

# Variance Components, Heritabilities and Gain Estimates for Growth Chamber and Field Performance of *Populus tremuloides*: Gas Exchange Parameters

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## Summary

Five populations of trembling aspen from Alberta, Canada were tested under both field (north and south, grown 2 years) and corresponding growth chamber (north and south, grown 12 weeks) conditions and gas exchange traits (net assimilation (NA), stomatal conductance ( $G_s$ ), photosynthetic water use efficiency (WUE)) were measured. Differences among populations were not significant for most traits however clone-within-population explained substantially more variation in nearly all analyses. Plants grown in a drier potting mix showed significantly lower net assimilation in the southern chamber. By the end of the growth chamber experiment (83 days), there was a significant positive correlation between net assimilation and both height, and root dry weight in both chambers. Similar correlations were not found in the field. There was also no relationship between the growth chamber and field performance of clones. Broad-sense clone mean heritability estimates for NA,  $G_s$  and WUE ranged from 0.28 to 0.80, 0.73 to 0.92, and 0.44 to 0.80 respectively. Estimates from the field sites were much more variable and rarely as high. Gain estimates for net assimilation in the northern chamber averaged 16% (12.6% to 17.8%) across all three test dates but were far more variable (5.9% to 22.4%) across dates in the southern chamber which averaged 11%. Overall, trembling aspen in Alberta exhibits substantial genetic variation at the clonal level for gas exchange traits with limited differentiation at the population level.

*Key words:* trembling aspen, gas exchange, heritability, gain, variances.

*FDC:* 232.11; 165.3; 165.5; 161.14.16; 176.1 *Populus tremuloides*.

## 1.0 Introduction

The use of physiological measurements to assist in the determination of superior genotypes for tree improvement is relatively new (STETTLER et al., 1997), although the need for better cooperation and understanding between physiologists, silviculturalists and geneticists has been suggested for some time (KOEHN, 1987; KRAMER, 1948, 1986).

Many studies done on selected poplar hybrids suggest that physiological traits can be used for early clonal screening (CEULEMANS and IMPENS, 1980, 1983; GAUTHERUM et al., 1967) and substantial benefits could be gained by allowing breeders to 'cull' phenotypes sooner, thereby reducing overall field test costs (LEDIG, 1969). So far, however, assessment of heritability and gain estimates based on physiological traits has largely been unexplored (NIENHUIS et al., 1994; SRIVASTAVA and JAIN, 1994). Two obvious concerns with using physiological traits are: 1) establishing the link between physiological performance (e.g. net assimilation) and growth; and 2) because most physiology studies are greenhouse based, establishing the relationship between growth chamber and field performance. Previous studies on *Populus* have shown both high and low

correlations between photosynthetic performance and growth (BARIGAH et al., 1994; GAUTHERUM et al., 1967; HUBER and POLSTER, 1955; OKAFA and HANOVER, 1978; REIGHARD and HANOVER, 1990) and, with studies involving relatively few clones, generally show a positive relationship between greenhouse and field performance (but see CEULEMANS et al., 1987). However, 'field' conditions in these experiments are typically well tended and watered potted plants grown outside (ISEBRANDS et al., 1988; NELSON and EHLERS, 1984).

Although poplars have been studied by physiologists for many years, these studies have typically been restricted to very few (BOURDEAU, 1958), and often hybrid clones (BASSMAN and ZWIER, 1991; CEULEMANS and IMPENS, 1980; FOOTE and SCHAEDEL, 1976; JURIK et al., 1984; MICHAEL et al., 1990; NELSON, 1985; NELSON and EHLERS, 1984; NELSON and ISEBRANDS, 1983; REGEHR et al., 1975). For tree improvement purposes, the need for quantitative parameter estimates demands that substantially more genotypes be tested and that testing be done on unselected native clones, in addition to hybrids (DANG et al., 1994; DUNLAP et al., 1993; SEILER and JOHNSON, 1988).

We present data on gas exchange (net assimilation, stomatal conductance and water use efficiency) of 20 to 29 native, unselected male clones of trembling aspen (*Populus tremuloides* MICHAUX) from Alberta, Canada. Clones were grown under both growth chamber and field conditions. Genetic variation among populations and clones-within-populations was assessed, a comparison of field and growth chamber performance was made, and physiological responses were compared with yield measurements. Heritability and gain estimates were also calculated for net assimilation.

## 2.0 Materials and Methods

For collection protocol, greenhouse propagation and growth chamber set-up as well as the field site locations and establishment, see THOMAS et al. (1997). In the growth chamber study stecklings (rooted cuttings) were grown under 350  $\mu\text{mol}$  to 450  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$  at pot height. Light was supplied by four high-intensity-discharge (HID) mercury halide lamps (400 W) and four high-intensity-discharge (HID) sodium lamps (400 W). Limited availability of growth chambers did not permit experimental replication at the chamber level. The 'moisture' treatment (Metromix *versus* Metromix plus sand, see THOMAS et al. (1997) was considered a split-plot treatment for analysis purposes.

### 2.1 Data collection

Gas exchange was measured three times in the growth chambers (Days 41, 62 and 83 of growth). All test plants were removed from the growth chamber immediately prior to measuring. Measurements were made using a portable infrared gas analyzer (IRGA) (ADC LCA-3, Analytical Development Company, Hoddesdon, England) with the broad leaf cuvette

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Table 1. – Source of variation, associated p-values and heritabilities ( $H^2_c$ ) (s.e.) for net assimilation (NA), stomatal conductance to  $H_2O$  ( $G_s$ ) and water use efficiency (WUE) for field data in the combined sites analysis at 4 test dates. Significant p-values are in bold.

