Paper:
http://dx.doi.org/10.1139/cjfr-2014-0253
Effects of Harvesting and Drought on CO₂ and H₂O Fluxes in an

Aspen Dominated Western Boreal Plain Forest: Early Chronosequence Recovery

R.M. Petrone¹, L. Chasmer², C. Hopkinson², U. Silins³, S.M. Landhäusser³, N. Kljun⁴, K.J. Devito⁵

¹Department of Geography & Environmental Management, University of Waterloo, 200 University Ave West, Waterloo, Ontario, Canada, N2L 3G1. P: 519-888-4567, F: 519-746-0658, E: rich.petrone@uwaterloo.ca

²Department of Geography, University of Lethbridge, Lethbridge, Alberta, Canada, T1K 3M4.

³Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada, T6G 2H1.

⁴Department of Geography, University of Swansea, Singleton Park, Swansea UK, SA2 8PP.

⁵Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, T6G 2E9.
ABSTRACT

The following study examines the hydrological recovery of regenerating boreal aspen and mixed-wood species, and the sensitivity of that regeneration to drought within the first five years of establishment. The results of this study indicate that ET fluxes and WUE rebounded quickly as a result of new vegetation foliage growth and wet conditions found within the first two years following harvest. However, a period of dry years had a significant influence on rates of post-harvest growth, carbon dioxide (CO₂), and water fluxes at these sites.

The first and second years of regeneration were marked by early spring thaw and higher than normal precipitation, while air temperatures remained slightly above the 30-year normal. During this period, average measured height of vegetation tripled at both sites and cumulative ET was approximately 60% of that prior to harvest by the end of the second year of growth. By the third year (2009), the site became a sink for atmospheric CO₂ during the snow-free season (DOY 128-238), despite low precipitation during the latter half of the summer. Volumetric soil moisture content (VMC) in 2009 was highest (on average) of the five years examined, due to heavy snowfall and a late start to the growing season (where air temperatures consistently exceed 0°C), resulting in sustained productivity. However, cumulative annual precipitation also declined to 79% (in year 3, 2009) and 57% (in 2010) of the 30-year normal for that region, leading to significant (lagged) declines in forest productivity in 2010 and 2011. This resulted in the site becoming a source of CO₂ to the atmosphere during the 2010 and 2011 growing seasons (annual balance was not measured). Throughout the drought period (2009, 2010 and 2011) average growth rates (stand height) increased by only 15% (2009), 11% (in 2010), and 14% (in 2011) of that in 2008. Water use efficiency (WUE) also declined in 2010 and 2011, while differences in light use efficiency (LUE) did not vary significantly because foliage was maintained. The results
of this study indicate that regenerating mixed-wood stands are sensitive to drought, and respond relatively quickly to changes in soil moisture regime. This is important as regional drying as a result of predicted climatic changes combined with increased industrial activity may result in significant decline in productivity within these stands over broad regions.
INTRODUCTION
The northern Boreal forest covers approximately 29% of North America (Brandt, 2009) and is a
significant sink for atmospheric CO₂ due to broad area coverage and the prevalence of highly
productive deciduous trees (Gower et al. 2001). Trembling aspen (Populus tremuloides Michx.)
is the most widespread deciduous broadleaf tree species in North America, occurring over a wide
range of site conditions with the greatest continuous expanse found in the western boreal forest
(WBF) (Little 1971; Rowe 1972; Walter and Breckle 1991; Peterson and Peterson 1992).
Recently there have been several northern boreal forest initiatives examining energy, ET and
carbon fluxes, such as the Boreal Ecosystem Atmosphere Study (BOREAS) and the Boreal
Ecosystem Research and Monitoring Sites (BERMS) projects (Griffis et al. 2003; Black et al.
1996; Kljun et al. 2007; Gower et al. 1997; Barr et al. 2007). These studies indicate that despite
their short growing season, aspen dominated forests are more productive than evergreen sites
(Griffis et al. 2003). More recently, the BERMS project has incorporated three harvested and
three previously burned jack pine sites (Mkhabela et al. 2009; Amiro et al. 2006; Howard et al.
2004; Zha et al. 2009), and on later chronosequence regenerating stands. Currently, there is only
one chronosequence study of a one year old harvested aspen site (Amiro 2001), and no study has
investigated the short-term impact of harvesting of aspen forests on ecosystem carbon and water
balances in the WBF in general, nor in the sub-humid, drought prone climate of the Boreal Plains
region (BP) specifically.

Under normal atmospheric conditions, maximum photosynthetic capacity of trembling
aspen is more than double that of other boreal species: jack pine (Pinus banksiana Lamb.) and
black spruce (Picea mariana), resulting in greater cumulative net ecosystem production (NEP)
than either of these two species (Griffis et al. 2003; Zha et al. 2013). Warming and earlier spring
snowmelt may also increase the onset of budburst and growing season length (Barr et al. 2007; Kljun et al. 2007), resulting in substantial increases in gross ecosystem production (GEP) during years with adequate soil moisture (Arain et al. 2002). However, there is strong evidence that increased warming and periodic droughts are affecting the health and productivity of Boreal forest ecosystems in some regions (Michaelin et al. 2011). Air temperatures and precipitation are expected to increase through the 21st Century (IPCC, 2007), which may lead to increased productivity within the Boreal zone (Zha et al. 2013). However, Zha et al. (2013) also caution that increased productivity under relatively normal, non-limiting conditions does not account for the possibility of water stress due to increased evapotranspiration. For example, periods of drought, shifting precipitation patterns and maximum air temperature extremes may be responsible for declining forest health observed in southern and central parts of the Boreal forest (Goetz et al. 2005; Zhang et al. 2009; Goetz et al. 2011; Michaelian et al. 2011).

