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Projections of water, carbon, and nitrogen dynamics under future climate change in an alpine tundra ecosystem in the southern Rocky Mountains using a biogeochemical model

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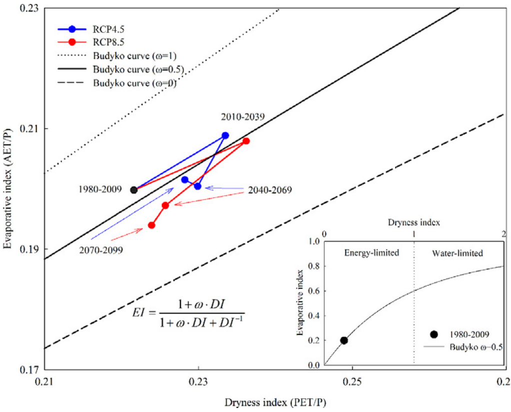
HIGHLIGHTS

- Future dynamics of water, carbon, and nitrogen are projected in an alpine tundra.
- Budyko curve applied to examine evapotranspiration and runoff under RCP scenarios.
- Advanced snowmelt in spring and lower soil moisture in summer are projected.
- Future dynamics of C N are significantly affected by altered hydrological patterns.
- Extended growing season and elevated CO_2 affect major C N pools and fluxes.

GRAPHICAL ABSTRACT



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ABSTRACT

Using statistically downscaled future climate scenarios and a version of the biogeochemical model (PnET-BGC) that was modified for use in the alpine tundra, we investigated changes in water, carbon, and nitrogen dynamics under the Representative Concentration Pathways at Niwot Ridge in Colorado, USA. Our simulations indicate that future hydrology will become more water-limited over the short-term due to the temperature-induced increases in leaf conductance, but remains energy-limited over the longer term because of anticipated future decreases in leaf area and increases in annual precipitation. The seasonal distribution of the water supply will become decoupled from energy inputs due to advanced snowmelt, causing soil moisture stress to plants during the growing season. Decreases in summer soil moisture are projected to not only affect leaf production, but also reduce decomposition of soil organic matter in summer despite increasing temperature. Advanced future snowmelt in spring and increasing rain to snow ratio in fall are projected to increase soil moisture and decomposition of soil organic matter. The extended growing season is projected to increase carbon sequestration by 2% under the high radiative forcing scenario, despite a 31% reduction in leaf display due to the soil moisture stress. Our analyses demonstrate that future nitrogen uptake by alpine plants is regulated by nitrogen supply from mineralization, but plant nitrogen demand may also affect plant uptake under the warmer scenario. PnET-BGC

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simulations also suggest that potential CO_2 effects on alpine plants are projected to cause larger increases in plant carbon storage than leaf and root production.

1. Introduction

There is growing evidence that some high-mountain environments have experienced and are projected to experience future increases in temperature that are more rapid than the global land average, possibly due to snow albedo feedbacks, or changes in cloud coverage, surface water vapor, radiative flux, and atmospheric aerosols (Collins et al., 2013; Pepin et al., 2015). The Colorado Rocky Mountains have undergone a 1.4 °C increase in mean annual temperature from 1963 to 2012, and temperatures are projected to increase by 1.4 °C to 3.6 °C and 3.1 °C to 5.3 °C from 1971–2000 to 2055–2084 under the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathways (RCP) 4.5 and 8.5 scenarios, respectively (Lukas et al., 2014). Projected changes in annual precipitation from 1971–2000 to 2035–2064 in Colorado range from −5% to +6% and −3% to +8% under the RCP4.5 and RCP8.5 scenarios, respectively. The only season showing increases in future precipitation in Colorado by a majority of general circulation models (GCMs) is winter (Lukas et al., 2014) (33 out of 37 GCM simulations from the fifth phase of the Coupled Model Intercomparison Project (CMIP5) found positive trends). The lack of agreement among GCM projections in future annual precipitation in Colorado is consistent with other mid-latitude regions in the contiguous United States (Romero-Lankao et al., 2014).

Alpine tundra ecosystems are considered to be particularly vulnerable to global change due to the nature of their resource utilization and magnitude of projected climate change. Over the past several decades, observations at different scales in alpine tundra ecosystems have shown changes in species composition (Elmendorf et al., 2012a), phenology (Parmesan, 2006), ecosystem function (Elmendorf et al., 2012b), and biogeochemical cycles (Ernakovich et al., 2014) in response to increasing temperature and altered seasonal precipitation. Primary production of alpine tundra ecosystems can be affected directly by the altered physical environment, or indirectly through changes in biotic and abiotic factors, such as snow pack depth and duration, which determine the start of growing season and the growing season soil moisture regime (Bowman and Fisk, 2001). Many biogeochemical processes in the alpine tundra, including those involving carbon, nitrogen, and water, show distinct patterns during snow-cover and snow-free seasons, which makes them sensitive to future increases in temperature. For instance, the rate of soil organic matter (SOM) decomposition, which is primarily controlled by soil temperature and moisture during the growing season, is also correlated with the duration of the snowpack and associated microbial activity beneath the snow (Seastedt et al., 2001). Nitrogen uptake during the growing season is primarily related to plant production, and parallels N accumulation in plant biomass. In contrast, nitrogen assimilation in winter is largely influenced by the subnivean microbial community (Fisk et al., 2001).

Since alpine tundra supplies water for many downstream uses, there is considerable interest in how future changes in precipitation, snowpack accumulation and loss, and evapotranspiration affect water resources. While previous climate change simulations have largely focused on responses in community composition and the structure of alpine tundra ecosystems (Johnson et al., 2011; Sverdrup et al., 2012), climatic effects on biogeochemical cycling at the watershed scale are less well studied, especially in response to projections from IPCC climate change scenarios.

In this study, we revised and validated a biogeochemical model, PnET-BGC, using observations from an alpine tundra ecosystem at Niwot Ridge, Colorado. We evaluated the ability of the monthly time-step, lumped-parameter model with prescribed vegetation inputs that depict the plant functional traits to capture temporal variations of major biogeochemical processes in this ecosystem of high spatial-heterogeneity. Simulations of biogeochemical processes involving water, carbon, and nitrogen were made under two RCP scenarios through the end of the 21st century to examine the effects of future increases in temperature, altered seasonal precipitation, and elevated atmospheric CO_2 concentrations on carbon sequestration/storage, nitrogen mineralization and uptake, and evapotranspiration and runoff of the alpine tundra ecosystem.

Admittedly, the deductive reasoning nature of modeling precludes using this approach to discover novel explanatory variables for current or future biogeochemical patterns. The goal of this research was to quantitatively examine the effects of multiple climatic and environmental factors that are gradually changing over the long-term on the future hydrology and biogeochemistry of the alpine tundra in the southern Rocky Mountains. This is achieved by incorporating understanding and synthesizing up-to-date knowledge on ecosystem function into the algorithm and parameters of the process-based model. Note that our goal is not to predict the future, but rather to help manage uncertainty by narrowing the possible range to a subset of plausible futures that pertain directly to vulnerabilities of specific resources and management objectives (Littell et al., 2011). The simulations are used to examine general biogeochemical principles rather than predict the behavior of a specific ecosystem (Green and Sadedin, 2005). For this reason we use the term projection, not prediction, when describing the simulated model outputs about the future. In this study, we tested the hypotheses that 1) climate change in the alpine tundra under the RCP scenarios will result in soil moisture stress on vegetation in summer; 2) advanced future snowmelt in spring and increasing rain to snow ratio in fall will alter the soil moisture regime and affect the dynamics of water, carbon, and nitrogen in the ecosystem; and 3) future extended growing season and elevated atmospheric CO_2 concentrations may have large impacts on ecosystem functions of the alpine tundra.

2. Materials and methods

2.1. Site description

The Niwot Ridge Long-Term Ecological Research (LTER) site is located in the Front Range of the Colorado Rocky Mountains. The area includes an 8-km, east-west oriented ridge and several nested watersheds that comprise the Green Lakes Valley (Bowman and Seastedt, 2001). The Niwot Ridge LTER site is bounded on the west by the Continental Divide, and elevation ranges from 4000 m.a.s.l. at Arikaree Peak to 3250 m. a.s.l. at the subalpine forest. Model simulations in this study were conducted for the Saddle, a 0.89 km^2 alpine tundra site on a flat ridge-top at 3500 m above the sea level at which ecology and biogeochemistry are most intensively studied in Niwot Ridge. Plant species at the Saddle are spatially heterogeneous, and genera include *Carex*, *Caltha*, *Deschampsia*, *Acomastylis*, *Kobresia*, *Selaginella*, *Trifolium*, and *Salix*. Community structure at Niwot Ridge can be largely explained by the snow gradient which is a function of wind and topography (Walker et al., 2001). Six physiognomic-habitat-based units (noda) were identified at the Saddle as the standard for differentiating plant communities in other studies at alpine tundra of Niwot Ridge (May and Webber, 1982).

