Discovery of Geographically Robust Hybrid Poplar Clones

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Abstract

Hybrid poplar clonal growth in the states (regions) of Minnesota (MN), Indiana (IN), Michigan (MI), and New York (NY) USA was analyzed to discover 10 geographically robust (geo-robust) clones, all *P. deltoides* x *P. nigra* (D x N) hybrids previously tested and screened in MN, that were broadly adapted across latitudinal and longitudinal ranges of 9 and 20 degrees, respectively. The clonal effect for growth explained 25 to 36 % of the total variance, 2.5–4.1 times the clone x site interaction. Clone explained 24 to 46 % of total variation in canker occurrence on two sites. Genetic gain in growth was calculated relative to commercial check clones. Genetic gain in growth of geo-robust clones exceeded that of random clones by 24 to 44 %. Geo-robust clones and the best clones on each site were not significantly different on the MN sites, but best clones outperformed geo-robust clones on the other sites by 10 to 39 % genetic gain. Geo-robust clones grew faster than commercial check clones on all but the MI site. The reduction in genetic gain for growth due to using broadly adapted clones relative to the best clones has to be compared to the additional costs and benefits of multiple breeding zones.

Key words: *breeding zones, clonal adaptability, genotype x environment interaction, hybrid poplars, Populus*

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Introduction

Hybrid poplars are one of the primary dedicated energy crops needed to meet national targets for bioenergy in the USA (US DOE, 2016). However, investments in hybrid poplar programs are not expected to support narrow breeding zones or the tailoring of individual clones to specific sites (Nelson et al., 2018), ie., *specialist* genotypes (Zalesny et al., 2009). Accordingly, the emphasis of our hybrid poplar breeding program at the Natural Resources Research Institute (NRRI) has evolved so that we are now identifying families and clones that are fast-growing and broadly adapted to a range of soils, climates and geographic regions, ie., *generalist* genotypes (Zalesny et al., 2009). Fortunately, two studies preceding the one reported here provide evidence that this approach may be successful. Nelson et al. (2018, 2019) documented a strong clonal effect for growth rate that accounted for 3–4 times more of the variation than the clone x site (genotype x environment, G x E) interaction on a range of sites in Minnesota (MN, USA) and Indiana (IN, USA), and no change of rank between six sites in MN nor between two sites without irrigation or fertilization in IN.

The focus of the NRRI program is the *Populus deltoides* x *Populus nigra* (D x N, DN) cross. Both *P. deltoides* and *P. nigra* are riparian species and are within the *Aigeiros* section of *Populus*. Whereas *P. deltoides* is a North American species, *P. nigra* is a pan-European species that extends into Asia Minor. The *P.*

deltoides female parent of MN origin provides resistance to *Septoria* (*Sphaerulina musiva*) canker and adaptability to harsh northern temperate conditions. The *P. nigra* male parent imparts varying amounts of rust resistance. Moreover, the *P. nigra* component in D x N hybrids contributes rootability among individual D x N pedigreed selections so that unrooted cuttings can be used for plantation establishment, which is critical for commercial deployment. D x N clones developed in MN did surprisingly well in northwestern and southwestern IN field tests 5–9 degrees latitude south and 8–9 degrees longitude east of where the clones were developed in northern MN (Nelson et al., 2019), with significant representation in the top 10th percentile for growth. An even more surprising result of that study was that the clonal rank for growth rate did not change for 19 clones common to six test sites in northern MN and the two IN sites. Our hypothesis is that D x N hybrids with a female parent of MN origin can provide very broad adaptability to sites of wide latitudinal and longitudinal range. Cooperative studies in Michigan (MI, USA) and New York (NY, USA) being reported here with clones common to the previous MN and IN tests provide an opportunity to further test and possibly extend the adaptability inferences associated with our hypothesis. This meta-analytic study takes advantage of the greater power of clonal populations for detecting G x E interactions, in contrast to using families and seed sources (Bentzer et al., 1988; Yu and Pulkkinen, 2003) and the statistical robustness of non-parametric rank correlations.

Materials and Methods

Study design

The MN, MI and NY field tests were conducted using randomized complete blocks, while the IN field tests were designed as a completely random design within four cultural treatment blocks. The details of the MN and IN experimental designs are described in Nelson et al. (2018, 2019). The MI (Escanaba) and NY (Cornell, Tully) designs each entailed six blocks, and each clone was represented by a single-tree plot located randomly within each block.

Plant material

Clone selection for tests–

The clones in the MN and IN tests are described in Nelson et al. (2018, 2019). The clones in the MI and NY tests are listed in Table 1. Seventy-three percent of the clones in the MI and NY tests were D x N hybrids, 96 % of which had *P. deltoides* parents of MN origin and were bred, tested and screened in MN by the NRRI Hybrid Poplar Program. The NRRI breeding and testing process is diagrammed in Nelson et al. (2018). The commercial standard clone, NM6, was embedded in all trials as a check. Some trials also included two other commercial standard check clones, DN5 (IN, Cornell and Tully) and DN2 (MN, MI).

Table 1
Characteristics of clones established on the Escanaba, Cornell and Tully sites.

