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Allometric Relationships for Aboveground Woody Biomass Differ Among Hybrid Poplar Genomic Groups and Clones in the North-Central USA

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Abstract

Allometric biomass equations were developed based on harvests of 198 trees from 15 field sites in the north-central USA, with the trees representing 4 hybrid poplar genomic groups and a total of 11 clones within these groups. Specifically, equations were developed to describe woody (branch + stem) total dry weight (TDW) as a function of diameter at breast height (DBH), along with hypothesis tests of differences among genomic groups and clones for equation intercepts and slopes. Inclusion of groups or clones improved model fit ($r^2 = 0.90$ or 0.91, respectively) compared to the generic model consisting of only DBH ($r^2 = 0.85$). Differences in equation parameters translated into significant differences among groups and clones for estimated TDW when compared at mean DBH (20 cm). Equations were also developed to describe branch-to-stem weight ratio (BSR) as a function of TDW and tree height (H), also with hypothesis tests of differences in intercepts and slopes among genomic groups and clones. Inclusion of genomic groups somewhat improved model fit ($r^2 = 0.57$) compared to the generic model consisting of only TDW and H ($r^2 = 0.53$), whereas model fit improved more markedly with the inclusion of clones ($r^2 = 0.75$). Our results indicate that group- and clone-specific equations (rather than generic ones) are warranted for hybrid poplars, and that group-specific equations are adequate for estimating TDW whereas clone-specific equations are more appropriate for estimating BSR.

Keywords Allometric equations · Bioenergy · Biofuels · Phytotechnologies · *Populus* · Short-rotation woody crops

Introduction

Short-rotation woody crops (SRWCs), such as *Populus* species and their hybrids (hereafter referred to as hybrid poplars), are an integral component of environmental sustainability portfolios worldwide [1, 2], and this is especially true in the north-central USA [3–5]. Hybrid poplar is one of several purpose-grown woody feedstocks used for bioenergy, biofuels, and bioproducts [6]. The production of hybrid poplar biomass is also vital for the success of phytotechnologies such as phytoremediation wherein soil contaminants are taken up and sequestered in root, wood, and leaf tissues [7–9]. Similarly, hybrid poplars grown in riparian management systems have provided ecological benefits along with marketable products [10]. Through genetic improvement efforts, an array of hybrid poplar genotypes have been developed and may be selected for deployment at a given site based on knowledge of genotype × environment interactions [11]. Biomass production is a logical metric for selection, as the goods and services derived from woody crops generally scale with tree biomass. However, measuring tree biomass is often resource-intensive and involves destructive sampling which may be undesirable in some situations; thus, researchers and resource managers are often reliant upon allometric (i.e., growth of stems and branches relative to the entire tree) equations to estimate woody biomass from easier, non-destructive measurements such as diameter at breast height (DBH).

Equations for total aboveground biomass have been developed at various resolutions for genotypes used in certain geographic regions. For example, equations have been developed for broad species groups in the USA [12, 13], hybrid poplars

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in general in Sweden [14], and specific genomic groups (trees of similar parentage) and clones (trees of identical genetic make-up) in Canada [15–17]. In the north-central USA, however, development of biomass equations has been limited to relatively few hybrid poplar clones [18–20]. Meanwhile, a generalized aboveground biomass equation based on several older clones [21] has been widely used to estimate total aboveground biomass for both older and newer genotypes in the region [11, 22]. It has been unclear, however, whether the newer genotypes adhere to the same allometric relationships or are sufficiently different to warrant unique equations.

In addition, information about biomass allocation between branches and stems is largely lacking for both older and newer clones in the region. At the relatively wide spacings that are typical of the region (often from 2 × 2 to 3 × 3 m), the ratio of branch-to-stem weight tends to increase with tree size during the first few years of establishment while the trees are essentially open-grown [19], and then decreases with time as canopy closure is reached and competition for light results in allocation primarily to vertical growth [23]. In this way, competition produces changes in tree form, such as the ratios of diameter-to-height [24] or height-to-stem area [23]. To the extent that such changes in tree form coincide with changes in branch-to-stem ratio [25], the former can be useful as a predictor of the latter. For branch-to-stem models that already contain a covariate for tree size (e.g., total aboveground biomass as in Headlee et al. [19]), the addition of height as a covariate equates to adding a metric of tree form, as the relationship between height and branch-to-stem ratio is determined after adjusting for differences in total aboveground biomass. A similar approach has been used to model the crown ratio as a function of DBH and height for eucalypt trees [26].

In this study, we describe the development of biomass equations based on harvests of 198 hybrid poplar trees from two different regional testing networks that were deployed between the years of 1987 and 2001 at 15 sites across the north-central USA. Specifically, equations were developed to predict woody (branch + stem) total dry weight (TDW) as a function of diameter at breast height (DBH), with hypothesis testing for differences in equation intercepts and slopes among 4 genomic groups and 11 clones within these groups. Similarly, equations were developed to predict branch-to-stem weight ratio (BSR) as a function of TDW and tree height (H), also with hypothesis testing for differences in intercepts and slopes among the genomic groups and clones. The resulting equations are presented and discussed in the context of model fit and potential utility, and the observed differences among genomic groups and clones are also discussed in terms of possible causes and implications for generating improved estimates of hybrid poplar biomass production and allocation. As such, the current study builds off of information learned from two previous biomass studies in the region [11, 27].