2.2. Model structure

The deterministic biogeochemical model, PnET-BGC, was used to examine water, carbon, and nitrogen dynamics at the Saddle of Niwot

Ridge (Gbondo-Tugbawa et al., 2001; Ollinger et al., 2009). PnET-BGC uses inputs of solar radiation, air temperature, precipitation, and atmospheric CO_2 concentration at a monthly time step to simulate hydrologic and biogeochemical processes involving vegetation, soil, and surface waters. The model also uses monthly wet atmospheric deposition and constant dry to wet deposition ratios of 10 elements as inputs. Plant functional traits are parameterized as vegetation type-specific values in PnET-BGC. Relative concentrations of 10 elements to nitrogen in SOM and vegetation are considered as fixed parameters in the model. The model simulates the initiation of leaf and stem production to certain growing degree days, and simulates leaf drop based on leaf carbon balance after certain Julian days. In this study, we defined the length of growing season as the duration of leaf presence. PnET-BGC considers potential CO_2 fertilization effects on vegetation by which elevated atmospheric CO_2 concentrations increase internal leaf CO_2 concentrations increasing photosynthesis and water use efficiency (WUE). PnET-BGC uses total precipitation as an input, and calculates rain to snow ratio and snowmelt as a function temperature. The model simulates monthly snow accumulation and loss based on inputs from precipitation and outputs through sublimation and snowmelt. In this study, we defined the length of snow-covered period as the duration in which snow water equivalent is greater than 20 cm. A detailed description of the model structure is provided in Appendix S1.

Several key processes of plant functional characteristics and soil properties were revised in algorithms and parameters to accommodate the nature of alpine tundra ecosystems. PnET-BGC was originally developed for and has been largely applied to forest ecosystems. In this study, processes associated with wood carbon and nitrogen were removed from the model, including wood carbon and nitrogen allocation, wood respiration and turnover, and live and dead wood carbon and nitrogen. Accordingly, several stem components were added in the model to represent alpine tundra vegetation. In previous versions of PnET, a minimum ratio of annual foliar to wood production was set to depict the physiological constraint on carbon allocation that foliage production is regulated by the wood production that provides the physical support to leaves (Aber et al., 1995). This constraint was removed from the model to accommodate alpine tundra. The new set of carbon and nitrogen pools was added in the model to represent the non-structural carbohydrates and lipids and storage organs such as tubers and rhizomes. We also developed an algorithm of dead biomass carbon and nitrogen pools which receive inputs after leaf and stem senescence and transfers these nutrients monthly to the soil organic matter pool by a predetermined percentage. Previous studies at Niwot Ridge and other alpine and arctic tundra sites demonstrated that rates of SOM decomposition tend to increase as snow pack accumulates, while minimal variation was observed in soil temperature and soil moisture (Brooks et al., 1998; Liptzin et al., 2009). This pattern is attributed to microbial activity underneath continuous snow cover (Fisk et al., 2001). Based on the observations at Niwot Ridge, our model incorporated this relationship with an exponential increase in rates of SOM decomposition over the snow-covered period which conservatively allows rates to double under a continuous snowpack of approximately eight months. Snow sublimation is an important component of the snow mass balance in alpine tundra ecosystems. However, accurate simulation of snow sublimation (MacDonald et al., 2010; Sexstone et al., 2018; Strasser et al., 2008) often requires detailed information on snowpack which may not be readily available (e.g., height of saltation layer, height of turbulent suspension layer) and large number of input factors which inevitably introduce additional uncertainty (e.g., aerodynamic roughness length, specific air humidity immediately above snow surface). In this study, we used wind speed as an input to PnET-BGC, and calculated the proportion of snowpack to be lost through sublimation as a function of monthly wind speed. Detailed descriptions and values of model parameters used in this study are provided in Table S1.

2.3. Simulation procedures

Similar to previous applications of PnET-BGC, the model was run from 1000 A. D. to 1850 with background climate and atmospheric deposition inputs for a spin-up period. Starting from 2011, downscaled projected future climate under the RCP4.5 and RCP8.5 scenarios from the four GCMs were applied in PnET-BGC with and without application of the algorithm of potential CO_2 fertilization effects on vegetation. We present a time series of the model outputs, and compare the long-term average and interannual variability of simulations for 1986–2010 with those projected for 2076–2100. To address interannual variability of model outputs for the 2076–2100 period, we report the mean values of projections using the four GCMs. A detailed description of the simulation procedures is provided in Appendix S2.

To examine future hydrological responses to climate change, we used a Budyko curve approach to explore future partitioning of precipitation into evapotranspiration and runoff (Budyko, 1974). We used similar methods from a previous study on water yield of multiple ecosystems (Creed et al., 2014) and their concepts of *dynamic deviation* and *elasticity* to interpret our projections of the future hydrological status of the Saddle at Niwot Ridge. The Budyko curve describes the relationship between the potential evapotranspiration (PET) and actual evapotranspiration (AET) of a watershed, each standardized by the quantity of precipitation (P) (i.e., the evaporative index ($EI = AET/P$) is examined as a function of the dryness index ($DI = PET/P$)). The dynamic deviation is defined as the change in EI relative to the Budyko curve as climate varies. This metric is a measure of the extent to which the allocation of precipitation to ET and runoff deviates from theoretical expectations under changing climate. Elasticity is defined as the ratio of the change in DI to the change in EI, and is a measure of a watershed's ability to maintain water partitioning consistent with the Budyko curve as climate varies. A watershed has high elasticity if the DI changes with climate warming with only limited change in EI (Creed et al., 2014). The Budyko curve used in this study considered the plant-available water coefficient (ω) which represents the relative difference in the ways plants use water for transpiration and reflects rooting depth (Zhang et al., 2001). Zhang et al. (2001) found that a ω of 2 best describes forested watersheds, and a ω of 0.5 is best for grassland and cropland watersheds. Bare soil has ω of less than 0.5 because the rate of soil evaporation becomes water limited before plant transpiration (Zhang and Dawes, 1998). We used a Budyko curve with $\omega = 0.5$ to evaluate dynamic deviation and elasticity in this study.

Two parameters were used to quantify the effects of drought on alpine plants and SOM decomposition, respectively. Plant soil moisture stress index (DWater), which is defined as the ratio between actual and potential transpiration, describes the degree of water stress on plants. DWater values approach 0 when plants are under extreme water stress and approaches 1 when water stress is alleviated. Soil moisture index is defined as the ratio between water content and water holding capacity of soil, and is related to the rate of SOM decomposition. Note that these parameters are different from the plant-available water coefficient (ω) in the application of the Budyko curve described above.

2.4. Climate change scenarios and downscaling

We selected future climate change scenarios produced by four general circulation models (GCM: CCSM4, HadGEM2-CC, MIROC5, and MRI-CGCM3) from CMIP5 (Taylor et al., 2012). The use of multiple GCMs encompasses the ability of different models to accurately project different climate outputs (e.g. maximum temperature, minimum temperature, precipitation, solar radiation). Our selection of General Circulation Models was based on the following criteria: 1) models must simulate maximum and minimum temperature, precipitation, and solar radiation as outputs; 2) simulations by selected models must agree with observations relatively well in terms of climate sensitivity to greenhouse gas emissions; and 3) outputs of regional GCM simulations may not consistently perform poorly in many regions and for many variables.

Meteorological outputs from the individual GCM were statistically downscaled by the Asynchronous Regional Regression Model (ARRM) approach, then used as inputs to PnET-BGC model (Stoner et al., 2013). The ARRM downscaling technique first builds a statistical relationship between daily observed climatology at the site and past simulated climate at the regional scale for each month during a period over 30 years using piecewise quantile regression, then applies the regression parameters to regional GCM projections to generate station-based future climate. Evaluation of the performance of ARRM downscaling method (Dixon et al., 2016) and its effects on ecological and hydrological modeling (Hay et al., 2014; Pourmokhtarian et al., 2016) have been reported in recent studies.

We summarized downscaled future air temperature and precipitation which are inputs to PnET-BGC, and showed projection of future snow water equivalent and snow-covered periods in supporting information (Appendix S3).

2.5. Model performance and sensitivity analysis

We used three metrics, normalized mean error (NME), normalized mean absolute error (NMAE), and normalized root mean square error (NRMSE) to evaluate model performance in the validation process (Janssen and Heuberger, 1995).

$$NME = \frac{\overline{P} - \overline{O}}{\overline{O}}$$

$$NMAE = \frac{\sum_{i=1}^{n} (|P_i - O_i|)}{n\overline{O}}$$

$$NRMSE = \frac{\sqrt{\frac{\sum_{i=1}^{n} (P_i - O_i)^2}{n}}}{\overline{O}}$$

where $\overline{P}$ and $\overline{O}$ are means of predicted and observed values, P_i and O_i are predicted and observed values at time i, and n is the number of observations. NME > 0 indicates overestimation, and a value < 0 indicates underestimation. NMAE ranges from 0 to ∞, with 0 being optimal.