Year	NA				$G_s$				WUE			
	1993		1994		1993		1994		1993		1994	
	June	Aug	June	Aug	June	Aug	June	Aug	June	Aug	June	Aug
Source*	p-values				p-values				p-values			
L	<0.01	<0.01	0.05	0.05	0.02	0.04	0.10	0.07	0.88	0.28	0.76	0.72
P	0.76	0.45	0.29	0.26	0.47	0.84	0.93	0.40	0.86	0.52	0.39	0.49
LP	0.23	0.19	0.91	0.68	0.65	0.18	0.42	0.75	0.02	0.43	0.49	0.23
B(L)	0.41	0.07	0.01	<0.01	0.08	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
C(P)	0.15	0.26	0.26	0.72	0.50	0.36	0.54	0.83	0.19	0.05	0.72	0.24
LC(P)	<0.01	0.74	0.01	0.05	0.04	0.25	<0.01	0.25	0.09	0.97	0.18	0.65
PB(L)	0.52	0.49	0.08	0.21	<0.01	0.43	0.50	0.24	0.90	0.72	0.74	0.23
B(L)C(P)	0.99	0.01	0.99	0.90	0.99	0.94	0.97	0.51	0.91	0.24	0.03	0.77
$H^2_c$	0.25	0.19	0.24	0	<0.01	0.11	0	0	0.22	0.33	0	0.20
	(0.18)	(0.23)	(0.22)		(0.20)	(0.25)			(0.23)	(0.14)		(0.22)

\*) Source effects where L is location, P is population, B(L) is block-within-location, C(P) is clone-within-population, LC(P) is location by clone-within-population interaction, PB(L) is population by block-within-location and B(L)C(P) is block-within-location by clone-within-population interaction.

(PCL(B)). Saturating light (a minimum of 1500  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$  RODEN and PEARCY, 1993) was provided by a 12 volt quartz halogen light (MR-16, Phillips, Somerset, NJ, USA) for both field and greenhouse measures. All gas exchange measurements were expressed on a projected leaf area basis. Leaves usually filled the entire cuvette (6.25  $\text{cm}^2$ ); when necessary measured leaf area was determined using a leaf area meter (Li-Cor 3100, Lambda Instruments Corporation, Lincoln, Nebraska). Gas exchange was done on the first fully expanded leaf from the top, based on observation of the leaf size relative to the other leaves. The leaf plastochron index (LPI) (LAMOREAUX et al., 1978) was not used due to the number of different clones (CEULEMANS et al., 1988) and environmental treatments. In general, however, for the growth chamber plants, leaf 6 to 10 on the terminal shoot was used for gas exchange measurements, which is similar to the LPI of 7 used by OKAFO and HANOVER, (1978) for the same species. Net assimilation (NA,  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ), photosynthetic water use efficiency (WUE,  $\mu\text{mol CO}_2 \text{ fixed/mmole H}_2\text{O transpired}$ ) and stomatal conductance to  $H_2O$  ( $G_s$ ,  $\text{mmol m}^{-2}\text{s}^{-1}$ ) were calculated according to the equations of VON CAEMMERER and FARQUHAR, (1981) based on instantaneous measurements. Four clones from each population were measured in the growth chamber while up to six clones per population were measured in the field study. Two individuals were measured per clone per moisture treatment per chamber in the growth chamber study (160 total per test date per chamber) with up to three replicates per clone per block per site in the field study (maximum of 348 total per test period). Field measurements were taken in both June and August of 1993 and 1994. Plants within a site were measured over 1 to 2 days and both sites were measured within a week of each other at each test period.

## 2.2 Statistical models and data analysis

Data were analysed following the linear models presented in THOMAS et al. (1997) for combined chamber analysis, combined field analysis and individual field site analysis. Individual chamber analysis was done using the following model:

[1]

$$Y_{ijkl} = \mu + M_i + P_j + C_{k(j)} + M_i P_j + M_i C_{k(j)} + e_{l(ijk)}$$

where  $Y_{ijkl}$  is an observation on the  $l$ th tree from the  $k$ th clone in the  $j$ th population and  $i$ th moisture,  $\mu$  is the overall mean,  $M_i$  is the effect of the  $i$ th moisture ( $i = 1,2$ ),  $P_j$  is the effect of the  $j$ th population ( $j = 1, \dots, 5$ ),  $C_{k(j)}$  is the effect of the  $k$ th clone nested in the  $j$ th population ( $k = 1, \dots, 4$ ),  $M_i P_j$  is the interaction of the  $i$ th moisture and the  $j$ th population,  $M_i C_{k(j)}$  is the interaction of the  $i$ th moisture and the  $k$ th clone nested in

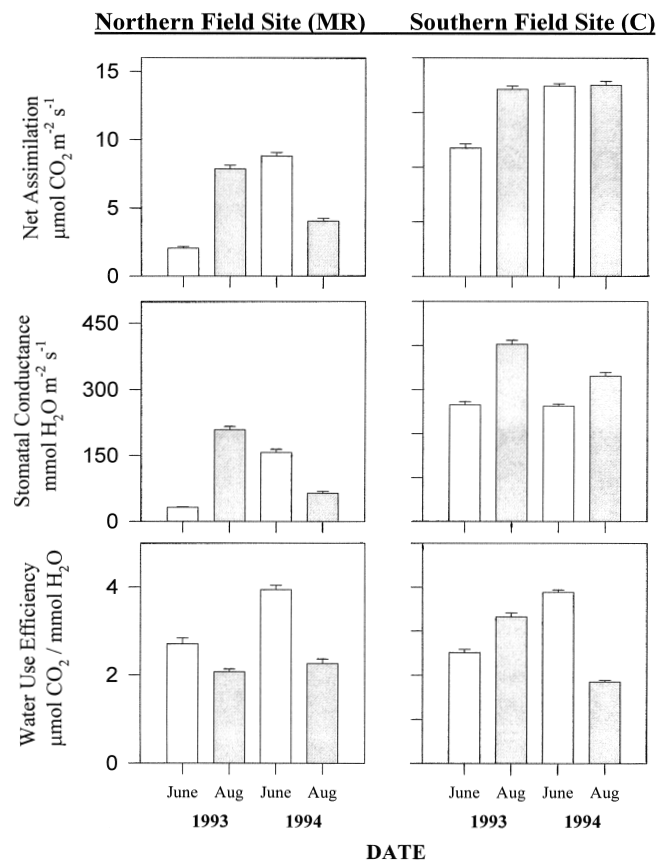


Figure 1. – Means (s.e.) of all trembling aspen clones for net assimilation ( $\text{mmol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ), stomatal conductance ( $\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$ ) and photosynthetic water use efficiency ( $\text{mmol CO}_2 \text{ fixed/mmole H}_2\text{O transpired}$ ) for each date and field site. Where MR = Meander River and C = Calgary.

the  $j$ th population and  $e_{l(ijk)}$  is the random error. Moisture was considered to be a fixed factor while all other terms were considered random effects. For analyses including chamber, differences are presented graphically by date and trait.

Variance components were calculated by hand using the appropriate mean square values and corresponding expected mean square coefficients generated from PROC GLM, RANDOM/TEST option (SAS Inc., 1985). Negative variance components were assumed to be zero (FINS et al., 1992). For all analyses sources of variation were considered significant at  $\alpha = 5\%$ .

