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Structure, production and resource use in some old-growth spruce/fir forests in the Front Range of the Rocky Mountains, USA

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Abstract

Old-growth forests of Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) dominate much of the landscape of the Rocky Mountains. We characterized the structure, biomass and production of 18 old-growth (200–450-year-old) spruce/fir forests in Rocky Mountain National Park, Colorado, as well as the stand-level supply and use of light and nitrogen. Stands were chosen to span a broad range of elevation, aspect, and topography. Aboveground tree biomass in these old-growth forests averaged 253 Mg/ha (range 130–488 Mg/ha), with aboveground net primary production of 3700 kg ha^{-1} yr^{-1} (range from 2700 to 5200 kg ha^{-1} yr^{-1}). Within stands, trees >35 cm in diameter accounted for 70% of aboveground biomass, but trees <35 cm contributed 70% of the production of woody biomass. Differences in slope and aspect among sites resulted in a range of incoming light from 58 to 74 TJ ha^{-1} yr^{-1}, and tree canopies intercepted an average of 71% of incoming light (range 50–90%). Aboveground net primary production (ANPP) of trees did not relate to the supply of light or N, but ANPP correlated strongly with the amount of light and N used ($r^2 = 0.45-0.54$, $P < 0.01$). Uptake of 1 kg of N was associated with about 260 kg of ANPP, and one TJ of intercepted shortwave radiation produced about 78 kg of ANPP. Across these old-growth stands, stands with greater biomass showed higher rates of both ANPP and resource use; variation in aboveground biomass was associated with 24% of the variation in N use ($P = 0.04$), 44% of the light use ($P = 0.003$), and 45% of the ANPP ($P = 0.002$).

Keywords: Conifer forests; Net primary production; Resource gradient

1. Introduction

Forests of Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) cover about one million ha of the Rocky Mountains in Colorado, USA. Although logging has been extensive in some local areas, most of these spruce/fir forests are in mature or old-growth age classes (Alexander, 1987; Robertson, 1992). Some general features of these forests have been well documented, such as basal area, density of trees, and age (cf. Aplet et al., 1988; Robertson, 1992; Rebertus et al., 1992), but biomass and net primary production have

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been estimated in only a few stands (Aplet et al., 1989; Arthur and Fahey, 1992; Prescott et al., 1989; Peet, 2000). Most of the spruce/fir forests within Rocky Mountain National Park and the adjacent Roosevelt National Forest are greater than 200 years in age, affording an opportunity to characterize the structure, production, and resource use of these forests across relatively broad environmental gradients. As part of a larger project on the potential effects of climate change on Rocky Mountain forests (Stohlgren et al., 1995), we examined old-growth spruce/fir forests across broad gradients of elevation, aspect, and topography.

2. Methods

During the summer of 1992, we selected 18 old-growth stands in Rocky Mountain National Park (near Milner Pass and the Cache la Poudre River) and the adjacent Neota Creek Wilderness in the Roosevelt National Forest in northern Colorado. We chose these stands to span a range of aspect and topographic position, and to insure a broad range of resource supplies (incoming light, available water and nutrients). The stands were dominated by Engelmann spruce and subalpine fir, and a few plots also had lodgepole pines (*Pinus contorta* Dougl. Ex.Loud.). Average ages for the dominant trees ranged from 200 to 450 years (Table 1), but the variation in age among stands did not relate to stand biomass ($r^2 = 0.00, P = 0.92$). Precipitation averages about 1.2 m yr^{-1}, with two-thirds as snow (Baron and Mast, 1989). Temperatures are cool in summer (near 14 °C monthly mean in July) and cold in winter (near −6 °C monthly mean in January). The soils are not classified to series, but are largely Typic Cryoboralfs and Lithic Cryochrepts with textures of clay loam to silt loam (Table 1). At each location, we established a 20 m × 20 m plot and measured all trees for diameter at breast height and total tree height. Increment cores were used to estimate 10-year stem increment and sapwood area. Sapwood was marked on the cores in the field, and both sapwood and 10-year increments were measured in the laboratory with a dissecting microscope.

