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1 **Effects of Harvesting and Drought on CO₂ and H₂O Fluxes in an**
2 **Aspen Dominated Western Boreal Plain Forest: Early Chronosequence Recovery**

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1 **ABSTRACT**

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

8 The first and second years of regeneration were marked by early spring thaw and higher
9 than normal precipitation, while air temperatures remained slightly above the 30-year normal.
10 During this period, average measured height of vegetation tripled at both sites and cumulative
11 ET was approximately 60% of that prior to harvest by the end of the second year of growth. By
12 the third year (2009), the site became a sink for atmospheric CO₂ during the snow-free season
13 (DOY 128-238), despite low precipitation during the latter half of the summer. Volumetric soil
14 moisture content (VMC) in 2009 was highest (on average) of the five years examined, due to
15 heavy snowfall and a late start to the growing season (where air temperatures consistently exceed
16 0°C), resulting in sustained productivity. However, cumulative annual precipitation also declined
17 to 79% (in year 3, 2009) and 57% (in 2010) of the 30-year normal for that region, leading to
18 significant (lagged) declines in forest productivity in 2010 and 2011. This resulted in the site
19 becoming a source of CO₂ to the atmosphere during the 2010 and 2011 growing seasons (annual
20 balance was not measured). Throughout the drought period (2009, 2010 and 2011) average
21 growth rates (stand height) increased by only 15% (2009), 11% (in 2010), and 14% (in 2011) of
22 that in 2008. Water use efficiency (WUE) also declined in 2010 and 2011, while differences in
23 light use efficiency (LUE) did not vary significantly because foliage was maintained. The results

1 of this study indicate that regenerating mixed-wood stands are sensitive to drought, and respond
2 relatively quickly to changes in soil moisture regime. This is important as regional drying as a
3 result of predicted climatic changes combined with increased industrial activity may result in
4 significant decline in productivity within these stands over broad regions.

1 INTRODUCTION

2 The northern Boreal forest covers approximately 29% of North America (Brandt, 2009) and is a
3 significant sink for atmospheric CO₂ due to broad area coverage and the prevalence of highly
4 productive deciduous trees (Gower et al. 2001). Trembling aspen (*Populus tremuloides Michx.*)
5 is the most widespread deciduous broadleaf tree species in North America, occurring over a wide
6 range of site conditions with the greatest continuous expanse found in the western boreal forest
7 (WBF) (Little 1971; Rowe 1972; Walter and Breckle 1991; Peterson and Peterson 1992).
8 Recently there have been several northern boreal forest initiatives examining energy, ET and
9 carbon fluxes, such as the Boreal Ecosystem Atmosphere Study (BOREAS) and the Boreal
10 Ecosystem Research and Monitoring Sites (BERMS) projects (Griffis et al. 2003; Black et al.
11 1996; Kljun et al. 2007; Gower et al. 1997; Barr et al. 2007). These studies indicate that despite
12 their short growing season, aspen dominated forests are more productive than evergreen sites
13 (Griffis et al. 2003). More recently, the BERMS project has incorporated three harvested and
14 three previously burned jack pine sites (Mkhabela et al. 2009; Amiro et al. 2006; Howard et al.
15 2004; Zha et al. 2009), and on later chronosequence regenerating stands. Currently, there is only
16 one chronosequence study of a one year old harvested aspen site (Amiro 2001), and no study has
17 investigated the short-term impact of harvesting of aspen forests on ecosystem carbon and water
18 balances in the WBF in general, nor in the sub-humid, drought prone climate of the Boreal Plains
19 region (BP) specifically.

20 Under normal atmospheric conditions, maximum photosynthetic capacity of trembling
21 aspen is more than double that of other boreal species: jack pine (*Pinus banksiana* Lamb.) and
22 black spruce (*Picea mariana*), resulting in greater cumulative net ecosystem production (NEP)
23 than either of these two species (Griffis et al. 2003; Zha et al. 2013). Warming and earlier spring

1 snowmelt may also increase the onset of budburst and growing season length (Barr et al. 2007;
2 Kljun et al. 2007), resulting in substantial increases in gross ecosystem production (GEP) during
3 years with adequate soil moisture (Arain et al. 2002). However, there is strong evidence that
4 increased warming and periodic droughts are affecting the health and productivity of Boreal
5 forest ecosystems in some regions (Michaelin et al. 2011). Air temperatures and precipitation are
6 expected to increase through the 21st Century (IPCC, 2007), which may lead to increased
7 productivity within the Boreal zone (Zha et al. 2013). However, Zha et al. (2013) also caution
8 that increased productivity under relatively normal, non-limiting conditions does not account for
9 the possibility of water stress due to increased evapotranspiration. For example, periods of
10 drought, shifting precipitation patterns and maximum air temperature extremes may be
11 responsible for declining forest health observed in southern and central parts of the Boreal forest
12 (Goetz et al. 2005; Zhang et al. 2009; Goetz et al. 2011; Michaelian et al. 2011).

13 Despite their broad distribution aspen forests are acutely sensitive to drought over a
14 period of years (Krishnan et al. 2006; Kljun et al. 2007; Michaelin et al. 2011). Within a mature
15 aspen stand, Kljun et al. (2007) found that NEP was a significant sink for CO₂ (more than double
16 that of an average year) during the first year of drought because soil moisture storage within
17 deeper layers of the soil profile could be accessed. During the second and third years of drought,
18 NEP declined to well-below average levels (Krishnan et al. 2006; Kljun et al. 2007), while rates
19 of growth and foliage amount declined significantly (Krishnan et al. 2006). Using remote sensing
20 data and aerial photography beyond stands, Michaelian et al. (2011) found substantial mortality
21 (>55%) of some aspen and mixed broad-leaf stands in the southern Boreal zone as a result of the
22 same drought examined in Krishnan et al. (2006) and Kljun et al. (2007). Over broad areas,
23 declines in ecosystem productivity may be a visual sign of drought stress due to reduced

1 precipitation and/or increased drying in these regions (Goetz et al. 2005; Zhang et al. 2009;
2 Goetz et al. 2011; Michaelian et al. 2011), however, actual mechanisms for change and species
3 sensitivity to drought are not well understood. As climate warming trends increase, widespread
4 aridity may have substantial but relatively unknown influences on ecosystem dynamics (Kurz et
5 al. 2008). To date, no studies have examined the sensitivity of recently harvested and
6 regenerating aspen stands to prolonged drought and water stress (Zha et al. 2013).

7 The following study examines two regenerating aspen-mixedwood stands following
8 harvest within the BP ecozone of the Canadian Boreal forest. This region contains the greatest
9 proportion of trembling aspen stands (Peterson and Peterson 1992), and is characterized as a
10 mosaic of fragmented upland forests, riparian ecosystems, and pond-peatland complexes
11 (Petrone et al. 2008; Rizzo and Wiken 1989). The BP region is also prone to periods of
12 significant drought, where evapotranspiration (ET) exceeds precipitation (P) (Marshall et al.
13 1999; Devito et al. 2005), and heavy anthropogenic disturbance from resource extraction. The
14 objectives of this study are:

- 15 1. Quantify water and CO₂ exchanges within two regenerating mixed-aspen stands for the
16 first five years following harvest.
- 17 2. Examine the resiliency of stands to a period of drought by reporting on growing season
18 trajectories of production efficiencies (water use efficiency, light use efficiency), soil
19 moisture influences, and changes in growth.

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

22 **SITE CHARACTERISTICS**

1 Two recently harvested upland trembling aspen stands were established as part of a larger study
2 within the Utikuma Regional Study Area (URSA), located in the BP ecozone, north-central
3 Alberta (56° 6' N, 116° 32' W) (Figure 1a) (Devito et al. 2005). Climate in this area is sub-humid
4 with mean annual precipitation ranging between 481 mm and 518 mm (Environment Canada,
5 2010), and 30-year monthly mean temperatures ranging between -14.6 to 15.8 °C (Ecoregions
6 Working Group 1989). The BP is a glacial landscape characterized by small variations in
7 topography (655-670 m above sea level (a.s.l.)), heterogeneous upland moraine landforms, and
8 adjacent pond/peatland complexes.