Broad-sense heritabilities were calculated on a clone mean basis following the equations presented in THOMAS et al. (1997). The individual chamber heritabilities used the following equation:

$$[2] H^2_C = \frac{\sigma^2_C}{\frac{K3\sigma^2_C}{K3} + \frac{K1\sigma^2_{MC}}{K3} + \frac{\text{Error}}{K3}}$$

where K3 is the coefficient associated with the variance due to clone-within-population ( $\sigma^2_C$ ) and K1 is the coefficient associated with the variance due to the moisture by clone-within-population interaction term ( $\sigma^2_{MC}$ ) (see Appendix 1). Gain calculations followed the equation presented in THOMAS et al. (1997). Standard errors for heritabilities followed NYQUIST, (1991) (see THOMAS et al. (submitted)). Correlation analysis was used to examine the relationship between net assimilation and both height and root dry weight.

### 3.0 Results

#### 3.1 Field analyses

For the combined sites analyses many higher order interactions were significant and heritability estimates were low and highly variable (Table 1). Therefore, analysis was done by individual site, trait and date (Figure 1, Tables 1, 2). Field net assimilation (NA) values were generally much higher in Calgary than Meander River and higher than growth chamber values. In the field there was no correlation found between NA and growth (not shown).

In the separate site analysis clone-within-population accounted for more of the variation, and, therefore heritabilities were generally higher than for the combined site analysis although the results remained variable (Table 2). Population was significant only once in all the analyses (water use efficiency [WUE], Meander River, June 1993, Table 2). Block accounted for a substantial amount of the variation at the Calgary site, likely due to shading of one block by mid-afternoon during the growing season. In June 1993, at Meander River, despite the droughty conditions and low NA rates (Figure 1), clone-within-population still explained 11.8% of the variation (Table 2a). Clone-within-population explained 18.5% of the variation in Calgary for the same date. By 1994, both field sites had reasonably stable heritability values for NA, (Tables 2a, d) although values for Calgary were lower. Despite the higher mortality at Meander River, clone-within-population explained three times as much of the variation in NA in 1994 as it did at Calgary.

#### 3.2 Growth chamber analyses

Combined growth chamber analyses showed no significant population effect for any of the three gas exchange traits while clone-within-population was significant only for stomatal conductance ( $G_S$ ) on Day 41 (Table 3). Chamber by clone-

Table 2. – Source of variation, degrees of freedom (Df), p-values, percent variance (% Var) explained and heritabilities ( $H^2_c$ ) (s.e.) for the northern field site (a, b, c, respectively) and the southern field site (d, e, f respectively) for net assimilation (NA), stomatal conductance to  $H_2O$  ( $G_S$ ) and water use efficiency (WUE), for June and August of 1993 and June and August of 1994. Significant p-values are in bold.

a) Northern Field Site, NA										
Year		1993					1994			
Date		June		August		June		August		
Source*	Df <sup>#</sup>	p-value	% Var	p-value	% Var	p-value	% Var	p-value	% Var	
P	4	0.42	1.0	0.47	2.63	0.93	0	0.10	6.74	
B	1	0.81	0	0.17	4.30	0.61	0	<b>0.02</b>	<b>6.71</b>	
PB	4	0.87	0	0.49	0	0.09	4.85	0.74	0	
C(P)	24	0.18	11.8	0.77	0	<b>&lt;0.01</b>	<b>19.07</b>	0.07	12.39	
BC(P)	24	0.27	8.0	<b>&lt;0.01</b>	<b>44.15</b>	0.97	0	0.81	0	
Error	74		79.3		48.91		76.08		74.16	
$H^2_c$		0.33 (0.27)			0	0.51 (0.11)		0.41(0.16)		
b) Northern Field Site, $G_S$										
Year		1993					1994			
Date		June		August		June		August		
Source*	Df <sup>#</sup>	p-value	% Var	p-value	% Var	p-value	% Var	p-value	% Var	
P	4	0.62	0.47	0.52	0	0.74	0	0.20	6.74	
B	1	0.96	0	0.61	0	0.15	2.25	0.40	0	
PB	4	0.61	0	0.23	4.46	0.40	0.27	0.52	0	
C(P)	24	0.79	0	0.32	5.07	<b>0.02</b>	<b>17.48</b>	0.18	11.83	
BC(P)	24	<b>0.03</b>	<b>28.10</b>	0.56	0	0.91	0	0.21	9.66	
Error	74		71.43		90.48		80.01		71.77	
$H^2_c$		0			0.18 (0.28)	0.48 (0.13)		0.34(0.27)		
c) Northern Field Site, WUE										
Year		1993					1994			
Date		June		August		June		August		
Source*	Df <sup>#</sup>	p-value	% Var	p-value	% Var	p-value	% Var	p-value	% Var	
P	4	<b>0.04</b>	<b>8.70</b>	0.39	4.70	0.45	2.69	0.29	1.75	
B	1	<b>&lt;0.01</b>	<b>17.25</b>	<b>0.03</b>	<b>20.06</b>	<b>&lt;0.01</b>	<b>34.66</b>	<b>&lt;0.01</b>	<b>66.60</b>	
PB	4	0.78	0	0.46	0	0.70	0	0.42	0.03	
C(P)	24	0.10	7.67	0.82	0	0.69	0	0.64	0	
BC(P)	24	0.89	0	<b>&lt;0.01</b>	<b>33.04</b>	<b>0.01</b>	<b>21.09</b>	0.55	0	
Error	74		66.38		42.20		41.57		31.62	
$H^2_c$		0.32 (0.16)			0	0		0		
d) Southern Field Site, NA										
Year		1993					1994			
Date		June		August		June		August		
Source*	Df <sup>#</sup>	p-value	% Var	p-value	% Var	p-value	% Var	p-value	% Var	
P	4	0.38	0.57	0.07	11.16	0.32	0.96	0.41	0.53	
B	1	0.35	0.04	0.07	4.85	<b>&lt;0.01</b>	<b>18.56</b>	<b>&lt;0.01</b>	<b>45.39</b>	
PB	4	0.32	0.44	0.43	0	0.35	0.41	0.13	2.34	
C(P)	24	<b>&lt;0.01</b>	<b>18.51</b>	0.37	1.96	<b>0.05</b>	<b>6.68</b>	0.13	3.97	
BC(P)	24	0.99	0	0.64	0	0.97	0	0.80	0	
Error	104		80.45		82.04		73.39		47.77	
$H^2_c$		0.54 (0.09)			0.12 (0.29)	0.33 (0.14)		0.31 (0.19)		
e) Southern Field Site, $G_S$										
Year		1993					1994			
Date		June		August		June		August		
Source*	Df <sup>#</sup>	p-value	% Var	p-value	% Var	p-value	% Var	p-value	% Var	
P	4	0.62	0	0.20	1.86	0.70	0	0.45	0.36	
B	1	0.14	6.06	<b>&lt;0.01</b>	<b>19.66</b>	<b>&lt;0.01</b>	<b>44.85</b>	<b>&lt;0.01</b>	<b>60.87</b>	
PB	4	<b>&lt;0.01</b>	<b>10.61</b>	0.61	0	0.78	0	0.19	1.53	
C(P)	24	<b>&lt;0.01</b>	<b>8.45</b>	0.16	4.07	<b>0.05</b>	<b>5.78</b>	0.54	0	
BC(P)	24	0.99	0	0.93	0	0.91	0	0.56	0	
Error	104		74.88		74.41		49.36		37.24	
$H^2_c$		0.37 (0.10)			0.23 (0.17)	0.39 (0.14)		0		
f) Southern Field Site, WUE										
Year		1993					1994			
Date		June		August		June		August		
Source*	Df <sup>#</sup>	p-value	% Var	p-value	% Var	p-value	% Var	p-value	% Var	
P	4	0.52	0	0.61	1.45	0.48	0	0.68	0	
B	1	<b>&lt;0.01</b>	<b>6.49</b>	<b>&lt;0.01</b>	<b>61.10</b>	<b>&lt;0.01</b>	<b>18.91</b>	<b>&lt;0.01</b>	<b>32.25</b>	
PB	4	0.87	0	0.80	0	0.45	0	0.06	3.60	
C(P)	24	<b>0.02</b>	<b>15.66</b>	0.76	0	<b>0.03</b>	<b>10.39</b>	0.70	0	
BC(P)	24	0.81	0	0.70	0	0.89	0	0.96	0	
Error	104		77.85		37.46		70.69		64.15	
$H^2_c$		0.51 (0.13)			0	0.45 (0.13)		0		