Despite their broad distribution aspen forests are acutely sensitive to drought over a period of years (Krishnan et al. 2006; Kljun et al. 2007; Michaelin et al. 2011). Within a mature aspen stand, Kljun et al. (2007) found that NEP was a significant sink for CO₂ (more than double that of an average year) during the first year of drought because soil moisture storage within deeper layers of the soil profile could be accessed. During the second and third years of drought, NEP declined to well-below average levels (Krishnan et al. 2006; Kljun et al. 2007), while rates of growth and foliage amount declined significantly (Krishnan et al. 2006). Using remote sensing data and aerial photography beyond stands, Michaelian et al. (2011) found substantial mortality (>55%) of some aspen and mixed broad-leaf stands in the southern Boreal zone as a result of the same drought examined in Krishnan et al. (2006) and Kljun et al. (2007). Over broad areas, declines in ecosystem productivity may be a visual sign of drought stress due to reduced
precipitation and/or increased drying in these regions (Goetz et al. 2005; Zhang et al. 2009; Goetz et al. 2011; Michaelian et al. 2011), however, actual mechanisms for change and species sensitivity to drought are not well understood. As climate warming trends increase, widespread aridity may have substantial but relatively unknown influences on ecosystem dynamics (Kurz et al. 2008). To date, no studies have examined the sensitivity of recently harvested and regenerating aspen stands to prolonged drought and water stress (Zha et al. 2013).

The following study examines two regenerating aspen-mixedwood stands following harvest within the BP ecozone of the Canadian Boreal forest. This region contains the greatest proportion of trembling aspen stands (Peterson and Peterson 1992), and is characterized as a mosaic of fragmented upland forests, riparian ecosystems, and pond-peatland complexes (Petrone et al. 2008; Rizzo and Wiken 1989). The BP region is also prone to periods of significant drought, where evapotranspiration (ET) exceeds precipitation (P) (Marshall et al. 1999; Devito et al. 2005), and heavy anthropogenic disturbance from resource extraction. The objectives of this study are:

1. Quantify water and CO$_2$ exchanges within two regenerating mixed-aspen stands for the first five years following harvest.

2. Examine the resiliency of stands to a period of drought by reporting on growing season trajectories of production efficiencies (water use efficiency, light use efficiency), soil moisture influences, and changes in growth.

Sensitivity to drought and long-term feedbacks will provide important insights into aspen stand dynamics and response to soil moisture deficits (all else being equal).

SITE CHARACTERISTICS
Two recently harvested upland trembling aspen stands were established as part of a larger study within the Utikuma Regional Study Area (URSA), located in the BP ecozone, north-central Alberta (56° 6’ N, 116° 32’ W) (Figure 1a) (Devito et al. 2005). Climate in this area is sub-humid with mean annual precipitation ranging between 481 mm and 518 mm (Environment Canada, 2010), and 30-year monthly mean temperatures ranging between -14.6 to 15.8 °C (Ecoregions Working Group 1989). The BP is a glacial landscape characterized by small variations in topography (655-670 m above sea level (a.s.l.)), heterogeneous upland moraine landforms, and adjacent pond/peatland complexes.

Harvested areas examined in this study (Figure 1b) are located on nearby uplands (within 200 m of each other) and share an adjacent pond between them (Devito et al. 2005). Both pre-harvest aspen stands had regenerated from wildfire in 1962 and were approaching maturity when they were harvested. In March 2007, the northern-most study area (NSA) was harvested, and approximately one year later (February 2008), the southern study area (SSA) was harvested, both with minimal damage to roots as a result of deep snow (>60cm) and frozen ground. In the years immediately following harvest, there was increased prevalence of fireweed (*Epilobium angustifolium*), blue-joint reed grass (*Calamagrostis canadensis*), and yellow sweet clover (*Melilotus officinalis*). Within three (four) years of harvest, the regenerating canopy had an average height of at least 1.1 m (Figure 1c). Remaining tree debris that could not be used for commercial purposes was left in large slash piles within the site (Figure 1c), and was burned the winter following harvest (2008/2009).

**DATA COLLECTION AND METHODS**

_Meteorological Data Collection_
Hydro-meteorological data were collected throughout the year on short-stature (4.3 m) towers at each harvest site, coincident with energy and mass exchanges. Variability in temporal measurements and inter-/intra-annual climate were examined throughout the year, and more specifically during the snow-free period from May 8 to August 26th (DOY 128-238), 2007-2011 (NSA), and 2008-2009 (SSA). Half-hourly (averaged) atmospheric measurements included air temperature ($T_a$, °C), and relative humidity (RH, %) (height = 1.3 m a.g.l., 0.5 m above canopy (HOBO Onset Pro Temperature/RH, Hoskin Scientific, Vancouver, Canada)). Radiation measurements included above canopy net radiation ($Q^*$, W m$^{-2}$), measured at a height of approximately 4 m a.g.l. (NRLite radiometers, Kipp and Zonen, The Netherlands). Wind speed and direction were measured using RM Young (Young Inc. Michigan USA) wind monitors, and were used primarily to locate the origin of half-hourly flux footprints.

Soil measurements included moisture, temperature and heat fluxes collected at sites located 20 m, 25 m, and 85 m from each tower and averaged. Soil heat fluxes ($Q_G$) were measured using two heat flux transducers (HFT-03; Campbell Scientific, USA) at each site, buried 0.05 m below the litter fall horizon (LFH) - soil interface. Soil temperature and heat storage in the upper 0.05 m were measured using a thermopile (TCAV-L; Campbell Scientific, USA) inserted at 0.025 and 0.075 m below the soil surface. Soil volumetric moisture content (VMC, %) (CS616 TDR; Campbell Scientific, USA; calibrated for study site soils) and soil temperatures (107B Thermistors; Campbell Scientific, USA) were recorded at depths of 0.01, 0.10, 0.30, 0.50 and 1.0 m below the LFH-mineral soil interface at each site (Redding and Devito 2008; Brown et al. 2013). VMC data were corrected for soil bulk density and temperature. Ground water levels were measured using well data adjacent to eddy covariance towers, and at
two sites at the riparian/stand edge. Cumulative precipitation was measured within an open area near the NSA using hand gauges and a tipping bucket rain gauge (R. M. Young Inc.).