Clone ID	Cross	Female Parent Origin	Male Parent Origin	Common Clones to All Sites (inc IN)	Common Clones to All Sites Except IN
502.37	DxM	unknown	unknown	Yes	Yes
6300	DxN	D109	N964-1	No	No
21700	DxN	D109	N949-2	No	No
22700	DxN	D109	N949-2	No	No
23300	DxN	D109	N949-2	No	No
24400	DxM	D109	M1052-3	No	No
31500	DxN	D109	N964-1	No	No
41700	DxN	288-5	N944-4	No	No
20113214	DxN	D109	N949-2	No	No
22021008	DxN	D125	N40	No	Yes
22021009	DxN	D125	N40	No	No
22021018	DxN	D125	N40	No	No
22021021	DxN	D125	N40	No	No
22021048	DxN	D125	N40	No	Yes
22057002	DxN	D121	N40	No	No
22057006	DxN	D121	N40	No	No
22057030	DxN	D121	N40	No	No
22057032	DxN	D121	N40	No	No
22066086	Dx(TD)	180-1	50-197	No	No
22066094	Dx(TD)	180-1	50-197	No	No
22069011	DxN	180-1	N88	No	No
22090032	TDx(D)	52-225	D113	No	No
22091021	TDx(D)	52-225	D105	No	No
22091022	TDx(D)	52-225	D105	No	Yes
22091039	TDx(D)	52-225	D105	No	No
22091051	TDx(D)	52-225	D105	No	No
99001111	DxN	D121	N947-5	No	No
99007071	DxN	D121	N949-2	Yes	Yes
99007108	DxN	D121	N949-2	No	Yes
99007115	DxN	D121	N949-2	Yes	Yes
99007116	DxN	D121	N949-2	Yes	Yes
99008002	DxN	D121	N944-4	No	Yes
99008070	DxN	D121	N944-4	No	Yes
99008080	DxN	D121	N944-4	No	No
99008081	DxN	D121	N944-4	No	No
99008098	DxN	D121	N944-4	No	No
99037044	DxN	D200	N964-6	No	No
99037017	DxN	D200	N964-6	No	No
99037039	DxN	D200	N964-6	No	No
99037046	DxN	D200	N964-6	No	No
99037049	DxN	D200	N964-6	Yes	Yes
99037051	DxN	D200	N964-6	No	No
99037053	DxN	D200	N964-6	No	No
99038002	DxN	D200	N944-4	No	No
99038003	DxN	D200	N944-4	No	Yes
99038005	DxN	D200	N944-4	No	Yes
99038007	DxN	D200	N944-4	No	No
99038013	DxN	D200	N944-4	Yes	Yes
99038022	DxN	D200	N944-4	No	Yes
99038026	DxN	D200	N944-4	No	No
99038036	DxN	D200	N944-4	No	No
99059016	DxN	D123	N949-2	Yes	Yes
99059043	DxN	D123	N949-2	No	Yes
99098008	DxN	14 Crookston	N964-6	No	No
99105008	DxN	14 Crookston	N944-4	Yes	Yes
99105088	DxN	14 Crookston	N944-4	No	Yes
152x11861	DxM	*P. deltoides* '152'	*P. maximowiczii* '11861'	No	Yes
23001 3057	TDx(D)	52-225	D133	No	No
23059 32018	DxN	D110	SO N147	No	No
9732-11	DxN	D125	N946-2	Yes	Yes
9732-19	DxN	D125	N946-2	No	Yes
9732-24	DxN	D125	N946-2	Yes	Yes
9732-31	DxN	D125	N946-2	No	Yes
9732-32	DxN	D125	N946-2	No	No
D105	OP *P. deltoides*	UM OP family 904 mother	wind pollinated	No	No
D109	OP *P. deltoides*	UM OP family 400 mother	wind pollinated	No	No
D110	OP *P. deltoides*	UM OP family 908 mother	wind pollinated	No	No
D111	OP *P. deltoides*	UM OP family 908 mother	wind pollinated	No	No
D113	OP *P. deltoides*	UM OP family 400 mother	wind pollinated	No	No
D124	OP *P. deltoides*	UM OP family 400 mother	wind pollinated	No	No
D125	OP *P. deltoides*	UM OP family 400 mother	wind pollinated	No	No
DN164	DxN	unknown	unknown	No	No
DN2 (commercial check clone)	DxN	unknown	unknown	No	No
DN5 (commercial check clone)	DxN	unknown	unknown	No	No
NC14106	DxM	unknown	unknown	No	No
NM6 (commercial check clone)	NxM	unknown	unknown	Yes	Yes

D = *Populus deltoides*, N = *P. nigra*, M = *P. maximowiczii*, T = *P. trichocarpa*. OP = open pollinated

Plant propagation

Propagation methods for the MN and IN tests are described by Nelson et al. (2018, 2019). Rooted cuttings were used in the MI test and propagation methods were the same as for the MN test, as described by Nelson et al. (2018). Unrooted cuttings (20.3 cm in length) were utilized in the NY tests, with cuttings harvested in winter from dormant stools in a cutting orchard at the University of Minnesota North Central Research and Outreach Center (NCROC) nursery near Grand Rapids, MN, and stored at sub-freezing temperatures.

Study locations

The geographic coordinates and information on soils and climate for the MI and NY test sites are in Table 2. The MN and IN sites are described in Nelson et al. (2018, 2019). The latitudinal and longitudinal ranges for the MN, IN, MI and NY sites were 9 degrees and 20 degrees, respectively. All tests were established on agricultural soils.

Table 2
Location, soil and climate information for Escanaba, Cornell and Tully test sites.

Site	Escanaba	Cornell	Tully
County	Delta	Ontario	Onondaga
Nearest town	Escanaba, MI	Geneva, NY	Tully, NY
Latitude	45.7712	42.8810	42.7959
Longitude	-87.1992	-77.0119	-76.1177
Slope%	1 – 6	0 – 3	0 – 3
Soil texture	fine sandy loam	silt loam	gravelly loam
Soil pH	6.5	6.8	6.5
Soil particulate organic matter (%)	1.58	4.4	5
Soil bulk density (g/cm3)	1.43	1.17	1.25
Average high/low temperature (◦ C)	24.2/-13.9	26.6/-8.9	24.4/-12.2
Growing degree days during study (base 10 ◦C/30 ◦C)	1,967	2,653	2,256
Long term average precipitation (mm)	724	850	1164

Soil data from https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm
Climate data from https://www.usclimatedata.com/ U.S. Climate Data, three-decade (1981–2010) averages (National Centers for Environmental Information, NOAA).

Plantation establishment and maintenance

Establishment and weed control methods for the MN and IN sites are described in Nelson et al. (2018, 2019).

