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SUBALPINE FOREST CARBON CYCLING: SHORT- AND LONG-TERM INFLUENCE OF CLIMATE AND SPECIES

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Abstract. Ecosystem carbon cycle feedbacks to climate change comprise one of the largest remaining sources of uncertainty in global model predictions of future climate. Both direct climate effects on carbon cycling and indirect effects via climate-induced shifts in species composition may alter ecosystem carbon balance over the long term. In the short term, climate effects on carbon cycling may be mediated by ecosystem species composition. We used an elevational climate and tree species composition gradient in Rocky Mountain subalpine forest to quantify the sensitivity of all major ecosystem carbon stocks and fluxes to these factors. The climate sensitivities of carbon fluxes were species-specific in the cases of relative aboveground productivity and litter decomposition, whereas the climate sensitivity of dead wood decay did not differ between species, and total annual soil CO_2 flux showed no strong climate trend. Lodgepole pine relative productivity increased with warmer temperatures and earlier snowmelt, while Engelmann spruce relative productivity was insensitive to climate variables. Engelmann spruce needle decomposition decreased linearly with increasing temperature (decreasing litter moisture), while lodgepole pine and subalpine fir needle decay showed a hump-shaped temperature response. We also found that total ecosystem carbon declined by ~50% with a 2.8°C increase in mean annual temperature and a concurrent 63% decrease in growing season soil moisture, primarily due to large declines in mineral soil and dead wood carbon. We detected no independent effect of species composition on ecosystem C stocks. Overall, our carbon flux results suggest that, in the short term, any change in subalpine forest net carbon balance will depend on the specific climate scenario and spatial distribution of tree species. Over the long term, our carbon stock results suggest that with regional warming and drying, Rocky Mountain subalpine forest will be a net source of carbon to the atmosphere.

Key words: Abies lasiocarpa; *climate; Colorado, USA; ecosystem carbon cycle; gradient analysis;* Picea engelmannii; Pinus contorta; *Rocky Mountains; species composition; subalpine forest.*

INTRODUCTION

Climate change projected for the coming century is likely to alter ecosystem carbon fluxes and pool sizes, resulting in either positive or negative feedbacks to the climate system (Woodwell et al. 1978, 1998, Lashof et al. 1997). The magnitude of these feedbacks may not be consistent over space or time, but may be predicted in part by the relative sensitivities of different ecosystem processes to the direct and indirect effects of climate change. Climate change can directly alter ecosystem processes by speeding or slowing temperature- and moisture-dependent rates such as primary productivity, nitrogen mineralization, or organic matter decay (Kirschbaum 1995, Hart and Perry 1999, Saleska et al. 1999, Shaw and Harte 2001). If process rates are under species-specific constraints, mean process rates and process sensitivity to climate changes can vary with plant community composition (Chapin et al. 1995, Hobbie 1996, Hobbie and Chapin 1998, Eviner and Chapin 2003). Over the long term, persistent climate changes may alter the species composition of an ecosystem and thereby indirectly affect ecosystem processes and potential C cycle feedbacks to climate (Pastor and Post 1988, Harte and Shaw 1995, Saleska et al. 2002). Indirect and direct effects are likely to interact to yield rate changes that are not easily predicted (Hobbie et al. 2000), particularly where responses occur on a range of time scales (Dunne et al. 2004).

The ability to predict C feedbacks to climate change requires a mechanistic understanding of how C cycling is affected by both species composition and climate. In forest ecosystems, whole-system climate manipulations as employed in shorter-stature ecosystems (e.g., Chapin et al. 1995, Harte et al. 1995, Luo et al. 2001) are not feasible. Similarly, intentional manipulation of tree community composition through species addition or removal requires decades for trees to mature and additional time for slowly cycling C pools, such as soil and dead wood, to approach equilibrium (Kueppers et al. 2004). Spatial climate gradients reflect long-term adjustments of species and ecosystems to climate conditions if soils, light levels, and other environmental factors are held constant and human impacts are min-

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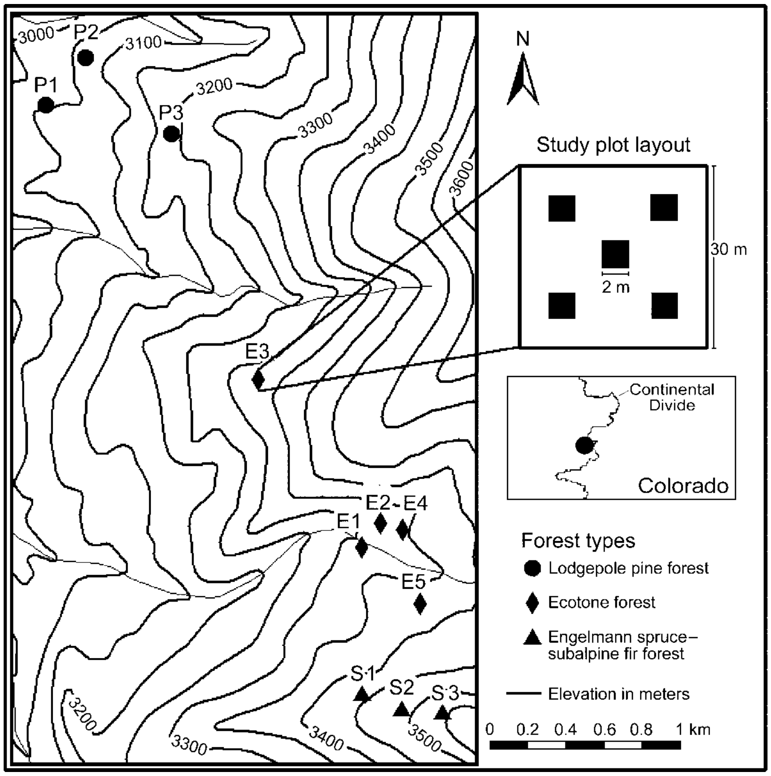

FIG. 1. Arrangement of research plots along an elevational climate and forest type gradient in the Fossil Ridge Wilderness, Gunnison County, Colorado, USA.

imized (Jenny 1941, Vitousek and Matson 1991, Amundson and Jenny 1997). Therefore a carefully selected spatial climate gradient should reflect differences in C cycling due to differences only in climate and species composition, providing an alternative approach to manipulative experiments. Small-scale manipulations can be used to supplement gradient observations and determine the sensitivity of individual processes to climate differences, as well as to distinguish climate from species effects.

We used a gradient approach to investigate how C cycling in subalpine forest in the Rocky Mountain region varies with climate and whether the spatial patterns we observed were influenced by tree species composition. Subalpine forest, while relatively small in spatial extent, will experience more rapid and larger climate changes than forests at lower elevations due to snow-albedo feedbacks (Beniston et al. 1997, Giorgi et al. 1997). Subalpine forest is also a useful study system because the mountainous topography results in substantial differences in climate and vegetation over relatively short horizontal distances, and in the Rocky Mountain region this forest type has relatively low tree species diversity. By measuring all of the major C stocks and flows along gradients in climate and species composition, we were able to quantify the sensitivity of subalpine forest C cycling to variation in these factors on the landscape.

METHODS

Study sites

We measured ecosystem C stocks and fluxes along a 500-m elevation gradient centered at 38°43′27.21″ N latitude and 106°39′3.92″ W longitude, in the Fossil Ridge Wilderness, Gunnison County, Colorado, USA (Fig. 1). The Fossil Ridge Wilderness is a 12 840-ha roadless area on the western slope of the Rocky Mountains that was designated as federally protected wilderness in 1993. A fence prevents cattle from entering the research watershed, although grazing was permitted historically. The fire regime in Rocky Mountain subalpine forests is thought to have been minimally impacted by 20th century fire suppression, due to the difficulty of controlling the large, intense fires characteristic of these forests and to 100+ year fire return intervals (Schoennagel et al. 2004). The last fire in the Fossil Ridge Wilderness was in 1980, burning ~80 ha of lodgepole and bristlecone pine (G. Chonka, *personal communication*), although there was no evidence of this fire near our study plots. There is no recorded history or evidence (e.g., stumps) of logging in or near our research area. The largest current direct human impact in this forest is private and commercially guided hunting, which has resulted in local wood gathering for campfires. Overall, this area has been minimally impacted by historic and current human activities, allow-

PLATE 1. Fossil Ridge Wilderness as seen looking north from plot S3. Engelmann spruce trees can be seen in the foreground, while lodgepole pine dominates the opposite slope. Photo credit: L. M. Kueppers.

ing us to assume that most differences along the gradient are due to environmental and ecological factors.

