JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 113, G03013, doi:10.1029/2007JG000680, 2008

How alpine plant growth is linked to snow cover and climate variability

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Received 28 December 2007; revised 14 March 2008; accepted 4 June 2008; published 30 July 2008.

[1] Recent climate models predict future changes in temperature and precipitation in the Alps. To assess the potential response of alpine plant communities to climate change, we analyzed specific and combined effects of temperature, precipitation, and snow season timing on the growth of plants. This analysis is based on data from 17 snow meteorological stations and includes plant growth records from the same sites over 10 years. Using multiple regression and path analysis, we found that plant growth was primarily driven by climatic factors controlled by the timing of the snow season. Air temperature and precipitation before snow-up and after melt-out yielded the greatest direct impact on maximum plant height as well as growth rates. The variability of environmental drivers between sites versus between years had different effects on plant growth: e.g., sites with early melt-out dates hosted plant communities with tall, slow-growing vegetation. But interannual variations in melt-out dates at a given site did not produce measurable differences in plant growth performance. However, high temperatures after melt-out invariably resulted in a shortened growth period. We speculate that the plant growth patterns we observed in response to climate variation between sites are indicative of the long-term responses of alpine plant communities to persistent climate changes. With most climate models indicating shorter winters, we thus expect alpine grasslands in the Alps to display an enhanced biomass production in the future.

Citation: Jonas, T., C. Rixen, M. Sturm, and V. Stoeckli (2008), How alpine plant growth is linked to snow cover and climate variability, *J. Geophys. Res.*, *113*, G03013, doi:10.1029/2007JG000680.

1. Introduction

[2] Plant growth takes place in summer, yet winter is equally important in determining the composition and health of plant communities in arctic and alpine ecosystems [*Ellenberg*, 1988; *Jones et al.*, 2001]. Winter determines the length of the snow-free season as well as the state of soil and plants at the start of the growing season [*Keller et al.*, 2005; *Körner*, 2003]. Low air temperatures, the build-up and melt of a snow cover, and limited sun light are the main attributes of winter. At first glance, these seem to be simple variables whose impact on plants should be readily apparent. However, they are linked in complex ways that can produce counter-intuitive results. Snow can shield plants from low ambient temperatures and harsh winds, yet at the same time reduce the amount of light available for photosynthesis. If deep enough, snow (not air temperature) will dominate the thermal balance of the ground [*Haeberli*, 1973]. It will also control the amount of liquid soil moisture available during the winter for soil microbes [*Schimel et al.*, 2004]. A deep snowpack can also delay spring melt by several weeks [*Rixen et al.*, 2003]. In short, simple winter environmental variables such as temperature, snow precipitation, and light are anything but simple. Understanding how they impact arctic and alpine ecosystems remains a challenge.

[3] The need for this understanding is particularly pressing now. Data already indicate that the climate of Earth's high altitude and latitude regions is changing more rapidly than elsewhere [*ACIA*, 2004; *IPCC*, 2007]. These climate models are consistent in suggesting that these trends will not only continue, but potentially accelerate. Already, the vegetation in these regions is responding. Alpine species have been migrating upward [*Grabherr et al.*, 1994; *Walther et al.*, 2005], while in the Arctic, shrubs have become more abundant and extended their range [*Sturm et al.*, 2001; *Tape et al.*, 2006].

[4] Our ability to predict future vegetation states in arctic and alpine locations hinges on how well we sort out the specific and combined impact of changing winter climate variables on alpine plant communities. Three methods have been used to date to assess these impacts. The first has been experimental manipulation. Investigators have enhanced snow depth through the use of snow fences [*Wahren et al.*, 2005], or reduced it by shoveling off the snow manually [*Starr et al.*, 2000; *Wipf et al.*, 2006]. The second has been response prediction using linked bio- and geo-physical models [*Gottfried et al.*, 1999; *Keller et al.*, 2005]. The third method, one that forms the basis of this study, is to

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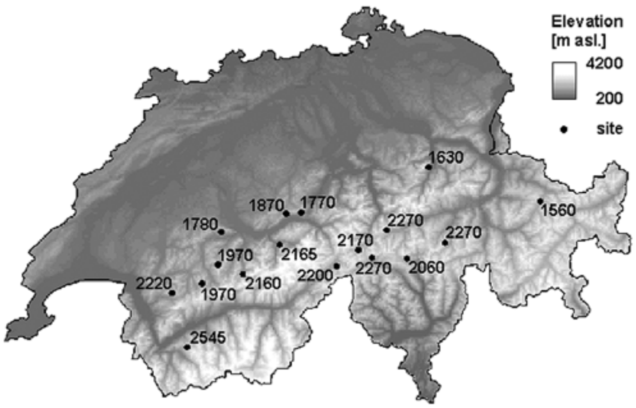

Figure 1. Site locations (black dots) in Switzerland. Site elevation is given in m asl.

make use of natural experiments to assess how winter variables impact plant growth. For example, data on changes in plant growth rates or species composition from locations where there are long, detailed records of weather and snow cover can be analyzed using statistical methods to identify specific plant responses to climate variability [*Inouye and McGuire*, 1991; *Inouye et al.*, 2002; *Walker et al.*, 1995, 1994].

