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REGULAR ARTICLE

Modeling sugar content of farmer-managed sugar beets (*Beta vulgaris* L.)

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ABSTRACT

We measured or estimated leaf and root physical and chemical traits of spatio-temporally heterogeneous field-grown sugar beet throughout its ontogeny during three growing seasons. The objective was to quantify the impact of temporal changes in these traits on root sugar content [S(R); g 100 g-1 root dry weight]. Artificial Neural Network (ANN), in conjunction with thermal time (ºCd), adequately delineated the boundaries (mean ± standard deviation, S.D.) between S(R) during early (41.6 ± 6.2), med (54.5 ± 3.0), and late ontogeny (63.4 ± 2.4), corresponding, respectively to low, medium, and high S(R). Calibration and validation Partial Least Squares (PLS) regression models, using plant physical and chemical traits, predicted and validated sugar content of sugar beet leaves [S(L)] and roots [S(R)] throughout its ontogeny with significant probabilities. Most physical and all chemical traits exhibited dynamic changes throughout plant ontogeny and, consequently, negatively or positively impacted S(R). The positive impact of S(L) and root volume (RV) on S(R) diminished towards the end of the growing season; whereas, the positive impact of root density (RD) and carbon:nitrogen (C:N) ratio in leaves [C:N(L)] and roots [C:N(R)] persisted throughout plant ontogeny. Specific leaf area (SLA), in particular, exhibited negative, then positive impact on S(R). The utility of physical and chemical traits of field-grown sugar beets in building reliable PLS models was confirmed using multivariate analysis on secondary statistics (residual mean square errors, RMSE and validation coefficients of determination, Q^2) which discriminated between and correctly classified low (100%), medium (95%) and high (97%) S(R) groups. The findings may have implications to design management practices that can enhance C:N ratio and C-sequestration in roots, maintain optimum, but not excessive, N level in developing leaves and roots, optimize root sugar content and minimize its variation under field conditions.

Key Words: *sugar content; artificial neural network; PLS model; physical plant traits; C:N ratio.*

Abbreviations: Artificial Neural Network, ANN; Carbon (%) in Leaf, C(L); Carbon (%) in Roots, C(R); Carbon:Nitrogen ratio in Leaf, C:N(L); Carbon:Nitrogen ratio in Roots, C:N(R); Leaf Area, cm^2, LA; Leaf Dry Weight, g, LDW; Leaf:Root Dry Weight Ratio, L:R; Nitrogen (%) in Leaf, N(L); Nitrogen (%) in Root, N(R); Plant Dry Weight, g, PDW; Root Density, g ml^{-1}, RD; Root Dry Weight, g, RDW; Root Volume, ml, RV; Specific Leaf Area, cm^2g^{-1}, SLA; Specific Leaf Weight, g m^{-2}, SLW; Sugar content in Leaves, g $100g^{-1}$ dry weight, S(L); and Sugar content in Roots, g $100g^{-1}$ dry weight, S(R).

INTRODUCTION

Approximately 55% of total sugar beet production in the United States is located in Minnesota (MN) and North Dakota (ND) (Maung and Gustafson, 2010). Although it is predominantly grown for sugar production (Khan, 2008), sugar beet qualifies as an advanced biofuel feedstock to produce ethanol with minimal nitrogen requirements and simpler sugar-to-ethanol conversion as compared to corn. Typical root fresh weight yields in MN range from 50-60 Mg ha^{-1} with 15-19% sugar content (Khan, 2008); whereas, on average, corn biomass (stover) and grain yields in the same region range from 7-10 and from 6-8 Mg ha^{-1}, respectively (NAAS-USDA, 2010).

Sugar beet if grown properly does not flower and continues to accumulate sugar throughout its ontogeny (Jaggard et al., 2009). However, field-grown and farmer-managed sugar beet crops are inevitably heterogeneous populations typically produced by crossing parental lines that are not hybrids. Therefore, such populations may not efficiently utilize external inputs (i.e., incident solar radiation, N fertilizer, water, etc.) and may not achieve their biomass and sugar content production potential (Jaggard et al., 2009; Nouri et al., 2009). Potential yield is usually lost in such non-uniform stands because space and resources are not efficiently and equally utilized by all plants (Çakmakçi et al., 1998; Jaggard et al., 2009). To increase potential yield, it was suggested to either increase the rate at which the foliage expands per unit of thermal time (ºCd), or modify management practices so that seedlings emerge from soil earlier for a better canopy development, or both (Bloch et al., 2006a; Jabro et al., 2009; Jaggard et al., 2009). However, a large number of factors (e.g., N supply, plant density, edaphic and weather conditions) may adversely influence canopy development (Çakmakçi et al., 1998; Hoffmann and Blomberg, 2004). Most modern varieties usually take 1050 ºCd from sowing to achieve 90% foliage cover; however, when the linear relationship between root dry weight and ºCd is considered (de Reffey et al., 2010), achieving higher root and sugar yields in the short-growing season climates of west-central MN (<2,500 ºCd) becomes a challenging task.

