Agronomy **2012**, *2*, 14-27; doi:10.3390/agronomy2010014

OPEN ACCESS

agronomy

ISSN 2073-4395

www.mdpi.com/journal/agronomy

Article

Modeling Long-Term Trends in Russet Burbank Potato Growth and Development in Wisconsin

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Received: 8 February 2012; in revised form: 7 March 2012 / Accepted: 7 March 2012 / Published: 14 March 2012

Abstract: Improving understanding and prediction of the potato (*Solanum tuberosum)* tuber size over the growing season is important due to its effects on crop price and marketing. Several models have been proposed to describe potato growth and development, but are based on short-term data and have little use for predicting yields or in-season management decisions. This analysis uses long-term data collected from 1979 to 1993 in central Wisconsin to describe growth and development of the Russet Burbank potato variety. This paper describes average number of potato tubers per plant and tuber length as influenced by thermal time and stem number per plant over 14 years. For each plant variable, data analysis uses multivariate techniques to fit a hierarchical logistic model with parameters potentially depending on stem number per plant. Analysis finds that the average number of potato tubers and average tuber length were affected by thermal time and stem number per plant. Estimated models are biologically relevant, provide an understanding of seasonal thermal variability and stem number per plant effects on average tuber set and growth, and can be used to describe yearly variation in average potato growth and development. Increased understanding of potato growth in response to thermal time and stem number per plant can improve management recommendations and predictions of crop economic value.

Keywords: potato tuber number per plant; potato tuber length; potato stem number per plant; hierarchical logistic model; thermal time; growing degree days

1. Introduction

Models describing potato (*Solanum tuberosum*) growth and development can identify interactions among management practices (e.g., planting date, planting density, irrigation timing, and nutrient applications), climatic variables (e.g., temperature, light, precipitation, carbon dioxide) and plant factors (e.g., per plant stem density, plant height, number of tubers, *etc.*) and the relative importance of each factor for potato tuber growth. A properly calibrated and validated model can aid in exploring and describing natural phenomena with respect to plant growth, interactions as described above and feedback regarding changes in plant growth throughout the growing season [1]. As an extension, a calibrated and validated biophysical model can improve management recommendations by predicting the potato tuber size and yield responses to management decisions and stress events such as drought, excessive temperature, or nutrient deficiency. Predicting the potato tuber size distribution and yield is also important for determining price. Potato market classes have varying pay scales across tuber size classes and contracts with established prices for chipping, frozen processed and freshmarket. For example, price premiums are awarded for chip potatoes with tubers between 50 and 100 mm in diameter, and for potato tubers greater than 285 grams [2–4]. Price premiums for fresh market russet and red potato varieties vary annually for tubers in specific tuber size categories [5]. A properly calibrated and validated model predicting tuber size and yield response could provide practical in-season management recommendations based on weather events, easily measured plant variables (e.g., per plant stem density, plant height, plant growth stage), and current pricing schedules. These recommendations can assist grower decision making processes to best take advantage of these pricing schedules and harvest at the optimal time.

Several experiments have studied the dependence of potato growth and development on a variety of factors, including cultivar, thermal time based on soil and air temperature, light, irrigation, nutrient management, and planting density and orientation [3,6–13]. These experiments have often investigated potato tuber set, tuber size and distribution, and total yield in response to one of several variables [3,6,10,11,13,14].

Interactions and correlations among potato plant organs, with respect to total tuber set and tuber length predictions, have not been extensively related to variation in yield. However, management practices (potato seed production, seed storage, seed size, *etc.*) are known to affect stem and tuber numbers per plant; and have been utilized to describe density-dependent crop yield responses [3,8,15]. The number of tubers per plant increases with increasing stem density [3,7,16], with some finding that that both the average tuber size and the cumulative proportion of tuber sizes vary with stem density, while average tuber size decreased with increasing stem number and with tuber numbers per square meter [3].