9 Harvested areas examined in this study (Figure 1b) are located on nearby uplands (within
10 200 m of each other) and share an adjacent pond between them (Devito et al. 2005). Both pre-
11 harvest aspen stands had regenerated from wildfire in 1962 and were approaching maturity when
12 they were harvested. In March 2007, the northern-most study area (NSA) was harvested, and
13 approximately one year later (February 2008), the southern study area (SSA) was harvested, both
14 with minimal damage to roots as a result of deep snow (>60cm) and frozen ground. In the years
15 immediately following harvest, there was increased prevalence of fireweed (*Epilobium*
16 *angustifolium*), blue-joint reed grass (*Calamagrostis canadensis*), and yellow sweet clover
17 (*Melilotus officinalis*). Within three (four) years of harvest, the regenerating canopy had an
18 average height of at least 1.1 m (Figure 1c). Remaining tree debris that could not be used for
19 commercial purposes was left in large slash piles within the site (Figure 1c), and was burned the
20 winter following harvest (2008/2009).

21 **DATA COLLECTION AND METHODS**

22 *Meteorological Data Collection*

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

12 Soil measurements included moisture, temperature and heat fluxes collected at sites
13 located 20 m, 25 m, and 85 m from each tower and averaged. Soil heat fluxes (Q_G) were
14 measured using two heat flux transducers (HFT-03; Campbell Scientific, USA) at each site,
15 buried 0.05 m below the litter fall horizon (LFH) - soil interface. Soil temperature and heat
16 storage in the upper 0.05 m were measured using a thermopile (TCAV-L; Campbell Scientific,
17 USA) inserted at 0.025 and 0.075 m below the soil surface. Soil volumetric moisture content
18 (VMC, %) (CS616 TDR; Campbell Scientific, USA; calibrated for study site soils) and soil
19 temperatures (107B Thermistors; Campbell Scientific, USA) were recorded at depths of 0.01,
20 0.10, 0.30, 0.50 and 1.0 m below the LFH-mineral soil interface at each site (Redding and Devito
21 2008; Brown et al. 2013). VMC data were corrected for soil bulk density and temperature.
22 Ground water levels were measured using well data adjacent to eddy covariance towers, and at

1 two sites at the riparian/stand edge. Cumulative precipitation was measured within an open area
2 near the NSA using hand gauges and a tipping bucket rain gauge (R. M. Young Inc.).

3 *Eddy-Covariance Instrumentation and Processing*

4 Net ecosystem exchange (NEE), latent (Le) and sensible (H) energy exchanges, and friction
5 velocity were measured using eddy covariance instrumentation for the snow-free period,
6 coincident with hydro-meteorological data. Instrumentation deployment followed the same
7 protocols for set-up and data processing for each site so that measurements between sites would
8 be intercomparable. Instrumentation consisted of an open-path infrared gas analyzer (IRGA)
9 (model LI-7500, LI-COR Inc., NE) and a three-dimensional sonic anemometer (model CSAT3,
10 Campbell Scientific, UT) installed at a height of 4.3 m a.g.l. (approximately 1 m above the top
11 of the vegetation canopy by year five of growth (NSA)), per site. Fluxes were sampled at a rate
12 of 20 Hz and averaged over half hourly periods using a CR23X data logger (Campbell Scientific,
13 UT). Briefly, NEE correction procedures (Giroux, 2012) included filtering for periods of low
14 friction velocity ($<0.35 \text{ m s}^{-1}$) (Petrone et al. 2007), and rotation of vertical and horizontal wind
15 velocities to zero (Kaimal and Finnigan, 1994). Gaps within eddy covariance data were filled
16 based on the mean moving windows over 14-day periods (Falge et al. 2001), and quality
17 controlled to remove outliers exceeding two standard deviations of the mean (Papale et al. 2006).
18 Gross ecosystem production (GEP) was estimated from half- hourly estimates of net ecosystem
19 production (where $\text{NEP} = -\text{NEE}$), assumed positive when the ecosystem is a sink for atmospheric
20 CO_2 , and total ecosystem respiration (Re). Night-time NEP was used as a direct estimate of Re
21 during periods when friction velocity was greater than the minimum threshold. For periods
22 below this threshold, Re was estimated using an empirical model as a function of within canopy
23 air temperature. Daytime GEP was estimated as the difference between NEP and Re ($\text{GEP} =$

1 NEP + Re), where daytime Re was determined from the same empirical model used for night-
2 time Re (Griffis et al. 2003).

3 A flux footprint parameterization based on a full-scale Lagrangian particle model (Kljun
4 et al. 2002; Kljun et al. 2004) was used to estimate contribution areas for mass fluxes at both
5 sites during the summer of 2009. The footprint is defined as the probability of contribution by
6 CO₂ and water fluxes per unit area upwind of the eddy covariance system. While most inputs
7 were obtained from eddy covariance and wind direction, roughness length (z_{0m}) and zero plane
8 displacement (d) of vegetation were mapped at 1 m resolution within 10 degree wind sectors
9 based on canopy height from airborne light detection and ranging (LiDAR) data ($z_{0m} = 1/10$
10 height; $d = 2/3$ height of trees) (Chasmer et al. 2011). Wind sectors were used to constrain the
11 iterative footprint model, which was then accumulated over the growing season.

12 *Efficiency Parameters*

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

$$21 \quad IPAR = PAR(1 - e^{(-LAI_e * k)}) \quad [1]$$

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

$$4 \quad GEP_{Landsberg} = P_{max} \left(1 - e^{-\alpha(PAR - I_{comp})} \right), \quad [2]$$

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

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

11 *Stand Mensuration*

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

1 photography (processed with DHP and TRACwin software ; Leblanc, 2008) acquired at 17 and
2 14 coincident locations within the NSA and SSA, respectively.

3 *Airborne LiDAR Data Collection and Processing*

4 Airborne Light Detection And Ranging (LiDAR) remote sensing data were used to compare
5 spatial changes in canopy height and cover between 2008 and 2011 (and pre-harvest conditions
6 in 2002). LiDAR data were collected in September 2008 for Alberta Sustainable Resource
7 Development using an Optech Inc. ALTM 3100EA (Optech Inc., Canada). The system was
8 operated at a flying height of 1400 m a.g.l., with a laser pulse repetition frequency of 50 kHz,
9 and a scan angle of $\pm 25^\circ$. Data collected in August 2011 was acquired and processed by the
10 authors using a slightly different sensor model (Optech Inc. ALTM3100) operated at a flying
11 height of 1800 m a.g.l. The laser pulse repetition frequency was 50 kHz, with a scan angle of
12 $\pm 23^\circ$. A 50% overlap of scan lines was adopted to reduce laser ‘shadowing’ by canopies and to
13 ensure sampling of both sides of trees. LiDAR data were also collected in 2002 and is used to
14 briefly describe pre-harvest stand structural characteristics (Hopkinson et al. 2005 and Chasmer
15 et al. 2011).

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

1 **RESULTS**

2 *Site Climate Variability*

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

19 Growing season average air temperatures (T_a) for the period studied (except 2009) were
20 slightly warmer than the 30-year normal (at Slave Lake Airport, Alberta; Environment Canada,
21 2010), but no period stood out as being significantly warmer than any other period ($P=0.64$ using
22 Kruskal-Wallis test) (Table 1; Figure 2). 2007 was also marked by the earliest spring thaw (the
23 date when air temperatures were consistently greater than 0°C), of the years studied (March 19th),

1 while the latest spring thaw occurred on April 6th, 2009. The winter (identified as December 1st
2 to March 31st) of 2008/2009 was also 7° colder than the 30-year normal for this region (Slave
3 Lake Airport, Alberta; Environment Canada, 2010), and was certainly the coldest during the
4 period studied.