We conducted a sensitivity analysis to evaluate uncertainty in the output of the deterministic model caused by inaccuracy of different model inputs (Saltelli et al., 2004). A first-order sensitivity index approach was selected for its reliability, efficiency, and relatively low computational expense (Jørgensen and Bendoricchio, 2001; Saltelli et al., 2005). This unit-independent index is defined as

$$S_{Xi}^{Y} = \frac{\partial^{Y}/_{Y}}{\partial^{X_i}/_{X_i}}$$

where Y is a model output of interest, and X_i is a model input. A higher positive $S^{Y}{}_{Xi}$ value indicates a greater sensitivity of a model output to a model input. A negative $S^{Y}{}_{Xi}$ value indicates that increases in value of an input results in a decrease of the value of an output. The sensitivity analysis was conducted by examining the changes in model outputs during 2006–2010 period in response to a 10% increase in an input factor. The three metrics used to evaluate model performance and the first order sensitivity index approach have been previously applied to PnET-BGC (Fakhraei et al., 2017; Pourmokhtarian et al., 2012; Valipour et al., 2018).

3. Results

3.1. Model performance and sensitivity analysis

PnET-BGC simulations capture monthly variation in snow water equivalent at the Saddle for most years during 1982–2010, with the exception of a large underestimation in 1984 (Halfpenny, 2016; Walker, 2016; Williams, 2016) (NME = 0.02, NMAE = 0.34, NRMSE = 0.48; Fig. S3; Table S2). This underestimation is likely due to an error in measurement of precipitation at the meteorology station because the observed maximum snow water equivalent in the spring of 1984 was much higher than the sum of observed precipitation (model input) during the preceding fall and winter. Year-to-year variation in aboveground net primary production (NPP) is generally captured by the model except for 1985 (May and Webber, 1982; Walker et al., 2016) (NME = −0.01, NMAE = 0.07, NRMSE = 0.09; Fig. S4; Table S2). The underestimation of aboveground NPP for 1985 is attributed to simulated soil moisture stress to vegetation at the start of the growing season in 1984 due to the underestimation of snow water equivalent, which results in low carbon balance for 1984 and affects productivity in 1985. We compare simulated monthly soil moisture index for 1982–2003 with observations calculated from gravimetric and volumetric soil moisture (Seastedt, 2017; Walker, 2017) (NME = 0.96, NMAE = 1.08, NRMSE = 1.27; Fig. S5; Table S2). The timing of seasonal variation in soil moisture is captured by the model for most years, but the content is generally overestimated. Model simulations also captures the timing and magnitude of peak stream discharge at the Saddle for most years during 1999–2010 except for 2002, but generally overestimates stream discharge at the start of snowmelt (Caine, 2018) (NME = 0.53, NMAE = 0.73, NRMSE = 1.03; Fig. S6; Table S2). Meltwater flow through deep snowpack is considered one of the least understood aspects in snow hydrology (Williams et al., 2010). The simple relationship between temperature and snowmelt used in PnET-BGC does not depict the complex "thaw-freeze-thaw" process as meltwater passes through the deep snowpack. Future experiments that quantitatively examine this process are needed to improve the model algorithm of snowmelt for alpine tundra ecosystems which affects model performance of soil moisture and stream discharge.

Long-term continuous measurements of transpiration are not available for the Saddle. We compare simulated transpiration at Saddle (1986–2010) with observed transpiration (1961–1990) at the nearby site D-1 (Greenland and Losleben, 2001) 3750 m above the sea level (250 m higher than the Saddle) (Fig. S7). Simulated monthly transpiration at the Saddle for 1986–2010 is slightly higher than observations at D-1 for 1961–1990. We attribute this difference to the higher temperature at the lower-elevation site in the more recent period. The model also simulated other major ecosystem processes for which continuous long-term measurements are not available at the Saddle. Model outputs are comparable with measurements of most ecosystem variables by different individual studies (Table S3).

Sensitivity analysis shows that model simulations of carbon pools and fluxes are generally more responsive to certain parameters including foliar respiration as a fraction of maximum photosynthesis (BFolResp), leaf retention time (FolRet), half saturation light level (HalfSat), optimum temperature for photosynthesis (PsnTOpt), specific leaf weight (SLWmax), the constant in the equation of WUE as a function of vapor pressure deficit (WUECnst), and meteorological inputs including photosynthetically active radiation (PAR) and precipitation (Table S4 a). Model simulations of both carbon and water dynamics are responsive to input factors related to sublimation of snow including wind speed and percentage of sublimation at average wind speed (SnowRedisNorm) (Table S4 a b). Model simulations of hydrologic processes are also responsive to leaf retention time (FolRet), precipitation, and input factors that have great effect on photosynthesis including the slope of leaf N and maximum photosynthetic rate (AmaxB), leaf N content in litter (FLPctN), half saturation light level (HalfSat), and photosynthetically active radiation (PAR) (Table S4 b). Sensitivity analysis indicates that model simulations of nitrogen dynamics are highly responsive to input factors that have great effect on carbon and water pools and fluxes. Simulations of nitrogen mineralization and uptake are also responsive to maximum N content in plant N pool (MaxNStore) and leaf N content in stem and root litter (STPctN and RLPctN) which have negligible effect on simulations of carbon and water (Table S4 c). This sensitivity analysis suggests that uncertainty in the above-mentioned input factors are likely major contributors to uncertainty in model outputs. To reduce the uncertainty in simulations of carbon, water, and nitrogen dynamics at the Saddle, improvements on measurement accuracy in these model inputs are needed.

3.2. Climate-driven changes in alpine plant dynamics

We simulated actual and potential transpiration at the Saddle under climate change scenarios, and found small changes by the end of this century. Actual transpiration changes from 35 (long-term average) ± 6 (interannual variability) cm/yr in 1986–2010 to 38 (long-term average) ± 5 (mean interannual variability of projections using inputs from four GCMs) cm/yr and 37 ± 5 cm/yr in 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively (Table S7). Potential transpiration is projected to increase from 39 ± 6 cm/yr in 1986–2010 to 44 ± 6 cm/yr and 43 ± 6 cm/yr in 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively. As shown on the Budyko curve, the dryness and evaporative index values are projected to increase from 1980–2009 to 2010–2039, and then decrease until the end of the century (except for 2070–2099 under the RCP4.5 scenario) (Fig. 1). There is an overall tendency for the hydrologic status of Saddle to shift towards a lower plant-available water coefficient (ω) in the Budyko curve under the climate change scenarios. However, the small variation in dynamic deviation coupled with the modest range of projected dryness index values yields high elasticity (e > 0.5, especially for 1980–2009 to 2010–2039 under the RCP4.5 scenario and 1980–2009 to 2040–2069 under the RCP8.5 scenario) (Table S6).

Future carbon cycling of alpine plants is associated with changes in growing season soil moisture, atmospheric CO_2 concentration, and growing season length. Summer and fall are the driest seasons at Niwot Ridge. Index values (DWater) of plant soil moisture stress during the growing season suggest modest to severe future drought during summer and fall under the climate change scenarios. The projections by the four GCMs indicate that the minimum plant soil moisture stress index value during the growing season decreases from 0.72 ± 0.13 in 1986–2010 period to 0.68 ± 0.16 (0.71 ± 0.17 with CO_2 effects) and 0.63 ± 0.16 (0.66 ± 0.16 with CO_2 effects) for 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively (Fig. 2 a b; Table S7). Future leaf net primary production responds to projected soil moisture conditions by decreasing from 48 ± 7 g C m^{-2} yr^{-1} in 1986–2010 period to 41 ± 5 g C m^{-2} yr^{-1} (43 ± 5 g C m^{-2} yr^{-1} with CO_2 effects) and 33 ± 5 g C m^{-2} yr^{-1} (36 ± 5 g C m^{-2} yr^{-1} with CO_2 effects) in 2076–2100 period under the RCP4.5 and RCP8.5 scenarios, respectively (Fig. 2 c d; Table S7). Projections without CO_2 effects show that leaf net primary production is more strongly correlated with the mean plant soil moisture stress index value (Fig. 3, $r = 0.57$) than the minimum ($r = 0.53$) during summer and fall in the previous year.

