Using Flow Gauges to Determine Stem and Root Conductance in Hybrid Poplars.

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Abstract

A study was conducted using sap flow gauges to determine stem and root conductance in hybrid poplars at two sites near Swift Current, Saskatchewan. At the Rushlake site, sap flow rates were compared between Canam and Walker poplars using Dynamax (Model SGA-10) stem flow gauges. The primary objective was to determine if the difference in susceptibility to mid-summer terminal shoot dieback in Walker and Canam poplar clones could be attributed to leaf-specific conductance. Walker poplars appear to be well-suited to mesic sites and, under good soil moisture conditions, perform better than Canam. However, they are susceptible to mid-season terminal shoot dieback, while Canam poplars do not seem to be as susceptible. We suspect that this is primarily attributable to a greater leaf-specific conductance (LSC) of Canam poplars. As a tertiary cause, perhaps Canam poplars achieve a more complete stomatal closure during periods of extended vapor pressure deficits. The gauges were mounted at the distal ends (where the shoot diameter is about 10 mm) of actively growing branches near the crown of each tree. For a period of 14 days, the sap flow rates of each tree were measured. Preliminary results indicate that Canams did indeed have a greater LSC and showed higher stem flow rates than Walker poplars. Under the study conditions at the Rushlake site, air temperatures were not of sufficient magnitude to determine differences in leaf stomatal closure between the Canam and Walker trees. The LSC characteristics, however, would have benefited the Canam poplars in functioning under extended vapor pressure deficits. A secondary objective was to determine if differences in root conductances of poplars subjected to varying saline conditions were possible to measure using sap flow gauges. Although great care must be taken during gauge installation on tree roots, we found it is possible to measure root sap conductance on trees subjected to varying levels of salinity.

Introduction

Recently, advancement in technologies have allowed researchers to investigate plant transpiration by measuring sap flow. This is done using flow gauges that are attached to the plant stems. The advantages of these gauges are that they do not disturb the plant root medium as many lysimeters do, are non-destructive, require no calibration, and do not affect the transpiration behavior of the plant during measurement. Other advantages include: (1) that the proper installation and functioning of gauges can be ascertained, and the reliability of the measurements can be assessed by studying the raw data, (2) the potential accuracy resulting from a properly installed sap flow system under moderate sap flow conditions can be excellent, and (3) long-term observations are possible (Angadi et al. 2003). Several sap flow gauges employ the heat balance concept. The most popular has been a gauge based on initial designs by Sakuratani (1981), Sakuratani (1984), further refined by Baker and van Bavel (1987), and Steinberg et al. (1989). They are currently available commercially under the label (Dynamax Corp., Texas). Past studies, validating this technology have demonstrated that distribution of vascular tissue, sap flow rate, and stem type affect the flow system (Cohen et al. 1993). Data from Zhang and Kirkham (1995), however, suggest that sap flow rate is more important than stem anatomy in determining the precision of such a gauge.

Heat balance techniques have been used for many objectives, such as studying weed-crop competition, partitioning sap flow into various portions of the plant, identifying responses to high CO_2 concentration, measuring genetic variation to water relations, quantifying responses to different plant stresses and evaluating herbicide resistance (Akanda et al. 1996). The objectives of this report are: (1) to determine if differences in leaf-specific conductance (LSC) can be measured between two selected poplar (Populus *deltoides* Bartr. X. P. *xpetrowskyana* Scneid.) clones (Canam and Walker) using the heat-balance sap flow gauges, and (2) to apply sap flow gauges to poplar roots. The first objective was addressed in the Rushlake Experiment. It is known that Walker poplars favour mesic sites and, under good moisture conditions, perform better than Canam poplars. However, the Walker trees are susceptible to mid-season die-back of terminal shoots, while the Canams do not seem to be as susceptible. It is hypothesized that this could be attributable to a greater LSC of Canam poplars and/or a more complete stomatal closure in Canams under high vapor pressure deficits. The second objective was to explore the technology, as reported by Coners and Leuschner (2002), of using sap flow gauges to measure root sap conductance of poplars (Smith Experiment). Specifically, the roots of Walker poplars growing on a saline site were monitored with the purpose of observing differences in root conductance in response to changes in the electrical conductivity of the soil.

