Agricultural and Forest Meteorology 252 (2018) 241–255

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

# Limitations to winter and spring photosynthesis of a Rocky Mountain subalpine forest

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ARTICLE INFO

*Keywords:*
Conifer
Climate change
Xylem temperature
*Pinus contorta*
*Abies lasiocarpa*
*Picea engelmanii*

ABSTRACT

Temperate and boreal conifer forests are dormant for many months during the cold season. Climate change is altering the winter environment, with increased temperature, altered precipitation, and earlier snowmelt in many locations. If significant enough, these changes may alter patterns of dormancy and activity of evergreens. Here we studied the factors limiting photosynthetic activity of a high-elevation subalpine forest that has undergone substantial warming in recent decades. We tested the hypothesis that this warming has been significant enough to allow photosynthesis during sunny warm days in winter. Using thermal imagery, we found that foliage in winter was sometimes near the temperature optimum for photosynthesis, but no net carbon gain occurred for most of the cold season. Water transport was limited by blockage of sap transport by frozen boles, but not by frozen soils. Foliar carotenoid content was much higher during winter, driven largely by increases in the pool size of the photoprotective xanthophyll cycle. There was no seasonal change in chlorophyll or lutein content. Net carbon uptake began only as boles thawed, with no difference in timing among tree species, and the spring increase in canopy-level photosynthetic capacity occurred before sap transport was detected. The seasonality of gross primary productivity (GPP) was strongly linked to seasonality of xanthophyll cycle deepoxidation state in all species. Seasonality of GPP was detectable with two metrics of canopy color – the Green Chromatic Coordinate and Green-Red Vegetation Index (a proxy for the newly proposed MODIS-based chlorophyll/carotenoid index or CCI). Both indices were significantly correlated with GPP. Together these results indicate the potential for airborne or near-surface remote sensing of leaf color to serve as a metric of photosynthetic activity in evergreen forests, and to monitor physiological changes associated with the progression in and out of winter dormancy.

## 1. Introduction

The climate of seasonally snow-covered ecosystems is changing, affecting the seasonality of winter and the timing of biophysical events related to photosynthetic downregulation. In many locations, late winter air temperature is increasing (Kapnick and Hall, 2012; Pederson et al., 2013), total accumulations of snow are decreasing (Hamlet et al., 2005; Mote et al., 2005), relatively more winter precipitation falls as rain instead of snow (Knowles et al., 2006), and snowmelt occurs earlier (Clow, 2010; Stewart et al., 2005). Climate models indicate that these changes will continue (Brown and Mote, 2009; Nogués-Bravo et al., 2007; Scalzitti et al., 2016).

Evergreen plants in seasonally snow-covered locations endure the physiological stress of winter while still absorbing appreciable sunlight. Most undergo biochemical downregulation of photosynthesis that manifests as a decrease in photosynthetic capacity and alterations in pigment composition associated with photoprotection (Adams et al., 2004; Öquist and Huner, 2003; Verhoeven, 2014). Overwintering evergreens have been shown to utilize two forms of sustained thermal energy dissipation to cope with excess absorbed light, a rapidly-

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https://doi.org/10.1016/j.agrformet.2018.01.025
Received 27 February 2017; Received in revised form 21 December 2017; Accepted 18 January 2018

reversible form that is important when favorable temperature for photosynthesis may occur periodically, and a slowly-reversible form that is associated with more sustained downregulation of photosynthesis in colder climates (Verhoeven, 2014). Both forms involve xanthophyll cycle pigments, and may operate in synergy (Porcar-Castell, 2011). Despite this, some conifers maintain appreciable photosynthetic capacity in winter (Nippert et al., 2004; Schaberg et al., 1998; Schulze et al., 1967).

Physiological activity and phenology of plants are responding to the persistent changes in winter climate. The combination of decreasing snow cover and increasing air temperature has complex biophysical and biogeochemical effects on plants and soils (Brooks et al., 2011; Groffman et al., 2001; Kreyling, 2010). The phenology of small plants that spend winter under the snow is strongly altered by earlier snowmelt (Steltzer et al., 2009). Trees and shrubs that extend above the snowpack are responding to warming generally with earlier leaf expansion in spring and later senescence in autumn (Polgar and Primack, 2011). Spring greenup occurs earlier across the northern hemisphere (Barichivich et al., 2013; Piao et al., 2011). Earlier spring and later autumn influence annual gross primary productivity (GPP) and ecosystem respiration ($R_{eco}$) (Richardson et al., 2010, 2009). Thus, the carbon cycle of seasonally snow-covered biomes is being modified on a large scale as climate changes, and this is detectable in the amplitude and timing of the seasonal cycle of atmospheric $CO_2$ (Forkel et al., 2016).

