



# Productivity of an Australian mountain grassland is limited by temperature and dryness despite long growing seasons

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## ABSTRACT

Changing climates have extended growing seasons and increased vegetation productivity in many northern ecosystems, but less is known about Southern Hemisphere counterparts. Among the more dramatic changes are reductions in winter snow cover in mountainous ecosystems in southeastern Australia; some forecasts predict almost complete absence of snow by 2050. We used the eddy covariance technique in a montane grassland (Nimmo) of the Snowy Mountains, which was a carbon sink of  $26 - 185 \text{ g C m}^{-2} \text{ yr}^{-1}$  from 2007–2014 but was temperature- and moisture-limited. Higher soil temperatures increased net productivity at a rate of about  $2.2 \text{ g C m}^{-2} \text{ month}^{-1}$  per  $1^\circ \text{C}$ , when soil water content was not limiting. Carbon uptake of Australian mountain grasslands may therefore increase in a warming climate, provided growing season precipitation remains adequate. We used the MODIS normalized difference vegetation index (NDVI) to monitor phenology at Nimmo from 2001–2016. We also recorded daily estimates of greenness from digital imagery (i.e. PhenoCam) and found close correspondence between satellite and near-surface greenness indices in 2015, suggesting that remote sensing can reliably extend PhenoCam records. Mean growing season length (244 days) did not change over the study period and was two weeks longer than mountain grasslands in the Northern Hemisphere. The longer Australian growing season is not correlated with productivity and is likely attributable to the lower latitude of the Snowy Mountains ( $36^\circ \text{S}$ ) and mild Australian climate. Green-up of the grassland advanced by 16 days over the past 15 years, seemingly as a result of increasing August (late winter) temperature. Grass senescence (i.e. yellowing) was most closely related to vapor pressure deficit in March (early autumn). When high temperatures ( $\geq 14^\circ \text{C}$ ) and low rainfall ( $\leq 50 \text{ mm}$ ) resulted in high March VPD ( $\sim 0.7 \text{ kPa}$ ), grass yellowed nearly 3 months early and the growing season was  $< 200$  days. These results suggest there is a tipping point beyond which high summer VPD prevents late-season recovery of Australian mountain grasslands.

## 1. Introduction

Changes in climate have shifted the seasonal activities of many terrestrial and aquatic species in recent decades (IPCC, 2014). Hundreds of studies have documented advancement of plant phenology in spring (Parmesan and Yohe, 2003; Root et al., 2003) with an overall response rate of  $2.8 \text{ days decade}^{-1}$  in the Northern Hemisphere (Parmesan, 2007). Changes in autumn phenology have received much less attention (Gallinat et al., 2015), despite its importance for ecosystem productivity and carbon storage. A recent meta-analysis found that autumn leaf senescence in the Northern Hemisphere has been

delayed by  $0.3 \text{ days yr}^{-1}$  (Gill et al., 2015). The combination of earlier springs and later autumns has resulted in longer growing seasons in Europe (Menzel et al., 2006), North America (Piao et al., 2007), and Asia (Ibáñez et al., 2010). Extension of the growing season by one day increased vegetation productivity by  $5.8 - 15.7 \text{ g C m}^{-2} \text{ yr}^{-1}$  across a range of northern ecosystems (Churkina et al., 2005; Danielewska et al., 2015; Dragoni et al., 2011; Keenan et al., 2014; Piao et al., 2007; Richardson et al., 2010). Ecosystem respiration has also increased, particularly in autumn, reducing the net increase in carbon uptake to  $2.8 - 7.2 \text{ g C m}^{-2} \text{ yr}^{-1}$  per day extension of the growing season (Piao et al., 2007, 2008; Richardson et al., 2010). Much less is known about

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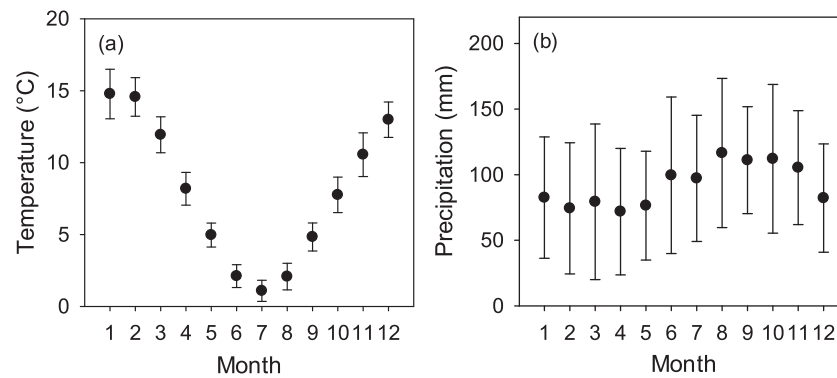


Fig. 1. Seasonal variation in mean monthly (a) air temperature and (b) precipitation at the Nimmo grassland from 1970–2016. Error bars represent standard deviations. The ANUClimate dataset (<http://www.anuclimate.org>) is gridded at 0.01° (approximately 1 km) and provides continuous, site-specific daily data interpolated from ground-based observations.

ecosystems in the Southern Hemisphere, despite their importance in the global carbon cycle (Beringer et al., 2016; Cleverly et al., 2016; Jung et al., 2010; Poulter et al., 2014; Zhao and Running, 2010).