Materials and Methods

Theory and Operation of Sap Flow system

The gauges used in this experiment were Dynamax (Model SGA-10) stem flow gauges, (Dynamax Inc, Houston, TX, USA) and have been described in detail by Baker and van Bavel (1987), Steinberg et al. (1989), and Ham and Heilman (1990). A small flexible foil heater of fixed width completely encircles the stem or root and constantly emits heat energy, measured as a flux, to a small portion of the conductive tissue. Each heat balance gauge is fitted with foam covers, weather shields, and multiple layers of aluminum foil to reduce unwanted heat and radiative exchanges and ensure steady-state energy transfer. Assuming no energy storage within the gauge installation, the input of heat flux to the system (Q), electrically powered in joules per second, equals the sum of the outward or radial heat loss through the insulation shielding surrounding the gauge (Qr), the axial heat conducted in both directions (Qv), and the convective heat carried by the sap flow (Qf):

$$Q = Qr + Qv + Qf \qquad \text{[in joules per second]}$$

The fluxes Qr and Qv are calculated electronically in this gauge using measured temperature gradients, fixed coefficients, and the conductive cross-sectional area of the stem or root (Ac) in cm^2. With the assumption that the specific heat capacity (Cp) of the sap equals that of water at 25 ^oC (4.18 joules per gram per ^oC), and a measure of the temperature difference in the sap caused by Q moving into and out of the measurement reach (T_{out} - T_{in}), the Qf-flux can be converted to sap flow (F) in grams per second (or hour):

$$F = \frac{Qf}{Cp\,(T_{out} - T_{in})} \qquad \text{[in grams per second]}$$

Rush Lake Experiment

The sap flow gauges were installed on three Canam and three Walker trees growing in a poplar plantation established in 1999 within a mesic site near the village of Rushlake, about 30 km east of Swift Current, Saskatchewan. Dynamax (Model SGA-10) gauges were installed at the distal ends of actively growing branches near the crown of each tree (branch diameters: 10.0, 10.1, and 12.9 mm for the Canam and 9.4, 10.0, and 10.7 for the Walker). Due to difficulty with the connections of the cable for Walker poplar #2 tree, these measurements were not used. The average height of the Canam and Walker trees measured 5.95 and 5.81 m, respectively. The branches were fairly smooth and required minimum preparation for gauge attachment except to remove one or two leaves and a light sanding of the nodes. Before installing the gauges, a thin layer of electrical insulating compound (G4, Dow Corning Corp., Midland MI) was applied to improve thermal contact and to protect the heater from water vapour condensation (Dynamax 2000). White foam insulation, foam 'O'rings above and below the gauges, and reflective-painted PVC weather shields were used to weather-proof the gauges (Dynamax 2000). In addition, at least three layers of aluminum foil were wrapped around the installation to seal it from direct radiation (Angadi et al. 2003). Connecting wires were taped to the tree trunk and covered with aluminum foil near the gauges to avoid temperature fluctuations. Following installation, the portion of the branch above and below the gauge was sealed with electrical insulating compound to prevent moisture penetration. A constant four volts from a 12 V deep-cycle Marine battery passed through a datalogger transformer to each gauge. The effective branch thermal conductivity was assumed to be 0.42 W m^{-1} $^oC^{-1}$, as suggested by Sakuratani (1981). The effective thermal conductivity of each gauge installation (Ksh) was estimated during low sap flow periods, from early morning observations (Dynamax 2000). When convective heat loss was less than 5% of the total heat supplied, flow rates were electronically set to zero. Gauge signals were scanned every 30 s using a data logger (Model 10X, Campbell Scientific, Logan Utah), and mean values were calculated every 30 min and stored. The trees in this study were continuously monitored for 14 days beginning 14 July, 2004 at midnight. Because sap flow rates depend on the total leaf area existing downstream from the gauge, the sap flow readings in this study were adjusted for leaf area (Heilman and Ham 1990). Following the field measurements, the leaves on each branch distal to the flow gauges were removed, taken to the lab, and measured for leaf area. The total leaf area (TLA) distal to each gauge was then calculated by summing individual leaf areas. The total leaf area distal to each gauge measured 2129.6, 3000.5 and 5028.2 cm^2 for the Canams and 2375.3 and 2785.3 for the Walkers. A standard total leaf area of 2500 cm^2 was chosen to scale and standardize all branch sap flow rates (RFB) to facilitate clonal comparisons:

$$RFB = \frac{F}{TLA/2500}$$

Night time leaf water potentials were measured using a Model 1000 Plant Water Status Console (PMS Instruments) to determine the effective soil water availability to the plant at the beginning of the test. Sap flow data were quantified using a paired t-test, comparing the mean values for each clone (SAS 1995).