The sugar beet plant is unique in that the source (leaves) and sink (root) are anatomically directly connected and, therefore, any developmental changes of one have direct and immediate impact on the other, and eventually on the sugar content of roots [S(R)] throughout ontogeny (Shaw et al., 2002; de Reffye et al., 2010). Leaf growth and development, quantified by leaf area (LA), dry leaf weight (DLW), leaf specific area (LSA) or weight (LSW), as well as by the ratio of leaf dry weight:root dry weight (L:R) and leaf sugar content [S(L)] have direct effects on the growth and development of the root as the storage organ (Bloch and Hoffmann, 2005; Hoffmann, 2005). Alternatively, root volume (RV), density (RD) and dry weight (RDW) may have positive or negative impact on leaf growth and development, and eventually on S(R) (Lawlor, 2002; Launay et al., 2009). Therefore, modeling the interrelationships between these variables and their direct and indirect impact on sugar content throughout ontogeny may help improve crop management, assist farmers to reduce external inputs, and increase potential yield (de Reffey et al., 2010). The objective of this study was to quantify the impact of temporal changes in physical and chemical traits of leaves and root, and model sugar content in roots of heterogeneous populations of farmer-managed sugar beet in a major sugar beet growing region of the United States.

MATERIAL AND METHODS

FIELD EXPERIMENT

A common-garden field experiment in a complete randomized design was carried out during three years (2006, 2007 and 2009) at three locations in west-central Minnesota, USA. Sugar beet (*Beta vulgaris*) commercial variety was planted at a population density of 15-17 seedlings m^{-2}, then thinned to ~10 plants m^{-2} and managed for a target average fresh root yield of 55 Mg ha^{-1} and average sugar content of 18% sugar on fresh weight basis with inputs (fertilizers, herbicides, etc.) and management practices recommended for the region. Random whole plant samples (5 plants per sample, location and year) were collected starting at ~150 Julian days, or about 900 ^{o}Cd, and continued until full maturity at harvest time (~ 2,000-2,300 ^{o}Cd, min 5 ^{o}C; 7 samplings yr^{-1}). Each plant was separated into leaves and root, and then physical measurements were recorded or estimated on leaves and root of each plant. The relationship between S(R) and Log10(^{o}Cd) was used as an initial guide to classify S(R) data into those with low, medium and high sugar content during the growing season.

PHYSICAL MEASUREMENTS

Separate digital images of each root and its leaves, with a scale photographed in each image, were taken using a Nikon SLR digital camera with high resolution, and then images were converted to 8-bit binary (gray scale) format using the software package ImageJ (Rasband, 2010). The 8-bit images were used to calculate number and area of leaves, and root dimensions. Root and leaf samples at each sampling date were dried at 45 ^{o}C for 170-200 hours to a constant dry weight and the following physical traits were recorded or calculated for each sample: total plant dry weight, total leaf dry weight, total leaf area, leaf specific weight, leaf specific area, root dry weight, root volume, root density, and leaf:root dry weight ratio.

CHEMICAL ANALYSIS

Carbon and nitrogen were determined at each sampling date on leaf and root sub-samples using a LECO FP-428 analyzer (LECO, St. Joseph, MI), then the C:N ratio was calculated. Sugar content (sucrose, glucose and fructose) was determined using leaf and root sub-samples and expressed as g of total sugars per 100 g of leaf or root dry weight. The sugar content determination followed the procedure outlined in Hendrix (1993).

STATISTICAL ANALYSIS

Statistical moments (mean, S.D.) were estimated for all physical and chemical traits, including sugar content in leaves and roots, and then used for subsequent estimation of secondary (i.e., derived) statistics and model coefficients. A Multilayer Perception (MLP) Artificial Neuron Network (ANN) with 17[input]-10[hidden]-1[output] neurons (StatSoft, 2010) was used to classify the sugar content of sugar beet roots into three broad categories (low, medium and high) based on a matrix of 17 physical and chemical traits measured on plants, leaves and roots of 103 samples during three growing season. Mean and S.D. of sugar content in roots, and the corresponding statistics in leaves for each category are presented in Fig. 1.

MODELING APPROACH

Partial Least Squares (PLS) regression models were developed to predict S(R) in each category (i.e., low, medium and high sugar content) of samples identified through ANN analyses. Statistics of the calibration (R^2) and validation (Q^2, regression coefficients, and loadings of independent variables on the first partial least squares regression component, PLSC1) models were plotted in one dimension for each category to visualize the quantitative relationships between independent and dependent variables, and relationships between independent variables. The one-dimensional plots were used to identify trait dynamics throughout the growing season and how they impacted S(R). The validation procedure was performed by building a calibration model using 75% of data points and then deploying the model to predict the remaining 25% (StatSoft, 2010).

An estimate of the model intercept (β_o) and the residual mean squares error (RMSE), in addition to the validation coefficient of determination (Q^2) of each PLS model were plotted for the leaf and root low-, medium-, and high-sugar content categories. Loadings of independent variables (physical root and leaf traits, C:N ratios in roots and leaves, or both, along with correlation coefficient between RMSE and each of β_o and Q^2, in each case were listed as indicators of trait dynamics throughout the growing season. Finally, a matrix of

RMSE and Q^2 estimates derived from the PLS models for S(L) and S(R) in each of the low, medium and high S(R) categories was used in a discriminant analysis to verify the initial ANN-MPL classification, and to validate the use of physical and chemical traits in building reliable PLS models for field-grown sugar beets.