\* Source effects where P is population, B is block, PB is population by block interaction, C(P) is clone-within-population and BC(P) is block by clone-within-population interaction.

# Degrees of freedom given are maximum values for each site since clone-within-population (4 to 6) varied slightly and replicates varied (1 to 3) across dates and clones.

within-population was significant for all three of the test dates for  $G_S$  and for Day 62 for both NA and WUE. Despite this evidence of variability in clone performance among chambers,

Table 3. – Source of variation, associated p-values and heritabilities ( $H^2_c$ ) (s.e.) for net assimilation (NA), stomatal conductance to  $H_2O$  ( $G_s$ ) and water use efficiency (WUE) for combined chamber analysis at three test dates. Significant p-values are in bold.

Days	NA			$G_s$			WUE		
	41	62	83	41	62	83	41	62	83
Source*	p-values			p-values			p-values		
CH	non-estimable			non-estimable			non-estimable		
P	0.47	0.66	0.19	0.60	0.13	0.57	0.61	0.77	0.36
C(P)	0.77	0.79	0.12	<b>0.02</b>	0.09	0.07	0.31	0.72	0.09
CHP	0.38	0.65	0.39	0.34	0.26	0.82	0.79	0.77	0.11
CHC(P)	0.07	<b>&lt;0.01</b>	0.33	<b>&lt;0.02</b>	<b>&lt;0.01</b>	<b>0.05</b>	0.09	<b>&lt;0.01</b>	0.35
M	0.16	0.53	0.78	0.52	0.29	0.71	0.16	0.49	0.48
CHM	0.18	0.55	0.17	<b>0.01</b>	0.78	0.66	0.29	0.38	0.28
MP	0.71	0.66	0.32	<b>&lt;0.01</b>	0.60	0.96	0.99	0.79	0.59
MC(P)	0.54	<b>0.03</b>	0.33	0.60	0.07	0.39	0.83	<b>&lt;0.02</b>	0.73
CHMP	0.91	<b>0.04</b>	0.49	0.99	0.24	0.03	0.79	<b>0.04</b>	0.76
CHMC(P)	0.08	0.85	0.48	0.17	0.99	0.25	0.12	0.95	0.29
$H^2_c$	0	0	0.55	0.67	0.38	0.59	0.28	0	0.67
			(0.22)	(0.14)	(0.20)	(0.19)	(0.30)		(0.16)

\*) Source effects where CH is chamber, P is population, C(P) is clone-within-population, CHP is chamber by population interaction, CHC(P) is chamber by clone-within-population interaction, M is moisture, CHM is chamber by moisture interaction, MP is moisture by population interaction, MC(P) is moisture by clone-within-population interaction, CHMP is chamber by moisture by population interaction and CHMC(P) is chamber by moisture by clone-within-population interaction.

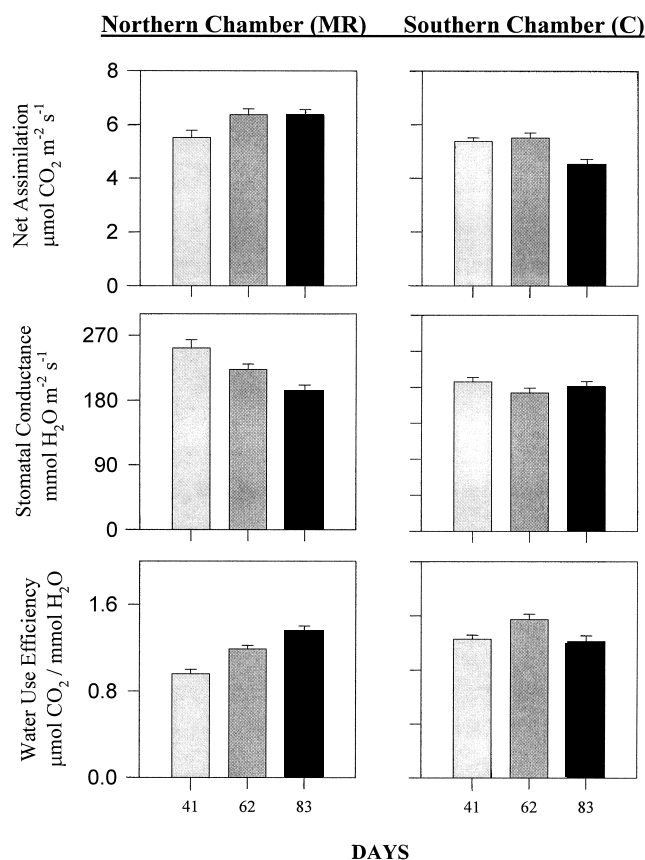


Figure 2. – Means (s.e.) for net assimilation ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), stomatal conductance ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and photosynthetic water use efficiency ( $\mu\text{mol CO}_2 \text{ fixed} / \text{mmol H}_2\text{O transpired}$ ), for trembling aspen clones (average of all populations) on each date in the 2 growth chambers.

heritabilities for  $G_s$  were quite high since clone-within-population accounted for 39.5%, 16.7% and 20.9% of the variation over the three test dates respectively, but was lower for both NA and WUE. Due to the significant interactions, subsequent analysis of variance calculations were done on an individual chamber basis for gain estimates.