Eddy-Covariance Instrumentation and Processing

Net ecosystem exchange (NEE), latent (Le) and sensible (H) energy exchanges, and friction velocity were measured using eddy covariance instrumentation for the snow-free period, coincident with hydro-meteorological data. Instrumentation deployment followed the same protocols for set-up and data processing for each site so that measurements between sites would be intercomparable. Instrumentation consisted of an open-path infrared gas analyzer (IRGA) (model LI-7500, LI-COR Inc., NE) and a three-dimensional sonic anemometer (model CSAT3, Campbell Scientific, UT) installed at a height of 4.3 m a.g.l. (approximately 1 m above the top of the vegetation canopy by year five of growth (NSA)), per site. Fluxes were sampled at a rate of 20 Hz and averaged over half hourly periods using a CR23X data logger (Campbell Scientific, UT). Briefly, NEE correction procedures (Giroux, 2012) included filtering for periods of low friction velocity (<0.35 m s⁻¹) (Petrone et al. 2007), and rotation of vertical and horizontal wind velocities to zero (Kaimal and Finnigan, 1994). Gaps within eddy covariance data were filled based on the mean moving windows over 14-day periods (Falge et al. 2001), and quality controlled to remove outliers exceeding two standard deviations of the mean (Papale et al. 2006).

Gross ecosystem production (GEP) was estimated from half-hourly estimates of net ecosystem production (where NEP = -NEE), assumed positive when the ecosystem is a sink for atmospheric CO₂, and total ecosystem respiration (Re). Night-time NEP was used as a direct estimate of Re during periods when friction velocity was greater than the minimum threshold. For periods below this threshold, Re was estimated using an empirical model as a function of within canopy air temperature. Daytime GEP was estimated as the difference between NEP and Re (GEP =
NEP + Re), where daytime Re was determined from the same empirical model used for nighttime Re (Griffis et al. 2003).

A flux footprint parameterization based on a full-scale Lagrangian particle model (Kljun et al. 2002; Kljun et al. 2004) was used to estimate contribution areas for mass fluxes at both sites during the summer of 2009. The footprint is defined as the probability of contribution by CO$_2$ and water fluxes per unit area upwind of the eddy covariance system. While most inputs were obtained from eddy covariance and wind direction, roughness length ($z_0 m$) and zero plane displacement ($d$) of vegetation were mapped at 1 m resolution within 10 degree wind sectors based on canopy height from airborne light detection and ranging (LiDAR) data ($z_0 m = 1/10$ height; $d = 2/3$ height of trees) (Chasmer et al. 2011). Wind sectors were used to constrain the iterative footprint model, which was then accumulated over the growing season.

Efficiency Parameters

In this study, light use efficiency (LUE), water use efficiency (WUE) and Landsberg light response curves were used to assess resource use through the growth period per year. LUE, the use of light by vegetation for photosynthesis (Schwalm et al. 2006; Chasmer et al. 2008), was determined as the ratio of GEP to intercepted photosynthetically active radiation (IPAR). Above and below-canopy intercepted and reflected PAR measurements were not acquired for stands due to the low height, dense cover and lack of definitive understory immediately following harvest. Therefore, IPAR was estimated using site average effective LAI (LAIe) from ceptometer measurements:

$$IPAR = PAR(1 - e^{-LAIe k})$$

[1]
where $k$ is an assumed extinction coefficient of 0.5 for both sites. The relationship between intercepted PAR (at the top of the canopy) and GEP was also determined using a Landsberg light response curve (e.g. Turner et al. 2002; 2003):

$$GEP_{\text{Landsberg}} = P_{\text{max}} \left(1 - e^{-a(P_{\text{PAR}} - I_{\text{comp}})} \right),$$

which demonstrates the maximum average GEP ($P_{\text{max}}$), the slope (scaling factor) of the initial rise of GEP with incoming PAR ($a$), and the point at which GEP is zero (the light compensation point, $I_{\text{comp}}$).

Water use efficiency (WUE), the total amount of biomass produced by photosynthesis for every gram of water lost through transpiration (Rosenberg et al. 1983), was determined from the ratio of GEP to ET (for dry periods only (no precipitation + one day to allow for drying)).

**Stand Mensuration**

Vegetation structure was sampled in three 15 m by 15 m plots per site, at the time of peak foliage (second week in July) per year (Brown et al. 2010). Measurements included: tree height (Vertex hypsometer; Sweden), diameter at breast height (DBH) at 1.3 m a.g.l. (Vernier caliper), and LAIe. Site average LAIe was estimated using a ceptometer (AccuPAR LP-80 ceptometer Decagon Devices Inc., WA). Measurements of PAR radiation by the ceptometer were acquired on overcast days along two (east-west and north-south) 100 m transects per site. PAR measurements were sampled at a height of ~0.25 m a.g.l., every 5 m at centre, and again at a distance of two meters perpendicular to the transect (left and right of centre). LAIe estimates from ceptometer measurements were checked and calibrated using digital hemispherical
photography (processed with DHP and TRACwin software; Leblanc, 2008) acquired at 17 and 14 coincident locations within the NSA and SSA, respectively.

Airborne LiDAR Data Collection and Processing

Airborne Light Detection And Ranging (LiDAR) remote sensing data were used to compare spatial changes in canopy height and cover between 2008 and 2011 (and pre-harvest conditions in 2002). LiDAR data were collected in September 2008 for Alberta Sustainable Resource Development using an Optech Inc. ALTM 3100EA (Optech Inc., Canada). The system was operated at a flying height of 1400 m a.g.l., with a laser pulse repetition frequency of 50 kHz, and a scan angle of ±25°. Data collected in August 2011 was acquired and processed by the authors using a slightly different sensor model (Optech Inc. ALTM3100) operated at a flying height of 1800 m a.g.l. The laser pulse repetition frequency was 50 kHz, with a scan angle of ±23°. A 50% overlap of scan lines was adopted to reduce laser ‘shadowing’ by canopies and to ensure sampling of both sides of trees. LiDAR data were also collected in 2002 and is used to briefly describe pre-harvest stand structural characteristics (Hopkinson et al. 2005 and Chasmer et al. 2011).