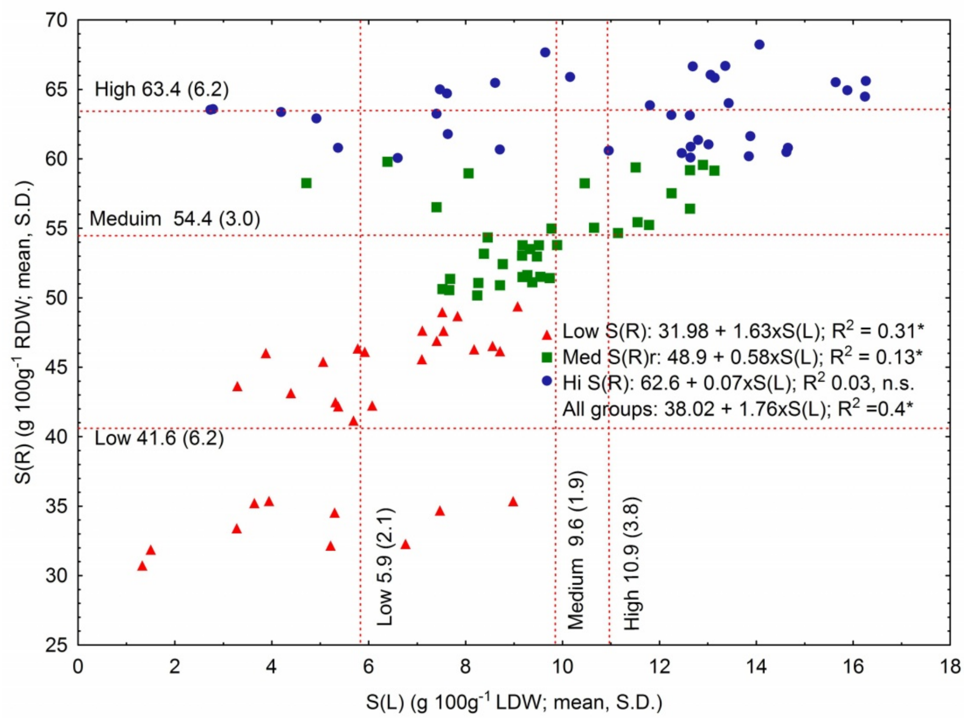

Figure 1. Descriptive statistics [mean and (S.D.)], univariate relationships and predictive equations between sugar content in leaves, S(L), and roots, S(R) in g 100 g^{-1} of leaf (LDW) and root (RDW) dry weight, respectively, during early (low sugar content), med (medium sugar content), and late (high root sugar content) ontogeny of sugar beets sampled during three growing seasons.

RESULTS

ROOT SUGAR CONTENT AND ONTOGENY

A Partial Least Squares (PLS) regression model described S(R) throughout the growing season as a function of S(L) as follows:

$$Y = 38.02+1.76 \times S(L);\ R^2 = 0.4;\ P < 0.05 \quad (1)$$

However, when Log_{10} thermal time [Log_{10}(ºCd)], S(L), and their interaction during the growing season, were included, the validation PLS model accounted for 60% of variation in S(R) [$Q^2 = 0.60$; $P < 0.05$], as follows:

$$Y = 38.5+1.754xS(L)+0.31xLog_{10}(^{o}Cd)-2.9xS(L)xLog_{10}(^{o}Cd) \quad (2)$$

The PLS model in (2) suggests that S(L) and ºCd have positive impacts on S(R); however, as the growing season progressed, the interaction between these two factors tended to cause a decrease in S(L). The two-way dependency of S(R) on S(L) and ºCd is supported by a strong multiple correlation ($r = 0.75$; $P < 0.0001$) found between S(R) and both predictors in (2) above.

ANN CLASSIFICATION

The Multilayer Perception (MLP) Artificial Neural Network (ANN), with 17[input]-10[hidden]-1[output] neurons, classified the whole data set into three S(R) categories (i.e., low, medium and high) based on a matrix of 17 physical and chemical traits measured on plants, leaves and roots of 103 samples during three growing season. The R^2 values for the training, testing and validation samples were 89.7, 88.0 and 85.5, respectively, indicating that the classification, as reported in Fig. 1 was confirmed with large level of accuracy. Descriptive statistics [low (41.6 ± 6.2), medium (54.5 ± 3.0), and high (63.4 ± 2.4 g $100g^{-1}$ dry weight) S(R)] and sample distribution based on the relationship between sugar content in leaves and roots of the three categories (Fig. 1) suggest that the relationship estimated by R^2 of PLS regression models, declined, and eventually disappeared at the end of the growing season. The overlap between the medium and high root sugar content categories (and the corresponding sugar content in leaves) was evident almost throughout the growing season. However, when the whole growing season was considered, a significant relationship (R^2 = 0.40; $P < 0.05$) was found between sugar content in leaves and roots.

PLS MODELS FOR INDIVIDUAL S(R) CATEGORIES

The PLSC1 calibration (R^2 = 0.86; $P < 0.01$) and validation (Q^2 = 0.81; $P < 0.01$) models accounted for most of the variation in the "Low" S(R) category (Fig. 2A). Most physical traits loaded positively and were significantly correlated with PLSC1. However, C(L) although had a positive impact on S(R), and unlike C:N(L), C:N(R) and C(R), was not significant; whereas both N(L) and N(R) had negative impacts on S(R) at this stage. Specific leaf weight (SLW), and L:R, unlike other leaf and root traits, loaded negatively on PLSC1 and, presumably, contributed to low S(R). Leaf area, SLA and LDW were closely related to each other and, based on their similar loadings on PLSC1, closely linked to RDW, RV, and, to a lesser extent, RD. Finally, S(L) and RD, although were positively correlated with PLSC1, their positive regression coefficients were not significant. The following explanatory variables had significant regression coefficients in the PLSC model (Fig. 2A), in predicting S(R) in the "early-season, low-sugar content" S(R) category:

$$Y = 33.0+2.5e\text{-}03xPDW+5.1e\text{-}04xLDW+1.3e\text{-}03xLA-9.3e\text{-}4xSLA+1.97e\text{-}03xSLW-3.9e\text{-}05xL{:}R+2.04e\text{-}03xRDW+7.9e\text{-}03xRV-1.7e\text{-}05xN(L)+3.75e\text{-}05xC{:}N(L)-1.9e\text{-}05xN(R)+2.5e\text{-}05xC(R)+3.6e\text{-}04x\ C{:}N(R) \quad (3)$$