Vegetation along the gradient is largely determined by elevation and associated differences in climate (Peet 2000). The forest is dominated by lodgepole pine (*Pinus contorta*) at lower elevations and Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at upper elevations, with all three tree species co-occuring in an ecotone between 3300 and 3400 m (see Plate 1). This transition in species dominance is one that has been reported to recur with paleoclimate change (Markgraf and Scott 1981, Fall 1997). These species are widespread in the Rocky Mountain region, although Engelmann spruce and subalpine fir are replaced by white spruce and balsam fir in the boreal Rockies (Peet 2000). The sparse understory is composed of common juniper (*Juniperus communis*), *Vaccinium myrtillus*, and other low shrubs, tree seedlings, graminoids, and flowering plants. We selected 11 research plots (each 30 × 30 m) ranging in elevation from 3040 to 3552 m, establishing three in the pine forest, three in the spruce–fir forest, and five in the ecotone (Fig. 1). We took four GPS readings at each plot and used the *x* and *y* coordinates with a digital elevation model to estimate mean plot elevation. The highest elevation plot was approximately 50 m below treeline. All plots had northwest aspects with slope angles $<30°$, had similar stand densities, and were in forest patches at least 130 years old. The plots were on the Schofield-Peeler gravelly to very stony sandy loam soil series, classified as a Typic cryoboralf derived from Pre-Cambrian granite (Fox 1977). The soils are very rocky with strong horizonation, having thicker organic horizons at higher elevations. Within each plot we established five 2 × 2 m evenly spaced subplots where we clustered most of our flux measurements (Fig. 1).

Climate

Mean annual temperature and mean total annual precipitation at the nearby National Weather Service Taylor Park weather station (2800 m) are 0.5°C and 422 mm, respectively. Monthly mean temperature peaks in July at 13.4°C. Peak total monthly precipitation occurs in August with the monsoon rains, although precipitation is spread fairly evenly throughout the year. During the years of the study (1999–2002), annual and growing-season temperatures were warmer than the 1949–2003 means, and annual and growing season precipitation were generally within the range of normal interannual variability. However, the first year of the study, 1999, had record high total annual precipitation, due to high spring and summer rainfall.

We measured microclimate variables directly in every plot to quantify relative differences in climate. We measured soil temperature 15 cm below the ground surface in every subplot and air temperature 1.5 m above ground at the center of each plot, both hourly from July 1999 to October 2001 using Hobo dataloggers (Onset Computer, Bourne, Massachusetts, USA). We excluded outlier values and filled missing data using regressions with other sensors in the same plot, then aggregated the measurements into daily means. We calculated annual means and growing degree days (the sum of daily air degrees over 5°C) for 2000, the only year for which we had complete records in all plots. We estimated the mean date of snowmelt as the first day in spring that a majority of soil temperature probes recorded means $>1°C$, averaging 2000 and 2001 dates for each plot. We calculated the mean length of winter for 1999–2000 and 2000–2001 as the number of days between the date when plot daily mean soil temperature dipped below 1°C in fall and the date of snowmelt in spring, averaging the two winters.

We measured growing season gravimetric soil moisture in the top 10 cm of soil, three times in every subplot in 2000: immediately after snowmelt, 6 wk after snowmelt, and in mid-October. We calculated the median of these measurements for each plot as an index of relative soil moisture because the frequency distributions of the measurements were skewed. We also measured soil moisture with fiberglass resistance sensors (Soil Moisture Equipment, Santa Barbara, California, USA) buried 15 cm below the ground surface in every subplot. We recorded resistance every 2 wk throughout the 2000 growing season to determine intraseasonal variation in soil moisture.

Carbon stocks

Aboveground tree biomass.—We calculated aboveground tree biomass from previously published, species-specific allometric equations using measurements of diameter at breast height (dbh) and tree height. During the summer and early fall of 1999 we measured the dbh of every tree $>$1.4 m tall in each plot using a steel diameter tape. We measured the height of short trees (less than $\sim$2.5 m) directly and the height of tall trees geometrically using a clinometer. For aspen, a minor component of the aboveground biomass in our study sites, we used a single equation from sites in Alberta (Peterson et al. 1970, Stanek and State 1978). For lodgepole pine, we based the equation for small ($<$10 cm dbh) trees on published raw data (from Colorado [Moir 1972]) and used separate equations for large trees (from Alberta [Johnstone 1970, Stanek and State 1978]). We used a single equation for the closely related white spruce (*Picea glauca*) to calculate Engelmann spruce biomass (from New Brunswick [Baskerville 1965, Stanek and State 1978]). For subalpine fir, we used separate equations for small trees (from British Columbia [Wang et al. 2000]), and large trees (from Alberta [Singh 1982] and from British Columbia [Stanek and State 1978; J. P. Kimmins, *unpublished manuscript*]). We calculated leaf area index (LAI) for each plot as the sum of each tree's LAI divided by the plot area, using species-specific allometric equations for LAI (Kaufmann et al. 1982).

Understory biomass.—Between 11 and 25 August 2000, we harvested live aboveground understory biomass from six evenly spaced 1-m^2 quadrats per plot. We subdivided the biomass into categories: pine, spruce, and fir seedlings; *Vaccinium myrtillus*; buffalo berry (*Shepherdia canadensis*); common juniper; forbs; graminoids; and other. We dried all samples for 48 h at 65°C before weighing.

Dead wood.—We measured the biomass of snags and coarse woody debris ($>$10 cm diameter) in each study plot in 2001 (Kueppers et al. 2004). We measured fine woody debris biomass ($\geq$2.5 cm and $<$10 cm diameter), in 12 1×1 m quadrats, evenly spaced along two parallel 30-m transects running across each plot. We measured the volume of each piece of wood geometrically and calculated mass by multiplying volume by plot mean wood density, determined from five oven-dried (65°C) subsamples. In calculating plot mean biomass we included zeros for quadrats containing no fine woody debris.

Forest floor.—We collected forest floor from 12 15×15 cm areas in a corner of each fine woody debris quadrat. We sampled to the top of the mineral soil and included needles, cones, and branches $<$2.5 cm diameter. We dried the material at 65°C, weighed it, and calculated mean plot-level forest floor biomass. We determined forest floor C content on a subset of six samples per plot, by grinding oven-dry samples to a fine powder and analyzing them on a Carlo Erba elemental analyzer (CE Elantec, Lakewood, New Jersey, USA).

Mineral soil carbon.—In 2000, we measured the C content and bulk density of the soil by collecting quantitative samples from three soil pits per study plot. We dug the soil pits to 60 cm depth and sampled by soil horizon and 10 cm depth increment, starting at the top of the O horizon, if present. Soil samples were returned to the laboratory, dried at 100°C, passed through a 2-mm sieve, and weighed to determine bulk density. In some cases, cobbles and boulders prevented us from obtaining a quantitative sample. For these, we took qualitative samples for C analysis and estimated the sample bulk density from the other pits in the plot. We removed roots from subsamples of the $<$2 mm soil fractions, ground the subsamples to a fine powder, and analyzed them for C on a Carlo Erba elemental analyzer (CE Elantec).

Because the pits were so rocky, we measured the mass of all rocks $>$5 cm removed from each soil pit, converted rock mass to volume using a measured rock density of 2.3 g/cm, measured the total volume of each soil pit geometrically, and calculated the volume fraction of each pit containing the $<$5-cm soil size fraction. To calculate the total C inventory in the mineral soil, we multiplied the percentage of C of each sample by the horizon- and depth-increment-specific bulk density (which accounted for rocks $<$5 cm). We then summed the C content of the $<$5-cm size fraction for the whole profile and corrected for the volume of soil $<$5 cm in each pit, yielding a C content per unit area. The correction assumes no trend in rockiness with depth.