Interactions between vegetative and vegetative reproductive potato plant tissues and correlations among potato plant organs, with respect to vegetative tissues, have been demonstrated, although few models have been parameterized for both vegetative and reproductive growth patterns [3,7,16]. However, numerous models using several functional forms exist to simulate reproductive tissue growth patterns in potatoes, including linear (hierarchical) and non-linear (e.g., expolinear, hyperbolic, and logistic) models. The logistic equation has great utility for modeling plant growth processes due its simplicity and the biological interpretation of parameters estimated. Logistic models have described several aspects of plant growth processes, including vegetative and vegetative reproductive organ growth and development over a season [17]. Recently, a logistic model predicted yield response to applied nitrogen in bermudagrass (*Cynodon dactylon*) [18], tall fescue (*F. arundinacea*) [18], and corn (*Zea mays*) [19]. The logistic model also described the leaf area index of soybean (*Glycine max*) [20], wheat (*Triticum aestivum*) kernel growth, and the concentration and uptake of nitrogen, phosphorus and potassium in green beans (*Phaseolus vulgaris* cv. Carlo Cleo and Mutin) [21]. The logistic model has not been used to model potato reproductive and vegetative tissues together, as dependent upon each other. Modeling reproductive tissue dependence upon vegetative growth has the potential to increase the descriptive strength of the fitted model.

As previously mentioned other models have been used to model potato growth and development. A hierarchical model, utilizing a beta function, has been used to describe vegetative, tuberization, and late bulking phases of potato growth [22]. Similarly, potential and commercial yields were predicted using a step-wise procedure to build a potato plant growth model [23]. Expolinear growth equations correlated daily solar radiation and air temperature to dry matter accumulation across years [24]. In addition, hyperbolic models related crop yield to competition within wheat [25,26], corn [27], soybeans [28], and potatoes [6]. However, the hierarchical model, expolinear model and hyperbolic models are inherently complex and parameter estimates offer little biological interpretation.

The goal of this analysis was to describe potato growth and development throughout the growing season using a long-term data set. Specific objectives were to describe (i) potato tuber length throughout the growing season as a function of thermal time and stems per plant, and (ii) potato tuber set per plant throughout the growing season as a function of thermal time and stems per plant.

2. Experimental Setup

Annual field scale trials from 1979 to 1993 evaluated the potato growth and development for the Russet Burbank variety in Wisconsin. Experiments were conducted at the Hancock Agricultural Research Station, near Hancock, WI (latitude: 44°8’23” N; longitude: 89°31’23” W; elevation: 328 m). The soil type was Plainfield sand (sandy, mixed mesic, Typic Udipsamments). Russet Burbank variety potato seed was purchased annually from a commercial seed farm located in Antigo, WI. Potato seed ranged from generation 3 to generation 5 certified seed. Seed pieces, machine cut to an average size of 56.7 grams per seed piece, were planted at 30.48 cm in-row seed piece spacing between April 15 and April 30 across the entire field each year. Crop management strategies used each year were based on best management practices developed at the University of Wisconsin-Madison [29] and consistent across years. Target nitrogen rates were 269 kg applied nitrogen per hectare, split applied at planting, emergence, and tuberization. Supplemental nitrogen was added based upon potato petiole nitrate analysis. Target phosphorous rates ranged from 112 to 168 kg P_2O_5 applied per hectare. Potash was broadcast applied the fall before potato production at an application rate of 336 kg K_2O per hectare.

Each season, within field plant sampling occurred weekly from the time of tuber set through harvest. Specific initial sampling dates ranged from May 28 to June 25 and final sampling dates ranged from August 4 to September 4. Each year there were between 8 and 15 sampling dates in total. On each sampling date, twenty plants were sampled from a field in potato production with number of stems, number of tubers, and individual tuber length measured for each plant. Thermal time was measured by growing degree days accumulated over the potato growing season beginning May 1 using the average daily air temperature and a base of 4.4 °C [22].

2.1. Data Analysis

First, measured plant variables were averaged across the twenty plants sampled on each date within each year. These averages were analyzed graphically to identify relationships among the variables and with thermal time. Next, multivariate exploratory techniques, including principal components analysis, were used to determine correlations among the measured response variables and thermal time. These correlations were used to generate statistically testable hypotheses relevant to each specified objective. To test specific hypotheses, the data were subjected to linear and non-linear regression analyses using R version 2.10.1 and Statistica version 9.1 (Statsoft, Incorporated, Tulsa, OK, USA).

The goal of the analysis was to identify the best non-linear model relating average potato tuber length, average tuber set to thermal time and to determine how stems per plant affected these relationships through thermal time. After assessing several functional forms (hyperbolic, polynomial, and quadratic), a logistic model was selected for the relationship of each response variable to thermal time. This selection was based on model fit criteria, including the Akaike information criterion (AIC), the pseudo-R^2 and percent of variation explained by the model, as well as the ability to interpret biologically each estimated model parameter [25,30,31].