Allometric equations were used to calculate stemwood and branchwood biomass and leaf area. We used equations from Kaufmann et al. (1982) for foliage biomass of spruce, fir and pine. Stem biomass equations came from Kimmins (1997) for spruce, Gholz et al. (1979) for fir, and Olsson et al. (1998) for pine. Wood biomass 10 years ago was calculated by applying these equations to the diameters at that time, and

Table 1
Site and soil descriptions

Plot No.	Aspect (°)	Elevation (m)	% Slope, slope position	Median soil depth (m)	Soil texture fractions (%)		
					Sand	Silt	Clay
1	346	3400	30, upper	0.26	51	26	23
2	346	3390	30, upper	0.41	49	24	27
3	346	3420	30, upper	0.48	53	23	24
4	333	3320	40, lower	0.31	54	22	24
5	338	3220	40, lower	0.32	47	26	26
6	41	3180	35, lower	0.50	56	22	22
7	37	3180	40, lower	0.59	45	23	32
8	58	3180	40, lower	0.43	38	24	38
9	155	3220	35, lower	0.29	48	28	25
10	134	3220	50, lower	0.43	53	25	22
11	158	3220	45, lower	0.39	42	26	32
12	232	3205	30, lower	0.29	54	27	19
13	242	3205	30, lower	0.27	44	32	24
14	236	3200	45, lower	0.60	71	17	13
15	245	3200	45, lower	0.32	37	27	36
16	223	3200	25, lower	0.32	41	33	26
17	223	3205	25, lower	0.40	50	27	23
18	223	3200	20, lower	0.23	48	27	25

subtracting that mass from the present mass estimates; division of this difference by 10 provided an annual estimate. Foliage productivity was estimated as the biomass of needles collected (on a semi-monthly basis for 2 years) from 15 l traps (0.125 m^2) per stand (placed systematically on a 4 m × 5 m grid). Leaf areas were estimated from measured sapwood areas and regression equations from Kaufmann et al. (1982) for spruce and fir, and from Long and Smith (1985) for pine. These methods of estimating pools and fluxes may have some biases (given the lack of opportunity for destructive sampling in the National Park and Wilderness), but we are confident the relative patterns among the stands should be very robust.

Incoming light was calculated as potential total shortwave radiation based on latitude, slope and aspect. For our hypothesis test, we assumed that cloud cover would be similar across the study sites. Light interception was measured with a Decagon Ceptometer, at 15 points along a transect through each plot in early July, between 10 AM and 2 PM. Annual light use was calculated as incoming light times the fraction intercepted.

Nitrogen supply was indexed with ion exchange resin bags (Binkley and Matson, 1983). Fifteen sets of separately bagged anion exchange resins (14 ml Sybron IONAC ASB-IPOH, 4.2 $mmol_c$ per bag) and cation exchange resins (14 ml Sybron IONAC c-251 H^+, 4.9 $mmol_c$ per bag) were buried adjacent to each other 5 cm below the forest floor on a 4 m × 5 m grid, and left in place for 1 year (July 1992–1993). After collection, each set of resin bags was cut open and composited (within sites) and the anion and cation resins extracted with 100 ml of 2 M KCl. Sample extracts were frozen until nitrate and ammonium analyses were done by flow injection (Lachat Instruments, 1986, 1987). Nitrogen uptake was estimated as the N content of litterfall plus the N content of wood increment. The N contents of litterfall and wood samples (from tree cores) were determined using a Leco 2000 C/N analyzer.

We used frequency histograms and cumulative frequency plots to examine patterns in structure. Frequency histograms for within-stand patterns were developed by converting the number (or biomass or production) of trees within a plot to proportions of the plot total, and then these within-plot proportions were averaged across stands to represent the average within-stand patterns. For example, if a plot contained 50 trees, and two trees were in the 20–30 cm diameter class, then 0.04 of the trees in this plot were 20–30 cm in diameter. For stand level patterns, the cumulative values for each plot were tallied. Linear regressions were used to test for associations between production and resource supply and use.

