Modeling and Analysis

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Economic impact of yield and composition variation in bioenergy crops: *Populus trichocarpa*

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Abstract: To achieve a bio-based economy, it is necessary to consider variability within a feedstock population. We must understand the range of key phenotypic characteristics when selecting economically advantageous genotypes for domestication in an optimized supply chain. In this analysis we measured cell-wall composition traits in a large natural variant population of *Populus trichocarpa*. The results were combined with agronomic growth data from the matching genotype to conduct various techno-economic analyses, evaluating the impacts of physical and compositional variability and determining the ultimate phenotypic drivers for yield and economic metrics. Here we show that, although ethanol yield per land area per year and minimum fuel selling price were most strongly impacted by tree size, when considering the largest 25% of trees, size and carbohydrate content were nearly identical influences on minimal fuel selling price, highlighting the need to focus on both size and carbohydrate content in selecting economically optimal feedstocks. © 2020 The Authors. *Biofuels, Bioproducts, and Biorefining* published by Society of Chemical Industry and John Wiley & Sons, Ltd

Key words: high-throughput compositional analysis; feedstock variability; techno-economic analysis; bioethanol; minimum fuel selling price

Introduction

Economically viable production of bio-based products and advanced fuels requires robust, high-yielding feedstocks produced using sophisticated breeding, transgenesis, or genome editing techniques. The development of sustainable feedstocks will require high-throughput analytical capabilities for the screening and selection of desirable plant phenotypes. *Populus* spp. are particularly well-suited for use as a bioenergy crop and as a model system for understanding the genetic regulation of economically important phenotypes. Given that these species are fast growing and are widely adapted to diverse environments across North America, they are easily deployable for commercial production.[1] Further, because *Populus* remains largely undomesticated, natural populations of these species exhibit high genetic diversity, which translates into high phenotypic variation among individuals of the same species. This phenotypic diversity includes key traits that impact economics including biomass yield and biomass

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composition.[2] Establishing the extent of naturally occurring variation informs the genetic potential of the species as a feedstock and can be directly modeled to predict economic gains or potential trait tradeoffs.

The identification of the function of key genes for economic phenotypes allows either targeted genetic engineering or improved breeding by genomic selection.[3] High-throughput pipelines have been developed that allow production of modified biomass targeting individual genes related to plant cell-wall chemistry and anatomy.[4,5] These phenotypes require detailed analysis to determine which changes can be optimized for economically advantageous feedstock production. Cell-wall composition can be obtained through traditional wet chemistry methods but often involves both labor and time-intensive measurements.[6,7] Standard methods outlined in ASTM International and National Renewable Energy Laboratory (NREL) Laboratory procedures for carbohydrate composition take an hour or more per sample.[7] Pyrolysis molecular beam mass spectrometry (pyMBMS) can be employed as a high-throughput method to obtain information about the lignin composition of a sample but does not easily yield accurate information about the carbohydrate composition in a single-species set.[8–10] High-throughput methods for hydrolysis of biomass in 96-well plates have been developed; however, this method still requires a time-consuming high performance liquid chromatography (HPLC) step.[11,12]

The use of proton nuclear magnetic resonance spectroscopy (^{1}H NMR) as a screening method has gained traction in recent years with the development of automated sample changers for nuclear magnetic resonance (NMR) spectrometers. Mixture analysis by NMR has become increasingly popular and has been applied to biomass hydrolysates previously.[13] Often, the anomeric proton region from 4.4 and 5.4 ppm is relied on to quantify sugars in solution. However, this method has several drawbacks, most notably the large water peak in the middle of the sugar anomeric region that can obscure the signals of interest at neutral pH in biomass hydrolysates.[14,15] Suppression of the water peak is easily achieved but also adversely affects the peaks of interest. Alternatively, by combining HPLC-derived data with NMR spectra and building partial least squares (PLS) models, accurate concentrations of five different monomeric sugars can be predicted using the aliphatic sugar peaks between 3.1 and 4.2 ppm, even given the severe overlap of signals described previously.[13] This type of analysis is ideally suited to determine the sugar composition variation across a single species, such as the *Populus trichocarpa* population here, because it can be achieved in a higher throughput manner than traditional HPLC methods – both due to the decreased upstream processing using our scaled-down hydrolysate preparation and the reduced run-times using ^{1}H NMR.

Feedstock cost is one of the greatest operational expenses in a biorefinery, so understanding which feedstocks are advantageous relative to one another in terms of both cost and quality should be an important consideration for any biorefinery.[16,17] No formally accepted standard of lignocellulosic biomass quality has been defined previously, but several metrics may be used. Process yield, defined as amount of fuel produced per unit of feed, is one metric that evaluates the impact of a feedstock on total production. In biorefineries where fermentation is the primary conversion route, such as in the production of ethanol, high process yield would correspond to feedstocks where a higher percentage of usable sugars (glucose, xylose, and arabinose) can be evolved through pretreatment and / or enzymatic hydrolysis steps, which then can go on to fuel.[18–20] However, growers are typically concerned with achieving the highest biomass yields for a given land area with little consideration given to process yield or quality. To reconcile the gap between grower and biorefinery, both biomass yield and process yield can be combined and normalized to define the metric of fuel yield per land area per year.[21] This metric not only can be an important consideration when evaluating the land footprint required to reach a fuel production target, but may also serve as a negotiating point between the biorefinery and grower, or grower and plant breeders, in determining feedstock price. From an economic standpoint, the minimum fuel selling price (MFSP) needed to achieve a net present value of zero for a process facility is often used to summarize the entire biorefinery in terms of economic drivers such as capital expense, operating expense, and revenue, where feedstocks that lead to the lowest MFSP can be regarded as the best performers. While not a direct measure of feedstock quality, MFSP can serve as a bottom-line economic indicator of the value of quality and quantity and, through a series of sensitivity analyses, can determine which feedstock characteristics are most impactful.