In the "Medium" S(R) category (Fig. 2B, middle panel), the PLSC1 calibration (R^2 = 0.69; $P <$ 0.01) and validation (Q^2 = 0.46; $P < 0.01$) models accounted for a smaller portion of the variation. At this stage in the ontogeny of sugar beets, most physical and chemical traits loaded on PLSC1 in a similar manner as they did on PLSC1 of the "Low" S(R) category; however, C(L) had negative, but not significant, impact on S(R). Also, a larger portion of the variation in S(R) was unaccounted for by model (4, see below) as compared with model (3). In addition, a larger gap (0.23) was found between the calibration (R^2 = 0.69) and validation (Q^2 = 0.46) models in this case as compared to a much smaller gap (0.05) found for the "Low" S(R).The following explanatory variables had significant regression coefficients in the PLSC model (Fig. 2B), describing root sugar content (Y) in the "med-season, medium-sugar content" S(R) category:

$$Y = 52.3+2.9e\text{-}05xPDW+1.06e\text{-}05xLDW+6.06e\text{-}04xLA-1.2e\text{-}05xSLA+1.4e\text{-}05xSLW-4.8e\text{-}07xL{:}R+1.85e\text{-}05xRDW+1.01e\text{-}04xRV-1.8e\text{-}07xN(L)+4.7e\text{-}07xC{:}N(L)-1.9e\text{-}07xN(R)+1.6e\text{-}07xC(R)+4.7e\text{-}6xC{:}N(R) \quad (4)$$

The PLSC1 calibration (R^2 = 0.82; $P < 0.01$) and validation (Q^2 = 0.56; $P < 0.01$) models accounted for an intermediate portion of the variation in the "High" root sugar content category (Fig. 2C) as compared with the "Low" and "Medium" sugar categories. The following explanatory variables had significant regression coefficients in the PLSC model, describing root sugar content (Y) in the "late-season, high-sugar content" S(R) category:

$$Y = 62.3\text{-}3.4\text{e-}04\text{xPDW-}1.47\text{e-}04\text{xLDW+}3.2\text{e-}04\text{xLA+}1.4\text{e-}04\text{xSLA-}1.5\text{e-}04\text{xSLW-}2.6\text{e-}04\text{xRDW-}1.6\text{e-}03\text{xRV+}9.5\text{e-}08\text{xRD-}3.3\text{e-}06\text{xN(L)+}3.4\text{e-}06\text{xC(L)+}1.9\text{e-}05\text{xC:N(L)+ }2.2\text{e-}06\text{xC(R)+}7.5\text{e-}05\text{xC:N(R)} \quad (5)$$

