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Object: Final response to bg-2015-9

Dear Editor,

I have completed revision of the manuscript "*Growth response of temperate mountain grasslands to inter-annual variations of snow cover duration*". I was pleased with the overall positive comments from the two reviewers and the associate editor, and I have endeavoured to incorporate suggestions into this revised version.

I have performed further analyses to specifically address comments from reviewer 2. Because they did not change the main conclusions of the paper, I propose to present these additional results in supplementary materials to keep the manuscript concise.

Below, I provide a point-by-point response to the reviewers' comments. The original reviewers' comments are indicated in italics while responses are in regular font. Note that I used blue text to keep track of changes made to the manuscript.

I think the manuscript has improved because of these changes and I thank you for considering it for publication in *Biogeosciences*.

Yours sincerely,

Dr. Philippe Choler

REVIEWER #1

General comments:
The manuscript "Growth response of temperate mountain grasslands to inter-annual variations of snow cover duration" discusses the influence of snow and other meteorological drivers on grassland growth. This study shows the importance of the growing season length and especially autumn dynamics on yearly productivity. The manuscript was a joy to read and I have little or no comments on either methodology or the overall manuscript structure. The path analysis was new to me, and provides a refreshing (visual) way to analyze causative relationships between variables.

I thank reviewer #1 for this positive assessment of the manuscript.

Although, it's my opinion that there might be room for some discussion on snow-removal or freeze-thaw experiments. Although the study addresses changes under current climate conditions, the author mentions potential consequences of changes in snow melt dates due to climate change.
Within this context, the potential absence of snow (for part of the winter) is also a potential scenario, increasing freeze-thaw cycles. Discussing this line of research would marry the author's observational analysis with experimental work and further strengthen the manuscript. Below I attached some references potential references. However, I'll leave including this discussion to the discretion of the author as it will only strengthen the manuscript but does not influence its current merit.
Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods JA Dunne, J Harte, KJ Taylor - Ecological Monographs, 2003
Recurrent soil freeze–thaw cycles enhance grassland productivity J Kreyling, C Beierkuhnlein, K Pritsch. . . - New Phytologist, 2008

I fully agree that the lack of snow or the presence of a shallow snowpack during winter have strong impacts on the current distribution of plant and soil microbial communities and on ecosystem functioning. This has been shown in local-scale studies we conducted in alpine pastures (e.g. Zinger, L & al. 2009, Baptist & al. 2010). In the context of this study, it would have been highly relevant to not only to test for the effect of presence-absence of snow, but also for the effect of snowpack height and, most importantly, soil temperature on the growth of pastures across the examined mountain ranges. The modelling of alpine soil tempratures at different soil depths using the SAFRAN-CROCUS-MEPRA modelling platform is currently under development and there will be future opportunities to examine these linkages at the regional scale. This point has been included in the discussion and the suggested references have been added (lines 466-477).

Finally an open question for the author; given that all meteorological drivers are available why not pursue / include a modelling approach using the simple framework as presented previously (2010 Biogeosciences / Ecosystems)?

Although it would be beyond the scope of this work to propose a process-based, dynamic modelling of the growth of alpine pastures in response to environmental forcing, I am convinced that this study opens the way to such developments. A sentence has been added in the conclusions to mention this perspective (lines 546-548). .

REVIEWER #2

The manuscript from Choler entitled "Growth response of temperate mountain grasslands to inter-annual variations of snow cover duration" shows a novel analysis conducted in the French Alps using satellite *data and downscaled meteorological forcing to determine: first, the relative contribution of the growing season length and maximum normalized difference vegetation index (NDVImax) in determining the inter-annual variations of primary productivity; second, to evaluate the effects of snow-cover on phenology and productivity. Last but not least, Choler analyzes the sensitivity of the integral of NDVI to inter-annual variations of temperature and precipitation during the growing season. By using a hierarchical path analysis, the author concludes that inter-annual variations in the integral of NDVI are driven by year-to-year variations in the length of the snow-free period. The author also demonstrates that the period spanning from peak standing biomass to the first snowfall accounted for two thirds of NDVIint. The article is clearly written, despite many typos that need to be corrected (please see minor comments below) and the analysis is well conceived. The result that the integral of NDVI from the peak of the season to the first snowfall controls the inter-annual variability of the productivity in these ecosystems is novel and interesting. As well as the combined use of the normalized difference snow index (NDSI) and NDVI to derive the length of the snow-free period. I strongly recommend this paper for publication in Biogeoscience.*

I thank reviewer #2 for this positive assessment of the manuscript.

However, I would encourage the author to describe better some of the assumptions, which can have important impacts on some of the results. For instance the assumption that the integral of NDVI times PAR is the productivity of the ecosystem is strong. In these ecosystems NDVI tends to be quite impacted in the senescence period (mainly due to the dry/green ratio and canopy structure), vegetation indices more related to the green biomass can better approximate productivity in the senescence period. Enhanced Vegetation Index could be in this case a good substitution of NDVI, as well as other indices based on the red-edge portion of the spectrum. An analysis showing that the integral of EVI and NDVI in the senescence phase are unbiased would be convincing.

I agree that several sources of uncertainties may affect the estimate of GPP from remotely sensed data. However, the focus of the study is to examine <u>inter-annual variations</u> of proxies of GPP in response to meteorological drivers. Thus, the key assumption is that these sources of uncertainties remain consistent across years for a given polygon. I have made this point stronger in the discussion (lines 518-531).

As mentionned in the first version of the manuscript (lines 216-217), I did not find any significant change when EVI was used instead of NDVI. In particular, the period spanning from peak standing biomass to the first snowfall accounted for two thirds of EVIIint, as is the case for NDVIint. Inter-annual variations in EVIint are of the same order of magnitude as those for NDVIint. Path coefficients are also very similar whatever the vegetation index. To address this point, I have added a figure in Supplementary Material (Fig. S3) and added a section in Material and Methods the text (lines 235-244).

As suggested, I have further discussed the risk of overweighting the contribution of the senescing period to the yearly productivity when using NDVI. I also mentionned than comparative studies using MODIS-derived (NDVI, EVI) and MERIS-derived (MTCI) vegetation indexes would represent an interesting follow-up study (lines 510-517).

Also the assumption that the light use efficiency is constant across all the 121 sites used is strong. In my opinion using a light use efficiency model for this analysis, that links timing and integrals of NDVI, is probably not going to change the main outcomes, but I would encourage the author to mention that the direct translation between integrals of NDVI times PAR and productivity is not always robust. At page 20 line 8 the author assumes that LUE is constant in each polygon. But in my opinion here is maintained constant across all the polygons. Please discuss the limitations.

It is true that I have considered LUE as a constant across polygons and years. There is still a debate on the relevance of using vegetation specific LUE in remote sensing studies of productivity. Following the meta-analysis of Yuan & al. (2014) I have made the assumption that variations in light-use efficiency are adequately captured by variations in NDVI because this vegetation index well correlates with structural and physiological properties of canopies (e.g. leaf area index, chlorophyll). Following reviewer's suggestion, I have made this point clearer in the discussion (lines 518-531).

As mentioned before, the combined use of NDSI and NDVI is of great interest and a novel contribution to the field. The use of the criteria NDSI/NDVI < 1 to estimate the length of the snow-free period is arbitrary as almost all the thresholds applied in the phenology field. I suggest testing how much sensitive is the snow-free season length to different selections of NDSI/NDVI. Would be also beneficial an evaluation of the threshold using data from high-resolution satellite data or in sites with phenological cameras where the snow-free period can be easily identified.

This revised version includes two supplementary figures related to the use of the NDVI/NDSI ratio. Figure S2 shows that the length of the snow free period (Psf) is relatively insensitive to variations in NDVI/NDSI thresholds. Changes of this ratio within the range 0.9 - 1.1 leads to a Psf increase/decrease of less than 3 days. In addition, this has no impact on the main results of the path analysis.

Unfortunately, there are not enough ground-based observations to evaluate the accuracy of the remotely sensed estimates of TSNOWmelt and TSNOWfall at the scale of this study. Figure S1 presents data collected at one site (corresponding to one MOD09A1 pixel) from 2012 onwards. Ground truthing includes visual inspection of the site, analysis of images acquired with time-lapse cameras and continuous monitoring of soil temperature and snow height. It is shown that the NDVI/NDSI ratio provides a good estimate of snowcover dynamics at that site.

Up to now, the use of high-resolution remote sensing data to evaluate the performance of the method has been hindered by the insufficient temporal coverage of these images and the difficulties in implementing spatially explicit gap-filling methods to provide continuous time series of the presence/absence of snow at high spatial resolution. I referred to a recent study we conducted in a high elevation watershed to illustrate the challenges of this kind of study (Carlson & al. 2015).

To address this specific point, I have modified the Material and Methods section (lines 196-207) and the discussion (lines 398-406).

At page 15 line 25 the author writes "Essentially, the two contrasting scenarios for the initial period of growth observed in this study were either a fast growth rate during a shortened growing period in the case of a delayed snowmelt, or a lower growth rate over a prolonged period following a warm spring". The author discusses this statement as follow: "Alltogether, these results strongly suggest that intrinsic growth constraints limit the ability of high elevation grasslands to enhance their growth under ameliorated atmospheric conditions. Other severely limiting factors – including nutrient availability in the soil – may explain this low responsiveness . . .." I fully agree with this explanation, but there are few papers recently published that showed that another explanation could be to the different phenologies of the different species/communities of the grassland. For instance, consistently to this study, Julitta et al., (2014) shows a lower rate of increase of the green chromatic coordinates (gcc) derived from digital repeated photography in springs with exceptional early snow-melt. However, Julitta et al found that the ecosystem-level phenology was the combined effect of the different phenology of the two main communities (forbs and grass) present at the site that respond in a completely different way to early and late snow-melt, and spring photoperiod and temperature. The interannual variability of gcc extracted for each community was instead less pronounced than the one observed at the ecosystem level. I would suggest to the author to add these considerations.

This point has been included in the discussion (lines 454-456).

As a minor comment I suggest the author to double-check for spelling the article. For example: P2 line 15 "negligeable" P3 line 24 "seasonaly" P4 line 1 "reponse" P4 line 23 "reolution" P16 line 11 "Alltogether"

The manuscript was reviewed to correct typos.