As interest in poplar as a lignocellulosic feedstock grows, so too will the need to understand its variability across a population given its limited domestication. There is a need to comprehend this variation as a range of physical and compositional phenotypes, and also to understand how these phenotypes impact overall feedstock quality and biorefinery economics. Determining which phenotypes are most advantageous to a biorefinery can provide insights into which feedstocks are ideal, accelerating research and domestication

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by guiding plant breeders into focusing on attributes that are the most influential to improving yields, while simultaneously reducing production costs. In this paper, we present the larger economic impact that a broad range of natural variation in plant growth and cell wall composition for *P. trichocarpa* has on the bioenergy landscape in terms of MFSP, process ethanol yield, and field ethanol yield.

Materials and methods

Plant materials

The natural variant *P. trichocarpa* population comprising 1089 individuals was selected to represent the species range stretching from 38.8° to 54.3°N latitude from California, USA, to British Columbia, Canada. Details of field establishment, growing conditions and maintenance were described previously.[22,23] Increment cores were collected from 3-year-old trees at the Corvallis OR experiment station (44° 34′ 14.81″ N, 123° 16′ 33.59″ W) in December 2013. Cores were oven dried at 50 °C and were then ground through a 20-mesh screen using a Wiley mini-mill (Swedesboro, NJ, USA). Diameter at breast height (DBH), in centimeters, was measured on 7-year old trees from the Clatskanie, OR field site (46° 6′ 11″ N, 123° 12′ 13″ W).

Hydrolysate preparation

Samples for sugar composition analysis were first prepared by undergoing starch removal and ethanol extraction, followed by a two-stage acid hydrolysis using a scaled-down version of the NREL laboratory analytical procedure 'Determination of Structural Carbohydrates and Lignin from Biomass'.[6] To begin, 7.5 mg (±0.05 mg) of milled and extracted biomass samples were weighed into 5 mL microwave reaction vials. Then, 75 µL of 72% H_2SO_4 was stirred into the samples and the tubes were placed in a heat block and held at 30 °C for 1 h, with stirring every 5–10 min. This was followed by the addition of 2.1 mL of water to dilute the total acid concentration of the solution to 4% before being autoclaved at 121 °C for 1 h. Once the samples cooled to room temperature, they were neutralized to pH 7 with a predetermined amount of $CaCO_3$ (Alfa Aesar by Thermo Fisher Scientific, Tewksbury, MA, USA). The hydrolysates were then filtered at 1.0 µm for solids removal. Filtered liquid hydrolysate samples were preserved with sodium azide and stored at 4 °C in 1.5 mL microfuge tubes for up to 1 week. Samples were cold filtered at 0.2 µm immediately prior to NMR analysis. For standard samples used to build models, HPLC was used to determine sugar concentrations as described previously.[6,7,13]

^{1}H nuclear magnetic resonance analysis

For quantitative ^{1}H NMR analysis, liquid hydrolysates were prepared by adding 50 µL of D_2O stock solution containing 0.1 mg mL^{-1} TSP-d_4 (Cambridge Isotope Labs, Andover MA, USA), for NMR locking and chemical shift reference, to 450 µL of hydrolysate in NMR sample tubes. The final concentration of TSP-d_4 in each sample was 0.01 mg mL^{-1}. A Bruker Avance III spectrometer (Bruker Bio-Spin, Billerica, MA, USA) at 14.1 T (600.16 MHz) equipped with a Bruker 5 mm BBO probe and a Sample Jet automatic sample changer was used to collect ^{1}H spectra of hydrolysates. Suppression of the water peak was achieved using a NOESY-1D with presaturation, a recycle delay of 5 s, and a total of 64 scans. Four inch NMR sample tubes were placed in 96-tube racks for use in the 5 mm shuttle mode of the Sample Jet. Samples were run over the course of a 6-month period with each rack containing standards to ensure both consistent hydrolysis and quantitative NMR analysis. Spectra were acquired at 298 K and processed with automatic phase correction, baseline correction, and chemical shift referencing to TSP-d_4.

Partial least squares models for sugar composition

Spectral bucketing was performed using Brukers AMIX software. Spectra were divided into 0.005 ppm buckets in the region of 3.10–4.15 ppm for a total of 210 buckets. Bucketed data were used to build PLS models for subsequent predictions in the Unscrambler v. 10.5 (CAMO A/S, Trondheim, Norway). The formation of methanol during hydrolysis interferes with the quantitative NMR analysis of sugars; thus, the methanol peak centered at 3.37 ppm and, spanning four buckets (3.2925–3.2775 ppm), was set to zero. Twenty samples from eight biomass feedstocks (poplar, eucalyptus, pine, bagasse, wheat straw, corn stover, alfalfa, and switchgrass) were used to construct PLS models with HPLC-determined concentrations for five monomeric sugars (glucose, xylose, galactose, arabinose, and mannose) and coordinating NMR spectra, as described previously.[13]

Pyrolysis molecular beam mass spectrometry analysis

Pyrolysis Molecular Beam Mass Spectrometry (py-MBMS) can be employed as a high-throughput method to obtain information about the lignin composition of a sample but does not easily yield accurate information about the carbohydrate composition in a single-species set.[8–10] Py-MBMS analysis of samples was performed as described elsewhere.[9,24–27] 4 mg of debarked, ground (20-mesh)

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destarched and extracted biomass samples were pyrolyzed using a Frontier PY2020 unit (Frontier Laboratories Ltd., Fukushima, Japan) at 500 °C for 30 s. Mass spectral data was acquired using an Extrel Super-Sonic MBMS Model Max 1000 (Extrel, Pittsburgh, PA, USA) and processed using Merlin Automation software (Extrel, Pittsburgh, PA, USA). Spectra werecollected from *m/z* 30 to 450 at 17 eV. Lignin content was estimated relative to NIST 8492 *Populus deltoides* standard of 26.2 wt % lignin content (Klason) by summation of ion intensities of *m/z* 120, 124, 137, 138, 150, 152, 154, 164, 167, 168, 178, 180, 181, 182, 194, 208 and 210 from mean-normalized spectra. Relative syringyl (S) values were calculated by summation of mean-normalized ion intensities of *m/z* 154, 167, 168, 182, 194, 208, 210 and relative guaiacyl (G) values were determined by summation of ion intensities of *m/z* 124, 137, 138, 150, 164, 178.