LiDAR data were classified and processed in TerraScan (TerraSolid, Finland) and output into ground and non-ground (vegetation) classes, after removal of outliers. Several gridded products were derived following Chasmer et al. (2011), including a digital elevation model (DEM, m), a digital surface model (DSM, m) of canopy heights plus topography, and a canopy height model (CHM (m) = DSM – DEM). The difference between the 2008 and 2011 CHMs quantify growth characteristics of regenerating species throughout the two sites (Figure 1c), residual mature aspen trees that were left over after harvest, and slash piles that were burned during the winter following the LiDAR survey.
RESULTS

Site Climate Variability

Climatology during the five years of study was marked by two years of wetter than normal conditions directly after harvest followed by a 2-year dry/drought period that began approximately 2.5 years after harvest (NSA; 1.5 years after harvest at SSA). Harvest years 2007 (at NSA) and 2008 (at SSA) were the wettest in 13 years, exceeding the 30-year normal for the region (Table 1). Above average rainfall and snow accumulation in 2007 and 2008 maintained high soil VMC into June 2009 (maximum average of 0.42 m$^3$ m$^{-3}$; Figure 2). Higher than normal rates of precipitation continued with above average snow accumulation into spring 2009. By summer 2009, both sites experienced significant declines in precipitation (Table 1; Figure 6e), while initially high VMC declined through the July and August period (2009), and remained low through 2010 and 2011 as a result of low cumulative rainfall (Table 1; Figure 2). Minimum average soil moisture of 0.27 m$^3$ m$^{-3}$ occurred in the summer 2010, while July ground water levels ranged from 4-6 m (at towers) and 1-2 m below the surface near the riparian edge. Ground water levels measured near the towers were lowest during the wettest year in 2007 as a result of a previous dry period, peaking in 2009 (with shallowest levels) in response to precipitation inputs in 2007 and 2008. Ground water levels decreased again in 2010 and 2011, lagging drought, while precipitation returned to near-normal conditions by mid-summer 2011.

Growing season average air temperatures (Ta) for the period studied (except 2009) were slightly warmer than the 30-year normal (at Slave Lake Airport, Alberta; Environment Canada, 2010), but no period stood out as being significantly warmer than any other period (P=0.64 using Kruskal-Wallis test) (Table 1; Figure 2). 2007 was also marked by the earliest spring thaw (the date when air temperatures were consistently greater than 0°C), of the years studied (March 19$^{th}$),
while the latest spring thaw occurred on April 6th, 2009. The winter (identified as December 1st to March 31st) of 2008/2009 was also 7° colder than the 30-year normal for this region (Slave Lake Airport, Alberta; Environment Canada, 2010), and was certainly the coldest during the period studied.

*Energy Exchanges*

Although Q* did not vary significantly between sites or years (Figure 2), the partitioning of Q* into latent (Qe) and sensible (Qh) heat exchanges did (Figure 3). Both sites exhibited similar changes in Qh and Qe following harvest, with slightly greater proportions of average Q* used for Qe (Table 1). Qe increased through the growing season, peaking in late June/early July, while Qh peaked earlier in the season (June) and declined through July and August with increased foliage cover and rates of evapotranspiration. Decline in Qe through 2011 (average = 32% of Q*) occurred as a lagged response to drought, showing little rebound to earlier (2007-2009) levels by the end of the study period (Figure 3).

*Spatial and Temporal Changes in Vegetation Growth Following Harvest*

Rates of growth of regeneration species also appeared to be affected by drought between mid-2009 into 2011. This was observed at NSA, which had the longest record of structural measurements (Table 2). At both sites, average canopy height tripled during the first two years of establishment. Growth rates at SSA were not influenced by drought during the second year of growth, likely because soil moisture was retained from previous warm/wet years. Between 2008 and 2009, growth rates slowed to 15% of total growth between 2007 and 2008, and 11% of total growth between 2009 and 2010 (compared with 2008-2009), and increased slightly in 2011 (14%) (Table 2). It is not known what the growth rate would have been if conditions were similar
to the first two years of growth, throughout the five-year period, however, a decline in growth  
rate in 2010, followed by slight rebound in 2011 indicates that arid conditions may have had  
some influence. Average LAIe estimates measured in July of each year doubled between years 1  
and 2 of growth at both sites, but declined to 21% of growth by year 3; 5% (year 4); and 7%  
(year 5) (at NSA) (Table 2). Diameter at breast height (DBH) also more than doubled between  
years 1 and 2 of growth, but declined to 26% (2009), 15% (2010), and 11% (2011) compared  
with previous years’ growth. This indicates that foliage growth rates were most affected by  
drought over the three-year period, and a late start to the growing season in 2009.  

Spatial variability of growth rates determined from two airborne LiDAR surveys (2008  
and 2011) (Figure 4) were greatest at the NSA as expected (due to the timing of harvest in 2007),  
and exceeded 2 m in some areas, while at SSA (harvested one year later), site average growth  
rates were approximately 1.3 m over the three-year period. Interestingly, growth rates at both  
sites were greatest in areas adjacent to mature aspen residuals; trees that were not cleared during  
harvest, and near edges where harvested areas were adjacent to mature trees (Figure 4c). A total  
of 53 mature trees remained at NSA following harvest, while only 13 remained at SSA. Areas  
with greater rates of growth did not correspond with parts of sites that characterized by taller  
trees pre-harvest (Figure 4a), or variations in topography.  

CO₂ and Water Vapor Exchanges  

Areas sampled by eddy covariance instrumentation are shown in Figure 5. The greatest  
probability of fluxes occurred within 71 m (stdev. = 8 m) of the eddy covariance system (NSA),  
and 98 m (stdev. = 8 m) (SSA). Prevailing wind directions did not vary greatly between sites,  
originating from NW (NSA) and SSW (SSA) during the years studied for each site. When
combined with spatial variations in canopy growth (Figure 4d), areas sampled by eddy covariance at NSA were slightly more productive than SSA due to an additional year of growth.

