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EFFECTS OF INTERANNUAL CLIMATE VARIATION ON ABOVEGROUND PHYTOMASS IN ALPINE VEGETATION¹

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Abstract. Relationships between peak annual vascular aboveground phytomass and annual climate variation in alpine plant communities located on Niwot Ridge, Colorado, were analyzed using path analysis. The five community types, fellfield, dry meadow, moist meadow, wet meadow, and snowbed, represent a snow depth–soil moisture gradient and broadly represent the most common vegetation types on east-facing slopes of the Front Range alpine zone. Using nine successive years of data, this is the first longer term analysis of alpine phytomass and climate and one of the longest nonagricultural production records available. Live phytomass ranged from 97 g/m² (snowbed) to 237 g/m² (fellfield). Among-community differences in phytomass were greater than differences among years, but there was also significant phytomass variation among years. Path analysis indicated that climate accounted for 15–40% of the variation in phytomass. The dry communities, fellfield (exposed rocky summit areas dominated by cushion and mat plants) and dry meadow, were most sensitive to previous year precipitation, the moist and wet meadow communities were most sensitive to current growing season soil moisture, and the snowbed community was most sensitive to date of snow release. Because of the relatively high amount of variation attributable to variables related to precipitation, changes in precipitation regimes that may occur in alpine ecosystems will likely result in changes in phytomass that are detectable with clip-harvest methods.

Key words: *alpine tundra; climate change; Colorado; ecosystems; path analysis; phytomass; plant community; soil moisture.*

INTRODUCTION

Multiple stresses, including low temperatures, high winds, short growing seasons, low nutrient availability, and soil moisture, may all limit plant growth and primary production in alpine and arctic environments (Billings and Bliss 1959, Savile 1972, Rehder 1976a, b, Rehder and Schäfer 1978, Webber 1978, Bliss 1985, Chapin and Shaver 1985, Sundriyal 1992). These many limiting factors result in low levels of primary productivity and phytomass compared to other ecosystems. Data from the International Biological Program

(IBP) Tundra Biome sites indicate live, aboveground, vascular phytomass in forb- and graminoid-dominated tundra communities ranges from 18 to 505 g/m²; net annual aboveground production ranges from 16 to 356 g/m² (Wielgolaski et al. 1981).

Laboratory and experimental field studies have demonstrated that temperature, moisture, and nutrients limit growth of tundra species (Bliss 1985, Chapin and Shaver 1985), but there is little quantitative information available on how tundra phytomass varies as a function of climate and site variables. The availability of ultimate controlling resources under actual field conditions is dependent upon climate and site conditions that are highly variable in both time and space. Phytomass incorporates physiologic controls over growth as well as evolutionary responses to field conditions, making it difficult to sort out proximal and ultimate

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controls. For example, growth of arctic and alpine plants may halt while there are still resources available (Sorenson 1941, Svoboda 1977), which is presumably an adaptation to unpredictable growing season length.

We used a 9-yr record of phytomass, climate, and soil moisture to determine (1) the response of aboveground vascular phytomass to interannual variation in climate, and (2) how five plant communities differ from one another in the response of their phytomass to climate variation. Our study area was in the alpine zone of the Front Range in Colorado. This is the longest continual record of annual phytomass variation in alpine tundra, and it allows an analysis of the relationship of phytomass and climate that would not be possible with data collected over only 1–3 yr (for example, Scott and Billings 1964, Webber and May 1977, May and Webber 1982).

The IBP Tundra Biome data (Wielgolaski et al. 1981) indicate that phytomass and net annual aboveground primary production (NAPP) of forb- and graminoid-dominated communities are highly correlated ($r = 0.968$; Wielgolaski et al. 1981: Table 6.5) in arctic and alpine tundra. We did not assume, however, that phytomass necessarily equaled NAPP. The aboveground portions of most erect alpine forbs and graminoids die back completely during the winter, so that peak aboveground phytomass approximates NAPP for most species, but there are exceptions. Cushion plants maintain live aboveground tissue over winter, and it is difficult to accurately sort current and previous year growth for these species. *Kobresia myosuroides*, a sedge that dominates large areas in the Colorado Front Range alpine zone, has a complex phenology that complicates determination of NAPP using simple clip-harvest methods. Leaves of this species are produced in spring and fall. Fall leaves are dormant over winter and elongate the following spring (Bell and Bliss 1979). Because similar mechanisms may exist in other alpine species, we consider only live aboveground phytomass here, but we use both the current and previous year climate data in our analysis.

We used path analysis (Wright 1934, Li 1975) to examine phytomass–climate relationships. A path diagram (Fig. 1) represents both an a priori analytical model and a hypothesis of relationships. Using path analysis conventions, straight lines with single arrows represent possible causal relationships, and arcs represent unanalyzed correlations. Our model proposes that nine measured variables may affect phytomass directly or indirectly: (1) precipitation during the previous year growing season, (2) precipitation during the previous winter, (3) precipitation from beginning of thaw season to snow melt, (4) precipitation after snow melt, (5) thawing-degree days (thawing-degree days are the sum of mean daily temperatures for all days when the mean temperature is above 0°C) during the previous year growing season, (6) thawing-degree days from beginning of thaw season to snow melt, (7) thawing-degree days after the current year snow melt, (8) soil

moisture, and (9) snow-free date. Precipitation prior to snow melt, including both winter and summer components, and thawing-degree days prior to snow melt may act indirectly through their effects on soil moisture and date of snow-cover loss (snow-free date). Previous year data were included because there are at least three ways that the previous year's climate or soil moisture could affect the current year's growth: (1) by directly affecting this year's production, (2) by directly affecting last year's production, and (3) by affecting the survival of last year's production into the current year.

STUDY AREA

Data were collected from a saddle ("the Saddle") on Niwot Ridge, a tundra upland ≈ 60 km west of Boulder, Colorado, at 40°03' N, 105°36' W. The ridge begins on the Continental Divide at 4085 m above sea level, extends eastward as a narrow, sparsely vegetated arête for ≈ 2 km, and then widens into continuously vegetated knolls and shallow saddles that stretch another 7 km to the east. The Saddle is at 3650 m elevation and is ≈ 25 ha in size, with rising slopes to the east and west and falling slopes to the north and south. Slopes range from 0 to 25% but are mostly $< 10\%$.

The Niwot Ridge climate has been monitored at station "D-1" (Marr 1961), ≈ 1.5 km west of the Saddle, since 1951 and on the Saddle since 1981 (Losleben 1983–1990, Greenland 1989). The climate is characterized by (1) a short growing season, having only 4 mo (May through August) when mean monthly temperatures are above 0°C, (2) high among-year variability in monthly mean temperatures, and (3) high seasonal variability in precipitation, with maxima in the winter and spring and a minimum in the fall (Greenland 1989). Mean annual temperature is -3.7°C . The warmest months are June, July, and August, with means of 4.6°, 8.2°, and 7.1°C, respectively. By September the mean minimum temperature is below 0°C (-0.57°C). Mean annual precipitation is 930 mm, and average precipitation during the three warm months is relatively low, 60, 50, and 62 mm, respectively. The major precipitation months are January and March, with mean amounts of 102 and 128 mm, respectively. Total annual precipitation amounts are highly variable, with a nearly threefold difference (541–1427 mm) between the driest and wettest years recorded. The Niwot Ridge summer precipitation regime is intermediate in comparison to other North American alpine sites that have reasonably long records. The Sierra Nevada to the west has extreme summer drought, and the Mt. Washington area in the northern Appalachians has high summer precipitation (Billings 1988). Although there is no apparent summer moisture deficit, water budget analyses indicate a potential for a July–September deficit, because the different field capacities and radiation budgets on different slope angles and aspects create a spatial mosaic of water availability that is strongly controlled by topography and substrate (Greenland 1989).