In the individual chamber analysis more variation was explained by clone-within-population, thus heritability values were higher and less variable (Table 4). Chamber mean values by date and trait are presented in Figure 2. The decrease in NA in the Calgary (southern) chamber on Day 83 corresponds to a decrease in growth by this date (THOMAS et al., 1997) and, subsequently, a drop in the heritability values. In contrast, NA values for the Meander River (northern) chamber were similar on Day 62 and 83 despite a drop in  $G_s$  in this time period. Plants were still actively growing in the northern chamber at Day 83 (THOMAS et al., 1997).

Despite the significant chamber by clone-within-population interaction there was some consistency in clone performance between chambers, particularly by the end of the experiment (Day 83). A significant positive correlation was found for NA on Day 83 ( $r^2 = 0.32$ ,  $p < 0.01$ ), and for  $G_s$ , on Day 41 ( $r^2 = 0.40$  and  $p < 0.01$ ), 62 ( $r^2 = 0.24$  and  $p = 0.03$ ) and Day 83 ( $r^2 = 0.19$  and  $p = 0.06$ ) for WUE.

There was also evidence of good correlations between clone physiological performance and growth. In the northern chamber, there was a significant positive correlation between NA and both height and root dry weight for Day 83 (height:  $r^2 = 0.27$ ,  $p = 0.02$ , root dry weight:  $r^2 = 0.42$ ,  $p < 0.01$ ). In the southern chamber, height was positively correlated with NA on Day 62 ( $r^2 = 0.40$ ,  $p < 0.01$ ) and Day 83 ( $r^2 = 0.40$ ,  $p < 0.01$ ) while root dry weight and NA were positively correlated on Day 83 ( $r^2 = 0.53$ ,  $p < 0.01$ ).

There was no significant moisture effect in the combined chamber analysis (Table 3). However, the individual southern chamber analysis showed a significant moisture effect on Days 41 ( $p = 0.04$ ) and 62 ( $p = 0.03$ ) for NA, and WUE values also appear to track this trend ( $p = 0.09$ , Day 41 and  $p = 0.10$ , Day 62). On each test date trees in the wetter mix (Metromix) had higher NA.

Generally, there was little correlation between clone performance in the growth chambers and in the field. No correlation was found between clone means in the growth chambers and field for NA (Day 62: southern growth chamber versus June 1994 Calgary,  $r^2 = 0.002$ , Day 62: northern growth chamber versus June 1994 Meander River,  $r^2 = 0.02$ ). There

**Table 4.** – Source of variation, degrees of freedom (Df), p-values, percent variance (% Var) explained and heritabilities ( $H^2_c$ ) (s.e.) for the northern chamber (a, b, c respectively) and the southern chamber (d, e, f respectively) for net assimilation (NA), stomatal conductance to  $H_2O$  ( $G_S$ ) and water use efficiency (WUE), for Days 41, 62 and 83 of growth. Significant p-values are in bold.

a) Northern Chamber, NA							
Days		41		62		83	
Source*	Df	p-value	% Var	p-value	% Var	p-value	% Var
M	1	0.73		1.00		0.56	
P	4	0.23	8.3	0.55	0.0	0.50	0.0
C(P)	15	0.13	19.8	<b>0.02</b>	<b>31.2</b>	<b>0.04</b>	<b>28.9</b>
MP	4	0.89	0.0	0.07	12.8	0.33	2.3
MC(P)	15	<b>0.05</b>	<b>22.8</b>	0.35	3.8	0.41	2.4
Error	40		49.2		52.3		70.0
$H^2_c$		0.46 (0.23)		0.68 (0.15)		0.61(0.18)	
b) Northern Chamber, $G_S$							
Days		41		62		83	
Source*	Df	p-value	% Var	p-value	% Var	p-value	% Var
M	1	0.11		0.29		0.83	
P	4	0.42	0.8	<b>0.01</b>	<b>36.6</b>	0.86	0.0
C(P)	15	<b>&lt;0.01</b>	<b>76.7</b>	<b>&lt;0.01</b>	<b>32.0</b>	<b>0.01</b>	<b>35.7</b>
MP	4	0.94	0.0	0.57	0.0	<b>0.05</b>	<b>13.8</b>
MC(P)	15	0.17	4.2	0.79	0.0	0.37	2.9
Error	40		18.3		31.4		47.7
$H^2_c$		0.92 (0.04)		0.80 (0.07)		0.73 (0.13)	
c) Northern Chamber, WUE							
Days		41		62		83	
Source*	Df	p-value	% Var	p-value	% Var	p-value	% Var
M	1	0.57		0.90		0.84	
P	4	0.44	1.1	0.81	0.0	0.24	8.3
C(P)	15	0.14	18.5	0.09	19.3	<b>&lt;0.01</b>	<b>43.1</b>
MP	4	0.69	0.0	0.09	13.1	0.11	4.8
MC(P)	15	0.17	15.0	0.36	4.4	0.80	0.0
Error	40		65.4		63.2		43.9
$H^2_c$		0.44 (0.24)		0.52 (0.21)		0.80 (0.07)	
d) Southern Chamber, NA							
Days		41		62		83	
Source*	Df	p-value	% Var	p-value	% Var	p-value	% Var
M	1	<b>0.04</b>		<b>0.03</b>		0.27	
P	4	0.97	0.0	0.75	0.0	0.07	27.7
C(P)	15	0.11	16.0	<b>&lt;0.01</b>	<b>52.2</b>	0.27	6.6
MP	4	0.62	0.0	0.94	0.0	0.30	2.9
MC(P)	15	0.64	0.0	0.28	5.2	0.32	5.2
Error	40		84.0		42.6		57.6
$H^2_c$		0.43 (0.21)		0.80 (0.10)		0.28 (0.32)	
e) Southern Chamber, $G_S$							
Days		41		62		83	
Source*	Df	p-value	% Var	p-value	% Var	p-value	% Var
M	1	0.75		0.54		0.40	
P	4	0.87	0.0	0.51	0.0	0.47	0.0
C(P)	15	<b>&lt;0.01</b>	<b>60.5</b>	<b>&lt;0.01</b>	<b>55.7</b>	<b>&lt;0.01</b>	<b>50.3</b>
MP	4	0.54	0.0	0.22	1.5	0.52	0.0
MC(P)	15	0.43	0.9	0.96	0.0	0.08	13.6
Error	40		38.6		42.8		36.1
$H^2_c$		0.86 (0.07)		0.84 (0.06)		0.76 (0.11)	
f) Southern Chamber, WUE							
Days		41		62		83	
Source*	Df	p-value	% Var	p-value	% Var	p-value	% Var
M	1	0.09		0.19		0.35	
P	4	0.99	0.0	0.61	0.0	0.06	20.9
C(P)	15	<b>&lt;0.01</b>	<b>48.1</b>	<b>&lt;0.01</b>	<b>54.4</b>	0.25	14.8
MP	4	0.35	1.1	0.89	0.0	0.29	7.1
MC(P)	15	0.65	0.0	0.13	10.1	0.28	14.2
Error	40		50.8		35.5		42.9
$H^2_c$		0.79 (0.08)		0.80 (0.10)		0.45 (0.13)	