3. Results and discussion

3.1. Patterns in structure and production across stands

These old-growth forests averaged about 1150 trees/ha, with a 3-fold range in aboveground tree biomass, from 130 to 488 Mg/ha (Table 2; Fig. 1). Basal area (at 1.4 m height) averaged 63 m^2/ha, with a range 36–104 m^2/ha. Aboveground net primary production spanned about a 2-fold range from 2700 to 5200 kg ha^{-1} yr^{-1}. Forty-five percent of the trees in the stands were spruce, and spruce accounted for 38% of stand biomass and 55% of stand growth (Fig. 2). Across all stands, only about 9% of the trees (=100 trees/ha) were greater than 50 cm in diameter, and fewer than 1% (=10 trees/ha) were greater than 70 cm in diameter. More than 70% of these old-growth plots had no trees >70 cm in diameter.

Robertson (1992) summarized characteristics for 600 old-growth stands of spruce/fir in the Arapaho and Roosevelt National Forests (adjacent to Rocky Mountain National Park). This broader range of stands averaged 54.6 m^2/ha of basal area (S.D. = 21.7), which was somewhat lower and more variable than the old-growth stands in this study (63 m^2/ha, S.D. = 15.5; Table 1). The numbers of stems per hectare were similar between the two studies, with 790 stems/ha >12 cm diameter in the National Forests, and 730 stems/ha from our study.

Arthur and Fahey (1992) estimated biomass and production for twenty 400 m^2 plots in the Loch Vale Watershed in Rocky Mountain National Park. Stand basal area averaged 40 m^2/ha, with 124 Mg/ha of aboveground tree biomass and 2570 kg ha^{-1} yr^{-1} of aboveground tree net primary production. Prescott et al. (1989) characterized two 600 m^2 plots in an old-growth stand of Engelmann spruce and subalpine fir in Alberta, and found a basal area of 40 m^2/ha,

Table 2
Tree characteristics

Plot	Average dominant age (year)	Average diameter (mm)			Tree density (trees/ha)				Stand basal area (m^2/ha), total	Stand leaf area index, total	Aboveground tree biomass (Mg/ha)				Aboveground net primary production (kg ha^{-1} yr^{-1})		
		Spruce	Fir	Pine	Spruce	Fir	Pine	Total			Spruce	Fir	Pine	Total	Wood	Foliage	Total
1	400	37	15		300	275	0	575	36.4	6.2	114	15	0	130	1240	1450	2700
2	400	38	23		550	325	0	875	76.7	14.9	260	65	0	325	1920	1620	3540
3	250	31	20		650	250	0	900	57.5	7.1	185	32	0	217	2210	1810	4020
4	200	34	22		400	750	0	1150	65.0	8.9	143	130	0	273	2480	1730	4220
5	200	29	21		750	775	0	1525	77.6	9.4	202	111	0	313	2650	1660	4310
6	350	35	23		325	825	0	1150	63.7	7.6	136	138	0	274	2030	1790	3820
7	350	23	20		875	475	0	1350	52.9	9.9	162	66	0	228	1890	2100	3990
8	250	29	20		650	475	0	1125	57.4	7.6	183	55	0	237	1760	1790	3550
9	450	27	17		300	1000	0	1300	39.6	9.6	70	90	0	161	1220	1140	2350
10	200	18	16	28	925	200	450	1575	55.5	5.8	83	14	97	194	1210	1120	2330
11	300	28	13	20	750	900	50	1700	60.1	9.7	80	47	4	132	1760	1520	3280
12	450	24	21		425	1025	0	1450	55.1	13.3	81	156	0	237	2900	1510	4410
13	450	44	24		350	350	0	700	68.4	8.4	219	67	0	285	1450	1970	3420
14	400	34	21		300	800	0	1100	53.6	9.4	109	114	0	223	1460	1460	2920
15	450	40	21		525	575	0	1100	85.3	9.7	312	83	0	394	2020	2140	4160
16	400	48	16		500	600	0	1100	103.7	11.5	434	54	0	488	2570	2630	5200
17	400	36	20		350	675	0	1025	56.6	8.2	176	88	0	264	2280	2010	4290
18	400	51	17		275	575	0	850	69.5	7.8	123	58	0	180	1870	2380	4240
Average	325	34	19	24	510	600	30	1140	63.0	9.2	171	77	6	253	1940	1770	3710
S.D.	120	8	3	4	205	252	103	294	15.5	2.2	90	40	22	87	495	383	748