Coarse roots.—We measured coarse root ($>$2 mm diameter) biomass between 0 and 60 cm depth by collecting all coarse roots taken from the three soil pits per plot (mean pit volume 0.145 ± 0.008 m^3, $n = 33$). We separated coarse roots from the soil by hand and weighed them in the field using a spring-loaded balance. We dried a subset of roots from each plot in the laboratory at 65°C and weighed them to determine a fresh mass to dry mass conversion factor.

Fine roots.—We measured fine-root biomass ($<$2 mm diameter) in the top 15 cm of soil with a 6 cm diameter core in each subplot, taken between 7 and 22 September 2000, roughly when we expected root biomass to peak (Arthur and Fahey 1992). We immediately placed the samples on ice and returned them to the laboratory where they were kept at 4°C. We broke up the soil cores under running water over 425-μm, 850-μm, and 2-mm mesh sieves and removed decaying organic matter, fungi, and mosses from the root samples by hand. To distinguish live from dead we used a combination of cues including color, physical resilience, adhesion between stele and cortex, and root structure (Vogt and Persson 1991). We only examined root fragments $>$5 mm long and recorded the dates of root sampling and sorting, confirming that progressive root death did not affect our measurements. We oven-dried the samples for 48 h at 65°C before weighing them.

For all stocks other than forest floor and soil C, we converted biomass to C by assuming plant biomass is 50% C.

Carbon fluxes

Tree biomass increment.—We calculated aboveground tree biomass increment as the plot-level sum of differences in live tree biomass between 1999 and 2002. In June 2002 we remeasured dbh on all trees measured in 1999, as well as on saplings that had grown to 1.4 m since 1999. We calculated 2002 tree biomass using 1999 height (or 2002 height for new trees), 2002 dbh, and the same allometric equations used in 1999. We did not exclude 2002 dbh measurements that were smaller than those from 1999, as has been done by other researchers (e.g., Raich et al. 1997). We applied a plot- and size-class-specific mean change in dbh for outlier values (1–3 trees per plot, 20 of 1378 trees across all plots). We estimated mortality as the total biomass of trees that were live in 1999 but dead in 2002 and divided biomass increment and mortality by the time between measurement periods (2.8 yr) to yield annual rates.

Litterfall.—We collected litterfall monthly during the growing seasons between August 1999 and July 2001, from mesh-lined 0.14-m^2 litter traps placed in each subplot. The June collections included litter from the previous October–May. The litter traps were ~0.5 m above the ground surface and therefore did not receive litter from most of the understory. We separated the litter by species (pine, spruce, and fir), and/or component, dried it at 65°C, weighed it, and calculated plot mean annual totals for two years, August 1999–July 2000 and August 2000–July 2001. We assumed litterfall was 50% C, dry mass.

Aboveground net primary productivity.—We calculated aboveground net primary productivity (ANPP) as the sum of annual biomass increment plus mean annual fine litterfall for each plot. Standard errors of plot-level ANPP reflect interannual variation in litterfall only. Aboveground net primary productivity estimates do not include understory productivity, produced plant matter that was consumed by herbivores or parasites, volatile organics lost to the atmosphere, or organics leached from the canopy into the soil (Clark et al. 2001). We also assumed that trees that had died between 1999 and 2002 did not accumulate biomass between 1999 and their death. As a result, our values for ANPP are slight underestimates.

Litter decomposition.—In July and August 1999, we collected freshly senesced lodgepole pine needles in tarps under canopy trees in the pine and pine-dominated ecotone forests and Engelmann spruce and subalpine fir needles under trees in the spruce–fir and spruce–fir-dominated ecotone forests. We air-dried the needles in the laboratory, sorted them by species, removed green and highly decomposed needles, and placed 4.0 g into 10 × 15 cm nylon mesh litter bags. The litter bags had 1.6-mm mesh on top and 0.2-mm ''no-see-um'' nylon tent mesh on the bottom, to prevent needle loss (Rustad and Cronan 1988, Hobbie 1996). We divided the litterbags (n = 825) evenly among the subplots and anchored them to the ground surface at one corner. We retrieved litterbags after 2, 10, 14, 22, and 26 mo, dried them at 65°C, hand-sorted the samples to remove contamination, and weighed them. To correct the initial sample masses for the difference between air-dry and oven-dry mass, we oven-dried ~15 initial samples of air-dried litter per species to obtain mean correction factors of 0.929 ± 0.002 for pine, 0.85 ± 0.02 for spruce, and 0.888 ± 0.007 for fir. We used a single exponential decay model to calculate decay rate constants (k) for each species and plot separately.

We estimated coarse woody debris decay rates using radiocarbon to determine the age of dead wood and a Monte Carlo routine to estimate the exponential decline in wood tissue density with age (Kueppers et al. 2004). For both wood and needle decay, we assumed that the C decay rate was equivalent to mass decay rate.

Soil CO_2 flux.—We measured in situ soil respiration biweekly throughout the snow-free season of 2000, using flexible-volume static chambers and soda lime traps (Edwards 1982). Within 6 ± 1 d after snowmelt in each plot, we placed a 16.5 cm diameter plastic ring in each subplot, pressing the rings 1 cm into the soil surface. We clipped live plants within the sample area at the soil surface. We allowed the soils to equilibrate for at least 0.5 h before placing a 5.9 cm diameter container with 8.5 g of 6–12 mesh granular oven-dried soda lime onto a three-legged platform in the center of the ring and closed the chamber, sealing the lip with vacuum grease (Dow Corning high vacuum grease, Fisher Scientific, Hampton, New Hampshire, USA) for the 24-h measurement period. The chamber lids were equipped with a stopcock open to a partially inflated mylar balloon that acted as flexible volume, minimizing the effect of pressure changes within the chamber on diffusion of CO_2 from the soil (Lund et al. 1999). We corrected every measurement by blanks (n = 11 per sample date) that were treated the same as the measurement samples, but left in the field in chambers with solid bottoms. We also adjusted the measurements by

TABLE 1. Study plot climate and tree biomass characteristics.

Plot	Forest type	Elevation (m)	Mean temperature		Growing-degree days (day-°C)	Soil moisture† (%)	Date of snowmelt (day of year)	Winter length (d)	Lodgepole pine AGB‡ (%)	Basal area (m^2/ha)	Leaf area index (m^2/m^2)
			Air (°C)	Soil (°C)							
P1	pine	3040	1.88	2.81	920	28.4	129	195	100	38.3	6.7
P2	pine	3072	2.20	3.93	1001	15.9	125	176	100	25.5	4.4
P3	pine	3200	1.86	3.60	923	18.5	125	176	100	27.3	4.8
E1	ecotone	3308	−0.72	2.08	529	24.2	146	223	71	43.4	12.0
E2	ecotone	3323	0.02	2.54	630	21.4	144	211	81	38.1	9.2
E3	ecotone	3328	0.82	2.93	761	20.2	140	205	87	44.6	10.3
E4	ecotone	3334	−0.38	2.74	562	40.2	142	209	52	50.8	17.4
E5	ecotone	3392	−0.46	2.31	566	58.8	147	213	20	53.6	23.1
S1	spruce–fir	3456	−0.13	1.59	644	60.2	156	234	0	43.4	20.4
S2	spruce–fir	3520	−0.58	1.48	560	79.2	152	223	0	50.1	23.9
S3	spruce–fir	3552	−0.37	2.23	605	52.9	150	226	0	22.4	10.8

† Median growing-season gravimetric soil moisture.
‡ AGB = aboveground biomass.

the mass ratio of H_2O released (and evaporated) per molecule CO_2 adsorbed (Grogan 1998). The ratio of soil area to soda lime area was 12.8% for the summer measurements, and the maximum change in mass of the soda lime was 3%. Because snowmelt progressed from low to high elevations, we made slightly more measurements in the lower elevation plots (12–13 vs. 10–11 measurements).