Smith Experiment

The Smith Experiment consists of a poplar plantation established in 1998 on a mesic saline soil and located about 3 km southwest of Swift Current, Saskatchewan. Four Walker trees, ranging 3.3, 3.34, 3.85, and 4.85 m in height were selected. The two taller trees (average height 4.35 m) indicated less salinity and were compared with two smaller trees indicating greater salinity (average height 3.32 m). One root of about 10 mm in diameter (resulting in calculated cross-sectional root areas of 0.64, 0.95, 0.97, and 1.27 cm^2), on the south side of each tree was located and fitted with a (Model SGA-10) sap flow gauge. Care was taken to minimize soil disturbance in excavation and installation of the gauge on the root. The small pit was then covered with plywood, black plastic and foil-backed insulation to isolate the installation. As at the Rushlake site, gauge signals were scanned every 30 s using a data logger (Model 10X, Campbell Scientific, Logan Utah) and mean values were calculated every 30 min and stored. The trees were monitored for sap flow for 5 days from the 10^{th} to the 14^{th} of August, 2004. Following the logic of Heilman and Ham (1990), the sap flow readings in this study were adjusted for cross-sectional root area (Ac). A standard root area of 1.0 cm^2 was used to scale and standardize all root sap flow rates (RFR) to facilitate tree comparisons.

$$RFR = \frac{F}{(Ac/1)}$$

Following the field measurements, the gauges were dismantled, and the soil immediately surrounding the entire length of the root was extracted and analyzed for electrical conductivity (saturated paste extracts). Results were averaged to obtain a mean electrical conductivity for each root. Sap flow data were quantified using a paired t-test, comparing the mean values for each site (SAS 1995).

Results and Discussion

Rushlake Site

Most experiments using the heat balance technique have been done under controlled environmental conditions with plants grown in pots. The precision of the heat flow gauges have been evaluated and verified by also measuring the transpiration of plants growing in sealed pots and weighing the pot at specific intervals to determine water loss (Angadi et al., 2003; Zhang and Kirkham, 1995). A few experiments have been done under field conditions, mainly with large, woody, perennial plants. For a list of these experiments see Zhang and Kirkham (1995).

A constraint with field measurements of large plants using flow gauges is verifying the accuracy of the data. Senock and Ham (1993) overcame this difficulty by applying a mathematical analysis to show that changes in sap flow rate (F) are inversely proportional to (T_{out}-T_{in}) under moderate to high flow conditions. Thus, the shape of the (T_{out}-T_{in}) or ()T) response curve over 24 hours can be used to assess data accuracy and optimum heat input (ie., the sap temperature rise,)T, should not exceed 8 ^{o}C in the morning and should be above 0.3 ^{o}C during the peak flow period (Dynamax 2000)). When the curve is generally concave-up, with the minimum difference occurring sometime during midday, the data contains few errors (less than 10%) (Senock and Ham, 1993). Under these conditions, the curve is a mirror image of the curve for the sap flow rate (i.e., maximum sap flow rate on days without clouds occurs at solar noon). Our data in Figures 1 and 2 concurs. When the curve is generally concave-down, with a maximum difference occurring sometime during midday, the gauge signals the presence of errors (Senock and Ham, 1993). Our data in Figures 1 and 2 suggest a high degree of data accuracy for this test.

The data in Table 1, indicate that the Canam trees have a much higher average hourly sap flow rate (adjusted for leaf area) during the period from 07:00 to 20:00 hours each day than that for Walker trees. The average accumulated daily sap flow rate (adjusted for leaf area) measured in g day $^{-1}$ is significantly higher for Canams as well (Table 1), indicating the possibility of a higher LSC for the Canam compared to Walker poplars. In comparing the sap flow rates of the two poplar clones at high temperatures (Table 2), Canams continued to display higher flow rates when mean hourly temperatures were 25 ^{o}C or higher, as well as when they were 30 ^{o}C or higher. The Canam sap flow rates compared at different temperatures with the average sap flow rates in Table 1, resulted in a 33.6% increase at temperatures 25 ^{o}C or higher and by 44.2% at 30 ^{o}C or higher. Conversely the Walker poplars displayed slightly lower flow rate increases (32.6 and 39.9 % respectively). This suggests that the Canams are more easily able to keep up with the transpiration demands during warm summer days as compared to Walkers. Flow rates continued to increase significantly as temperatures increased, indicating low vapor pressure deficit conditions even at 30 ^{o}C or higher. Soil moisture conditions were near field capacity as indicated by night time leaf water potentials (-0.236 MPa for Canams and 0.204 for Walkers). Figure 2, showing mean flow rates measured in g hr^{-1} during a 24 hour period on July 18th of a typical, warm summer day and Figure 3, showing mean sap flow rates for the 14 day study period, support this inference as well. Figure 3 also indicates the response of the gauges to changes in evaporation demands due to diurnal temperature fluctuations as well as precipitation events. Of note, under extended precipitation events and/or periods of high humidity, the gauges need to be checked often for moisture accumulation between the heater and the plant. The presense of such water interferes with heat transfer.