NSA and SSA were net sources of CO₂ to the atmosphere during the May to August period for the first 2 years post-harvest (annual C balance was not measured), and NSA was a greater source of CO₂ than SSA during those first two years following harvest (Table 1, Figure 6). NSA became a slight sink for CO₂, by the end of the third year after disturbance (2009), resulting in total cumulative NEP of 17 g C m⁻². Low precipitation and low VMC during the latter half of 2009 to 2011 resulted in net loss of CO₂ to the atmosphere by 2010 (201 g C m⁻²) through 2011 (180 g C m⁻²) for the period measured (Table 1; Figure 6). NEP was significantly positively correlated with soil VMC in year 1 (2007) ($R^2 = 0.65, p < 0.05$) and 3 (2009) ($R^2 = 0.55, p < 0.05$) following harvest at NSA, and in year 2 (2009) ($R^2 = 0.55, p < 0.05$) at SSA, but neither site was greatly influenced by other drivers (e.g. VPD, Tair or RH). Growing season cumulative GEP and NEP were positively linearly correlated with annual foliage growth (LAIe) ($R^2 = 0.93; 0.95$, respectively), height ($R^2 = 0.87; 0.89$, respectively) and DBH ($R^2 = 0.87; 0.91$, respectively).

Cumulative ET estimates of 222 mm (NSA) and 220 mm (SSA) were found during the May to August period for the first year of post-harvest growth. By the second year of growth, a cool spring initially limited ET fluxes at NSA until approximately DOY 159, when ET began to increase as a result of warmer air temperatures and residual VMC. Cumulative ET fluxes on the same day in 2009 were suppressed, coinciding with cool Ta and a late start to the season (Figure 2; Figure 6). A warm, dry May to August period in 2010 resulted in the greatest cumulative ET fluxes exceeding annual P for that year. By 2011, ET was reduced to 2007 levels until DOY 211.
as a result of very low rainfall (cumulative $P < 20$ mm from January 1st) and reduced soil moisture conditions that remained low until mid-June (Figure 2; Figure 6).

**Post-Harvest Efficiency**

Water use efficiency (WUE) increased steadily during the first three years of growth at NSA, reaching an average WUE of $3.3 \text{ g C/g H}_2\text{O}$ (RM ANOVA on ranks, $p < 0.05$ for differences between years) (Figure 7a). Slightly higher efficiencies were recorded during the first two growth at SSA compared with the first two years of growth at NSA, but were not significantly different. At NSA, WUE decreased by 57% of 2009 amounts in 2010 ($1.89 \text{ g C/g H}_2\text{O}$) in response to decreased soil moisture content, declining foliage growth rates, and reduced GEP. WUE then rebounded to $2.44 \text{ g C/g H}_2\text{O}$ in 2011 with increased precipitation during the latter part of the summer.

Average LUE was slightly less during the second year of growth at SSA ($1.35 \text{ g C MJ}^{-1}$) compared with NSA ($1.58 \text{ g C MJ}^{-1}$), in response to differences in measured LAIe (used to estimate IPAR) and C uptake (Figure 7b). LUE peaked in 2009 ($1.63 \text{ g C MJ}^{-1}$) and declined to $1.42 \text{ g C MJ}^{-1}$ and $1.23 \text{ g C MJ}^{-1}$, on average in 2010 and 2011. Unlike drought responses of mature aspen stands (e.g. Kljun et al. 2007), rates of foliage growth and intercepted radiation declined, but foliage was not lost from the canopy. Therefore, LUE was relatively stable through the drought period as growth matched GEP.

Similar responses of GEP compared with intercepted PAR (Landsberg light response curves; Figure 8) illustrate a slightly different trend to Figure 7b. Use of light for photosynthesis increases during the first three years of rapid growth at NSA (first two years at SSA), and maximum average GEP ($P_{\text{max}}$) levels off with increasingly greater amounts of light, per year.
(approximately 52, 88, and 137 Wm$^{-2}$ for years 2007 to 2009, respectively at NSA). By 2010, $P_{\text{max}}$ was lower than the maximum rates of increase observed in 2009 (0.32 g C m$^{-2}$ 30-min$^{-1}$), declining to 0.18 g C m$^{-2}$ 30-min$^{-1}$. At SSA, $P_{\text{max}}$ reached 0.11 g C m$^{-2}$ 30-min$^{-1}$ and 0.21 g C m$^{-2}$ 30-min$^{-1}$ within the first two years of harvest (2008, 2009), indicating increased productivity with light interception in year 2, compared with NSA at the same stage of growth. GEP at SSA also leveled off at greater amounts of incident PAR than NSA (approximately 78 and 161 Wm$^{-2}$, 2008 and 2009, respectively).

**DISCUSSION**

An extreme drought that began in July 2001 and lasted through 2003 (Barr et al. 2007) within western parts of the Canadian Boreal zone prompted a series of reports on the sensitivity of boreal forest species to drought (e.g. Krishnan et al. 2006; Barr et al. 2007; Kljun et al. 2007; Michaelian et al. 2011). The results of these studies suggest that drought poses a significant threat to Boreal forest species, especially as drying is expected to increase with climate warming in these regions (Hogg and Bernier, 2005; Hogg et al. 2008; Michaelian et al. 2011). Warming could also lead to a variety of complex feedbacks of critical concern to forest managers, including: natural disturbance (fire and insects), impacts to forest health, and productivity of mature and regenerating forests (Hogg and Bernier, 2005). The results of our study suggest that rapidly regenerating stands are not immune to drought, and may be as sensitive (if not more so) to soil moisture deficits that occur in response to extreme temperatures and drying. These findings are especially important for the Western Boreal Plains ecozone, where anthropogenic disturbance is significant and lengthy periods of regional drying occur with greater frequency (Petrone et al. 2007).
Regional Implications of Drought

A number of large-scale remote sensing studies have shown declines in the Normalised Difference Vegetation Index (NDVI) within central parts of the Boreal zone from the mid 1980’s (Zhou and Running, 2010; de Jong et al. 2011; Epstein et al. 2013). Large-area mapping of vegetation productivity and land cover change using remote sensing provides an additional indicator of some long-term impacts of climate-related disturbance. However, authors do not necessarily agree on the hydrological and meteorological drivers of large-scale changes or the directionality of positive and negative feedbacks (Hogg and Bernier, 2005).