Materials and Methods

Fifteen study sites were harvested between 2009 and 2011 from two regional networks of hybrid poplar plantings that were previously established in the north-central USA [28]. Summary information about the individual sites, including locations and basic climate and soil data, is provided in Table 1. Four of the sites were from a network planted at 3 × 3 m spacing during 2000 to 2001 [11, 22], and are hereafter referred to as 10-year-old plantings, while the remaining 11 sites were from a network planted at 2.4 × 2.4 m spacing during 1987 to 1991 [21, 31, 32] and are hereafter referred to as 20-year-old plantings (Fig. 1). From these networks, trees representing 4 genomic groups [*Populus deltoides* Bartr. ex Marsh × *P. deltoides* ‘DD’; *P. deltoides* × *P. nigra* L. ‘DN’; *P. nigra* × *P. maximowiczii* A. Henry ‘NM’; (*P. trichocarpa* Torr. et Gray × *P. deltoides*) × *P. deltoides* ‘TDD’] and consisting of a total of 11 clones (‘C916000’, ‘C916400’, ‘C918001’, ‘DN34’, ‘DN182’, ‘NM2’, ‘NM6’, ‘NC13563’, ‘NC13624’, ‘NC13649’, ‘NC14018’) were harvested for the current study (Table 2). Up to 4 trees per clone were harvested at each site, resulting in a total of 198 trees harvested.

In the field, trees were marked with paint at breast height (i.e., 1.37 m), felled, measured for height, and a main leader was identified for the purposes of classifying biomass as belonging to the stem or to the branches. The branches were then removed from the main leader, chipped into large plastic bins, and total fresh weight (to the nearest 0.1 kg) of the branches was recorded for each tree. The stem was cut into segments, placed in large plastic bins, and total fresh weight of the stem was similarly recorded for each tree. Subsamples of branch and stem biomass were then taken to determine the ratio of fresh weight to dry weight. Specifically, a subsample of the branch chips for each tree was randomly pulled from the plastic bin, and a subsample from each stem was obtained in the form of a cross-sectional disk cut at breast height. All subsamples were weighed in the field to determine fresh weight to the nearest 0.1 g; in addition, cross-sectional disks were measured for outside-bark diameter to the nearest 0.1 cm. The material was then transported to the analytical laboratory at the Institute for Applied Ecosystem Studies in Rhinelander, WI, USA, and dried in an oven at 55 °C until constant weight was reached. Dry weight was recorded with the same precision as fresh weight. The ratio of dry to fresh weight for each subsample was then used to estimate total dry weight of each component of each tree based on the fresh weight recorded in the field. Under the drying conditions in this study (55 °C with prevailing humidity of approximately 70%), the residual moisture content of the wood after drying is estimated to be approximately 11% by weight [33]. Samples were dried at this temperature and humidity to avoid volatilization of

Table 1 Site information from 10-year-old and 20-year-old planting networks established between 1987 and 2001 and harvested between 2009 and 2011. Mean heights (+/− standard error) at harvest time, soil texture, average annual precipitation (P), and average growing season (April to October) temperatures (T) are given. Adapted from Headlee et al. [28]

Site	State[a]	Net.	Year est.	Year cut	Height (m)	Soil texture[b]	P (mm)[c]	T (°C)[c]
Ames	IA	10	2000	2010	15.1 ± 0.4	Fine sandy loam	881	17.0
Arlington	WI	10	2000	2010	18.0 ± 0.3	Silt loam	869	14.7
Escanaba	MI	10	2001	2009	12.5 ± 0.2	Fine sandy loam	728	12.6
Waseca	MN	10	2000	2011	16.3 ± 0.4	Clay loam	907	15.9
Belgrade	MN	20	1990	2011	17.2 ± 0.4	Loam	653	15.3
Bemidji	MN	20	1988	2010	17.9 ± 0.3	Loamy sand	676	12.7
Fairmont	MN	20	1988	2011	18.7 ± 0.2	Clay loam	831	16.5
Granite Falls	MN	20	1987	2011	21.4 ± 0.8	Loam	727	15.3
Lamberton	MN	20	1988	2011	18.7 ± 0.9	Clay loam	710	15.6
Lancaster	WI	20	1991	2010	22.5 ± 1.3	Silt loam	898	15.5
Milaca	MN	20	1989	2011	19.4 ± 0.3	Silt loam	748	14.1
Mondovi	WI	20	1988	2011	19.3 ± 0.3	Silt loam	881	15.4
Rhinelander	WI	20	1988	2010	21.5 ± 0.6	Loamy sand	675	13.0
Ulen	MN	20	1989	2010	14.4 ± 0.5	Loam	628	14.3
Warren	MN	20	1989	2010	20.8 ± 0.7	Fine loamy sand	548	13.4

[a] *IA* Iowa, *MI* Michigan, *MN* Minnesota, *WI* Wisconsin

[b] Soil texture information obtained from USDA Natural Resources Conservation Service (NRCS) [29]

[c] Climate data (30-year climate averages from 1981 to 2010) obtained from National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center [30]

nitrogen and carbon, the data from which are being used in companion studies. For the current study, all weights are recorded at 11% moisture content.

Additional calculations were required for one of the 10-year-old plantings (i.e., Escanaba), as the portion of the stem within the live crown was not separated from the branches prior to weighing. For these trees, the dry weight of the stem within the live crown was estimated for each tree using its specific gravity multiplied by its approximate volume. Specific gravity was measured in the lab as described by Headlee et al. [28], and volume was estimated using the formula for the volume of a cone (volume = $^1/_3$ height × area of the base; where "height" is the measured length of the live crown and "area of the base" is calculated from the stem diameter measured at the base of the live crown). The estimated stem weight within the live crown was then used to adjust the component weights for each tree (i.e., subtracted from branch weight and added to stem weight).