[5] Each of the above methods has its strengths and weaknesses. In snow manipulation experiments, investigators often inadvertently alter several aspects of the snow, sometimes in unrealistic ways. This can confound their analysis. For instance, it is rarely possible to alter the depth of the snow without also affecting its density and thermal properties. Likewise, bio-geo-modeling is still problematic. Unless the complex biophysical linkages that operate within plant communities are fully coded into the models, the model output is unlikely to be reliable, particularly when projecting over decadal timescales. Natural experiments pose difficulties as well: (1) it is unclear how best to characterize the natural winter environment in ways meaningful for biota, and (2) it is hard to establish cause and effect when environmental variables are uncontrolled. Snow depth, snow quality, air and soil temperature, date of first snow, snow duration: we know all of these affect plants, but some variables (like snow depth) produce their impact through time-integrated effects, while others, like sharp frosts and rain-on-snow, produce contingencies with unexpected consequences. There is no clear-cut method of characterizing these driver variables in ways that fully encompass how changes in their magnitude, frequency, or intensity will impact plants. Yet despite these difficulties, we still think natural experiments offer promise in making rapid advances toward achieving a predictive capability. Natural experiments do not require setting up and monitoring of dedicated vegetation plots, so they can be applied widely. They rely on standard, rather than specialized records, which are usually longer than the records from dedicated plots. That way, individual and combined effects of environmental variables on plant growth can be investigated, which is much harder to do in manipulation experiments where an attempt is usually made to alter just one of several variables.

[6] In this study, we use data from automatic weather stations to characterize the climate and the seasonal snow cover at 17 alpine sites in Switzerland. The same stations, fortuitously, capture plant growth as well. We identify a simple set of plant response variables based on the growth pattern of the vegetation. We then break down the weather/snow data into a number of simple time and environmental state variables whose impact on the plants can be examined singularly and in concert. Using multiple regression analysis, we identify the 6 most important forcing variables, which we then use in structural equation modeling (SEM) to produce driver-response maps. Path analysis reveals the relative importance of each of the links between explanatory and response variables and indicates how the growth performance of the investigated plant communities is linked to the climatologic forcing variables. These data form the basis from which we are able to explore the response of alpine plants to changes in climate (such as those detailed in future scenarios by the IPCC). While here we look only at changes in the Swiss Alps, the method is also suitable for other arctic and alpine systems.

2. Data and Methods

[7] Since 1996, the Swiss Federal Institute for Snow and Avalanche Research (SLF) has run a meteorological network that monitors snow and weather [*Rhyner et al.*, 2002]. To date, about 105 stations have been installed throughout the Swiss Alps. At each station standard meteorological parameters such as snow depth, air temperature, wind speed, and soil temperature are measured every 30 min.

[8] Snow depth is measured using an ultrasonic snow depth sensor (SR50, Campbell Scientific, USA). It turns out that these devices also can be used to track vegetation height (h) in summer. We tested this aspect of the ultrasonic sensor using artificial and manipulated natural vegetation. From these tests we concluded that (1) the sensor was sensitive to plants within a radius of 75 cm below the aiming point for a sensor 6 m above ground, and (2) the sensor could pick up the reflection of leaves or flowers if they occupied just 4% of the sensor footprint. Note that the sensor was set-up to respond to the nearest target (i.e., the highest plants). Its accuracy is about 2 cm. We compared ultrasonic sensor plant growth records with manual measurements from 6 sites. Biomass and vegetation height were sampled twice during the growing period, a first time when plants reached approximately 1/3 of their maximum height (h_{max}) and again at approximately 2/3 h_{max}. The correlation between ultrasonic and manually measured heights was r^2 = 0.96. The correlation for biomass was r^2 = 0.89. Note that this correlation was only tested for within the (height) growth period and does not preclude additional biomass production after attaining the maximum height. We also tested the ultrasonic sensor plant growth records against remote sensing NDVI data with an astonishingly good consistency between the timing of the maximum NDVI and when the plants reached their maximum height [*Fontana et al.*, 2008].

[9] From the 105 existing SLF station sites, we identified 17 sites (Figure 1) that feature undisturbed subalpine and alpine grasslands with a homogeneous vegetation of at least 10 cm height at full growth. To ensure clear determination of plant growth parameters, the analysis was restricted to

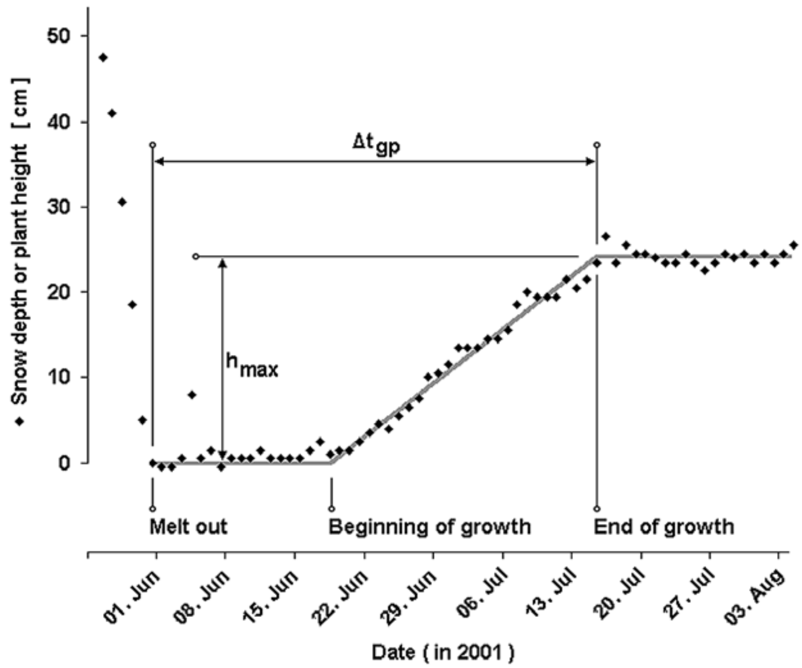

Figure 2. Sample data (black dots) from the ultrasonic sensor at Tujetsch (2270 m asl). A 3-leg linear fit (gray line) has been used to determine our five plant-growth indices (see list below, Δt_{gp} denotes the growth period and h_{max} the maximum vegetation height). In case of ephemeral snowfall after melt out (5 June in this example) affected data could be identified by means of surface temperature data and subsequently discarded from the fitting procedure.