Snow depth on the Saddle is spatially variable, rang-

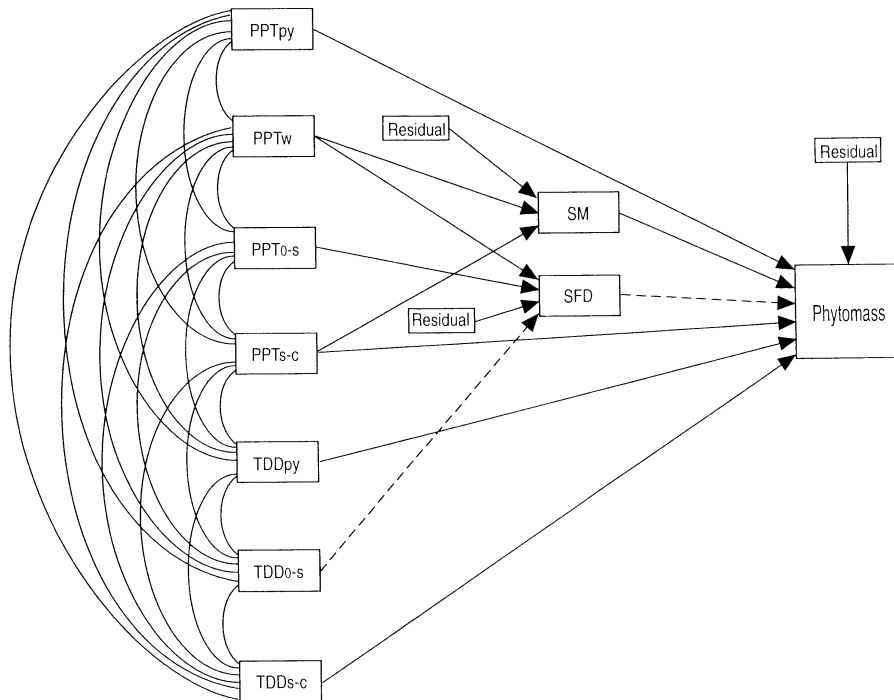


FIG. 1. Hypothesized relationships among climate variables and vascular phytomass on Niwot Ridge, Colorado. — possible causal pathways; --- a predicted negative relationship. Abbreviations are: PPTpy, precipitation in the previous year growing season; PPTw, winter precipitation; PPT0-s, precipitation from beginning of thaw season to snow melt; PPTs-c, precipitation from snow melt to date of harvest; TDDpy, thawing-degree days in the previous year growing season; TDD0-s, thawing-degree days from beginning of thaw season to snow melt; TDDs-c, thawing-degree days from snow melt to harvest; SM, soil moisture; SFD, snow-free date.

ing from 0 m on the knolls to >5 m at the northeast-facing base of the west knoll. Exposed sites are blown free of snow except during relatively calm spring storms when these sites can receive up to 1 m of snow. During 9 yr of measurement the average date for the entire Saddle to become snow-free was 18 August, and in 1984 some snow remained in the deepest snowbeds throughout the year (J. Halfpenny, *personal communication*).

METHODS
Phytomass

May (1973) defined six plant communities in the Saddle, five of which, fellfield (exposed rocky summit areas dominated by cushion and mat plants), dry meadow, moist meadow, wet meadow, and snowbed, are the basis of our long-term phytomass study (Table 1). These five communities broadly represent the most common vegetation types in the Front Range alpine zone, as well as the major soil patterns. Two 10-m transects in each community, each parallel to a permanent plot established by May (1973), were used for phytomass sampling. Five 20 × 50 cm quadrats, located at 2-m intervals along each transect (total of five samples per plot, 10 samples per plant community and year), were completely cleared of live and dead phytomass at peak season, which occurs during the 1st wk of August. Sampling was done in 1982 through 1990

inclusive; new transects parallel to and 1 m away from the old were established in 1987 in order to avoid resampling any ground over the course of the study.

Samples were returned to the laboratory, frozen, and sorted into the following fractions at a later date: graminoid, forb, vascular cryptogam (single species *Selaginella densa*), shrub (foliar), live woody, and dead, including both standing dead and litter. The most abundant graminoid, *Kobresia myosuroides*, and the most abundant forb, *Acomastylis rossii*, were sorted separately to indicate contributions of dominant species. Only green portions of *Kobresia myosuroides* were counted as live. After sorting, samples were dried at 60°C for 48 h or until dry, and weighed to the nearest 0.1 g.

Climate and soils

Daily climate summaries, including air temperature, radiation, humidity, and precipitation, have been maintained in the Saddle since 1981. Details of methods and instrumentation are in Losleben (1983–1990). Weekly gravimetric soil moisture estimates were made for each plot in 1983 through 1989. Two small soil cores, ≈1 cm in diameter and 5 cm long, were taken from the soil surface adjacent to each end of each permanent plot, weighed, dried for 24 h at 105°C, and reweighed to calculate mass loss as a percentage of dry mass.

TABLE 1. The six plant communities of the Niwot Ridge Saddle, as determined from polar ordination (May and Webber 1982). The fellfield, dry meadow, moist meadow, wet meadow, and snowbed communities comprise 97% of the vegetated area in the Saddle and were the focus of the phytomass studies.

Community	Dominant species	Snow-free days	Average date of release from snow
Fellfield	<i>Trifolium dasyphyllum</i> , <i>Silene acaulis</i> , <i>Paronychia pulvinata</i>	>200	<1 June
Dry meadow	<i>Kobresia myosuroides</i> , <i>Selaginella densa</i> , <i>Acomastylis rossii</i>	150–200	<1 June
Moist meadow	<i>Acomastylis rossii</i> , <i>Deschampsia caespitosa</i>	100–150	14 June
Shrub tundra	<i>Salix planifolia</i> , <i>S. glauca</i>	100–150	16 June
Wet meadow	<i>Caltha leptosepala</i> , <i>Carex scopulorum</i>	100	5 July
Snowbed	<i>Sibbaldia procumbens</i> , <i>Carex pyrenaica</i>	<75	20 July

Climate and soil moisture data were used to derive the nine variables that are hypothesized to have a direct or indirect relationship to vascular phytomass (Fig. 1). Precipitation was partitioned into three variables: (1) winter precipitation measured as depth of water equivalent, representing total precipitation from October of the previous year through May of the current year, and all presumed to fall as snow, (2) summer precipitation from 1 June to snow-free date (at a particular plot), (3) summer precipitation from snow-free date to harvest date. Winter precipitation data are from station D-1 due to a problem with the Saddle gauge during two winters. Snow-free date varies spatially, therefore the summer precipitation numbers were different for each plot. The assumption is that water that falls as rain while a plant is still covered by snow is unavailable to that plant for growth, but may affect date of snowmelt. Thawing-degree days (TDD) were calculated from daily temperature to represent a cumulative index of energy available for growing plants or melting snow. TDD were also partitioned into premelt season and postmelt season components. The day of the year on which a plot was free of snow is a measure of effective growing season length, since all clip harvests were made at the same time. Soil moisture data were collected weekly following snowmelt and were averaged over the growing season. The last two climate variables used in the analyses were previous year growing season precipitation and temperature. It was assumed that all precipitation that falls during the summer is depleted, and that there is no direct between-year effect on soil moisture.

Additional soils were collected from the top 10 cm in 30 plots as part of an earlier study in 1971 (May 1973). The following analyses were completed on these samples: organic matter percentage, water holding capacity, texture, pH, base saturation, cation exchange capacity, Ca^{+2} , Mg^{+2} , NO_3^- , NH_4^+ , PO_4^{-2} , Fe^{+1} , and Al^{+3} . Methods are described in May (1973).

Statistical methods

It is difficult to assess the influence of a single variable or even to adequately assess the combined variance of

a set of variables when there are complex interactions among variables during regression analysis (Draper and Smith 1981). Path analysis (Wright 1934, Li 1975) is an extension of multiple regression, but it allows for explicit analysis and display of correlations among the variables. Path analysis can test a particular hypothetical model of relationships or simply guide the interpretation of multiple regression. The method developed in the field of population genetics (Li 1975, Maddox and Antonovics 1983, Mitchell-Olds 1987, Crespi 1990); it has also proven useful in the analysis of vegetation–environment interactions, which are often complicated by intercorrelations among variables (Hermy 1987, Edwards and Armbruster 1989, Wesser and Armbruster 1991).

The data were subjected to path analysis as indicated in Fig. 1 and as described by Kerlinger and Pedhazur (1973) and Li (1975). Path coefficients are standardized multiple regression coefficients of the original variables. Path analysis of total live phytomass was done separately for each community and for the three individually sorted species in the communities where they were most abundant. Correlation coefficients, path coefficients, and other statistics were calculated using StatView 4.0 (Haycock et al. 1992) on a Macintosh IIx computer.