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Title

Growth response of temperate mountain grasslands to inter-annual variations of snow cover duration

Running title

Growth response of grasslands to snow cover duration

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ABSTRACT (284 WORDS)

A remote sensing approach is used to examine the direct and indirect effects of snow cover duration and weather conditions on the growth response of mountain grasslands located above the tree line in the French Alps. Time-integrated Normalized Difference Vegetation Index (NDVIint), used as a surrogate for aboveground primary productivity, and snow cover duration were derived from a 13-year long time series of the Moderate Resolution Imaging Spectro-radiometer (MODIS). A regional-scale meteorological forcing that accounted for topographical effects was provided by the SAFRAN–CROCUS–MEPRA model chain. A hierarchical path analysis was developed to analyze the multivariate causal relationships between forcing variables and proxies of primary productivity. Inter-annual variations in primary productivity were primarily governed by year-to-year variations in the length of the snow-free period and to a much lesser extent by temperature and precipitation during the growing season. A prolonged snow cover reduces the number and magnitude of frost events during the initial growth period but this has a negligible impact on NDVIint as compared to the strong negative effect of a delayed snow melting. The maximum NDVI slightly responded to increased summer precipitation and temperature but the impact on productivity was weak. The period spanning from peak standing biomass to the first snowfall accounted for two thirds of NDVIint and this explained the high sensitivity of NDVIint to autumn temperature and autumn rainfall that control the timing of the first snowfall. The ability of mountain plants to maintain green tissues during the whole snow-free period along with the relatively low responsiveness of peak standing biomass to summer meteorological conditions led to the conclusion that the length of the snow-free period is the primary driver of the inter-annual variations in primary productivity of mountain grasslands.

Introduction

Temperate mountain grasslands are seasonally snow-covered ecosystems that have to cope with a limited period of growth (Körner, 1999). The extent to which the length of the snow-free period controls the primary production of mountain grasslands is still debated. On the one hand, snow cover manipulation experiments and time series analyses of ground-based measurements generally showed a decrease in biomass production under shortened growing season length (Wipf and Rixen, 2010; Rammig et al., 2010). On the other hand, several studies pointed to the increasing risk of spring frost damage and summer water shortage following an early snowmelt and the associated detrimental effects on biomass production (Baptist et al., 2010; Ernakovich et al., 2014; Inouye, 2000). In addition, both soil microbial nitrogen immobilization and accumulation of inorganic nitrogen are enhanced under deep and long-lasting snowpacks (Brooks et al., 1998), and plants may benefit from increased flush of nutrients and ameliorated soil water balance following unusually long winters. To better understand the growth response of alpine grasslands to changing snow cover duration it thus seems pivotal (i) to assess the contribution of the different components of the growth response, particularly the duration of the favorable period of growth and the peak standing biomass; (ii) to account for the effect of meteorological forcing variables on both snow cover dynamics and on plant growth, and (iii) to disentangle the direct and indirect effects, i.e. effects mediated by other forcing variables, of snow cover on land surface phenology and primary productivity.

From a phenomenological point of view, annual primary production may be viewed as the outcome of two things namely the time available for biomass production and the amount of biomass produced per unit of time. For seasonally snow-covered ecosystems, this translates into two fundamental questions: to what extent does the length of the snow-free period determine the length of plant activity? and (ii) what are the main drivers controlling the instantaneous primary production rate of grasslands during the snow-free period? A number of studies have provided evidence for the non-independence of these two facets of growth response by noting that the biomass production rate increases when snow melting is delayed and that grasslands are able to partially recover the time lost when the winter was atypically long (Walker et al., 1994; Jonas et al., 2008). However, most of these studies focused on the initial period of growth - i.e. from the onset of greenness to the time of peak standing biomass - and therefore little is known about the overall relationship between the mean production rate and the total length of the snow-free period. Eddy covariance measurements have shown that the amount of carbon fixed from the peak standing biomass to the first snowfall represents a significant contribution to the Gross Primary Productivity (GPP) (e.g. Rossini et al., 2012). Accounting for the full period of plant activity when examining how primary production of grasslands adjusts to inter-annual variations in meteorological conditions seems thus essential.

Remote sensing provides invaluable data for tracking ecosystem phenology over broad spatial scale as well as inter-annual variations of phenological stages over extended time periods (Pettorelli et al., 2005). For temperature-limited ecosystems, numerous studies focused on arctic areas have established that the observed decadal trend toward an earlier snowmelt has translated into extended growing season and enhanced greenness (Myneni et al., 1997; Jia et al., 2003). By contrast, the phenology of high elevation grasslands has not received the same degree of attention, partly because there are a number of methodological problems in using remote sensing data in topographically complex terrain, including scale mismatches, geolocation errors, and vegetation heterogeneity (Fontana et al., 2009; Tan et al., 2006). That said, some studies have used moderate resolution imagery to document the contrasting responses of low and high vegetation to the 2003 heat wave in the Alps (Jolly, 2005; Reichstein et al., 2007) or to characterize the land surface phenology of high elevation areas in the Rockies (Dunn and de Beurs, 2011), the Alps (Fontana et al., 2008) or the Tibetan plateau (Li et al., 2007). However, none of these studies has comprehensively examined the direct and indirect effect of meteorological forcing variables and snow cover duration on the different components of annual biomass production in mountain grasslands.

In this paper, I used remotely sensed time series of the Normalized Difference Snow index (NDSI) and of the Normalized Difference Vegetation Index (NDVI) to characterize snow cover dynamics and growth response of mountain grasslands. Time-integrated NDVI (NDVIint) and the product of NDVI and Photosynthetically Active Radiation (PAR) were taken as surrogates of aboveground primary productivity, while maximum NDVI (NDVImax) was used as an indicator of growth responsiveness to weather conditions during the summer. My main aim is to decipher the interplay of snow cover dynamics, weather conditions and growth responsiveness affecting NDVIint. Specifically, I addressed three questions: (i) What is the relative contribution of the growing season length and NDVImax in determining the inter-annual variations of primary productivity ? (ii) What are the direct and indirect effects of the snow cover dynamics on productivity ? and (iii) What is the sensitivity of NDVIint to inter-annual variations in temperature and precipitation during the growing season? The study was based on 121 grassland-covered high elevation sites located in the French Alps. Sites were chosen to enable a remote sensing characterization of their land surface phenology using the Moderate Resolution Imaging Spectro-radiometer (MODIS). Meteorological forcing was provided by the

SAFRAN–CROCUS–MEPRA model chain that accounts for topographical effects (Durand et al., 2009c). I implemented a hierarchical path analysis to analyze the multivariate causal relationships between meteorological forcing, snow cover, and NDVI-derived proxies of grassland phenology and primary productivity.

Material and methods

Selection of study sites

The selection of sites across the French Alps was made by combining several georeferenced databases and expert knowledge. My primary source of information was the 100 m-resolution CORINE land cover 2000 database produced by the European Topic Centre on Spatial Information and Analysis (Commission of the European Communities, 1994) that identifies 44 land cover classes based on the visual interpretation of high-resolution satellite images and from which I selected the class 3.2.1 corresponding to 'Natural grasslands'. Natural grasslands located between 2000 m and 2600 m above sea level were extracted using a 50 m-resolution Digital Elevation Model from the Institut Géographique National (IGN). I then calculated the perimeter (P), area (A) and the mean slope of each resulting group of adjacent pixels, hereafter referred as polygons, and kept only those that had an area greater than 20 ha, an index of compactness ($C= 4\pi A/P^2$) greater than 0.1, and a mean slope smaller than 10°. The first two criteria ensured that polygons were large enough and sufficiently round-shaped to include several 250m MODIS contiguous cells and to limit edge effects. The third criterion reduced the uncertainty in reflectance estimates associated with steep slopes and different aspects within the same polygon. Moreover, steep slopes usually exhibit sparser plant cover with low seasonal amplitude of NDVI, which reduces the signal to noise ratio of remote sensing data. Finally, I visually double-checked the land cover of all polygons by using 50 cm-resolution aerial photographs from 2008 or 2009. This last step was required to discard polygons located within ski-resorts and possibly including patches of sown grasslands, and polygons too close to mountain lakes and including swampy vegetation. I also verified that all polygons were located above the treeline.

Climate data

Time series of temperature, precipitation and incoming short-wave radiation were estimated by the SAFRAN–CROCUS–MEPRA meteorological model developed by Meteo-France for the French Alps. Details on input data, methodology, and validation of this model are provided in Durand & al. (2009a; 2009b). To summarize, the model combines observed data from a network of weather stations and estimates from numerical weather forecasting models to provide hourly data of atmospheric parameters including air temperature, precipitation and incoming solar radiation. Simulations are performed for twenty-three different massifs of the French Alps (Fig. 1), each of which is subdivided according to the following topographic classes: 300 m elevation bands, seven slope aspect classes (north, flat, east, south-east, south, south-west and west) and two slope classes (20° or 40°). The delineation of massifs was based on both climatological homogeneity, especially precipitation, and physiographic features. To date, SAFRAN is the only operational product that accounts for topographic features in modelling meteorological land surface parameters for the different massifs of the French Alps.

MODIS data

The MOD09A1 and MOD09Q1 surface reflectance products corresponding to tile h18.v4 (40◦N-50◦N, 0◦E-15.6◦E) were downloaded from the Land Processes Distributed Active Archive Center (LP DAAC) (ftp://e4ftl01.cr.usgs.gov). A total of 499 scenes covering the period from 18-02-2000 to 27-12-2012 were acquired for further processing. Data are composite reflectance, i.e. representing the highest observed value over an 8-day period. Surface reflectance in the red (RED), green (GREEN), near-infrared (NIR) and mid-infrared (MIR) were used to calculate a Normalized Difference Vegetation Index (NDVI) at 250 m following:

$$NDVI = (NIR - RED) / (NIR + RED) \qquad \text{(eqn. 1)}$$

and a Normalized Difference Snow Index (NDSI) at 500 m using the algorithm implemented in Salomonson and Appel (2004):

$$NDSI = (GREEN - MIR) / (GREEN + MIR) \qquad \text{(eqn. 2)}$$

NDVI and NDSI values were averaged for each polygon. Missing or low quality data were identified by examining quality assurance information contained in MOD09Q1 products and interpolated using cubic smoothing spline. NDVI or NDSI values that were two times larger or smaller than the average of the two preceding values and the two following values were considered as outliers and discarded. Time series were gap-filled using cubic spline interpolation and smoothed using the Savitzky-Golay filter with a moving window of length $n = 2$ and a quadratic polynomial fitted to $2n + 1$ points (Savitzky and Golay, 1964).

A high NDSI and low NDVI were indicative of wintertime whereas a low NDSI and a high NDVI were indicative of the growing season (Fig. 2). Here I used the criteria $NDSI / NDVI < 1$ to estimate the length of the snow-free period, hereafter referred as Psf, at the polygon level (Fig. 2). This ratio was chosen as a simple and consistent way to set the start (TSNOWmelt) and the end (TSNOWfall) of the snow-free period across polygons and years. Ground-based observations corresponding to one MOD09A1 pixel (Lautaret pass, 6.4170° longitude and 45.0402° latitude) and including visual inspection, analysis of images acquired with time-lapse cameras and continuous monitoring of soil temperature and snow height showed that this ratio provides a fair estimate of snowcover dynamics (Fig. S1). Further analyses also indicated that Psf is relatively insensitive to changes in the NDVI/NDSI thresholds with 95% of the polygon x year combinations exhibiting less than 2 days of shortening when the threshold was set to 1.1 and less than 3 days of lengthening when the threshold was set to 0.9 (Fig. S2). Finally, changing the threshold within this range had no impact on the main results of the path analysis. The yearly maximum NDVI value (NDVImax) was calculated as the average of the three highest daily consecutive values of NDVI and the corresponding middle date was noted TNDVImax.