MI (Escanaba) site:

The clonal trial at Michigan State University Forest Biomass Innovation Center (FBIC) contained 56 clones and was established at 1.5 x 2.4 m spacing with containerized, pre-rooted 'mini' cuttings in July 2008, using dibble bars. To prepare the site, the remaining stubble from a winter wheat crop was sprayed with glyphosate and rototilled 10 days later. Vegetative buds on the containerized plants had already elongated at the time of planting. Accord® (glyphosate) herbicide was applied at 0.96 liters of active ingredient (a.i.) per hectare with a shielded sprayer, seven days post planting. Midway through the first two growing seasons, mechanical weed maintenance was done with a tiller and spring harrow. After the first two growing seasons and when plants were dormant (December 2009), a pre-emergent herbicide tank mix of Pendulum Aqua Cap® (pendimethalin) (2.26 a.i./hectare) and Scepter 70DG® (imazaquin) (0.29 liters a.i./hectare) was applied. Spot treatments of insecticide (*Bacillus thuringiensis* (BT), mixed as 9.9 ml dry powder per 3.79 liters) were applied as needed to control mourning cloak butterfly (*Nymphalis antiopa*) larvae.

NY (Cornell) site:

The clonal trial at Cornell University was located at Cornell AgriTech in Geneva, NY, contained 49 clones (identical to 49 of 50 clones in the Tully trial) and was established at 1.8 x 1.8 m spacing in June 2012. The 2011 wheat crop on this site while it was fallowed was sprayed with glyphosate in May 2012 to kill existing vegetation. The site was moldboard plowed and disked several times to prepare it for planting.

Dormant hardwood cuttings (20.3 cm in length) were hand-planted with a dibble bar. A pre-emergent herbicide was applied on the following day (June 22nd). The pre-emergent chemical product used was SureGuard® and was applied at the label rate of 420.32 grams per hectare (or 210/16 grams active ingredient per hectare). Due to the dry weather conditions, a drip-irrigation system was completed on the day of planting and was used to provide irrigation during the periods of dry weather in the first growing season as needed. A minor number of replants were needed and were made after three assessments in July 2012.

NY (Tully) site:

The clonal trial at the SUNY ESF Tully site contained 50 clones (49 identical to the 49 clones in the Cornell trial) and was established at 1.8 x 1.8 m spacing in late May 2012 with unrooted cuttings shipped at sub-freezing temperatures in ice chests from NRRI. The trial location had been fallow for two years prior to planting and was most recently planted with a winter rye cover crop in the fall of 2010. In late April 2012, the field was sprayed with glyphosate (2.2 kg ai ha^{-1}) and then rototilled ten days later.

Each dormant hardwood cutting (20.3 cm in length) was driven into the ground with a rubber mallet at a predetermined position. A single bud was left aboveground for each cutting.

The field was sprayed with a pre-emergent herbicide cap (Goal® 1.1 kg ai/ha) within one week of planting. A small amount of spot spraying was done with glyphosate during the first growing season to kill weeds that sprouted when the pre-emergence cap broke down or was disturbed. Initial

assessment of survival was conducted in June and July 2012. About 4–5 replacement cuttings per block were planted on June 11th. Initial survival measured in July 2012 was 98 %.

Measurements

Stand age at measurement was: MN and Cornell – 4 years, Escanaba and Tully – 5 years, IN – 3 years. Growth parameters used in ranking and genetic gain calculations were: MN – basal area (cm^2), IN – tree bole volume (cm^3), Escanaba and Cornell – DBH^2, Tully – tree height. Diameters were not measured at the Tully site; height was the only growth parameter measured there.

Canker scoring was not done at the IN or Cornell sites. Canker score had different bases for MN, Escanaba and Tully. The canker scoring system for MN, as described in Nelson et al. (2018), was as follows: 0 = cankers absent, 1 = cankers present but rare, 2 = cankers present with multiple areas of sunken, necrotic tissue on main bole or branches. For the Escanaba trial, the following scoring was used: 1 = no cankers (absent), 2 = slight cankering, 3 = moderate cankering, 4 = severe cankering. At the Tully site, the following scoring was used: 1 = no cankers (absent), 2 = cankers present but rare, 3 = obvious moderate to heavy incidence of *Septoria* (*Sphaerulina musiva*) canker(s) with typical sunken canker.

Statistical analyses

Growth parameters chosen for the ANOVA tests were: MN –>basal area (Nelson et al., 2018); IN –>total tree bole volume calculated from diameter and height as described in Nelson et al., 2019; Escanaba –>DBH, DBH^2 and tree height; Cornell –>DBH^2 and tree height; Tully –>tree height. For plantations of a given age and spacing, the allometric relationships between tree height, diameter, diameter squared, basal area and bole volume should theoretically produce approximately the same statistical test results for any of these four parameters. This assumption was confirmed by the ANOVA for DBH, DBH^2 and height at Escanaba and Cornell (see Table 5). Diameter squared (DBH^2) was used in clone ranking and rank similarity tests for Escanaba and Cornell to be as similar as possible to the MN and IN growth parameters, which utilized basal area and total tree bole volume, respectively. Tree height was also used for ranking clones on the Escanaba and Cornell sites to compare with the ranking using DBH^2. Canker scores were not taken for the IN and Cornell sites, and different canker scoring systems were used for MN, Escanaba and Tully, so canker scores cannot be directly compared for these sites. ANOVA tests were performed in R 3.5.1 by using function aov from the R basic package to achieve the sum of squares for clone types and errors. This test used one of the growth parameters as y variable and clone as x variable. To compute the variance components of growth parameters, a random effects model was fitted by the lmer function from the package of *lme4*, and clone was the only predictor and treated as a random variable. The site and site x clone effects could not be calculated for the Escanaba, Cornell and Tully sites due to differences in clone populations, measurement variables and age of measurement.