The specific three-parameter logistic functional form used was:

$$Y(t) = \frac{\alpha}{1 + \exp\left(\frac{\beta - t}{\gamma}\right)} \quad (1)$$

For this model Y is the response variable (average potato tuber length and average tuber set) and t is thermal time, here measured as growing degree days accumulated over the potato growing season using a base of 4.4 °C from an assumed planting date of May 1. As a logistic model, α is the maximum value or upper asymptote of the response variable Y, β is the inflection point where the response variable reaches half of its maximum value, and γ is a scaling factor that governs how rapidly the response variable reaches its maximum.

These biological parameters (α, β, and γ) estimate thermal time effects on crop development as measured by average tuber set and average tuber length. However, these parameters themselves may potentially depend on other variables. For example, stems per plant may influence the maximum value (α) of average tuber length. The potential for these parameters to depend on other explanatory variables is denoted here as $\alpha(X)$, $\beta(X)$ and $\gamma(X)$, where X is a vector of explanatory variables. Based on this model, analysis identified explanatory variables and functional forms for each parameter most consistent with the data for the two response variables: average potato tuber length and average tuber set.

The following process was used to identify explanatory variables and appropriate functional forms for each response variable. First, subsets of the data set were defined based on pre-selected data bin ranges for each potential explanatory variable, e.g. average stem number in overlapping ranges of 0–3, 2–4, 3–5, 4–6, 5–7, 6–8, 7–9, and 8–10. Second, a logistic model was fit to estimate α, β, and γ for the data within each subset. Third, estimated parameters were plotted against the mid-point of the bin range defining each subset to visually identify potential functional forms consistent with each parameter's dependence on the explanatory variable. As an example, Figure 1 plots the estimated α's and β's for average tuber length for bins defined by the stem number. Fourth, based upon these plots, potential functional forms for the dependence of α, β, and γ on the explanatory variables were identified. For example, Figure 1 suggests a linear function, $\alpha = \alpha_0 - \alpha_{stems}\,Stems$, should be used for $\alpha(X)$, where *Stems* is the average stem number per plant and α_0 and α_{stems} are parameters that estimate the impact on tuber length, but no function was used to estimate the effect of stem number per plant on β, *i.e.*, $\beta(X) = \beta$, as no relationship was apparent. Fifth, the identified functions $\alpha(X)$, $\beta(X)$ and $\gamma(X)$ were substituted for α, β, and γ in equation (1) and the full model fit to estimate the parameters of the $\alpha(X)$, $\beta(X)$ and $\gamma(X)$ functions (e.g., α_0 and α_{stems}). Substitutions were evaluated using t-tests for the new parameters (e.g., α_0 and α_{stems}) and goodness-of-fit criteria, including both the biological interpretation of each parameter and AIC, to assess significance of each estimated parameter and overall model fit.

Parameter estimates for each response variable were compared across years and F-tests were conducted to determine if analysis by year described more of the variation in data than when pooled across years. The tuber set model was not improved by addition of yearly estimates, and thus only the combined results are presented. Following model selection and parameterization procedures, individual models and the parameters varied for the four response variables (Table 1). Final functional forms were:

$$\text{Average Tuber Length} = \frac{\alpha_0 + \alpha_{stems} Stems}{1 + \exp\left((\beta - t)/(\gamma_0 + \gamma_{stems} Stems)\right)} \tag{2}$$

$$\text{Average Tuber Set} = \frac{\alpha_0 + \alpha_{stems} Stems}{1 + \exp\left((\beta - t)/\gamma\right)} \tag{3}$$

where *Stems* is the average stems per plant and t is accumulated growing degree days (base 4.4 °C).

Equations (2) and (3) imply that the two response variables each follow a logistic curve in response to thermal time and that the logistic curves for average tuber length and average tuber set also both depend on the stems per plant. Specifically, the maximum (α) of average tuber length and average tuber set both depend linearly on stems per plant. In addition, the scaling factor (γ) that governs how rapidly average tuber length reaches its maximum also depends linearly on stems per plant.

Figure 1. Logistic model *α* and *β* parameter estimates plotted against the mid-point of the stem number per plant data bin ranges 0–3, 2–4, 3–5, 4–6, 5–7, 6–8, 7–9, and 8–10 to visually assess relationship between estimated parameters and measured plant variables.