Feedstock supply chain and cost models

To estimate the cost of poplar delivered to the biorefinery, a simulation model of the poplar supply chain (harvest, transport, storage, and chipping) was constructed in ExtendSim (Imagine That Inc., San Jose, CA, USA). The feedstock requirement was assumed to match the refinery demand of 2000 dry metric tons per day with a 90% process uptime. In the model, poplar was harvested, delimbed, and transported to the biorefinery as logs. The logs were stored until needed by the biorefinery and then chipped. The log was the only part of the tree transported and used by the biorefinery, with limbs and leaves considered waste and assumed to have no economic value.

The harvest process utilized seven harvest crews. Each harvest crew consisted of two feller-bunchers to cut and fell the trees ($176/h machine $^{-1}$), five grapple skidders to drag the trees to the loading area ($154/h machine $^{-1}$), and three stoke boom delimbers to delimb the trees ($129/h machine $^{-1}$). It was assumed that 1800 h per year were available for harvest operations. Separate crews were used for transporting logs to the refinery. The transportation crews consisted of four to eight log trucks ($127 h machine $^{-1}$) with a loader ($129/h machine $^{-1}$) at the field and a loader at the refinery. The number of log trucks per crew varied based on the average distance between the field and the refinery in order to utilize the loaders most effectively and minimize log truck waiting time during loading and unloading. The hourly cost for each transport crew truck was estimated to be between $766 and $1274 per hour, depending on the number of log trucks used.

The biorefinery contained two chippers to chip logs ($233 h^{-1} machine^{-1}). The chippers were assumed to operate 12 months per year with a large enough chipped inventory so that typical downtime events would not starve the biorefinery. Three additional loaders were necessary at the refinery in order to manage the feedstock supply as well as feed the two chippers. The hourly cost for chipping along with the additional loaders was estimated at $853 per hour. All hourly costs included fuel and labor.

The number of fields needed to supply the biorefinery's demand was calculated assuming trees are harvested once every 7 years, each field contained 1980 trees per hectare, a constant field size of 20.2 ha, and 1 field per 2.6 km^2. With a fixed daily requirement at the refinery and a fixed spatial field density, the required supply chain footprint varies only as a function of tree size. The production cost, cost to establish and maintain fields prior to harvest, was assumed to be $1290 ha^{-1}.[1]

The yield (dry metric tons/ha) range considered in this analysis was determined based on tree diameter of 7-year old poplar trees from the poplar population data sets that contained measurements for one to three ramets of each genotype in the study. Trees with DBH values of less than 9 cm were excluded from the study because the supply region would be too large, making transportation cost excessive, and the harvesting process selected for this study is not appropriate for smaller stems. The stem biomass (kg tree $^{-1}$) was calculated by Eqn (1):

$$m_{tree} = 0.0741 * DBH^{2.27} \quad (1)$$

where m_{tree} = mass of single poplar stem (kg tree^{-1}).[28] The yield per hectare was then calculated for each diameter assuming a planting density of 1980 trees per hectare.

Final delivered cost to the biorefinery for the genotype was calculated by taking the average of delivered costs for all ramets of that genotype. Feedstock was delivered cost ($ dry metric ton $^{-1}$) was a function of yield and can be approximated by equation 2,

$$\text{Cost}_{\text{Delivered}} = -0.0239x^3 + 1.5468x^2 - 34.157x + 302.79 \quad (2)$$

where x = DBH (cm) at year.

Techno-economic analysis

A representative subset of 204 samples with similar averages, standard deviations, and extremes of composition was chosen for analysis. Where full compositional data was not available for ash, extractives, acetate, and sucrose, these were set at fixed values of 1.08, 1.64, 3.52 and 0.07 weight percent, respectively, based on measurements from a small set of other samples. Then carbohydrate sugar and lignin percentages were linearly scaled on these values to reach 100% mass closure. For each sample in the subset, a process simulation for cellulosic ethanol production, made available by NREL,[29]

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was completed using Aspen Plus Version 7.2 (AspenTech, Bedford, MA, USA) following similar process assumptions to the work performed by Humbird *et al.* with feedstock composition modified for each run to be representative of the individual poplar feed.[16] Despite a change in feedstock from the originally modeled corn stover to poplar, biological conversion, and processing assumptions were assumed to be similar and any changes in feed handling, pretreatment, and biomass recalcitrance were not considered in this analysis. While we used the Humbird[16] stover model, this is comparable with the earlier yellow poplar model of Wooley *et al.*[30] There are several studies,[2,31] showing the variability of sugar solubilization via pretreatment and enzymatic hydrolysis. However, these data are from unoptimized laboratory conditions and were used as screens with incomplete solubilization. We did not attempt to extrapolate to optimized process conditions and costs at this time.

Economic assumptions of tax rate (21%), onstream time (90%), plant startup time (0.5 years), and cost year (2016) were updated to be consistent with recent design cases,[32] and the feedstock cost for each sample was taken as the average of feedstock costs for the genotype. A discounted cashflow rate of return analysis for each sample was performed, incorporating results from the Aspen Plus simulation to determine the MFSP, calculated by setting the net present value of the ethanol facility to be zero for an after-tax internal rate of return of 10% over a 30-year lifetime. Overall ethanol production was normalized to the per ton basis for calculation of process ethanol yields. The products of process ethanol yields and biomass yields were normalized, based on the 7-year growth cycle, to a per year basis for determination of field ethanol yields.