Total photosynthesis of alpine plants is not only associated with leaf display but also the growing season length and atmospheric CO_2 concentrations. Average length of the growing season increases from 3 months for 1986–2010 to 3.6 ± 0.4 months and 4.1 ± 0.2 months for 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively (Fig. 2 e f; Table S7). Annual photosynthesis is projected to increase from 319 ± 86 g C m^{-2} yr^{-1} during 1986–2010 to 384 ± 95 g C m^{-2} yr^{-1} (497 ± 117 g C m^{-2} yr^{-1} with CO_2 effects) and 325 ± 103 g C m^{-2} yr^{-1} (464 ± 138 g C m^{-2} yr^{-1} with CO_2 effects) for 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively (Fig. 2 g h; Table S7). Note that the impact of potential CO_2 fertilization effects on total photosynthesis is projected to be greater than the impact of climatic factors, especially under the RCP8.5 scenario. Future stem NPP is projected to increase with carbon storage in thick roots and non-structural carbohydrates/lipids (see results below), while fine root NPP is projected to decrease with leaf NPP. As a result of the

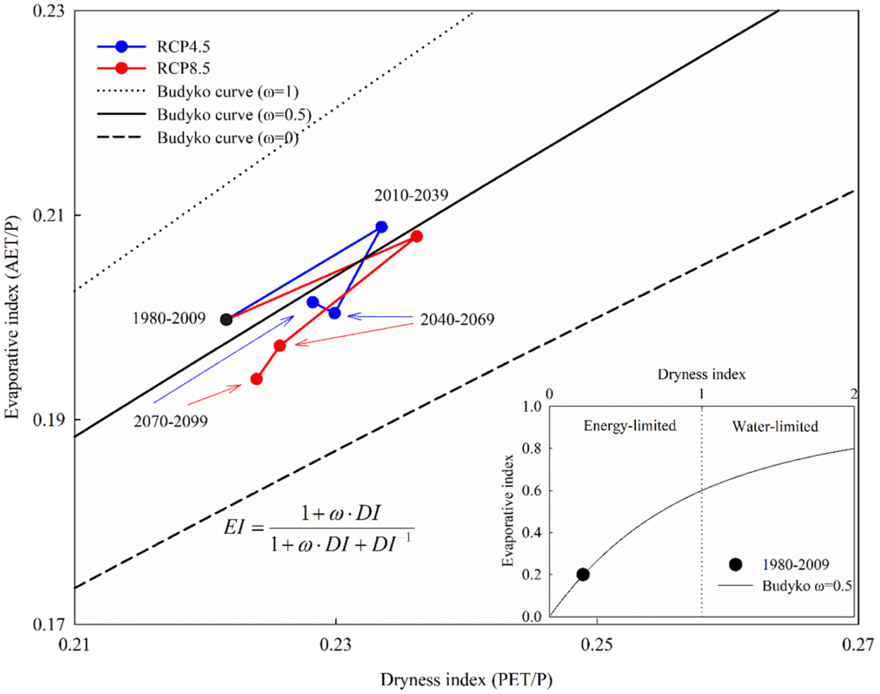

Fig. 1. Past simulation and future projections of dryness index and evaporative index at the Saddle of Niwot Ridge during 30-year periods under the Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios. Values shown are average of simulations using four General Circulation Models without CO_2 fertilization effects.

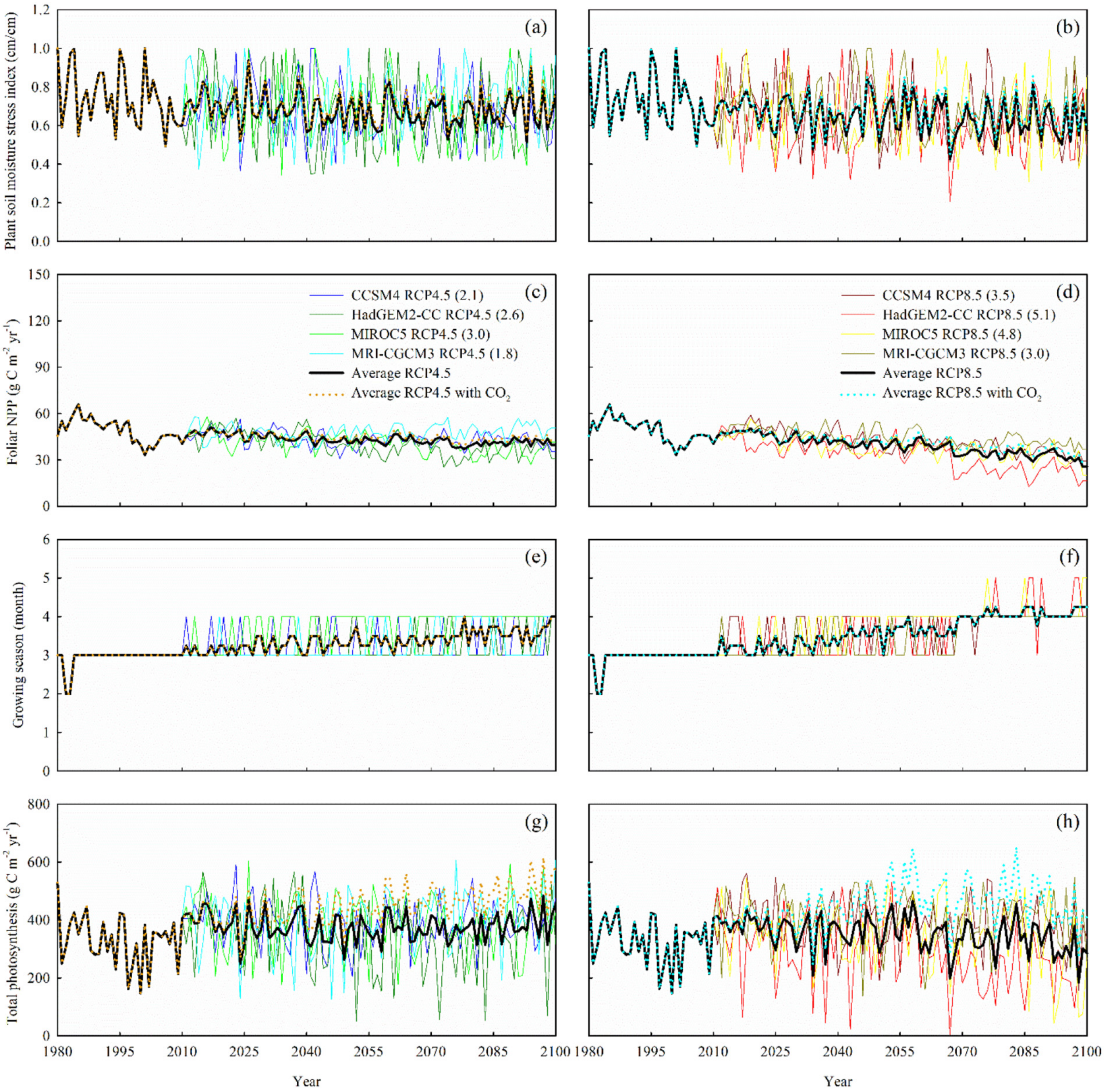

Fig. 2. Past simulations (1980–2010) and future projections (2011—2100) of plant soil moisture stress index (a, b), foliar net primary production (NPP) (c, d), growing season length (e, f), and photosynthetic rate (g, h) at the Saddle of Niwot Ridge under the Representative Concentration Pathway (RCP) 4.5 (a, c, e, g) and 8.5 (b, d, f, h) scenarios. Projections shown use climate inputs from four General Circulation Models (GCMs). The values in parentheses for GCM labels indicate increases in annual mean temperature from 1986–2010 to 2076–2100.

projected changes in vegetation components, total NPP shows little change or decreases when potential CO_2 fertilization effects are not considered, and increases when potential CO_2 fertilization effects are included in simulations (Fig. 4; Table S7).

Future carbon storage in live and dead plant biomass responds to changes in photosynthesis at the Saddle. Projections of carbon storage in live plant tissue (storage organs and non-structural carbohydrates and lipids) show increases from 287 ± 77 g C m^{-2} in the 1986–2010 period to 480 ± 95 g C m^{-2} (716 ± 117 g C m^{-2} with CO_2 effects) and 421 ± 96 g C m^{-2} (702 ± 133 g C m^{-2} with CO_2 effects) for 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively (Fig. 5 a b; Table S7). Dead plant biomass exhibits various responses to future climate depending on the radiative forcing scenario and GCM selected. During 2076–2100, dead plant biomass is projected to be 228 ± 20 g C m^{-2} (299 ± 25 g C m^{-2} with CO_2 effects) under the RCP4.5 scenario and 197 ± 20 g C m^{-2} (284 ± 27 g C m^{-2} with CO_2 effects) under the RCP8.5 scenario, compared with 206 ± 33 g C m^{-2} for 1986–2010 (Fig. 5 c d; Table S7). Similar to the patterns of total photosynthesis, the impact of potential CO_2 fertilization effects on carbon storage in live and dead plant biomass is projected to be greater than the impact of climatic factors, especially under the RCP8.5 scenario.