The Gross Primary Productivity (GPP) of grasslands could be derived from remote sensing data following a framework originally published by Monteith (Monteith, 1977). In this approach, GPP is modelled as the product of the incident Photosynthetically Active Radiation (PAR), the fraction of PAR absorbed by vegetation (fPAR) and a light-use efficiency parameter (LUE) that expresses the efficiency of light conversion to carbon fixation. It has been shown that fPAR can linearly related to vegetation indices under a large combination of vegetation, soil– and atmospheric conditions (Myneni and Williams, 1994). Assuming that LUE was constant for a given polygon, I therefore approximated inter-annual variations of GPP using the time-integrated value of the product NDVI x PAR, hereafter referred as GPPint, over the growing season and calculated as follows:

$$\text{GPPint} \sim \sum_{t=1}^{T} \text{NDVI}_t \times \text{PAR}_t \qquad \text{(eqn. 3)}$$

where T is the number of days for which NDVI was above NDVIthr. I set NDVIthr = 0.1 having observed lower NDVI usually corresponded to partially snow-covered sites and or to senescent canopies (Fig. 2). The main findings of this study did not change when I varied NDVIthr in the range 0.05-0.15. As a simpler alternative to GPPint, i.e. not accounting for incoming solar radiation, I also calculated the time-integrated value of NDVI, hereafter referred as NDVIint following:

$$\mathrm{NDVIint} = \sum_{t=1}^{T} \mathrm{NDVI}_t \qquad \text{(eqn. 4)}$$

The periods from the beginning of the snow-free period to TNDVImax, hereafter referred as Pg, and from TNDVImax to the end of the first snowfall, hereafter referred as Ps, were used to decompose productivity into two components: NDVIintg and GPPintg, and NVIints and GPPints (Fig. 2). Note that the suffix letters g and s are used to refer to the first and the second part of the growing season, respectively.

The whole analysis was also conducted with the Enhanced Vegetation Index (Huete et al., 2002) instead of NDVI. The rationale for this alternative was to select a vegetation index which was more related to the green biomass and thus may better approximate GPP especially during the senescence period. I did not find any significant change in the main results when using EVI. In particular, the period spanning from peak standing biomass to the first snowfall accounted for two thirds of EVIint as is the case for NDVIint (Fig. S3A) and inter-annual variations in EVIint were of the same order of magnitude as those for NDVIint (Fig. S3B). Because results from the path analysis (see below) were also very similar with EVI-based proxies of productivity, I chose to present NDVI-based results only.

Path analysis

Path analysis represents an appropriate statistical framework to model multivariate causal relationships among observed variables (Grace et al., 2010). Here, I examined different causal hypotheses of the cascading effects of meteorological forcing, snow cover duration and phenological parameters (TNDVImax, Pg, and Ps) on NDVIint and GPPint. To better contrast the processes involved during different stages of the growing season, separate models were implemented for the period of growth and the period of senescence. The set of causal assumptions is represented using directed acyclic graphs in which arrows indicate which variables are influencing (and are influenced by) other variables. These graphs may include both direct and indirect effects. An indirect effect of X1 on Y means that the effect of X1 is mediated by another variable (for example X1->X2->Y). Path analysis tests the degree to which patterns of variance and covariance in the data are consistent with hypothesized causal links. To develop this analysis, three main assumptions have been made: (i) that the graphs do not include feedbacks (for example, X1->X2->Y->X2); (ii) that the relationships among variables can be described by linear models and (iii) that annual observations are independent, i.e. the growth response in year n is not influenced by previous years because of carryover effects.

Since I chose to focus on the inter-annual variability of growth response, I removed between-site variability by calculating standardized anomalies for each polygon. Standardized anomalies were calculated by dividing annual anomalies by the standard deviation of the time series making the magnitude of the anomalies comparable among sites.

For each causal diagram, partial regression coefficients were estimated for the whole dataset and for each polygon. These coefficients measure the extent of an effect of one variable on another while controlling for other variables. Model estimates were based on maximum likelihood, and Akaike Information Criterion (AIC) was used to compare performance among competing models. Only ecologically meaningful relationships were tested. The model with the lowest AIC was retained as being the most consistent with observed data.

I used the R software environment (R Development Core Team, 2010) to perform all statistical analyses. Path coefficients and model fit were estimated using the package *lavaan* (Rosseel, 2012).

Results

One hundred and twenty polygons fulfilling the selection criteria were included in the analyses. These polygons spanned 2° of latitude and more than 1° of longitude and were distributed across seventeen massifs of the French Alps from the Northern part of Mercantour to the Mont-Blanc massif (Fig. 1). Their mean elevation ranged from 1998 m to 2592 m with a median of 2250 m. Noticeably, many polygons were located in the Southern and in the innermost part of the French Alps where high elevation landscapes with grassland-covered gentle slopes are more frequent essentially because of the occurrence of flysch, a bedrock on which deep soil formation is facilitated.

A typical yearly course of NDVI and NDSI is shown in Figure 2. The date at which the NDSI/NDVI ratio crosses the threshold of one was very close to the date at which NDVI crosses the threshold of 0.1. On average, NDVImax was reached fifty days after snowmelt, a period corresponding to only one third of the length of the snow-free period (Fig. 3A). Similarly, NDVIg accounted for one third of the NDVIint (Fig. 3B). The contribution of the first part of season was slightly higher for GPPint though it largely remained under 50% (Fig. 3C). Thus, the maintained vegetation greenness from TNDVImax to TSNOWfall explained the dominant contribution of the second part of the growing season to NDVI-derived proxies of grassland productivity.

Most of the variance in NDVIint and GPPint was accounted for by between-polygon variations that were higher during the period of senescence compared to the period of growth (Table 1). Inter-annual variations of NDVIint and GPPint represented 25% of the total variance and were particularly pronounced at the end of the examined period with the best year (2011) sandwiched by two (2010, 2012) of the three worst years (Fig. 4A). The two likely proximal causes of these inter-annual variations, i.e. Psf and NDVImax, showed highly contrasted variance partitioning. Between-year variation in Psf was four to five times higher than that of NDVImax (Table 1). The standardized inter-annual anomalies of Psf showed remarkable similarities with those of NDVIint and GPPint both in terms of magnitude and direction (Fig. 4B). By contrast, the small inter-annual variations of NDVImax did not relate to inter-annual variations of NDVIint or GPPint (Fig. 4C). For example, the year 2010 had the strongest negative anomaly for both Psf and NDVIint whereas the NDVImax anomaly was positive. There were some discrepancies between the two proxies of primary productivity. For example, the heat wave of 2003, which yielded the highest NDVImax, exhibited a much stronger positive anomaly for GPPint than for NDVIint and this was due to the unusually high frequency of clear sky during this particular summer.

The path analysis confirmed that the positive effect of the length of the period available for plant activity largely surpassed that of NDVImax to explain inter-annual variations of NDVIint and GPPint. This held true for NDVIintg or GPPintg - with an over dominating effect of Pg (Fig. 5A, C) - and for NDVIints or GPPints - with an over dominating effect of Ps (Fig. 5B, D). There was some support for an indirect effect of Pg on productivity mediated by NDVImax, as removing the path Pg-> NDVImax in the model decreased its performance (Table 2). In addition to shortening the time available for growth and reducing primary productivity, a delayed snowmelt also significantly decreased the number of frost events and this had a weak positive effect on both NDVIintg and GPPintg (Fig. 5A, C). However, this positive and indirect effect of TSNOWmelt on productivity, which amounts to (-0.46) x (-0.08) = 0.04 for NDVIintg and (-0.46) x (-0.13) = 0.06 for GPPintg, was small compared to the negative effect of TSNOWmelt on NDVIintg (-1 x 0.96 for NDVIintg and -1 x 0.95 for GPPintg). Apart from its effect on frost events and Ps, TSNOWmelt had also a significant positive effect on TNDVImax with a path coefficient of 0.57, signifying that grasslands partially recover the time lost because of a long winter to reach peak standing biomass. On average, a one-day delay in the snowmelt date translates to a 0.5-day delay in TNDVImax (Fig. S4A).

Compared to snow-cover dynamics, weather conditions during the growing period had relatively small effects on both NDVImax and productivity (Fig. 5). For example, removing the effects of temperature on NDVImax and precipitation on NDVIintg did not change model fit (Table 2). The most significant positive effects of weather conditions were observed during the senescence period and more specifically for GPPints with a strong positive effect of temperature (Fig. 5D). The impact of warm and dry days on incoming radiation explained why more pronounced effects of temperature and precipitation are observed for GPPint (Fig. 5D), which is dependent upon PAR (see eqn. 3), than for NDVIint (Fig. 5B).

Meteorological variables governing snow cover dynamics had a strong impact on primary productivity (Fig. 5). A warm spring advancing snowmelt translated into a significant positive effect on NDVIintg and GPPintg - an indirect effect which amounts to (-0.62) x (-1) x 0.95 =0.59 (Fig. 5A, C). Heavy precipitation and low temperature in October-November caused early snowfall and shortened Ps, which severely reduced NDVIints and GPPints (Fig. 5B, D). Overall, given that the senescence period accounted for two thirds of the annual productivity (Fig. 3B, C), the determinants of the first snowfall were of paramount importance for explaining inter-annual variations of NDVIint and GPPint.

Path coefficients estimated for each polygon showed that the magnitude and direction of the direct and indirect effects were highly conserved across the polygons. The climatology of each polygon was estimated by averaging growing season temperature and precipitation across the 13 years. Whatever the path coefficient, neither of these two variables explained more than 8% of variance of the between-polygon variation (Table 3). The two observed trends were (i) a greater positive effect of NDVImax on NDVIintg in polygons receiving more rainfall, which was consistent with the significant effect of precipitation on NDVImax (Fig. 5A) and (ii) a smaller effect of temperature and Ps on GPPints and NDVIints, respectively, suggesting that the coldest polygons were less responsive to increased temperatures or lengthening of the growing period (see discussion).

Discussion

Using a remote sensing approach, I showed that inter-annual variability in NDVI-derived proxies of productivity in alpine grasslands was primarily governed by variations in the length of the snow-free period. As a consequence, meteorological variables controlling snow cover dynamics are of paramount importance to understand how grassland growth adjusts to changing conditions. This was especially true for the determinants of the first snowfall, given that the period spanning from the peak standing biomass onwards accounted for two-thirds of annual grassland productivity. By contrast, NDVImax - taken as an indicator of growth responsiveness - showed small inter-annual variation and weak sensitivity to summer temperature and precipitation. Overall, these results highlighted the ability of grasslands to track inter-annual variability in the timing of the favorable season by maintaining green tissues during the whole snow-free period and their relative inability to modify the magnitude of the growth response to the prevailing meteorological conditions during the summer. I discuss below these main findings in light of our current understanding of extrinsic and intrinsic factors controlling alpine grassland phenology and growth.

