Agricultural and Forest Meteorology 253–254 (2018) 176–189

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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

Effects of forest tent caterpillar defoliation on carbon and water fluxes in a boreal aspen stand

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A R T I C L E I N F O

Keywords:
Forest tent caterpillar
Eddy covariance
Gross ecosystem production
Ecosystem respiration
Net ecosystem production
Evapotranspiration

A B S T R A C T

Insect outbreaks can significantly influence carbon (C) and water balances of forests. Forest tent caterpillars (FTC) (*Malacosoma disstria* Hübner) are one of the most prominent insects found in aspen forests in Canada and have the potential to considerably influence regional C and water fluxes. In the summer of 2016, an FTC infestation occurred in a ca. 100 -year-old trembling aspen (*Populus tremuloides*) stand in the southern boreal forest where the longterm research site known as Old Aspen (OA) is located. The infestation led to nearly complete defoliation of the canopy during the leafing out period when photosynthesis, and thus C uptake, is progressing towards maximum levels. We used 21 years of eddy-covariance (EC) and climate measurements covering pre-infestation and infestation periods to estimate the impact of the FTC infestation on net ecosystem production (NEP), gross ecosystem production (GEP) and evapotranspiration (E). Defoliation in 2016 reduced annual NEP to $-130\ g\ C\ m^{-2}\ y^{-1}$ and GEP to $798\ g\ C\ m^{-2}\ y^{-1}$, respectively, which were much less than their 20-year means (NEP = $118 \pm 53\ g\ C\ m^{-2}\ y^{-1}$, GEP = $1057 \pm 74\ g\ C\ m^{-2}\ y^{-1}$), and resulted in the most negative annual NEP value of the 21 years of measurements at the OA site. NEP for 2016 was even lower than values observed during three drought years (2001–2003). However, FTC infestation caused little effect on annual E. FTC infestation reduced the near-surface remotely-measured greenness index, green chromatic coordinate (GCC), to ~0.32 on June 10 in comparison to ~0.40 in other years. The defoliation, observable from space as reductions in normalized difference vegetation index (NDVI) values, also showed a negligible effect on E but a large effect on the C fluxes.

1. Introduction

Nearly a tenth of all present-day global forest cover exists within Canada, which extends across 38% of the country's 9.1 million km^2 land area (FAO, 2015). Ecosystem disturbances such as wildfires, harvesting, insect outbreaks, and storms can have large effects on the carbon (C) balance of these forests (Amiro et al., 2010). Impacts of insect outbreaks on C balance tend to vary greatly depending on the species of insects and their host vegetation. Two types of insects that are known to significantly alter C balance of a forest stand are: (1) *Coleoptera* (bark beetles) and (2) *Lepidoptera* (moths and butterflies) (Hicke et al., 2012; Peterson and Peterson, 1992). The latter, which are defoliators (also known as folivores), feed directly on tree leaves, thereby reducing the leaf area and affecting tree growth and mortality (Cook et al., 2008; Hogg et al., 2008). Such insect herbivores are often host-specific at the level of tree genus. In aspen stands (*Populus* spp.), the primary species of *Lepidoptera* capable of defoliation are the forest tent caterpillar (FTC) (*Malacosoma disstria* Hübner), large aspen tortrix (*Choristoneura*

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https://doi.org/10.1016/j.agrformet.2018.01.035
Received 7 June 2017; Received in revised form 5 January 2018; Accepted 26 January 2018

conflictana), Bruce spanworm (*Operophtera bruceata*), aspen leaf miner (*Phyllocnistis populiella*), and gypsy moth (*Lymantria dispar*) (Peterson and Peterson 1992). The FTC in particular has been characterized as the most consequential insect of trembling apen in the prairie provinces (Brandt, 1995), with several major outbreaks in the Canadian prairie provinces occurring between 1937 and 1990 (Brandt et al., 2003). FTC outbreaks tend to be periodic (separated by intervals of 9–13 years) and short-lived, lasting no longer than 1–2 years, though small areas of residual infestation can linger 4 years or longer (Cooke et al., 2009; Cooke and Lorenzetti, 2006). Despite the widespread, and sometimes severe, defoliation events caused by FTC, outbreaks rarely result in tree mortality on their own (Volney and Fleming, 2000), with the exception of oubreaks in locations where unusually frequent, long-lasting defoliation has occurred (Man and Rice, 2010). When FTC defoliation coincides with or immediately follows drought, increases in tree mortality have been observed (Hogg et al., 2008).

The life cycle of FTC has been previously described by Ives and Wong (1988), but we provide a brief summary here. Larvae hatch early in spring, which coincides temporally with the flushing of aspen leaves. Larvae do not actually produce a silken "tent", but instead leave trails of silk while traveling to feed and rest in small silken masses spun on tree trunks or larger branches. After approximately 5 weeks, mature larvae form silken cocoons and pupate for about 10 days before emerging as moths. They then go on to lay eggs, which become larvae 4 weeks later but do not hatch until the following spring.