Results and discussion

Natural variation in *P. trichocarpa* populations – sugar composition

More than 900 poplar samples from a natural variant population were prepared in duplicate for high-throughput analysis by ^{1}H NMR as described previously.[13] The entire analysis was completed over the course of 6 months. Partial least square models were used to predict the concentrations of glucose and xylose, plus three minor sugars. The percentage error between HPLC and ^{1}H NMR prediction was less than 10%. Histogram plots of the sugar compositions are given in Fig. 1 with bin widths calculated based on the standard deviations for each model, and maximums, minimums, and standard deviations (σ) were as follows: (a) max = 0.57,

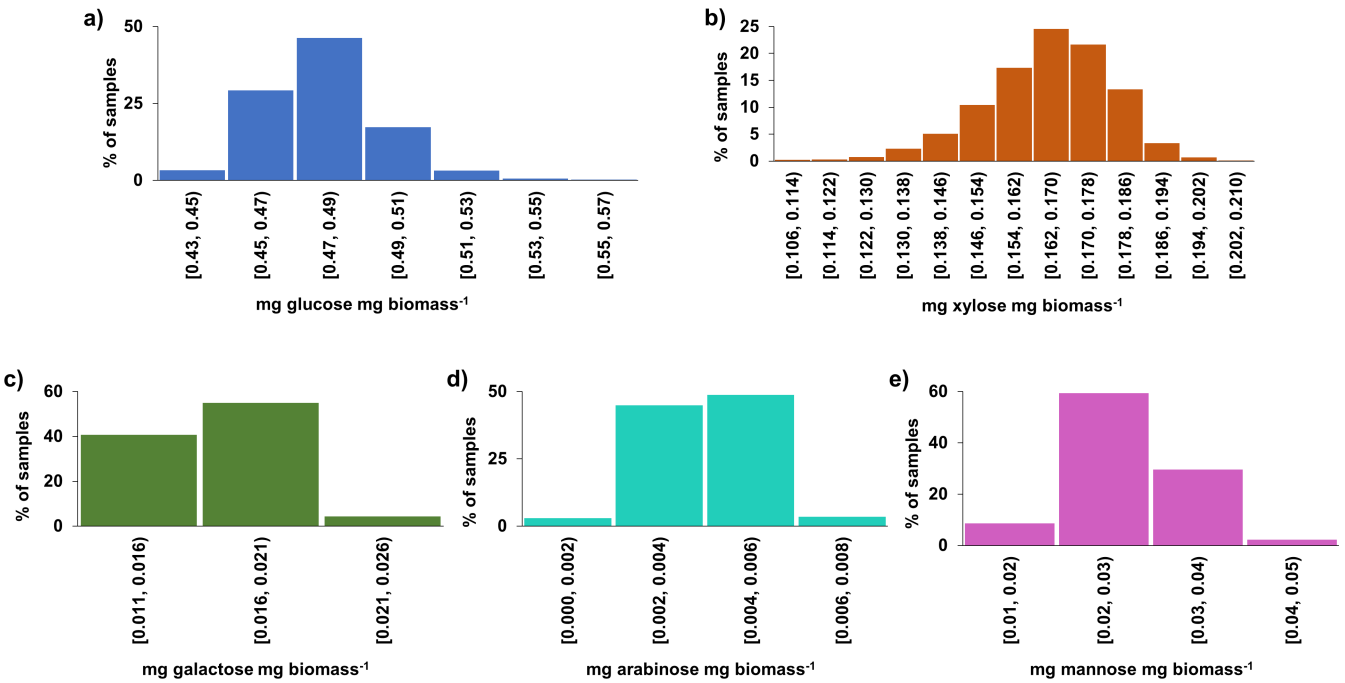

Figure 1. Frequency distribution (n = 924) of sugar composition across the natural variant *P. trichocarpa* population. Bin width is equal to the standard deviation for each monomeric sugar's model as follows: (a) σ = ±0.02 mg glucose mg biomass $^{-1}$; (b) σ = ±0.008 mg xylose mg biomass^{-1}; (c) σ = ±0.005 mg galactose mg biomass $^{-1}$; (d) σ = ±0.005 mg arabinose mg biomass $^{-1}$; (e) σ = ±0.01 mg mannose mg biomass^{-1}.

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min = 0.43, σ = ±0.02 mg glucose mg biomass $^{-1}$; (b) max = 0.204, min = 0.106, σ = ±0.008 mg xylose mg biomass $^{-1}$; (c) max = 0.025, min = 0.011, σ = ±0.005 mg galactose mg biomass $^{-1}$; (d) max = 0.019, min = 0.000, σ = ±0.005 mg arabinose mg biomass $^{-1}$; and (e) max = 0.05, min = 0.01, σ = ±0.01 mg mannose mg biomass $^{-1}$.

Glucose and xylose have much broader distributions around their mean values than the three minor sugars and have statistically relevant differences at ±1 standard deviation. There is less variation in the abundance of minor sugars, and the observed concentrations approach the detection limit for both HPLC and NMR. These lower concentrations of minor sugars are expected given that xylans are the main hemicelluloses in hardwood species, followed by small amounts of mannans and uronic acids.[33] There also appear to be genotypes within the natural variant population that display glucose and xylose compositions outside of the previously reported cellulose and hemicellulose content of various poplar species.[34] In some cases, the glucose content, and therefore cellulose content, is significantly higher, with one sample in the population comprising 57% glucose. This sample also contains the lowest xylose concentration (10.6%), the lowest arabinose concentration (0%/not detected), and one of the highest mannose concentrations (5%).