The statistical assumptions of path analysis are that the relationships among variables are linear, additive, and causal, and that the residuals are correlated neither amongst themselves nor with the variables. The assumptions of multiple regression, that the variables are normally distributed and independent, i.e., not collinear, also hold for path analysis (Kerlinger and Pedhazur 1973). Analysis of residuals indicated no evidence that the assumptions were not met. Serial autocorrelation analysis indicated no problems with independence of sampling among years.

Seven degrees of freedom were used to assess the statistical significance of the path coefficients. There were 9 yr of phytomass data but only 8 yr of soil moisture data. There were two plots per plant community, but some variables (winter precipitation and previous year data) were the same for all plots.

TABLE 2. Niwot Ridge climate, 1982–1990. Winter precipitation data are from the D-1 Station at the west end of the ridge; other data are from the Saddle. Note that winter precipitation data begin in October of the previous year. (Source: Niwot Ridge LTER climate database, Losleben 1983–1990.)

Year	Winter precipitation (October–May snow fall as water equivalent depth, mm)	Growing season precipitation (1 June to freezing date, mm)	Thawing-degree days (°C-days)
1982	822	266	688
1983	1118	260	780
1984	1120	461	793
1985	764	223	791
1986	998	249	737
1987	846	243	1090
1988	913	135	1057
1989	905	192	832
1990	847	396	1033

The goal of standard multiple regression is to maximize the explained variance in a variable based on a linear combination of independent variables. Path analysis, on the other hand, is based on an a priori model of relationships. This approach presumes some logical conception of how the variables are related. In the case of standard multiple regression, the signs of the coefficients are often ignored. In path analysis, however, a sign that is the reverse of that expected may indicate a problem with the model. For example, it is logical that increased precipitation should result in increased soil moisture, as predicted in our model. There is no logical way that adding water to soil could make it drier. It is possible, however, that there could be a negative correlation coefficient between these variables. There are three primary reasons why a path or

regression coefficient may have a sign opposite that which is expected logically: (1) the variables are correlated in the expected manner, but collinearity caused the sign to switch, (2) there is no actual relationship between the variables, and the correlation is spurious, or (3) there is no direct relationship between the variables, but they are correlated due to a third variable that was not included in the model (Kerlinger and Pedhazur 1973, Li 1975). The recommended action when a sign is not as expected logically is to reconsider the path model (Li 1975). We assumed that our basic model was correct as far as the signs of coefficients went, but we did not assume that any hypothesized causal pathway existed. Therefore path coefficients with the wrong sign, i.e., variables that should logically have a positive correlation but had a negative correlation, or vice versa, were presumed to have no causal relationship and were removed from the model. In no case could we detect that collinearity caused the wrong sign, and in all cases the removed variables were by themselves statistically insignificant. The possibility exists that in some cases our logic was incorrect, and we removed an important variable. The final models are simple, statistically conservative, and internally consistent, however, which was our goal. Deletion of variables always caused a decrease in the total variance explained by the model.

We used two-way analysis of variance (ANOVA) to test for significant differences in total live phytomass among communities and years and for a community-year interaction. We used one-way ANOVA to test if differences among years in phytomass components, e.g., total graminoid, total forb, total shrub, *Kobresia myosuroides*, *Acomastylis rossii*, and *Selaginella densa*, were statistically significant. ANOVAs of among-community differences have 4 df (five communities) in the numerator; those of among-year differences have 8 df

TABLE 3. Growing-season soil moisture percentages in the Niwot Ridge Saddle, 1982–1989. Values represent means ± 1 SE. The number of samples is in parentheses.

	Fellfield	Dry meadow	Moist meadow	Wet meadow	Snowbed
1982	34.4 ± 3.7 (28)	65.6 ± 4.0 (28)	93.8 ± 10.9 (26)	131.9 ± 12.2 (15)	68.9 ± 7.5 (12)
1983	45.6 ± 3.4 (28)	65.4 ± 2.9 (28)	90.4 ± 5.9 (28)	144.4 ± 7.3 (16)	34.3 ± 2.6 (8)
1984	39.3 ± 2.6 (36)	69.9 ± 3.7 (36)	117.7 ± 66.3 (31)	115.1 ± 5.9 (17)	61.4 ± 3.5 (7)
1985	32.3 ± 3.1 (40)	63.6 ± 3.9 (40)	91.9 ± 5.1 (38)	133.5 ± 13.0 (27)	35.1 ± 3.7 (21)
1986	33.5 ± 2.5 (40)	70.8 ± 5.7 (36)	106.7 ± 10.2 (33)	146.0 ± 9.5 (20)	28.1 ± 2.6 (8)
1987	33.8 ± 3.4 (36)	55.3 ± 3.5 (36)	64.2 ± 3.8 (36)	133.3 ± 6.1 (16)	26.9 ± 2.7 (16)
1988	32.3 ± 2.5 (36)	63.6 ± 4.2 (36)	88.5 ± 12.1 (36)	142.6 ± 7.3 (26)	35.2 ± 3.7 (18)
1989	18.8 ± 5.3 (8)	50.9 ± 9.7 (8)	74.6 ± 12.6 (8)	139.3 ± 14.3 (6)	46.6 ± 17.7 (4)
All years	33.7 ± 1.3 (78)	63.1 ± 1.0 (80)	90.3 ± 3.7 (77)	133.9 ± 2.6 (72)	39.5 ± 2.0 (70)

TABLE 4. Live vascular phytomass (g/m²) in each of five plant communities in the Niwot Ridge Saddle, 1982–1989. Values represent means \pm 1 SE. Shrubs represent foliar growth only.