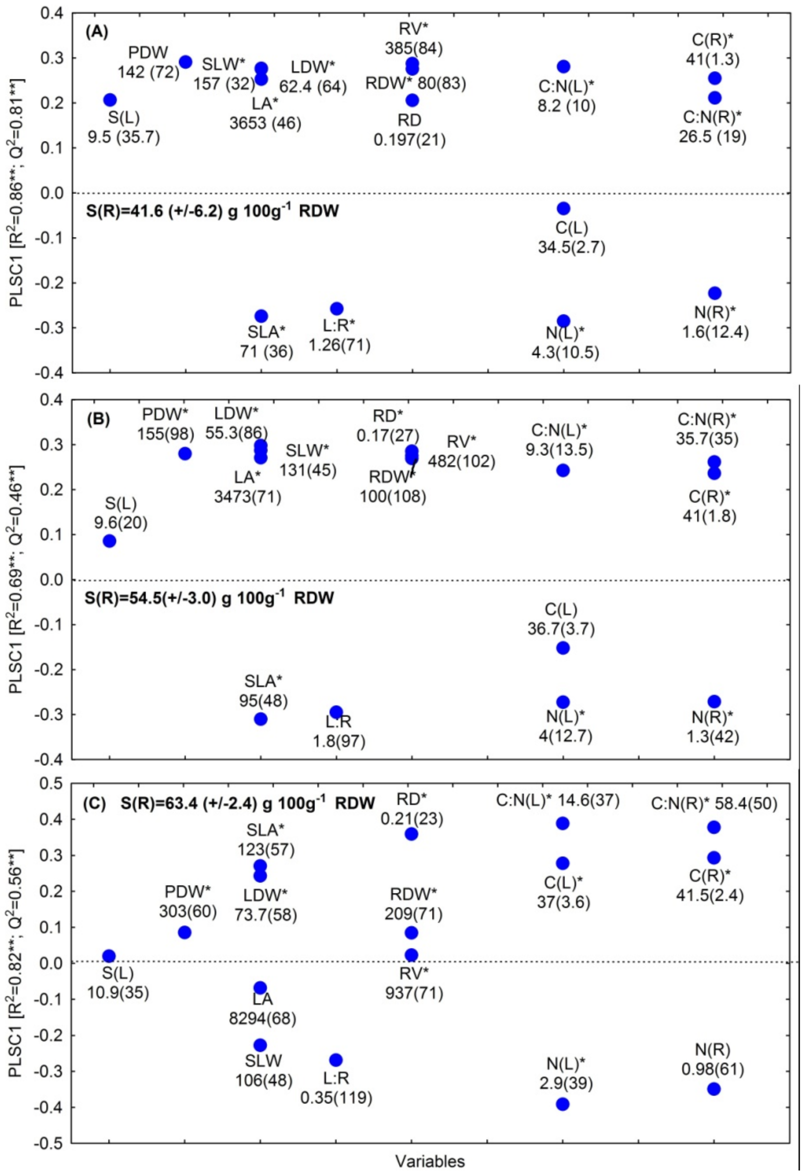

Figure 2. Mean and (coefficient of variation), calibration (R^2) and validation (Q^2) model coefficients and loadings (i.e., correlation coefficients between variables and the first Partial Least Squares Regression Component, PLSC1; *Y-axis*) of physical and chemical traits measured on plant, leaves and root of sugar beet with low (41.6 ± 6.2 g 100g^{-1} root dry weight; A), medium(54.5 ± 3.0 g 100g^{-1} root dry weight; B), and high (63.4 ± 2.4 g 100g^{-1} root dry weight; C) sugar content in roots on PLSC1 [see *Abbreviations* for trait name and unit of measurement; an "*" denotes a significant (P < 0.05) impact of a trait on S(R)].

Three variables, [S(L), L:R, and N(R)], had negative, but not significant impact on S(R) in the "High" S(R) category. In addition, 50% of the remaining variables tended to cause a decrease in S(R) at this stage. Of significant importance are C(L), C(R), C:N(L), and C:N(R) as positive determinants of S(R).

PHYSICAL AND CHEMICAL TRAIT DYNAMICS

Secondary statistics (i.e., RMSE, β_o, Q^2 and loadings of physical and chemical traits on PC1) for the low-, medium-, and high-S(L) (Fig. 3A) and for the low-, medium-, and high-S(R) (Fig. 4), and the correlation coefficients between RMSE and each of β_o and Q^2 confirm trait dynamism for most, but not all, traits throughout ontogeny. The first principal component (PC1) accounted for 69, 71, and 43% of variation in 10 physical and two chemical traits of the low-, medium, and high-S(L) categories, respectively. Loadings of five physical traits (PDW, LDW, RV, RDW, and L:R ratio) remained relatively stable throughout ontogeny (Fig. 3A); whereas, loadings of S(L), LA, SLW, SLA, C:N(L), and C:N(R) showed medium to large levels of decline, especially late in ontogeny.

Estimates of RMSE and their correlation with β_o differed as to the S(L) category and the composition of independent traits used in developing the respective PLS models. RMSE estimates were slightly larger for the medium- as compared with the low-S(L) category and whether physical, chemical or both trait sets were used to estimate PLS model coefficients. A large increase in RMSE estimate was observed for the high-S(L) category. Nevertheless, negative and significant relationships were found between RMSE and β_o, the strongest of which ($r = -0.86$; $P < 0.001$) was found for the high-S(L) category.

Notwithstanding the loadings of physical and chemical traits on PC1 (see above), a gradual decrease in the validation Q^2 for S(L) was observed as sugar beet plants approached maturity and a concomitant change in some leaf and root physical and chemical traits. Correlation coefficients between RMSE and validation Q^2 (Fig. 3B) were small and non-significant for low-S(L) and high-S(L), but not for the medium-S(L) category ($r = 0.66$; $P < 0.05$). Very little, if any, impact is evident on the magnitude and trend of the relationship between RMSE and validation Q^2 whether physical, chemical, or both groups of traits were used as predictors.

The gradual increase in β_o, as a natural consequence of increasing S(R), and the concomitant decrease in RMSE of S(R) is statistically supported by the declining negative relationship between these two model parameters from -0.78 ($P < 0.001$) for the low-S(R), to -0.62 ($P < 0.05$) for the medium-S(R), and finally to -0.50 ($P < 0.05$) for the high-S(R) categories (Fig. 4A). Independent variables displayed medium to large levels of dynamism as quantified by their loadings on, and the amount of variation accounted for by PC1 in different S(R) categories; however, they did not substantially affect the magnitude and the relationship between RMSE and β_o.

A significantly stronger and negative relationship was found between RMSE and Q^2 for all three S(R) categories (-0.96; $P < 0.0001$) (Fig. 4B). The impact of physical traits on S(R) estimates declined dramatically as sugar beet plants approached maturity. However, the rate of decline (i.e., change in Q^2 value) was smaller when C:N(L) and C:N(R) alone or in combination with physical traits were used as S(R) predictors.

DISCRIMINATION BETWEEN S(R) CATEGORIES

The discriminant analysis resulted in almost total separation and correct classification of 100% of low-, 95% of medium-, and 97% of high-S(R) categories based on secondary statistics. The largest Mahalanobis squared distance ($D^2 = 49.6$; $P < 0.0001$) was found between the low- and high-S(R) categories, followed by D^2 (39.4; $P < 0.001$) between low- and medium-S(R); whereas, the shortest, albeit significant, distance ($D^2 = 22.1$; $P < 0.005$) was found between medium- and high-S(R). The first of two canonical discriminant functions (CANDISC-1) accounted for 0.72 of total variation and separated the low- from medium- and high-S(R) categories; whereas, the second discriminant function (CANDISC-2) accounted for the remaining 0.28 of total variation and separated the medium- and high-S(R) categories from each other.