Table 1. Mean Hourly Sap Flow (g hr^{-1}) Between 07:00 and 20:00 Hr and the Total Daily Sap Flow (g day^{-1}), From 14 July to 27 July 2004 Adjusted for Leaf Area, as Measured by the Heat Balance Method Using Dynamax (Model SGA-10) Heat Flow Gauges Mounted on Actively Growing Canam and Walker

	Average sap flow		Total daily sap flow	
	Canam	Walker	Canam	Walker
	g hr^{-1}	g hr^{-1}	g day^{-1}	g day^{-1}
	40.27	18.87	554.30	261.03
Paired t-test:				
Mean difference	21.64		293.27	
Standard error	0.64		28.77	
Prob >|t|	<0.0001		<0.0001	
Degrees of freedom	376		13	

Table 2. Mean Hourly Sap Flow (g hr^{-1}), Adjusted for Leaf Area When the Mean Hourly Temperature Reached 25 °C or Higher, and 30 °C or Higher From 14 July to 27 July 2004 as Measured by the Heat Balance Method Using Dynamax (Model SGA-10) Heat Flow Gauges Mounted on Actively Growing Canam and Walker

	25 °C or higher		30 °C or higher	
	Canam	Walker	Canam	Walker
	g hr^{-1}	g hr^{-1}	g hr^{-1}	g hr^{-1}
Sap flow	53.80	25.03	58.06	26.40
Paired t-test:				
Mean difference	28.77		31.66	
Standard error	0.76		1.24	
Prob >|t|	<0.0001		<0.0001	
Degrees of freedom	176		66	

Smith Site

The site was characterized for salinity in 1998 when the trees were originally planted. The salinity in the vicinity of the two trees displaying moderate growth ranged from 0.6 dS m^{-1}

in the top 30 cm of the soil profile to 1.07 dS m^{-1} at a depth of 120 cm. The salinity of the trees displaying less than moderate growth ranged from 0.73 dS m^{-1} in the top 30 cm of soil profile to 10.03 dS m^{-1} at a depth of 120 cm. The soil electrical conductivity in close proximity to the roots of the low salt trees was 0.58 dS m^{-1}, while the soil growing the salt-affected trees measured 0.54 dS m^{-1} just following the sap flow measurements. All monitored roots were located in the top 45 cm of the soil profile.

According to Senock and Ham (1993), Figure 4 suggests confidence in the accuracy of the recorded flow measurements. When comparing both the mean hourly and the accumulated daily sap flow rates, the low salt trees indicated somewhat higher rates of flow even though both sets of measured roots were experiencing similar saline conditions during the test period (Table 3). The higher flow rates may be due to greater root surface area in contact with the soil, and/or more vigorous respiration activity of the larger trees, resulting in greater flow. To verify this, above-ground sap flow (adjusted for leaf area) and detailed root measurements would need to be included. Figure 5, showing mean sap flow rates through the roots for the five day study period, indicates the response of the gauges to changes in evaporation demands due to diurnal temperature fluctuations.

Table 3. Mean Hourly Sap Flow (g hr^{-1}) Between 07:00 and 20:00 Hr and the Total Daily Sap Flow (g day^{-1}), From 10 August to 14 August, 2004 Adjusted for Root Area, as Measured by the Heat Balance Method Using Dynamax (Model SGA-10) Heat Flow Gauges Mounted on Actively Growing Roots of Walker Poplars Growing in Low (Low Salt) and Moderately Saline (Salt-affected) Environments.

	Average daily sap flow		Total daily sap flow	
	Low salt	Salt-affected	Low salt	Salt-affected
	g hr^{-1}	g hr^{-1}	g day^{-1}	g day^{-1}
	42.86	39.20	1161.92	1060.32
Paired t-test:				
Mean difference	3.66		101.6	
Standard error	1.11		22.06	
Prob >|t|	<0.0012		<0.01	
Degrees of freedom	134		4	

Conclusions

We found that it was possible to measure differences in sap flow between poplar clones under moderate to high flow conditions. Preliminary results indicate that Canams appears to have a higher LSC than Walkers under mesic conditions. Under the conditions existing during the study period at the Rushlake site, 30 ^{o}C temperatures were not sufficient to determine differences in leaf stomatal closure between Canams and Walkers. Sap flow readings must be standardized to facilitate clonal or varietal comparisons. This can be done with total leaf area or cross-sectional areas of stems and roots. Although great care must be taken during gauge installation on tree roots, it is possible to measure root sap conductance on trees subjected to varying levels of salinity. Regardless of the field situation, or the species investigated, a critical evaluation of the effect of ambient conditions on gauge performance should be done to ensure reliable plant water use estimates (Shackel et al. 1992). Under highly variable environmental conditions (precipitation events or periods of high humidity) the gauges need to be monitored closely to ensure dry contact between the heater and the plant stem as the presense of water greatly impedes heat transfer.