data from these 17 sites. Most of the sites were meadows moderately grazed by cattle, a common type of ecosystem for the Swiss Alps. The sites were dominated by grass and herb species characteristic of plant communities related to *Poion alpinae* [*Ellenberg*, 1988]. All sites were open, flat, and generally not exposed to wind. They ranged from 1560 to 2545 m asl. For the 17 sites there were 111 data records available. Of these, 82 records covering the 10 winter seasons between 1996 and 2006 could be evaluated according to the procedures described below.

2.1. Plant Growth Data (System Response)

[10] Aboveground plant growth did not usually occur until 2 to 3 weeks after the snow had melted (Figure 2). Once begun, the growth was nearly linear until the vegetation had reached its maximum height (h_{max}). By fitting the growth signal with a 3-leg linear fit (Figure 2, gray line), we were able to compute the following dates or indices: (1) melt out (date), (2) beginning of growth (date), (3) end of growth (date), (4) growth period Δt_{gp} (duration), and (5) maximum vegetation height h_{max}. Focusing on plant growth performance, we define h_{max} and Δt_{gp} as our two key plant response parameters indicating the amount and speed of biomass production.

2.2. Snow and Weather Data (System Drivers)

[11] In order to statistically analyze the effect of winter drivers on plant growth we needed to convert continuous snow and weather data into a small number of relevant discreet indices. We did so in two steps: first, by calculating a large set of potential drivers (as outlined below), and then by culling this list to produce a final set of four key drivers using statistical techniques.

[12] Availability of light, energy and water are widely recognized as essential for plant growth. To capture these factors from the available meteorological measurements we used the following data: (1) air temperature, (2) soil temperature, (3) snow depth, and (4) precipitation.

[13] The SLF stations measure the first three of the above factors, but are not equipped with precipitation gages. As substitution for respective on-site measurements, we used precipitation gage records from the meteorological network NIME run by the Federal Office of Meteorology and Climatology MeteoSwiss [*Begert et al.*, 2005]: for each of our sites we averaged data from three nearby NIME stations from the same meteorological basin and typically within a radius of 10 km. Site-representative measurements of incoming solar radiation were not available.

[14] In order not to presuppose which parts of the year were most relevant for plant growth, the four above listed snow and weather factors were evaluated over a relatively large set of 10 time intervals (Figure 3 and Table 1). Some of the intervals we evaluated were defined by fixed dates (Figure 3, see Average Periods). Others were defined relative to the specific timing of the seasonal snow cover (Figure 3, see Specific Periods). Average Periods (AP) reflect the observed range of snow-up and melt-out dates between years and sites. In contrast, Specific Periods (SP) relate to the actual snow-up and melt-out dates for a given plant growth record.

[15] As expected, not all combinations of the four snow and weather factors convolved with the 10 intervals listed in Table 1 provided reasonable environmental indices. We excluded indices that were undefined (e.g., soil freezing did not occur during or after the melt-out period), known to be relatively insignificant (e.g., mean air temperatures during

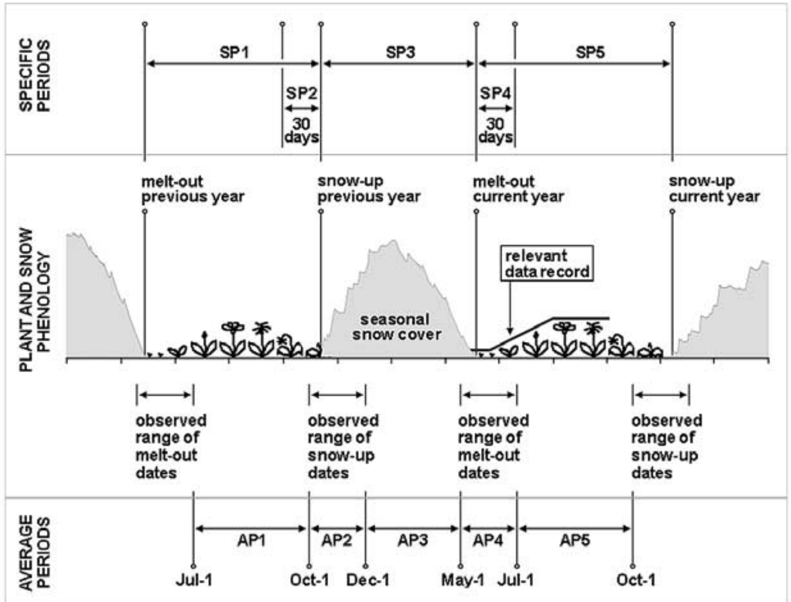

Figure 3. Definition of average and specific periods used in the data analysis. Melt-out was defined as the date of the first snow-free day in spring, while snow-up was defined as date of the last day in fall featuring a snow depth below 10 cm. See also Table 1.

snow covered period [e.g., *Taras et al.*, 2002]), or that confounded timing and averaging issues (e.g., snow depth averaged over AP2 – AP4). On the other hand, we added negative degree sums of air temperature as an alternative proxy for freezing soil because direct measurements could be biased by local heterogeneity in soil moiture distribution. This process led to 29 environmental drivers (listed in Table 2) that were used in the driver-response analysis.