Three secondary statistics [RMSE and Q² of S(L), and Q² of S(R)] had decreasing negative standardized coefficients on CANDISC-1; whereas, RMSE of S(R) had a positive standardized loading. The three secondary statistics [RMSE of S(L), Q² and RMSE of S(R)], all had positive standardized coefficients on CANDISC-2.

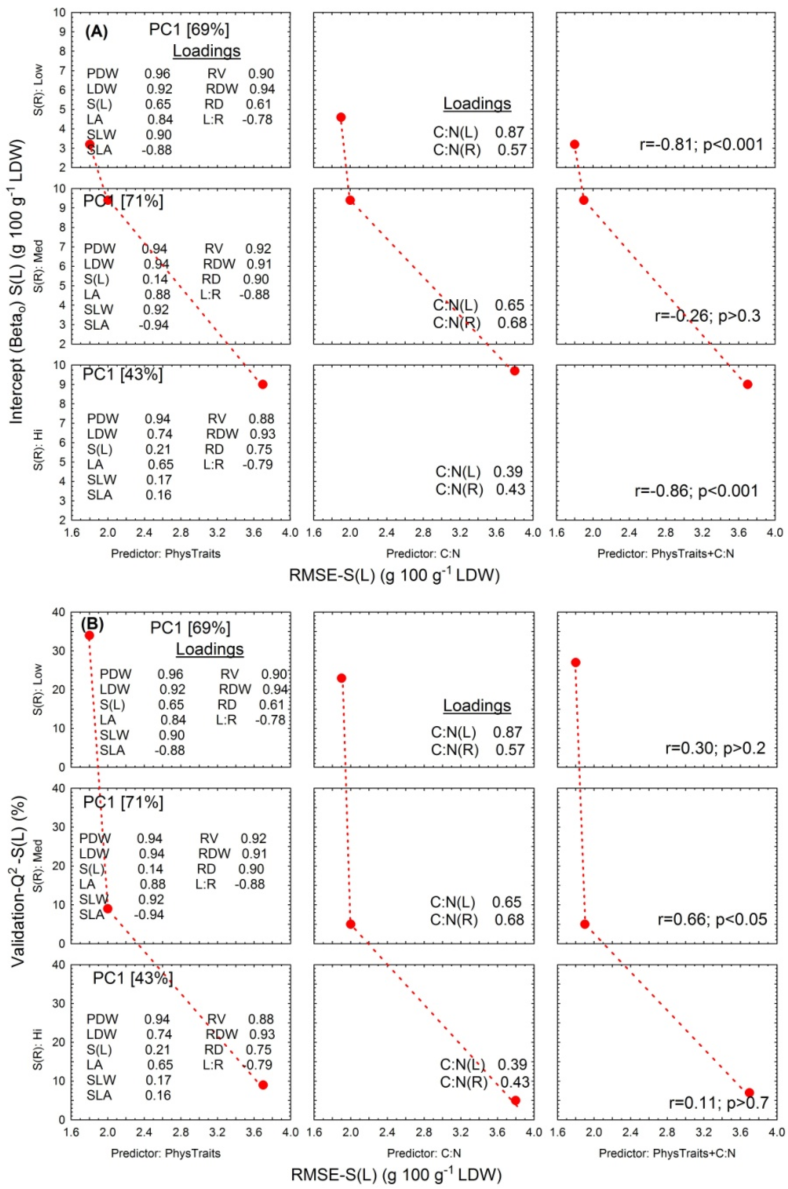

Figure 3. Leaf-based relationships (r- values) between secondary statistics (residual mean squares error, RMSE and each of validation coefficient of variation, Q^2, and partial least squares regression intercept, β_o) of sugar content (g $100g^{-1}$ dry matter), and loadings on the first principal component (PC1) derived from plant, leaves, and root physical and chemical traits of sugar beet with low, medium, and high root sugar content.

DISCUSSION

ROOT SUGAR CONTENT AND ONTOGENY

A reasonably large portion of variation (Q² = 60%) in S(R) under the short growing season of west-central MN was accounted for by S(L), thermal time, and their interaction. The power of S(L) in accounting for variation in S(R) declined over time and disappeared altogether at the last sampling dates (Fig. 1) indicating that there is no feedback inhibition or sink limitation to store sugar in the developing storage roots (Launay et al., 2009). However, the negative regression coefficient (-2.9; Equation 2) of S(L) x Log10(ºCd) suggests that ºCd, in particular, may become a limiting factor late in ontogeny under short growing seasons (de Reffey et al., 2010). Therefore, to increase potential biomass and S(R) yields, new management practices that allow for early seedling emergence, uniform population density, and high N use efficiency (Hoffmann, 2005; Jaggard et al., 2009); and new varieties that can achieve ~90% foliage cover at lower thermal time (~850 ºCd) are needed (de Reffey et al., 2010).