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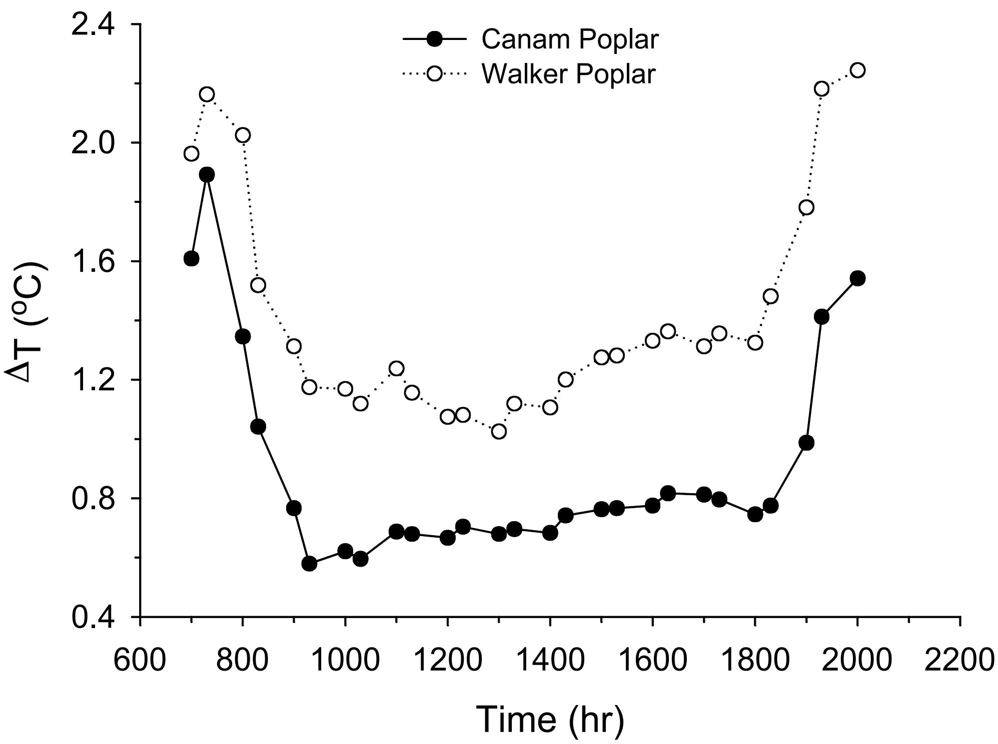

Figure 1. The difference in branch temperatures ()T) measured as the sap enters (T_{in}) and leaves (T_{out}) the flow gauge, plotted from 07:00 to 20:00 hour on 18 July 2004 (Julian day = 200).