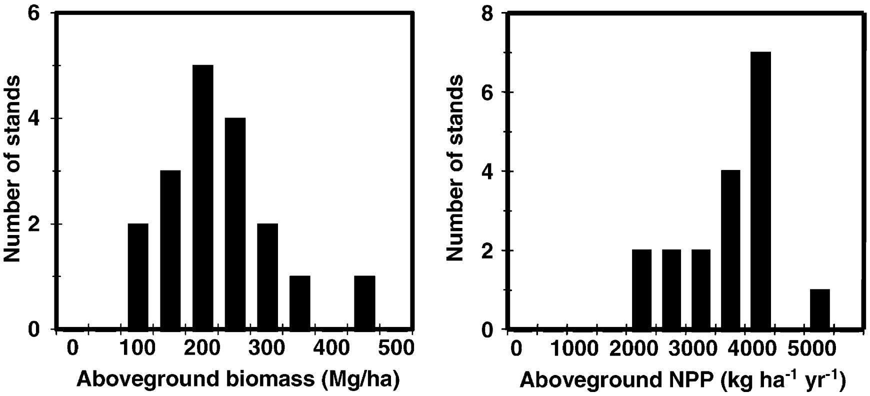

Fig. 1. Distribution of aboveground tree biomass (left) and net primary production (right).

aboveground tree biomass of 144 Mg/ha, and aboveground tree net primary production 3830 kg ha^{-1} yr^{-1}. The average biomass and tree production of the Loch Vale stands of Arthur and Fahey (1992) fell below the range of values we found for 18 stands elsewhere in the same Park, whereas Prescott et al. (1989) reported biomass and tree production values that are within the range of our stands.

3.2. Patterns in structure and production within stands

Within stands, half of the trees were smaller than 15 cm in diameter and accounted for less than 5% of stand biomass (Fig. 3). Stand biomass was distributed relatively evenly among trees from 25 to 65 cm diameter, whereas woody production was concentrated in trees of 15–35 cm diameter. Trees >35 cm in diameter accounted for 70% of aboveground biomass, but trees <35 cm contributed 70% of the production of woody biomass. The same story is illustrated by size ranking rather than diameter (Fig. 4); the largest 20% of the trees contributed about half the biomass of the stands, but contributed just 24% of stand production. This pattern of modest growth by the dominant trees in the stand contrasts markedly with the pattern in younger, more productive stands. For example, Binkley et al. (in press) found that the largest 25% of trees in a plantation of *Eucalyptus saligna* in Hawaii accounted for 60% of the total wood production. Similar within-stand data are not available for younger stands of Engelmann spruce and subalpine fir, and direct assessments are needed of within-stand patterns with relation to stand age to improve our understanding of the role of stand structure in driving age-related changes in stand-level production (Ryan et al., 1997).

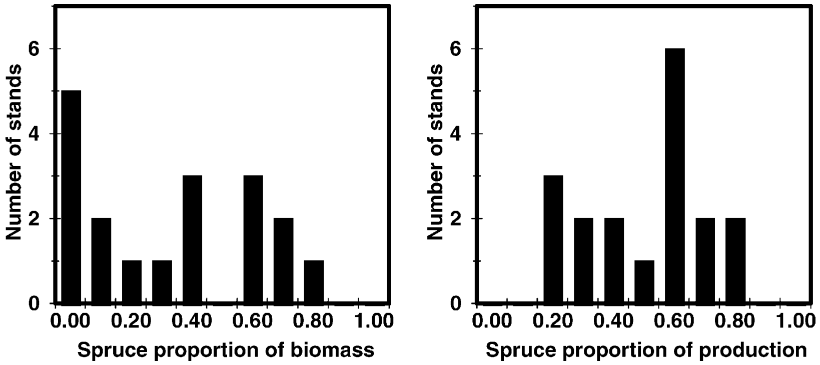

Fig. 2. Proportion of aboveground biomass (left) and woody production (right) comprised of spruce. Spruce accounted for a disproportionately large fraction of growth relative to biomass.