The canker scores for Escanaba and Tully are ordinal values and thus cannot be analyzed with ordinary ANOVA methods. The clone effect on canker score was analyzed with the ordinal logistic model fit method. Model fitting was performed in JMP Pro 14. Pseudo R^2 was calculated by McFadden's R squared measure.

The growth parameters and canker score were averaged for each clone within each site. The mean values of growth parameters were ranked from the largest = 1 to the smallest. Growth parameters and canker score were averaged for all clones within each site to calculate average site values. Spearman's Test of Rank Correlation was used to compare similarity of ranks between sites. Two Spearman's Tests were done to compare clone ranks between sites: 1) 12 clones common to all sites (MN, IN, Escanaba, Cornell and Tully); and 2) 27 clones common to all sites excluding IN. Spearman's Test was also used to compare clone rankings based on DBH^2 and tree height within the Escanaba and Cornell sites.

Genetic gains for growth rate were calculated as the increase in growth for clones over the mean growth of the commercial check clones, divided by mean growth of the check clones. The genetic gains for Tully could not be directly compared or combined with genetic gain values for the MN, IN, Escanaba and Cornell sites because only height was measured at Tully, and height has a much lower coefficient of variation than does DBH^2 (Table 3).

Table 3

Mean site growth parameters and canker scores for all clones on the Escanaba, Cornell and Tully sites.

Site	Age measured (years)	Spacing (m)	Parameter	Unit	Count (number of clones)	Mean	Standard Deviation (CV)
Escanaba	5	1.5 x 2.4	DBH	cm	56	5.59	1.66 (29.70%)
			DBH^2	cm^2	56	33.87	20.22 (59.70%)
			Height	m	56	7.55	0.98 (12.98%)
			Canker score		56	1.93	
Cornell	4	1.8 x 1.8	DBH	cm	49	8.65	1.42 (16.42%)
			DBH^2	cm^2	49	78.99	24.01 (30.40%)
			Height	m	49	7.87	0.72 (9.15%)
Tully	5	1.8 x 1.8	Height	m	50	8.55	1.03 (12.05%)
			Canker score	m	50	1.49	

CV = is coefficient of variation

No canker scoring for Cornell. Canker scores have different bases for Escanaba and Tully (see Measurements section for canker scoring systems), and so means cannot be directly compared. Canker scores are ordinal variables; standard deviation cannot be calculated.

Geographic regions in this study are defined as MN, IN, MI (Escanaba) and NY (Cornell, Tully). Inter-regional clones are identified as those within the upper 10th and/or 25th percentile in two or more sites in different regions. Geographically robust (geo-robust) clones are considered all inter-regional clones without cankering. Clonal groups for each site included geo-robust clones, best clones, and other (random) clones.

Growth and genetic gains were compared for the three clonal groups within each site. Comparisons used geo-robust clones present on a site and an equal number of top-ranked clones (best clones) and equal number of other (random) clones that are not geo-robust or best clones for the site. Inclusion of the other (random) clone group was to eliminate the possibility that estimated genetic gain for geo-robust clones was not due to chance, as the populations are generally improved. As variances for growth and genetic gain were unequal for clonal groups within each site (determined by box plots), we used the non-parametric Steel-Dwass method (JMP Pro 14) to detect differences between the clonal group means within each site.

Results

Means and analysis of variance

Survival at age of measurements averaged 87 % for the six MN sites (range 78 %–95 %) and 97 % for the two IN sites, and was 99 % for the Escanaba MN site, 97 % for the Cornell NY site and 95 % for the Tully NY site. Site means for growth rate parameters for the six MN field tests and the two IN field tests are in Nelson et al. (2018, 2019). The site means for growth parameters and canker scores at Escanaba, Cornell and Tully are in Table 3. Growth at Escanaba was substantially slower than the mean performance in MN and IN and at Cornell and Tully. Canker scoring was done differently at the MN, Escanaba and Tully sites. As a consequence, canker scores cannot be directly compared between sites. However, the mean canker scores in Nelson et al. (2018) and in Table 3 do indicate that cankers were not frequent in the MN, MI and NY sites on which canker incidence was monitored, although specific clones were heavily cankered on certain sites (Table 4). Table 4 shows growth parameter values and canker scores for each clone at Escanaba, Cornell and Tully. Growth rates and canker scoring for clones on the MN sites are in Nelson et al. (2018), and growth rates for IN are in Nelson et al. (2019).

Table 4
Mean clone values for growth parameters used for ranking growth and canker scores for the Escanaba, Cornell and Tully sites.