Year		Fellfield	Dry meadow	Moist meadow	Wet meadow	Snowbed
1982	Graminoids	25.8 \pm 5.3	86.6 \pm 17.0	48.9 \pm 6.9	42.6 \pm 10.2	2.8 \pm 0.8
	Forbs	151.3 \pm 19.5	90.4 \pm 17.6	136.3 \pm 17.3	72.6 \pm 14.4	68.2 \pm 13.9
	Shrubs	0	0	0	6.7 \pm 4.2	0
	<i>K. myosuroides</i>	2.3 \pm 1.3	50.8 \pm 12.5	1.5 \pm 1.5	0	0.1 \pm 0.1
	<i>A. rossii</i>	31.2 \pm 8.7	17.8 \pm 6.1	56.9 \pm 12.4	9.8 \pm 8.2	18.2 \pm 6.4
	<i>Selaginella densa</i>	16.4 \pm 5.9	14.2 \pm 3.3	2.6 \pm 2.6	0	0
	Total live	193.5 \pm 23.7	191.2 \pm 15.7	187.8 \pm 19.4	121.8 \pm 19.5	71.0 \pm 14.1
1983	Graminoids	34.6 \pm 6.0	100.2 \pm 13.5	62.6 \pm 8.5	46.3 \pm 9.0	3.7 \pm 1.3
	Forbs	145.0 \pm 14.2	69.6 \pm 14.3	162.5 \pm 19.2	79.6 \pm 15.7	72.6 \pm 7.4
	Shrubs	0	0	0.6 \pm 0.6	2.2 \pm 1.5	0 \pm 0
	<i>K. myosuroides</i>	6.3 \pm 3.5	67.5 \pm 14.6	1.7 \pm 1.7	0	0
	<i>A. rossii</i>	29.5 \pm 11.0	7.1 \pm 3.3	80.8 \pm 17.0	16.6 \pm 11.3	10.7 \pm 3.8
	<i>Selaginella densa</i>	14.3 \pm 3.6	11.5 \pm 3.5	0	0	0
	Total live	193.9 \pm 15.7	181.3 \pm 17.7	225.7 \pm 21.1	128.1 \pm 15.0	76.3 \pm 8.4
1984	Graminoids	39.4 \pm 9.2	132.1 \pm 20.2	68.3 \pm 9.5	46.1 \pm 12.5	6.3 \pm 1.4
	Forbs	217.6 \pm 30.8	100.1 \pm 21.5	162.2 \pm 11.1	89.4 \pm 18.4	63.9 \pm 11.0
	Shrubs	0	0	0	0	0
	<i>K. myosuroides</i>	2.4 \pm 1.3	75.4 \pm 16.8	0 \pm 0	0	0
	<i>A. rossii</i>	49.1 \pm 20.2	29.1 \pm 13.8	75.0 \pm 13.2	22.3 \pm 10.3	8.9 \pm 4.0
	<i>Selaginella densa</i>	24.8 \pm 5.0	10.3 \pm 2.9	3.4 \pm 2.6	0	7 \pm 3.9
	Total live	281.8 \pm 30.3	242.9 \pm 31.3	234.0 \pm 11.1	135.6 \pm 22.0	77.5 \pm 10.8
1985	Graminoids	48.6 \pm 10.4	123.0 \pm 16.8	65.4 \pm 7.5	79.3 \pm 18.1	8.0 \pm 2.8
	Forbs	246.1 \pm 34.5	140.8 \pm 38.6	206.7 \pm 15.8	99.3 \pm 27.7	114.7 \pm 10.4
	Shrubs	0	0	0	3.0 \pm 1.8	0
	<i>K. myosuroides</i>	0.4 \pm 0.4	83.4 \pm 19.9	2.5 \pm 2.5	0	0
	<i>A. rossii</i>	44.6 \pm 11.2	26.3 \pm 12.5	71.4 \pm 11.7	20.5 \pm 13.1	13.4 \pm 6.0
	<i>Selaginella densa</i>	48.8 \pm 9.9	45.3 \pm 14.3	1.5 \pm 1.5	0	0
	Total live	343.6 \pm 36.0	309.1 \pm 27.2	274.0 \pm 14.2	181.7 \pm 38.6	122.8 \pm 10.7
1986	Graminoids	43.5 \pm 11.0	110.0 \pm 17.7	73.0 \pm 10.0	64.7 \pm 12.9	10.0 \pm 4.8
	Forbs	199.2 \pm 24.2	105.3 \pm 24.0	163.0 \pm 14.0	95.8 \pm 18.9	102.0 \pm 7.9
	Shrubs	0	0	0.2 \pm 0.2	5.4 \pm 2.7	0
	<i>K. myosuroides</i>	1.5 \pm 1.0	67.2 \pm 20.5	1.2 \pm 1.2	0	0
	<i>A. rossii</i>	36.0 \pm 12.1	28.4 \pm 11.0	63.1 \pm 13.1	10.1 \pm 5.7	15.6 \pm 5.3
	<i>Selaginella densa</i>	15.8 \pm 4.9	18.8 \pm 6.5	0.7 \pm 0.7	0	0
	Total live	258.6 \pm 26.6	234.1 \pm 16.1	236.8 \pm 14.5	166.0 \pm 25.4	112.0 \pm 11.8
1987	Graminoids	26.4 \pm 4.7	130.0 \pm 9.8	52.7 \pm 8.4	77.8 \pm 13.9	10.2 \pm 2.4
	Forbs	215.0 \pm 34.3	97.4 \pm 25.4	153.1 \pm 18.9	83.0 \pm 17.9	104.9 \pm 6.6
	Shrubs	0	0	1.4 \pm 1.3	8.2 \pm 4.4	0 \pm 0
	<i>K. myosuroides</i>	1.7 \pm 1.1	87.3 \pm 17.4	4.6 \pm 3.6	0	0
	<i>A. rossii</i>	44.4 \pm 6.2	14.3 \pm 6.4	66.7 \pm 11.9	1.9 \pm 1.9	17.1 \pm 6.0
	<i>Selaginella densa</i>	21.7 \pm 4.7	12.8 \pm 4.5	0	0	0
	Total live	263.3 \pm 33.7	240.5 \pm 17.5	207.0 \pm 19.1	169.0 \pm 19.7	114.9 \pm 6.8
1988	Graminoids	34.1 \pm 7.3	110.2 \pm 12.0	46.4 \pm 9.5	71.8 \pm 10.1	7.5 \pm 2.4
	Forbs	203.3 \pm 18.3	135.5 \pm 25.6	144.1 \pm 12.0	75.3 \pm 15.2	80.1 \pm 5.6
	Shrubs	0 \pm 0	0 \pm 0	1.9 \pm 1.3	8.3 \pm 3.5	0 \pm 0
	<i>K. myosuroides</i>	1.6 \pm 0.8	78.7 \pm 20.0	6.1 \pm 4.2	0 \pm 0	0 \pm 0
	<i>A. rossii</i>	32.7 \pm 6.3	32.6 \pm 13.9	34.6 \pm 8.1	4.7 \pm 4.7	9.7 \pm 4.0
	<i>Selaginella densa</i>	45.8 \pm 9.4	16.3 \pm 4.6	0 \pm 0	0 \pm 0	0 \pm 0
	Total live	283.4 \pm 18.3	261.9 \pm 22.5	194.7 \pm 17.8	160.6 \pm 11.2	87.7 \pm 6.4
1989	Graminoids	18.8 \pm 2.9	102.1 \pm 12.7	34.4 \pm 7.1	69.5 \pm 10.5	6.2 \pm 2.5
	Forbs	138.8 \pm 19.6	60.3 \pm 14.9	184.1 \pm 24.2	98.1 \pm 17.7	91.0 \pm 9.1
	Shrubs	0 \pm 0	0 \pm 0	4.0 \pm 4.0	9.0 \pm 4.0	0 \pm 0
	<i>K. myosuroides</i>	0.7 \pm 0.6	68.5 \pm 15.9	4.0 \pm 3.4	0 \pm 0	0 \pm 0
	<i>A. rossii</i>	45.7 \pm 17.9	16.7 \pm 8.8	72.1 \pm 19.1	4.9 \pm 2.8	14.3 \pm 5.8
	<i>Selaginella densa</i>	16.8 \pm 5.2	11.7 \pm 4.2	0 \pm 0	0 \pm 0	2.9 \pm 2.9
	Total live	174.3 \pm 19.7	174.0 \pm 8.6	222.7 \pm 28.8	176.7 \pm 20.1	100.1 \pm 8.9
1990	Graminoids	24.0 \pm 2.7	103.5 \pm 15.8	52.7 \pm 8.6	84.1 \pm 17.0	7.8 \pm 2.5
	Forbs	133.2 \pm 13.4	84.6 \pm 20.1	162.3 \pm 20.8	124.4 \pm 15.4	104.9 \pm 13.9
	Shrubs	0 \pm 0	0 \pm 0	2.7 \pm 2.7	5.1 \pm 2.3	0 \pm 0
	<i>K. myosuroides</i>	2.2 \pm 1.0	62.6 \pm 17.6	8.7 \pm 6.9	0 \pm 0	0 \pm 0
	<i>A. rossii</i>	30.2 \pm 10.5	21.1 \pm 10.2	51.3 \pm 11.4	4.6 \pm 3.5	14.3 \pm 5.5
	<i>Selaginella densa</i>	6.6 \pm 1.7	9.2 \pm 2.5	0 \pm 0	0 \pm 0	0 \pm 0
	Total live	163.8 \pm 12.0	197.4 \pm 16.7	217.7 \pm 22.8	213.6 \pm 21.4	112.8 \pm 15.4

TABLE 4. Continued.

Year		Fellfield	Dry meadow	Moist meadow	Wet meadow	Snowbed
All years	Graminoids	33.1 ± 2.5	110.8 ± 5.1	56.7 ± 3.0	7.0 ± 0.8	65.4 ± 4.5
	Forbs	185.7 ± 9.4	98.2 ± 7.9	164.0 ± 5.9	90.9 ± 6.1	89.1 ± 3.7
	Shrubs	0	0	1.1 ± 0.5	5.3 ± 1.0	0
	<i>K. myosuroides</i>	22.0 ± 0.5	71.3 ± 5.7	3.2 ± 1.1	0	0
	<i>A. rossii</i>	38.1 ± 3.9	21.5 ± 3.3	63.9 ± 4.5	10.6 ± 2.6	<0.1
	<i>Selaginella densa</i>	23.5 ± 2.4	16.7 ± 2.3	1.0 ± 0.5	0	0
	Total live	237.4 ± 10.0	225.8 ± 7.8	222.8 ± 6.6	161.6 ± 7.9	97.2 ± 3.9

(9 yr) in the numerator. Denominator degrees of freedom are 89 in both cases (2 plots × 9 yr × 5 communities = 90 sources of variation).