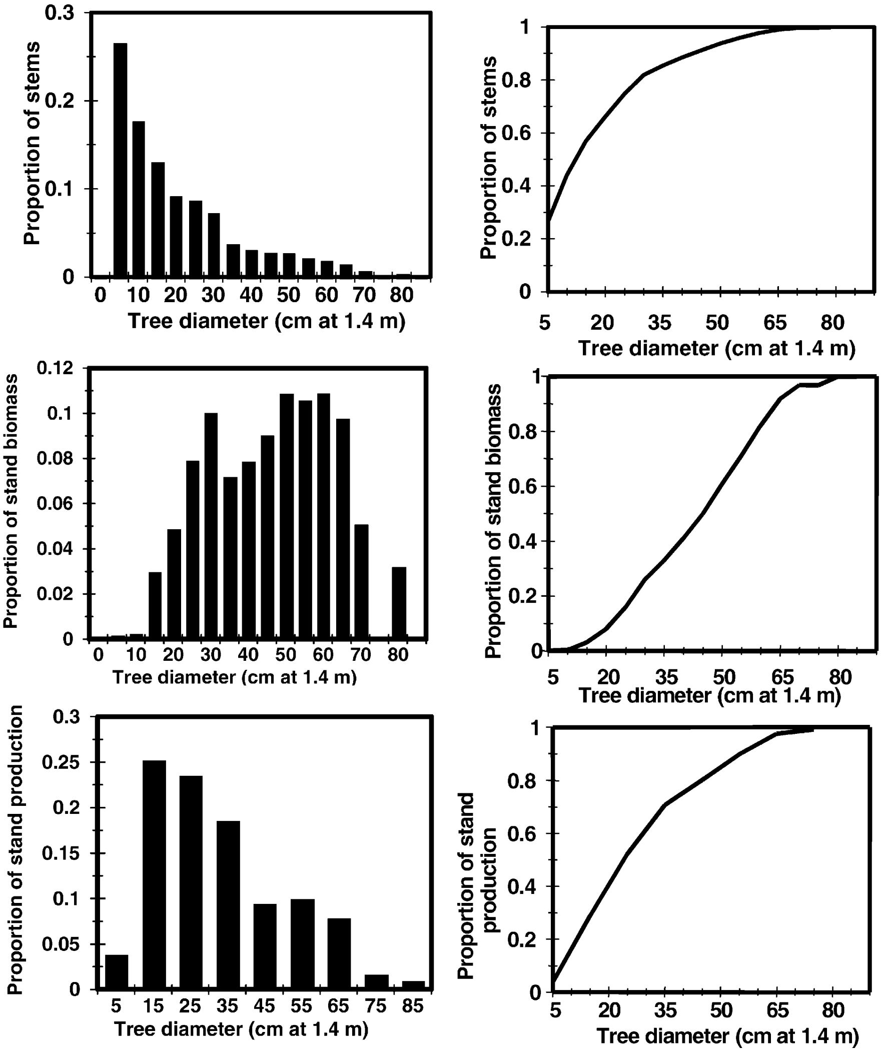

Fig. 3. Average within-stand patterns in tree numbers (upper), stand biomass (middle) and woody (stem + branch) production (lower) by diameter class.

3.3. Patterns in stand production and resource supply and use

Across all stands, ANPP averaged 42 g/m^2 of leaf area (S.D. $= 9$). Plots with higher leaf area had significantly lower rates of ANPP/LA ($r^2 = 0.36$, $P < 0.01$); a stand with an LAI of 7 would average 47 g ANPP/m^2 LA, whereas a stand with an LAI of 12 would average 35 g ANPP/m^2 LA. These rates of production per unit of leaf area are notably lower than rates reported for young and old forests of lodgepole pine in the Medicine Bow Mountains of southern Wyoming. Olsson et al. reported rates from 100 to 150 g ANPP/m^2 of LA (across an age range 30–200 years), and Smith and Resh reported rates of 80–100 g ANPP/m^2 of LA for stands between 30 and 260 years old. Callaway et al. (2000) measured an age sequence of whitebark pine (*Pinus albicaulis* Engelm.) and subalpine fir, and found rates a constant rate of about 90 g ANPP/m^2 LA from stand age 70–460 years. In all three age sequences, ANPP/LA was largely independent of age. The rates of ANPP were similar across