In spring, the sharp decrease of NDSI and the initial increase of NDVI were simultaneous events (Fig. 2). Previous reports have shown that NDVI may increase independently of greenness during the snow melting period (Dye and Tucker, 2003) and this has led to the search for vegetation indices other than NDVI to precisely estimate the onset of greenness in snow-covered ecosystems (Delbart et al., 2006). Here I did not consider that the period of plant activity started with the initial increase of NDVI. Instead I combined NDVI and NDSI indices to estimate the date of snowmelt and then used a threshold value of NDVI = 0.1 before integrating NDVI over time. By doing this, I strongly reduced the confounding effect of snowmelt on the estimate of the onset of greenness. That said, a remote sensing phenology may fail to accurately capture the onset of greenness for many other reasons, including smoothing procedures applied to NDVI time series, inadequate thresholds, geolocation uncertainties, mountain terrain complexity and vegetation heterogeneity (Cleland et al., 2007; Tan et al., 2006; Dunn and de Beurs, 2011; Doktor et al., 2009). Assessing the magnitude of this error is difficult as there have been very few studies comparing ground-based phenological measurements with remote sensing data, and furthermore most of the available studies have focused on deciduous forests (Hmimina et al., 2013; Busetto et al., 2010; but see Fontana et al., 2008). Ground-based observations collected at one high elevation site and corresponding to a single MOD09A1 pixel provide preliminary evidence that the NDVI/NDSI criterion adequately captures snowcover dynamics (Fig. S3). Further studies are needed to evaluate the performance of this metric at a regional scale. For example, the analysis of high-resolution remote sensing data with sufficient temporal coverage is a promising way to monitor snow cover dynamics in complex alpine terrain and to assess its impact on the growth of alpine grasslands (Carlson et al., 2015). Such an analysis has yet to be done at a regional scale. Despite these limitations, I am confident that the MODIS-derived phenology is appropriate for addressing inter-annual variations of NDVIint because: (i) the start of the season shows low NDVI values and thus uncertainty in the green-up date will marginally affect integrated values of NDVI and GPP, and (ii) beyond errors in estimating absolute dates, remote sensing has been shown to adequately capture the inter-annual patterns of phenology for a given area (Fisher and Mustard, 2007; Studer et al., 2007), and this is precisely what is undertaken here.

Regardless of the length of the winter, there was no significant time lag between snow disappearance and leaf greening at the polygon level. This is in agreement with many field observations showing that initial growth of mountain plants is tightly coupled to snowmelt timing (Körner, 1999). This plasticity in the timing of the initial growth response, which is enabled by tissue preformation, is interpreted as an adaptation to cope with the limited period of growth in seasonally snow-covered ecosystems (Galen and Stanton, 1991). Early disappearance of snow is controlled by spring temperature, and our results showing that a warm spring leads to a prolonged period of plant activity are consistent with those originally reported from high latitudes (Myneni et al., 1997). Other studies have also shown that the onset of greenness in the Alps corresponds closely with year-to-year variations in the date of snowmelt (Stockli and Vidale, 2004) and that spring mean temperature is a good predictor of melt out (Rammig et al., 2010). This study improves upon previous works (i) by carefully selecting targeted areas to avoid mixing different vegetation types when examining growth response, (ii) by using a meteorological forcing that is more appropriate to capture topographical and regional effects compared to global meteorological gridded data (Frei and Schär, 1998), and (iii) by implementing a statistical approach enabling the identification of direct and indirect effects of snow on productivity.

Even if there were large between-year differences in Pg, the magnitude of year-to-year variations in NDVImax were small compared to that of NDVIint or GPPint (Table 1 and Fig. 4). Indeed, initial growth rates buffer the impact of inter-annual variations in snowmelt dates, as has already been observed in a long-term study monitoring seventeen alpine sites in Switzerland (Jonas et al., 2008). Essentially, the two contrasting scenarios for the initial period of growth observed in this study were either a fast growth rate during a shortened growing period in the case of a delayed snowmelt, or a lower growth rate over a prolonged period following a warm spring. These two dynamics resulted in nearly similar values of NDVImax as TSNOWmelt explained only 4% of the variance in NDVImax (Fig. S4B). I do not think that the low variability in the response of NDVImax to forcing variables is due to a limitation of the remote sensing approach. First, there was a high between-site variability of NDVImax, indicating that the retrieved values were able to capture variability in the peak standing aboveground biomass (Table 1). Second, the mean NDVImax of the targeted areas is around 0.7 (Fig. 4B), i.e. in a range of values where NDVI continues to respond linearly to increasing green biomass and Leaf Area Index (Hmimina et al., 2013). Indeed, many studies have shown that the maximum amount of biomass produced by arctic and alpine species or meadows did not benefit from the experimental lengthening of the favorable period of growth (Kudo et al., 1999; Baptist et al., 2010), or to increasing CO2 concentrations (Körner et al., 1997). Altogether, these results strongly suggest that intrinsic growth constraints limit the ability of high elevation grasslands to enhance their growth under ameliorated atmospheric conditions. More detailed studies will help us understanding the phenological response of different plant life forms (e.g. forbs and graminoids) to early and late snowmelting years and their contribution to ecosystem phenology (Julitta et al., 2014). Other severely limiting factors - including nutrient availability in the soil - may explain this low responsiveness (Körner, 1989). For example, Vittoz & al. (2009) emphasized that year-to-year changes in the productivity of mountain grasslands were primarily caused by disturbance and land use changes that affect nutrient cycling. Alternatively, one cannot rule out the possibility that other bioclimatic variables could better explain the observed variance in NDVImax. For example, the inter-annual variations in precipitation had a slight though significant effect on NDVImax (Fig.

5A, C) suggesting that including a soil water balance model might improve our understanding of growth responsiveness, as suggested by (Berdanier and Klein, 2011). Many observations and experimental studies have also pointed out that soil temperature impacts the distribution of plant and soil microbial communities (Zinger et al., 2009), ecosystem functioning (Baptist and Choler, 2008), and flowering phenology (Dunne et al., 2003). More specifically, the lack of snow or the presence of a shallow snowpack during winter increase the frequency of freezing and thawing events with consequences on soil nutrient cycling and aboveground productivity (Kreyling et al., 2008; Freppaz et al., 2007). Thus, an improvement of this study would be to test, not only for the effect of presence-absence of snow, but also for the effect of snowpack height and soil temperature on NDVImax and growth responses of alpine pastures. Regional climate downscaling of soil temperature at different depths is currently under development within the SAFRAN-CROCUS-MEPRA model chain and there will be future opportunities to examine these linkages. Nevertheless, the results showed that at the first order the summer meteorological forcing was instrumental in controlling GPPints, without having a direct effect on NDVImax (Fig.5B, D). In particular, positive temperature anomalies and associated clear skies had significant effects on GPPints. Moreover, path analysis conducted at the polygon level also provided some evidence that responsiveness to ameliorated weather conditions was less pronounced in the coldest polygons (Table 3), suggesting stronger intrinsic growth constraints in the harshest conditions. Collectively, these results indicated that the mechanism by which increased summer temperature may enhance grassland productivity was through the persistence of green tissues over the whole season rather than through increasing peak standing biomass.

The contribution of the second part of the summer to annual productivity has been overlooked in many studies (e.g. Walker et al., 1994; Rammig et al., 2010; Jonas et al., 2008; Jolly et al., 2005) that have primarily focused on early growth, or on the amount of aboveground biomass at peak productivity. Here, I showed that the length of the senescing phase is a major determinant of inter-annual variation in growing season length and productivity and hence that temperature and precipitation in October-November are strong drivers of these inter-annual changes (Fig. 5B, D). The importance of autumn phenology was recently re-evaluated in remote sensing studies conducted at global scales (Jeong et al., 2011; Garonna et al., 2014). A significant long-term trend towards a delayed end of the growing season was noticed for Europe and specifically for the Alps. In the European Alps, temperature and moisture regimes in late autumn and early winter are possibly under the influence of the North Atlantic Oscillation (NAO) phase anomalies (Beniston and Jungo, 2002). This opens the way for research on teleconnections between oceanic and atmospheric conditions and the regional drivers of alpine grassland phenology and growth.

Eddy covariance data also provided direct evidence that the second half of the growing season is a significant contributor to the annual GPP of mountain grasslands (Chen et al., 2009; Rossini et al., 2012; Li et al., 2007; Kato et al., 2006). However it has also been shown that while the combination of NDVI and PAR successfully captured daily GPP dynamics in the first part of the season, NDVI tended to provide an overestimate of GPP in the second part (Chen et al., 2009; Li et al., 2007). Possible causes include decreasing light-use efficiency in the end of the growing season in relation to the accumulation of senescent material and/or the "dilution" of leaf nitrogen content by fixed carbon. Noticeably, the main findings of this study did not change when NDVI was replaced by EVI, a vegetation index which is more sensitive to green biomass and thus may better capture primary productivity. Consistent with this result, Rossini et al. (2012) did not find any evidence that EVI-based proxies performed better than NDVI-based proxies to estimate the GPP of a subalpine pasture.

Further comparison with other vegetation indexes - like the MTCI derived from MERIS products (Harris and Dash, 2010) – will contribute to better evaluate NDVI-based proxies of GPP.

A strong assumption of this study was to consider that the LUE parameter is constant across space and time. There is still a vivid debate on the relevance of using vegetation specific LUE in remote sensing studies of productivity (Yuan et al., 2014; Chen et al., 2009). Following Yuan & al. (2014) I have assumed that variations in light-use efficiency are primarily captured by variations in NDVI because this vegetation index correlates with structural and physiological properties of canopies (e.g. leaf area index, chlorophyll and nitrogen content). Multiple sources of uncertainty affect remotely sensed estimates of productivity and it is questionnable whether the product NDVI times PAR is a robust predictor of GPP in alpine pastures. The estimate of absolute values of GPP and its comparison across sites was not the aim of this study that focuses on year-to-year relative changes of productivity for a given site. It is assumed that limitations of a light-use efficiency model are consistent across time and that these limitations did not prevent the analysis of the multiple drivers affecting inter-annual variations of remotely sensed proxies of GPP. At present, there is no alternative for regional-scale assessment of productivity using remote sensing data. In the future, possible improvements could be made by using air-borne hyperspectral data to derive spatial and temporal changes in the functional properties of canopies (Ustin et al., 2004) and assess their impact on annual primary productivity.