Clone	Escanaba			Cornell		Tully		
	Mean DBH^2 (cm^2)	Rank	Mean Canker Score	Mean DBH^2 (cm^2)	Rank	Mean Height (m)	Rank	Mean Canker Score
502.37	61.51	8	3.00	102.30	10	9.60	8	2.17
6300	18.11	44	1.17					
21700	15.62	50	1.33					
22700	22.91	32	1.40					
23300	28.26	26	1.00	72.66	29	8.76	31	1.17
24400	20.29	39	1.33					
31500	31.41	24	1.20					
41700	65.91	6	1.00	82.79	25	9.24	12	1.00
20113214				93.34	16	9.15	16	2.00
22021008	20.68	36	3.17	90.64	21	9.64	7	1.67
22021009	30.68	25	3.40					
22021018	52.63	12	3.80					
22021021				54.43	43	8.16	33	1.33
22021048	23.93	30	3.40	68.39	32	9.21	13	1.20
22021051	47.04	15	3.60					
22057002	27.90	27	4.00					
22057006	21.94	33	4.00					
22057030	32.07	23	2.17					
22057032	77.00	3	3.33					
22066086	21.38	34	3.50					
22066094	20.46	37	1.83					
22069011	43.16	16	1.67					
22090032	13.87	52	3.00					
22091021	25.60	29	2.80					
22091022	21.15	35	2.50	59.42	36	8.77	29	1.40
22091039				23.13	49	7.49	43	2.00
22091051				38.93	46	8.85	25	1.75
99001111	17.54	46	1.00					
99007071	17.83	45	3.60	120.18	1	9.27	10	2.00
99007108	60.98	9	1.00	55.07	41	8.06	34	1.17
99007115	83.81	1	1.00	86.33	23	8.32	32	1.50
99007116	15.70	49	1.17	87.29	22	9.13	17	1.50
99008002	56.84	10	2.67	103.05	9	8.94	23	1.83
99008070	34.17	22	1.00	75.40	27	7.93	36	2.33
99008080	23.92	31	1.50					
99008081				100.98	11	9.26	11	1.33
99008098				103.65	8	9.13	18	1.33
99037017				106.55	5	9.93	3	1.17
99037039	14.87	51	2.00					
99037044	10.09	54	1.50	58.35	37			
99037046				90.86	20	9.69	5	1.67
99037049	5.81	56	1.00	57.27	38	9.21	14	1.33
99037051				99.62	13	9.95	2	1.17
99037053	19.38	42	2.33					
99038002				74.52	28	8.03	35	2.50
99038003	55.23	11	1.00	105.31	7	9.98	1	1.17
99038005	50.17	14	1.17	97.30	15	8.95	22	1.33
99038007				71.74	30	8.79	28	2.33
99038012	7.96	55	2.00					
99038013	74.57	4	1.00	100.40	12	7.79	39	2.00
99038022	18.58	43	1.00	79.95	26	8.81	27	1.17
99038026				92.99	17	9.89	4	1.00
99038036	16.69	48	1.00					
99059016	77.25	2	1.00	97.85	14	8.97	21	1.00
99059019	19.65	41	1.40					
99059043	19.81	40	1.17	62.49	35	7.67	40	1.00
99098008	20.45	38	1.00					
99105008	51.74	13	1.17	54.40	44	6.88	47	1.50
99105088	13.51	53	1.00	39.56	45	6.29	49	1.00
152x11861	63.75	7	2.83	69.57	31	9.51	9	2.20
23001 03057						5.14	50	1.50
23059 32018						7.84	38	2.20
9732-11	27.66	28	2.20	112.43	3	9.04	19	2.00
9732-19	41.49	17	1.83	116.67	2	9.68	6	1.17
9732-24	36.73	20	1.60	106.10	6	9.18	15	1.17
9732-31	16.85	47	1.17	110.37	4	8.87	24	1.83
9732-32				54.79	42	8.81	26	1.17
D105				56.22	39	7.91	37	1.00
D109				84.96	24	7.67	41	1.00
D110				37.42	48	7.30	45	1.33
D111				37.63	47	6.79	48	1.00
D113				67.73	34	7.22	46	2.00
D124				92.57	19	7.48	44	1.33
D125				68.06	33	8.77	30	1.00
DN164	34.20	21	2.17					
DN2	40.08	18	2.75					
DN5				56.19	40	7.64	42	1.33
NC14106	38.68	19	1.20					
NM6	67.29	5	1.33	92.78	18	9.04	20	1.00

No canker scoring for Cornell. Canker scores have different bases for Escanaba and Tully (see Measurements section), and so cannot be directly compared.
The basis for clone rankings for MN is basal area (see Nelson et al., 2018), whereas in IN it was tree bole volume (see Nelson et al., 2019). **Commercial check clones DN2, DN5 and NM6 are in bold.**

Table 5
ANOVA and variance components for growth variables for the Escanaba, Cornell and Tully sites.

Site	Variable	Unit	Parameters	Degrees of freedom	Sum of Squares	Variance components	Variance components, %
Escanaba	DBH	cm	Clone	55	846	1.859	27.73%
			Error	262	1268	4.844	72.27%
	DBH^2	cm^2	Clone	55	127415	276.8	27.15%
			Error	262	194651	742.8	72.85%
	Height	m	Clone	55	288.16	0.604	24.70%
			Error	262	480.56	1.841	75.30%
Cornell	DBH^2	cm^2	Clone	48	164179	436.5	34.58%
			Error	243	200612	825.7	65.42%
	Height	m	Clone	49	149	0.3848	33.36%
			Error	248	191	0.7686	66.64%
Tully	Height	m	Clone	49	258	0.6368	27.60%
			Error	235	389	1.6702	72.40%

Results from the analysis of variance for growth on the Escanaba, Cornell and Tully sites are shown in Table 5. The growth parameters showed significant variations among clones, which explained around 25–35 % of total variance at Escanaba, Cornell and Tully. This is comparable to 28 % for the MN sites and 36 % for the IN sites for growth. Variance components for all four regions indicate a strong clonal effect on growth rate. DBH, DBH^2, and height had similar variance components for the clone effect at the Escanaba and Cornell sites (Table 5), suggesting that the use of DBH or DBH^2 at Tully would have given a similar clone effect with DBH or DBH^2 as the measured variable.

The significant pseudo R^2 values (Table 6) for both the Escanaba and Tully sites indicate a significant clone effect on canker incidence. However, the pseudo R^2 for Tully is only 0.24, which suggests that most of the variation in canker incidence on that site is due to error. The pseudo R^2 for Escanaba is 0.46, indicating that variance in canker score is equally explained by clone and error on that site.

Table 6
The ordinal logistic model fit for canker score using clone as the predictor variable for the Escanaba and Tully sites.

Site	Predictor Variable	Degree of Freedom	Prob>ChiSq	Pseudo R^2
Escanaba	Clone	55	<0.0001	0.4633
Tully	Clone	49	<0.0001	0.2378

Model fitting was performed in JMP Pro 14. Prob < 0.05 indicates a significant fit.
Pseudo R^2 was calculated by McFadden's R squared measure.