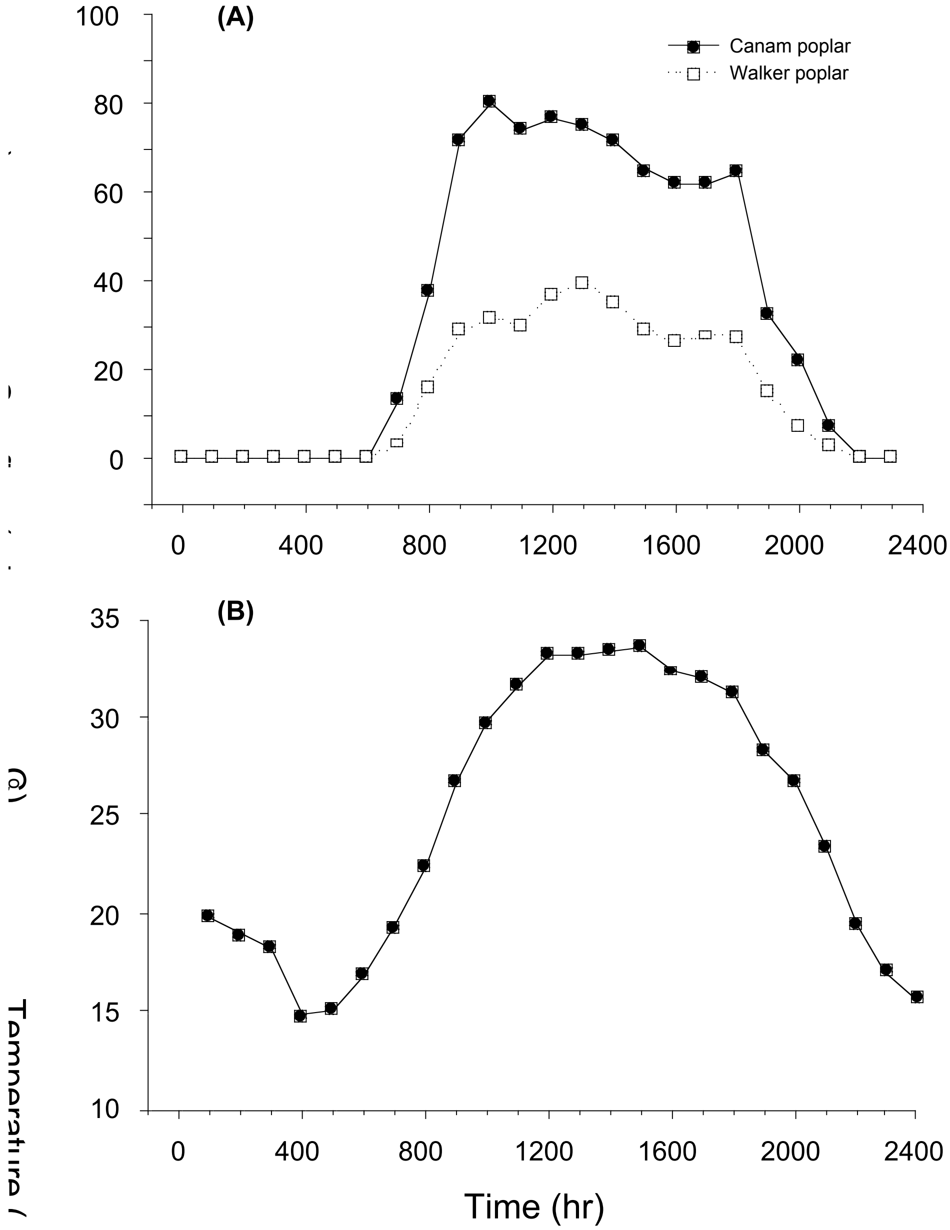

Figure 2. (A) Mean hourly sap flow (g hr^{-1}), adjusted for leaf area, as measured by the heat balance method using Dynamax (Model SGA-10) heat flow gauges mounted on actively growing branches of Canam and Walker poplars, and (B) mean hourly temperature (^oC), measured on site for 18 July 2004 (Julian day = 200).