The data were pooled across sites and used to develop allometric equations. For total dry weight of the tree (TDW; kg), log-transformed TDW was used as the dependent variable, with log-transformed diameter at breast height (DBH; cm) as a covariate using the linear form:

$$\log_{10}(\mathrm{TDW}) = a_0 + a_1 \times \log_{10}(\mathrm{DBH}) \tag{1a}$$

which in non-linear terms may be expressed as:

$$\mathrm{TDW} = 10^{a0} \times \mathrm{DBH}^{a1} \tag{1b}$$

For branch-to-stem dry weight ratio (BSR; kg kg^{-1}) of the tree, log-transformed BSR was used as the dependent variable, with log-transformed TDW and log-transformed tree height (H; m) as covariates using the linear form:

$$\log_{10}(\mathrm{BSR}) = b_0 + b_1 \times \log_{10}(\mathrm{TDW}) + b_2 \times \log_{10}(\mathrm{H}) \tag{2a}$$

which in non-linear terms may be expressed as:

$$\mathrm{BSR} = 10^{b0} \times \mathrm{TDW}^{b1} \times \mathrm{H}^{b2} \tag{2b}$$

When using multiple predictor variables, correlation between the covariates (a.k.a., multicollinearity) may be an issue. We tested for multicollinearity between TDW and H using the variance inflation factor (VIF) method; the resulting value of VIF = 2.873 was less than the threshold value of 10, above which multicollinearity would be considered a concern [34].

Generic equations (without genomic group or clone effects) were developed for comparison of model fit (i.e., r^2 and coefficient of variation, *CV*) with group- and clone-specific equations, and all equations were fit using PROC GLM in SAS® (SAS Institute, Cary, NC) using Type III sums of squares. The group- and clone-specific equations were developed with analysis of covariance (ANCOVA) hypothesis testing techniques [35]. Specifically, the null hypotheses of the intercepts (a_0, b_0) and slopes (a_1, b_1, b_2) being equal among genomic groups and clones were tested for TDW (i.e., Equation 1a) and BSR (i.e., Equation 2a). When significant evidence was indicated by *F*-

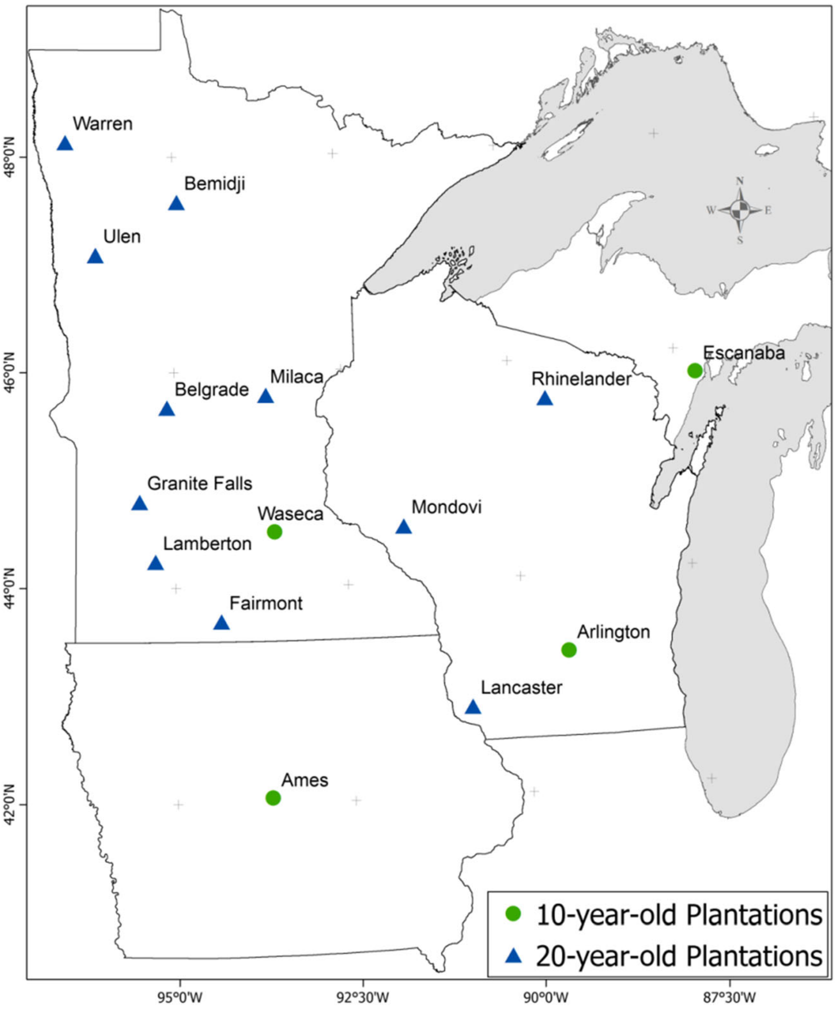

Fig. 1 Map of hybrid poplar field sites in the north-central USA that were harvested for this study. Adapted from Headlee et al. [28]

tests ($p < 0.05$), the null hypothesis was rejected and group- or clone-specific values were fit. If significant differences in slopes were detected, indicating differences among groups or clones varied depending upon the value of the covariate(s), then null hypotheses of no differences among groups or clones were also tested for TDW or BSR at the mean levels of the covariate(s). When significant differences were indicated ($p < 0.05$), multiple comparisons tests (with Tukey adjustment to control for experiment-wide error) were conducted to identify significant differences among least squares means of individual groups or clones. Because the equations were fit using log-transformed data and then converted to the original units of measure, the