2.3. Statistical Analysis

[16] The statistical analysis had two goals: (1) to identify the key factors that directly drive plant growth in the Swiss Alpine, and (2) to analyze the complex network of relationships between system drivers and responses. As outlined above, the analysis is based on 82 data records from the SLF station sites, each featuring two plant growth indices as response variables and 29 environmental indices as potential explanatory variables (Table 2). To also include timing variables in the analysis we added snow-up and melt-out dates and the duration of snow covered period as supplementary environmental factors. The data analysis was structured in four steps

[17] 1. As a matter of principle, plant growth data will display variability between sites and between years. Because there are different reasons for why plant communities show a different growth performance in one year at two separate sites versus at one site in two separate years, we analyzed for between-sites effects and between-years effects separately. Between-sites effects consider the consequences of persistent spatial differences in climate for plant growth. As different climatic regimes result in different plant communities, between-sites effects reflect the variability of growth due to climate-driven differences in species composition. This part of the analysis was performed on residuals with respect to year as random factor. Between-years effects, in contrast, consider the growth response of plant communities at a given site to interannual climate variations. Hence, between-years effects primarily reflect the growth response of plant communities with established species compositions to perturbations in the local climate. This part of the analysis

Table 1. Definition of Periods for Data Aggregation

Period Acronym	Description	Start and End Date
AP1	Average snow-free period previous year	1 Jul to 31 Sep of the previous year
AP2	Average snow-up period	1 Oct to 30 Nov of the previous year
AP3	Average snow-covered period	1 Dec of the previous year to 30 Apr of the current year
AP4	Average melt-out period	1 May to 30 Jun of the current year
AP5	Average snow-free period current year	1 Jul to 31 Sep of the current year
SP1	Specific growing season previous year	Between melt-out and snow-up dates of the previous year
SP2	Month before snow-up	30-day period just before the snow-up date of the previous year
SP3	Specific snow-covered period	Between snow-up in the previous year and melt-out in the current year
SP4	Month after melt-out	30-day period just after the melt-out date of the current year
SP5	Specific growing season current year	Between melt-out and snow-up dates of the current year

Table 2. Environmental Drivers and Notation Used in Analysis[a]

Interval	Air Temperature	Soil Temperature	Snow Depth	Precipitation	Reference Term
AP1	m			s	
AP2	m, dgs	df		s	"during snow-up"
AP3		df		s	
AP4	m, dgs			s	"during melt-out"
AP5	m			s	
SP1	m			s	
SP2	m, dgs	df	ds	s	"before snow-up"
SP3		df	m	s	
SP4	m, dgs		ds	s	"after melt-out"
SP5	m			s	

[a]Here m, mean value; dgs, degree sum of night (20:30 to 4:30) temperatures below -2°C; df, number of days with soil frost; ds, number of days with snow cover; s, total precipitation over interval; AP1-AP5, SP1-SP5 denote periods as defined in Figure 3.

was performed on residuals with respect to the site as random factor.

[18] 2. To minimize problems arising from correlated explanatory variables, the environmental drivers were pooled into factor classes according (approximately) to their reciprocal correlations (Table 3). Interestingly, temperature and precipitation data were correlated in spring, but not in autumn.

[19] 3. We employed multiple regression analysis to identify those key environmental drivers with the strongest direct influence on plant growth. A total of four regression models were optimized, to account for between-sites and between-years effects on both response variables, respectively. Best fit models were identified using stepwise factor selection algorithms based on Akaike's Information Criterion [*Akaike*, 1981], on condition that per factor class at most one driver may be included in the model.

[20] 4. We used the key drivers and response variables to assemble a path analysis diagram. The diagram was optimized by means of structural equation modeling (SEM) using AMOS 5 [*AMOS*, 1999]. Both path analysis and SEM are multiple regression techniques that allow for explicit analysis of the correlation among variables. In a path model, the magnitude of a path coefficient (i.e., a standardized regression coefficient) indicates the relative impact of the driver variable on the response variable. SEM is an extension of path analysis [*Shipley*, 1999; *Wright*, 1934] that allows an estimation of the appropriateness of the path model selection using a χ^2-test [*Mitchell*, 1992]. Our optimized path model provides a graphical cause-and-effect map that we use to examine the complex relationships between driving meteorological variables and vegetation responses. In this technique causality is assumed rather than demonstrated.

3. Results

3.1. Plant Phenology and Snow Climatology

[21] To give an overview of the phenology of plant growth and seasonal snow cover at our sites, we have computed some statistics on dates and periods defined in Figures 2 and 3 (see Table 4). The sites experienced on average 200 d/year during which a snow cover was present. The typical melt-out date was 27 May. The plants consistently waited two weeks after melt out before they began to grow. A similar "safety" period has been noted for arctic plants [*Jackson and Bliss*, 1984; *Ram et al.*, 1988; *Scott*, 1977; *Svoboda*, 1977; *Walker et al.*, 1995]. Probably not just coincidentally, it is the same period of two weeks after melt-out before episodic below-freezing temperatures ceased to occur at our sites (data not shown). Around 40 d after melt-out, the plants reached their maximum height (h_{max}). Given that the sites have on average 165 snow-free days, the growth period covered only a small fraction (1/4) of the potential growing season.

[22] The interannual variation in the dates for melt-out and for end of growth was almost the same (10.2 d, 10.4 d respectively). However, the variation in the length of the interval between these two dates (Δt_{GP}) was significantly smaller (6.4 d), indicating some direct link between the timing of the melt-out and of the plant growth phenology [cf. *Walker et al.*, 1995].