Detailed (high spatial resolution) remote sensing studies, such as Michaelian et al. (2011) examined pre- and post-drought trembling aspen mortality using aerial photography over a broad area extending through the southern Boreal forest of Alberta and Saskatchewan to the border between prairie and aspen ‘parkland’ (a heterogeneous region of aspen and grassland patches). They found that mature aspen parkland was most severely affected by the three-year (2001-2003) western boreal drought, resulting in net reduction of boreal aspen biomass by 20% four years following drought. Normal losses from mortality in these stands are 7%, but Michaelian et al. (2011) note that these losses could increase as prairie climates move north as a result of warming and drying trends at grassland edges. Within 150 immature and mature aspen plots within the same regional area studied by Michaelian et al. (2011), Hogg et al. (2008) noted similar declines in aspen health as a result of the same drought, with regional declines in stem growth approximating 30% through the drought period, and into the following years. Spatial declines in growth were directly attributed to stress from low soil moisture (Hogg et al. 2008; Michaelian et al. 2011).

Climate Similarities to the Western Boreal Forest Drought of 2001-2003
The climate conditions for drought in this study were similar to that found during the 2001-2003 severe western Boreal drought described in Krishnan et al. (2006), Barr et al. (2007), Kljun et al. (2007), and others. Within a mature aspen stand located in south-central Saskatchewan, Kljun et al. (2007) describe the first two years of study as having relatively normal (during year 2000) and slightly above average air temperatures. The growing season started earlier than usual. Similar pre-drought conditions were also observed in this study, with slightly warmer (and wetter) than normal conditions during the two years leading up to drought. At the height of drought (2002), the mature aspen stand experienced colder than normal air temperatures and a late start to the growing season (end of April) (Kljun et al. 2007). Similarly, we also observed colder than normal air temperatures during the year of initial drought conditions, where average air temperatures were 7°C colder. A late spring thaw (April 6th 2009) also occurred during the first drought year in this study. Krishnan et al. (2006) found significant declines in precipitation to approximately 55% of the 30-year mean over the three-year drought period in Saskatchewan. In this study, annual cumulative precipitation measured in 2010, when drought was most severe, was 59% of the 30-year regional mean. Although drought within the BP ecozone did not last as long, similarities in air temperature and precipitation patterns allow for some comparison between mature and regenerating stands.

**Implications of Drought on Rates of Aspen Growth**

Regenerating aspen/mixed-wood within the BP ecozone experienced significant declines in height, leaf area and stem diameter growth. Sensitivity to drought may have been buffered, in part, by a relatively high water table in 2009 (Table 1), measured at the boundary between the peatland-pond ecosystem adjacent to the two harvested sites and within close proximity of each tower. Declining growth rates occurred with greatest magnitude in 2010, approximately one year
after declines in precipitation were observed (Table 2). During this period, average VMC and depth to ground water were lower than other years, contributing to drought stress and reduced rates of growth (Table 1). Bernier et al. (2002) suggest that direct linkages between transpiration and the closure of leaf stomata as a result of declines in soil moisture conditions might significantly impact the regeneration of aspen in areas prone to drought (e.g. Hogg et al. 2005).

In our study, LAIe was most significantly affected in 2010 (5% of pre-drought growth rates), followed by declines in rates of growth of vegetation height (11% of pre-drought growth rates). Krishnan et al. (2006) found a 30-40% decrease in aspen leaf area and stem growth following the 2001-2003 drought within a mature aspen stand, indicating that regenerating stands may be more sensitive to drought, assuming linear growth rates under ‘normal’ conditions. Kurz and Apps (1999) indicate that the growth of stands, from regeneration to maturity, follows a logistical relationship with increasing rates of growth often starting at around 10 years, while Peichl et al. (2010) observed a tripling of canopy height between years 1 and 4 of white pine seedling growth. This may indicate greater declines in regenerating aspen growth during drought periods, however, without knowing the true trajectory of growth, differences are difficult to quantify.

Variability of CO₂ and Water Fluxes

During the first two years of growth, the proportion of Q* used for ET to an average maximum of 52% in 2009 (Table 1), coinciding with warm, wet years of 2007 and 2008 at NSA, and 2008 at SSA (Zermeno-Gonzalez and Hipps, 1997; Kochendorfer et al., 2011). In the first year of drought (2009), the NSA was a slight sink for CO₂ and had the highest growing season NEP of all years studied (Figure 6), while SSA remained a source of CO₂ to the atmosphere. The slight C sink at NSA was due to non-limiting soil water supply, increased light use and water use.
efficiencies (Figure 8), and rapid foliage development as part of long-term growth. Re was also reduced during this period, but had little influence on gross ecosystem production (GEP) (Table 1). Barr et al. (2007) and Kljun et al. (2007) found similar results within mature aspen forests during the first year of the 2001-2003 drought, where significant foliage cover continued to promote gross ecosystem photosynthesis (P), despite slight declines in Re, resulting in the greatest cumulative NEP (in 2001, first year of drought) of all other years examined (Kljun et al. 2007). After one year of drought, Barr et al. (2007) found that reduced LUE acted to limit photosynthesis and growth, while also reducing NEP and Re. By the year following the drought period (2004), Krishnan et al. (2007) found that significant foliage loss and a later start to the growing season resulted in reduced gross ecosystem photosynthesis, and the lowest NEP in 11 years of study. Within the NSA regenerating aspen stand, NEP following drought declined to almost half that immediately following harvest, and saw only slight rebound in 2011 (Table 1). WUE also declined significantly during the last two years of study, indicating that water stress had a significant, prolonged influence on the use of CO₂ for growth. Further, the proportion of Q* used for evapotranspiration during the drought period remained at near pre-drought levels, however, in 2011 this declined significantly to 32% (with increased partitioning to sensible heat fluxes) as a lagged response to drought conditions. Mkhabela et al. (2009) illustrate similar observations, noting that decreased WUE over many years following harvest results from a greater E to ET ratio, lower levels of leaf development and low C uptake.