Table 2 Hybrid poplar genomic groups and clones in the current study. Planting networks (10- and 20-year-old), number of sites and trees sampled, and ranges of diameters at breast height (DBH) of sample trees are shown

Genomic group—parent species	Clones	Net.	Sites	Trees	DBH (cm)
‘DD’—*Populus deltoides* × *P. deltoides*	C916000	10	4	14	13.0–27.8
	C916400	10	4	15	13.5–29.8
	C918001	10	4	15	8.9–24.9
‘DN’—*P. deltoides* × *P. nigra*	DN34	10, 20	15	57	12.4–30.2
	DN182	20	10	37	15.1–34.2
‘NM’—*P. nigra* × *P. maximowiczii*	NM2	10	3	10	15.2–27.3
	NM6	10	2	6	18.0–27.6
‘TDD’— (*P. trichocarpa* × *P. deltoides*) × *P. deltoides*	NC13563	10	4	15	15.2–25.3
	NC13624	10	3	9	11.4–17.2
	NC13649	10	3	9	13.5–19.0
	NC14018	10	4	11	14.0–25.3

least squares means are equivalent to geometric means and thus represent underestimates of their arithmetic counterparts. If desired, a correction factor calculated from the standard error may be applied to the means to better approximate their arithmetic values, as described by Sprugel [36]. Trees of clones ‘NM6’, ‘NC13624’, and ‘NC13649’ were included in the development of generic and group-specific equations, but were not fit for clone-specific equations due to their small sample sizes ($n <$ 10). Finally, the clone ‘DN34’ was present in both planting networks (10- and 20-year-old) in sufficient numbers ($n = 57$) to test for differences between networks in slopes and intercepts for each equation (TDW and BSR), as well as differences between networks in the predicted values of TDW and BSR at the mean level of the covariates. The tests for these network-specific equations for ‘DN34’ were conducted in the same manner as described above for the group- and clone-specific equations.

Results

For TDW, the covariate $\log_{10}$ DBH was significant ($p <$ 0.0001). The generic equation showed a relatively strong model fit ($r^2 = 0.85$; $CV = 5.1\%$), although the fit was improved when genomic groups were included in the model ($r^2 = 0.90$; $CV = 4.3\%$). The relationship between TDW and the covariate DBH is shown by group in Fig. 2. The F-tests for genomic group-specific equations indicated that the null hypothesis of equality among groups should be rejected for slopes ($p = 0.0117$) but not for intercepts ($p = 0.0569$). Relative to the generic equation, model fit was also improved when clones were included in the model ($r^2 = 0.91$; $CV = 4.2\%$). The F-tests for clone-specific equations indicated that the null hypotheses should be rejected for equal intercepts ($p = 0.0048$) and equal slopes ($p = 0.0015$) among clones. Best-fit estimates of intercepts and slopes are given in Table 3 for the generic, group-specific, and clone-specific equations.

Table 3 Coefficient estimates (with standard errors in parentheses) for total dry weight (TDW; kg tree^{-1}) equations. Generic equation represents data from all genomic groups pooled together. Trees of clones NM6, NC13624, and NC13649 were included in the generic and genomic group equations, but were not fit for clone-specific equations due to low sample size ($n < 10$)

Equations	Group/ clone	a_0		a_1	
Generic TDW	All	− 1.03	(0.09)	2.33	(0.07)
Group TDW	DD	− 0.65	(0.13)	2.01	(0.10)
	DN	− 1.02	(0.13)	2.36	(0.10)
	NM	− 0.50	(0.38)	1.94	(0.29)
	TDD	− 0.42	(0.21)	1.78	(0.17)
Clone TDW	C916000	− 0.25	(0.31)	1.69	(0.24)
	C916400	− 0.86	(0.26)	2.19	(0.20)
	C918001	− 0.74	(0.18)	2.10	(0.15)
	DN34	− 1.27	(0.18)	2.55	(0.14)
	DN182	− 0.76	(0.19)	2.17	(0.14)
	NM2	− 0.63	(0.42)	2.00	(0.32)
	NC13563	− 0.52	(0.41)	1.85	(0.32)
	NC14018	− 0.67	(0.44)	1.99	(0.34)

Based on the inequality of slopes for groups and clones in the TDW equations, least squares means were adjusted to the mean level of the covariate (DBH = 20 cm) and tested for significant differences among groups and clones. Significant differences were observed for both genomic groups ($p <$ 0.0001) and clones ($p < 0.0001$), and therefore multiple comparisons analyses were conducted to identify statistically significant differences among individual groups and clones (Fig. 3). For the genomic groups, adjusted TDW was significantly higher with group DN than with groups DD and TDD. Groups NM and DD were also significantly higher than group TDD. For the clones, adjusted TDW was significantly higher with clones ‘DN34’ and ‘DN182’ than with clones ‘C916000’, ‘NC13563’, and ‘NC14018’. The remaining clones were intermediate and did not differ significantly from any other