We estimated over-winter flux rates by placing two containers with a total of 70 g soda lime in each chamber from late October or early November 2000 to within a day or two of 2001 snowmelt in each plot, using chamber lids without mylar balloons. The ratio of soda lime to exposed soil area was 25.5%, and the maximum change in mass was 11%, a level at which adsorption efficiency should still be about 80%. To ensure that there was enough humidity in the soil chambers to enable CO_2 adsorption, we dripped several milliliters of water onto the soda lime prior to sealing the chamber lids (Grogan and Chapin 1999). The chambers were covered by at least 30 cm of snow for most of the winter. Because the soda lime method tends to overestimate fluxes when rates are low and underestimate fluxes when rates are high (Nay et al. 1994), we report winter and growing-season rates calibrated to infrared gas analysis measurements based on the curve in Grogan (1998).

We calculated the total annual flux (as megagrams of CO_2-C per hectare per year) by multiplying each plot mean daily rate by the number of days to the previous measurement. In most cases this was 14 d; however, for the first measurement in spring we multiplied this first rate by the number of days to the date when the over-winter flux measurement was ended in the subsequent year. In every plot, snowmelt in 2000 and 2001 occurred within several days of the same date. In the fall, we extended the mean over-winter daily flux rate back to the last growing season measurement date, which was 23 October in most plots and 9 October in the three highest elevation plots.

Statistical analysis

We evaluated the relationships among elevation, six different climate variables, and a continuous index of species composition (the fraction of tree aboveground biomass [AGB] that was pine) using Pearson correlation coefficients and highlight those statistically significant at $P < 0.05$ after a Bonferroni correction for multiple comparisons ($P < 0.0063$). We conducted simple linear regression analyses to evaluate the effects of

TABLE 2. Pearson correlation, *r*, matrix of climate and species composition characteristics of the study plots.

Characteristic	Elevation	Air temperature	Soil temperature	Growing-degree days	Soil moisture	Snowmelt date	Winter length
Elevation	**1.00**						
Air temperature	**−0.84**	**1.00**					
Soil temperature	−0.78	0.83	**1.00**				
Growing-degree days	−0.81	**1.00**	0.81	**1.00**			
Soil moisture	0.76	−0.64	−0.79	−0.60	**1.00**		
Snowmelt date	**0.90**	**−0.91**	**−0.93**	**−0.88**	0.75	**1.00**	
Winter length	0.83	**−0.89**	**−0.94**	**−0.87**	0.68	**0.97**	**1.00**
Pine fraction	**−0.89**	0.75	0.81	0.71	**−0.93**	**−0.87**	−0.81
Pine fraction in ecotone	−0.87	0.58	0.36	0.58	**−0.99**	−0.61	−0.15

Notes: Data for correlations are given in Table 1. All correlations significant after a Bonferroni correction for multiple comparisons are given in boldface type. For each comparison, *n* (number of plots) = 11, except those with pine fraction in the ecotone forest for which *n* = 5.

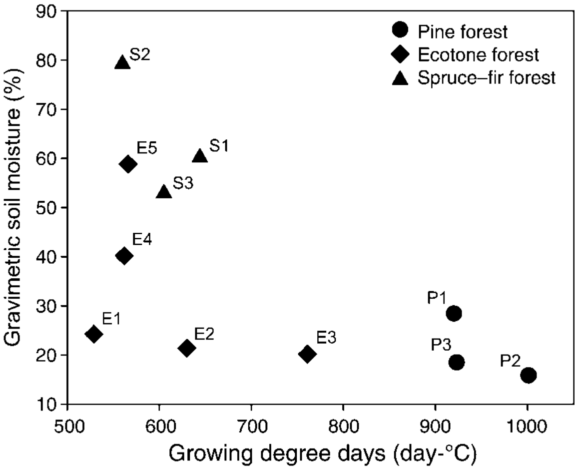

FIG. 2. Location of individual study plots in growing-season climate space.

climate variables on all ecosystem C stocks and fluxes. We only discuss relationships with $P < 0.05$ after a Bonferroni correction, unless otherwise noted. Because most climate variables were highly correlated with one another, we did not construct multiple regression models except when examining soil CO_2 flux rates over time. In some cases, nonlinear models better represented trends in the data. In these cases, we omit the linear form from our results and report the functional form and means-corrected regression statistics for the nonlinear relationships separately.

Because species composition changed with climate along the full gradient, we utilized variation in species composition (pine fraction) within the ecotone where climate variation was more limited to help distinguish climate from species composition effects on C cycling. We also examined the residuals of the strongest C stock–climate regressions for patterns with species composition. We calculated all statistics using Systat version 8.0 (SPSS 1998).

RESULTS

Plot climate and species composition

The range in annual temperature along the gradient is similar to projections for regional annual temperature change within this century (National Assessment Synthesis Team 2000). Mean annual air temperature in the year 2000 spanned 2.92°C, and mean annual soil temperature spanned 2.45°C along the gradient, with colder plots occurring at higher elevations (Tables 1 and 2). Summer warmth, as measured by year 2000 growing-degree days, was highest in the low-elevation, pine forest plots (Table 1). Air temperature and growing-degree days were lowest in plot E1, probably due to its low topographic position, where cold air drainage occurred. Growing-degree days, annual air temperature, and annual soil temperature were positively correlated with one another along the gradient (Table 2). Snowmelt occurred 31 d later in the latest melting plot compared to the earliest melting plot, while mean winter length differed by 58 d along the gradient (Table 1). Snowmelt date and length of winter were positively correlated, increased with elevation, and were negatively correlated with annual air and soil temperature and growing-degree days (Table 2).

Median growing season gravimetric soil moisture ranged from 15.9% to 79.2% among the plots, with the two wettest plots (S1 and S2) in spruce–fir forest (Table 1). These two also had the latest dates of snowmelt, which could have allowed soil moisture to remain high in early summer when rainfall was scarce. Soil moisture, as measured with resistance sensors and expressed as the mean sum of ranks by plot, was moderately correlated to gravimetric soil moisture ($r = -0.61$; higher resistance indicates drier soil). The lack of high correlation could be due to the fact that resistance was measured 5 cm deeper than gravimetric moisture, where soils may have retained water further into the growing season. Overall, the climatic range of the study plots encompassed warm–dry, cool–dry, and cool–wet environments, with no relatively warm–wet plots (Fig. 2).

Changes in tree species composition along the gradient were reflected in the relative proportion of aboveground biomass that was lodgepole pine (Table 1). This fraction decreased with increasing elevation, soil moisture, and snowmelt date (Table 2). Within the ecotone forest, where variation in climate was less pronounced than along the full gradient, pine fraction was tightly correlated with soil moisture (Table 2).

Ecosystem carbon stock relationships with climate, species composition

Climate variables were not consistently strong explanatory variables for live plant C pools along the gradient. Total tree AGB C was not related to climate (Table 3) along the full gradient, perhaps in part because we used tree size and canopy maturity as plot selection criteria. Understory biomass was low (<1 Mg C/ha in all plots) and patchily distributed. Shrub and tree seedling biomass accounted for most (71–99%) of the understory biomass, and graminoids were always 5% or less of the total (see Appendix A for all C stock values). Total understory C tended to increase with soil moisture along the gradient, although the trend was not statistically significant (Table 3). We also found no significant patterns between total or live fine-root C and climate (Table 3). Coarse-root C decreased with increasing soil temperature and increased with soil moisture along the gradient (Table 3), reflecting differences in C allocation either as climate changed or as tree species composition changed.

Dead wood and soil C were closely related to climate. Total dead wood C was a significant but variable fraction of ecosystem C, decreasing strongly as air temperature and growing-degree days increased (Kueppers

TABLE 3. Correlation coefficients, r, and probabilities, P, from simple linear regression analyses of all measured ecosystem C pools vs. climate variables.