Grasslands cover about one-third of Earth's land surface (Adams et al., 1990) and contribute significantly to terrestrial carbon fluxes (Gilmanov et al., 2010; Scurlock and Hall, 1998). Grassland productivity is largely controlled by the amount and timing of precipitation and corresponding seasonal fluctuations in soil water content (Knapp et al., 2002; Parton et al., 2012; Peng et al., 2013). Temperature is also an important regulator of grassland productivity (Zha et al., 2005) and growing season length (Liu et al., 2006), particularly in high-elevation grasslands. By using a coupled vegetation–hydrology model, Hufkens et al. (2016) predicted grassland growth will shift to earlier spring emergence, reduced summer cover, and later autumn senescence in the future. Overall, the longer growing seasons are expected to increase North American grassland productivity in the future, despite increasing aridity (Hufkens et al., 2016). Such predictions may not extend to mountain grasslands, however, where water from the melting snowpack is often important for productivity. Despite increases in growing season length, soil moisture constrains productivity of subalpine and alpine grasslands (Berdanier and Klein, 2011; Körner, 2003). Increasing aridity has caused a > 50% decline in productivity of a subalpine grassland in the Rocky Mountains, USA over the last four decades (Brookshire and Weaver, 2015). In high-elevation ecosystems, the usual correlation between growing season length and productivity (i.e. longer growing seasons, higher productivity; Galvagno et al., 2013) can sometimes even be reversed (i.e. longer growing seasons, lower productivity; Hu et al., 2010; Sloat et al., 2015).

Mountain ecosystems cover only 11,000 km<sup>2</sup> (< 1%) of Australia's total land area (Williams and Costin, 1994), but grasslands cover about 70% of Australia (McIvor, 2005). The Snowy Mountains are located in southeastern Australia, and since the 1960s, have seen a 40% reduction in snow cover (Bormann et al., 2012; Green and Pickering, 2002; Nicholls, 2005). Snow patches in the Snowy Mountains are more variable than in other parts of the world, as inter-annual melt dates vary by as much as 22 weeks, relative to 1–5 weeks in Northern Hemisphere sites (Green and Pickering, 2009). The area receiving at least one day of snow cover per year in the Snowy Mountains is expected to decrease by up to 85% by 2050 (Hennessy et al., 2008) due to warming of 1–2°C (CSIRO and BoM, 2015). Large losses of snow cover are predicted as the low latitude and relatively mild climates of much of the high country have, for many thousands of years, provided only marginal conditions for the presence of snow (Slatyer et al., 1985). Projected declines in precipitation of about 20% by 2050 compound the effects of rising temperatures on snow cover (Hennessy et al., 2003).

We quantified long-term changes in phenology (2001–2016) and productivity (2007–2013) of a montane grassland (Nimmo; Snowy Mountains, Australia) to determine how climate change may impact Australian mountain ecosystems. At 1340 m elevation, our study site is

located below the alpine treeline (1800 m; Mason and Williams, 2008) and above the winter snow line (1200 m; Slatyer et al., 1985), but receives less than  $28 \pm 24$  days of snow cover each year (Slatyer et al., 1985) and is therefore described as montane (NPWS, 2003). Our objectives were to determine: (1) if productivity and growing season length have changed over the study period, (2) which climate variables drive changes in productivity and phenology at Nimmo, and (3) how this Australian montane grassland compares to those in the Northern Hemisphere. We quantified ecosystem CO<sub>2</sub> fluxes using the eddy covariance technique and characterized seasonal phenology patterns using the normalized difference vegetation index (MODIS-NDVI). We also compared satellite data to a near-surface greenness index measured using digital repeat photography.

## 2. Materials and methods

### 2.1. Site description

Our montane grassland site (Nimmo, 36° 12' 57" S, 148° 33' 10" E, 1340 m a.s.l.) is located on a floodplain within the Gungarlin River valley in the Snowy Mountains, New South Wales, Australia (Fig. S1). The Nimmo site is situated about 35 km northeast of Mount Kosciuszko, the highest mountain in Australia (2228 m). Mean annual temperature at the site is ~7.5°C, and mean annual precipitation is ~1100 mm, mainly falling in winter (Fig. 1b). The vegetation community is broadly characterized as sod tussock grassland (Benson, 1994) and is dominated by the C<sub>3</sub> perennial snow grass, *Poa sieberiana*. The soil is a chernic tenosol derived from granite bedrock, which is generally acidic (pH = 5.0), low in nutrients (total soil N = 3.8 g m<sup>-2</sup>, total soil P = 1.2 g m<sup>-2</sup>), and rich in organic matter (17%; McHugh, 2016). Ecosystem carbon storage ( $13.8 \pm 0.6$  kg C m<sup>-2</sup>; McHugh, 2016) at Nimmo is comparable to global estimates for temperate montane grasslands (14.0 kg C m<sup>-2</sup>; Adams et al., 1990). The Nimmo site is intermittently grazed at low-intensity by cattle from late spring to late autumn, typically by about 130 cow-calf pairs on approximately 475 ha of private land.

The closest long-term climate station (Cabramurra, 35° 56' 24" S, 148° 22' 48" E, 1482 m a.s.l.) is 34 km northwest and 142 m higher elevation than Nimmo. The ANUClimate dataset (<http://www.anuclimate.org>) was used to examine annual temperature, precipitation, and relative humidity trends at the site from 1970–2016. The 0.01° gridded dataset (approximately 1 km) provides continuous, site-specific daily data interpolated from ground-based observations (Xu and Hutchinson, 2013). Climate data were available at Nimmo from 2007–2014, and temperature, precipitation, and relative humidity from the ANUClimate dataset were used for other study years (2001–2006, 2014–2016). All climate data were converted to daily and monthly averages for data analysis.

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