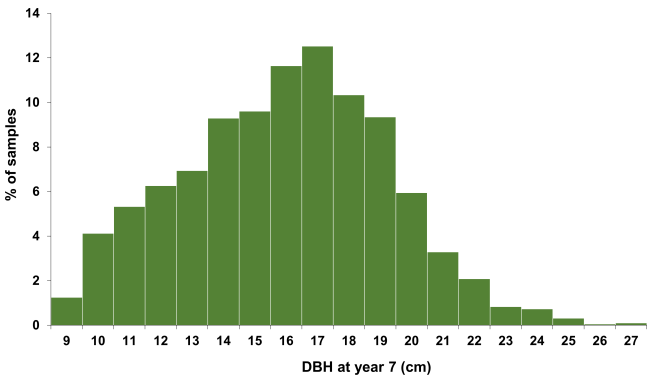

Figure 2. Frequency distribution (n = 1916) of diameter of breast height at age 7 measurements in a natural variant *P. trichocarpa* population. Bin width is equal to 1 cm.

Natural variation in *P. trichocarpa* populations – lignin composition

A Py-MBMS analysis of a subset of 204 samples was selected based on representative sugar content distribution as determined via the NMR method described above. The dataset of composition is included in a downloadable file.[38] The subset of samples had an estimated average lignin content of 0.246 (σ = ±1.1) mg mg biomass $^{-1}$, ranging from 0.192 to 0.266 mg lignin mg biomass $^{-1}$. The syringyl to guaiacyl ratio (S/G) of lignin monomers for the subset was 2.1 (σ = ±0.1), ranging from 1.8 to 2.5.

Natural variation in *P. trichocarpa* growth

The ramets for the genotypes used in the compositional analysis were not the same ramets for the diameter at breast height measurements at age 7 (DBH7). The ramets used for the compositional analysis were harvested at age 3 in Corvallis, OR, while the DBH7 values came from measurements taken of the same genotype in different fields in Clatskanie, OR, with one to three replicate ramets measured for each genotype. We have assumed that the composition will correlate between these sample sets. After

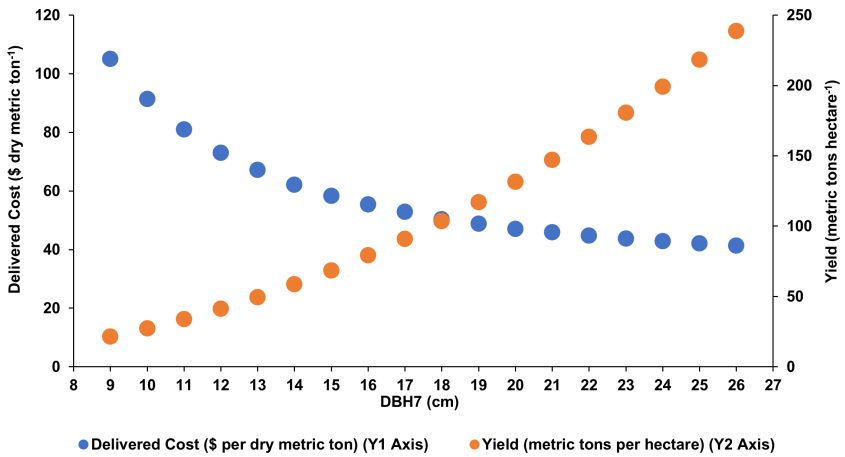

Figure 3. Delivered cost and field yield distributions compared to DBH7 as the measure of total tree mass. *Y*1 axis, left, delivered cost ($ dry metric ton^{-1}); *Y*2, right, yield (metric tons hectare^{-1}); *X* axis, DBH7 (cm).

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3 years, the proportion of juvenile wood in the sample cores will have decreased. Likewise, DeMartini *et al.*[36] observed in one poplar tree with ring-to-ring variability decreasing with age. Across the population, the mean DBH7 was 15.9 cm with a standard deviation of 3.3 cm. Figure 2 shows the variation of DBH7 across all measured trees.

Feedstock cost model

The frequency distribution of poplar diameter data (Fig. 2) was used to calculate feedstock cost delivered to the biorefinery. The delivered cost, shown in Fig. 3, includes the total cost to plant and maintain the fields, harvest, transport, and chip the poplar feedstock. As the annual biorefinery demand, density of fields in poplar production (hectares/mi), and the number of trees planted per hectare were held constant for each simulation, the key impacts of tree size on cost were harvest efficiency and transportation cost. With increasing tree diameter, and thus mass, fewer trees are needed which reduces the equipment and labor required to harvest and transport the total feedstock mass. Increasing tree diameter also reduces the number of fields needed to meet biorefinery demand which reduces the supply radius and transportation distance. Shorter transport distances reduce the log transport time, truck return time to collect the next load, and total number of trucks needed. As DBH7 increases from 9 to 26 cm, the delivered cost decreases by nearly 60%. As tree mass, and thus yield, was calculated as an exponential function of diameter in this analysis (Eqn 1), delivered cost was more significantly impacted by tree size at the lower range of tree diameters considered. It should be noted that this is a techno-economic cost and not necessarily the price that a biorefinery would pay for feedstock. We assume that as the incurred cost of feedstock increases or decreases, so would the purchase price of the feedstock.

Techno-economic analysis

Figure 4 provides the frequency distributions and summary of results for the subset of 204 poplar samples used in techno-economic analyses (TEA). Results are shown for (a) MFSP: min = \$0.52 L^{-1}, max = \$0.65 L^{-1}, $\bar{x}$=\$0.56 L^{-1}, σ = \$0.02 L^{-1} (4.47%), bin width is 0.01 \$ L^{-1}; (b) Process ethanol yield: min = 360 L dry metric ton $^{-1}$, max = 400 L dry metric ton $^{-1}$, $\bar{x}$=376 L dry metric ton $^{-1}$, σ = 5 L dry metric ton $^{-1}$ (1.48%), bin width is 3 L ton $^{-1}$; (c) Field ethanol yield: min = 1400 L ha $^{-1}$ year $^{-1}$, max = 11 100 L ha $^{-1}$ year $^{-1}$, $\bar{x}$=4810 L ha $^{-1}$ year $^{-1}$, σ = 1840 L ha $^{-1}$ year $^{-1}$ (38.2%), bin width is 1000 L ha $^{-1}$ year $^{-1}$. The MFSP varied moderately among samples (σ = ±4.47%) while process ethanol yield maintained a relatively small variability relative to the mean (σ = ±1.48%). Field ethanol yield varied the most relative to the mean (σ = ±38.2%) as well as over the range of observed values, with the maximum value approximately eight times the minimum. Table 1 lists the range of the costs for several aggregated sectors, including feedstock.