Projections by four GCMs do not show uniform long-term changes in future nitrogen uptake. Simulated nitrogen uptake at the Saddle is 6.8 ± 2.1 g N m^{-2} yr^{-1} from 1986 to 2010. Average nitrogen uptake projected by the four GCMs for the 2076–2100 period are 7.8 ± 1.5 g N m^{-2} yr^{-1} (8.2 ± 1.6 g N m^{-2} yr^{-1} with CO_2 effects) and 7.9 ± 1.6 g N m^{-2} yr^{-1} (8.6 ± 1.7 g N m^{-2} yr^{-1} with CO_2 effects) under the RCP4.5 and RCP8.5 scenarios, respectively (Table S7). Projections without CO_2 effects indicate that nitrogen uptake is more strongly correlated with net nitrogen mineralization under the RCP4.5 scenario (Fig. 6 a, $r = 0.96$) than the RCP8.5 scenario (Fig. 6 b, $r = 0.95$). Projected nitrogen uptake is also significantly correlated with total NPP under the RCP8.5 scenario (Fig. 6 d, $r = 0.25$), but no significant correlation is observed under the RCP4.5 scenario (Fig. 6 c).

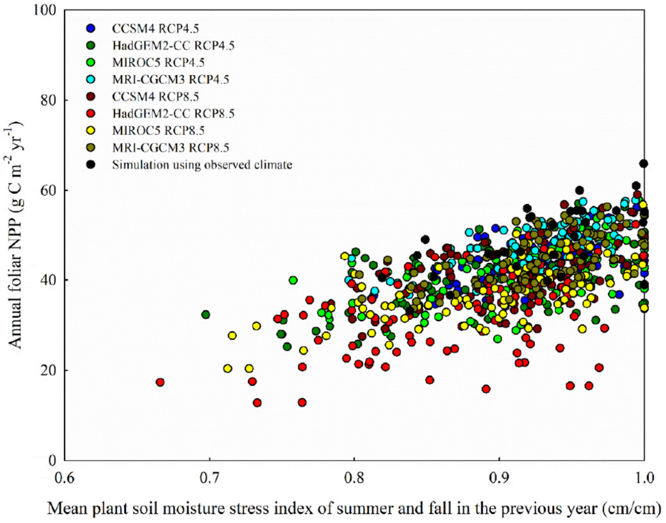

Fig. 3. Relation of annual foliar net primary production (NPP) with mean plant soil moisture stress index (Dwater) during summer (JJA) and fall (SON) in the previous year under the Representative Concentration Pathway (RCP) 4.5 and 8.5 scenarios. Color symbols indicate projections using future climate input from four General Circulation Models from 2011 to 2100; black symbols indicate simulations using observed climate inputs from 1980 to 2010.

3.3. Climate-driven changes in alpine soils

Future decomposition of soil organic matter is projected to respond to altered snow cover, growing season soil moisture and the temperature regime with distinct annual and seasonal patterns. Annual rates of SOM decomposition are projected to show little change without considering potential CO_2 effects on vegetation, but slightly increase when potential CO_2 effects are considered (Table S7). Projections without potential CO_2 effects on vegetation depict decreases in summer SOM decomposition, but increases during other seasons (Fig. 7 c d; Table S8). Seasonal patterns of soil moisture without CO_2 effects on vegetation show that during summer the soil moisture index is projected to decrease from 0.77 ± 0.11 in 1986–2010 to 0.68 ± 0.11 and 0.52 ± 0.10 in 2076–2100 under the RCP4.5 and RCP8.5 scenarios, respectively. In contrast, during other seasons the soil moisture index is projected to increase from 1986–2010 to 2076–2100 under the RCP4.5 and RCP8.5 scenarios (Fig. 7 a b; Table S8). Note that soil moisture is projected to be much higher in spring than in summer by the end of the century under the RCP8.5 scenario.

The projection of net nitrogen mineralization is primarily affected by future decomposition of soil organic matter. Simulations indicate that the mean annual rate of nitrogen mineralization is 8.2 ± 2.9 g N m^{-2} yr^{-1} for 1986–2010. Projections indicate increases in nitrogen mineralization to 9.5 ± 1.9 g N m^{-2} yr^{-1} (9.8 ± 2.0 g N m^{-2} yr^{-1} with CO_2 effects) and 9.9 ± 1.9 g N m^{-2} yr^{-1} (10.5 ± 2.0 g N m^{-2} yr^{-1} with CO_2 effects) under the RCP4.5 and RCP8.5 scenarios, respectively (Table S7). Seasonal results for projections without potential CO_2 fertilization effects on vegetation show net N mineralization is expected to decrease in summer but increase during other seasons under both low and high radiative forcing scenarios (Table S8).

4. Discussion

Previous studies at Niwot Ridge have largely focused on the response of ecosystem structure to future climate change. Long-term observations have shown that more significant changes in plant species distribution have occurred near the higher boundary at 3700 m.a.s.l. and lower boundary at 3300 m.a.s.l. (the subnival and treeline ecotones) rather than the center of alpine tundra at 3500 m.a.s.l. where the Saddle site is located (Suding et al., 2015). Although warming and snow manipulation experiments at the Saddle have demonstrated changes in species diversity at the habitat level in response to altered climate factors (Gasarch and Seastedt, 2015; Walker et al., 2006), long-term observations suggest that ecosystem structure at the landscape level has been surprisingly stable except for an increase in the coverage of shrub species from 0.24% in 1946 to 1.29% in 2008 (Formica et al., 2014; Spasojevic et al., 2013), which is similar to the patterns observed at an arctic tundra site (Wilson and Nilsson, 2009). An experiment using a combination of warming, snow manipulation, and nitrogen fertilization in the moist meadow community at the Saddle demonstrate that ecosystem functions are not likely to be indirectly affected by climate change through interacting species (Farrer et al., 2015). These findings help justify our study that uses a model with prescribed vegetation inputs that depict the plant functional traits to examine how ecosystem functions respond to future changing climate. The agreement of model simulations with observations in major ecosystem variables suggests the robustness of the generalized model using a monthly time-step for the alpine tundra ecosystem with high spatial heterogeneity of snowpack and high β-diversity of plant species.

4.1. Effects of increasing temperature and altered precipitation on water, carbon, and nitrogen cycling

Low and high temperature limits of net photosynthesis are adapted by alpine plants with prostrate morphology to avoid low leaf temperature in winter under high wind speed and extremely low air temperatures and tolerate high leaf temperatures in summer when solar radiation peaks and wind calms (Billings and Mooney, 1968; Körner, 1982, 1999a; Pisek et al., 1973). The wide range of optimal temperature for net photosynthesis by alpine plants results in little direct temperature effect on carbon sequestration under future climate change scenarios at Niwot Ridge. Our projections are consistent with a manipulation experiment at an Alaskan tundra site in which photosynthetic capacity of seven plant species was relatively unchanged throughout the growing season (Starr et al., 2008). However, increasing temperature indirectly affects leaf conductance and carbon assimilation through altered potential transpiration and soil moisture stress, because vapor pressure deficit is projected to increase under future temperature, leading to decreases in water use efficiency (Law et al., 2002) and increases in rates of potential transpiration per unit of leaf area (see below for potential CO_2 effects). Despite the increasing demand, rates of actual transpiration are limited by available soil moisture. Projected increases in summer precipitation are not enough to compensate for the loss of soil moisture through transpiration, which causes soil moisture stress for alpine plants and negatively affects rates of photosynthesis at Niwot Ridge. Alpine plants respond to low soil moisture by producing less leaf area in the following year and operating at “full power”, rather than allocating excessive carbon to photosynthetic machinery and suffering from periodic “shut down” (Körner, 1999b). Repeated future soil moisture stress during the growing season is projected to decrease leaf display at Niwot Ridge especially under the high radiative forcing scenario. Our findings of future soil moisture control over productivity at the alpine tundra ecosystem are consistent with remote sensing observations at an Arctic tundra site, which suggest decreases in vegetation growth following earlier snowmelt (Gamon et al., 2013). A meta-analysis of warming experiments also found slight declines in canopy height and coverage of herbaceous plants from three alpine tundra ecosystems (Walker et al., 2006). We noticed several short-term field studies conducted in Arctic and Antarctic tundra ecosystems report unchanged or increasing productivity in response to warming. However, some of these ecosystems did not exhibit soil moisture stress during the growing season (Day et al., 2008; Hobbie and Chapin, 1998), while other studies found similar relative effects of soil moisture on plant productivity as our projections (Oberbauer et al., 2007).