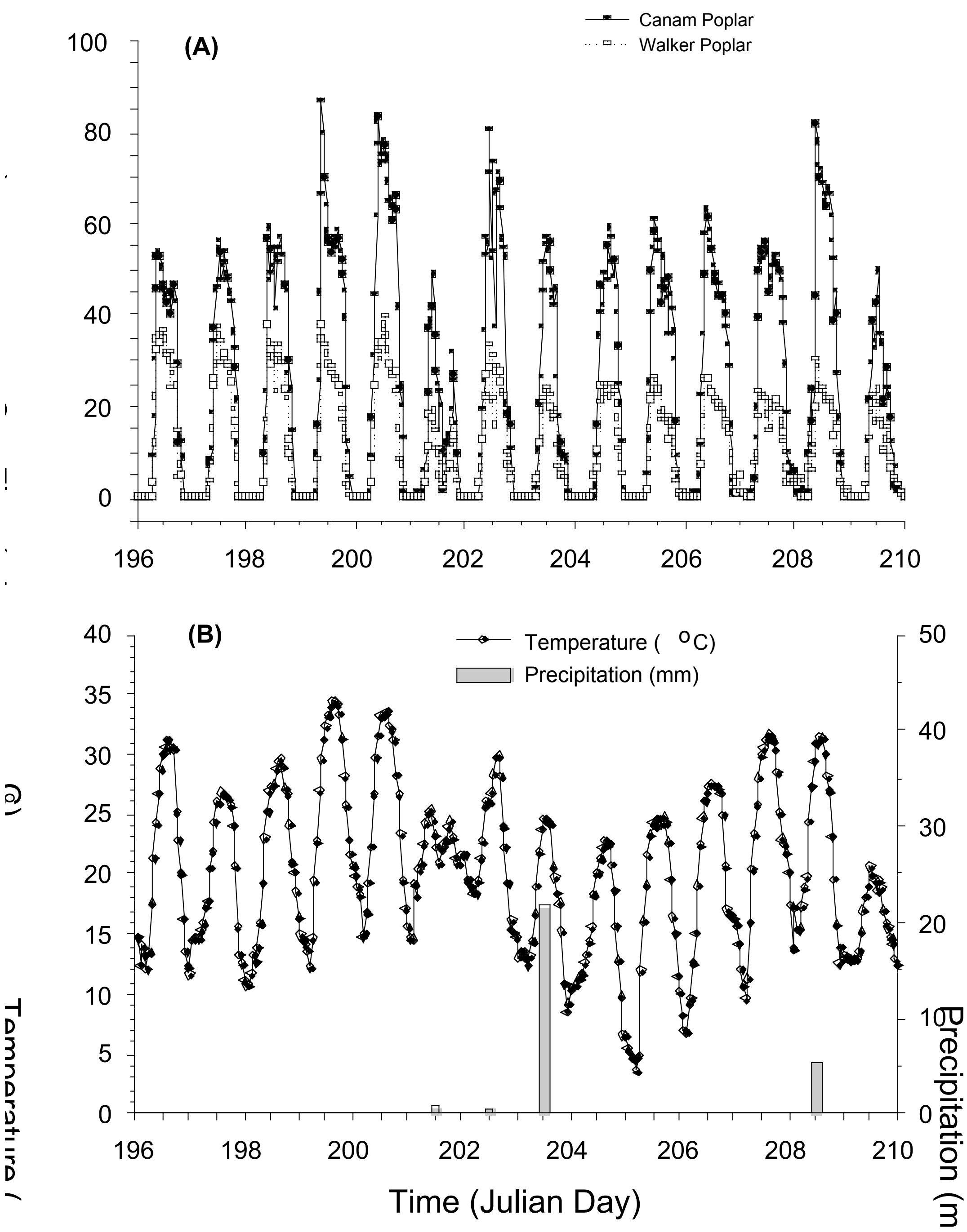

Figure 3. (A) Mean hourly sap flow (g hr^{-1}) adjusted for leaf area, from 14 July to 27 July 2004 as measured by the heat balance method using Dynamax (Model SGA-10) heat flow gauges mounted on actively growing branches of Canam and Walker poplars, and (B) diurnal mean hourly temperature fluctuations and precipitation events.

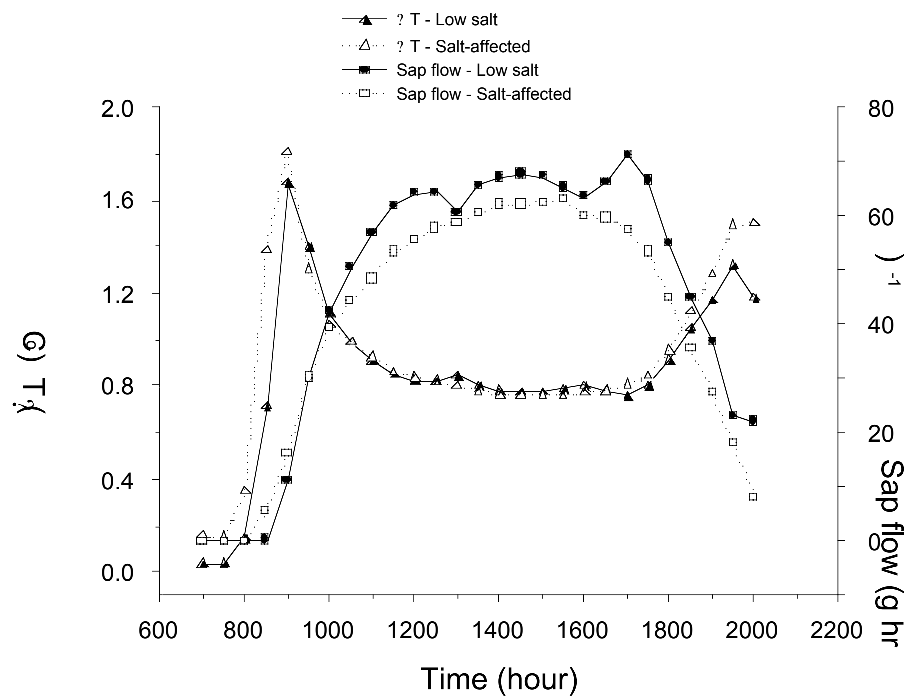

Figure 4. The difference in root temperatures ()T) measured as the sap enters (T_{in}) and leaves (T_{out}) the flow gauge and the mean adjusted diurnal sap flow (g hr^{-1}) from 7:00 to 20:00 hr as measured by stem flow gauges mounted on actively growing roots of Walker poplars subjected to low (low salt) and moderate salinity (salt-affected) for 12 August 2004 (Julian day = 225).