5 *Energy Exchanges*

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

14 *Spatial and Temporal Changes in Vegetation Growth Following Harvest*

15 Rates of growth of regeneration species also appeared to be affected by drought between mid-
16 2009 into 2011. This was observed at NSA, which had the longest record of structural
17 measurements (Table 2). At both sites, average canopy height tripled during the first two years of
18 establishment. Growth rates at SSA were not influenced by drought during the second year of
19 growth, likely because soil moisture was retained from previous warm/wet years. Between 2008
20 and 2009, growth rates slowed to 15% of total growth between 2007 and 2008, and 11% of total
21 growth between 2009 and 2010 (compared with 2008-2009), and increased slightly in 2011
22 (14%) (Table 2). It is not known what the growth rate would have been if conditions were similar

1 to the first two years of growth, throughout the five-year period, however, a decline in growth
2 rate in 2010, followed by slight rebound in 2011 indicates that arid conditions may have had
3 some influence. Average LAI estimates measured in July of each year doubled between years 1
4 and 2 of growth at both sites, but declined to 21% of growth by year 3; 5% (year 4); and 7%
5 (year 5) (at NSA) (Table 2). Diameter at breast height (DBH) also more than doubled between
6 years 1 and 2 of growth, but declined to 26% (2009), 15% (2010), and 11% (2011) compared
7 with previous years' growth. This indicates that foliage growth rates were most affected by
8 drought over the three-year period, and a late start to the growing season in 2009.

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

18 *CO₂ and Water Vapor Exchanges*

19 Areas sampled by eddy covariance instrumentation are shown in Figure 5. The greatest
20 probability of fluxes occurred within 71 m (stdev. = 8 m) of the eddy covariance system (NSA),
21 and 98 m (stdev. = 8 m) (SSA). Prevailing wind directions did not vary greatly between sites,
22 originating from NW (NSA) and SSW (SSA) during the years studied for each site. When

1 combined with spatial variations in canopy growth (Figure 4d), areas sampled by eddy
2 covariance at NSA were slightly more productive than SSA due to an additional year of growth.

3 NSA and SSA were net sources of CO₂ to the atmosphere during the May to August
4 period for the first 2 years post-harvest (annual C balance was not measured), and NSA was a
5 greater source of CO₂ than SSA during those first two years following harvest (Table 1, Figure
6 6). NSA became a slight sink for CO₂, by the end of the third year after disturbance (2009),
7 resulting in total cumulative NEP of 17 g C m⁻². Low precipitation and low VMC during the
8 latter half of 2009 to 2011 resulted in net loss of CO₂ to the atmosphere by 2010 (201 g C m⁻²)
9 through 2011 (180 g C m⁻²) for the period measured (Table 1; Figure 6). NEP was significantly
10 positively correlated with soil VMC in year 1 (2007) ($R^2 = 0.65, p < 0.05$) and 3 (2009) ($R^2 =$
11 $0.55, p < 0.05$) following harvest at NSA, and in year 2 (2009) ($R^2 = 0.55, p < 0.05$) at SSA, but
12 neither site was greatly influenced by other drivers (e.g. VPD, Tair or RH). Growing season
13 cumulative GEP and NEP were positively linearly correlated with annual foliage growth (LAIe)
14 ($R^2 = 0.93; 0.95$, respectively), height ($R^2 = 0.87; 0.89$, respectively) and DBH ($R^2 = 0.87; 0.91$,
15 respectively).

16 Cumulative ET estimates of 222 mm (NSA) and 220 mm (SSA) were found during the
17 May to August period for the first year of post-harvest growth. By the second year of growth, a
18 cool spring initially limited ET fluxes at NSA until approximately DOY 159, when ET began to
19 increase as a result of warmer air temperatures and residual VMC. Cumulative ET fluxes on the
20 same day in 2009 were suppressed, coinciding with cool Ta and a late start to the season (Figure
21 2; Figure 6). A warm, dry May to August period in 2010 resulted in the greatest cumulative ET
22 fluxes exceeding annual P for that year. By 2011, ET was reduced to 2007 levels until DOY 211

1 as a result of very low rainfall (cumulative P < 20 mm from January 1st) and reduced soil
2 moisture conditions that remained low until mid-June (Figure 2; Figure 6).

3 *Post-Harvest Efficiency*

4 Water use efficiency (WUE) increased steadily during the first three years of growth at NSA,
5 reaching an average WUE of 3.3 g C/g H₂O (RM ANOVA on ranks, $p < 0.05$ for differences
6 between years) (Figure 7a). Slightly higher efficiencies were recorded during the first two
7 growth at SSA compared with the first two years of growth at NSA, but were not significantly
8 different. At NSA, WUE decreased by 57% of 2009 amounts in 2010 (1.89 g C/g H₂O) in
9 response to decreased soil moisture content, declining foliage growth rates, and reduced GEP.
10 WUE then rebounded to 2.44 g C/g H₂O in 2011 with increased precipitation during the latter
11 part of the summer.

12 Average LUE was slightly less during the second year of growth at SSA (1.35 g C MJ⁻¹)
13 compared with NSA (1.58 g C MJ⁻¹), in response to differences in measured LAI_e (used to
14 estimate IPAR) and C uptake (Figure 7b). LUE peaked in 2009 (1.63 g C MJ⁻¹) and declined to
15 1.42 g C MJ⁻¹ and 1.23 g C MJ⁻¹, on average in 2010 and 2011. Unlike drought responses of
16 mature aspen stands (e.g. Kljun et al. 2007), rates of foliage growth and intercepted radiation
17 declined, but foliage was not lost from the canopy. Therefore, LUE was relatively stable through
18 the drought period as growth matched GEP.

19 Similar responses of GEP compared with intercepted PAR (Landsberg light response
20 curves; Figure 8) illustrate a slightly different trend to Figure 7b. Use of light for photosynthesis
21 increases during the first three years of rapid growth at NSA (first two years at SSA), and
22 maximum average GEP (P_{max}) levels off with increasingly greater amounts of light, per year

1 (approximately 52, 88, and 137 Wm^{-2} for years 2007 to 2009, respectively at NSA). By 2010,
2 P_{max} was lower than the maximum rates of increase observed in 2009 ($0.32 \text{ g C m}^{-2} \text{ 30-min}^{-1}$),
3 declining to $0.18 \text{ g C m}^{-2} \text{ 30-min}^{-1}$. At SSA, P_{max} reached $0.11 \text{ g C m}^{-2} \text{ 30-min}^{-1}$ and 0.21 g C m^{-2}
4 30-min^{-1} within the first two years of harvest (2008, 2009), indicating increased productivity
5 with light interception in year 2, compared with NSA at the same stage of growth. GEP at SSA
6 also leveled off at greater amounts of incident PAR than NSA (approximately 78 and 161 Wm^{-2} ,
7 2008 and 2009, respectively).

8 **DISCUSSION**

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

23

1 *Regional Implications of Drought*

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

9 Detailed (high spatial resolution) remote sensing studies, such as Michaelian et al. (2011)
10 examined pre- and post-drought trembling aspen mortality using aerial photography over a broad
11 area extending through the southern Boreal forest of Alberta and Saskatchewan to the border
12 between prairie and aspen 'parkland' (a heterogeneous region of aspen and grassland patches).
13 They found that mature aspen parkland was most severely affected by the three-year (2001-
14 2003) western boreal drought, resulting in net reduction of boreal aspen biomass by 20% four
15 years following drought. Normal losses from mortality in these stands are 7%, but Michaelian et
16 al. (2011) note that these losses could increase as prairie climates move north as a result of
17 warming and drying trends at grassland edges. Within 150 immature and mature aspen plots
18 within the same regional area studied by Michaelian et al. (2011), Hogg et al. (2008) noted
19 similar declines in aspen health as a result of the same drought, with regional declines in stem
20 growth approximating 30% through the drought period, and into the following years. Spatial
21 declines in growth were directly attributed to stress from low soil moisture (Hogg et al. 2008;
22 Michaelian et al. 2011).