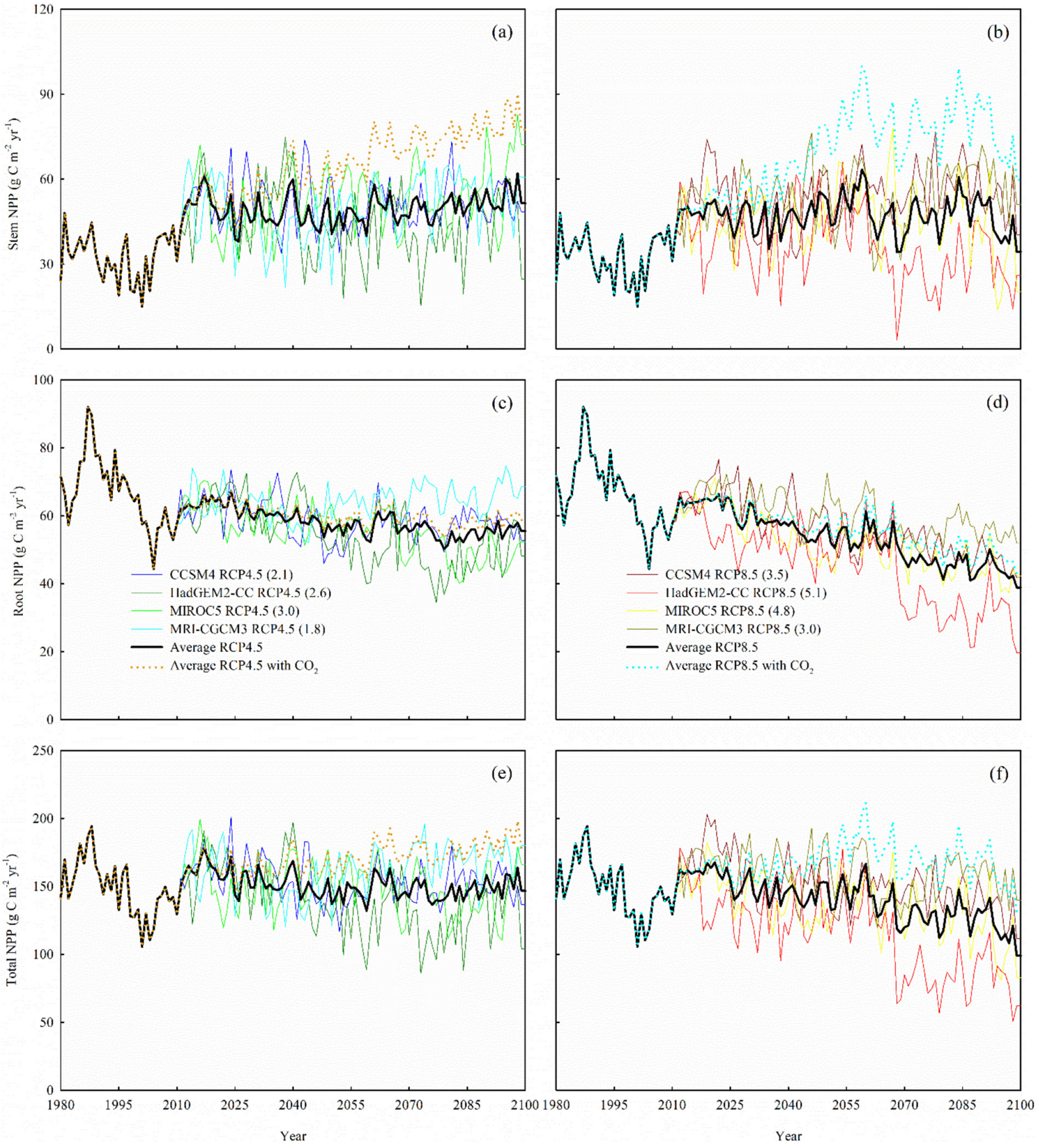

Fig. 4. Past simulations (1980–2010) and future projections (2011–2100) of stem (a, b), root (c, d), and total net primary production (NPP) (e, f) at the Saddle, Niwot Ridge under the Representative Concentration Pathway (RCP) 4.5 (a, c, e) and 8.5 (b, d, f) scenarios. Projections shown use climate inputs from four General Circulation Models (GCMs). The values in parentheses for GCM labels indicate increases in annual mean temperature from 1986–2010 to 2076–2100.

Decreasing snowmelt and increasing potential transpiration results in decreasing soil moisture during summer. The effect of decreasing summer soil moisture outweighs the direct effect of increasing temperature on SOM decomposition, resulting in decreases in SOM decomposition. Our projections show paradoxical results of increasing soil moisture in fall with decreasing precipitation and increasing temperature. This pattern is due to an increase in the rain to snow ratio in fall because the temperature is projected to increase from just below freezing to above freezing under the future climate scenarios. Projected increases in both temperature and soil moisture in fall lead to increases in rates of SOM decomposition.

Projected changes in climate and hydrology shift Saddle's relative position on the Budyko curve, as evapotranspiration is projected to become more water-limited over the short-term due to the temperature-induced increases in leaf conductance (data not shown), but remains energy-limited over the long-term because of anticipated future decreases in leaf area and increases in annual precipitation. Future earlier snowmelt (Fig. 7 e f) and decreasing summer soil moisture (Fig. 7 a b) indicate that climate change may decouple the timing of water and energy supply at Niwot Ridge, resulting in less favorable conditions for the alpine plants (Fig. 2 a b). The overall tendency of Saddle to shift on the Budyko curve from a higher to a lower plant-available water coefficient (ω) (Zhang et al., 2001) in the future indicates that the alpine plants may alter their use of soil water for transpiration due to temperature-induced decreases in leaf area. Our projections contrast with findings from previous studies which concluded a large response

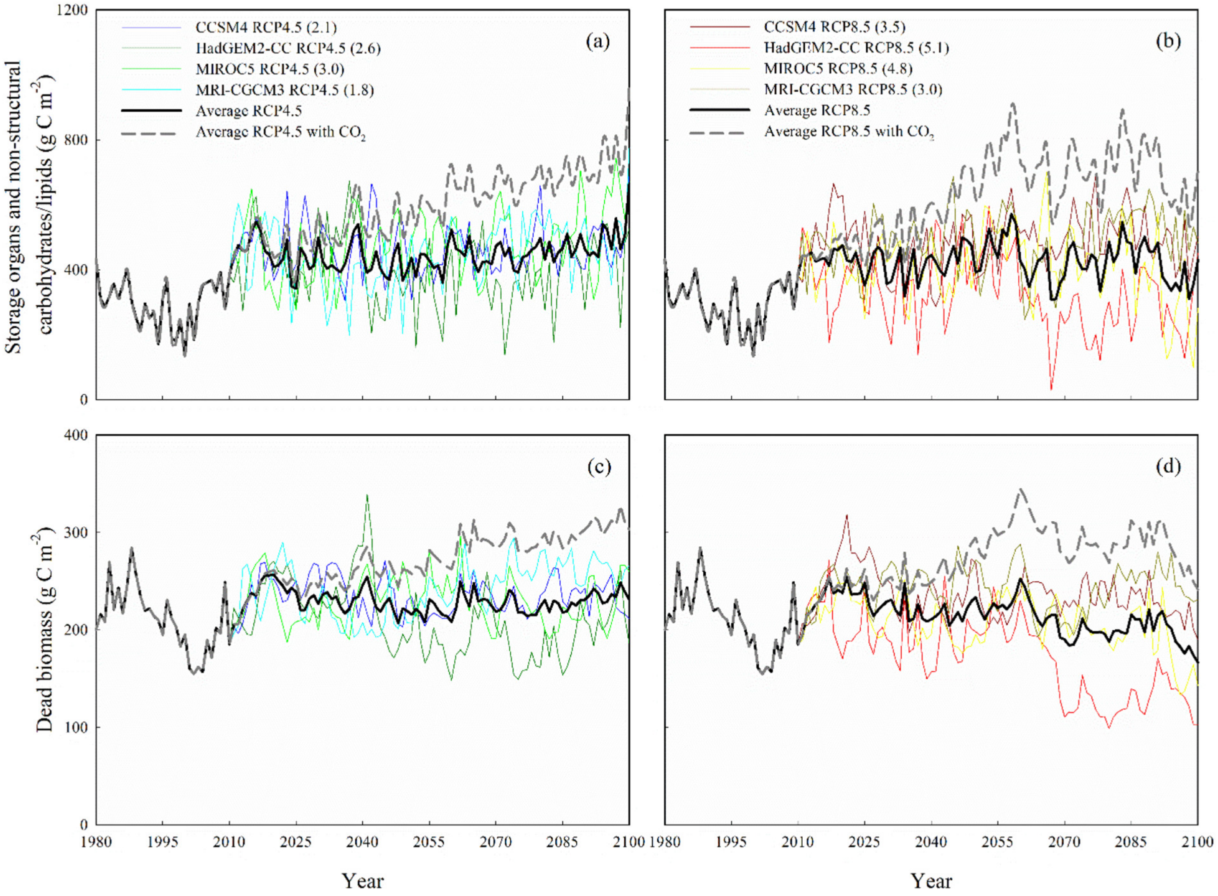

Fig. 5. Past simulations (1980–2010) and future projections (2011–2100) of carbon storage in storage organs and non-structural carbohydrates/lipids (a, b) and dead biomass (c, d) at the Saddle of Niwot Ridge under the Representative Concentration Pathway (RCP) 4.5 (a, c) and 8.5 (b, d) scenarios. Projections shown use climate inputs from four General Circulation Models (GCMs). The values in parentheses for GCM labels indicate increases in annual mean temperature from 1986–2010 to 2076–2100.

in actual evapotranspiration to climate variability, low elasticity values, and low resilience for alpine tundra ecosystems (Creed et al., 2014; Jones et al., 2012). These studies assumed water storage is at steady state when calculating actual evapotranspiration. Although the implications for water-yield at alpine tundra sites using the Budyko curve approach is accurate, our analysis suggests that the response in actual evapotranspiration to future climate variability at Niwot Ridge may not be as drastic as previously indicated.