To determine the phenotypic drivers of the poplar samples to each quality attribute, MFSP, process ethanol yield, and field ethanol yield were plotted against the mass fraction of fermentable carbohydrates and DBH7 in Fig. 5. Both MFSP and field ethanol yield showed trends against DBH7 (b, f) while no relationships were observed when MFSP and field ethanol yield were plotted against the mass fraction of fermentable sugars (a, e). Conversely, process ethanol yield showed a strong trend against mass fraction of fermentable carbohydrates (c), while no trend was observed when plotted against DBH7 (d). This led us to the

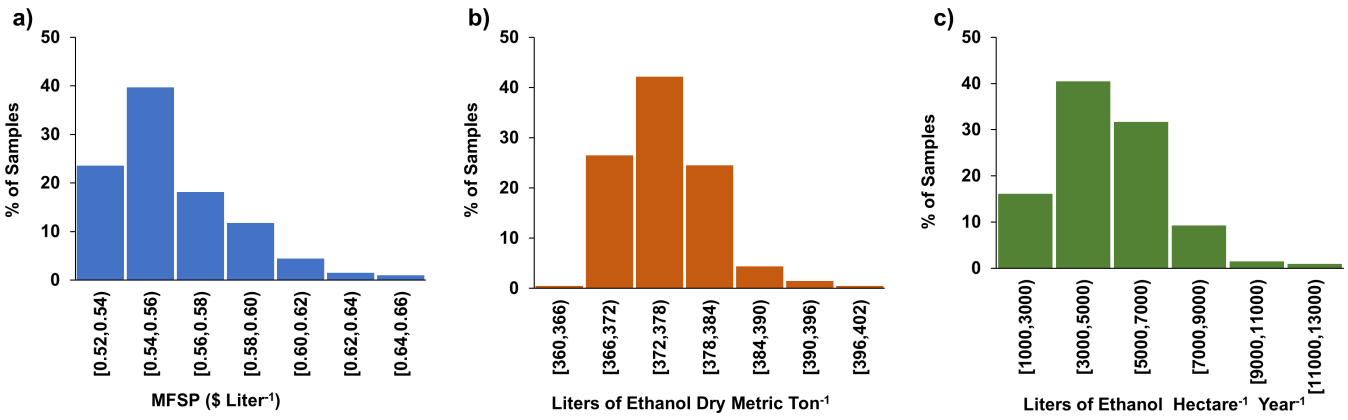

Figure 4. Frequency distribution for poplar subset (n = 204) incorporated in the techno-economic analysis highlighting economic and yield metrics as follows with bin width equal to standard deviation: (a) MFSP, σ = ±\$0.02; (b) process ethanol yield, σ = ±6; and (c) field ethanol yield, σ = ±2000.

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Table 1. Range of costs and revenues in the biorefinery TEA across the population of 204 genotypes studied.

	Average	Min	Max	Standard deviation
Total capital investment ($MM)	452	448	456	1.5
Ethanol revenues ($MM year^{-1})	138	128	165	6.3
Yearly feedstock costs ($MM year^{-1})	34.3	25.7	56.9	6.0
Variable operating costs minus feedstock ($MM year^{-1})	40.0	38.1	44.5	0.9
Electricity credits ($MM year^{-1})	5.8	2.3	7.4	0.7

observation that size (DBH7) and carbohydrate percentage are not correlated across this population. Figure 6 illustrates this lack of relationship for glucose; there was a similar lack of correlation for other carbohydrates as well as lignin and S/G (data not shown). Thus, across the entirety of variability in the natural population, MFSP and field ethanol yield are most strongly influenced by allometric attributes, while process ethanol yield is most strongly influenced by compositional attributes. This agrees with recent literature[37,38] on more general biomass feedstock cost versus quality impacts. Here the results are extended into genotypic and phenotypic variability within populations. A more in-depth analysis on MFSP is given in the discussion section.