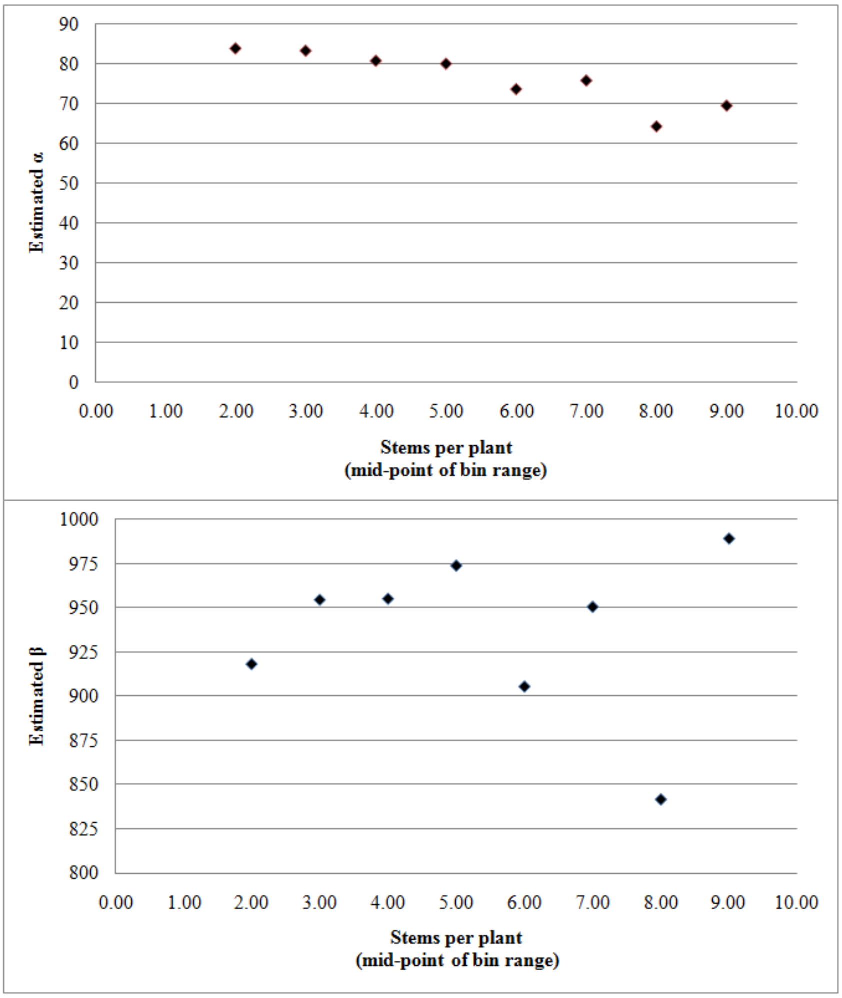


Table 1. Response variables, explanatory variables and estimated parameters utilized in describing the relationships between response variables.

Parameter	Definition
α	The maximum value or upper asymptote of the response variable (Average Tuber Length (mm) or Average Tuber Number).
α_0	Estimated intercept parameter of the linear function describing the dependence of α on the explanatory variable.
α_{stems}	Estimated slope parameter of the linear function describing the dependence of α on the explanatory variable.
β	The inflection point where the response variable reaches half of its maximum value.
γ	The scaling factor that governs how rapidly the response variable reaches its maximum value.
γ_0	Estimated intercept parameter of the linear function describing the dependence of γ on the explanatory variable.
γ_{stems}	Estimated slope parameter of the linear function describing the dependence of γ on the explanatory variable.

Table 1. *Cont.*

Parameter	Definition
Stems	Average stem number per plant.
t	Thermal time, here measured as growing degree days accumulated over the potato growing season using a base of 4.4 °C.

3. Experimental Results

Average tuber length varied with average stem number per plant within the context of a logistic model over the fourteen years and all sampling dates (Table 2). When combining data across years, the model described 76.6% of the tuber length variability and had a correlation coefficient of 0.875. However, parameter estimates for individual years were found to explain more of the variation in average tuber length than a single model across all years based on an F-test (Table 2). Due to the large sample size and associated power of statistical F and t-tests, individual year estimates for α, β, and γ were different across all years, while α_{stem} differed for all but 2 years. Equation (2) was estimated individually by year. Stem number per plant did not affect maximum tuber length (α) in 1979, 1982, and 1990 (Table 3). Stem number per plant did not affect the scaling factor (γ) in any individual year, as indicated in Table 2, so Table 3 only reports estimates of γ, rather than for γ_0 and γ_{stems}.