23 *Climate Similarities to the Western Boreal Forest Drought of 2001-2003*

1 The climate conditions for drought in this study were similar to that found during the 2001-2003
2 severe western Boreal drought described in Krishnan et al. (2006), Barr et al. (2007), Kljun et al.
3 (2007), and others. Within a mature aspen stand located in south-central Saskatchewan, Kljun et
4 al. (2007) describe the first two years of study as having relatively normal (during year 2000)
5 and slightly above average air temperatures. The growing season started earlier than usual.
6 Similar pre-drought conditions were also observed in this study, with slightly warmer (and
7 wetter) than normal conditions during the two years leading up to drought. At the height of
8 drought (2002), the mature aspen stand experienced colder than normal air temperatures and a
9 late start to the growing season (end of April) (Kljun et al. 2007). Similarly, we also observed
10 colder than normal air temperatures during the year of initial drought conditions, where average
11 air temperatures were 7°C colder. A late spring thaw (April 6th 2009) also occurred during the
12 first drought year in this study. Krishnan et al. (2006) found significant declines in precipitation
13 to approximately 55% of the 30-year mean over the three-year drought period in Saskatchewan.
14 In this study, annual cumulative precipitation measured in 2010, when drought was most severe,
15 was 59% of the 30-year regional mean. Although drought within the BP ecozone did not last as
16 long, similarities in air temperature and precipitation patterns allow for some comparison
17 between mature and regenerating stands.

18 *Implications of Drought on Rates of Aspen Growth*

19 Regenerating aspen/mixed-wood within the BP ecozone experienced significant declines in
20 height, leaf area and stem diameter growth. Sensitivity to drought may have been buffered, in
21 part, by a relatively high water table in 2009 (Table 1), measured at the boundary between the
22 peatland-pond ecosystem adjacent to the two harvested sites and within close proximity of each
23 tower. Declining growth rates occurred with greatest magnitude in 2010, approximately one year

1 after declines in precipitation were observed (Table 2). During this period, average VMC and
2 depth to ground water were lower than other years, contributing to drought stress and reduced
3 rates of growth (Table 1). Bernier et al. (2002) suggest that direct linkages between transpiration
4 and the closure of leaf stomata as a result of declines in soil moisture conditions might
5 significantly impact the regeneration of aspen in areas prone to drought (e.g. Hogg et al. 2005).
6 In our study, LAI_e was most significantly affected in 2010 (5% of pre-drought growth rates),
7 followed by declines in rates of growth of vegetation height (11% of pre-drought growth rates).
8 Krishnan et al. (2006) found a 30-40% decrease in aspen leaf area and stem growth following the
9 2001-2003 drought within a mature aspen stand, indicating that regenerating stands may be more
10 sensitive to drought, assuming linear growth rates under 'normal' conditions. Kurz and Apps
11 (1999) indicate that the growth of stands, from regeneration to maturity, follows a
12 logistical relationship with increasing rates of growth often starting at around 10 years,
13 while Peichl et al. (2010) observed a tripling of canopy height between years 1 and 4 of
14 white pine seedling growth. This may indicate greater declines in regenerating aspen
15 growth during drought periods, however, without knowing the true trajectory of growth,
16 differences are difficult to quantify.

17 *Variability of CO₂ and Water Fluxes*

18 During the first two years of growth, the proportion of Q* used for ET to an average maximum
19 of 52% in 2009 (Table 1), coinciding with warm, wet years of 2007 and 2008 at NSA, and 2008
20 at SSA (Zermeno-Gonzalez and Hipps, 1997; Kochendorfer et al., 2011). In the first year of
21 drought (2009), the NSA was a slight sink for CO₂, and had the highest growing season NEP of
22 all years studied (Figure 6), while SSA remained a source of CO₂ to the atmosphere. The slight C
23 sink at NSA was due to non-limiting soil water supply, increased light use and water use

1 efficiencies (Figure 8), and rapid foliage development as part of long-term growth. R_e was also
2 reduced during this period, but had little influence on gross ecosystem production (GEP) (Table
3 1). Barr et al. (2007) and Kljun et al. (2007) found similar results within mature aspen forests
4 during the first year of the 2001-2003 drought, where significant foliage cover continued to
5 promote gross ecosystem photosynthesis (P), despite slight declines in R_e , resulting in the
6 greatest cumulative NEP (in 2001, first year of drought) of all other years examined (Kljun et al.
7 2007). After one year of drought, Barr et al. (2007) found that reduced LUE acted to limit
8 photosynthesis and growth, while also reducing NEP and R_e . By the year following the drought
9 period (2004), Krishnan et al. (2007) found that significant foliage loss and a later start to the
10 growing season resulted in reduced gross ecosystem photosynthesis, and the lowest NEP in 11
11 years of study. Within the NSA regenerating aspen stand, NEP following drought declined to
12 almost half that immediately following harvest, and saw only slight rebound in 2011 (Table 1).
13 WUE also declined significantly during the last two years of study, indicating that water stress
14 had a significant, prolonged influence on the use of CO_2 for growth. Further, the proportion of
15 Q^* used for evapotranspiration during the drought period remained at near pre-drought levels,
16 however, in 2011 this declined significantly to 32% (with increased partitioning to sensible heat
17 fluxes) as a lagged response to drought conditions. Mkhabela et al. (2009) illustrate similar
18 observations, noting that decreased WUE over many years following harvest results from a
19 greater E to ET ratio, lower levels of leaf development and low C uptake.

20 The partitioning of larger amounts of Q^* into ET early on within rapidly regenerating
21 stands is expected as water losses are increased from exposed soil surfaces (Ewers et al., 2005)
22 and initially low levels of leaf area. This may result in greater levels of plant water stress (due to
23 rapid removal of water via Q^*) from atmospheric demand and reduced soil moisture status. For

1 example, Allen et al. (2011) found that increased vegetation heterogeneity and roughness, creates
2 a ‘clothesline’ effect on stomatal conductance, whereby evaporative efficiency is increased in
3 areas that are not occluded by more heterogeneous vegetation types (wind is better able to
4 remove moisture from leaves and ground surface areas that are not sheltered by biomass). In
5 contrast, advection of air over dry, hot ground will increase latent energy exchanges by
6 vegetation (Philip, 1987), resulting in relatively high partitioning of post-harvest Q^* into ET, if
7 water is available. Despite results shown in this study, the rate at which regenerating stands
8 recover from drought continues to be a large gap in knowledge. CO_2 exchanges and the
9 efficiency with which C is used for photosynthesis is more sensitive to drought than regenerating
10 boreal jack pine (Chasmer et al. 2008). Kljun et al. (2007) suggest that mature jack pine and
11 black spruce located near the mature aspen stand may have been more resilient to the 2001-2003
12 drought as a result of topography and generally wetter soil conditions, on average. Further,
13 growing season estimates of the impacts of drought on CO_2 fluxes in our study are likely to be
14 conservative because we do not examine cumulative fluxes over an entire year.

15 **CONCLUSIONS**

16 This research has demonstrated that the atmospheric demand of the dry climate exerts a strong
17 control on stand ET and CO_2 uptake, but is ultimately limited by moisture available in the
18 rooting zone to meet the demands of transpiration. As long as soil moisture exceeds wilting point
19 values following harvest, ET and CO_2 uptake increase with growth of foliage (LAIe and canopy
20 height). The major results of this study are as follows:

- 21 1. The 5 years examined progressed from wet periods in 2007 and 2008 to a prolonged dry
22 period starting mid-way between 2009 and lasting into 2011.
- 23 2. Vegetation foliage amount increased substantially during the first two years of study, and

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

6 3. ET fluxes rebounded quickly as a result of the combined influence of bare soils, new
7 vegetation foliage growth and wet conditions found within the first two years following
8 harvest. However, ET became limited starting in the latter part of the growing season,
9 2009, which coincided with cooler air temperatures and lower soil moisture conditions.
10 Drought through 2010 and 2011 resulted in much lower ET levels similar to those found
11 in 2007 by 2011.