[23] As expected, there was a highly significant trend of smaller plants with increasing elevation. Moreover, melt-out occurred later with increasing altitude. We observed a delay of 3.5 to 4 d per 100 m at our sites, consistent with data in the literature [e.g., *Krautzer and Wittmann*, 2005]. In general, the timing of the plant development was delayed as a function of altitude, but the duration of the growth period remained approximately independent of altitude. Interestingly, the mean air temperature after melt-out was also uncorrelated with elevation ($p = 0.6$), as was the risk of post-melt-out frost ($p = 0.6$; dgs, see Table 2). Obviously, the effect of later melt-out with increasing altitude led to

Table 3. Factor Classes Used in Regression Analysis

Factor Class Function	Included Drivers
Timing and length of winter	Snow-up date, melt-out date, duration of SP3
Spring conditions	Air temperatures and precipitation during AP4 and SP4
Winter precipitation	Snow depth and precipitation during AP3 and SP3
Ephemeral snow in spring	Snow depth during SP4
Autumn temperatures	Air and soil temperatures during AP2 and SP2
Autumn precipitation	Precipitation during AP2 and SP2
Soil frost winter	Soil frost during AP3
Summer conditions[a]	Air temperature and precipitation during AP5 and SP5
Summer conditions previous year[a]	Air temperature and precipitation during AP1 and SP1
Ephemeral snow in autumn	Snow depth during SP2

[a]These two factor classes were merged when analyzing between-sites effects.

Table 4. Timing, Interannual Variability, and Altitudinal Trends of Growth and Climate

Phenology	Average Date or Duration	Interannual Variation[a]	Trend With Altitude Value at 2000 m	Gradient	Significance of Trend R^2	Significance of Trend p
Melt-out	27 May	10.2 days	25 May	+3.5 days/100 m	0.19	0.002
Beginning of growth	10 Jun	8.5 days	6 Jun	+5.1 days/100 m	0.43	0.000
End of growth	6 Jul	10.4 days	3 Jul	+4.0 days/100 m	0.24	0.001
Snow-up	9 Nov	14.0 days	No trend			
Growth period Δt_{gp}	39.5 days	6.4 days	No trend			
Snow-covered period SP3	200.1 days	18.3 days	196 days	+5.0 days/100 m	0.14	0.01
Max. vegetation height h_{max}				−3.7 cm/100 m	0.21	0.001

[a]One standard deviation.

similar temperature conditions after melt-out independent of elevation.

3.2. Identifying the Key Factors for Vegetation Growth

[24] The four best fit regression models are presented in Table 5. The explanatory variables listed in the table represent the key drivers with the strongest direct influence on plant growth at our sites. The results can be summarized as follows:

[25] 1. Air temperature and precipitation aggregated over SP2 (before snow-up) and SP4 (after melt-out) are the key meteorological factors.

[26] 2. The length of the snow covered period is the key timing factor.

[27] 3. Without exception, key drivers were aggregated over specific periods (SP), indicating that the timing of melt-out and snow-up dates is of paramount, albeit indirect importance.

[28] 4. Soil frost was not found to have a major influence on our plant growth indices. However, we noted an effect of air temperatures before snow-up when used as indirect indicator of frost (dgs, Table 2).

[29] 5. Of the above mentioned key drivers, only air temperature and precipitation after melt-out belong to the same factor class (Table 3).

[30] From these results, we were able to decide, which variables to include in the path models (Figures 4 and 5). As driving factors with direct links to the plant response variables, we used the key drivers (i.e., the explanatory variables) identified by the regression analysis (Table 5): duration of SP3, air temperature (dgs) during SP2, air temperature (m) during SP4, and precipitation during SP2. Only precipitation during SP4 was not included in the path models because it was collinear with the concurrent temperature variable (which appeared thrice in the best fit models). As indirect driving factors we used the two timing variables snow-up date and melt-out date. Given these preconditions, SEM helped us to optimize the detailed set-up of the path diagrams. The resulting model was applied to both between-sites and between-years analysis.

3.3. Between-Sites Effects

[31] The path diagrams (Figures 4 and 5) show a network of correlations between driving and response variables. To illustrate how to read these diagrams, we follow a path in Figure 4 that relates snow-up date to h_{max}: Places with earlier snow-up dates feature significantly higher temperatures before snow-up (p = ***, $R^2 = 0.7–0.8$), and places with higher temperatures before snow-up tend to attract taller plants (p = *, $R^2 = 0.2–0.3$). However, we note that there is an alternative link between snow-up date and plant height (via the length of the snow covered period), which dominates the overall effect between these two variables.

[32] Between-sites effects reflect how spatial differences in local climate influence the plant growth. As we have shown, site elevation is an important predictor for plant growth in alpine regions (Table 4). However, elevation itself has little direct relevance to plants. Rather, the elevation produces systematic variations in environmental drivers, and it is these that impact the plants. Here we intentionally exclude site elevation as an explicit factor so as not to confound the analysis for the climatologic drivers. Note also that variation in growth performance between sites may stem from differences in respective soils [*Körner*, 2003], which is not addressed in this paper.