	Air temperature		Soil temperature		Growing-degree days		Soil moisture		Snowmelt date		Winter length	
Carbon pool	r	P	r	P	r	P	r	P	r	P	r	P
Aboveground biomass	−0.31	0.35	−0.31	0.36	−0.37	0.26	0.21	0.53	0.21	0.54	0.22	0.53
Understory biomass†	−0.25	0.49	−0.49	0.15	−0.21	0.56	0.76	0.01	0.43	0.22	0.36	0.31
Coarse roots‡	−0.75	0.02	**−0.84**	**0.004**	−0.72	0.03	***0.98***	***0.0000***	0.77	0.02	0.74	0.02
Fine roots	−0.29	0.39	−0.45	0.17	−0.26	0.44	0.43	0.19	0.48	0.13	0.37	0.26
Fine woody debris	0.11	0.76	−0.13	0.70	0.12	0.71	0.15	0.67	−0.06	0.85	0.09	0.80
Coarse woody debris and snags§	**−0.93**	**0.002**	−0.77	0.04	**−0.92**	**0.004**	0.82	0.02	0.88	0.01	0.85	0.02
Forest floor	−0.15	0.66	−0.48	0.13	−0.12	0.73	0.38	0.24	0.33	0.33	0.44	0.18
Mineral soil (0–60 cm)¶	***−0.90***	***0.0004***	−0.50	0.16	***−0.91***	***0.0003***			0.66	0.03	0.58	0.06
Subsoil (30–60 cm)	**−0.77**	**0.004**	**−0.76**	**0.007**	**−0.75**	**0.008**	0.74	0.009	**0.82**	**0.002**	**0.80**	**0.003**
Total soil	−0.64	0.03	−0.62	0.04	−0.62	0.04			0.69	0.02	0.67	0.02
Ecosystem total	−0.71	0.01	−0.73	0.01	−0.73	0.01			0.67	0.02	0.68	0.02

Notes: Boldface type indicates significance at $P < 0.05$ and italics at $P < 0.01$, after a Bonferroni correction for multiple comparisons (P/6). Number of plots (n) = 11 in every case except those noted.

† Number of plots (n) = 10 (plot P1 excluded) for all climate variables.

‡ Number of plots (n) = 9 (plots E1 and E4 excluded) for all climate variables.

§ Number of plots (n) = 7 (plots E1, E2, E4, E5 excluded) for all climate variables (Kueppers et al. 2004).

¶ Number of plots (n) = 10 (plot E1 excluded) for air temperature and growing-degree days.

et al. 2004) (Table 3). Fine woody debris biomass was low and unrelated to climate indices along the gradient. Forest floor, or organic horizon, C was an important fraction of total ecosystem C, but on its own, was not significantly related to climate. Mineral soil C to 60 cm depth accounted for 16–31% of ecosystem C, decreased strongly with increasing air temperature and growing-degree days along the gradient (Table 3), and increased as a saturating function of soil moisture (r^2 = 0.58, root mean square error [RMSE] = 7.2 Mg C/ha, n = 11). The subsoil (30–60 cm) contained 14–38% of the total mineral soil C and was strongly related to most measured indices of climate, increasing with winter length and date of snowmelt and decreasing with air and soil temperature and growing degree days (Table 3). Mineral soil plus organic horizon C, or total soil C, increased nonlinearly with soil moisture (Fig. 3).

Total ecosystem C (the sum of the above C pools) showed linear trends with all measured climate indices (Table 3), but was best described by a nonlinear saturating function of soil moisture (Fig. 3). Allocation of C among ecosystem pools ranged from 28% to 64% in tree AGB, from 25% to 45% in organic and mineral soil C, and from 2% to 18% in dead wood (Appendix A). The highest elevation plot (S3) had the lowest fraction of ecosystem C in tree AGB and the highest fractions in soil and dead wood, reflecting the relatively hostile environmental conditions for tree growth and microbial decay near the elevational range limit of subalpine forest.

Due to the tight relationship between soil moisture and tree species composition in the ecotone, we were unable to use these plots to distinguish climate from species composition effects on individual C pools or on total ecosystem C. Residual analysis showed no pattern between the fraction of pine biomass and the

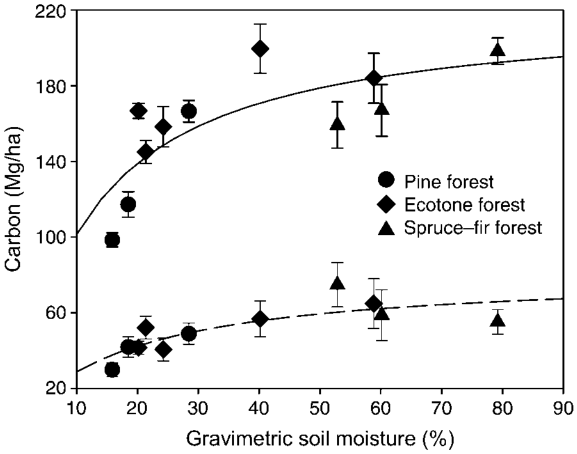

FIG. 3. The relationships between growing-season soil moisture and total organic and mineral soil (dashed line) and total ecosystem C (solid line) along the gradient. The regression equations are total soil C = 81(soil moisture)/(18 + soil moisture) (means-corrected r^2 = 0.68, root mean square error [RMSE] = 7.6 Mg/ha) and total ecosystem C = 221(soil moisture)/(11.8 + soil moisture) (means-corrected r^2 = 0.61, RMSE = 20.3 Mg/ha).

TABLE 4. Correlation coefficients, r, and probabilities, P, from simple linear regression analyses of select ecosystem C fluxes vs. climate variables.

	Air temperature		Soil temperature		Growing degree days		Soil moisture		Snowmelt date		Winter length	
Carbon flux	r	P	r	P	r	P	r	P	r	P	r	P
Relative AGBI†	***0.87***	***0.001***	0.66	0.04	***0.87***	***0.001***	−0.66	0.04	**−0.80**	**0.005**	−0.74	0.02
Total litterfall†	−0.59	0.07	−0.61	0.06	−0.60	0.07			0.59	0.08	0.62	0.06
Relative ANPP†	***0.87***	***0.001***	0.56	0.09	***0.89***	***0.0005***	−0.52	0.12	−0.69	0.03	−0.63	0.05
Pine relative ANPP‡	**0.88**	**0.004**	0.77	0.03	**0.87**	**0.005**	−0.75	0.03§	**−0.90**	**0.002**	−0.82	0.012
Pine relative AGBI‡	0.78	0.02	0.68	0.06	0.76	0.03	−0.57	0.14	**−0.87**	**0.005**	−0.79	0.02
Spruce needle decay	**−0.75**	**0.008**	−0.51	0.11	**−0.79**	**0.004**	0.24	0.48	0.55	0.08	0.53	0.09
Fir needle decay			−0.42	0.20			0.22	0.51	0.54	0.09	0.49	0.12
Soil CO_2 flux	0.50	0.12	0.58	0.06	0.47	0.14	−0.23	0.49	−0.59	0.06	−0.67	0.02

Notes: Boldface type indicates significance at $P < 0.05$ and italics at $P < 0.01$, after a Bonferroni correction for multiple comparisons ($P/6$). Number of plots (n) = 11 in every case except those noted. Abbreviations: AGBI, aboveground biomass increment; ANNP, aboveground net primary productivity.

† Number of plots (n) = 10 (plot S3 excluded) for all climate variables.

‡ Number of plots (n) = 8 (plots with no pine biomass, S1, S2, S3, excluded) for all climate variables.

§ Relationship not apparent when plot E5 is excluded (it has a large leverage on relationship).

residual variation in C stocks that was not explained by the strongest climate variable.