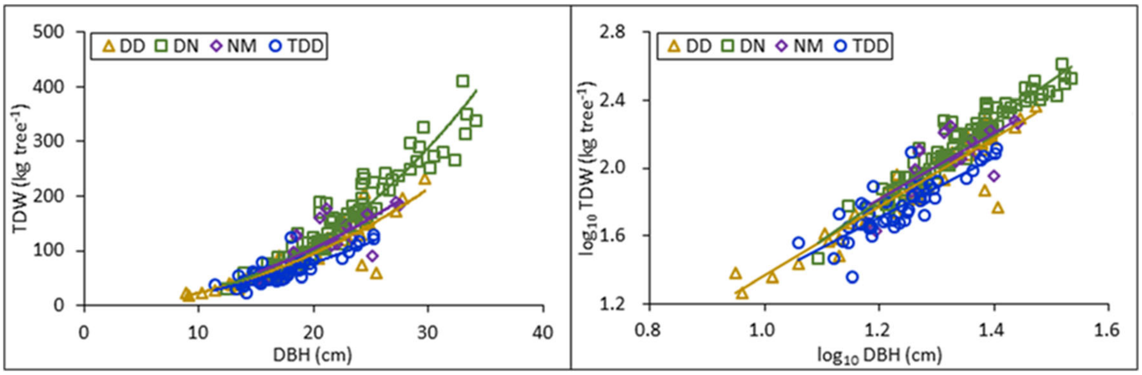

Fig. 2 Relationship of total dry weight (TDW; kg tree^{-1}) (at 11% moisture content) with diameter at breast height (DBH; cm) (left: untransformed; right; transformed) for genomic groups DD (gold triangles), DN (green squares), NM (purple diamonds), and TDD (blue circles). See “Materials and Methods” for genomic group descriptions

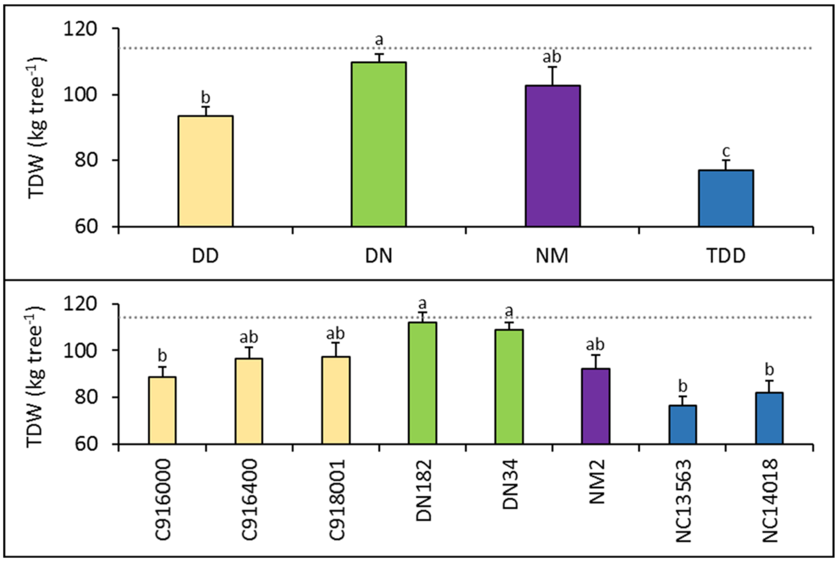

Fig. 3 Least squares means of total dry weight (TDW; kg tree^{-1}) for genomic groups (top) and clones (bottom) compared at mean tree DBH (20 cm). Significant differences ($p < 0.05$, with Tukey adjustment for multiple comparisons) are identified by different letters above the standard error bars. Columns of the same shade represent clones belonging to the same genomic group. The dashed line shows predicted TDW from an older equation for the region [21] at 20 cm DBH and 11% moisture content. See "Materials and Methods" for genomic group descriptions

clone. Compared to the estimates of TDW produced by the equation of Netzer et al. [21] (represented by the dotted line in Fig. 3; DBH = 20 cm and moisture content = 11%), the group- and clone-specific equations developed in this study produce somewhat lower estimates, particularly for groups DD, NM, and TDD and their respective clones.

For BSR, the covariates $\log_{10}$ TDW and $\log_{10}$ H were both significant ($p < 0.0001$). The generic equation showed a moderately strong model fit ($r^2 = 0.53$; $CV = 40.1\%$), and the fit was improved somewhat when genomic groups were included in the model ($r^2 = 0.57$; $CV = 39.3\%$). The relationship between BSR and the covariates TDW and H can be seen by group in Fig. 4. The *F*-tests for group-specific equations indicated that the null hypotheses of equality among groups should be rejected for the slope of TDW ($p = 0.0199$) but not for the slope of H ($p = 0.0574$) or the intercept ($p = 0.4480$). Relative to both the generic and group-specific equations, model fit improved markedly when clones were included in the model ($r^2 = 0.75$; $CV = 31.9\%$). The *F*-tests for the clone-specific BSR equations indicated that the null hypothesis of equal intercepts should be rejected ($p < 0.0001$), along with the null hypotheses of equal slopes for TDW ($p < 0.0001$) and H ($p < 0.0001$). Best-fit estimates of intercepts and slopes are given in Table 4 for the generic, group-specific, and clone-specific equations.