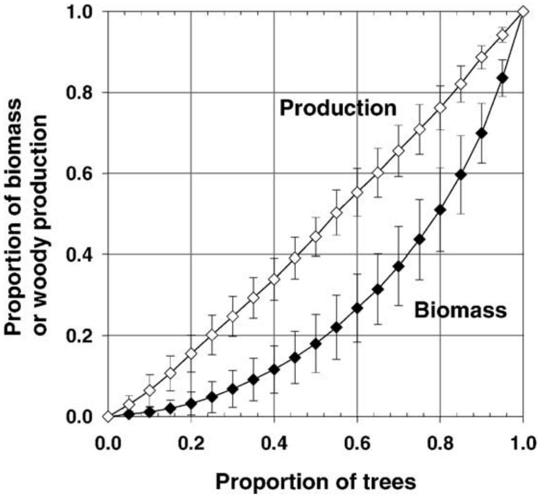

Fig. 4. Cumulative frequency diagrams for aboveground biomass and woody production (bars 1 standard deviation, $n = 18$ stands).

these forests, but leaf area for the spruce/fir forests were higher than the leaf areas for these other species and sites. The trend in leaf area among all stands (across species and sites) accounted for 72% of the variation in ANPP/LA $(\mathrm{ANPP/LA} = 150.5\,\mathrm{e}^{-0.134\mathrm{LA}}$, $P < 0.0001)$.

Differences among sites in slope and aspect generated a range of potential incoming light of 58–74 TJ ha^{-1} yr^{-1} (1 TJ = 10^{12} J; Fig. 5). The range in intercepted light was greater, from 29 to 60 TJ ha^{-1} yr^{-1}, as a result of a large range in stand leaf area index (2.5–5.3). Variation in leaf area explained about 27% of the variation in light interception $(P = 0.01)$, with an average light extinction coefficient of −0.37. Soil N supply, as indexed by resin bags, spanned a 9-fold range, whereas N uptake ranged over a 2.5-fold range (from 1.0 to 2.5 g N m^{-2} yr^{-1}).

Across the 18 plots, aboveground net primary production (ANPP) did not relate to the supply of light or N (Fig. 5), but ANPP correlated with both the amount of light and N used $(r^2 = 0.45–0.54, P < 0.01)$. Aboveground net primary production increased by 78 kg for each TJ (=78 μg/kJ) of intercepted light on an annual basis. The incoming light estimate is total shortwave radiation, and photosynthetically active

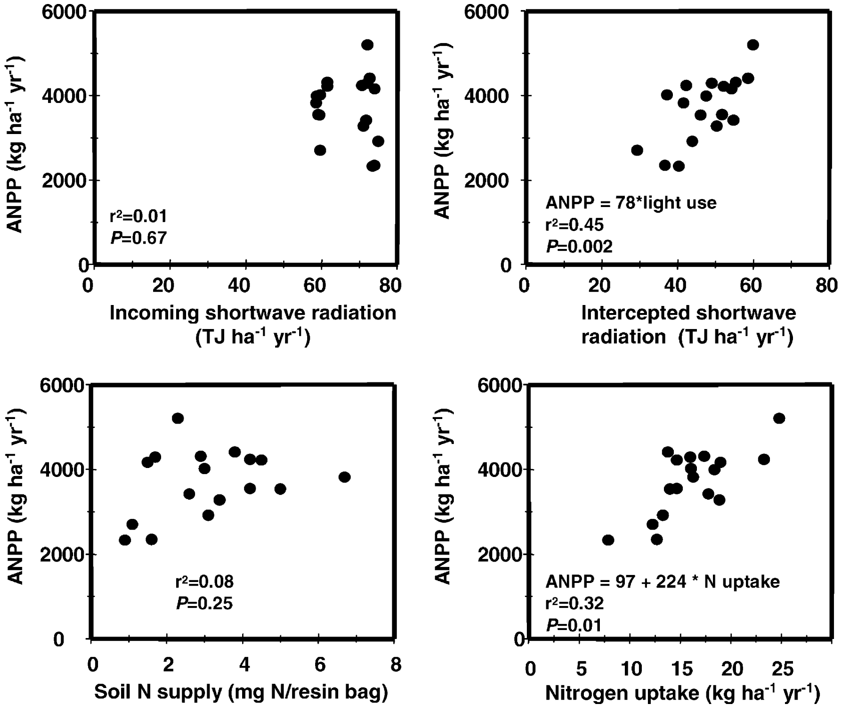

Fig. 5. Aboveground net primary production did not relate to the supply of either light or nitrogen, but related strongly to the amount of light intercepted or N taken up.