Table 2. Pooled parameter estimates and associated standard errors for Equations [2] and [3].

	Average Tuber Length (mm)		Average Tuber Number per Plant	
	Variance Explained: 76.6%		Variance Explained: 45.1%	
	R = 0.875		R = 0.672	
Parameter	**Estimate**	**SE**	**Estimate**	**SE**
α or α_0	89.23 ***	1.54	6.22 **	0.27
α_{stems}	1.85 ***	0.27	2.92 **	0.07
β	960.95 ***	11.33	528.89 **	6.55
γ or γ_0	274.95 ***	17.31	102.56 **	6.25
γ_{stems}	-8.19 *	4.11	NS	--

* Significant at the 0.05 probability level; ** Significant at the 0.01 probability level; *** Significant at the 0.001 probability level.

As stem number per plant increased, both the maximum average tuber length and tuber length growth rate decreased linearly (Figure 2). The average maximum tuber length (α) varied between 63.78 and 114.22 mm across years (Table 3). The rate at which tuber length increased was temperature dependent as indicated by the yearly variation in β and γ estimates. The point at which tubers reached half of their total length (β) varied between 720 and 1169 accumulated growing degree days over years. Stem number per plant affected average maximum tuber length by 0.7 to 4.7 times the average stem number across all years. The scaling parameter (γ) ranged from 198 to 322 accumulated growing degree days across years. Across all years and sampling dates, the total range in average tuber length was between 2.6 and 142.5 mm. Maximum tuber length (mm) for a given year was reached by 2000 to 2200 accumulated growing degree days.

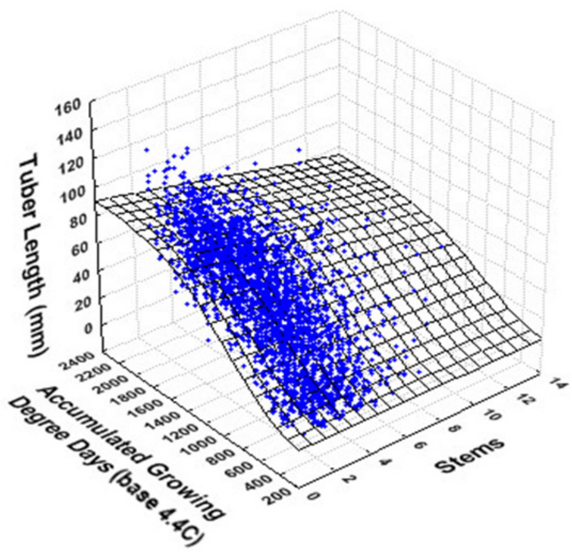
Table 3. Least squares estimated parameters for the logistic model describing average potato tuber length as a function of accumulated growing degree days and stem number per plant.

	α_0		α_{stem}		β		γ	
Year	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
1979	80.38 **	6.29	1.69	0.92	1005.19 **	40.50	245.69 **	17.24
1980	75.60 **	2.68	2.72 **	0.80	834.48 **	16.49	197.86 **	10.02
1981	114.22 **	6.91	4.73 **	1.29	1168.62 **	43.69	309.51 **	19.68
1982	63.21 **	2.54	1.67	0.89	922.05 **	19.74	205.39 **	10.74
1983	96.37 **	3.89	3.77 **	0.84	998.60 **	36.56	322.32 **	22.54
1984	77.84 **	3.83	1.42 **	0.54	968.51 **	28.28	264.93 **	19.98
1985	80.91 **	5.45	1.62 **	0.48	719.91 **	30.69	265.56 **	61.68
1986	91.17 **	3.99	2.35 **	0.85	866.74 **	27.07	287.48 **	15.61
1987	98.79 **	2.98	2.95 **	0.81	887.25 **	13.71	214.31 **	7.77
1988	96.74 **	3.25	2.78 **	0.65	1143.67 **	23.71	302.34 **	15.10
1989	93.62 **	3.47	1.99 **	0.70	978.20 **	20.13	251.11 **	14.57
1990	63.78 **	2.94	0.68	0.57	898.94 **	20.30	228.44 **	15.67
1991	86.49 **	3.10	2.63 **	0.63	932.97 **	26.22	287.13 **	20.73
1992	90.90 **	2.65	3.06 **	0.52	762.02 **	16.82	226.32 **	14.96
1993	84.24 **	2.53	2.38 **	0.58	784.20 **	17.64	239.93 **	13.38
Residual Square Error = 0.870								

* Significant at the 0.05 probability level; ** Significant at the 0.01 probability level; *** Significant at the .001 probability level.