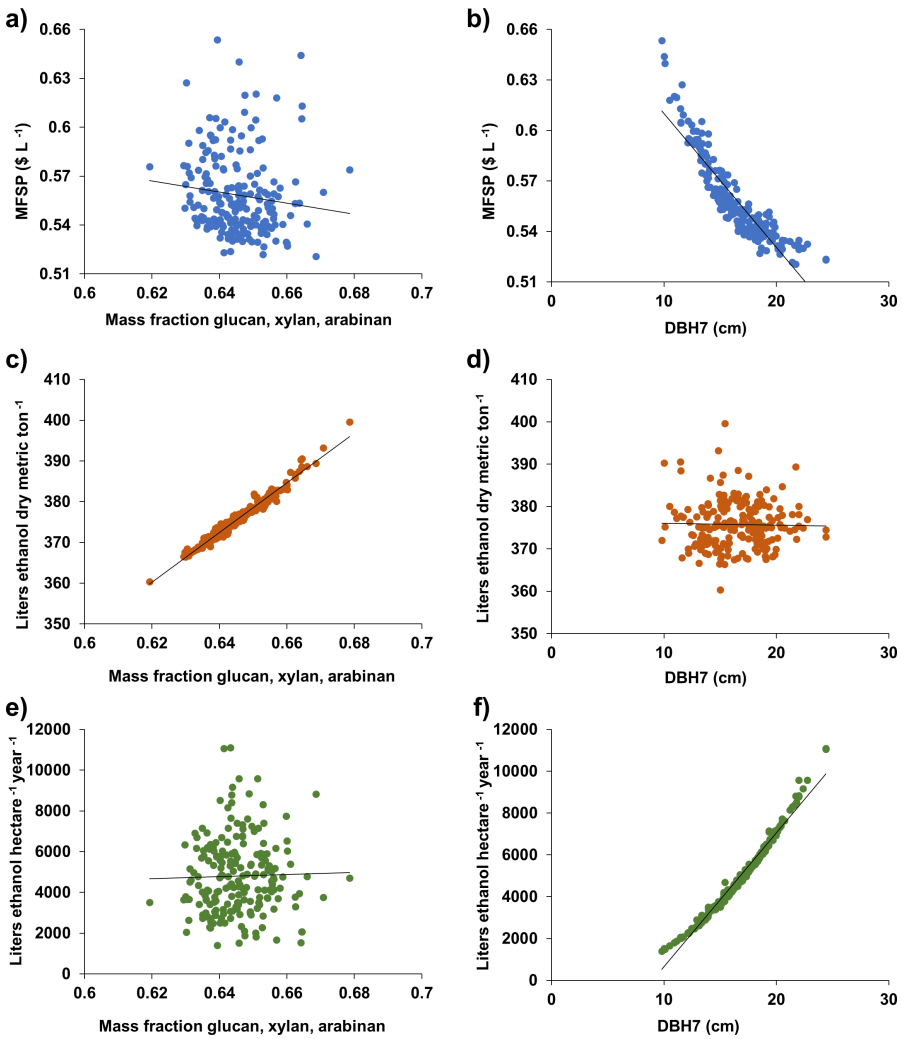

Figure 5. Relationships between (a, b) MFSP ($ gal $^{-1}$), (c, d) process ethanol yield (gal dry ton $^{-1}$), and (e, f) field ethanol yield (gal acre $^{-1}$ year $^{-1}$) against mass fraction fermentable carbohydrates (glucan, xylan, arabinan) and DBH7. R^2 values: (a) 0.015, (b) 0.816, (c) 0.969, (d) 0.001, (e) 0.001, and (f) 0.974.

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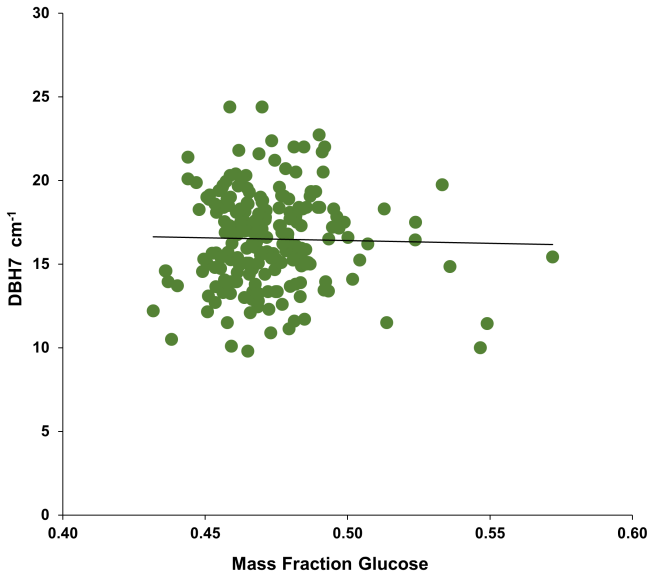

Figure 6. Relationship between DBH7 and mass fraction of glucose where R^2 = 0.0005.

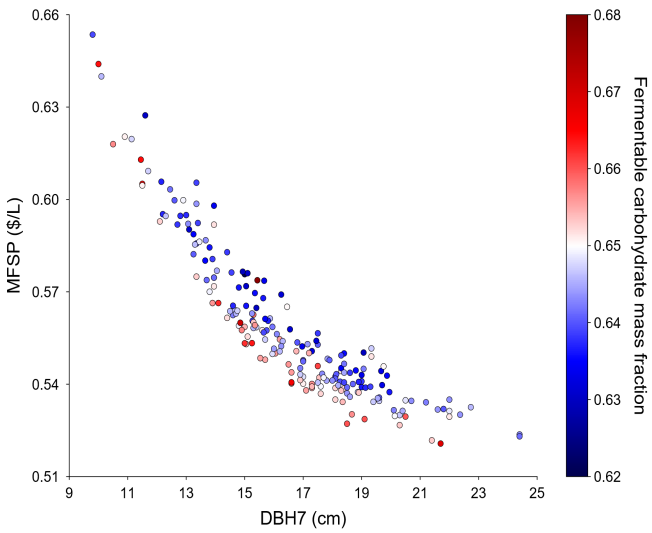

Figure 7. MFSP ($ L $^{-1}$) plotted against DBH7 (cm) with total mass fraction of fermentable carbohydrates (glucan, xylan, arabinan) shown for each sample by color.

Economic impact of yield and composition

The MFSP is a significant focal point in evaluating the economic feasibility of a biorefinery, so the relationship with physical and compositional phenotypes was examined. As shown in Fig. 5(a) and (b), across the population there is a correlation for MFSP to decrease as DBH7 increases (R^2 = 0.816), but no correlation is observed when MFSP is plotted against the fraction of fermentable carbohydrates (R^2 = 0.015). This is despite the strong relationship of fermentable carbohydrate mass fraction versus fuel yield (c) (R^2 = 0.969) where higher revenues can be expected through additional product sales. The reasoning for this can be determined through examination of population variability for each phenotype. For example, while total fermentable carbohydrate fraction varied across the population by only 9.58%, leading to fuel yield changes of 10.9%, DBH7 had over an order of magnitude more variation of 249% leading to differences between the minimum and maximum feedstock costs of 222%. With feedstock cost contributing significantly to MFSP, and given its high variability across the population due to high fluctuations in growth, any economic improvements due to enhanced yield of a few percent were far overshadowed by the spread in cost.