\*) Source effects where M is moisture (fixed factor therefore no variance estimate), P is population, C(P) is clone-within-population, MP is moisture by population interaction and MC(P) is moisture by clone-within-population interaction.

was also no relationship between field growth (caliper), and growth chamber NA, (Day 83: southern growth chamber *versus* June 1994 Calgary,  $r^2 = 0.12$ , northern growth chamber *versus* June 1994 Meander River,  $r^2 = 0.02$ ).

### 3.3 Gain estimates and clonal selection

Gain estimates are presented for NA only as this trait is highly dependent on  $G_S$  and is likely more directly related to yield (Table 5). Average gain estimates for the northern

chamber were quite consistent across the three dates (15.5% Day 41, 17.8% Day 62, 12.6% Day 83), whereas values fluctuate considerably in the southern chamber (5.9% Day 41, 22.4% Day 62, 5.2% Day 83). The phenotypic standard deviation (Table 5) is much smaller in the southern *versus* northern chamber for Days 41 and 83 as is the heritability estimate for Day 83. As with the growth/morphology data (THOMAS et al., 1997), there were large differences in gains among populations for NA. For example, on Day 62 in the southern chamber, gain estimates ranged from 7.9% (Lougheed) to 42.4% (Calgary) (Table 5e).

Since only four of six clones per population were tested for gas exchange in the growth chamber study, direct comparisons of relative clonal ranking cannot be made between the field and growth chamber experiment (Table 6). For the Dapp, Meander River and Little Buffalo populations, there was a high degree of consistency among chambers and test dates in terms of the top performing clone. However, Calgary and Lougheed populations were highly variable in this regard (Table 5).

## 4.0 Discussion

Despite the wide (9°) range in latitude and variation in sites (THOMAS et al., 1997, see Table 1) from which the populations were collected, more variation in performance existed at the clone-within-population than at the population level. This high level of clonal variation has also been found for morphological, growth and molecular traits in trembling aspen (CHELIAK and DANCİK, 1982; CHONG et al., 1994; EINSPAHR et al., 1967; JELINSKI and CHELIAK, 1992; LUND et al., 1992; REIGHARD and HANOVER, 1990; THOMAS et al., 1997).

If the quantitative genetic information about physiological traits is to prove useful in a tree improvement program, the relationships between carbon fixation and yield, and growth chamber *versus* field performance, must be established. So far, based on a variety of different poplar clones and hybrids, the relationship between growth performance and NA has been variable (BARIGAH et al., 1994; CEULEMANS and IMPENS, 1983; CEULEMANS et al., 1987; GATHERUM et al., 1967; HUBER and POLSTER, 1955; MICHAEL et al., 1990; OKAFO and HANOVER, 1978; REIGHARD and HANOVER, 1990). For aspen, in particular, previous studies reported a poor or negative correlation between both leaf and whole plant NA rates and productivity (OKAFO and HANOVER, 1978; REIGHARD and HANOVER, 1990). Our results, however, showed a strong positive correlation between net assimilation, on a leaf area basis, and height and root dry weight in the growth chamber experiment. Despite the encouraging results by CEULEMANS et al. (1987) showing a positive relationship between NA of 1-year old container plants and 5-year old field grown plants of selected interspecific poplar hybrids, we were unable to find a similar result. Correlations were not significant between growth chamber physiology and either field physiology or growth measurements.

In general, our growth chamber NA values were relatively low compared to some studies of field and growth chamber grown plants (GATHERUM et al., 1967; MONSON and FALL, 1989; NELSON and EHLERS, 1984; OKAFO and HANOVER, 1978; RODEN and PEARCY, 1993), but similar to values of BOURDEAU (1958) (6.3  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ) for greenhouse grown plants. It is possible that growth under non-saturating light conditions resulted in reduced photosynthetic capacity even under saturating light (NELSON and EHLERS, 1984; RODEN and PEARCY, 1993).

Differential gain estimates for NA between chambers may be a reflection of both a later bud-break and an earlier termina-

tion of growth in the southern chamber (THOMAS et al., 1997). Despite similar heritabilities between chambers for Days 41 and 62, the phenotypic standard deviation (Table 5) in the northern chamber was more than two times that of the southern chamber. On Day 83 the heritability value for the northern chamber was twice that of the southern chamber where most plants had set-bud already. The average gain values indicate that significant improvement in performance could be achieved with a relatively low selection intensity (1 in 4) and the positive correlation between height and NA means selection for one trait will not compromise selection for the other. If population were ignored (based on the genetic variation data) and the selection intensity were increased, substantial gains above the population mean would be possible with native sources of trembling aspen in Alberta.

Few studies have addressed questions about the quantitative genetics of physiological traits such as net assimilation, stomatal conductance or photosynthetic water use efficiency.