The partitioning of larger amounts of Q* into ET early on within rapidly regenerating stands is expected as water losses are increased from exposed soil surfaces (Ewers et al., 2005) and initially low levels of leaf area. This may result in greater levels of plant water stress (due to rapid removal of water via Q*) from atmospheric demand and reduced soil moisture status. For
example, Allen et al. (2011) found that increased vegetation heterogeneity and roughness, creates a ‘clothesline’ effect on stomatal conductance, whereby evaporative efficiency is increased in areas that are not occluded by more heterogeneous vegetation types (wind is better able to remove moisture from leaves and ground surface areas that are not sheltered by biomass). In contrast, advection of air over dry, hot ground will increase latent energy exchanges by vegetation (Philip, 1987), resulting in relatively high partitioning of post-harvest $Q^*$ into ET, if water is available. Despite results shown in this study, the rate at which regenerating stands recover from drought continues to be a large gap in knowledge. CO$_2$ exchanges and the efficiency with which C is used for photosynthesis is more sensitive to drought than regenerating boreal jack pine (Chasmer et al. 2008). Kljun et al. (2007) suggest that mature jack pine and black spruce located near the mature aspen stand may have been more resilient to the 2001-2003 drought as a result of topography and generally wetter soil conditions, on average. Further, growing season estimates of the impacts of drought on CO$_2$ fluxes in our study are likely to be conservative because we do not examine cumulative fluxes over an entire year.

**CONCLUSIONS**

This research has demonstrated that the atmospheric demand of the dry climate exerts a strong control on stand ET and CO$_2$ uptake, but is ultimately limited by moisture available in the rooting zone to meet the demands of transpiration. As long as soil moisture exceeds wilting point values following harvest, ET and CO$_2$ uptake increase with growth of foliage (LAIe and canopy height). The major results of this study are as follows:

1. The 5 years examined progressed from wet periods in 2007 and 2008 to a prolonged dry period starting mid-way between 2009 and lasting into 2011.

2. Vegetation foliage amount increased substantially during the first two years of study, and
declined in the final three years of study as a result of drought. Stand vegetation heights measured using airborne LiDAR increased by 1.15 m (stdev. 1.10 m at SSA) and 1.24 m (stdev. 1.34 at NSA), on average between 2008 and 2011. LAIe also doubled at SSA and NSA, respectively, between years 1 and 2, but declined significantly to between approximately 10% and 20% increases from years 3 to 5.

3. ET fluxes rebounded quickly as a result of the combined influence of bare soils, new vegetation foliage growth and wet conditions found within the first two years following harvest. However, ET became limited starting in the latter part of the growing season, 2009, which coincided with cooler air temperatures and lower soil moisture conditions. Drought through 2010 and 2011 resulted in much lower ET levels similar to those found in 2007 by 2011.

4. The effects of low moisture availability were also observed in the partitioning of Qe/Q*. In 2007 to 2009, large water availability resulted in greater Qe contribution to total Q*, but this percent contribution started to decrease by 2010 and as a result of very dry soil moisture conditions. ET continued to be suppressed in 2011, even though soil moisture conditions and precipitation began to increase, indicating a lag in soil moisture recharge and water use by vegetation.

5. During the wet periods: 2007, 2008 and into 2009, VMC and VPD had the greatest correspondence with ET fluxes. Plant foliage in rapid development phase, plus ground moisture contributions to flux may have contributed to this linkage. By 2010, VMC and Q* became greater drivers as a result of greater foliage and sensitivity/competition for light resources. CO₂ fluxes within the first 5 years of regeneration were not greatly influenced by hydro-meteorological driving mechanisms.
6. NSA and SSA were both net sources of CO$_2$ through the May to August period in the first two years of growth, as is expected, but became a net sink for C by the end of the third year. NEP became negative again, through years 4 and 5 as a result of sensitivity to Re and drought (lag) in 2010 (2011). This indicates that this rapidly regenerating stands within the boreal forest may eventually become a net sink for C during optimal growth conditions within the summer (MJJA) months. However, during the remainder of the year the system could still be a significant source of C. Thus, there is a need to further examine full year CO$_2$ and ET fluxes from these rapidly regenerating deciduous aspen clone stands.

7. Decreases in ET and NEP fluxes in later years indicate that there is a possible stomatal and GEP sensitivity to moisture stress at these sites, indicating that they could be sensitive to climatic changes and periods of drought.

8. WUE increases through wet years at the two sites, but decreases as a result of drought by 2010 and into 2011 (lagging the dry period). This may also be indicative of stomatal sensitivity to moisture stress as, over time, vegetation photosynthetic mechanisms and health may start to decline (e.g. Barr et al. 2006). Rapid increases in WUE between years 1 and 2 coincides with rapid foliage development. LUE also increases slightly through years 1-3 as a result of increased foliage, but is affected by stomatal sensitivity to drought in years 4 and 5, resulting in decreased LUE.

Rapid redevelopment of leaf area as result of high density regeneration of aspen through rapid root suckering returns stand ET to near (60% of) pre-harvest conditions and exhibits rapid increases in WUE and the slope of the light response curve within 3 years. Thus, as a result of their clonal structure, the intact root systems following the harvesting of above ground biomass
means that aspen are adept at making the most of the available resources (i.e. moisture, nutrients and light) and rapidly recovering in the years immediately following harvest. However, they are also sensitive to prolonged dry periods and drought, and may become significant sources of CO₂ through reduction in growth rates. This has a profound effect on the potential hydrological response of aspen dominated catchments that experience a range of disturbances that will result in the wholesale removal of mature above ground biomass. Thus, as forestry and other natural resource industries operating within the BP are mandated to manage pre- and post-disturbance water yields, information on this early chronosequence trajectory of regeneration and its use of soil moisture as influenced by climate cycles to meet the atmospheric demand of this sub-humid climate are vital information around which to base harvest and regeneration strategies.