[33] The path diagram (Figure 4) reveals that melt-out date is an important environmental driver of plant growth differences between sites. Although not directly linked to

Table 5. Best Fit Multiple Regression Models for Maximum Vegetation Height h_{max} and Length of the Growth Period Δt_{gp}[a]

Response Variable	Mode	Explanatory Variables Included in Best Fit Model (Standardized Coefficient β; Significance p)[b]	R^2	DOF
$\log(h_{max})$	Between sites	Duration of SP3 (−0.543; 0.000***)	0.300	77 + 3
		Air temperatures (dgs) during SP2 (0.388; 0.000***)		
		Air temperatures (m) during SP4 (0.323; 0.003**)		
Δt_{GP}	Between sites	Air temperatures (m) during SP4 (−0.582; 0.000***)	0.339	80 + 1
$\log(h_{max})$	Between years	Precipitation during SP2 (+0.300; 0.005**)	0.153	77 + 2
		Precipitation during SP4 (−0.254; 0.018*)		
Δt_{GP}	Between years	Air temperatures (m) during SP4 (−0.667; 0.000***)	0.445	80 + 1

[a]Terms and notation are discussed in section 2.
[b]Here ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

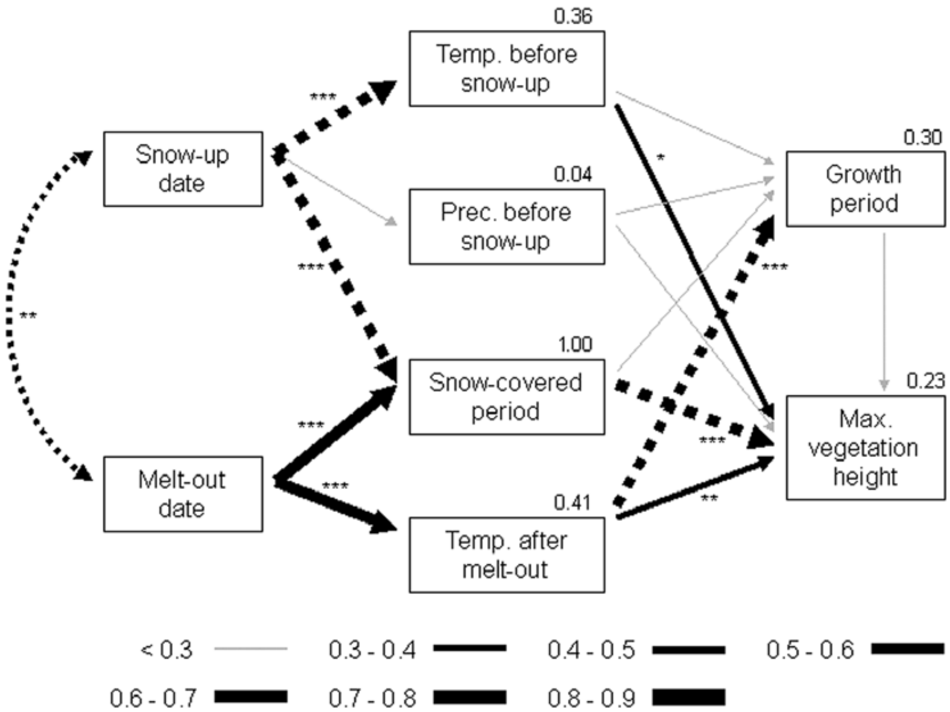

Figure 4. Path analysis diagram for between-sites effects. Values of the standardized regression coefficients are given by means of line weight (see inset legend), negative correlations are denoted by dotted lines, and positive correlations by solid lines, respectively. Multiple R^2 are given top right of the box of the respective response variable. The significance levels of correlations are denoted by *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$).

our growth indices, the melt-out date is closely associated with temperatures after melt-out and the duration of SP3. These two factors in turn display the strongest links to h_{max} and Δt_{gp}. More specific, sites with a late melt-out typically feature a longer-lasting seasonal snow cover and thus support plant communities with lower h_{max} values. At the same time, sites with a late melt-out also correspond to sites with warm temperatures after melt-out, which induce a

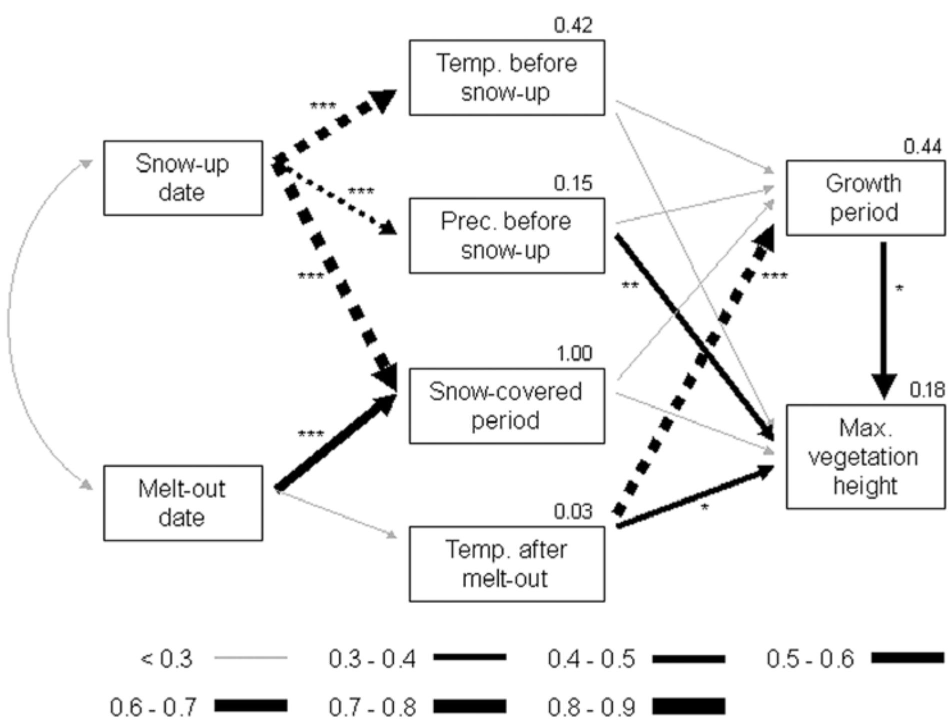

Figure 5. Path analysis diagram for between-years effects. Notation as in Figures 4.

shorter growth period. Both these effects are plausible considering the known propensity for plants to grow taller (1) at lower elevation where winter is shorter [*Ellenberg*, 1988] but also (2) along snow gradients from low to medium snow cover at the same elevation [*Friedel*, 1961].