Those that have looked at physiological responses have typically been restricted to six or fewer hybrid clones (BARIGAH et al., 1994; GATHERUM et al., 1967; LUUKKANEN and KOZLOWSKI, 1972; MICHAEL et al., 1990; MONSON and FALL, 1989; NELSON and EHLERS, 1984; NELSON and ISEBRANDS, 1983), or if more clones (18 to 20) were used they failed to consider family structure (CEULEMANS et al., 1987; CEULEMANS and IMPENS, 1983). Despite more recent work on poplars and *Salix sp.* having looked at both intraspecific and interspecific variation in physiological traits (DANG et al., 1994; DUNLAP et al., 1993, 1995; PEZESHKI and HINCKLEY, 1988; RODEN and PEARCY, 1993), heritability and genetic gain estimates in poplars have been limited to either leaf traits or growth and yield characteristics such as height, diameter or tree volume (BARNES, 1969; EINSPHAR et al., 1963, 1967; LI and WYCKOFF, 1993; THOMAS et al., 1997; VAN BUIJTENEN et al., 1959). The heritability values available for gas exchange traits have, so far, been restricted to herbaceous or agricultural crop species (NIENHUIS et al., 1994;

Table 5. – Heritabilities ( $H^2_c$ ), phenotypic standard deviations ( $\sigma_p$ ), population means, clone mean range, best clone-within-population, and gain estimates (based on selection differential for a 1 in 4 selection) for net assimilation ( $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ) for Days 41, 62 and 83 in the northern and southern growth chambers.

a. Northern Chamber, Day 41					
$H^2_c = 0.46, \sigma_p = 1.65$					
POPULATION					
Item	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	6.8	5.8	4.3	4.8	5.9
Clone mean range	5.5-8.3	3.4-7.2	1.6-6.4	2.8-7.2	4.7-7.4
Best clone	4	4	3	4	4
Gain %	10.0	10.7	22.1	23.1	11.5
b. Northern Chamber, Day 62					
$H^2_c = 0.68, \sigma_p = 1.38$					
POPULATION					
Item	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	7.4	6.7	6.5	5.4	5.9
Clone mean range	5.0-8.8	5.6-7.9	5.4-8.0	3.7-7.9	4.6-7.3
Best clone	5	4	3	3	3
Gain %	12.8	12.9	15.3	31.7	16.4
c. Northern Chamber, Day 83					
$H^2_c = 0.61, \sigma_p = 1.35$					
POPULATION					
Item	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	5.5	6.9	6.6	5.8	7.0
Clone mean range	4.2-6.3	5.1-8.3	5.1-8.6	3.6-7.5	5.7-7.5
Best clone	1	1	3	2	3
Gain %	9.0	12.9	19.0	18.0	4.0
d. Southern Chamber, Day 41					
$H^2_c = 0.43, \sigma_p = 0.74$					
POPULATION					
Item	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	5.4	5.6	5.3	5.3	5.4
Clone mean range	5.1-6.0	4.7-6.3	3.9-6.5	4.8-5.7	5.0-6.0
Best clone	3	3	3	2	1
Gain %	4.8	6.1	9.9	3.4	5.2
e. Southern Chamber, Day 62					
$H^2_c = 0.80, \sigma_p = 1.38$					
POPULATION					
Item	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	5.2	5.4	5.9	5.1	6.0
Clone mean range	3.6-7.9	4.7-5.9	4.7-7.3	3.9-6.0	4.3-8.2
Best clone	3	2	2	3	3
Gain %	42.4	7.9	18.6	15.0	28.2
f. Southern Chamber, Day 83					
$H^2_c = 0.28, \sigma_p = 0.83$					
POPULATION					
Item	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	3.1	4.4	4.8	4.5	5.9
Clone mean range	2.5-3.6	3.5-5.1	3.5-5.8	3.5-5.7	5.1-6.7
Best clone	5	4	3	3	3
Gain %	4.1	4.8	6.0	7.3	3.8

Table 6. – Heritabilities ( $H^2_c$ ), phenotypic standard deviations ( $\sigma_p$ ), population means, clone mean range, and best clone-within-population for net assimilation ( $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$ ) for June 1993, August 1993, June 1994 and August 1994 for the northern (Meander River) and southern (Calgary) field sites.

a. Northern Field Site, June 1993					
$H^2_c = 0.33, \sigma_p = 0.84$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	2.4	1.5	2.2	2.4	1.9
Clone mean range	1.8-3.1	0.8-3.3	1.9-3.0	0.6-3.3	1.6-2.5
Best clone	5	2	3	3	4
b. Northern Field Site, June 1994					
$H^2_c = 0.51, \sigma_p = 2.13$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	9.1	8.7	8.4	8.7	9.3
Clone mean range	7.2-10.7	6.6-11.2	5.2-11.6	6.4-11.8	6.5-12.0
Best clone	4	5	5	6	5
c. Northern Field Site, August 1994					
$H^2_c = 0.41, \sigma_p = 1.35$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	5.4	3.0	3.8	4.6	4.1
Clone mean range	4.6-6.9	2.0-4.7	2.9-6.3	2.6-6.3	3.2-5.5
Best clone	5	3	4	2	2
d. Southern Field Site, June 1993					
$H^2_c = 0.54, \sigma_p = 2.53$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	8.7	10.7	9.7	8.7	9.1
Clone mean range	6.5-12.1	8.5-12.6	8.5-10.3	4.5-10.9	5.8-13.3
Best clone	4	6	6	5	4
e. Southern Field Site, August 1993					
$H^2_c = 0.12, \sigma_p = 1.24$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	15.3	14.6	12.9	13.5	12.6
Clone mean range	13.5-16.9	12.8-16.0	11.7-13.7	12.2-15.3	10.7-14.0
Best clone	1	1	6	6	2
f. Southern Field Site, June 1994					
$H^2_c = 0.33, \sigma_p = 1.29$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	13.5	13.9	13.2	14.7	14.0
Clone mean range	12.4-15.7	12.0-14.9	12.1-14.3	12.4-16.5	13.4-15.3
Best clone	2	5	5	5	3
g. Southern Field Site, August 1994					
$H^2_c = 0.31, \sigma_p = 1.51$					
Item	POPULATION				
	Calgary	Lougheed	Dapp	Little Buffalo	Meander R.
Overall mean	15.7	13.9	13.9	13.9	13.6
Clone mean range	14.6-16.7	10.7-15.3	12.7-15.7	12.9-14.7	12.0-16.8
Best clone	5	1	1	6	1

SRIVASTAVA and JAIN, 1994). The broad-sense heritability value for NA reported by SRIVASTAVA and JAIN (1994) for soybean (0.63) was similar to those we report for the northern chamber.