RESULTS

Climate and soil moisture

Winter (October through May) precipitation at station D-1 ranged from 764 mm in 1985 to 1120 mm in 1984 (Table 2), representing a 1.5-fold difference in absolute magnitude. Growing season precipitation varied over the same period from 135 mm in 1988 to 461 mm in 1984, a difference of 3.4 times. Total annual thawing-degree days varied by as much as 1.6 times, from 688 degree-days in 1982 to 1090 degree-days in 1987.

Soil moisture percentages were lowest in the fellfield community, followed by snowbed, dry meadow, moist meadow, and wet meadow (Table 3). Individual samples ranged from 16 to 168% of dry mass, and within communities among-year differences varied by a factor of ≈2.

Phytomass

Phytomass averaged 189.7 ± 4.3 g/m² (mean ± 1 SE), with individual samples ranging from 16 (snowbed) to 514 g/m² (fellfield). The highest mean values were in the fellfield, dry meadow, and moist meadow communities, 237, 226, and 223 g/m², respectively, and the lowest values were in the snowbeds, with a mean of 97 g/m² (Table 4). Means were significantly different among communities ($F = 35.7, df = 4, 89, P \leq .001$)

and years ($F = 9.6, df = 8, 89, P \leq .001$; interaction $F = 2.3, df = 32, 89, P \leq .001$), and among-community variability was greater than among-year variability.

Individual species and growth forms exhibited greater spatial variability than total live phytomass. Differences in phytomass of a growth form or species among communities primarily represent their different abundances among communities. Although total live phytomass varied significantly among years in the fellfield, dry meadow, and snowbed communities, most components of the phytomass did not vary significantly among years in these communities (Table 5).

The three species that we sorted individually, *Acomastylis rossii*, *Kobresia myosuroides*, and *Selaginella densa*, had different patterns of among-year and among-community variability (Table 4). *K. myosuroides* primarily occurs in the dry meadow, where it dominates and contributes 27–38% of the phytomass. Phytomass values for *K. myosuroides* were significantly different among communities ($F = 135.6, df = 4, 89, P \leq .001$) but not among years ($F = 0.4, df = 8, 89$). *A. rossii* occurred in all communities, but was most abundant in the moist meadow where it dominates and contributes 18–35% of the live phytomass. Like those for *K. myosuroides*, phytomass values for *A. rossii* were significantly different among communities ($F = 41.5, df = 4, 89, P \leq .001$) but not among years ($F = 1.05, df = 8, 89$). *Selaginella densa*, a clubmoss, differed from the other two species in having significant variation among both communities ($F = 19.1, df = 4, 89, P \leq .001$) and years ($F = 6.9, df = 8, 89, P \leq .001$). *S. densa* is abundant in the fellfield and dry meadow com-

TABLE 5. *F* ratios and significance for ANOVAs comparing means of individual phytomass components among years for each community.

Phytomass component	Plant community				
	Fellfield	Dry meadow	Moist meadow	Wet meadow	Snowbed
Total graminoid	2.089	0.953	1.946	1.516	0.985
Total forb	3.138**	1.305	1.493	0.710	3.472**
Total shrub	Not present	Not present	0.751	1.016	Not present
Total live	5.949***	4.713***	1.841	1.563	3.274**
<i>Kobresia myosuroides</i>	1.304	0.416	0.719	Not present	1.000
<i>Acomastylis rossii</i>	0.450	0.664	1.081	0.908	0.379
<i>Selaginella densa</i>	5.584***	3.247**	0.861	Not present	2.219*

* $P \leq .05$, ** $P \leq .01$, *** $P \leq .001$.

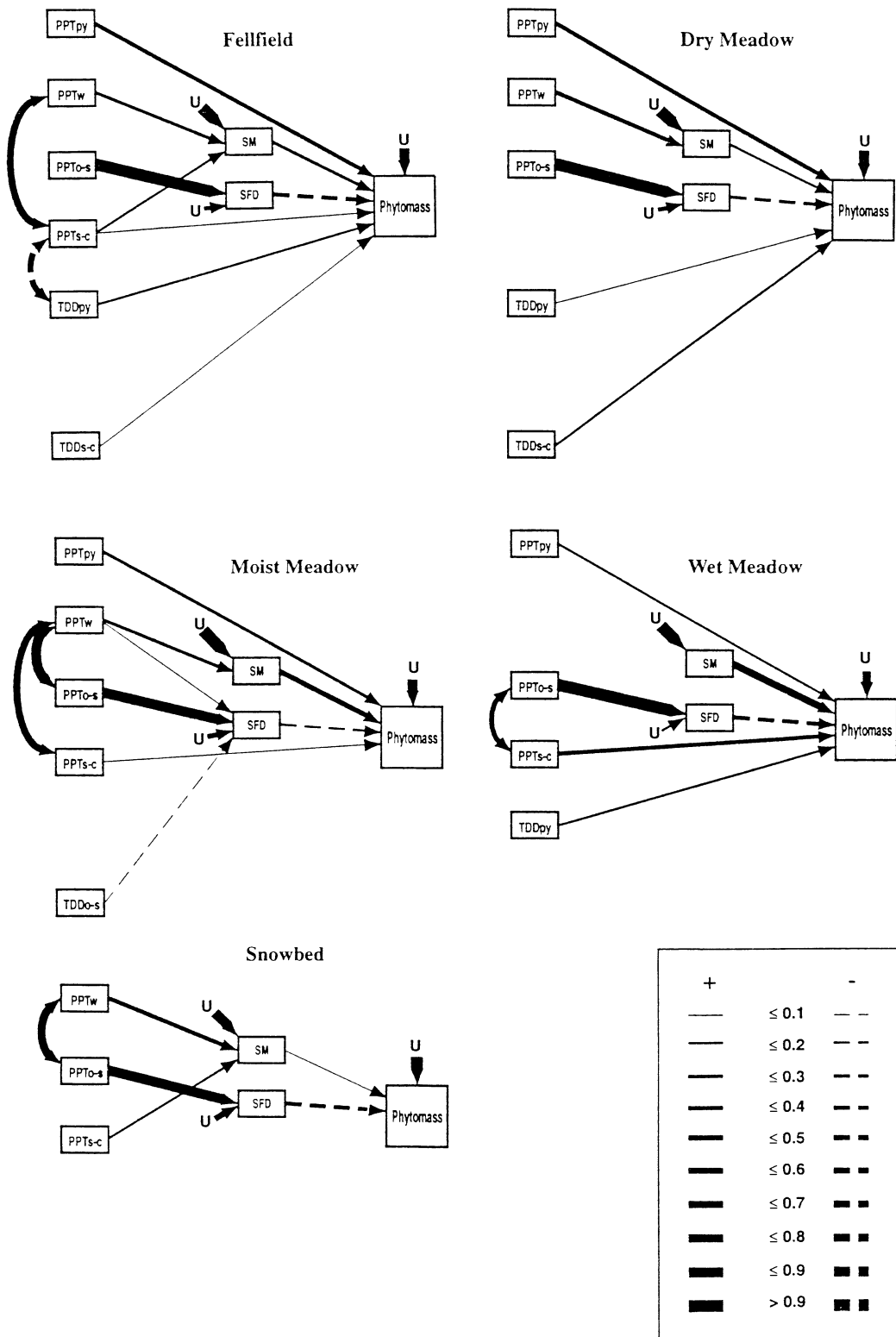


FIG. 2. Path diagram showing statistical influence of climate variables on live phytomass for each of five plant communities. Variable names are defined in Fig. 1 legend. Line widths indicate the magnitude of the path coefficients; dashed lines indicate a negative path coefficient.

TABLE 6. Path coefficients, *t* values, and coefficients of determination (*R*²) for the path diagrams in Fig. 2. Variable names are as in Fig. 1, and correlation matrices are in Appendix A.