[34] Interestingly, the correlation between melt-out date and maximum vegetation height is the result of a balance between two competing effects (lower half of Figure 4). Sites with a late melt-out on average feature long winters but also warm temperatures after melt-out. While the first effect is associated with lower vegetation, the opposite is the case for the second effect. In our data set the overall correlation between melt-out date and h_{max} is clearly dominated by the upper path (via duration of the snow covered period). However, the effect of the temperatures after melt-out (lower path) is not totally negligible. Perhaps one reason behind such complex plant growth behavior is that it entails a greater flexibility of alpine plant communities to climate variability. Note that also the association between snow-up dates and h_{max} constitutes a balance between two opposing effects (Figure 4). Here the lower path (via duration of the snow covered period) is superior to the upper path (via temperatures before snow-up). And thus, sites with an early onset of winter tended to attract plant communities with a lower h_{max}.

[35] Summarizing, winter length and temperatures after melt-out are the main direct drivers of plant growth differences between sites. However, it is striking that all strong correlations between explanatory variables and growth indices can be traced back further to snow-up and melt-out dates. Consequently, these timing variables must be of considerable indirect importance for plant growth in the Alps [see also *Friedel*, 1961; *Körner*, 2003].

3.4. Between-Years Effects

[36] Between-years effects consider the consequences of variations from average annual climate for the growth response of plant communities at given sites. The respective path diagram (Figure 5) reveals a very different driver-response pattern for between-years effects as compared to between-sites effects. Most remarkably and in contrast to Figure 4, the timing variables (snow-up and melt-out dates) are not indirectly associated with the growth response indices: not a single path between timing and growth variables consists of two considerably strong regressions. Also, the duration of the snow covered period is of no relevance to the plant growth with regards to between-years effects. Consistently, we found no response in the growth of the alpine plant communities investigated here to neither atypically short nor long winters. Similarly flexible growth behavior has also been found in other alpine and arctic vegetation types [e.g., *Muc*, 1977; *Walker et al.*, 1994]. We acknowledge, that atypical melt-out dates may entail frost damage or may influence plant reproduction rates [e.g., *Inouye*, 2000], however, such effects are not covered by our data set.

[37] Apart from timing issues there are considerable effects of interannual climate variations on plant growth. Again, spring temperatures influence growth speed, i.e., years with higher temperatures after melt-out typically displayed shorter growth periods. However, the effect of spring temperatures on the maximum vegetation height is more complex: while the direct path indicates that higher temperatures after melt-out had a positive effect on h_{max}, the opposite is the case when following the indirect path via Δt_{gp}. Here, the two effects counterbalance one another preventing any significant overall correlation between spring temperature and plant height.

[38] Finally, years with little precipitation before snow-up were found to result in smaller plants in the subsequent summer, an effect that has also been noted for alpine plant communities in the Rocky Mountains [*Walker et al.*, 1994]. Fall precipitation may influence nutrient uptake and storage late in the season. Moreover, many alpine plants preform leaf and flower buds in the previous year [*Billings and Mooney*, 1968] and may suffer from water shortage in autumn.

4. Discussion (Implications of Climate Change for Alpine Plant Communities)

[39] The combination of regression analysis with path diagrams specifically addressing between-years and between-sites effects reveals the complex response behavior of plant growth to climate variability in a way we believe is new and useful. First of all, the timing of melt-out and snow-up was found to be of remarkable (but indirect) importance to plant growth. For between-sites effects, all significant correlations between explanatory variables and plant growth indices featured strong connecting links to either snow-up or melt-out dates. We assume that persistent spatial patterns in timing of the snow season have led to long-term adjustments in plant species composition that ultimately caused the variation in growth performance between sites. Second, we identified temperature and precipitation before snow-up and after melt-out as the main climatologic drivers behind the observed spatial and temporal variability of plant growth. Of these, temperature after melt-out was the most relevant factor in both between-years and between-sites analysis. Our analysis thus implies that climate change affects alpine plant growth specifically by the interaction between shifts in the temperature-precipitation patterns with changes in the timing of the snow season. This finding is in general accordance with a large number of studies that have emphasized the importance of environmental variables related to snow cover on vegetation [e.g., *Choler*, 2005; *Schaefer and Messier*, 1995; *Sturm et al.*, 2001; *Walker et al.*, 1993].

[40] Perhaps a more novel finding is that the growth response to climate variability differed considerably depending on whether we analyzed for effects between years or between sites. Apart from differences between the specific correlations in Figures 4 and 5, the two path diagrams also differed by more general aspects. Between-years effects were generally less pronounced than between-sites effects. We interpret this to indicate that established plant communities have some flexibility in adjusting to interannual climate variations. Supporting this view, we observed that timing and length of the snow season did not lead to significant differences in plant growth between years. Also previous studies have concluded that the performance of arctic and alpine vegetation is rather conservative as an adaptation to the extreme environment and, therefore, shows little interannual variation [*Muc*, 1977; *Svoboda*, 1977; *Totland and Alatalo*, 2002; *Walker et al.*,

1994]. However, we believe the path analysis demonstrates the effect in a more specific and illustrative way.