As has been shown with other poplar/alder species (PEZESHKI and HINCKLEY, 1988) under well watered conditions, the drier potting mix reduced NA and WUE but had no effect on  $G_s$ . In general, however,  $G_s$  values were somewhat lower than those previously reported for open grown mature aspen trees (MCCAUGHEY and IACOBELLI, 1994) and showed a decrease from Day 62 to 83 in the northern chamber while WUE increased. This is expected because stomatal closure decreases water loss more than it decreases  $\text{CO}_2$  gain.

Although our field study had limitations, the plants were essentially left to grow (with some weeding) much like in an operational field plantation. Low NA and  $G_s$  values for Meander River are primarily a result of very dry conditions in June of 1993 and an early onset of fall in August 1994. Condi-

tions in Calgary were relatively favourable whereas the Meander River site was a comparatively poor site with a heavy clay (79%) soil. It is not surprising that given these conditions, we failed to find a relationship between NA in the field and growth chamber performance after only two years. Further we made multiple instantaneous gas exchange measures on a single leaf per plant, over the season, whereas CEULEMAN's et al. (1987) significant relationship between greenhouse and field grown plants, was based on means of multiple measurements on each plant several times in a single month thus normalizing fluctuations (ISEBRANDS et al., 1988), which are inherent in these readings.

Despite the lack of correlation between field and growth chamber performance, the heritability and gain values indicate that a longer field trial is warranted to further examine this relationship. With a longer field trial, and somewhat more care of the plantation, relationships between carbon fixation and

yield, and field and growth chamber performance, may become apparent. If so, and selection intervals can be substantially reduced, intensive silvicultural practices (eg: herbivore control, watering, fertilizing) may prove economical at an operational scale with a relatively short rotation.

BOURDEAU (1958) found a significantly higher respiration rate and slightly lower NA in female *versus* male aspen clones and he suggested that female clones were relatively smaller (caliper). Further studies of this species, including both classic tree improvement traits and physiological traits, should incorporate consideration of sex.

#### 4.1 Conclusions

The native populations of trembling aspen in Alberta exhibit substantial genetic (clonal) variation in gas exchange traits which should respond well to moderate selection in a tree improvement program. The lack of population variation will allow for inclusion of more widespread groupings of populations and more intensive selection, if desired. Intensive silviculture, in the form of an agricultural forestry system, may prove economical if gains of 15% to 20% in yield could be achieved.

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Appendix 1. — Expected mean square table for individual chamber analysis.

Individual growth chamber analysis.	
Source of Variation*	Expected mean squares
M	$\sigma^2 + K1\sigma_{MC}^2 + K2\sigma_{MP}^2 + K5\phi_M$
Population (P)	$\sigma^2 + K1\sigma_{MC}^2 + K2\sigma_{MP}^2 + K3\sigma_C^2 + K4\sigma_P^2$
Clone(P) (C)	$\sigma^2 + K1\sigma_{MC}^2 + K3\sigma_C^2$
MP	$\sigma^2 + K1\sigma_{MC}^2 + K2\sigma_{MP}^2$
MC	$\sigma^2 + K1\sigma_{MC}^2$
Error	$\sigma^2$

\*) Source of variation as described previously in text.  
Note: K1 = 2, K2 = 8, K3 = 4 and K4 = 16.

## Variance Components, Heritabilities and Gain Estimates for Growth Chamber and Field Performance of *Populus tremuloides*: Growth Parameters

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### Summary

Variance components, heritabilities and gain estimates are reported for 29 clones (five populations) of *Populus tremuloides* from Alberta, Canada, which were grown (two years) at two field sites (northern and southern Alberta) and in two controlled environment chambers (for 12 weeks). Results indicated more variation at the clone-within-population level than the population level. There was more variation accounted for by both clone-within-population and population in the growth chamber than in the field. Caliper: clone-growth chamber: 32%, field: 22% to 7%; caliper: population-growth chamber: 12%, field: 2%; height: clone-growth chamber: 7% to 27%; bud-burst: clone-growth chamber: 26%; root-to-shoot ratio: clone-growth chamber: 17%. Broad-sense clone mean heritabilities for caliper were also lower in the field (0.56 to 0.29), than in the growth chambers (0.80). Heritabilities in the growth chamber were: Bud-burst = 0.72, height = 0.74, root-to-shoot ratio = 0.59. Expected gains, estimated based on growth chamber data, were: 9% to 38% across populations for bud-burst, 11% to 24% for caliper, 12% to 22% for final height, and 8% to 19% for root-to-shoot. This study indicates that significant improvement in traits is possible in trembling aspen with a 17% selection intensity but that care must be taken in determining the size of the region that will comprise the population where selections are made.

*Key words:* trembling aspen, heritability, gain, variance components, growth chambers, field, morphology.

*FDC:* 232.11; 165.3; 165.5; 56; 176.1 *Populus tremuloides*.

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### 1.0 Introduction

Trembling aspen (*Populus tremuloides* MICHAUX) is the most widely distributed native tree species in North America (BURNS and HONKALA, 1990) and is a major component of the boreal forest. Its distribution in western Canada is largely controlled by moisture availability, particularly at its southern limit (HOGG, 1994). With an ever increasing demand on this timber resource by forest companies in western Canada, a need for quantitative genetic parameter estimates, such as baseline values of heritabilities and gains, has arisen. The study results presented here should assist the recent initiatives of the Western Boreal Aspen Cooperative, which is establishing a tree improvement program for aspen in Alberta (LI, 1995).

As is true of any tree improvement program, there are many years of investment required prior to accruing any benefits and therefore it is crucial that selections and testing consider future needs and possible environmental changes. Current general circulation models predict increases in atmospheric CO<sub>2</sub> and temperature (BOLIN et al., 1986), as well as reductions in soil moisture for the Canadian boreal forest (MANABE and WETHERALD, 1986). HOGG (1994) has shown that the regions at low elevations, where the majority of the future harvesting will be focussed, will be most affected by these changes in western Canada. Thus, the question of performance under moisture stress conditions could become very important over the next 30 to 50 years. A few studies (JIANG et al., 1989; WU et al., 1992) have indicated that early performance under controlled conditions may be reflective of later field performance and if testing and selections can be made based on growth chamber trials,