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

18 5. During the wet periods: 2007, 2008 and into 2009, VMC and VPD had the greatest
19 correspondence with ET fluxes. Plant foliage in rapid development phase, plus ground
20 moisture contributions to flux may have contributed to this linkage. By 2010, VMC and
21 Q^* became greater drivers as a result of greater foliage and sensitivity/competition for
22 light resources. CO_2 fluxes within the first 5 years of regeneration were not greatly
23 influenced by hydro-meteorological driving mechanisms.

- 1 6. NSA and SSA were both net sources of CO₂ through the May to August period in the
2 first two years of growth, as is expected, but became a net sink for C by the end of the
3 third year. NEP became negative again, through years 4 and 5 as a result of sensitivity to
4 Re and drought (lag) in 2010 (2011). This indicates that this rapidly regenerating stands
5 within the boreal forest may eventually become a net sink for C during optimal growth
6 conditions within the summer (MJJA) months. However, during the remainder of the year
7 the system could still be a significant source of C. Thus, there is a need to further
8 examine full year CO₂ and ET fluxes from these rapidly regenerating deciduous aspen
9 clone stands.
- 10 7. Decreases in ET and NEP fluxes in later years indicate that there is a possible stomatal
11 and GEP sensitivity to moisture stress at these sites, indicating that they could be
12 sensitive to climatic changes and periods of drought.
- 13 8. WUE increases through wet years at the two sites, but decreases as a result of drought by
14 2010 and into 2011 (lagging the dry period). This may also be indicative of stomatal
15 sensitivity to moisture stress as, over time, vegetation photosynthetic mechanisms and
16 health may start to decline (e.g. Barr et al. 2006). Rapid increases in WUE between years
17 1 and 2 coincides with rapid foliage development. LUE also increases slightly through
18 years 1-3 as a result of increased foliage, but is affected by stomatal sensitivity to drought
19 in years 4 and 5, resulting in decreased LUE.

20 Rapid redevelopment of leaf area as result of high density regeneration of aspen through
21 rapid root suckering returns stand ET to near (60% of) pre-harvest conditions and exhibits rapid
22 increases in WUE and the slope of the light response curve within 3 years. Thus, as a result of
23 their clonal structure, the intact root systems following the harvesting of above ground biomass

1 means that aspen are adept at making the most of the available resources (i.e. moisture, nutrients
2 and light) and rapidly recovering in the years immediately following harvest. However, they are
3 also sensitive to prolonged dry periods and drought, and may become significant sources of CO₂
4 through reduction in growth rates. This has a profound effect on the potential hydrological
5 response of aspen dominated catchments that experience a range of disturbances that will result
6 in the wholesale removal of mature above ground biomass. Thus, as forestry and other natural
7 resource industries operating within the BP are mandated to manage pre- and post-disturbance
8 water yields, information on this early chronosequence trajectory of regeneration and its use of
9 soil moisture as influenced by climate cycles to meet the atmospheric demand of this sub-humid
10 climate are vital information around which to base harvest and regeneration strategies.

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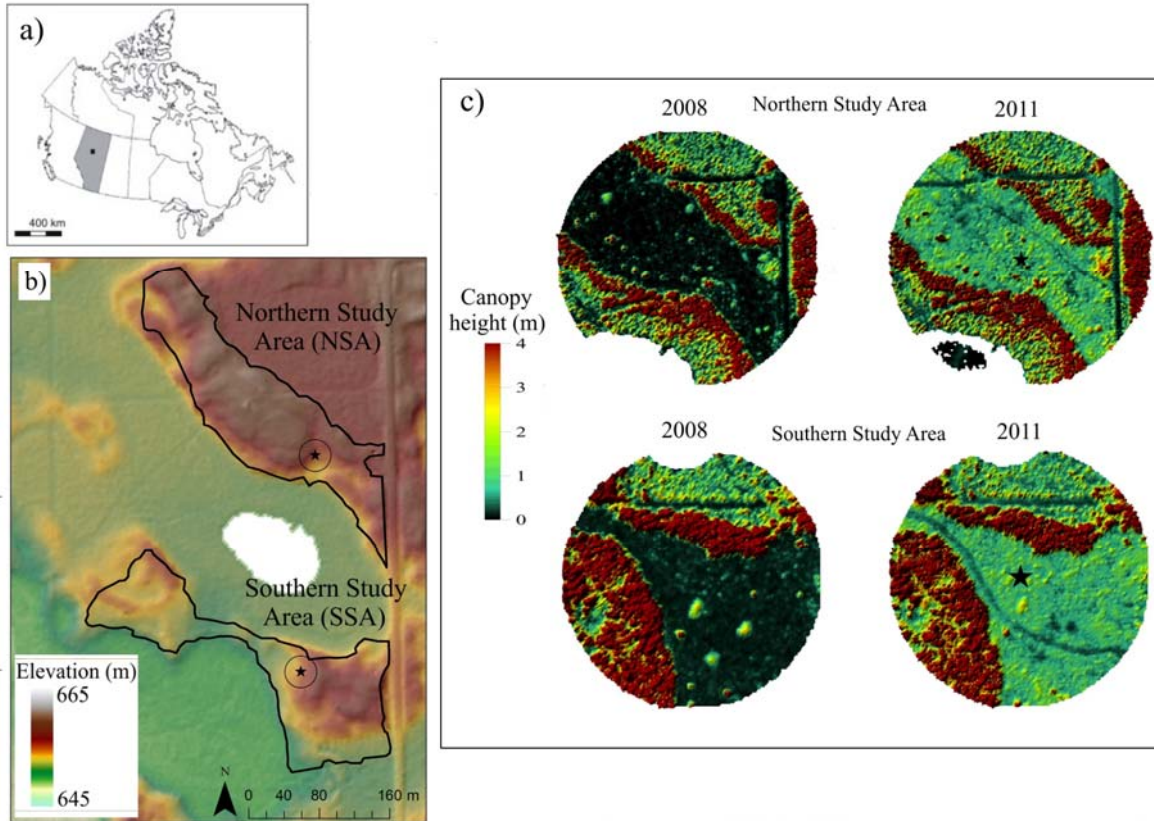
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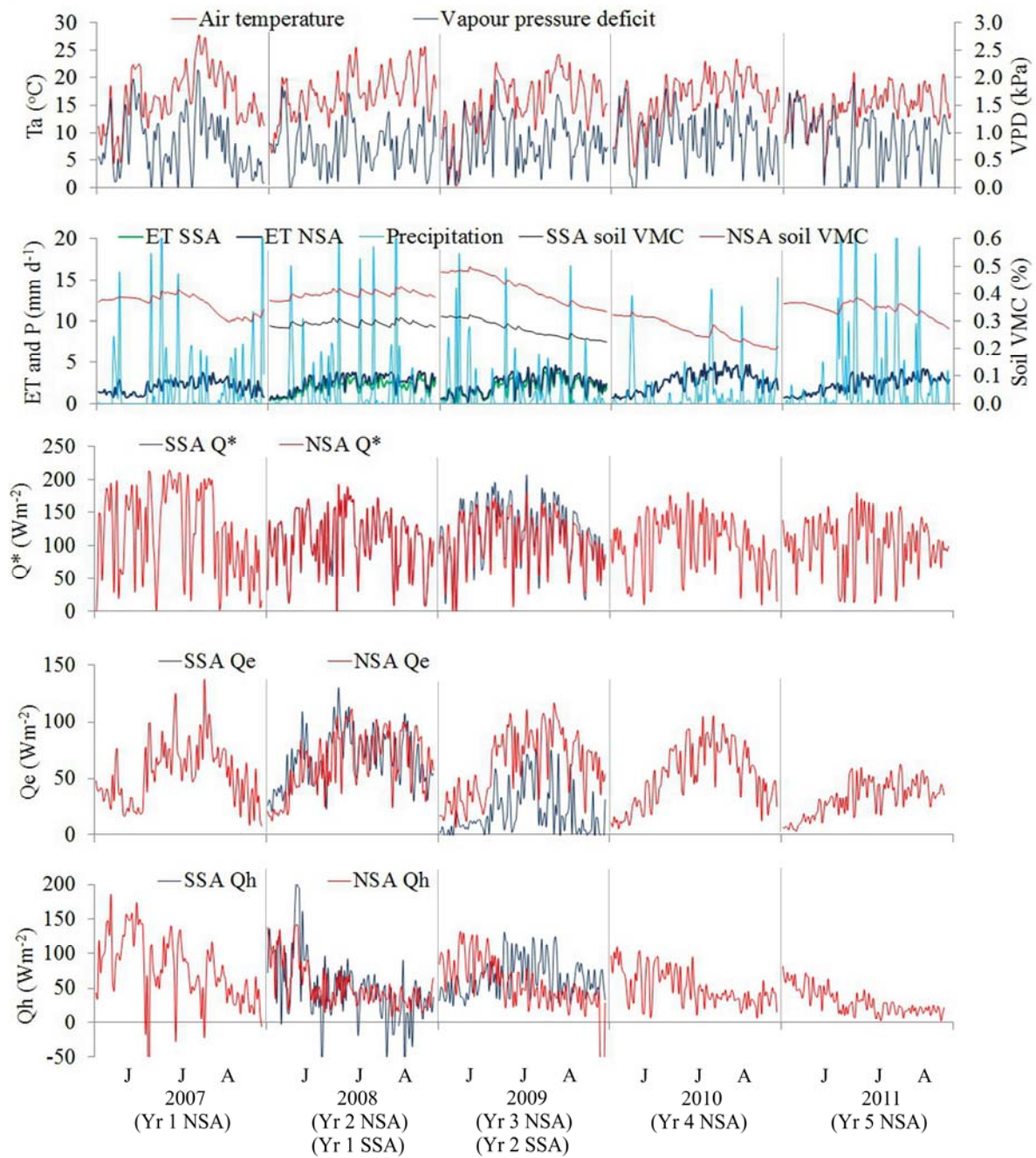
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1 Figures and Tables