Figure 2. Observed (points) and estimated average potato tuber length (smoothed curve) across accumulated growing degree days and stem number per plant in field trials near Hancock, WI from 1979–1993.

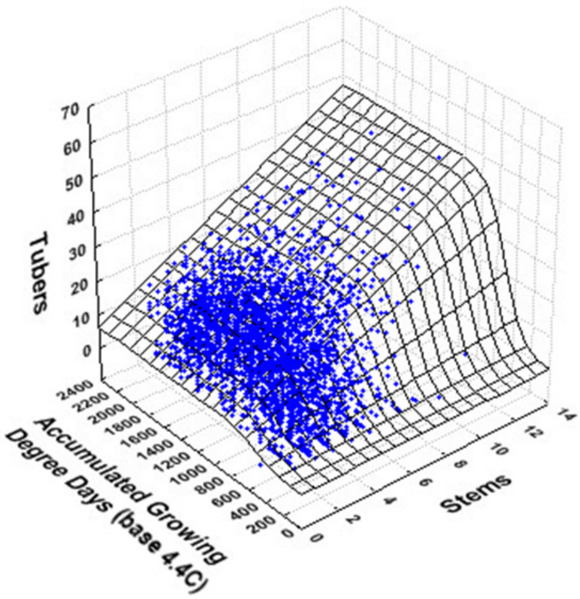
$$\text{Model: Average Tuber Length (mm)} = \left(\alpha_0 - \alpha_{stems} Stems\right) / \left(1 + \exp\left[\frac{\beta_0 - t}{\gamma_0 - \gamma_{stems} Stems}\right]\right)$$



Average tuber number per plant varied with stem number per plant and accumulated growing degree days across all sampling points, with a logistic model providing the best fit (Figure 3). Individual year parameter estimates did not differ based on F-tests, allowing for one model to be fit across years. The logistic model explained 45.1% of the variation in average tuber number with a correlation coefficient of 0.672. Average maximum tuber number per plant was linearly related to stem number per plant, within the simple logistic model (Table 2). The maximum average tuber number per plant (*α*) was estimated to be 6.22 plus 2.92 times the average stem number per plant. Similar to average tuber length, average tuber number per plant was temperature dependent. The accumulated growing degree days necessary for half tuber number (*β*) was 529, with maximum tuber number occurring at 1000 accumulated growing degree days or between July 3 and July 17 depending on the year. The scaling parameter (*γ*) was 102.6 accumulated growing degree days. The number of tubers per plant varied within the growing season and year, but ranged from between 1 and 58 tubers per plant.

Figure 3. Observed (points) and estimated average potato tuber number (smoothed curve) across accumulated growing degree days and stem number per plant in field trials near Hancock, WI from 1979–1993.

$$\text{Model: Average Tuber Length } (\text{mm}) = (\alpha_0 - \alpha_{stems} Stems) / \left(1 + \exp\left[\frac{\beta_0 - t}{\gamma_0}\right]\right)$$



4. Conclusions

Average tuber length and average tuber number per plant varied by year and within year. Much of the annual variation could be explained by stem number per plant and accumulated growing degree days, yet the model still remained relatively simple and biologically relevant. Introduced variation into the experiment could have originated from a number of sources over the course of this long-term experiment. Both across- and within-year variations in agronomic management (e.g., planting density, irrigation, pesticides, tillage, planting date) could potentially have affected growth. However, this is unlikely, as this experiment was conducted on an agricultural research station under the consistent direction from station superintendents and steps were taken to minimize management differences.

Similarly, plant measurement protocol inconsistency could potentially have been introduced across and within years. Sampling protocols were held consistent under the direction of the research personnel. Human introduced sampling error in collecting weekly sets of 20 plants and recording detailed measurements of plant organs could have increased the variation surrounding the true mean. However, the variability within our data is consistent with previously published estimates for each plant variable [6]. Spatial variability within each year and across years could have affected potato plant growth responses. This experiment was conducted over several fields located on the Hancock Agricultural Research Station and models were fit accurately to each of the specified plant growth parameters despite any variation introduced.