The factors governing the transition from the downregulated state of photosynthesis (winter dormancy) to spring activity are complex. Rather than an on-off switch, release from dormancy is intermittent with periods of activity based on re-establishment of photosynthetic metabolism and variability of weather (Ensminger et al., 2004; Sevanto et al., 2006; Turcotte et al., 2009). In some trees, photosynthetic activity can respond opportunistically to favorable periods during the otherwise cold season (Ensminger et al., 2004) if plants are able to maintain some photosynthetic capacity and water is available (Kolari et al., 2014; Nippert et al., 2004). Earlier snowmelt potentially leads to earlier phenological development and physiological activity of plants, but alternatively if air temperature is low during melt then carbon metabolism can be dramatically limited (Huxman et al., 2003; Winchell et al., 2016). Thus, as the climate warms, some plants may encounter a new regime where novel environmental conditions (combinations of photoperiod, air/soil temperature, snow cover, and water availability) result in physiological stress. The carbon cycle implications of such change remain highly uncertain.

For these reasons, we were motivated to examine the cold season carbon cycling of a high elevation coniferous forest in Colorado. This subalpine forest has undergone significant recent climate warming. Mean annual temperature has increased by ~1.1 °C/decade (Clow, 2010) to 2.7 °C in the 2000s (Mitton and Ferrenberg, 2012). Air temperature in each month February through May has significantly increased (McGuire et al., 2012), and April-May temperature has increased by 0.7 °C/decade (Kittel et al., 2015). Mean annual precipitation is about 800 mm, with a majority falling as snow. Total cold season precipitation has not changed, but the total now includes considerably more precipitation in April that used to occur in May (Kittel et al., 2015). This, combined with warmer cold season air temperature and thus higher convective heat flux during snowmelt when some bare ground is exposed, will likely lead to consistently earlier snowmelt. In most mountain basins of this region, total snow water equivalent is decreasing and snowmelt begins earlier than in recent decades (Clow, 2010).

Our primary objective was to evaluate the hypothesis that the climate has warmed sufficiently to allow the conifers at the Niwot Ridge forest to photosynthesize during favorable warm sunny periods in winter. A secondary objective was to determine if visible-wavelength imagery could be used to identify periods of activity and dormancy. We integrate data from a variety of sources, including a combination of microclimatic and micrometeorological observations, visible-wavelength and thermal imagery, and leaf-level pigment analyses. We anticipated that physiological differences might occur between co-dominant tree species in cold season activity or release from dormancy, and expected that initiation of sap transport would occur before net carbon uptake was detectable.

## 2. Material and methods

### 2.1. Study location

This study was conducted at the subalpine forest of the Niwot Ridge AmeriFlux Core site (US-NR1) in the Rocky Mountains of Colorado, U.S.A. (40.03°N, 105.55°W, 3050 m elevation). The flux tower is surrounded by a mix of evergreen needleleaf species: lodgepole pine (*Pinus contorta* Douglas ex Loudon), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Average tree height and leaf area index are 12–13 m and 3.8–4.2 $m^2$ $m^{-2}$, respectively, and the stem density is ~4000 stems $ha^{-1}$. This high elevation forest experiences cold winters with a persistent snowpack from October-November to May/June. Extensive site details are available in other publications (Burns et al., 2015; Monson et al., 2002). For the present study, observations are reported over a 1-yr period centered on the winter of 2015/2016. The study winter was a bit warmer than the monthly averages of 15 years preceding it (2000–2014) during January and February, but cooler than average for other months (Table 1). Peak snow water equivalent during the study winter was 419 mm, the 5th largest snowpack since the 2000 water year.

### 2.2. Meteorological parameters and carbon fluxes

Environmental conditions were monitored to examine their influence on forest activity and dormancy. Wind, down-welling photosynthetically active solar radiation (PAR), and net radiation (4-component) were measured above canopy, and air temperature both above canopy (21.5 m) and below (2 m), using standard sensors described in Burns et al. (2015). Soil moisture was measured with water content reflectometers (CS616, Campbell Scientific). Soil temperature was measured at 5 cm depth in mineral soil using a thermistor probe (CS107, Campbell Scientific). Snow water equivalent (SWE) data from a site 400 m distant from the flux tower were obtained from USDA/Natural Resources Conservation Service Snow Telemetry Network (site Niwot).

Net ecosystem exchange (NEE) of carbon dioxide was measured at 21.5 m above ground using the eddy covariance method, accounting for

**Table 1**
Comparison of air temperature during selected months between the study winter (2015/16) and the 15 years preceding it (2000–2014). Shown are the 15-year mean, standard deviation (SD), the maximum and minimum mean monthly temperature for each month, and the monthly means for the 2015/16 winter. The 2015/16 data are compared to the 15-year records and ranked in the last column.

| month | 15-year record | | | | 2015/16 | |
|---|---|---|---|---|---|---|
| | mean (°C) | SD (°C) | max (°C) | min (°C) | mean (°C) | 2015/16 rank |
| November | −2.5 | 2.0 | 0.2 | −7.1 | −3.5 | 5th warmest |
| December | −6.7 | 1.6 | −4.5 | −10.4 | −7.1 | 10th warmest |
| January | −6.4 | 1.5 | −3.5 | −9.3 | −6.0 | 6th warmest |
| February | −7.1 | 1.5 | −3.7 | −9.0 | −4.3 | 2nd warmest |
| March | −3.5 | 1.8 | 0.2 | −5.9 | −4.0 | 10th warmest |
| April | −0.2 | 1.7 | 2.4 | −3.5 | −0.9 | 7th warmest |