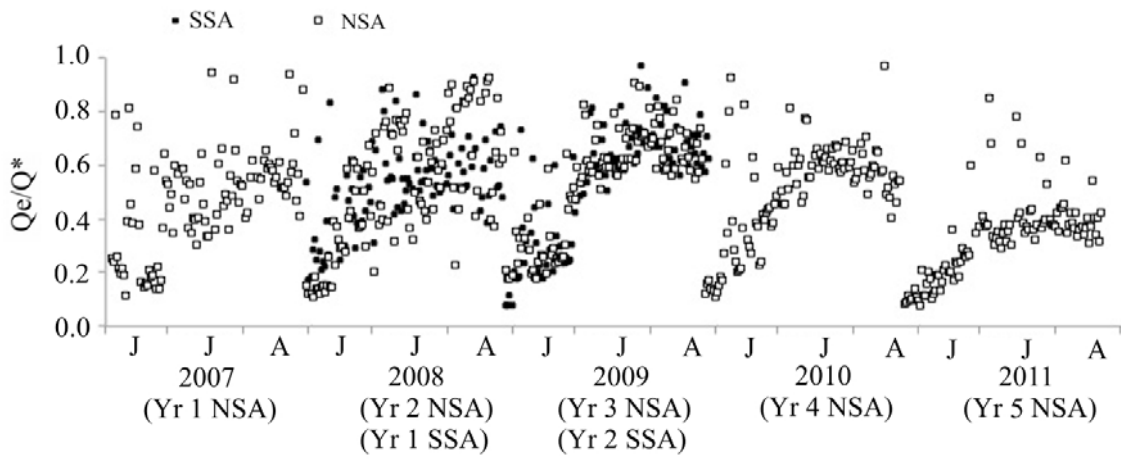
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3 Figure 1. a) Location of URSA in Alberta, Canada; b) The locations of the Northern Study Area (NSA)
4 and Southern Study Area (SSA) transposed on a shaded digital elevation model (DEM) derived from
5 airborne LiDAR. Areas of aspen harvest are outlined, while meteorological tower locations are indicated
6 by circles with stars; c) LiDAR-derived canopy height model (CHM) of NSA and SSA in 2008 and 2011
7 within a 100m radius of each tower. Large slash piles (2008 CHMs) appear as large quasi-circular masses
8 that are missing from the CHM in 2011.



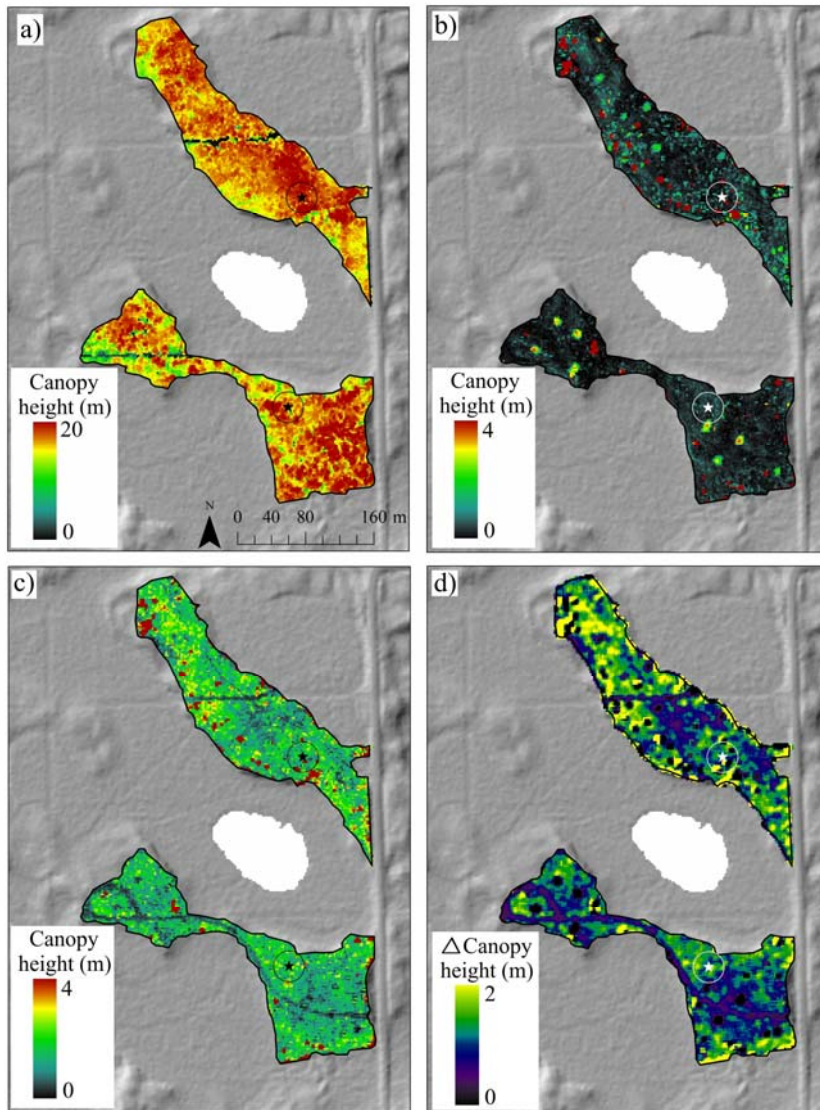
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2 Figure 2. June to August meteorological and hydrological variations throughout the 5 (NSA) and 2 (SSA)
 3 years of study.