Primary production is associated with the nitrogen demand of alpine plants throughout the growing season, while net nitrogen mineralization determines soil nitrogen availability because future nitrogen deposition is assumed to be constant in this study. Nitrogen demand of alpine plants is highest at the start of the growing season, then decreases in summer and fall as the demand for nitrogen is satisfied through continuous uptake. Our projections suggest future nitrogen uptake at Niwot Ridge is largely controlled by nitrogen supply than by nitrogen demand under both scenarios, with stronger control by the supply under the RCP4.5 scenario. The demand for nitrogen by the alpine plants is projected to affect uptake, to some extent, under the RCP8.5 scenario, but has little effect under the RCP4.5 scenario. This difference is because of greater decreases in NPP under the RCP8.5 than the RCP4.5 scenario, especially for foliar and root components which have higher nitrogen requirements.

4.2. Effects of extended growing season and reduced snowpack on alpine plants and soils

Alpine tundra ecosystems are characterized by short growing seasons. However, climate change is expected to have significant impacts on the length and timing of growing season in the future (Walker et al., 2001). Historic phenological records at Niwot Ridge (Holway and Ward, 1965; Walker et al., 1995) and other arctic tundra, alpine tundra, and subalpine meadow ecosystems (Arft et al., 1999; Dunne et al., 2003) have shown earlier initiation of growing season in response to climate warming. Projections of advanced spring transpiration at Saddle due to increasing temperature demonstrate effects of the extended growing season. As discussed previously, direct effects of increasing temperature on photosynthetic rate per unit of leaf area is negligible at Saddle due to the nature of alpine plants. However, simulations without potential CO$_2$ fertilization effects on vegetation show increases in annual photosynthesis per unit of ground area under the RCP4.5 scenario, while plant soil moisture stress is projected to become more severe and leaf area is projected to decrease. These seemingly contradictory results are due to the 20% increase in the length of growing season from 3 months in 1986–2010 to 3.6 months in 2076–2100. Similar results are also projected under the RCP8.5 scenario due to the extended growing season, in which plant soil moisture stress index and leaf production are projected to decrease by 12% and 31%, respectively, but annual photosynthesis per unit of ground area is projected to increase by 2% from 1986–2010 to 2076–2100. The additional carbon sequestration due to the extended growing season contributes to primary production, accumulates in live plant tissues, and transfers to dead plant tissues and soil organic matter which may further affect the leaching of dissolved organic carbon to surface water. A previous winter-warming experiment using snow fences and spring snow removal found 20% increase in aboveground NPP from an Arctic tundra, and attributed the response to phenological shifts and increased nitrogen availability (Natali et al., 2012). Our projections show similar increases in spring nitrogen

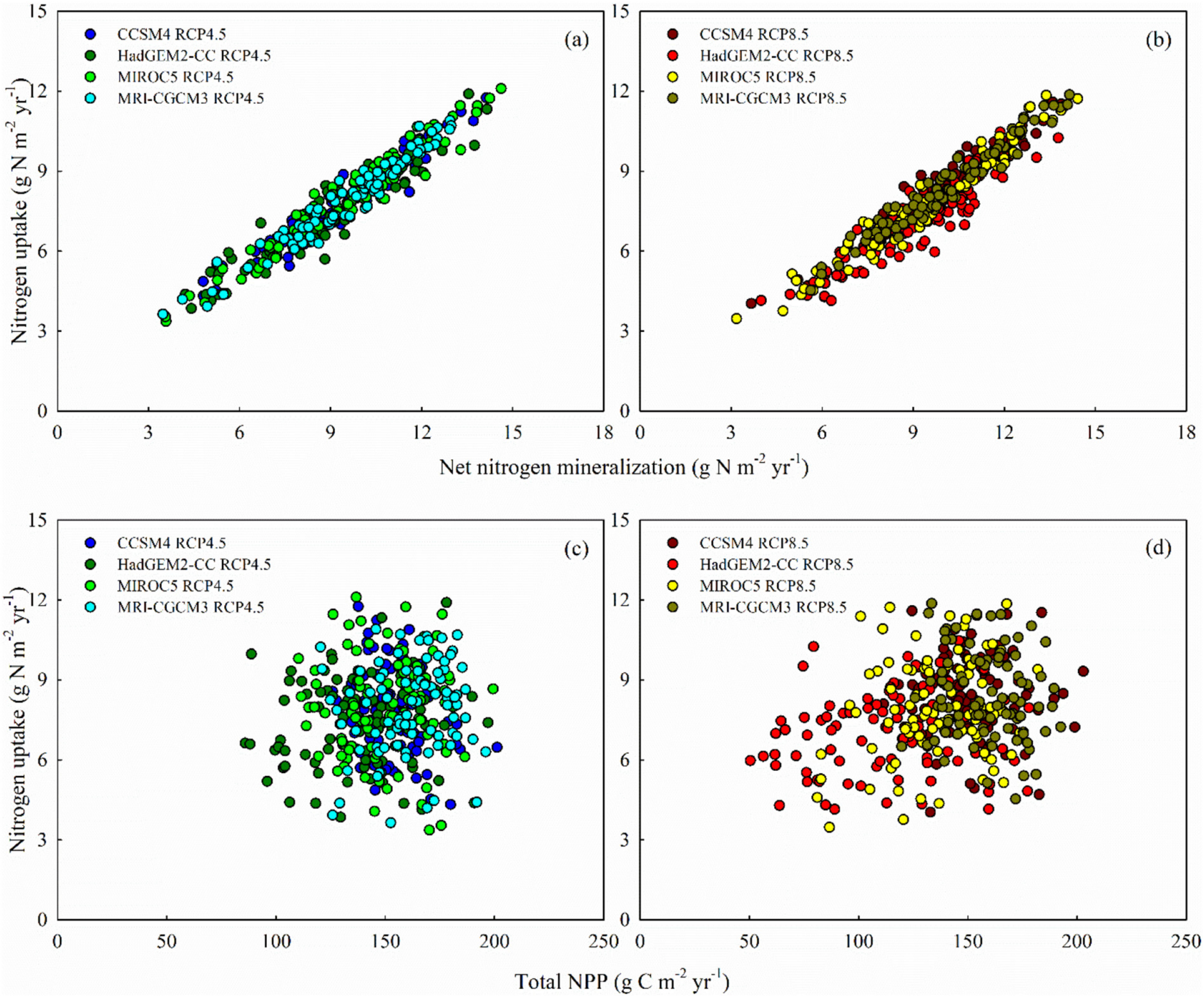

Fig. 6. Relation of annual nitrogen uptake with net nitrogen mineralization (a, b) and total net primary production (NPP) (c, d) under the Representative Concentration Pathway (RCP) 4.5 (a, c) and 8.5 (b, d) scenarios. Each symbol represents projection of a year between 2011 and 2100 using climate inputs from one General Circulation Model under the RCP4.5 or RCP8.5 scenario.

availability associated with warming. However, we do not find nitrogen induced increases in aboveground NPP because the increases in nitrogen availability in spring is largely offset by the decreases during summer.

Note that PnET-BGC simulates the initiation of growing season to certain growing degree days. Several manipulation experiments found that photoperiod (Keller and Körner, 2003) and nutrient supply (Smith et al., 2012) may be more important in controlling the phenology of some alpine plant species. In contrast to our results, a simulation study projected a shorter future growing season in alpine tundra because of the constraint on spring plant phenology by constant future photoperiod and earlier senescence in fall due to drier conditions (Ernakovich et al., 2014). Future improvements in PnET-BGC may quantitatively include such mechanisms to better describe current understanding of plant phenology.

Simulations by PnET-BGC of trends of snow water equivalent and duration of snow cover agreed with U.S. Department of Agriculture regional snowpack telemetry (SNOTEL) observations (Harpold et al., 2012). PnET-BGC considers snow-insulation effects and assumes constant soil temperature under the snowpack. Future shorter snow-covered period were expected to slightly decrease the rate of SOM decomposition in winter and spring due to reduced subnivean microbial activity. However, our projections indicate that this effect on future seasonal SOM decomposition is negligible compared with the effects of increasing winter soil moisture resulting from higher rain to snow ratio in fall and increasing spring soil moisture due to advanced snowmelt, which results in increases in SOM decomposition in winter and spring under the RCP scenarios.