Dependent variable	Independent variables	Path coefficient	<i>t</i>	<i>R</i> ²
Fellfield				
Soil moisture	WPPT	0.270	1.700	0.154
	PPTs-c	0.153	0.966	
Snow-free date	PPT0-s	0.942***	22.747	0.887
Total live phytomass	PPTpy	0.362*	2.722	0.340
	PPTs-c	0.046	0.340	
	TDDpy	0.144	0.862	
	TDDs-c	0.007	0.062	
	SM	0.206	1.600	
	SFD	-0.364*	-3.146	
Dry meadow				
Soil moisture	WPPT	0.388*	3.475	0.151
	PPT0-s	0.937***	22.167	
Snow-free date	PPTpy	0.397**	3.354	0.335
	TDDpy	0.082	0.643	
	TDDs-c	0.104	0.939	
	SM	0.195	1.785	
	SFD	-0.271*	-2.429	
Moist meadow				
Soil moisture	WPPT	0.300	1.926	0.089
	WPPT	0.019	0.176	
Snow-free date	PPT0-s	0.894	8.156***	0.831
	TDD0-s	-0.017	-0.319	
Total live phytomass	PPTpy	0.243	2.186	0.249
	PPTs-c	0.041	0.319	
	SM	0.430**	3.706	
	SFD	-0.137	-1.027	
Wet meadow				
Soil moisture	none			
Snow-free date	PPT0-s	0.935***	20.510	0.873
	PPTpy	0.109	0.883	
Total live phytomass	PPTs-c	0.391*	2.557	0.402
	TDDpy	0.165	1.052	
	SM	0.699***	5.759	
	SFD	-0.371*	-2.926	
Snowbed				
Soil moisture	WPPT	0.304*	2.390	0.148
	PPTs-c	0.166	1.309	
Snow-free date	PPT0-s	0.814***	10.673	0.663
Total live phytomass	SM	0.034	0.278	0.149
	SFD	-0.382*	-3.114	

* *P* ≤ .05, ** *P* ≤ .01, *** *P* ≤ .001.

munities and occurs only occasionally in the other communities. Its most extreme variation was in the fellfield, where it is most abundant. In that community *S. densa* phytomass was 7 g/m² in 1990 and 49 g/m² in 1985, an almost sixfold difference.

Path analysis

Path analysis of the effects of climate and soil moisture on total live phytomass indicated different patterns of climate effects in each community (Fig. 2). Path coefficients are in Table 6, and complete correlation matrices are in Appendix A. The variance in phytomass that was explained by the path model ranged from a high of 40% in the wet meadow community to a low of 15% in the snowbed community. Differences in the magnitudes of the path coefficients suggest dif-

ferent dynamics within the communities. Phytomass in the dry communities, fellfield and dry meadow, was most strongly related to precipitation in the previous year, but snow-free date and soil moisture were also relatively important. Phytomass in the moist meadow community had soil moisture as the most important explanatory variable, with previous year precipitation of secondary importance. Phytomass in the wet meadow community was explained primarily by soil moisture, with snow-free date and current season precipitation also significant. The final path model for snowbed phytomass had only two variables, soil moisture and snow-free date, with only snow-free date having statistical significance.

Soil moisture had 0–15% of its variance explained by the path analysis models (Fig. 2, Table 6). In all

communities except wet meadow, in which there were no relationships between climate and soil moisture consistent with the a priori path model, winter precipitation was most important in explaining soil moisture. Summer precipitation was of secondary importance in the fellfield and snowbed communities. Snow-free date was strongly related to climate, with 66–89% of the variance in snow-free date explained by the various path models (Fig. 2, Table 6). In all five communities, early season precipitation rather than winter snowfall was most important in explaining snow-free date, with high precipitation resulting in later melt. Early season precipitation is usually a mixture of rain and snow.

DISCUSSION

Patterns of variation in alpine phytomass

The aboveground phytomass values are in agreement with earlier data from Niwot Ridge (Webber and May 1977, May and Webber 1982) and within the range of values reported for alpine sites by the tundra biome project (Wielgolaski et al. 1981). The spatial variability in phytomass is high, and the overall range of values is similar to the range reported throughout the tundra biome. These data are a more representative sample for Niwot Ridge than those reported by Webber and May (1977), which were for a single sample in each community in a single year, 1973. Thus some differences in the present data from those numbers are expected. One of the main differences was the high phytomass values for fellfield, which were surprising given the dryness of these sites, their open canopies, and the dominance of their cover by low-growing cushion plants. The fellfield values are likely an over-representation of NAPP, because of difficulties accurately sorting annual growth from old leaf stems and bases in the tightly growing cushion species that dominate this community. Reexamination of stored samples supported this idea; samples with the highest values for forbs have abundant cushion plants. Forbs constitute from 72 to 82% of the fellfield phytomass (Table 4). The primary cushion species in fellfields is *Silene acaulis*, which forms cushions up to 70 cm diameter (Benedict 1989). Fellfield samples with high forb components invariably contained *S. acaulis* in abundance. A similar situation exists in the dry meadow community. Forb values are somewhat higher than would be expected if these were NAPP values, again due to an abundance of cushion plants. The dominant species in the dry meadow community, *Kobresia myosuroides*, is a caespitose sedge that forms dense tufts. Like the cushion plants, separation of old leaf bases from current growth is difficult. The consequences for both communities are that the values in Table 4 represent accurate estimates of phytomass but are overestimates of NAPP. The fact that phytomass in the fellfield and dry meadow communities represents >1 yr's produc-

tion could also explain why phytomass is most strongly related to the previous year's precipitation in those communities. In future studies it would be useful to quantify the over-winter survival in these two communities to better understand climate–production relationships.

The different relationships of phytomass in the five communities to climate and soil moisture indicate the different effects of climate within each community and the different limiting factors operating there. Increased precipitation in the previous year was the most significant variable in explaining higher phytomass in the driest communities, fellfield and dry meadow. Live tissue-nutrient concentrations of tundra plants are highest immediately after snow melt and gradually decrease throughout the growing season, due to a combination of translocation and dilution in new aboveground tissues (Chapin et al. 1975, Muc 1977, Dowding et al. 1981, Wielgolaski et al. 1981, Sundriyal and Joshi 1992). At the end of the growing season, nutrients are translocated back to belowground storage as aboveground tissue dies. The relationship of phytomass with previous year precipitation in the fellfield and dry meadow communities suggests that in these communities soil water limits either (1) photosynthesis as well as nutrient uptake and its consequent storage, or (2) survival of tissue between subsequent years. Either or both mechanisms may be acting, but more research would be needed to separate them.

Phytomass in the moist and wet meadow communities was also positively related to moisture, but in those cases it was current year soil moisture that influenced this outcome. Taylor and Seastedt (1994) documented a seasonal dry-down pattern of soil moisture in the moist meadow community on Niwot Ridge but could find no such pattern in the dry or wet meadow communities. Soil moisture is so consistently low in the dry meadow and fellfield communities that dry-downs likely occur immediately following precipitation events, so that no overall seasonal pattern can be detected. In the moist meadow there is sufficient soil moisture in the early season, with increasing drought as the season progresses, making among-year variation in soil moisture more important for production. Ehleringer and Miller (1975) studied water relations of five dominant species on Niwot Ridge along a gradient of water availability. They found evidence for water limitation of photosynthesis in all five species, with some of the lowest leaf water potentials recorded for alpine plants, but the actual effects of low moisture varied greatly among species and microsites, with different seasonal courses in different topographic positions. Our data corroborate this and other studies that indicate the importance of water stress in alpine tundra (e.g., Billings and Bliss 1959, Scott and Billings 1964, Kuramoto and Bliss 1970), by showing that phytomass is indeed higher in years with increased soil moisture.

The only community in which soil moisture or precipitation played no strong statistical role in explaining phytomass was the snowbed. This community has the shortest growing season and is strongly affected by date of release from snow, with earlier dates resulting in higher phytomass. This suggests that growing season length can be a limiting factor in alpine tundra, but only in deep snow areas. Other communities also have shortened growing season length when compared to nonalpine vegetation, but alpine species are well adapted to the short growing season, making other factors more important.