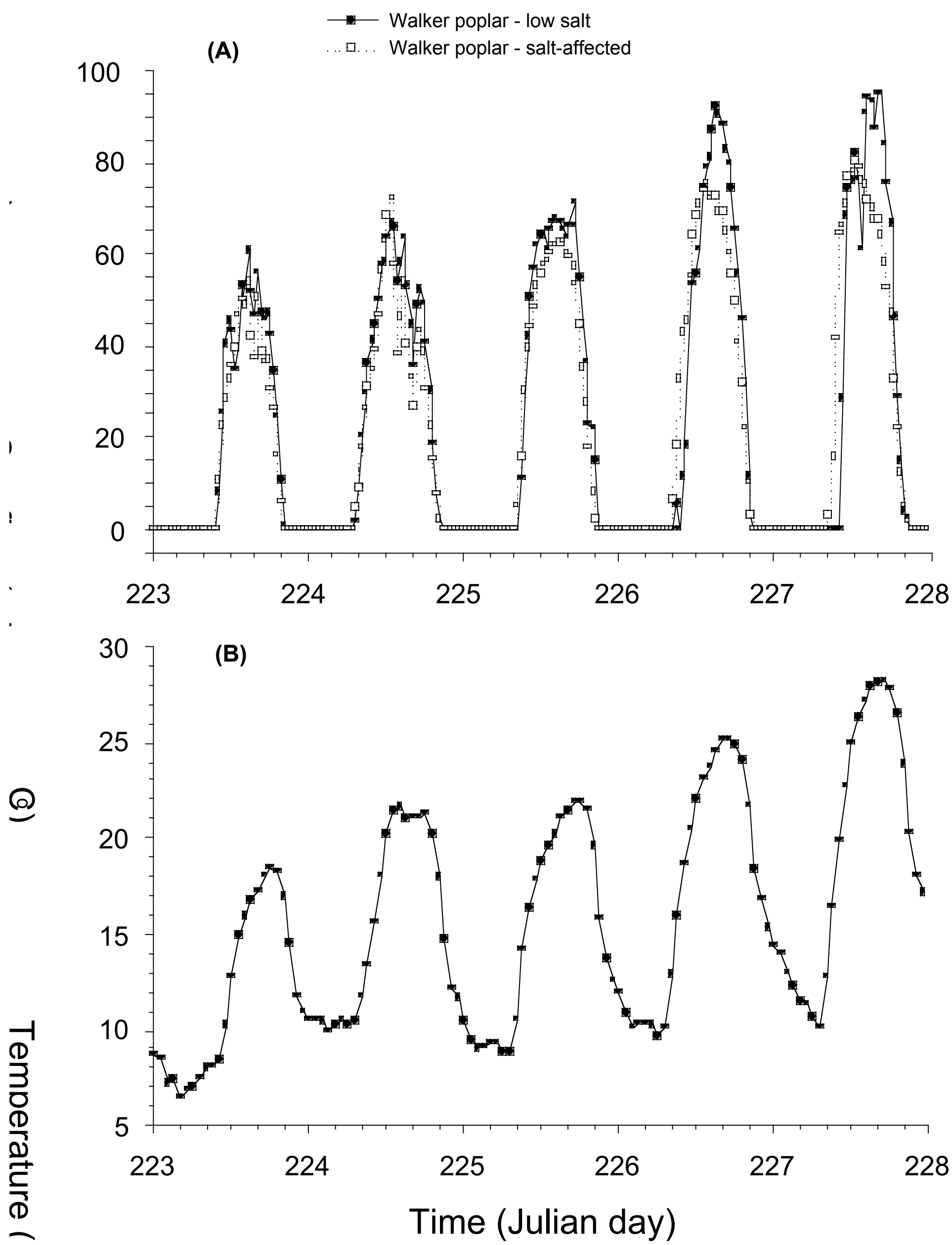

Figure 5. (A) Mean hourly sap flow (g hr^{-1}) adjusted for leaf area, from 10 August to 14 August 2004 as measured by the heat balance method using Dynamax (Model SGA-10) heat flow gauges mounted on actively growing roots of Walker poplars, and (B) diurnal mean hourly temperature fluctuations.