Tuber size response to stem number per plant and thermal time has been reported previously [6,13,32–35]. Consistent with previous reports, average tuber length decreased with increasing stem number per plant. Annual variation in stem number per plant and the rate of accumulating growing degree days occurred and resulted in a linear relationship between average tuber length and stem number per plant, which was explained by the logistic model. Measured values for average tuber length and stem number per plant were consistent with previously published values [6,8,35].

Average number of tubers per plant increased with increasing stem number per plant. This relationship has been observed and reported in previous research [6,13,32–35]. Interestingly, we were able to fit one model across all years of data and explain 45.1% of the variation in average number of tubers per plant using only thermal time and the number of stem number per plant. While average tuber number per plant has been demonstrated to remain constant under fixed experimental conditions [3,8], only limited accounts report non-plant population density variation in tuber number per plant [6,7]. The observed and estimated values for average tuber number per plant were greater than reported for sites in the western United States [3], but consistent with values reported in Wisconsin [6].

Overall, the model predicted a sigmoidal growth pattern for tuber length and the number of tubers per plant over the course of the growing season. Sigmoidal growth patterns have been observed previously in the literature in a number of species and plant organs, including potato tuber growth [17,20,21]. The logistic model has not been used extensively to model potato growth responses to stem number per plant and accumulated growing degree days. The logistic model provided the best fit and gave parameter estimates that could be interpreted biologically. Other growth models, such as the quadratic or square root models, are equally simple, but offer parameter estimates that have little biological meaning.

This analysis of long-term potato growth data demonstrates the ability to account for variation over several years and explains potato growth responses with a relatively simple and biologically relevant non-linear model. These estimated models provide a baseline on which to build updated best management practices for potato growers. Once properly validated and calibrated for various potato growing regions, the logistic model fit in this analysis can serve as a predictive tool to estimate average tuber length during a growing season with easily measured field variables (stem number per plant and accumulated growing degree days). In turn, accurately predicting tuber length response to easily measured variables can aid in monitoring potato tuber length throughout the growing season and in improving the evaluation of management practices and in-season crop marketing. Further, the effects of stem density on the alpha and gamma parameter estimates used to predict tuber length illustrate the increased solar energy (thermal time) required for the crop to reach a minimum average tuber length as average stem number per plant increase. A limitation of the data used in constructing this model is the use of average tuber length instead of average tuber weight. In addition, other tuber quality variables were not collected over the course of this experiment, such as specific gravity, starch percent, reducing sugar content, oil absorption, and flesh color. However, potato tubers for both fresh and chip production are visually graded and assessed for length to wide ratios (L:W) and the logistic model for average tuber length during the growing season provides growers with valuable information to aid in management practices and in-season crop marketing decisions. Further, annual variation in climate has been demonstrated to affect potato tuber L:W, specific gravity, and dry matter concentrations [36,37] Variability in potato tuber L:W, specific gravity and dry matter concentrations will add to the variability in average tuber weight. Average tuber length predictions made within this analysis inherently included variability that could be resolved by including factors (L:W, specific gravity, and dry matter concentration) that contribute to average tuber weight variation. Inclusion of L:W, specific gravity, dry matter concentration or average tuber weight in future analyses will explain additional variability in the data to increase accuracy and precision of the logistic model, but do not detract from the utility of this model as described. Describing the potato tuber size distribution remains important due to the effect of the tuber size distribution on crop price. Future methods of describing the potato size distribution are necessary to predict crop value [3,8,38].

This experiment was conducted over 14 years from 1979 to 1993. However, the data presented are still relevant to growers today. Throughout the experiment, Russet Burbank was the only potato variety planted for evaluation. Russet Burbank is the current standard potato variety to which new varieties are compared in fresh and processed markets in the United States. Russet Burbank comprised 44.6% of the 2010 fall planted potato acreage in Idaho, Maine, Minnesota, North Dakota, Washington and Wisconsin [39], the largest percentage of total acreage planted to a single variety in the United States in 2010. The limitations do not detract from the scientific utility and application of the model, as we were able to explain long-term variation, describe several potato plant organ growth patterns, and interpret correlations and interactions among variables measured across 14 years of field experiments conducted in central Wisconsin.

Acknowledgements

The authors acknowledge the contributions of Zhe Dun for assistance in data preparation. In addition, the authors appreciate the support from the staff at the University of Wisconsin, Madison Hancock Agricultural Research Station and the student hourly employees who contributed to the collection of data for this analysis.

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