



The International Society of Precision Agriculture presents the

# 15<sup>th</sup> International Conference on Precision Agriculture

## 26–29 JUNE 2022

Minneapolis Marriott City Center | Minneapolis, Minnesota USA

## Soil, Landscape, and Weather Affect Spatial Distributions of Corn Population and Yield

Kenneth A. Sudduth<sup>1</sup>, Lance S. Conway<sup>2</sup>, Newell R. Kitchen<sup>1</sup>

<sup>1</sup> USDA-ARS Cropping Systems and Water Quality Research Unit, Columbia, MO, USA

<sup>2</sup> University of Missouri, Department of Soil, Environmental, and Atmospheric Sciences, Columbia, MO, USA

A paper from the Proceedings of the  
15<sup>th</sup> International Conference on Precision Agriculture  
June 26-29, 2022  
Minneapolis, Minnesota, United States

**Abstract.** *As more planters are equipped with the technology to vary seeding rate, evaluation of the within-field relationships between plant stand density (or population) and yield is needed. One aspect of this evaluation is determining how stand loss and yield are related to soil and landscape factors, and how these relationships vary with different weather conditions. Therefore, this research examined nine site-years of mapped corn yield, harvest population, and soil and landscape data obtained for a central Missouri, USA field. Mechanical population sensors collected data during combine harvesting and provided information at the same scale as yield monitor measurements. Results showed spatial population variability at harvest was large in all site-years, with populations as much as 40% lower than seeding rate. Random forest machine learning models were created to relate population and yield ratio (or per-plant yield) to landscape data, proximal soil sensor data, and data from laboratory analysis of grid soil samples, both for a single year and multiple years. Single-year harvest population modeled very well (test set  $R^2 = 0.84$ ), with most important predictors including landscape and proximal sensor variables as well as soil-test phosphorus. Yield ratio also modeled well (test set  $R^2 = 0.65$ ), with the most important predictors being landscape properties. Direct modeling of multi-year population and yield ratio was not successful; however, models representing the temporal standard deviation in spatial population and yield ratio were moderately successful (test set  $R^2 = 0.50-0.52$ ), with the most important predictors being landscape variables, soil apparent electrical conductivity, soil organic matter, and cation exchange capacity. This case-study analysis showed the potential for explanatory modeling of spatial variability in harvest population and yield ratio, as well as their across-year temporal variability. Further research should investigate additional machine learning approaches more capable of modeling weather information in multiple-year analyses.*

**Keywords.** *Plant population, per-plant yield, corn, random forest, proximal soil sensors*

## Introduction

Technology is available to allow producers to adjust seeding rates within fields. However, the question of what seeding rate should be used at each within-field location remains unanswered. Although some research has suggested that variable-rate seeding of corn may not be appropriate for typical Midwestern US corn growing conditions when the yield vs. population production function is not known (Bullock et al., 1998), others have noted that variable-rate seeding may provide a benefit in fields with significant areas of shallow topsoil (Barnhisel et al., 1996).

Varying seeding rates may also be appropriate if the goal is to provide a uniform harvest population. Yield reductions due to lower than desired stands may be encountered in portions of fields subject to adverse emergence conditions and/or pest problems. If these areas of lower viability are temporally stable from year to year, or can be predicted prior to planting, seeding rates could be adjusted to compensate and achieve a desired harvest population across the field. In addition to the effects of mean population, increased variance in corn plant spacing due to planter inaccuracies or reduced emergence may also reduce yield (Nielsen, 1995). Nafziger (1996) reported that yields decreased due to missing plants, or “skips.” Adjacent plants compensated for 47% of yield loss due to a missing plant at 44,000 plants ha<sup>-1</sup>, but only for 19% of the loss at 74,000 plants ha<sup>-1</sup>.

Sensing systems that provide spatially-dense datasets of corn plant population at harvest would provide information to help determine appropriate seeding rates. We developed such a sensing system, consisting of a spring-loaded rod attached to a rotary potentiometer, mounted in front of the gathering chains on the row dividers of the combine head (Birrell and Sudduth, 1995). During harvesting, the corn stalks caused the rod to rotate backward, increasing the voltage potential across the potentiometer. When the stalk released the rod, a sharp decrease in voltage occurred. The potentiometer output was fed through a low-pass filter into an analog derivative circuit and digital filter circuit to convert the sharp drop in potential into a pulse recorded by a digital counter.