The link between winter snowfall, summer precipitation, and soil moisture differed among communities. In all cases the link between climate and soil moisture was fairly weak. There are at least two possible reasons for this. The first is simply our relatively small sample size, which weakens the statistical confidence of negative results. A second possibility is that the among-year variation in climate as a control on soil moisture is secondary to the role of topography and soil characteristics, particularly texture and organic matter content. Topographic variation is known to be a strong control on soil moisture (Swanson et al. 1988), and the five communities differed significantly in their soil characteristics (Appendix B). Our results support this conclusion, even given their low statistical power. Soil moisture in the fellfield and snowbed communities, where values were lowest, was most affected by climate, primarily winter snowfall, but also by summer precipitation. The dry and moist meadow communities, which have intermediate soil moisture values, had winter snowfall but not summer precipitation as important in explaining soil moisture. The wet meadow community had no significant relationships between soil moisture and climate. This is probably because the wet meadow community receives an almost constant supply of moisture from lateral flows due to nearby melting snowpack.

The lack of a strong response of any community to thawing-degree days appears unusual given the low growing season temperatures, yet similar results have been reported from the Arctic, and arctic plant species are less low-temperature sensitive than temperate species (Chapin 1983). The control of temperature on productivity of arctic plants is mainly an indirect one, through control of soil processes and nutrient availability (Chapin et al. 1987). Soils in the alpine zone of Colorado are not as cold as arctic soils, nor are they underlain by shallow permafrost, as in the Arctic, but they are cold relative to other ecosystems, and there is evidence for nutrient limitation in alpine tundra (Rehder 1976a, b, Gokceoglu and Rehder 1977, Rehder and Schäfer 1978, Bowman et al. 1993). Such an indirect effect, i.e., low soil temperatures leading to low nutrient availability, would likely show up more as a topographic effect than one related to among-year air temperature

differences. Also, a temperature response might be delayed. Our data indicated no significant response of growth to previous year thawing-degree days, but this is not a conclusive result given our small sample size.

The degree of among-year variability in phytomass that we have documented for Niwot Ridge has not been demonstrated in many other ecosystems. In high arctic tundra on Devon Island, annual productivity changed very little over a 3-yr period, despite a fourfold difference in thawing-degree days (Muc 1977); similar results have been reported for shortgrass prairie over a 5-yr period (Lauenroth et al. 1978) and for low-arctic tundra over 5 yr (Chapin and Shaver 1985). The Niwot Ridge data, on the other hand, varied significantly among years, but the differences were significant only for the whole community. Species differed in their response to specific factors and in their among-year patterns. Of the three selected species that were individually sorted, only aboveground phytomass of *Selaginella densa*, a nonvascular cryptogam, varied significantly among years. Chapin and Shaver (1985) suggested that the lack of among-year variability reported from arctic tundra was due to individualistic responses to multiple limiting factors, whereby different species or functional groups vary among years due to different ratios of resource availability, but overall community productivity remains relatively constant. They suggested that, in contrast to the hypothesis of Grime (1977), low-resource, or "extreme," environments such as tundra may have high levels of competition, because there are less than optimal amounts of resources available. This resource competition results in the community using all available resources in every year and therefore exhibiting a relatively constant productivity value.

The Chapin-Shaver (1985) competition hypothesis requires that (a) there is competition for available resources, (b) in a given year, certain species have some resources that are not limiting, so that they are able to compete effectively for the more limiting resources, and (c) the ratios of resources vary among years. Although we have not directly measured competition effects, the structure of the Niwot Ridge canopy compared to tussock tundra of Alaska suggests that competition may be less in alpine tundra, at least in certain communities. The Niwot Ridge canopy, particularly in the fellfield and snowbed communities, is primarily open, with 25–80% of the ground bare or lichen covered (M. Walker, unpublished data). Arctic tussock tundra, on the other hand, consists of a closed canopy with a dense, continuous moss cover. The moist meadow and wet meadow communities on Niwot Ridge, which have essentially continuous ground cover, showed minimal variation among years. These two communities may be more strongly limited by non-climatic factors such as soil nutrients or light, or they may be dominated by competition-adapted species, i.e., Grime's (1977) C-strategy.

Evolutionary factors may limit a species' ability to respond to annual variation in climate through variation in growth. The annual growth cycle of most tundra plants has two phases: (1) a rapid growth phase following snowmelt, where stored nutrients and carbohydrates are reallocated from below- to above-ground, and (2) a storage phase, where nutrients and carbohydrates are reallocated belowground (Mooney and Billings 1960, Chapin et al. 1975, 1980, 1986). Transplant experiments of *Acomastylis rossii* suggest ecotypic variation among the Niwot Ridge populations (May 1976). Intrinsic genetic controls on growth could be advantageous in an environment with a short growing season. Switching to belowground reallocation based on the earliest average date of resource depletion, rather than continuing growth throughout the period of available resources, which varies greatly among years, would assure that even in the most severe years the growth cycle is completed and sufficient reserves are available for rapid growth the following spring. This evolutionary control would dampen interannual variability. Ecotypic control and subsequent damping of variability in production has been implicated in *Eriophorum vaginatum*, the dominant species in Alaskan tussock tundra (Fetcher and Shaver 1990).

These three factors, (1) low competition, which is essentially in agreement with Grime (1977), (2) light or nutrient limitation, which is in agreement Chapin and Shaver (1985), and (3) ecotypic control, are not mutually exclusive. There is likely a gradient of competition intensity among different communities in arctic and alpine tundra as well as other ecosystems that have severe resource limitation. In the communities where competition is likely most intense (moist meadows and wet meadows), our data fit best with the Chapin-Shaver individualistic hypothesis, and the remaining communities seem to follow Grime's reduced competition hypothesis. Certainly, individual species are limited by different factors, but if a few single factors are more limiting than others, then interannual variation in the most limiting factors will control community response. Genetic controls over production can exist in any system and do not require competition or lack of it; they do, however, indicate a strong abiotic control over growth within the range of an ecotype. The present analysis suggests that the nature of growth limitation may be somewhat different in open and closed canopy arctic and alpine environments. Experimental analysis of potentially limiting growth factors in alpine tundra would be useful.

Climate change and the alpine ecosystem

Climate accounted for a significant amount of the interannual variation in alpine phytomass in 3 of 5 communities, but there was a large unexplained (residual) variance, from 60 to 85%. This residual variance is likely a function of ecotypic variation and other factors that we did not measure, in particular topog-

raphy and topographically controlled differences in soil characteristics and nutrient availability, which vary significantly among plant communities, as well as random variation or sampling error. Despite this high residual variance, the ability of simple linear statistics of climate and soil moisture to explain large amounts of variance in phytomass indicates a sensitivity of the system to variation in climate, and, in particular, variation in factors related to snowfall and precipitation. Many authors have established the importance of snow in controlling spatial patterns of species and factors important to plant growth (for example Braun-Blanquet 1932, Gjærevoll 1956, Billings and Bliss 1959, Johnson and Billings 1962, Bliss 1963, Canaday and Fonda 1974, Komárková 1979, Willard 1979, Walker et al. 1993). Consistent interannual patterns in snowpack due to topography and prevailing winds result in a complex of ecosystem factors, including most soil characteristics, that vary according to snow distribution.

Our analysis suggests that climate changes resulting in different snow cover and precipitation regimes could have significant direct impact on levels of primary productivity. Recent summaries of global climate models predict warming near the surface and increases in winter precipitation at midlatitudes (Mitchell et al. 1991). An important limitation of these models is that their spatial resolution is too coarse for examining local situations such as the Colorado Front Range alpine tundra. Although climate change at the global scale is predicted to be primarily changes in temperature, these changes will be expressed regionally as increases in the variability of the hydrologic cycle, i.e., either increasing drought or increasing storm severity (Hansen et al. 1991). The sensitivity of alpine vegetation to precipitation indicates the potential for changes in productivity in the short term. Sustained over long time periods, these changes would likely alter soil nutrient regimes and organic matter content in complex ways. Our path analyses suggest that changes in precipitation, growing season length, or soil moisture, which could result from either changes in timing or amount of snowfall or ratio of winter to summer precipitation, would likely have significant impact that would differ among alpine plant communities and species.

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APPENDIX A

TABLE A1. Correlation matrices for each of the five plant communities. Variable abbreviations are in Fig. 1 legend.