4.3. Potential contribution of elevated atmospheric CO_2 concentration on alpine tundra ecosystem functions

There is less consensus on the effects of elevated atmospheric CO_2 concentrations on carbon sequestration in alpine tundra ecosystems than for forests which have been the focus of the free-air CO_2 enrichment (FACE) studies. Some field studies have shown increased photosynthetic rate of alpine plants under elevated CO_2 concentrations (Körner and Diemer, 1987; Stocker et al., 1997), while another study showed that CO_2 stimulation of carbon sequestration declined within each growing season, and disappeared by the end of a four-year experiment (Körner et al., 1997). Several manipulation experiments reported downward adjustments of photosynthetic capacity by alpine plants under elevated CO_2 concentrations due to a large increase in total non-structural carbohydrates in leaves and an associated decrease in leaf nitrogen concentrations and Rubisco activity, which may or may not be enough to compensate CO_2 fertilization effects (Inauen et al., 2012; Körner and Diemer, 1994). This version of PnET-BGC was modified for alpine tundra ecosystems to consider CO_2 effects on vegetation. However, future improvements to the CO_2 fertilization algorithms can be made as relevant field studies become available.

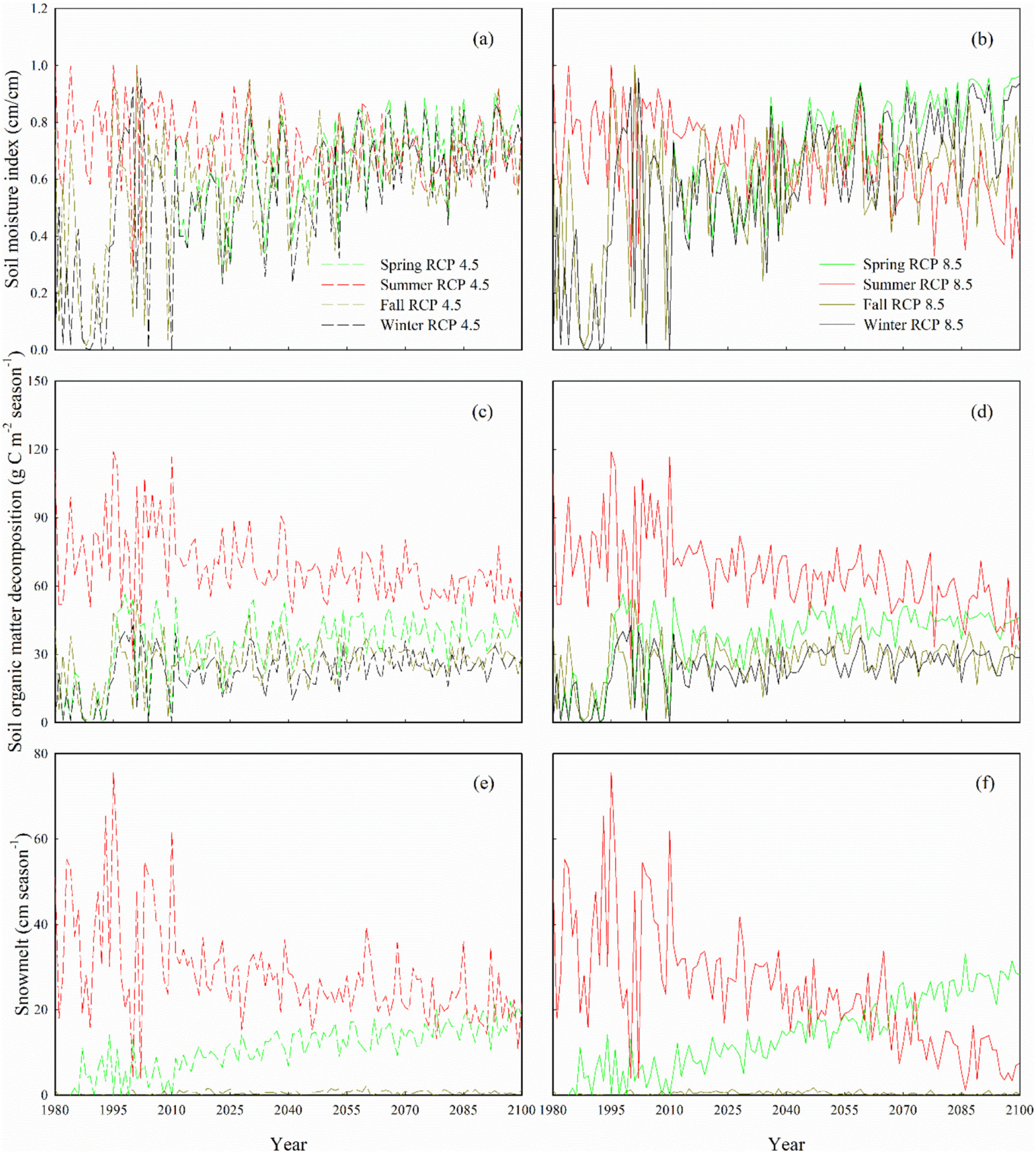

Fig. 7. Past simulations (1980–2010) and future projections (2011–2100) of seasonal soil moisture index (a, b), soil organic matter decomposition (c, d), and snowmelt (e, f). Results shown are the average projections using climate inputs from four General Circulation Models without CO_2 effects. Dashed lines represent the Represent Concentration Pathway (RCP) 4.5 scenario (a, c, e); solid lines represent the RCP8.5 scenarios (b, d, f).

Elevated atmospheric CO_2 concentrations are projected to affect major ecosystem functions at Saddle by increasing photosynthetic rates per unit of leaf area. As leaf and root production are largely affected by future temperature and precipitation, increases in rates of photosynthesis result in the accumulation of carbon in non-structural carbohydrates, lipids, and storage organ of alpine plants. Projected large increases in non-structural carbohydrates under elevated CO_2 concentrations are consistent with observations (Baxter et al., 1997; Körner, 2003; Poorter et al., 1997; Roumet et al., 1999; Zvereva and Kozlov, 2006) and simulations (Luo et al., 1997) for grassland and alpine tundra ecosystems. Carbon allocation to stems is expected to increase with elevated atmospheric CO_2 concentrations, as was observed by Tissue and Oechel (1987). Dead plant biomass is also expected to increase in response to the increases in stem NPP when potential CO_2 fertilization effects are considered. Simulations suggest that future elevated CO_2 concentration results in increases in carbon pools of live and dead plant biomass, but causes only slight increases in soil organic matter which leads to a negligible difference in rates of SOM decomposition from projections without potential CO_2 effects on vegetation.

Future elevated atmospheric CO_2 concentrations are also projected to increase water use efficiency of alpine plants, which is consistent with observations from stable isotopic approaches (Barbosa et al., 2010). Projected increases in water use efficiency result in lower rates of transpiration compared with projections without potential CO_2 effects. Decreased transpiration alleviates plant soil moisture stress on the alpine tundra ecosystem, and projects slightly higher leaf NPP compared with projections without potential CO_2 effects. Our projections of small reductions in transpiration and increases in soil moisture under elevated CO_2 concentrations are consistent with observations in the Jura Mountains of Switzerland (Lauber and Körner, 1997; Niklaus et al., 1998; Stocker et al., 1997). Projected positive growth responses to CO_2 enrichment have also been observed and attributed to CO_2-induced increases in soil moisture in grassland ecosystems (Dijkstra et al., 2010; Morgan et al., 2004). In PnET-BGC, root production is simulated as a function of leaf production. Elevated atmospheric CO_2 concentration is expected to result in slightly higher root primary production at Saddle under climate change scenarios, which is consistent with observations of transient CO_2-induced root growth under low soil moisture conditions in the Swiss Jura Mountains (Leadley et al., 1999).

5. Conclusions

To our knowledge this is the first comprehensive projections of water, carbon, and nitrogen dynamics in an alpine tundra under the RCP scenarios. Our analyses of changes in hydrology in the context of the Budyko curve demonstrate that future evapotranspiration of the watershed is becoming more water-limited over the short-term due to the temperature-induced increases in leaf conductance, but remains energy-limited over the long-term because warming-induced changes in leaf conductance are inadequate to offset projected decreases in leaf area and increases in annual precipitation. Seasonal hydrologic patterns suggest the timing of energy and water supply may be decoupled by climate change, resulting in soil moisture stress on alpine plants during the growing season and decreases in leaf production. Our simulations also indicate that future advanced snowmelt in spring and increasing rain to snow ratio in fall may decrease soil moisture and SOM decomposition in summer but increase soil moisture and SOM decomposition in other seasons. Model projections suggest that nitrogen uptake by the plants at Niwot Ridge is more regulated by future nitrogen supply than demand under both the low and high radiative forcing scenarios. However, the demand is expected to slightly affect nitrogen uptake under the RCP8.5 scenario. Our simulations indicate that potential CO_2 fertilization effects on alpine plants are projected to have large impacts on carbon storage in vegetation, but only negligible effects on leaf and root production.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.09.151.

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