The effect of varying combine operating conditions on sensor accuracy was evaluated by Sudduth et al. (2000). Performance was encouraging under most conditions, although actual population was underestimated at high populations. When compared to hand counts obtained at harvest under a range of operating conditions, the sensors underestimated population on average by 4.4% ( $r^2=0.93$ ) with a standard error of 3830 plants ha<sup>-1</sup>. However, when operating in test blocks without weak plants (and/or doubles) at speeds less than 2.5 m s<sup>-1</sup>, the average underestimation was reduced to 0.08% ( $r^2=0.96$ ) with a standard error of 2720 plants ha<sup>-1</sup>, or less than two plants in a 10-m transect. The underestimation and standard error of the predicted population was directly related to the stalk feed rate into the sensor. When the feedrate was restricted to less than 9 plants s<sup>-1</sup>, the standard error was 1800 plants ha<sup>-1</sup>. This threshold represented a travel speed of 2.0 m s<sup>-1</sup> at a population of 60,000 plants ha<sup>-1</sup>.

A large-plot study employing these harvest population sensors noted a stronger relationship between yield and harvest population than between yield and seeding rate and documented large and spatially-variable stand losses before harvest (Bauer et al., 2000). Sudduth et al. (2004) examined field-scale harvest population and corn yield data, finding significant correlations in only 5 of 8 site-years. Further, relationships of population and yield to soil and landscape properties were inconsistent and not often significant. In one site-year where improved instrumentation allowed quantifying individual plant spacings, there was an indication of stronger relationships between soil and landscape properties, population metrics, and yield.

Collectively, these studies showed the potential of utilizing population sensors for guiding future variable-rate seeding, but additional data collection and the application of more complex analysis methods were needed. Therefore, the goal of this research was to examine relationships among harvest plant spacing, corn yield, and soil, landscape, and weather data for a case-study field in central Missouri, USA using machine learning techniques. Specific objectives were to relate (1) harvest population, (2) yield ratio (i.e., per-plant yield), and (3) multi-year variability in those two measures to measured soil, landscape, and weather.

## Materials and Methods

Data were obtained on a 36-ha research field in central Missouri for nine years when corn was grown: 1999, 2001, 2003, 2005, 2007, 2009, 2011, 2013, and 2016. Since 1991 this field has generally been farmed in a corn-soybean rotation. From 2004 to 2014, it was the site of a precision agriculture system study (Yost, et al. 2017), and during those years corn was only grown in the south 15 ha. Before and after, corn was planted in the entire 36-ha field.

### Data Collection and Processing

Corn was harvested and yield data collected using a Gleaner R42 combine equipped with an AgLeader yield monitor and mechanical population sensors (Birrell and Sudduth, 1995) on each row. Yield datasets were cleaned using the Yield Editor 2 software tool (Sudduth and Drummond, 2007; Sudduth et al., 2012) to remove erroneous observations. The remaining 1-s observations were exported from the software for further analysis, after correction to market moisture.

For all site-years, “low speed” population data was processed on 1-s, providing the total number of plant detections for each row, along with GPS position and combine velocity. Then, the total number of plants and area covered for each row unit in 1-s was used to determine population for each row, as well as a mean population over all rows. Rarely, a sensor would malfunction and row data for any such interval was excluded from the mean population calculation. The 1-s mean populations were adjusted to compensate for plants miscounted at high feed rates (greater than 6.5 plants s<sup>-1</sup>) using Eq. 1 developed by Sudduth et al. (2000):

$$\text{Adjusted population} = \text{Raw population} * (0.758 + 0.371 * \text{Feedrate}) \quad (1)$$

where: Feedrate = estimated number of plants s<sup>-1</sup> entering each row of the combine head, as calculated from seeding rate and combine travel speed.

For 2003 and later, population data were processed both using the 1-s approach described above and a high-speed data acquisition system that recorded the times of individual plant detections in each row. The six row units on the combine were scanned at a 2-kHz frequency, providing a resolution of 1 mm at 7.2 km h<sup>-1</sup>. Using these data, along with velocity information, the spacing of each plant from the previously detected plant on that row was calculated. The distribution of these spacings was well-defined and consisted of multiple approximately Gaussian distributions corresponding to correct spacings, single skips, double skips, and doubles (Fig. 1). Proc NLIN in SAS was used to fit overlapping Gaussian distributions for each of the spacing categories, and parameters were determined separately for each year. Observations were classified as belonging to the distribution with the maximum frequency at that spacing.