The impact of transient defoliaton by insect herbivory on short-term fluxes has been the focus of some recent studies (e.g., Clark et al., 2010; Cook et al., 2008; Schäfer et al., 2010). Here, we examine an FTC infestation in 2016 that occurred at the boreal Old Aspen (OA) flux tower site in Saskatchewan (AmeriFlux ID "CA-Oas") for the first time in the 21-year period of long-term flux monitoring at this site. The infestation led to a complete defoliation of the stand as shown in Fig. 1. Motivated by the unique opportunity afforded by a FTC defoliation event occurring in an intensively-instrumented forest stand, we have examined the impacts of this transient disturbance on seasonal and annual C and water fluxes. Quantification of the impact of FTC on C and water fluxes in 2016, compared to pre-disturbance measurements from 1996 to 2015, required the separation of the FTC impact from climate effects during 2016. This was achieved by simulating the fluxes for the FTC-infestation period assuming there was no infestation, and determining the impact by subtracting the measured fluxes.

2. Materials and methods

2.1. Site description

The OA study site is a mature deciduous broadleaf forest located near the southern edge of the boreal forest in Prince Albert National Park, Saskatchewan, in the Boreal Plains ecozone (53.62889°N, 106.19779°W, WGS-84). The forest consists of trembling aspen (*Populus tremuloides* Michx.) with scattered (~10%) balsam poplar (*Populus balsamifera* L.) overstory and a hazelnut (*Corylus cornuta* Marsh.) understory. The understory accounts for 50% of the total leaf area (Arain et al., 2002; Barr et al., 2004). The stand is a uniformly aged stand that regenerated after a natural fire in 1919. The canopy height in 2002 was 21 m (Barr et al., 2012) and currently has a stem density of 486 trees ha^{-1} (personal communication: Jay Maillet 3 March 2017). The soil, an Orthic Gray Luvisol, has developed on clay-rich glacial till that occurs below an 8-10-cm thick LFH (litter-fermented-humic) layer and a 30-cm-thick silt loam layer (Barr et al., 2012). Mean (1960–2000) annual precipitation and air temperature from the closest long-term climate stations – Waskesiu Lake (53.55°N, 106.04°W, 532 m elevation) and Prince Albert Airport (53.13°N, 105.67°W, 428 m elevation) – are 422 mm and 0.6 °C, and 408 mm and 0.9 °C, respectively.

2.2. Climate measurements

A suite of climate variables were measured and reported as half-hourly average values. Air temperature was measured with temperature/humidity sensors (model HMP45C, Vaisala Oy, Finland), which were housed in aspirated radiation shields at a height of 37 m. Air temperature was also measured with a platinum resistance thermometer (PRT) and a 36-gauge chromel-constantan thermocouple (Omega Engineering Inc., Laval, Quebec), both housed in an aspirated radiation shield (model 076B, Met-One Instruments Inc., Grants Pass, OR) at 36 m. Precipitation was measured using both a tipping bucket rain gauge (model TR-525, Texas Electronics Inc., Dallas, TX, USA or model CS700, Campbell Scientific Inc. (CSI), Logan, UT, USA) and a weighing rain gauge (model 3000 with an Alter shield, Belfort Instruments, Baltimore, MD, USA) which were located at a height of ~2 m on a raised platform in the center of a natural clearing approximately 50 m northeast of the tower. Antifreeze was added in winter to prevent freezing and motor oil was added in summer to minimize evaporative losses from the weighing rain gauge. Shortwave and longwave radiation were measured at the 36-m (downwelling) and 30-m height (upwelling) with paired pyranometers (model CM11, Kipp & Zonen BV, Delft, The Netherlands) and paired pyrgeometers (model PIR, Eppley Laboratory Inc., Newport, RI, USA), respectively. Upwelling and downwelling components of photosynthetically active radiation (PAR) were measured at the same heights with paired quantum sensors (model LI-190SA, LI-COR Inc., Lincoln, NE). About 95% of the down-facing radiometers' canopy view would be within 43 m of the tower (Reifsnyder, 1967). Two profiles of soil temperature were measured at six depths (2, 5, 10, 20, 50, and 100 cm) with copper-constantan thermocouples.

2.3. Eddy-covariance flux measurements

We made year-round eddy-covariance (EC) measurements of fluxes of CO_2, water vapor, and sensible heat. These fluxes were measured using instruments mounted on a scaffold tower 39 m above the ground, including a tri-axial sonic anemometer (model R2 (1996–1999) or R3

Fig. 1. Photos of the forest tent caterpillar (FTC) defoliation event at the Old Aspen (OA) Fluxnet site taken on 16 June 2016 from the top of the tower within (a) and above the canopy (b). Panel (a) shows the branches stripped to the petioles with the FTC silken webs. In panel (b), the defoliated stand (over and understory) allows the green shrubbery on the forest floor to be seen.