Clone ranks

Clonal ranks for growth rate on the MN and IN sites are in Nelson et al. (2018, 2019). Clonal ranks for growth rate at Escanaba, Cornell and Tully are shown in Table 4. Except for NM6 ranking within the top 10th percentile at Escanaba, the three commercial check clones (NM6, DN2 and DN5) did not rank higher than the lower 68th percentile on any site. Spearman's Test results for the between-site comparisons are shown in Table 7. For the 12 clones common to all sites, clone ranks were not correlated at the $p < 0.05$ level for any site combinations. Clonal ranks in the 12-clone test for MN versus IN and Escanaba versus Tully were close to significant ($p > 0.05$, but < 0.10), although the Escanaba versus Tully rank coefficient was negative, indicating a reversal of rank order. In the 27-clone Spearman's Test for clones common to all sites except IN, only Cornell and Tully ranks were significantly correlated. Another Spearman's Test was done for rankings for DBH^2 and height within the Escanaba and Cornell sites. The rankings for DBH^2 and height were significantly correlated for both sites (Spearman's correlation coefficients 0.66–0.70, significant at $p < 0.001$), indicating that ranking based on height (Tully) is comparable to ranking based on DBH^2 (Escanaba and Cornell). As reported in Nelson et al. (2019), for the 19 clones common to the MN and IN sites, the Spearman's Rank Coefficient was positive and significant at the $p < 0.0001$, indicating no significant rank change in this comparison.

Table 7
Spearman's Tests of Rank Correlation for 12 clones common to all sites (MN, IN, Escanaba, Cornell and Tully) and for 27 clones common to all sites except IN. Growth parameters used for ranking were basal area for MN, tree bole volume for IN, DBH^2 for Escanaba and Cornell and tree height for Tully.

12 clones common to all sites:

Variable	MN	IN	Escanaba	Cornell	Tully
MN		**0.52**	-0.02	0.24	-0.01
IN	**0.52**		0.17	0.41	-0.04
Escanaba	-0.02	0.17		-0.09	**-0.50**
Cornell	0.24	0.41	-0.09		0.34
Tully	-0.01	-0.04	**-0.50**	0.34	

All p are > 0.05 for the 12-clone test (non-significant). Coefficients in bold in the 12-clone test have $p > 0.05$ and < 0.10.

27 clones common to all sites except IN:

Site	MN	Escanaba	Cornell	Tully
MN		-0.19	0.25	0.17
Escanaba	-0.19		0.19	0.030
Cornell	0.25	0.19		0.57*
Tully	0.17	0.030	0.57*	

Coefficients asterisked in the 27-clone test are significant at $p < 0.05$.

Identifying broadly-adapted clones

Inter-regional and geo-robust clones are identified in Table 8, with 10 clones being geographically robust. All of the geo-robust clones are D x N hybrids with MN *P. deltoides* female

parents, and all were tested and screened in MN. Seven of the geo-robust clones are females, three are males.

Table 8
List of clones in top 10th or 25th percentile for growth rate on two or more sites. MN is mean rank of six sites. IN is mean rank of two sites. *are inter-regional clones. Clones in bold are *geographically* robust (geo-robust) clones.

Clone (gender)	MN 10th	MN 25th	IN 10th	IN 25th	Escanaba 10th	Escanaba 25th	Cornell 10th	Cornell 25th	Tully 10th	Tully 25th	Cankered
99007071*(F)			X				X			X	yes
9732-19 (F)							X			X	no
9732-11* (F)		X					X				no
99037017(Unk)							X		X		no
9732-24*(F)	X							X			no
99038003*(F)	X					X		X	X		no
99008002*(M)						X			X		no
502.37* (M)						X		X	X		yes
99008081 (F)								X		X	no
99038013* (F)				X				X			no
99059016* (M)	X				X						no
41700* (F) (Aka 20173417)		X			X					X	no
152x11861*(M)						X				X	yes
99038005* (F)	X					X					no
99038022* (F)	X		X								no
99007116* (M)		X		X							no

Notes: *Inter-regional clones* are those within the top 10th and/or 25th percentile in growth rate in two or more regions out of the four regions. *Regions* are MN, IN, MI (Escanaba) and NY (Cornell, Tully). *Cankered* is a clone with moderate to heavy cankering on one or more sites in this study or in our experience in other field tests. **Geographically robust clones are inter-regional clones without cankering.** Gender: F = female, M = male, Unk = unknown = florals absent or not flowering at time of determination. Clone 41700 is numbered 20173417 in some previous reports. Clone values for MN and IN are from data in Nelson et al. (2018, 2019).

Genetic gains for geo-robust and best clones for each site

Genetic gains in growth relative to commercial check clones for geo-robust and best clones on each site are presented in Table 9. Specific clones used in the analysis for Table 9 are listed in Online Resource 1. Because all populations deployed in the trials were generally improved, and in order to eliminate the possibility that the genetic gains for the broadly adapted clones were not simply due to chance, we also compared genetic gains or reductions in growth for other (randomly chosen) clones not in the geo-robust and best clone populations (Table 9). In four out of five sites, the other (random) clones had a negative genetic gain, Cornell being the exception. For the sites for which genetic gain can be directly compared (MN, IN, Escanaba, Cornell), genetic gains for geo-robust clones exceeded that for the random clones by 24 to 44 %. Best clones and geo-robust clones were not significantly different in genetic gain and were significantly higher than other clones for the MN sites. For the IN sites, genetic gain for best clones was significantly higher (10–39 %) than for geo-robust clones, which in turn was higher than for other clones. Means for all sites showed a progression from best clones (highest genetic gain), geo-robust clones (intermediate genetic gain) to other clones (lowest genetic gain and negative for four out of five sites). However, except for MN and IN, geo-robust clones were not significantly different from other clones according to the Steel-Dwass test. But the trends in Table 9 are clear, so that the lack of rejecting the null hypothesis for the Escanaba, Cornell and Tully sites may be due to the small N (10) in each test not providing enough power to detect differences due to the large variance in the other clones category in all except the Escanaba site. The synthesis of all data indicates that the selection method for identifying geo-robust clones is valid.