VALIDATION PLS MODELS

The apparent differences between calibration (R^2) and validation (Q^2) coefficients of determination (Fig. 2) within and between S(R) categories are caused, for the most part, by the dynamic variation (expressed as C.V.) in physical and chemical traits throughout ontogeny. The steady increase in S(R) was associated with decreasing variation (S.D.) over time. This trend may suggest that the source, expressed as a negative and significant impact of SLA (Fig. 2A and 2B), could have been a limiting factor (Hoffmann and Blomberg, 2004; Kenter and Hoffmann, 2006). In addition, the declining L:R ratio (from 0.78 to 0.35, Fig. 2) may have contributed to this trend, knowing that most leaf weight in late ontogeny is attributed to petioles that can be considered as a sink (Launay et al., 2009) The sink components (i.e., RV, RDW and RD) were not limiting throughout ontogeny, although their C.V. values fluctuated over time, with RD being most stable and exhibited an increasingly positive impact on S(R). The decoupling of RD from each of RDW and RV, and the declining, albeit significant, impact of the last two sink components on S(R) late in ontogeny may offer the opportunity to overcome the physiologically-determined negative relationship between RDW and S(R) (Hoffman, 2005).

Nitrogen in leaves and roots, although declined in magnitude and increased in variability over time, had negative and mostly significant impact on S(R); this trend may have implications for N nutrition and management under field conditions (Hoffmann, 2005; Jaggard et al., 2009). However, in view of the more constant (~41%) and stable (C.V. 1.3-2.4%) carbon in roots, the C:N(R) ratio displayed an increase in magnitude (from 26.5 to 58.4) and variation (C.V. 19 to 50%) throughout ontogeny. The C:N ratios in leaves and roots, both of which had positive and significant impact on S(R), may directly impact S(R) through dry matter partitioning (Hoffman, 2005) and indirectly due to the linkage between N and carbohydrate metabolism (Lawlor, 2002).

PHYSICAL AND CHEMICAL TRAIT DYNAMICS

The dynamics of leaf and root development and their impact on root sugar content were adequately described by PLS regression models. Model coefficients (Equations 3-5) can contribute to the development and validation of potentially widely applicable morphogenetic model for sugar beet growth and production (de Reffey et al., 2010). Several trait (Fig. 2) whether they have static (e.g., RDW, RV), dynamic (e.g., LA, SLA and SLW), or decreasing loadings on PC1 over time [C:N(L) and C:N(R)] could be manipulated through novel management practices (Çakmakçi et al., 1998; Nouri et al., 2009; Jabro et al., 2010), plant nutrition (Shaw et al., 2002), or plant breeding and selection (Jaggard et al., 2009; de Reffye et al., 2010) for better resource utilization and sugar production.

The quantitative relationships between secondary statistics (i.e., model intercept, β, residual mean squares error, RMSE, and validation coefficient of determination, Q^2) for S(L) and S(R) (Fig. 3 and 4, respectively) provide some insights into the overall functioning of leaf and root physical and chemical traits, or both, and their ability to predict S(L) and S(R) over time. The most ideal combinations are to have PLS validation regression models with low RMSE and high Q^2 associated with high β values, especially when predicting S(R). These conditions were partially met for S(L) where small RMSE and high β values were associated during mid-season [i.e., medium S(L) category] (Fig. 3A), and where small RMSE and medium Q^2 values were associated early in ontogeny [i.e., low S(L) category] (Fig. 3B).

The lack of an ideal combination of all three secondary statistics can be explained on the basis of their biometrical relationships (r-values) throughout ontogeny. The relationships were not stable between RMSE and β, and mostly non-significant between RMSE and Q^2 when predicting S(L) (Fig. 3A and B). On the other hand, they were negative and decreased in magnitude between RMSE and β; and remained strongly negative between RMSE and Q^2 when predicting S(R) (Fig. 4A and B). Nevertheless, these secondary statistics, after removing β for obvious biometrical reasons, clearly discriminated between the three S(R) categories (Fig. 5).