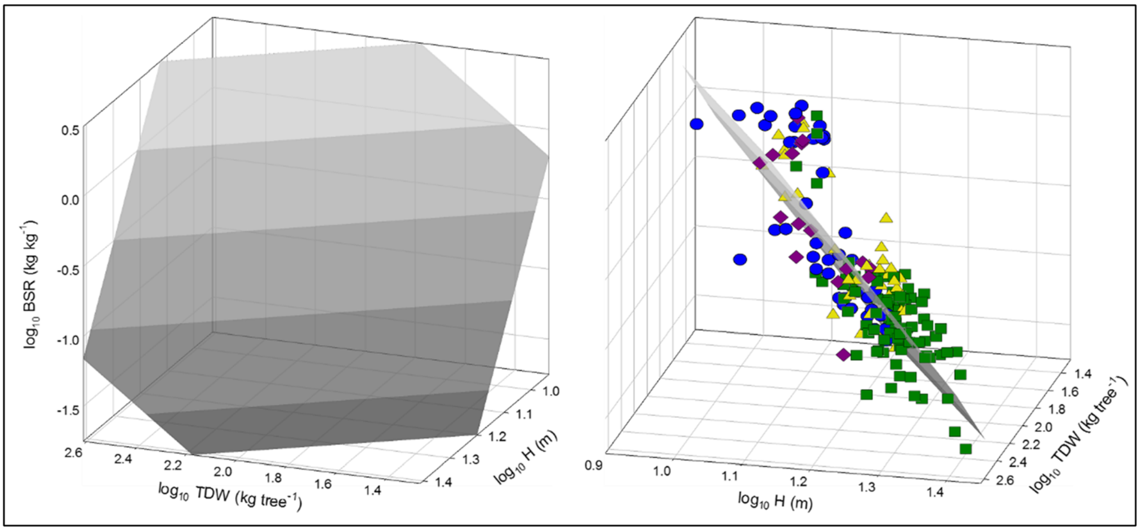

Fig. 4 Relationship of branch-to-stem dry weight ratio (BSR; kg kg^{-1}) to total dry weight (TDW; kg tree^{-1}) and tree height (H; m). Left: The relationship described by the generic regression equation (data pooled across genomic groups) is shown as a plane in three-dimensional space, where different shades correspond to different intervals of BSR. Right: The plane is rotated to the right approximately 90° to show model fit relative to genomic groups DD (gold triangles), DN (green squares), NM (purple diamonds), and TDD (blue circles). See "Materials and Methods" for genomic group descriptions

Table 4 Coefficient estimates (with standard errors in parentheses) for branch-to-stem dry weight ratio (BSR; kg kg^{-1}) equations. Generic equation represents data from all genomic groups pooled together. Trees of clones NM6, NC13624, and NC13649 were included in the generic and genomic group equations, but were not fit for clone-specific equations due to low sample size ($n < 10$)

Equations	Group/ Clone	b_0		b_1		b_2	
Generic BSR	All	3.83	(0.32)	1.29	(0.14)	− 5.89	(0.41)
Group BSR	DD	3.91	(0.81)	1.62	(0.28)	− 6.42	(0.98)
	DN	2.62	(0.69)	0.85	(0.22)	− 4.24	(0.77)
	NM	3.97	(1.48)	2.00	(0.51)	− 7.32	(1.66)
	TDD	4.07	(0.69)	2.01	(0.43)	− 7.22	(0.94)
Clone BSR	C916000	4.51	(1.16)	1.94	(0.45)	− 7.55	(1.32)
	C916400	6.94	(1.58)	1.45	(0.47)	− 8.43	(1.86)
	C918001	4.76	(1.26)	2.12	(0.46)	− 7.99	(1.65)
	DN34	3.79	(0.70)	1.06	(0.24)	− 5.50	(0.81)
	DN182	− 1.46	(1.12)	0.38	(0.27)	− 0.34	(1.14)
	NM2	2.53	(1.35)	1.72	(0.54)	− 5.65	(1.61)
	NC13563	7.97	(1.49)	0.91	(0.68)	− 8.84	(1.92)
	NC14018	11.45	(1.91)	1.57	(0.71)	− 12.59	(2.19)

Due to the inequality of slopes among genomic groups and clones in the BSR equations, least squares means were adjusted to the mean levels of the covariates (TDW = 100 kg; H = 16.5 m) and tested for differences among groups and clones. Significant differences were observed for both genomic groups ($p = 0.03$) and clones ($p < 0.0001$), and thus multiple comparisons analyses were used to identify statistically significant differences among individual groups and clones (Fig. 5). For the genomic groups, adjusted BSR was significantly higher with group DD than with group DN, while the remaining groups (NM and TDD) did not differ significantly from any other group. For the clones, adjusted BSR was significantly higher with clone 'C916400' than with clones 'C916000', 'DN34', 'DN182', and 'NC13563'. In addition, adjusted BSR was significantly higher with clones 'C918001' and 'DN34' than with clone 'DN182'; all remaining clones were intermediate and did not differ significantly from any other clone.

The tests for differences between planting networks for the clone 'DN34' indicated significant differences in the intercept ($p = 0.0384$) and slope ($p = 0.0430$) for the TDW equation. However, these differences did not translate to any significant difference in the predicted value of TDW at the mean level of the covariate (Table 5). For BSR, the networks also showed significant differences in the intercept ($p = 0.0003$), slope of TDW ($p = 0.0032$), and slope of H ($p = 0.0002$). As shown in Table 5, these differences did translate to a significant difference in predicted BSR for 'DN34' at the mean value of the covariates, with a value of 0.20 for the 10-year-old network and a value of 0.12 for the 20-year-old network.

Discussion

In this study, aboveground woody biomass was well-correlated with tree diameter for hybrid poplar genomic groups and clones growing across the region, as has been observed in other studies with hybrid poplars [14, 17, 21] and various other species [12, 13]. Our results also showed that this allometric relationship differed significantly among groups and clones. Specifically, TDW equation parameters