Table 9
The mean, standard deviations and genetic gains for growth versus commercial check clones among three clone groups for five site groups. The mean values were compared among three clone groups by the non-parametric Steel-Dwass method in JMP Pro 14. Data designated with different letters are significantly different from other clone groups within same site.

Site (N)	Clone type	Growth parameters				Genetic gain, %	
		Name	Unit	Mean	Standard deviation	Mean	Standard deviation
MN	Best clones	Basal area	cm^2	94.18^A	5.63	49.4^A	9.06
(10)	Geo-robust clones	Basal area	cm^2	88.36^A	13.05	40.1^A	20.73
	Other clones	Basal area	cm^2	60.73^B	18.40	-3.7^B	29.25
IN	Best clones	Tree volume	cm^3	14620^A	1602	66^A	18.25
(7)	Geo-robust clones	Tree volume	cm^3	11282^B	1602	28^B	18.02
	Other clones	Tree volume	cm^3	8165^C	1939	-7.29^C	22.11
Escanaba	Best clones	DBH^2	cm^2	68.86^A	8.81	28.3^A	16.31
(10)	Geo-robust clones	DBH^2	cm^2	47.86^{AB}	22.28	-10.7^{AB}	41.66
	Other clones	DBH^2	cm^2	24.90^B	12.51	-47.9^B	24.04
Cornell	Best clones	DBH^2	cm^2	108.66^A	6.09	45.7^A	8.29
(10)	Geo-robust clones	DBH^2	cm^2	97.25^B	10.67	29.7^B	15.22
	Other clones	DBH^2	cm^2	78.49^B	21.29	5.5^B	28.57
Tully	Best clones	Height	m	9.71^A	0.23	16.5^A	2.80
(10)	Geo-robust clones	Height	m	8.91^B	0.62	6.5^B	8.10
	Other clones	Height	m	8.11^B	1.21	-2.6^B	14.38

N is sample size for each clone group, equal to number of geo-robust clones on site. Check clone IDs: MN = DN2, NM6; IN = DN5, NM6; Escanaba = DN2, NM6; Cornell = DN5, NM6; Tully = DN5, NM6. Escanaba, Cornell and Tully are single sites. MN has 6 sites, described in Nelson et al. (2018). IN has 2 sites, described in Nelson et al. (2019).
Comparisons in table use geo-robust clones present on site and equal number of top-ranked clones (*best clones)* and equal number of other (random) clones that are not geo-robust or best clones for the site.

Discussion

According to genetic theory and empirical evidence, poplar hybrids are more likely to exhibit broad adaptability than pure natural species due to heterosis and increased heterozygosity (Lerner, 1954; Mitton and Grant, 1984; Gillespie and Turelli, 1989; Li and Wu, 1996; Wu, 1998; Zanewich et al., 2018). Recently, Zanewich et al. (2018) provided corroborating physiological evidence for this hypothesis by showing that heterosis in poplar hybrids is tied to phenotypic stability or environmental adaptability, with heterozygosity providing metabolic diversity that leads to better performance than parental pure species, particularly under suboptimal conditions. This body of

literature foretells and underpins the identification of the broadly adapted genotypes reported here.

The variation in mean growth performance between sites reflects the high plasticity (low stability) of hybrid *Populus* genotypes (Nelson et al., 2018; Yu and Pulkkinen, 2003). This result is in line with the concept that riparian tree species such as *P. deltoides* and *P. nigra* may display high genetic variation and phenotypic plasticity to buffer against the spatial and temporal heterogeneity of the riparian habitat (Guet et al., 2015). As explained in Nelson et al. (2018), plasticity/stability of clonal populations do not necessarily equate to G x E interaction, as the latter is determined by both clone rank changes and relative performance of clones on different sites, also known as variance-changing interaction (Des Marais et al., 2013). If growth rates of individual clones change substantially between sites but the response slopes are relatively parallel, G x E will be minimized.

A useful approach in further studies of clones adapted to wide geographic ranges would be to monitor phenology (shoot initiation and growth cessation). Such studies could lead to a better understanding of the physiological mechanisms behind the geographic robustness of these clones and refinements in clonal selection (Nelson et al., 2019). Another approach to elucidating the mechanisms of clonal site specificity is to correlate clonal performance with physiography and growing conditions, such as the work of Ghezehei et al. (2019).

The clonal effect for growth was strong and similar across all four regions (MN, IN, MI and NY) and was 2.5 to 4.1 times the clone x site (G x E) interaction for the MN and IN sites, respectively (Table 5) (Nelson et al., 2018; Nelson et al., 2019). The significant clonal effect on cankering at the Escanaba and Tully sites (Table 6) was expected from our experience with clone trials elsewhere over the last two decades.

The clonal populations tested here in all four regions were generally improved by the NRRI poplar program breeding process (Nelson et al., 2018), with only the Escanaba site having a commercial check clone (NM6) in the top 10th or 25th percentile for growth. Part of this improvement is undoubtedly the elimination of cold-susceptible clones and some diseased clones through prior screening in northern MN. For all sites except Escanaba, the commercial check clones ranked only within the lower 68th percentile, and as low as the lowest 18th percentile, for growth (Table 4) (Nelson et al., 2018; Nelson et al., 2019). Similarly, Zalesny et al. (2009) reported superior growth for another, earlier generation of experimental clones over that of commercial check clones in field tests encompassing sites in Minnesota, Wisconsin and Iowa ranging from 45.7 to 42.0 degrees N latitude and 95.2 to 89.4 degrees W longitude.

There have been a few hybrid poplar clone tests with at least 40 clones per test across broad geographic regions, including Riemenschneider et al. (2001), Rae et al. (2008), Zalesny et al. (2009) and the Nelson et al. (2018, 2019) studies tied to this paper. Rae et al. (2008) primarily used F_2 genotypes and thus is not comparable to the other cited studies, which used F_1 clones.