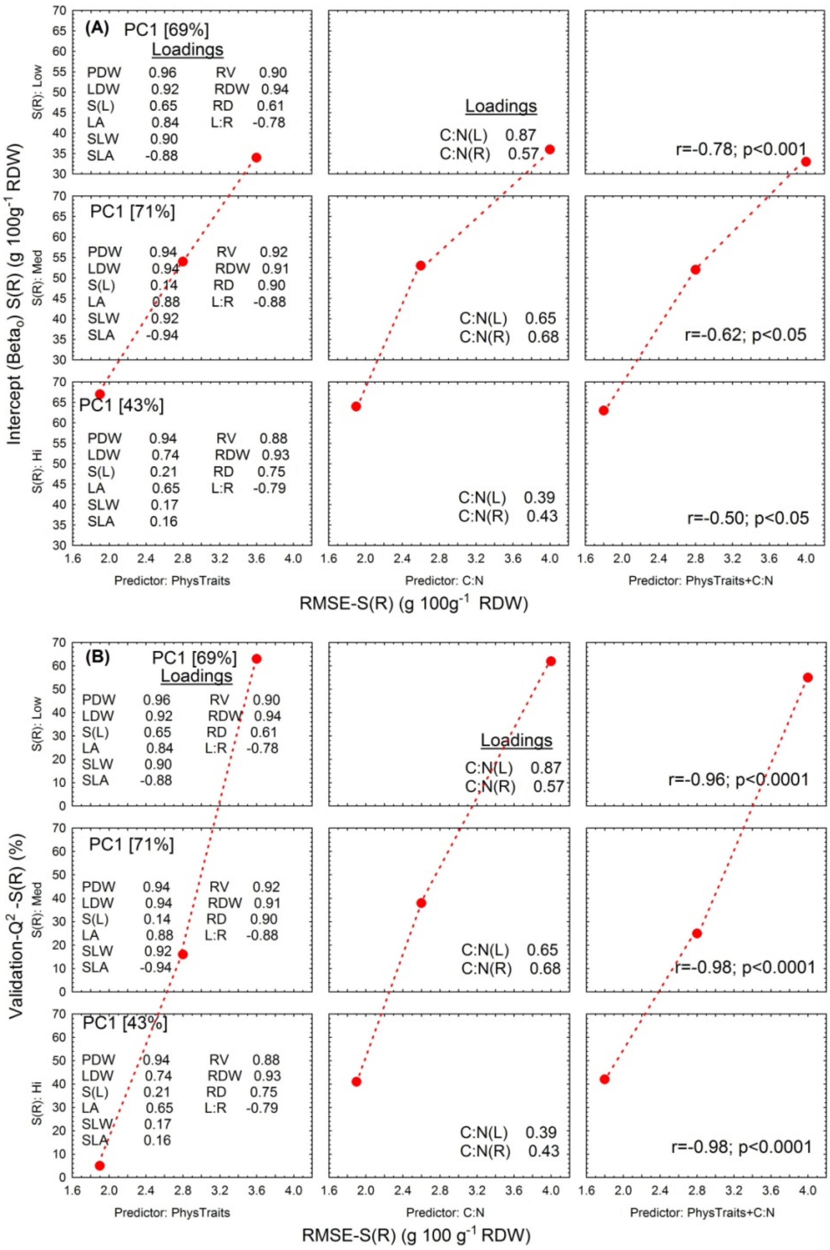

Figure 4. Root-based relationships (r- values) between secondary statistics (residual mean squares error, RMSE and each of validation coefficient of variation, Q^2, and partial least squares regression intercept, β_o) of sugar content (g $100g^{-1}$ dry matter), and loadings on the first principal component (PC1) derived from plant, leaves, and root physical and chemical traits of sugar beet with low-, medium-, and high-S(R).

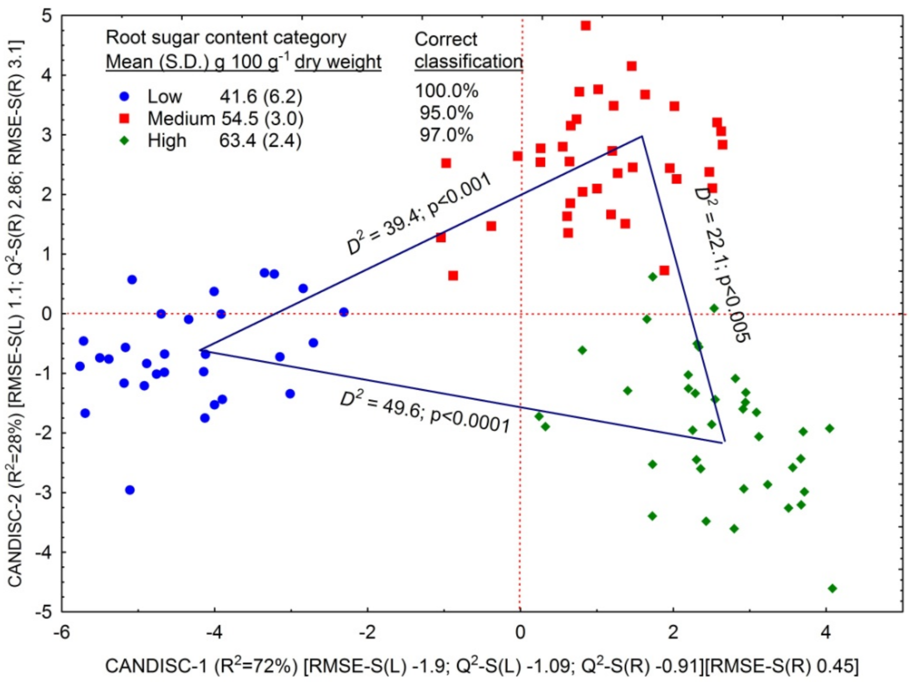

Figure 5. Discriminant analysis of sugar beet roots with low-, medium-, and high-S(R) sampled during three growing seasons and based on secondary statistics, followed by their standardized coefficients, and derived from plant, leaves and root physical and chemical traits.

CONCLUSIONS

Field-grown sugar beet crops are usually composed of highly heterogeneous plant populations due to complex interactions of variety, management practices, and edaphic factors with intra- and inter-annual weather variability. We used easily measured, or estimated, physical and chemical traits on leaves and roots of field-grown, farmer-managed sugar beet. We constructed models to help predict sugar content and identify which traits may have positive or negative impact on it in the developing roots throughout three growing seasons. During early growing season (< 170 Julian days), most leaf and root traits exhibited large (50% < C.V. < 70%) variation; whereas their carbon:nitrogen (C:N) ratios were less variable (C.V. < 20%); however, all had significant impact on root sugar content. During mid-growing season (180 < JD < 220; Julian days), root traits became increasingly more important than leaf traits in impacting root sugar content, displayed larger variation (70% < C.V. < 100%) and maintained a significant impact on root sugar content; however, their C:N ratios were less variable (C.V. 13.5-35%) and maintained a positive and significant impact on root sugar content. During late-growing season, leaf and root traits maintained the same trends and displayed larger variation; whereas their C:N ratios, although became more variable (C.V. 37-50%), they increased in magnitude and had stronger impact on root sugar content. The findings may have implications for farmers and agronomists to design management practices that can enhance carbon sequestration in roots, maintain an adequate, but not excessive, level of nitrogen in developing leaves and roots and minimize the variability in root sugar content.

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