<u>Fellfield</u>									
	PPTpy	PPTw	PPT0-s	PPTs-c	TDDpy	TDD0-s	TDDs-c	SM	SFD
PPTpy	1.000	-0.370	-0.349	-0.036	-0.421	-0.301	-0.079	0.276	-0.246
PPTw	-0.370	1.000	0.638	0.686	-0.299	-0.541	-0.101	0.362	0.538
PPT0-s	-0.349	0.638	1.000	0.121	-0.199	-0.494	-0.272	0.197	0.942
PPTs-c	-0.036	0.686	0.121	1.000	-0.520	-0.278	0.019	0.318	0.137
TDDpy	-0.421	-0.299	-0.199	-0.520	1.000	0.670	0.273	-0.491	-0.151
TDD0-s	-0.301	-0.541	-0.494	-0.278	0.670	1.000	0.654	-0.427	-0.300
TDDs-c	-0.079	-0.101	-0.272	0.019	0.273	0.654	1.000	0.094	-0.022
SM	0.276	0.362	0.197	0.318	-0.491	-0.427	0.094	1.000	0.212
SFD	-0.246	0.538	0.942	0.137	-0.151	-0.300	-0.022	0.212	1.000
Phytomass	0.446	-0.257	-0.450	-0.027	-0.077	-0.010	0.046	0.173	-0.425
<u>Dry meadow</u>									
	PPTpy	PPTw	PPT0-s	PPTs-c	TDDpy	TDD0-s	TDDs-c	SM	SFD
PPTpy	1.000	-0.389	-0.350	-0.061	-0.417	-0.343	-0.100	0.238	-0.165
PPTw	-0.389	1.000	0.607	0.715	-0.295	-0.319	-0.182	0.388	0.533
PPT0-s	-0.350	0.607	1.000	0.134	-0.195	-0.114	-0.413	0.016	0.937
PPTs-c	-0.061	0.715	0.134	1.000	-0.545	-0.218	-0.016	0.266	0.178
TDDpy	-0.417	-0.295	-0.195	-0.545	1.000	0.549	0.355	-0.296	-0.253
TDD0-s	-0.343	-0.319	-0.114	-0.218	0.549	1.000	0.783	-0.572	0.059
TDDs-c	-0.100	-0.182	-0.413	-0.016	0.355	0.783	1.000	-0.221	-0.183
SM	0.238	0.388	0.016	0.266	-0.296	-0.572	-0.221	1.000	-0.025
SFD	-0.165	0.533	0.937	0.178	-0.253	0.059	-0.183	-0.025	1.000
Phytomass	0.444	-0.303	-0.449	-0.114	-0.036	-0.123	0.100	0.248	-0.381
<u>Moist meadow</u>									
	PPTpy	PPTw	PPT0-s	PPTs-c	TDDpy	TDD0-s	TDDs-c	SM	SFD
PPTpy	1.000	-0.409	-0.207	-0.073	-0.406	-0.081	-0.179	0.098	0.0005
PPTw	-0.409	1.000	0.877	0.644	-0.303	-0.099	-0.223	0.298	0.806
PPT0-s	-0.207	0.877	1.000	0.592	-0.416	-0.005	-0.510	0.375	0.911
PPTs-c	-0.073	0.644	0.592	1.000	-0.485	0.228	0.024	0.190	0.522
TDDpy	-0.406	-0.303	-0.416	-0.485	1.000	0.319	0.417	-0.137	-0.516
TDD0-s	-0.081	-0.099	-0.005	0.228	0.319	1.000	0.554	-0.040	-0.024
TDDs-c	-0.179	-0.223	-0.510	0.024	0.417	0.554	1.000	-0.319	-0.508
SM	0.098	0.298	0.375	0.190	-0.137	-0.040	-0.319	1.000	0.300
SFD	0.0005	0.806	0.911	0.522	-0.516	-0.024	-0.508	0.300	1.000
Phytomass	0.282	-0.085	-0.057	0.034	-0.161	-0.245	-0.272	0.421	0.014
<u>Wet meadow</u>									
	PPTpy	PPTw	PPT0-s	PPTs-c	TDDpy	TDD0-s	TDDs-c	SM	SFD
PPTpy	1.000	-0.417	-0.256	0.030	-0.440	-0.048	-0.132	-0.036	-0.030
PPTw	-0.417	1.000	0.913	0.539	-0.357	0.327	-0.415	-0.029	0.850
PPT0-s	-0.256	0.913	1.000	0.605	-0.400	0.464	-0.650	-0.100	0.935
PPTs-c	0.030	0.539	0.605	1.000	-0.543	0.141	-0.036	-0.401	0.451
TDDpy	-0.440	-0.357	-0.400	-0.543	1.000	0.182	0.381	0.009	-0.468
TDD0-s	-0.048	0.327	0.464	0.141	0.182	1.000	-0.362	0.077	0.557
TDDs-c	-0.132	-0.415	-0.650	-0.036	0.381	-0.362	1.000	-0.122	-0.746
SM	-0.036	-0.029	-0.100	-0.401	0.009	0.077	-0.122	1.000	0.076
SFD	-0.030	0.850	0.935	0.451	-0.468	0.557	-0.746	0.076	1.000
Phytomass	0.034	-0.282	-0.246	-0.144	0.085	-0.046	0.078	0.512	-0.223
<u>Snowbed</u>									
	PPTpy	PPTw	PPT0-s	PPTs-c	TDDpy	TDD0-s	TDDs-c	SM	SFD
PPTpy	1.000	-0.490	-0.262	0.030	-0.317	-0.118	-0.083	-0.096	-0.304
PPTw	-0.490	1.000	0.760	0.274	-0.258	-0.135	-0.123	0.349	0.611
PPT0-s	-0.262	0.760	1.000	0.095	-0.306	0.157	-0.514	0.441	0.814
PPTs-c	0.030	0.274	0.095	1.000	-0.566	-0.390	0.609	0.250	-0.157
TDDpy	-0.317	-0.258	-0.306	-0.566	1.000	0.350	0.122	0.191	-0.209
TDD0-s	-0.118	-0.135	0.157	-0.390	0.350	1.000	-0.453	-0.251	0.463
TDDs-c	-0.083	-0.123	-0.514	0.609	0.122	-0.453	1.000	0.272	-0.744
SM	-0.096	0.349	0.441	0.250	0.191	-0.251	0.272	1.000	-0.071
SFD	-0.304	0.611	0.814	-0.157	-0.209	0.463	-0.744	-0.071	1.000
Phytomass	0.163	-0.392	-0.240	-0.028	-0.028	-0.199	0.083	0.061	-0.384

APPENDIX B

TABLE A2. Mean values of soil variables in each of five plant communities, and one-way analysis of variance comparing values among communities ($df = 4, 25$ in all cases). Data are from May (1973); Appendix III.

	<i>F</i> ratio	<i>P</i>	Plant community				
			Fellfield	Dry meadow	Moist meadow	Wet meadow	Snowbed
Number of samples			5	5	8	3	5
Organic matter (%)	4.318	.006	18.9	27.7	32.1	41.2	13.9
Water-holding capacity (% dry mass)	4.325	.006	104.2	149.7	175.6	223.0	91.2
Silt plus clay (%)	3.366	.019	43.9	43.1	50.8	65.2	36.7
pH	5.394	.0018	5.2	5.5	4.7	4.8	4.9
Base saturation (%)	11.478	.0001	60.7	78.9	30.9	0.4	29.7
Concentrations of positive charges							
CEC (mol/g)	2.573	.05	0.525	0.782	1.003	1.057	0.669
Ca ⁺² (mol/g)	7.363	.0003	0.245	0.510	0.195	0.305	0.065
Mg ⁺² (mol/g)	0.926	.481	0.030	0.025	0.032	0.025	0.093
NO ₃ ⁻ (mol/g)	3.169	.02	0.0005	0.0098	0.0020	0.0090	0.0008
NH ₄ ⁺ (mol/g)	2.379	.069	0.11	0.15	0.25	0.51	0.13
PO ₄ ⁻³ (mol/g)	0.700	.629	0.0025	0.0020	0.0021	0.0186	0.0014
Fe ⁺² (mol/g)	13.081	.0001	0.0031	0.0084	0.0089	0.0453	0.0053
Al ⁺³ (mol/g)	3.339	.0198	0.0500	0.0367	0.1400	0.1270	0.0967