The clonal composition of the Riemenschneider et al. (2001) and Zalesny et al. (2009) studies was very different from that of the present study. Those studies included disparate clone collections from a broad area of the Midwest USA. While D x N hybrids selected and tested in MN predominated in our study, out of the 43 genotypes tested by Riemenschneider et al. (2001) and the 187 evaluated by Zalesny et al. (2009), only two were D x N hybrids. Pure *P. deltoides* clones (non-hybrids) predominated in both of those earlier studies, while the field trials in our study included no pure *P. deltoides* in the MN and Escanaba tests, whereas they represented 2 % of the genotypes used in the IN study and 14 % of those used at Cornell and Tully. These differences in clone populations compromise our ability to make comparisons with the earlier studies.

In contrast to the present study and Nelson et al. (2018, 2019), Riemenschneider et al. (2001) reported a clone x location effect of 20.6 % for their earlier generation of clones, nearly double that of the clone effect for three sites, one each in MN (latitude 45.7 degrees N), WI (latitude 43.3 degrees N) and IA (latitude 42.0 degrees N). Likewise, Zalesny et al. (2009) stated that: "G x E interactions governed biomass production." In contrast to our study, Zalesny et al. (2009) included southern genotypes, which experienced winter dieback on the MN test site, and clones from the section *Populus* (the aspens), factors that are likely to have caused an increased G x E interaction. Clone mean rank correlations (Pearson's Correlation Coefficients) across sites in that study were all positive, ranged from 0.29 to 0.81 and were significant for 11 of 12 site comparisons. Significant ($p < 0.01$) Spearman's Coefficients of Rank Correlation between sites in our studies were: MN (6 sites) = +0.38 to +0.72; IN (2 sites) = +0.47 to +0.57; and Cornell and Tully (clones common to all sites except IN; see Table 7) = +0.57. While these Pearson's and Spearman's coefficients cannot be directly compared, the range of values between our studies and Zalesny et al. (2009) are broadly similar. Obviously, the genetic composition of the clonal populations will affect variances and ranks. Zalesny et al. (2009) did identify individual clones that were stable across sites, consistent with the idea of safely deploying a limited number of genotypes broadly adapted to heterogeneous growing conditions within and across regions, as we hypothesize.

The significant Spearman's Rank Coefficient between the Cornell and Tully sites for the 27 clones common to all sites except IN (Table 7) is not surprising, given the close proximity of these field plots. As explained in Nelson et al. (2019), the similarity of ranks for the MN and IN sites was unexpected. The results in the present study show that both population rank similarities and individual clone performance must be considered in identifying geo-robust clones. For example, even though clonal ranks were similar for the MN and IN sites, only two clones (99038022 and 99007116) were in the top 25th percentile for growth in both of these regions (Table 8).

Five of the 10 geo-robust clones (99038003, 99038013, 99038005; 9732-11 and 9732-24) are from only two full-sib D x N families (038, 032), indicating the family genome level and additive genetic variation (Berguson et al., 2017) are important in deriving geo-robust clones. However, it is unknown whether broad adaptability is strongly inherited, as heritability of growth stability, one component of adaptability, has been

shown to be low for other crops (Becker and Leon, 1988). Two of the geo-robust clones (99059016 and 9732-24) were identified as stable clones (Finlay and Wilkinson, 1963) across the six MN sites (Nelson et al., 2018), further evidence that the methods we used here for identifying geo-robust clones have validity.

Although genetic gains are substantial with deployment of broadly adapted clones, there is a significant growth cost in genetic gain in deploying geo-robust clones instead of the best clones in each region or site (Table 9), an expected pattern from a genecology perspective (Farmer, 1996). As surmised from Zalesny et al. (2009) and the provenance literature for *P. deltoides* and other northern temperate tree species (Eldridge et al., 1972; Ying and Bagley, 1976; Loehle, 1998), the genetic gain for geo-robust clones was highest for the MN sites, as the *P. deltoides* clonal parents were almost all from MN provenances, and the hybrid clones were screened and tested in that state. If we assume that the best clonal performance on each site was at the low end of improvement possible using a site-specific (narrow breeding zone) genetic improvement approach, we can conclude that the reductions in genetic gain over commercial check clones due to the use of geo-robust clones indicated in Table 9 are the minimums. The use of geo-robust clones on the Escanaba site actually produced a negative genetic gain, but all other sites exhibited large genetic gains for these clones, albeit less than the best clones for the sites. The genetic gain values for Tully cannot be compared directly with the other sites because tree height has a much lower coefficient of variation than do the other growth parameters. Excluding Tully, the geo-robust clones population averaged 21.8 % genetic gain, while the equal number of best clones averaged 47.4 %. If we assume Escanaba is an outlier and exclude it as well as Tully, the comparison reveals a 32.6 % genetic gain for geo-robust clones and 53.7 % for the best clones. The average ranks over all sites for the populations are: geo-robust clones = top 31th percentile, best clones = top 11th percentile.

Some reduction in genetic gain due to the use of broadly adapted clones was expected for our populations, as clone x site interaction was 9 to 11 % of total variation for the MN and IN sites, even though this is only 25 to 39 % of the amount of variation explained by clone (Table 5) (Nelson et al., 2018; Nelson et al., 2019). Under these genetic strictures, attempts to reduce G x E interaction will likely result in some reduction in genetic gain compared to using clones that are tailored to specific sites (Nelson et al., 2018).

From a practical investment perspective, the reduction in genetic gain for growth due to using broadly adapted clones has to be compared to the additional economic costs and benefits of multiple breeding zones. The costs of breeding *specialist* clones (Zalesny et al., 2009) and the concomitant necessity of narrow breeding zones are not trivial considerations when capital is limited.

There are two most important conclusions from this study. We have identified specific clones that can be deployed and may perform well over a wide geographic area delineated in this paper, with significant genetic improvement over current commercial clones. The results also suggest that one cost-effective approach may be a breeding and selection center in MN, with satellite testing of *Populus* from the MN program at strategic sites throughout much of the Midwest and Northeast USA.

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