Ecosystem carbon flux relationships with climate, species composition

Aboveground production and mortality.—Total aboveground net primary productivity (ANPP) was highest in the lowest elevation pine forest plot (P1) and lowest in the highest elevation spruce–fir forest plot (S3) (see Appendix B for all C flux values). Relative to the amount of tree biomass in each plot, ANPP ranged from 0.87%/yr to 1.82%/yr, with the maximum relative rate occurring in the highest elevation spruce–fir forest plot (S3). Aside from this high-elevation site, relative ANPP increased strongly with increasing temperature and summer warmth (Table 4). Within the ecotone forest, where species composition varied greatly while climate variation was somewhat less, overall relative ANPP increased with the fraction of total biomass that was lodgepole pine ($r^2 = 0.89$, $P = 0.02$, $n = 5$).

Tree biomass accumulation, or aboveground biomass increment (AGBI), accounted for 0–58% of ANPP. The highest elevation spruce–fir forest plot, S3, had the highest fractional biomass increase (1.06%/yr), while in all other plots relative AGBI increased strongly with temperature and growing-degree days and decreased with date of snowmelt along the gradient (Table 4). Litterfall, the other component of ANPP, did not differ significantly between years but differed among plots. We measured the greatest litterfall in the relatively wet ecotone forest plot where AGBI was lowest (E4) and the least in the highest elevation spruce–fir forest plot (S3). Total litterfall was only slightly related to climate, increasing as a saturating function of soil moisture ($r^2 = 0.50$, RMSE = 146 kg $C\cdot ha^{-1}\cdot yr^{-1}$, $n = 10$). Relative litterfall (mean litterfall mass per AGB) was not at all related to climate variables.

The plot-level patterns in ANPP were determined in part by distinct species responses to variation in climate. Pine ANPP as a fraction of pine AGB increased with growing-degree days and annual air temperature and decreased with later snowmelt along the gradient (Table 4), while spruce relative ANPP was not predicted well by climate variables, only trending greater in plots with longer winters ($r^2 = 0.30$, $P = 0.13$, $n = 9$). Pine relative AGBI decreased with later snowmelt date (Table 4), while spruce AGBI was insensitive to climate. The negative spruce increments in three plots reflected errors in measurement where trees gained biomass so slowly as to be undetectable and/or potential decreases in Engelmann spruce girth between our two measurement periods. Within the ecotone, mean pine AGBI (232 ± 55 kg $C\cdot ha^{-1}\cdot yr^{-1}$) was greater than mean spruce (−36 ± 73 kg $C\cdot ha^{-1}\cdot yr^{-1}$) and fir (15 ± 3 kg $C\cdot ha^{-1}\cdot yr^{-1}$) AGBI ($F_{3,12} = 7.328$, $P = 0.008$), suggesting that adult lodgepole pine was more successful than spruce or fir during the years of our measurements.

Finally, the fraction of C allocated to litterfall vs. additional biomass varied along the gradient, primarily tracking shifts in species composition. Allocation of ANPP to litterfall averaged 71 ± 6% across all plots, but ranged from 42% to 101% (greater than 100% indicates that AGBI was negative due to no or low growth and measurement error). While the overall litterfall fraction of ANPP decreased with increasing growing degree days ($r^2 = 0.63$, $P = 0.006$) and air temperatures ($r^2 = 0.65$, $P = 0.005$) and increased with snowmelt date ($r^2 = 0.54$, $P = 0.02$), winter length ($r^2 = 0.44$, $P = 0.04$), and as a saturating function of soil moisture ($r^2 = 0.54$, RMSE = 0.13, $n = 10$ in all cases), species-specific allocation fractions did not vary with climate. Spruce-dominated forest tended to allocate more ANPP to litterfall and pine-dominated forest allocated more to biomass increment. In the ecotone forest, where both

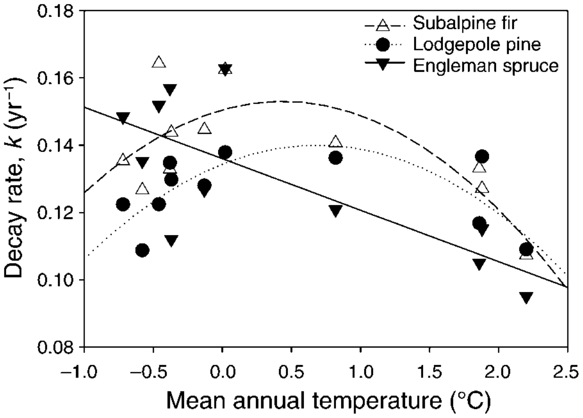

FIG. 4. The relationship between litter decay rate (*k*) and mean annual temperature for pine, spruce, and fir needles. Values are calculated from individual exponential decay models, each with 30 data points. The solid line shows least-squares linear regression through spruce data points (r^2 = 0.56, P = 0.008), the dotted line shows nonlinear regression through pine data (r^2 = 0.52, RMSE = 0.008 yr^{-1}), and the dashed line shows nonlinear regression through fir data (r^2 = 0.58, RMSE = 0.012 yr^{-1}).

species co-occur, spruce trees produced 66% more needle and cone litterfall per unit spruce biomass than did pine trees per unit pine biomass (0.78 ± 0.06%/yr vs. 0.47 ± 0.06%/yr). In addition, the litterfall fraction of ANPP showed a nonsignificant decreasing trend as the fraction of aboveground biomass that was lodgepole pine increased. Along the full gradient, the fraction of pine ANPP allocated to litterfall averaged 54 ± 3% (n = 8), while the median spruce allocation to litterfall was 89% (n = 9). This suggests that relationships between ecosystem-level litterfall allocation and climate variables are due not to the direct effects of climate, but to the shift in species composition along the climate gradient.

Tree mortality was not included in measures of ANPP. We recorded tree death in 7 of 11 plots, with 1–4 trees dying per plot between 1999 and 2002. The C flux associated with mortality was highly variable, totaling 14–2341 kg $\text{C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ where it occurred (Appendix B). The plot with the greatest mortality, S1, lost spruce and fir trees to what appeared to be beetle infestation. Other apparent causes of mortality in the plots were wind, lightning strikes, and dieback of trees that were shaded in the understory. In most plots, AGBI was greater than mortality, but in three plots where spruce growth was slow (E1, E4, S1) there was a net loss of standing biomass over the three years of the study.

Decomposition rates.—Needle litter mass loss was extremely slow in these sites, with decay rate constants (k) ranging from 0.095 ± 0.009 to 0.164 ± 0.012 yr^{-1}. These k values correspond to turnover times of approximately 6–11 yr. There were no differences in the mean k's among the three species, but the species differed in their sensitivity to climate. Rates of spruce needle decay decreased linearly with increasing annual temperature, while pine and fir needle decay had hump-shaped responses (Fig. 4). All three species showed responses to growing-degree days that were similar to their temperature responses (r^2 = 0.46, RMSE = 0.009 yr^{-1} for pine; r^2 = 0.57, RMSE = 0.012 yr^{-1} for fir), but, for the most part, did not have significant relationships with other climate variables (Table 4). Decomposition of pine litter had a fairly strong hump-shaped response to soil moisture (r^2 = 0.51, RMSE = 0.008 yr^{-1}, n = 11 in all cases). Across all sites, absolute mass loss per month did not differ between summer (June–October 2000–2001) and winter (October–June 2000–2002) for pine litter, but spruce and fir litter both lost mass more quickly over winter ($F_{2,126}$ = 4.047, P = 0.02; Fig. 5).

We measured dead wood decay only in a subset of plots (in and near P2, E2, and S2) and found no statistically significant differences in decay rate constants among the plots or between species (Kueppers et al. 2004). Dead wood turnover time ranged from 340 to 800 yr, with the fastest turnover time occurring in a pine forest plot (P2), where the climate was warmer and drier than in the other two plots sampled.