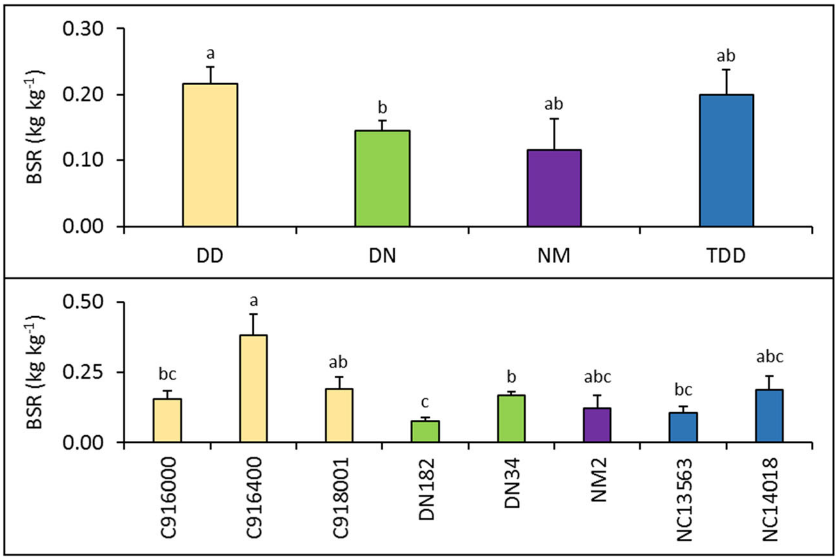

Fig. 5 Least squares means of branch-to-stem dry weight ratio (BSR; kg kg^{-1}) for genomic groups (top) and clones (bottom) compared at mean tree total dry weight (100 kg) and mean tree height (16.5 m). Significant differences ($p < 0.05$, with Tukey adjustment for multiple comparisons) are identified by different letters above the standard error bars. Columns of the same shade represent clones belonging to the same genomic group. See "Materials and Methods" for genomic group descriptions

Table 5 Coefficient estimates (with standard errors in parentheses) for clone 'DN34' by planting network (10- or 20-year-old), and least squares means of TDW (kg tree^{-1}) at 20 cm DBH and BSR (kg kg^{-1}) at 100 kg TDW and 16.5 m H. Means that differ significantly ($p < 0.05$) are denoted with different letters

Net.	a_0		a_1		TDW	b_0		b_1		b_2		BSR
10	− 0.76	(0.29)	2.15	(0.23)	110 a	7.46	(1.31)	3.13	(0.73)	− 11.8	(1.90)	0.20 a
20	− 1.46	(0.15)	2.68	(0.11)	107 a	1.57	(0.79)	0.77	(0.23)	− 3.30	(0.85)	0.12 b

differed significantly among genomic groups, which translated to significant differences in TDW at mean tree DBH (20 cm) for groups TDD (77 kg tree^{-1}) and DD (93 kg tree^{-1}) compared to group DN (110 kg tree^{-1}). Similarly, TDW equation parameters differed significantly among clones and translated to significant differences in TDW at mean tree DBH, with least squares means ranging from 76 kg tree^{-1} ('NC13563') to 112 kg tree^{-1} ('DN182'). This corroborates differences in allometric relationships among hybrid poplar groups and clones observed in south-central Canada [15, 16].

The differences in TDW equations and superior model fit for the group- and clone-specific equations recommend their use over the generic equation developed in the current study. At the mean tree DBH of 20 cm, for example, use of the generic equation would underestimate biomass by up to 12% or overestimate biomass by up to 24% depending upon the genotype. Truax et al. [16] similarly compared clone-specific equations versus generalized equations for five hybrid poplar clones (belonging to five separate genomic groups) growing in southern Québec, Canada, and found that their generalized equation resulted in underestimates of up to 14% and overestimates of up to 21% for aboveground woody biomass. In addition, comparison of our TDW equation estimates with those of an older, commonly used equation for the region [21] shows that our estimates are generally lower (see Fig. 3). While the estimates are only slightly lower for group DN (− 4%), the differences are more pronounced for groups NM (− 10%), DD (− 18%), and TDD (− 33%). Notably, the two clones in group DN in this study (i.e., 'DN34' and 'DN182') are older genotypes which were largely the basis for the older allometric equation for the region; in fact, the 20-year-old network from which DN trees were harvested in this study is the same network that was used to develop the older equation. In this context, our results suggest that the older equation reasonably describes the allometric relationship for the genotypes with which it was developed, but is likely to substantially overestimate TDW for groups NM, DD, and TDD and their respective clones. Thus, the new group- and clone-specific equations reported in the current study are expected to produce more accurate estimates of TDW for these genotypes. Because the clone-specific equations resulted in only slight improvements in model fit (r^2 = 0.91) compared to that for the group-specific equations (r^2 = 0.90), and no differences between clones within the same genomic group were observed (see Fig. 3), it appears the group-specific equations are likely to be adequate for estimating TDW of these genotypes.

The differences among genomic groups and clones in the relationship between TDW and DBH may be attributable to several factors, such as differences in wood density. A separate study on the specific gravity of our trees [28] showed that such differences exist among the genotypes and roughly correlate with the observed trends in TDW. For example, the group with the lowest adjusted TDW in the current study (i.e., TDD) was observed to have the lowest specific gravity (0.315 g cm^{-3}), while the group having the highest adjusted TDW (i.e., DN) was observed to have the highest specific gravity (0.354 g cm^{-3}), and the groups with intermediate TDW (i.e., DD and NM) had intermediate specific gravity (0.336 and 0.327 g cm^{-3}, respectively). Such differences in these and other wood properties in hybrid poplars have been reported elsewhere [37, 38]. For example, DeBell et al. [39] tested two *P. trichocarpa* × *P. deltoides* hybrids and one open-pollinated *P. trichocarpa* clone and reported significant differences for woody density and fiber length. Similarly, Geyer et al. [40] reported significant clonal differences among eleven clones belonging to two genomic groups (*P. deltoides*; *P. deltoides* × *P. nigra*) for wood density, while Pliura et al. [41] reported similar results for this trait from clones belonging to five genomic groups (*P. deltoides*; *P. deltoides* × *P. nigra*; *P. trichocarpa* × *P. deltoides*; *P. maximowiczii* A. Henry × *P. balsamifera L.*; *P. balsamifera* × *P. nigra*). In the current study, however, the relative differences in specific gravity (with group TDD being about 10% lower than group DN) are smaller than the relative differences in TDW (with group TDD being about 30% lower than group DN). Thus, it seems likely that other factors such as differences in bark thickness and/or stem taper may be similarly (or more) important for explaining the observed differences among genotypes in TDW at a given DBH.