[41] Our results allow assessing how alpine plant communities respond to climate change. For this purpose, it is important to carefully differentiate between effects that arise from (1) differences in species composition that have adapted to persistent spatial climate patterns (our between-sites effects), and from (2) the response of established species at a given site to interannual climate variations (our between-years effects). With this background, we argue that, at first, our between-years effects represent short-term responses of alpine plant communities to changing climate. If such climate perturbations become permanent, the growth performance will change with the species composition adapting to the new climate conditions. The long-term growth response to a persistent climate shift finally commences, when a new species composition is fully established. In analogy, we interpret our between-sites effects as representing the long-term responses of plant growth to persistent climate changes. Hence, our results reflect start and end point of the temporal trajectory of plant growth responses to a persistent shift in climate: between-years effects represent responses of a plant community at its present state, while between-sites effects represent responses of the vegetation after adapting to the new climate conditions. Several studies support this view, demonstrating that some alpine species have already shown upward migration in response to rising temperatures within the last decades [*Grabherr et al.*, 1994; *Keller et al.*, 2000; *Walther et al.*, 2005; see also *Tinner and Kaltenrieder*, 2005]. Moreover, the differences in our path diagrams (Figures 4 and 5) correspond to the conclusions of *Shaver et al.* [2000], who postulate very different short- and long-term effects in the response of arctic tundra to changing climate.

[42] Following the above approach, we apply our path diagrams to predict the growth response of alpine grasslands in Switzerland below 2500 m asl to expected climate change scenarios. However, we have to accept that predictive climate models available today do not yet provide projections for more complex indices such as temperatures after melt-out. Nevertheless, some conclusions can already be drawn.

[43] In the latest OcCC report [*OcCC-Consortium*, 2007] climate scenario calculations for the Swiss Alps are discussed in detail. According to these scenarios, by 2050 we can expect a temperature increase of 3°C in summer and 2°C in fall, winter, and spring. The summer precipitation will decrease by 20%, while the winter precipitation will increase by 10%. With a rising snow line, changes in temperature-precipitation patterns will only above 2000 m asl result in increasing amounts of snow in mid winter [*Abegg et al.*, 2007; *OcCC-Consortium*, 2007]. However, increasing peak snow depths will not necessarily translate into later melt-out dates, as at the same time warmer temperatures will also accelerate snow depletion. In fact, several recent studies consistently predict significantly earlier melt-out dates (by a few weeks), even at elevations between 2000 and 3000 m asl [*Beniston et al.*, 2003; *Jasper et al.*, 2004; *Keller et al.*, 2005]. Already melt-out records from the last 2–3 decades show a distinct trend toward earlier dates over mid elevation ranges [*Laternser and Schneebeli*, 2003; *Scherrer et al.*, 2004]. Even for records of Swiss stations up to 2500 m asl the same trend is visible, although less pronounced [*SLF*, 2006; see also *Beniston*, 2006].

[44] This climate scenario is specific enough to predict long-term effects on alpine plant communities using our path diagram in Figure 4. With earlier melt-out dates we expect a considerable shift in species composition favoring higher and faster growing plants. Thus, in the long run climate change will cause the alpine grasslands considered in this study to display enhanced biomass production. Unfortunately, short-term effects are harder to predict. In particular, we do not know how the combination of rising temperatures and earlier melt-out dates affect temperatures after melt-out. The same circumstances apply to predictions of precipitation before snow-up. But both environmental indices would be needed to also evaluate the short-term effects of climate change on alpine plant growth (see Figure 5).

5. Conclusions

[45] This study clarifies how the temporal and spatial variability of climate factors influences the growth performance of alpine grasslands. Based on climate and plant growth data from 17 sites in the Swiss Alps, our analysis revealed that plant growth was primarily controlled by climate factors aggregated in periods relative to melt-out and snow-up dates. In particular, we identified air temperature and precipitation after melt-out, and before snow-up respectively, as key meteorological factors that directly drove maximum plant height as well as growth rate. Variability of these environmental drivers between sites and between years had different effects on the growth response of the investigated plant communities. On the one hand, sites with a late melt-out typically experienced a longer seasonal snow cover and thus attracted plant communities with shorter vegetation. The same sites also featured warmer temperatures after melt-out, allowing for a faster growth. On the other hand, there was no correlation between the interannual variability of melt-out dates and our plant growth indices, i.e., plant height and growth speed. However, years with warm temperatures after melt-out resulted in a short growth period. Between-years effects were generally less pronounced than between-sites effects. This may be interpreted in a way that plant communities have some flexibility to interannual climate deviations.

[46] Given the clear differential responses of alpine plant communities to the temporal and spatial variability of temperature and precipitation, climate change scenarios as expected today are likely to have a significant impact on plant growth. In particular, earlier melt-out dates will cause a considerable shift in species composition favoring higher and faster growing plants. Thus, in the long run we expect alpine grasslands in the Alps to display an enhanced biomass production.

[47] **Acknowledgments.** We thank Sibyl Brugger for helping with the fieldwork, Werner Stahel for advising us with regards to the statistics, and Hansjörg Dietz and two anonymous reviewers for valuable comments on the manuscript. The precipitation data were provided by the Federal Office of Meteorology and Climatology MeteoSwiss. M. Sturm was supported by grants from the National Science Foundation-Office of Polar Programs.

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