radiation (PAR) would be about half of the total, giving a production of about 156 kg/TJ of PAR intercepted. We did not measure the extent of cloud cover through the year, but based on patterns for the Fraser Experimental Forest (70 km away), we estimate that incoming PAR would be about half of the potential PAR (M. Ryan, personal communication). Therefore our best estimate of production as a function of intercepted PAR is about 300 kg/TJ (=300 μg/kJ). Linder (1985) and Stenberg et al. (1995) reported production of 270–1700 μg/kJ of intercepted PAR, indicating a low production efficiency for our cold, high elevation forests.

On average, our forests produced about 260 g of ANPP per gram of N taken up (Fig. 1). Arthur and Fahey's (1992) plots in the Loch Vale of Rocky Mountain National Park yielded a similar estimate of 250 kg ANPP/kg N uptake; both production and N uptake were lower in their stands. Prescott et al. (1989) estimated that a 350-year-old spruce and fir forest in the Kananaskis Valley in Alberta produced from 250 to 280 kg ANPP/kg N uptake. Olsson et al. (1998) found a higher rate of 430 kg ANPP/kg N uptake for lower-elevation, old-growth (200+ year) stands of lodgepole pine in southeastern Wyoming. The higher production per unit of N in the lodgepole pine stand resulted from lower ANPP (50% lower than the average for spruce/fir in this study), and much lower N uptake (70% lower than spruce/fir).

As the supply or rate of use of a resource increases, the rate of production per unit of resource supply or use might change (Pastor and Bridgham, 1999). Hof et al. (1990) hypothesized that production per unit of resource used would be constant in relation to resource use, but that production per unit of resource supply in the environment should increase as the supply increases, as each leaf or root would obtain more resources. Our stands supported the first part of the Hof et al. (1990) prediction: aboveground net primary production per unit of light intercepted or nitrogen used showed no pattern with respect to light interception or nitrogen use ($r^2 = 0.07$ and 0.14, $P = 0.25$ and 0.013). However, the predicted pattern of increasing production per unit of resource supply was not supported for gradients in either light supply or nitrogen supply.

The hypothesis of increasing ANPP/unit resource used in relation to increases in resource supply had to be rejected for our suite of sites, but we are not confident that the idea itself is wrong. Hof et al. (1990) made this prediction with the assumption that the supply of other resources remained constant across gradients in the resource of interest. In our site, the supply of light correlated negatively with the supply of N ($r^2 = 0.30, P = 0.01$), confounding the examination of patterns between production and either light or N, and supplies of water probably differed substantially among stands.

Across our old-growth stands, larger stands showed higher rates of both ANPP and resource use; variation in aboveground biomass was associated with 24% of the variation in N use ($P = 0.04$), 44% of the light use ($P = 0.003$), and 45% of the ANPP ($P = 0.002$). We do not know why some stands were larger than others. Production did not relate to differences among sites in resource supply, and stand biomass did not relate to age, so we suspect that differences in stand biomass (and therefore resource use and production) may relate to stand-specific history, particularly the amount of tree mortality in recent decades.

We did not assess the rate of net biomass accumulation in these stands, but we suspect that mortality is probably removing tree biomass from the stand about as rapidly as production adds new biomass. We found that stand biomass was unrelated to the age dominant age ($r^2 = 0.00, P = 0.92$), even though some stands were twice the age of others. Arthur and Fahey (1992) used a steady-state model of decaying wood mass to estimate an annual rate of tree death in Loch Vale of Rocky Mountain National Park, and they concluded that bole production of 865 kg ha^{-1} yr^{-1} was almost matched by mortality of 810 kg ha^{-1} yr^{-1}. The combination of sustained moderate rates of net production and high mortality lead to complex forest structure that includes a substantial component of standing and fallen boles.

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