Figure 7 again plots MFSP versus DBH7 but gives the mass fraction of fermentable carbohydrates for each poplar in color with red showing higher carbohydrate mass fractions and blue showing lower carbohydrate mass fractions the dataset is provided.[38] The MFSP is most strongly influenced by DBH7, decreasing as diameter increases, while the range of MFSP for a given DBH7 trends towards being driven by the mass fraction of fermentable carbohydrates with higher fractions of glucan, xylan, and arabinan (red) towards the lower end of MFSP and lower fractions (blue) towards the higher end of MFSPs. When observed simultaneously, despite the primary influence on MFSP at this scale being diameter, there is a notable trend that, for any given DBH7, the highest MFSPs are samples with lower amounts of fermentable carbohydrates, while the lowest MFSPs contain the samples with the highest fermentable carbohydrates.

While DBH7 is decidedly influential on MFSP across the entirety of the poplar population, in practice only the largest trees will be of primary consideration when selecting a clone to plant in the field. To evaluate MFSP trends further among these trees, the poplars among the top 25% of DBH7 (n = 51) from the 204 analyzed samples were selected[38] and linear regressions were conducted on MFSP against both DBH7 and mass fraction fermentable carbohydrates. Among this subset, feedstock delivered cost varies between \$42.4 dry metric ton^{-1} to \$52.8 dry metric ton^{-1} (24.5%) helping to normalize against the high variability observed in the population, and the influence of composition on MFSP becomes more significant. Here, MFSP is correlated nearly as strongly to fermentable carbohydrates (R^2 = 0.321) as it is to DBH7 (R^2 = 0.365), with MFSP varying up to \$0.03 L^{-1}. For a biorefinery producing 246 million liters of ethanol per year with an MFSP of \$0.54 L^{-1}, the average among the largest 25% of trees, an improvement in profit by just \$0.01 L^{-1} to the ethanol selling price adds \$19.0 million in profits

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over the lifetime of the biorefinery. When extended to the entirety of the MFSP variation among this subset due, in part, to an improved fermentable sugar fraction, an \$0.03 L^{-1} improvement adds \$56.7 million in profits over the lifetime of the biorefinery. Thus, although physical attributes and biomass yield should be the primary considerations when selecting the most economically fit poplar clones, the quality in terms of its composition should be an equal consideration among the largest of trees and even modest yield and profit improvements due to enhanced sugar content can add significant value over the lifetime of a biorefinery.

Value proposition for genetic engineering or breeding of improved varieties

It has been shown that natural variation across the population carries significant economic impact but future genetic engineering of selected clones may allow for further improvement of carbohydrate content, adding additional value to harvested biomass. Thus, the economic benefits of carbohydrate content independent of tree size should be understood. To evaluate a hypothetical scenario whereby additional carbohydrate content is engineered into a tree, two clones of similar composition but of different size, were selected and the mass fraction of glucose was increased by an additional 5% absolute, while lignin content, considered to be of little economic value in ethanol production, was decreased to make up the mass balance. It should be noted that the intention in selecting these clones was not to recommend these particular clones over others, but that these were chosen due to compositional similarities and to highlight hypothetical modifications across different tree sizes. The MFSP was determined both before and after composition adjustments and the results are summarized in Table 2.

Through increased glucan, both BESC-878 and GW-9824 showed MFSP reductions of \$0.02 L^{-1} (3.9% and 4.0%), respectively. For the hypothetically engineered clone BESC-878, the MFSP (\$0.52 L^{-1}) matches the minimum observed in the natural population, despite DBH7 (17.6 cm) being significantly below the maximum from the data set (24.4 cm), highlighting how composition can compensate for economic losses in smaller trees, perhaps in a region where sub-optimal growing conditions may reduce maximum size. Our observations support the view that biomass yield and quality are not strongly correlated by genotype. This will allow for simultaneous breeding objectives of quality and yield; these can be pursued without additional cost or time, other than the minor cost of sampling and compositional analysis. While this analysis is hypothetical, future genetic engineering and breeding towards optimizing both composition and growth across the poplar species presents an opportunity for growers and biorefineries to improve productivity and increase revenues pushing the MFSP even lower and solidifying poplar as an optimal feedstock.

Future work

Future techno-economic assessments should be expanded to look at additional bio-based products and fuels, such as those produced from lignin, providing process and economic results in the context of alternative pathways and investigating potential new phenotypic drivers, such as overall lignin content or composition. Additional feedstocks and the initial base-case assumption of process similarity between stover and poplar should be examined. Studies should also examine the impact of biomass recalcitrance or digestibility on both conversion and pretreatment processing costs, perhaps by extrapolating from unoptimized laboratory screens. Further work is ongoing and includes genome-wide association studies to determine the genetic regulation of cell-wall sugar composition, and studies meant to address the effects of relevant genetic alterations and their impact on other growth and compositional characteristics of poplar trees. We believe that the trends seen in this study will generally hold when this type of analysis is repeated using future data on the linked variation of yield and composition in other biofeedstocks (e.g., switchgrass, miscanthus, sorghum, etc.).

Conclusions

We have shown how a range of natural variation in cell-wall composition for *Populus trichocarpa* impacts the economics associated with biorefinery processes and how phenotypic

Table 2. MFSP (\$ L^{-1}) comparison of natural poplar versus hypothetically engineered clones.

Poplar clone	DBH7 (cm)	Feedstock cost (\$ dry metric ton^{-1})	Mass fraction glucan	Mass fraction lignin	MFSP (\$ L^{-1})
BESC-878	17.6	53.51	0.457	0.243	0.54
BESC-878 (engineered)	17.6	53.51	0.507	0.193	0.52
GW-9824	15.3	61.22	0.450	0.241	0.56
GW-9824 (engineered)	15.3	61.22	0.500	0.191	0.54

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variation can drive breeding practices of poplar growers to develop optimized feedstocks to be used in such biorefineries. Within this population, tree size (DBH7) is the most influential driver of field ethanol yield and MFSP, but when selecting only the largest trees, the fraction of fermentable sugars becomes an equally important economic driver. This work will drive further research in developing a robust, sustainable feedstock for bio-derived fuels and products.

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