The differences in BSR equations and estimates among groups and clones indicate that these genotypes also allocated biomass differently. Specifically, BSR equation parameters differed significantly among genomic groups, which translated to significant differences in BSR at mean levels of TDW (100 kg) and H (16.5 m) for group DN (0.14 kg kg^{-1})

compared to group DD (0.22 kg kg^{-1}). Similarly, BSR equation parameters differed significantly among clones and translated to significant differences in BSR at mean levels of TDW and H, with least squares means ranging from 0.08 kg kg^{-1} (‘DN182’) to 0.38 kg kg^{-1} (‘C916400’). Such differences in biomass allocation among genotypes have been previously reported for hybrid poplars [10, 15, 16]. For example, Fortier et al. [10] tested five unrelated clones across four riparian management systems in southern Québec, Canada, and reported branch biomass varied among clones from 21 to 33% of aboveground woody biomass (equivalent to BSR of 0.27 to 0.50 kg kg^{-1}) at 6 years after planting. Similarly, Truax et al. [15] reported that branches comprised 21 to 31% of aboveground woody biomass (≈ BSR of 0.27 to 0.45 kg kg^{-1}) at 8 years after planting, and for the same plantings branches were 15 to 29% of aboveground woody biomass (≈ BSR of 0.18 to 0.41 kg kg^{-1}) at 13 years after planting [16].

Because the clone-specific BSR equations in the current study resulted in marked improvements in model fit (r^2 = 0.75) compared to that for the group-specific equations (r^2 = 0.57), and differences between clones within the same genomic group were observed (see Fig. 5), it appears that clone-specific equations are warranted for these genotypes. Less clear is whether these differences in biomass allocation resulted from inherent differences in “branchiness,” different responses to competition and/or site quality, or some combination of these (or other) factors. While some degree of meaning might ordinarily be inferred from clone-specific intercepts and slopes (e.g., greater inherent branchiness with higher intercepts, greater sensitivity to competition with steeper slopes of TDW, greater sensitivity to site quality with steeper slopes of H), caution against over-interpreting the data is necessary. Such inferences are best made when trees have been sampled throughout the rotation, whereas in the current study sampling was conducted at the typical rotation age (in the case of the 10-year-old trees) and beyond (in the case of the 20-year-old trees), with only one clone (i.e., ‘DN34’) sampled at both stages of stand development. In other words, the relatively wide range of sizes for sample trees in our study generally reflect gradients in site quality and the competitive status of individual trees within the sites, rather than a gradient of tree development through time. Thus, additional testing of these BSR equations at younger ages is recommended, in order to further evaluate their performance and/or improve model fit. Such research would improve our understanding of hybrid poplar biomass allocation in general, and would likely have important implications in terms of selecting genotypes for specific applications. For example, genotypes with less inherent branchiness could be advantageous for stem-only harvesting in pulp or bioenergy systems, whereas genotypes with greater inherent branchiness might be desirable for other purposes such as windbreaks or wildlife habitat.

While the network-specific TDW equations for ‘DN34’ differed significantly in slope and intercept, these differences did not translate to any significant difference in TDW at the mean level of the covariate (i.e., 110 and 107 kg tree^{-1} for 10- and 20-year-old networks, respectively). More specifically, the 10-year-old network had a higher intercept but lower slope compared to the 20-year-old network, such that the predicted values are similar in the middle of the data range and only differ at the extremes (where confidence in the predicted values is lowest). As such, the network-specific TDW equations for ‘DN34’ do not appear to provide a tangible advantage over the clone-specific equation for ‘DN34’. In contrast, the network-specific BSR equations for ‘DN34’ did translate to significantly different predicted values of BSR at the mean level of the covariates, with predicted values of 0.20 and 0.12 for the 10- and 20-year-old networks, respectively. One possible explanation for this difference is that there is an age component to BSR beyond the changes in TDW and H that coincide with age, such that including age as another covariate in BSR equations could further improve model predictions. Future studies should seek to sample trees across a gradient of ages (as opposed to just ages 10 and 20 as in the current study), so that the inclusion of age as a covariate for BSR may be more thoroughly investigated.

In summary, comparison of the TDW equations developed in the current study with the older equation commonly used in the region indicates that the older equation is not well-suited for estimating biomass of the newer genotypes that have been more recently deployed. Therefore, it is recommended that the TDW equations developed in this study be used when managing and modeling the productivity of these hybrid poplar genotypes in the north-central USA. Because the clone-specific equations resulted in only slight improvements in model fit compared to the group-specific equations, and no differences between clones within the same genomic group were observed, the group-specific equations may be sufficient for estimating TDW of these genotypes. Conversely, the clone-specific equations for BSR resulted in a marked improvement in model fit and differences among clones within groups were also observed, indicating that clone-specific equations are warranted for BSR. The group- and clone-specific equations reported here are thus expected to be useful for generating improved estimates of aboveground biomass production and allocation in the region. Future biomass productivity studies should incorporate whole-tree harvests followed by the development of genotype-specific allometric equations (including the newest set of genotypes available at that time), with a focus on biomass allocation over time, in order to maximize the information gained about the potential ecosystem services of hybrid poplars across the landscape.

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