Conclusions

I have shown that the length of the snow-free period is the primary determinant of remote sensing-based proxies of primary productivity in temperate mountain grasslands. From a methodological point of view, this study demonstrated the relevance of path analysis as a means to decipher the cascading effects and relative contributions of multiple predictors on grassland phenology and growth. Overall, these findings call for a better linkage between phenomenological models of mountain grassland phenology and growth and land surface models of snow dynamics. They open the way to a process-based, biophysical modelling of alpine pastures growth in response to environmental forcing following an approach used in a different climate (Choler et al., 2010). Year-to-year variability in snow cover in the Alps is high (Beniston et al., 2003) and climate-driven changes in snow cover are on-going (Hantel et al., 2000; Keller et al., 2005; Beniston et al., 1997). Understanding the factors controlling the timing and amount of biomass produced in mountain pastures thus represents a major challenge for agro-pastoral economies.

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Table 1

Variance partitioning into between-polygon and between-year components for the set of predictors and growth responses included in the path analysis.

		Percentage of variance	
Variable	Abbreviation	between polygons	between years
Date of snow melting	TSNOWmelt	53.6	46.4
Date of first snowfall	TSNOWfall	15.7	84.3
Length of the snow-free period	Psf	48.2	51.8
Length of the period of growth	Pg	27.9	72.1
Length of the period of senescence	Ps	40.5	59.5
Date of NDVImax	TNDVImax	41.4	58.6
Maximum NDVI	NDVImax	87.9	12.1
Time-integrated NDVI over Psf	NDVIint	73.3	26.7
Time-integrated NDVI over Pg	NDVIintg	37.6	62.4
Time-integrated NDVI over Ps	NDVIints	61.3	38.7
Time-integrated NDVIxPAR over Psf	GPPint	73.4	26.6
Time-integrated NDVIxPAR over Pg	GPPintg	32.5	67.5
Time-integrated NDVIxPAR over Ps	GPPints	53.9	46.1

Table 2

Model fit of competing path models. AIC is the Akaike Information Criteria value and ΔAIC is the difference in AIC between the best model and alternative models.

Model	Path diagram	d.f.	AIC	ΔAIC
NDVIintg	as in Fig. 5A	21	28539	0
	removing TEMPg -> NDVImax	22	28540	1
	removing PRECg -> NDVIintg	22	28538	-1
	removing FrEv -> NDVIintg	21	28588	49
	removing Pg -> NDVImax	22	28631	91
NDVIints	as in Fig. 5B	19	30378	82
	removing TNDVImax -> NDVImax	15	30296	0
GPPintg	as in Fig. 5C	21	29895	0
	removing TEMPg -> NDVImax	22	29896	1
	removing PRECg -> GPPintg	22	29924	29
	removing FrEv -> GPPintg	21	29965	70
	removing Pg -> NDVImax	22	29987	92
GPPints	as in Fig. 5D	19	31714	34
	removing TNDVImax -> NDVImax	15	31680	0

Table 3

Relationships between mean temperature or precipitation of polygons and the path coefficients estimated at the polygon level. Only significant relationships are shown. * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Path	Explanatory variable	Direction of effect	R^2 and significance
PRECg -> GPPintg	Temperature	-	0.04
TGspring -> TSNOWmelt	Precipitation	-	0.05*
NDVImax -> NDVIintg	Precipitation	+	0.07***
TEMPs -> NDVIints	Temperature	-	0.04*
TEMPs -> GPPints	Temperature	-	0.07***
PRECs -> NDVIints	Temperature	+	0.05*
NDVImax -> NDVIints	Temperature	+	0.03*
NDVImax -> GPPints	Temperature	+	0.04*
Ps -> NDVIints	Temperature	-	0.08***
Ps -> NDVIints	Precipitation	+	0.02*

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Figure caption

Figure 1. (A) Location map of the 121 polygons across the seventeen climatologically defined massifs of the French Alps. (B) Number of polygons per massif.

Figure 2. Yearly course of NDVI and NDSI showing the different variables used in this study: date of snowmelt (TSNOWmelt), maximum NDVI (NDVImax) and date of NDVImax (TNDVImax), date of snowfall (TSNOWfall), length of the snow-free period (Psf), length of the initial growth period (Pg), length of the senescence period (Ps), and time-integrated NDVI over the growth period (NDVIintg) and over the senescence period (NDVIints).

Figure 3. Frequency distribution of the relative contribution of Pg and Ps to Psf (A), of NDVIintg and NDVIints to NDVIint (B) and of GPPintg and GPPints to GPPint (C). Values were calculated for each year and for each polygon.

Figure 4. Inter-annual standardized anomalies for NDVImax (A), Psf (B), NDVIint (C) and GPPint (D).

Figure 5. Path analysis diagram showing the interacting effects of meteorological forcing, snow cover duration and NDVImax on NDVIint (A, B) and GPPint (C, D). For each proxy of productivity, separate models for the period of growth (A, C) and the period of senescence (B, D) are shown. Line thickness of arrows is proportional to standardized path coefficients which are indicated on the right or above each arrow.

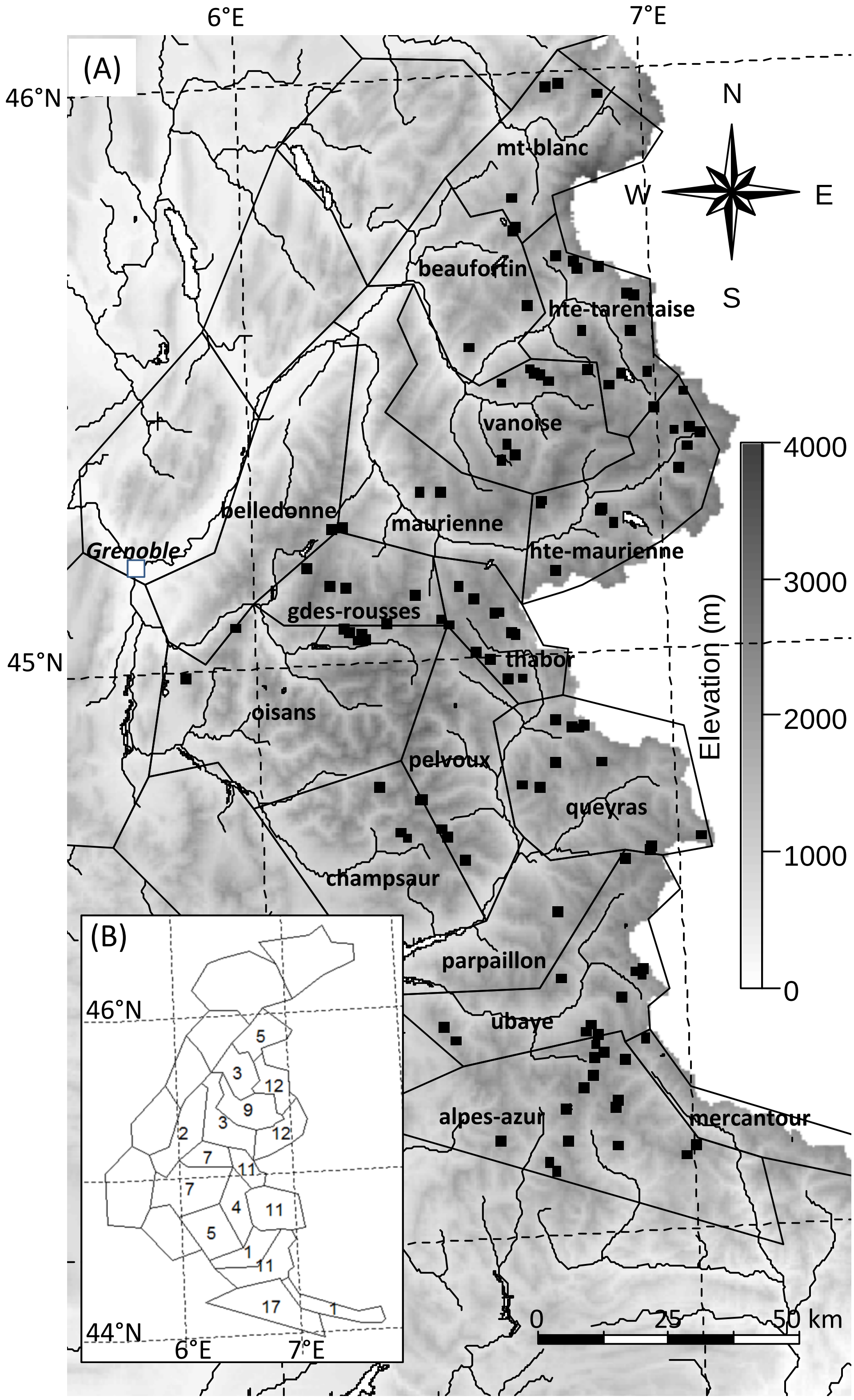
Values in italics indicate paths that can be removed without penalizing model AIC (see Table 2). Solid line (or dotted lines) indicates a significant positive (or negative) effect at $P<0.05$. Double lined arrows correspond to fixed parameters. Abbreviations include TEMP, averaged daily mean temperature (or senescence period); PREC averaged daily sum of precipitation; FrEv: number of frost events. Letter g (or s) is for the initial growth period (or the senescence period). Spring means the months of March and April. Fall means the months of October and November.

Figure S1. Ground-based observations of TSNOWmelt and TSNOWfall at Lautaret pass from 2012 onwards (dotted lines) superimposed on the NDVI and NDSI time series obtained from MODIS (8-days composite). The comparison is made for a single 500m MOD09A1 pixel that corresponds to a relatively flat area dominated by subalpine grasslands at a mean elevation of 2000 m.

Figure S2. Sensitivity of the length of the snow free period (Psf) to changes in the NDVI/NDSI thresholds. Psf changes are simulated for four thresholds and for the 1820 polygon x year combinations. Numbers above each boxplot indicate the percentage of combinations exhibiting a shortening of Psf larger than two days (when the threshold is increased) and a lengthening of Psf larger than three days (when the threshold is decreased).