**ACKNOWLEDGEMENTS**

The authors would like to acknowledge the financial support of the Natural Science and Engineering Research Council of Canada (Discovery Grants; Research Tools and Instrumentation; and Collaborative Research and Development (HEAD-2) programs), Northern Science Training Program, Cumulative Environmental Management Association (CEMA), Canadian Oilsands Network for Research and Development (CONRAD), Alberta Pacific Forest Products (AlPac) and Tolko Inc. LiDAR data provided by Alberta Environment and Sustainable Resource Development (AESRD). The authors would like to thank Kayla Giroux, Ronald Peter VanHaarlem, Scott Brown and George Sutherland for their assistance in the field. The authors would also like to thank the reviewers for their very thorough and insightful comments.
REFERENCES


Figure 1. a) Location of URSA in Alberta, Canada; b) The locations of the Northern Study Area (NSA) and Southern Study Area (SSA) transposed on a shaded digital elevation model (DEM) derived from airborne LiDAR. Areas of aspen harvest are outlined, while meteorological tower locations are indicated by circles with stars; c) LiDAR-derived canopy height model (CHM) of NSA and SSA in 2008 and 2011 within a 100m radius of each tower. Large slash piles (2008 CHMs) appear as large quasi-circular masses that are missing from the CHM in 2011.
Figure 2. June to August meteorological and hydrological variations throughout the 5 (NSA) and 2 (SSA) years of study.
Figure 3. Ratio of $Q_e$ to $Q^*$ at NSA and SSA for all years following harvest.
Figure 4. Spatial changes in canopy height derived from airborne LiDAR surveys collected in 2002, 2008, and 2011: a) pre-harvest canopy heights (August 2002); b) approximately six months after harvest at SSA, and 1.5 years after harvest at NSA (August 2008); c) 3.5 years after harvest (SSA) and 4.5 years after harvest (NSA); and d) residual changes in canopy height between 2008 and 2011 (smoothed using a 3 m x 3 m low pass filter to illustrate trends). Black areas in d) show removal of slash piles in 2008/2009.
Figure 5. Cumulative footprint probability density functions at a) NSA and b) SSA, with incremental (10%) contour lines for JD 128-238 (period of study) in 2009 when both sites were coincident. Footprints are overlaid onto a shaded relief image of the DEM to provide context and area coverage.
Figure 6. Cumulative growing season ET (a, b); NEP (c, d) and P (e) accumulated from the start of the growing season (May 8) for years following harvest at SSA (a, c) and NSA (b, d).
Figure 7. Box plot comparison of a) water use efficiency (WUE) and b) light use efficiency (LUE) at NSA and SSA. Lighter gray represents 5 growing seasons of WUE and LUE at NSA and darker gray represents 2 growing seasons of WUE and LUE at SSA. 2008 and 2009 at SSA are coincident with 1st and 2nd year growth with 2007 and 2008 at NSA. Central box plot lines represent average, box upper and lower edges represent 25th and 75th percentiles, and whiskers represent 5th and 95th percentiles. Greatest outliers are also shown (black circles).
Figure 8. Relationships between top of canopy incoming PAR and GEP for NSA and SSA sites. Dark, thick line illustrates Landsberg light response curves.
<table>
<thead>
<tr>
<th></th>
<th>Northern Study Area (NSA)</th>
<th>Southern Study Area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2007</td>
<td>2008</td>
</tr>
<tr>
<td>Total ET (mm)</td>
<td>222</td>
<td>278</td>
</tr>
<tr>
<td>Total NEP (g C m⁻²)</td>
<td>-426</td>
<td>-198</td>
</tr>
<tr>
<td>Total GEP (g C m⁻²)</td>
<td>257</td>
<td>615</td>
</tr>
<tr>
<td>Total Re (g C m⁻²)</td>
<td>-683</td>
<td>-813</td>
</tr>
<tr>
<td>Average, unforced energy balance closure ratio</td>
<td>0.88</td>
<td>0.89</td>
</tr>
<tr>
<td>Average Q* (W m⁻²)</td>
<td>120</td>
<td>109</td>
</tr>
<tr>
<td>Average (Qe/Q*) (July to Aug Qe/Q*)</td>
<td>(0.43</td>
<td>0.52</td>
</tr>
<tr>
<td>Tg (°C)</td>
<td>8.5</td>
<td>9.5</td>
</tr>
<tr>
<td>Ta (°C)</td>
<td>16.5</td>
<td>17.1</td>
</tr>
<tr>
<td>24 hr average VPD (kPa)</td>
<td>0.80</td>
<td>0.75</td>
</tr>
<tr>
<td>Daytime average PAR (W/m²)</td>
<td>107.8</td>
<td>110.7</td>
</tr>
<tr>
<td>WTcentre (m below ground surface)</td>
<td>524</td>
<td>410</td>
</tr>
<tr>
<td>WTedge (m below ground surface)</td>
<td>130</td>
<td>97</td>
</tr>
<tr>
<td>VMC (m³ m⁻³) at 10 cms below soil surface (min to max range)</td>
<td>0.36</td>
<td>(0.30 – 0.41)</td>
</tr>
<tr>
<td>Bowen’s Ratio</td>
<td>2.03</td>
<td>1.29</td>
</tr>
<tr>
<td>Pannual (mm)</td>
<td>530</td>
<td>504</td>
</tr>
<tr>
<td>Psummer (mm)</td>
<td>273</td>
<td>242</td>
</tr>
</tbody>
</table>

Table 1. Hydroclimatic data at the north (NHB) and south (SHB) harvest block for the period May 8 to August 26 from 2007 to 2011. ET represents total evapotranspiration, Tg is the ground temperature at 10 cm below the LFH-Mineral soil interface, Ta represents the average air temperature, VPD the average vapour pressure deficit, WTcentre and WTedge are the average depth of groundwater below the ground (BG) surface at the centre and riparian edge of the aspen hummock, respectively, VMC the volumetric moisture content, and Pannual and Psummer the total annual (Nov-Oct) and summer (May-Aug) precipitation depth for the study period.

Table 2. Measured average (standard deviation) vegetation structural characteristics, and growing season. Canopy Height = average height to top of trees; LAI = Leaf Area Index; DBH = Diameter at Breast Height.