Soil CO_2 *flux*.—Neither mean growing-season respiration rates (n = 10–13 measurements over time) nor winter daily respiration rate (n = 1 measurement over time) differed significantly from plot to plot, although daily mean growing-season rates were always higher than daily mean winter rates (paired $t_{10} = -12.713$, $P < 0.0001$). Mean daily winter soil CO_2 flux rates ranged from 0.63 ± 0.02 to 1.01 ± 0.04 g $\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ among plots, while growing season rates ranged from 0.84 ± 0.06 to 5.3 ± 3.7 g $\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ among plots and measurement dates. Growing-season CO_2 flux increased with soil temperature ($P < 0.001$) and soil moisture (P = 0.02) at the time of measurement, but was unrelated to plot variation in total soil C (full-model $F_{3,109}$ =

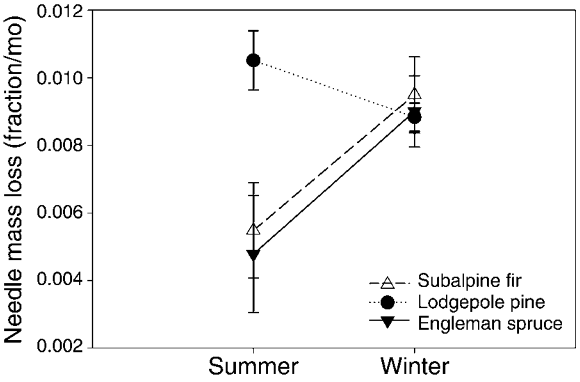

FIG. 5. Needle litter mass loss by species and season. Two-sample t tests between summer and winter mass loss rates found differences for subalpine fir (P = 0.03) and Engelmann spruce (P = 0.04), but not lodgepole pine (P = 0.09).

44.120, $P < 0.001$, $n = 113$, $r^2_{\mathrm{adj}} = 0.54$; dates having ''off meter'' moisture readings were excluded from analysis). Over the course of the growing season and within individual plots, soil moisture was not a significant factor, but soil temperature accounted for 16–90% of the variation in soil CO_2 flux in multiple regressions.

Total annual soil CO_2 flux ranged from 3.63 ± 0.11 to 6.00 ± 0.85 Mg C/ha in these forests. Annual soil respiration did not vary significantly with climate variables, although it tended to decrease with increasing winter length (Table 4). Winter length is also a strong predictor of both total growing season soil CO_2 flux and total winter flux, with the growing season total decreasing ($r^2 = 0.79$, $P < 0.001$, $n = 11$) and the winter total increasing ($r^2 = 0.57$, $P = 0.007$, $n = 11$) with longer winters. This results in the fraction of the total annual flux that occurs during winter increasing from 21% to 49% with longer winters ($r^2 = 0.91$, $P < 0.001$, $n = 11$).

Discussion

Our results suggest that most, though not all, Rocky Mountain subalpine forest stocks and fluxes of C are sensitive to climate within a range similar to projections for regional climate change within the next century. While ecosystem C stocks and forest species composition are each strongly related to climate, we found no evidence suggesting an independent effect of species on C stocks. In most cases, variations in C fluxes were related to climate variables, with the climate sensitivity of aboveground productivity and litter decay differing among species.

Ecosystem C stocks depend on climate

Along the Fossil Ridge gradient, plots with relatively warmer mean annual temperature and drier soil during the growing season stored less total ecosystem C, with an increase from −0.6° to 2.2°C mean annual temperature and a decrease from 79% to 16% median soil moisture resulting in an approximately 50% lower C content. Warmer plots had less mineral soil C, particularly in deeper soil layers, and less dead wood. Plots with relatively drier soils during the growing season had less coarse root C and a nonsignificant trend toward less understory C. The lack of trend in aboveground biomass could have been because we selected plots with similar stand densities and tree sizes. However, we did observe that the two warmest, driest plots had substantially less tree biomass than most other plots. While predictions for changes in regional precipitation and its timing remain largely uncertain, warmer temperatures will tend to advance snowmelt and increase evaporative demand during the growing season, both of which reduce growing season soil moisture. Therefore, we consider warmer, drier growing seasons an important potential outcome for long-term climate change in this region. If large decreases in C are observed with warming and drying, subalpine forests could become a substantial long-term source of C to the atmosphere.

We found no evidence for independent effects of species composition on individual or cumulative carbon stocks in these forest types. Spatial variation in tree species composition, both at a relatively local spatial scale within the ecotone and along the whole gradient, was strongly related to growing season water availability, with drier locations occupied by lodgepole pine and wetter locations occupied by Engelmann spruce and subalpine fir. As a result, residual analysis of carbon–climate regressions yielded no significant effects of species composition. We conclude that both species composition and C stocks are strongly and primarily influenced by climate. Over the long term, if species' distributions change to accommodate changes in local and regional climate, our measurements suggest that carbon stocks will reflect the dominant climate.

Ecosystem C flows depend on climate and species

All of the major ecosystem C flows we measured were sensitive to spatial and/or temporal variation in climate. In the case of aboveground productivity and needle decomposition, we found that tree species affect the flux sensitivity to climate, suggesting that forests dominated by different species may respond differently to short-term climate changes.

Productivity.—Relative AGBI and relative ANPP increased with warmer temperatures along the full elevation gradient. Because stand age decreased with increasing temperature, we cannot completely rule out its effect on rates of productivity. However, lodgepole pine tends to reach maturity at a younger age than spruce and fir, with reproduction occurring in as little as 10–20 yr for pine but 40+ yr for spruce and fir (Kimmins 1997). The overall trend between plot-level ANPP and temperature is probably due to two factors: (1) the shift in species composition from spruce–fir- to pine-dominated forest with warmer temperatures and (2) the increase in pine productivity with increasing temperatures. Evidence for (1) comes from the ecotone forest where plot productivity increased with increasing pine fraction. Since pine fraction increased with decreasing soil moisture within the ecotone and in these well-drained, seasonally dry, high elevation forests, we would not expect higher growing season moisture availability to depress growth rates, this pine-dependent increase in productivity is likely a true species effect. Regarding (2), along the full gradient, pine relative ANPP increased with temperature just as strongly as did total relative ANPP, indicating that pine growth is itself influenced by climate. Conversely, Engelmann spruce relative ANPP showed no response to temperature. The studied range in annual air temperature was more limited for spruce (1.54°C) than for pine (2.92°C), but even where the two species overlap in the ecotone, pine growth showed a trend with temperature while spruce did not.

Species differences in adaptation to seasonal climate variation could contribute to the observed differences in the growth rate response along the gradient. In these forests, initiation of photosynthesis and carbon uptake in spring is known to be affected by date of snowmelt and air temperature (Monson et al. 2002). Therefore, variation in the ability of species to take advantage of earlier than normal spring conditions could have repercussions for C gain. Similarly, observed species differences in the sensitivity to soil moisture of photosynthesis, sap flux, and conductance, particularly late in the growing season, can also affect C gain (Smith et al. 1984, Pataki et al. 2000, Monson et al. 2002). Such adaptations may explain the species-specific responses to interannual climate variability observed in tree rings (Villalba et al. 1994). The current physiological and tree ring evidence is consistent with our ecosystem-level results, suggesting that if climate change brings longer, warmer growing seasons to the region, lodgepole pine may benefit, while if the warming also results in drier growing seasons, Engelmann spruce and subalpine fir growth may not change or may decrease, particularly in moisture-limited sites. At the ecosystem scale, this implies that forests dominated by lodgepole pine may see increased growth, leading to a partial negative feedback to climate warming, while Engelmann spruce-dominated forests may not show a productivity response.

Needle decay.—The sensitivity of litter decay to changes in temperature and moisture was constrained by species composition, as has been seen for litter decomposition under climate warming manipulations (Taylor and Parkinson 1988, Hobbie 1996, McHale et al. 1998, Shaw and Harte 2001). Spruce litter decay decreased monotonically with increases in plot temperature, while pine and fir litter decay was fastest in sites with intermediate temperature. All three species had low decay rates in the warmest, driest plots suggesting that longer, warmer growing seasons may result in insufficient moisture in the surface litter layer during the growing season for microbial activity. Our measures of soil moisture were to 10 cm and thus probably underestimated the degree to which the litter layer dried in the summer months. As a result, annual air temperature and growing degree days yielded better (though inverse) indices of litter moisture status in summer. The hump-shaped responses of pine and fir indicate that they may be temperature limited under cold conditions and moisture limited, like spruce, under warmer conditions.

