moisture limitation. Shainsky and Radosevich (1992) showed that the increased presence of Douglas-fir seedlings can cause red alder seedlings to become progressively more moisture limited, and red alder growth is reduced, despite its greater height. Our study also showed that red alder growth responds negatively to water limitation, whereas Douglas-fir does not.

As the stand ages, and as more water demands are made by larger trees, water therefore becomes even more limiting and Douglas-fir competitiveness presumably increases because of its high tolerance of low soil moisture and through the formation of deep taproots (Fig. 3). As red alder leaf area decreases with declining soil water availability, a feedback mechanism could exist, where red alder growth is further reduced and even less light is captured. Thus, there can be multiple mechanisms enabling established Douglas-fir seedlings to persist under taller red alder as soil moisture becomes limited (Shainsky and Radosevich 1992).

A different situation would arise on a site where soil moisture is plentiful. In this case, red alder is more likely to suppress Douglas-fir, because competition for water is reduced. We found red alder growth increased more with high water availability than did Douglas-fir growth.

Our results show that red alder exhibits many mechanisms of foliage plasticity to light. Despite this, red alder is unable to regenerate successfully in its own understory. It is likely that the shade levels tested in this study were not extreme enough to simulate those found under a red alder canopy where light levels average 4% of open conditions (Chan et al. 1997). Despite large changes in leaf morphology (approximately a doubling of SLA) with only a slight decrease in

stem height, the mass of red alder grown under low light conditions averaged less than 25% of the mass of trees in grown under high light. Thus, foliage acclimation is not a sufficient response to ensure its survival and growth in the understory.

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