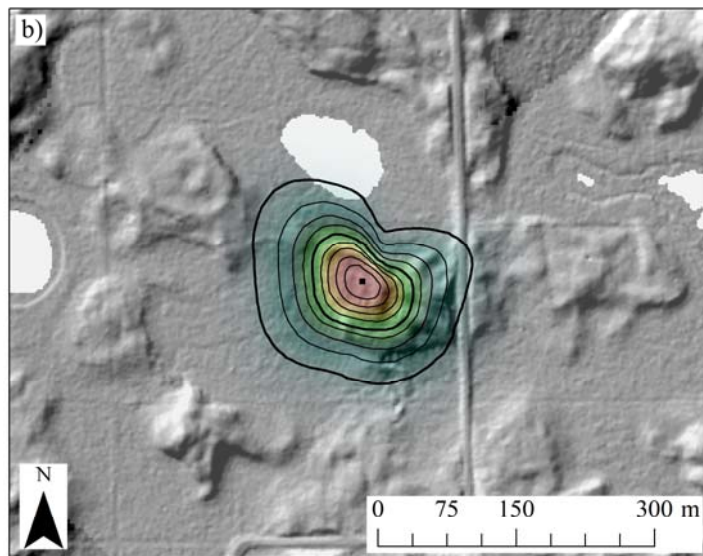
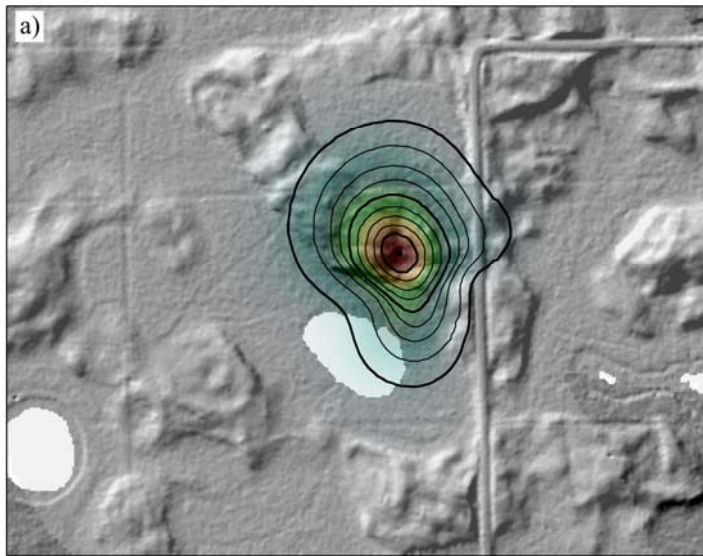
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2 Figure 3. Ratio of Q_e to Q^* at NSA and SSA for all years following harvest.

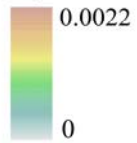


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
2 Figure 4. Spatial changes in canopy height derived from airborne LiDAR surveys collected in 2002, 2008,
 3 and 2011: a) pre-harvest canopy heights (August 2002); b) approximately six months after harvest at
 4 SSA, and 1.5 years after harvest at NSA (August 2008); c) 3.5 years after harvest (SSA) and 4.5 years
 5 after harvest (NSA); and d) residual changes in canopy height between 2008 and 2011 (smoothed using a
 6 3 m x 3 m low pass filter to illustrate trends). Black areas in d) show removal of slash piles in 2008/2009.



Footprint probability density function (%)

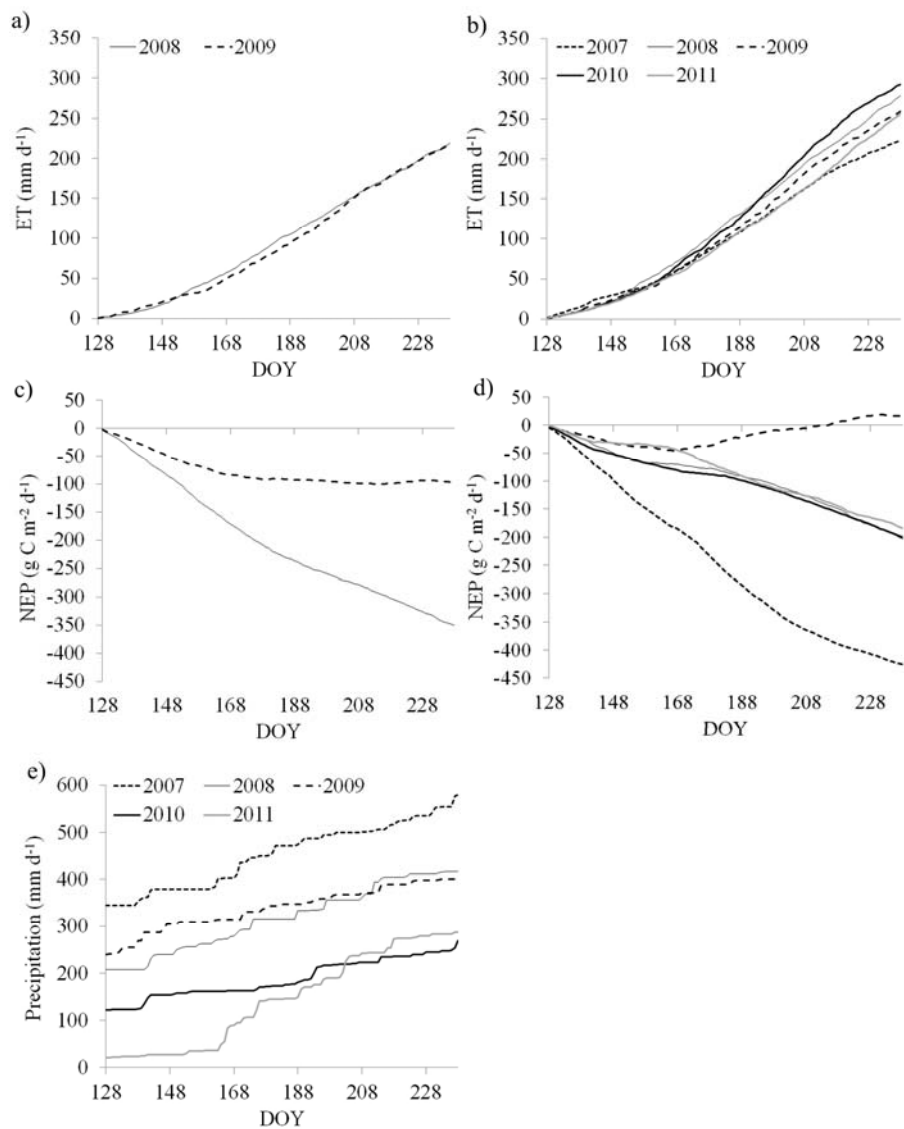


Footprint probability contour lines

-  Minor (10% increments)
-  Major (10%, 50%, 90%)

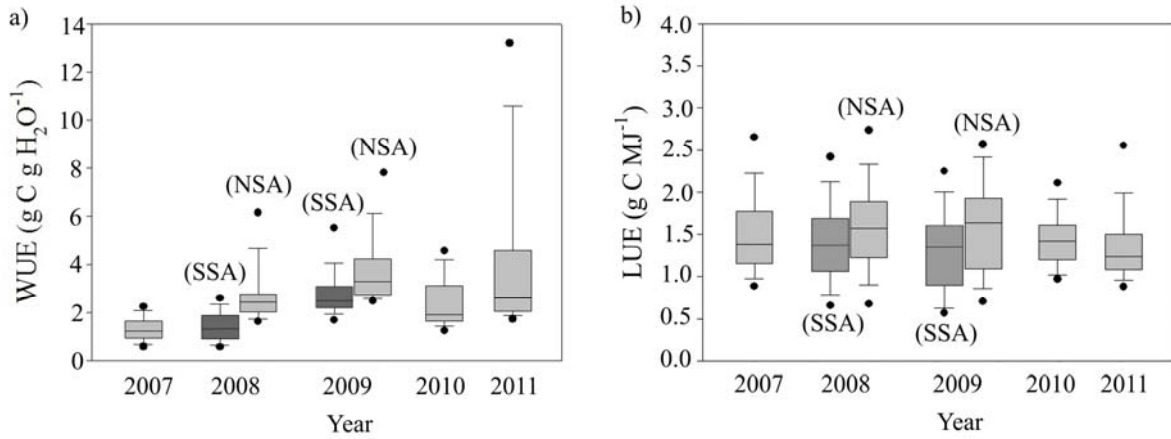
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2 Figure 5. Cumulative footprint probability density functions at a) NSA and b) SSA, with incremental
 3 (10%) contour lines for JD 128-238 (period of study) in 2009 when both sites were coincident. Footprints
 4 are overlaid onto a shaded relief image of the DEM to provide context and area coverage.