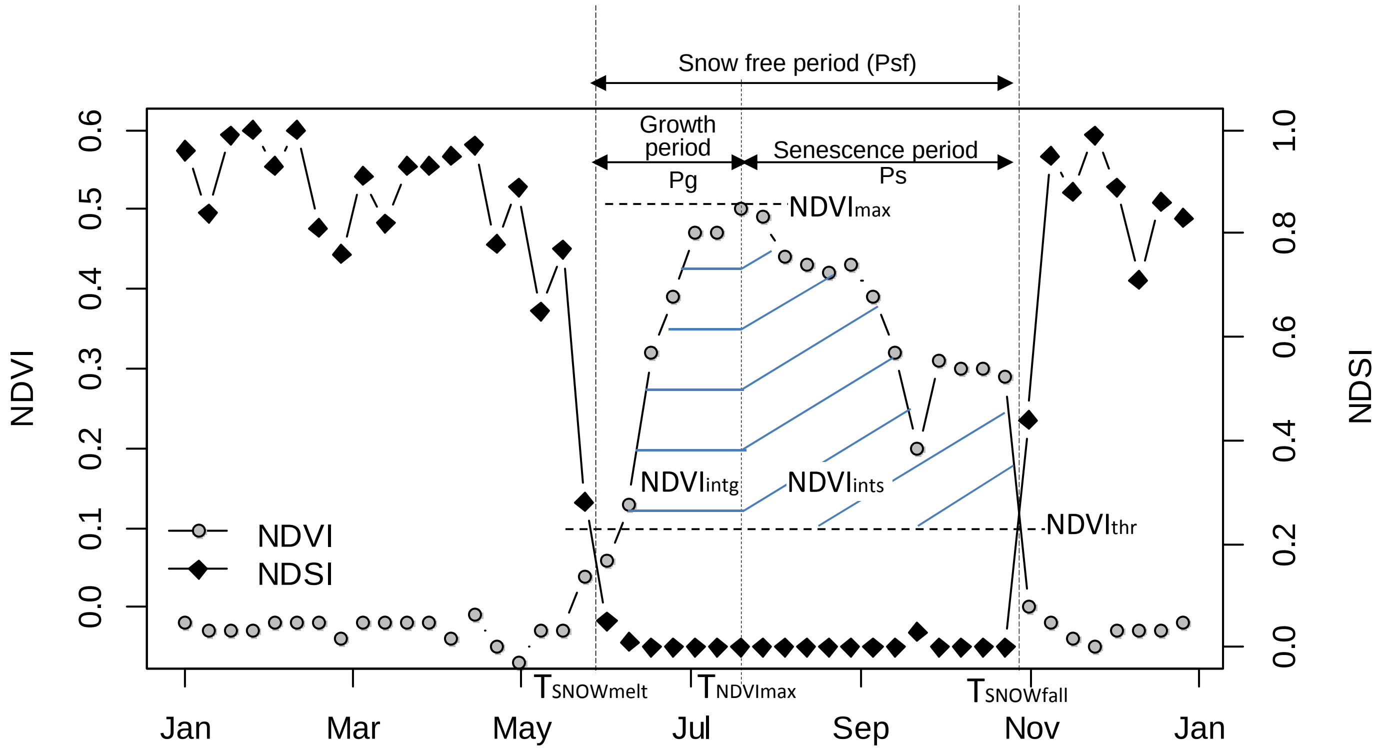
Figure S3. (A) Relationships between the inter-annual variations (standard deviation) of EVIint and NDVIint. One point corresponds to one polygon. (B) Frequency distribution of the relative contribution of EVIintg and EVIints to EVIint (to be compared to Fig. 3C). Values were calculated for each year and for each polygon.

Figure S4. Relationships between TSNOWmelt and TNDVImax (A) or NDVImax (B). Points correspond to every year x polygon combination. The dash-dotted line in (A) indicates a 1:1 relationship. Dotted lines show average values for each variable.



(A)
6°E
7°E
46°N
45°N
N
W
E
S
mt-blanc
beaufortin
hte-tarentaise
vanoise
belledonne
maurienne
hte-maurienne
Grenoble
gdes-rousses
thabor
oisans
pelvoux
queyras
champsaur
parpaillon
ubaye
alpes-azur
mercantour
Elevation (m)
4000
3000
2000
1000
0
0
25
50 km
(B)
46°N
44°N
6°E
7°E

Figure 1



Snow free period (Psf)
Growth period
Pg
Senescence period
Ps
NDVImax
NDVIintg
NDVIints
NDVIthr
NDVI
NDSI
TSNOWmelt
TNDVImax
TSNOWfall
Jan
Mar
May
Jul
Sep
Nov
Jan
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.0
0.2
0.4
0.6
0.8
1.0

Figure 2

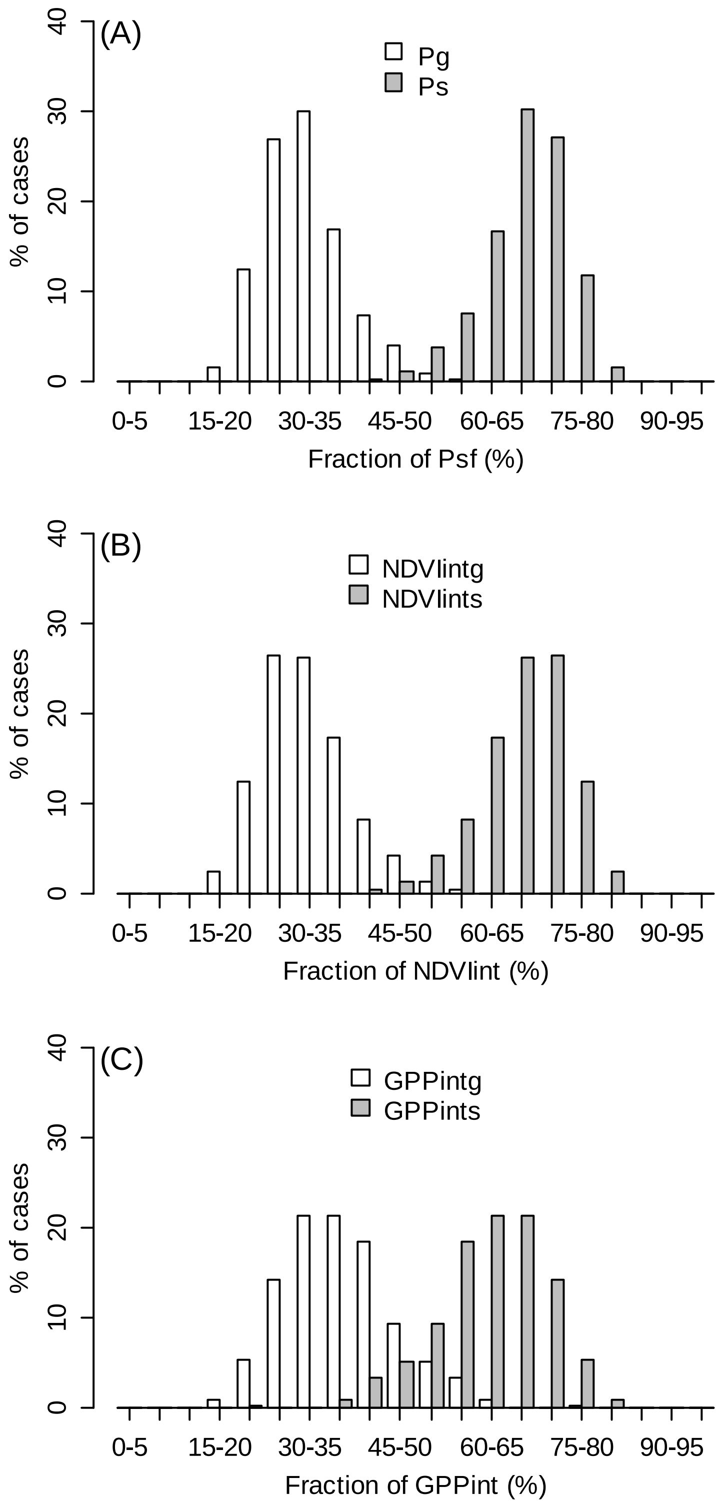

(A)
Pg
Ps
% of cases
0
10
20
30
40
0-5
15-20
30-35
45-50
60-65
75-80
90-95
Fraction of Psf (%)
(B)
NDVIintg
NDVIints
% of cases
Fraction of NDVIint (%)
(C)
GPPintg
GPPints
% of cases
Fraction of GPPint (%)