A substantial fraction of needle decay for all species occurred during winter under the snow, with spruce and fir litter actually losing more mass per month during the winter than during the summer. The importance of winter decay has been observed in other high-elevation and high-latitude ecosystems (Hobbie and Chapin 1996) and suggests that microbial communities in alpine environments may be better adapted to cold, wet conditions under snow than to warm, dry ones (Schadt et al. 2003). At Fossil Ridge, the cold, wet conditions under the snow appeared to favor formation of extensive networks of fungal mycelia on the litter surface that shrink away within days following snowmelt. Shorter winters in warmer plots may have reduced the length of time with conditions favorable to fungal-mediated decay. Greater mass loss rates in winter and slower overall rates of decay in plots with longer, warmer summers suggest that spruce and fir litter decayed readily under the snow, but was inhibited by warm, dry conditions during the summer. Pine litter may not have been as sensitive to seasonal variation in climate if other factors such as litter quality or physical properties limited decay. Pine had significantly higher initial C:N and lignin:N ratios than spruce and fir, but the species did not differ consistently in carbon fractions (Appendix C). The species-specific sensitivity of decay rates to climate suggests that if future climate change results in increased temperature or decreased winter length, both of which are projected for this region, all three species' litter may decay more slowly, except perhaps for fir or pine litter occurring in the coldest of sites.

Soil respiration.—Total annual soil respiration was not sensitive to climate variables, although numerous laboratory experiments and reviews of field data suggest that heterotrophic or total soil respiration should have varied with climate (e.g., Raich and Schlesinger 1992, Kirschbaum 1995, Zak et al. 1999, Kane et al. 2003). There are two possible explanations for the lack of a trend with climate. First, total and live fine-root biomass did not vary significantly with climate variables along the gradient. If, to first approximation, autotrophic (root) respiration is directly related to live fine-root biomass and therefore remained constant along the gradient, then an increase in heterotrophic respiration rate with temperature could have been canceled by a decrease in soil C (which was observed to decrease with temperature). Alternately, since soil respiration is affected by both temperature and moisture and these two variables were inversely correlated along the gradient, they could have had counteracting effects on respiration rates. Certainly a combination of these mechanisms is most likely, emphasizing the importance of controlled experiments and/or advanced techniques to partition soil CO_2 flux into heterotrophic and autotrophic sources (Hanson et al. 2000).

Winter respiration rates are difficult to measure accurately. Our mean estimate of 0.81 ± 0.03 g CO_2-$C \cdot m^{-2} \cdot d^{-1}$ was ~20–40% less than the rate of daily net ecosystem exchange (NEE; to the atmosphere) measured in a Colorado ecotone forest in early April 1999 and 2000, when a substantial fraction of the NEE (before snowmelt and detectable photosynthetic activity) was likely due to soil respiration (Huxman et al. 2003).

At Fossil Ridge, winter respiration (111–219 g $C \cdot m^{-2} \cdot yr^{-1}$) accounted for 21–49% of total annual soil respiration, increasing in proportion in sites where winters were longer. Although the soda lime method we used probably overestimated winter fluxes (Grogan and Chapin 1999), where winters are long and soils are sufficiently insulated against cold air temperatures, winter respiration can account for a substantial fraction of annual respiration (Sommerfeld et al. 1993, Fahnestock et al. 1999). Shorter winters and/or changes in the depth of snowpack and winter temperatures with climate change are all likely to alter the balance between winter and growing season soil respiration.

Conclusions

We found evidence that subalpine forest carbon cycling is strongly controlled by climate variables, with the sensitivity of several fluxes contingent on forest species composition. We also found that forest species composition and total ecosystem carbon are both related to growing-season soil moisture, with Engelmann spruce–subalpine fir forests and greater carbon stocks occurring under relatively moist conditions and lodgepole pine forests and substantially smaller carbon stocks occurring under relatively dry conditions. If the sensitivity of individual fluxes can be used to infer potential short-term responses to regional climate changes, absent shifts in species composition, our results suggest that warmer, drier conditions are likely to lead to increases in lodgepole pine productivity, decreases in needle decay rates, and increases in dead wood decay. Engelmann spruce productivity is not likely to respond to warming. The net effect of changes in flux rates will depend on particular scenarios for seasonal changes in moisture availability, spatial variation in subalpine forest species composition, and the sign and size of any change in soil respiration relative to an increase in productivity. It is plausible that warming could lead to short-term increases in ecosystem C storage in these systems. To more fully understand transient changes in regional net C balance with scenarios for climate change will require a model that can integrate both climate and species effects on the C fluxes within these forests.

While the climate sensitivity of C fluxes should be more closely related to short-term (years to decades) changes in climate, the climate sensitivity of C stocks should reflect long-term (centuries to millennia) adjustment of ecosystem C balance to equilibrium climate. As tree species composition and carbon cycling both adjust to warmer, drier conditions, our results suggest that subalpine forests may lose up to one-half their current carbon, primarily because of loss of slowly cycling mineral soil and dead wood C. Unfortunately, verifying the assumption of such a ‘‘space-for-time’’ substitution with paleoecological data is difficult, given the dynamic nature of ecosystem C cycling. Comparing the observed spatial patterns with predictions from a mechanistic and empirically based carbon cycle model would provide an alternative assessment.

Finally, our study design does not explicitly account for two processes critical to understanding long- and short-term C cycling in subalpine forests: fire and insect damage. Fire is known to structure forest ecosystems in the Rocky Mountains and is thought to be highly dependent on climate variability in subalpine forests (Romme and Knight 1981, Johnson and Larsen 1991, Schoennagel et al. 2004). Differences in the frequency of fire with climate along the gradient and/or with shifts in species composition could have contributed to the patterns we observed. More importantly, changes in fire frequency with climate change could have large effects on the time course of change in forest C balance. In boreal forests, fire released an equivalent of 10–30% of annual NPP to the atmosphere over the last 6500 years (Harden et al. 2000), and long-term differences in fire frequency are known to affect forest C balance (Wardle et al. 2003). Damage to trees by endemic spruce and mountain pine beetles can also profoundly influence forest structure (Romme et al. 1986, Veblen et al. 1991) and likely interacts with fire on the landscape (Veblen et al. 1994, Bebi et al. 2003). Recent work in Alaska, USA, and elsewhere suggests that insect damage may be constrained by climatic factors, raising the possibility that climate change may increase the area of influence of these biotic disturbance agents (Malmstrom and Raffa 2000).

Terrestrial carbon feedbacks to the climate system remain one of the largest sources of uncertainty in projections of future climate change (Cox et al. 2000, Dufresne et al. 2002). Current vegetation models used to estimate ecosystem responses to climate assume constant sensitivity to changes in temperature and moisture across vegetation types for some fluxes (e.g., a single Q10 for soil respiration) (Cramer et al. 2001). Although plant functional types are modeled as having different climate tolerances in terms of their geographic range, differences among types in the climate sensitivity of productivity, litter decay, and carbon allocation within the ecosystem are still poorly constrained. Further, we have found evidence that even within a single plant functional type (needle leaf evergreen temperate tree), species can differ in their sensitivity to climate along a spatial gradient. If the sensitivity of carbon cycling to climate change depends on characteristics other than those currently used to define plant functional types, vegetation models used to predict future climate change will need to be modified accordingly. For example, including a functional axis that distinguishes conservative from opportunistic life history strategies may improve our ability to predict changes in terrestrial carbon cycling. Finally, further work is needed to determine how to best use spatial gradients and other observational approaches to gain insight into the manner in which ecosystems will change over time with climate change.

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APPENDIX A

A table listing plot-level values of individual carbon stocks is available in ESA's Electronic Data Archive: *Ecological Archives* A015-060-A1.

APPENDIX B

A table listing plot-level values of individual carbon fluxes is available in ESA's Electronic Data Archive: *Ecological Archives* A015-060-A2.

APPENDIX C

A table listing the initial chemical characteristics of needle litter used in the decomposition experiment is available in ESA's Electronic Data Archive: *Ecological Archives* A015-060-A3.