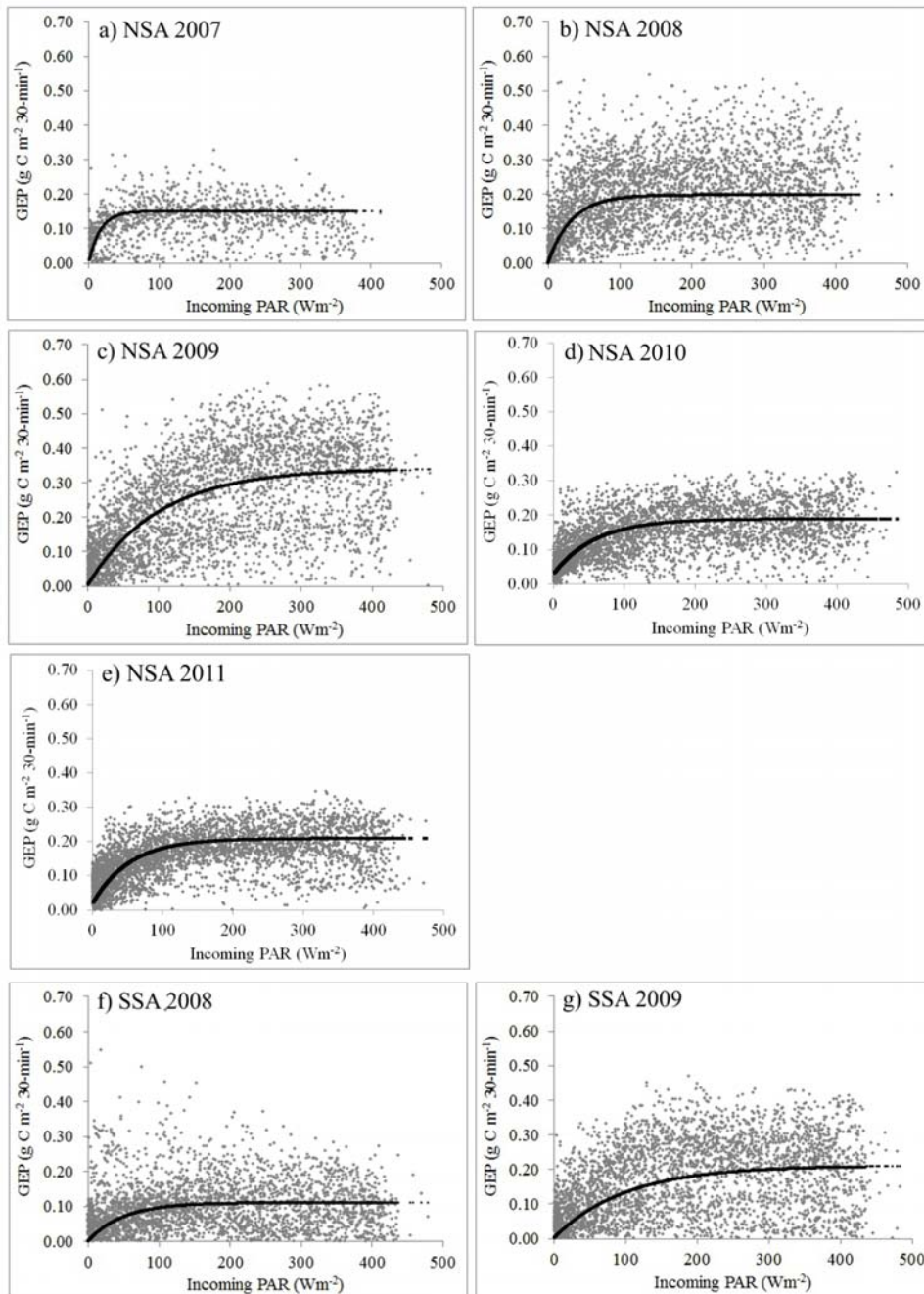
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2 Figure 6. Cumulative growing season ET (a, b); NEP (c, d) and P (e) accumulated from the start of the
 3 growing season (May 8) for years following harvest at SSA (a, c) and NSA (b, d).



1

2 Figure 7. Box plot comparison of a) water use efficiency (WUE) and b) light use efficiency (LUE) at
 3 NSA and SSA. Lighter gray represents 5 growing seasons of WUE and LUE at NSA and darker gray
 4 represents 2 growing seasons of WUE and LUE at SSA. 2008 and 2009 at SSA are coincident with 1st and
 5 2nd year growth with 2007 and 2008 at NSA. Central box plot lines represent average, box upper and
 6 lower edges represent 25th and 75th percentiles, and whiskers represent 5th and 95th percentiles. Greatest
 7 outliers are also shown (black circles).



1

2 Figure 8. Relationships between top of canopy incoming PAR and GEP for NSA and SSA sites. Dark,
 3 thick line illustrates Landsberg light response curves.

4

5

	Northern Study Area (NSA)					Southern Study Area	
	2007	2008	2009	2010	2011	2008	2009
Total ET (mm)	222	278	259	293	256	220	217
Total NEP (g C m⁻²)	-426	-198	17	-201	-180	-350	-97
Total GEP (g C m⁻²)	257	615	813	846	757	286	548
Total Re (g C m⁻²)	-683	-813	-796	-849	-760	-636	-645
Average, unforced energy balance closure ratio	0.88	0.89	0.92	0.9	0.9	0.84	0.89
Average Q* (W m⁻²)	120	109	108	103	103	108.2	116.7
Average (Qe/Q*) (July to Aug Qe/Q*)	0.43 (0.5)	0.52 (0.63)	0.43 (0.50)	0.51 (0.63)	0.32 (0.42)	0.57 (0.63)	0.30 (0.28)
Tg (°C)	8.5	9.5	9.2	9.4	8.4	9.8	9.6
Ta (°C)	16.5	17.1	15.3	17.1	14.9	16.3	13.5
24 hr average VPD (kPa)	0.80	0.75	0.84	0.90	0.88	0.76	0.59
Daytime average PAR (W/m²)	107.8	110.7	151.1	108.7	106.9	116.5	86.2
WT_{centre} (m below ground surface)	524	410	410	509	468	561	448
WT_{edge} (m below ground surface)	130	97	104	211	163	186	148
VMC (m³ m⁻³) at 10 cms below soil surface (min to max range)	0.36 (0.30 – 0.41)	0.40 (0.37- 0.42)	0.42 (0.33 – 0.50)	0.27 (0.19- 0.33)	0.34 (0.27- 0.38)	0.29 (0.27- 0.31)	0.27 (0.22- 0.32)
Bowen's Ratio	2.03	1.29	1.42	1.74	2.22	0.74	4.32
P_{annual} (mm)	530	504	391	282	489	Same as NSA	
P_{summer} (mm)	273	242	151	170	269		

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

9

	NSA					SSA	
	2007	2008	2009	2010	2011	2008	2009
Canopy Height (m)	0.54 (0.03)	1.63 (0.03)	1.88 (0.02)	2.09 (0.07)	2.39 (0.05)	0.58 (0.05)	1.59 (0.07)
LAI (m² m⁻²)	0.60 (0.1)	1.4 (0.1)	1.7 (0.09)	1.81 (0.06)	1.94 (0.06)	0.6 (0.1)	1.34 (0.07)
DBH (cm)	0.32 (0.08)	0.82 (0.07)	1.04 (0.08)	1.2 (0.08)	1.33 (0.06)	0.26 (0.04)	0.76 (0.07)

10
11 Table 2. Measured average (standard deviation) vegetation structural characteristics, and growing season.
12 Canopy Height = average height to top of trees; LAI = Leaf Area Index; DBH = Diameter at Breast
13 Height.

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