Figure 3

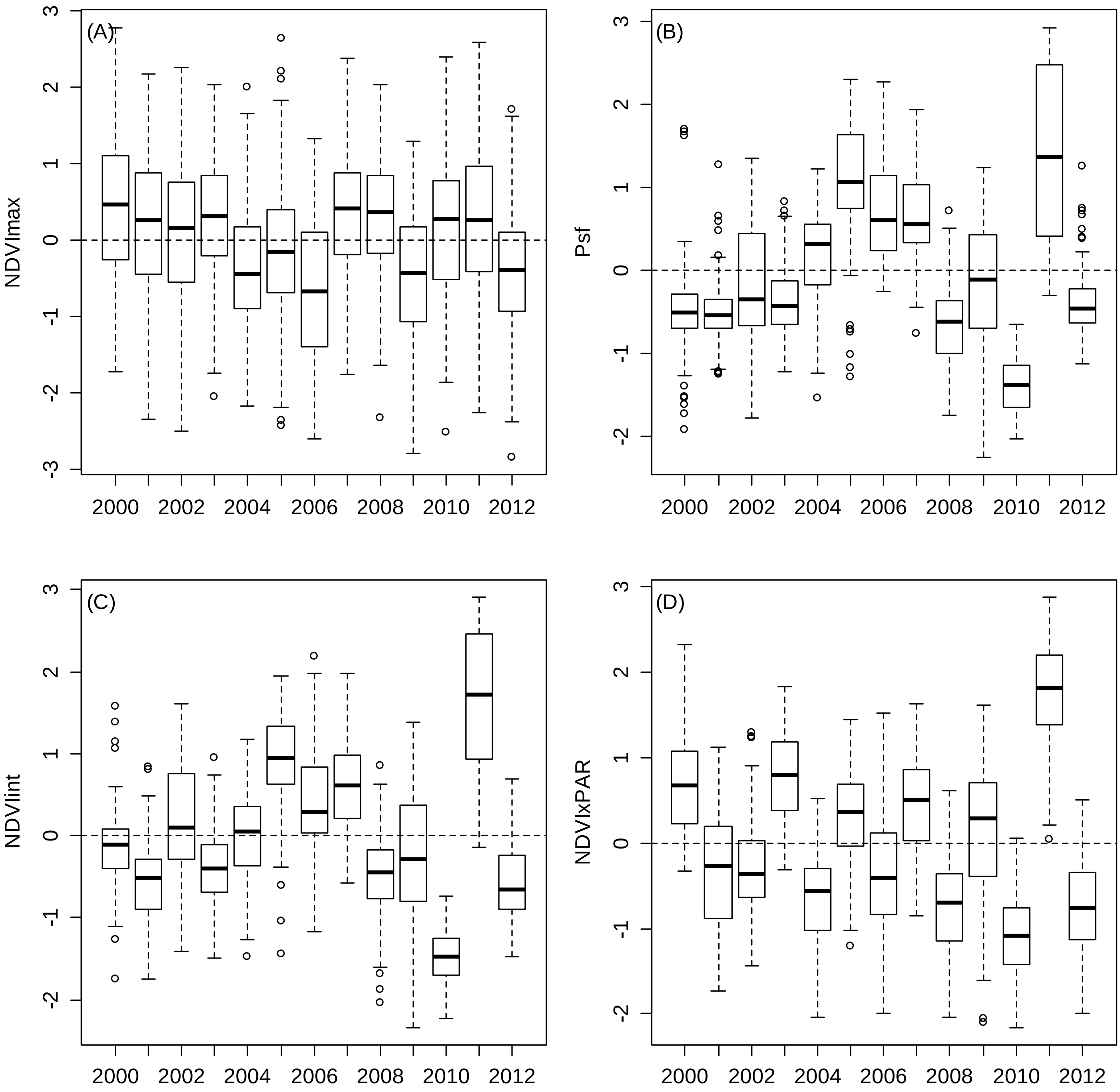
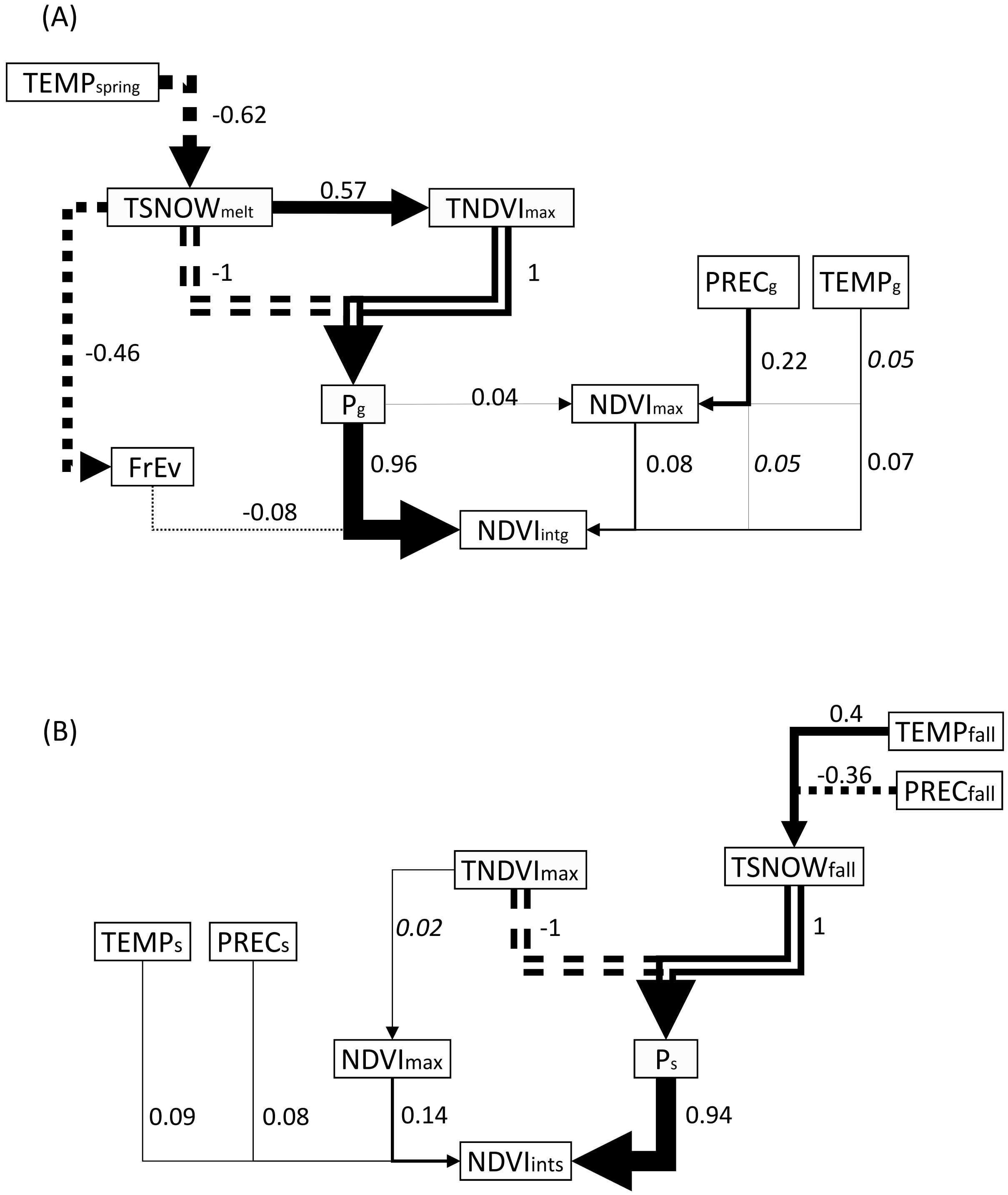

(A)
(B)
(C)
(D)
NDVImax
Psf
NDVIint
NDVIxPAR
2000
2002
2004
2006
2008
2010
2012

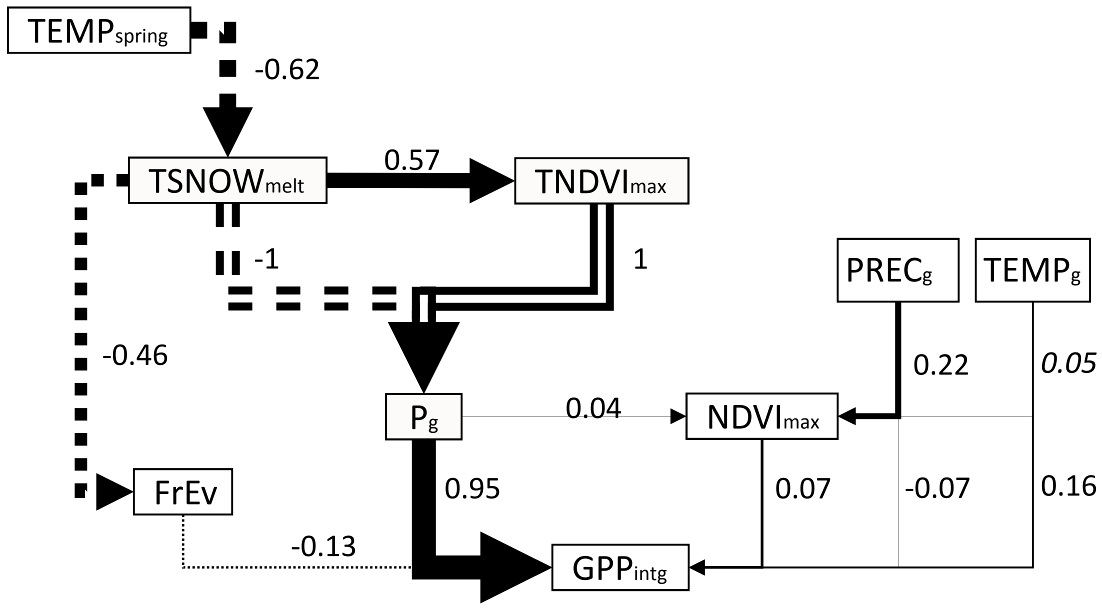
Figure 4



(A)
TEMPspring
-0.62
TSNOWmelt
0.57
TNDVImax
-1
1
PRECg
TEMPg
-0.46
0.22
0.05
Pg
0.04
NDVImax
FrEv
0.96
0.08
0.05
0.07
-0.08
NDVIintg
(B)
0.4
TEMPfall
-0.36
PRECfall
TNDVImax
TSNOWfall
TEMPs
PRECs
0.02
-1
1
NDVImax
Ps
0.09
0.08
0.14
0.94
NDVIints

Figure 5

(C)



(D)

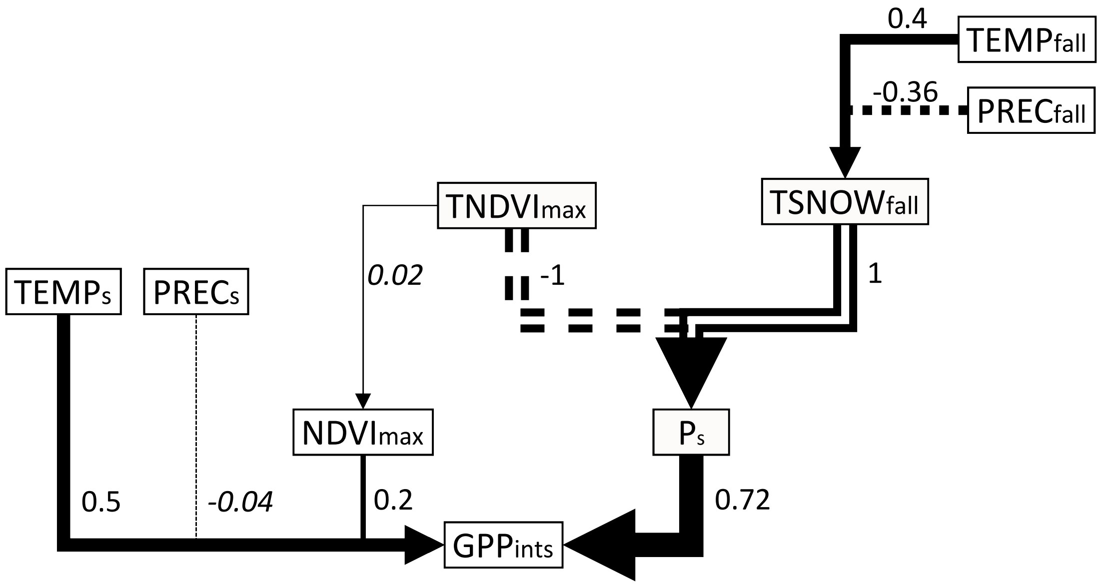


Figure 5 (continued)

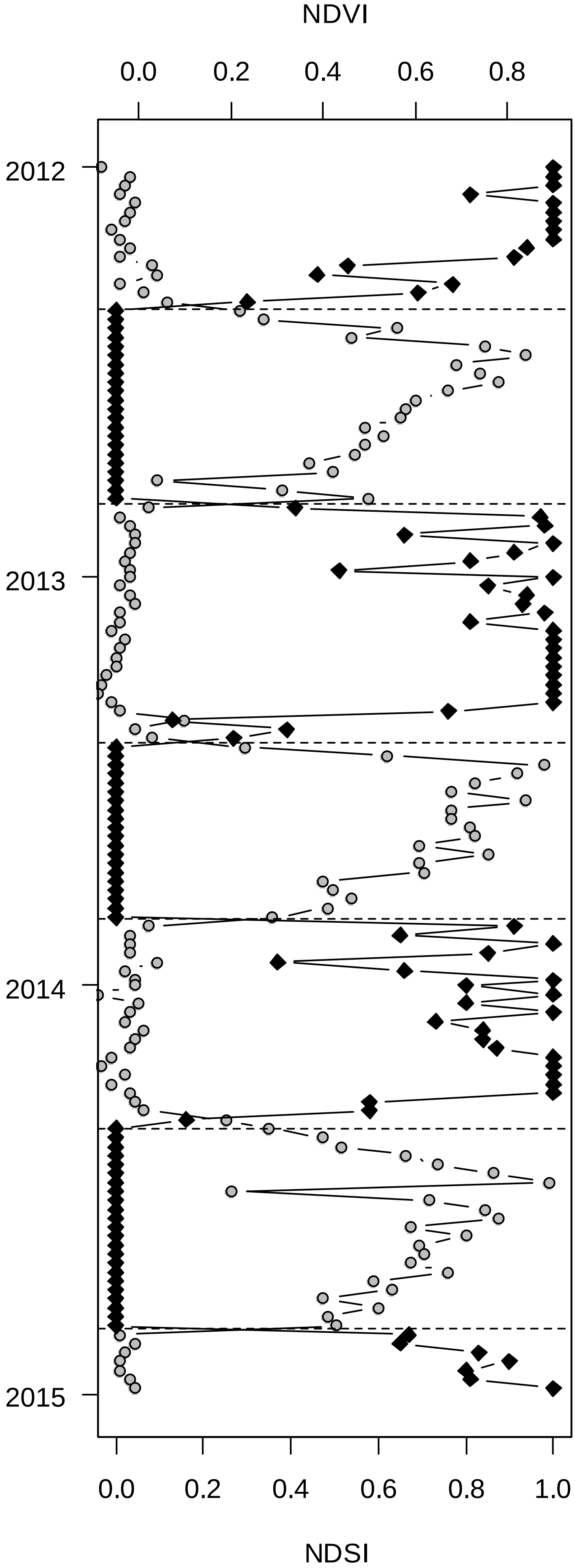


Figure S1

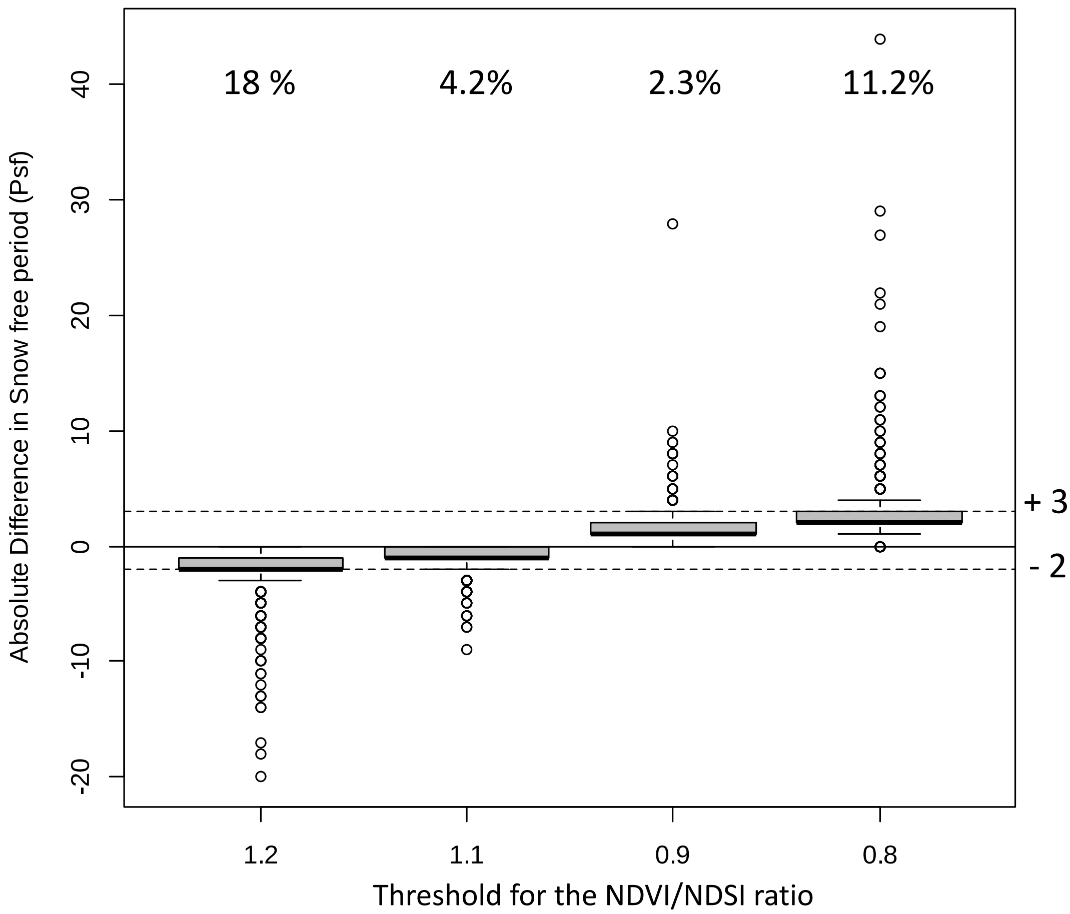
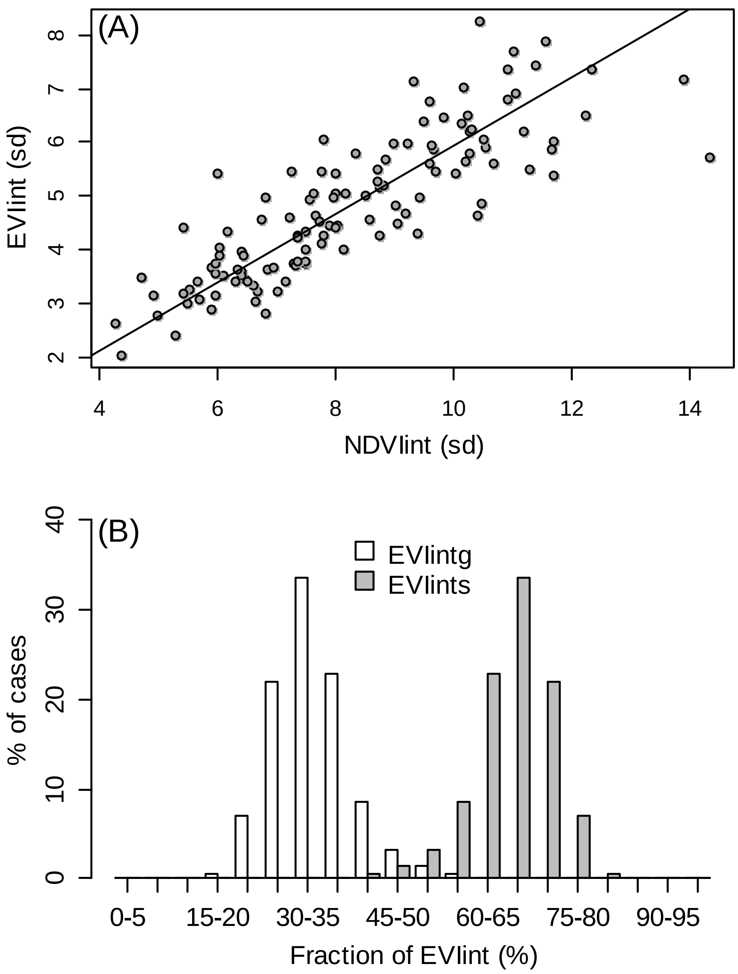

18 %
4.2%
2.3%
11.2%
+ 3
- 2
Absolute Difference in Snow free period (Psf)
40
30
20
10
0
-10
-20
1.2
1.1
0.9
0.8
Threshold for the NDVI/NDSI ratio

Figure S2



(A)
EVIint (sd)
NDVIint (sd)
(B)
EVIintg
EVIints
% of cases
Fraction of EVIint (%)

Figure S3

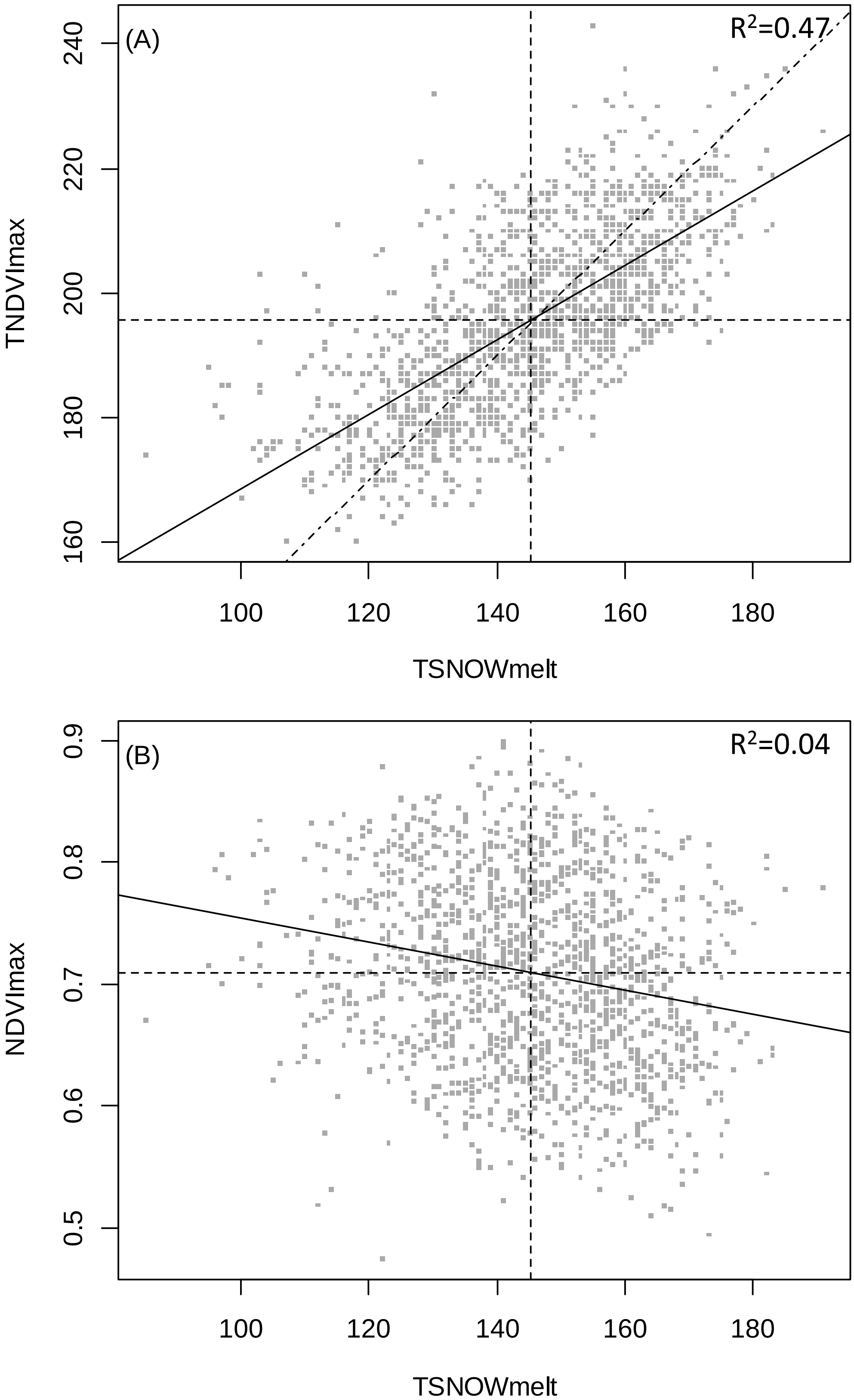

(A)
R^2=0.47
TNDVImax
160
180
200
220
240
100
120
140
160
180
TSNOWmelt
(B)
R^2=0.04
NDVImax
0.5
0.6
0.7
0.8
0.9
100
120
140
160
180
TSNOWmelt

Figure S4