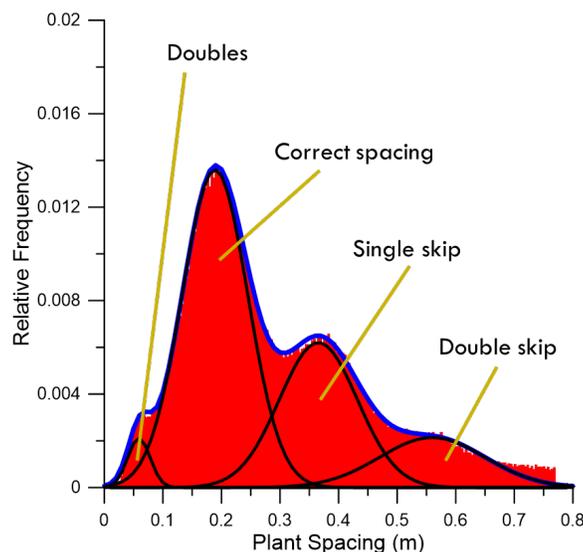


Fig. 1. Example 2013 plant spacing histogram (red bars), including overlapping Gaussian distributions defining doubles, plants at correct spacing, single skips, and double skips.

Other measurements used in the analysis included a standard suite of soil fertility measurements, proximal soil sensor data, and the landscape properties of slope, hillshade, and elevation. Grid soil samples were obtained to a 15-cm depth and analyzed for P, K, Ca, Mg, cation exchange capacity (CEC), organic matter (OM), and pH. Apparent soil electrical conductivity (ECa) was measured using a Veris 3100 instrument (Veris Technologies, Salina, KS, USA), providing shallow (ECsh; 0-0.3 m) and deep (ECdp; 0-1.0 m) data. Concurrently, a real time kinematic (RTK) GPS survey (vertical accuracy 3-5 cm) was conducted down the same transects to provide dense elevation data. Soil gamma radiation emissions were collected using an RSI-700 detector (Radiation Solutions Inc., Mississauga, ON, Canada) mounted to the front of a utility vehicle. Four measurements were available - total counts and counts of potassium uranium, and thorium. All proximal sensor data were obtained on an approximately 18 m transect spacing.

Appropriate semivariograms were created for the ECa, soil sample, gamma and RTK elevation datasets, and the data were kriged to a common 10-m grid for each field. Slope and hillshade were derived from the Spatial Analysis Toolbox in ArcGIS Pro (ESRI, Redlands, CA, USA). Slope was calculated in percent and was derived in a 3 x 3 cell moving window. For hillshade, the azimuth was set to 315 degrees, and the light source altitude to 45 degrees. The hillshade estimates were coded with integers between 0 and 255, increasing from dark to light. Population and yield data were aggregated to the same 10-m grid, rather than being kriged. This allowed the calculation of cell-specific standard deviations, as well as means, for both parameters. For the high-speed population data, the percentage of single skips, double skips, and large skips in each grid cell were also tabulated.

## Data Analysis

A machine learning approach was applied in all modeling strategies that utilized the field-scale data. A random forest (RF) algorithm was chosen due to consistent performance and the ability for model interpretation. The RF models were fit and interpreted with the 'randomForest', 'randomForestExplainer', and 'ICEbox' packages in R Statistical Software (R Core Team, 2022). The RF algorithm is a supervised ensemble learning technique that can be used for classification or regression problems. It uses a bagging technique, where the data are split and regression trees are created in parallel (Leo et al., 2021). Within each tree, the RF randomly selects features to create a prediction model. In our scenarios, the number of variables evaluated at each split in the decision tree (*mtry*) was set to 3. The final (bagged) model, in our scenario, was an average of 500 separate regression trees. These trees were developed on 80% of the data and tested on the remaining 20%. The Pearson correlation coefficient (*r*), coefficient of determination ( $R^2$ ) and root mean squared error (RMSE) were calculated to interpret performance of the model in the training and testing datasets.

Predictor significance was analyzed using the minimal tree depth distribution from the 'randomForestExplainer' package in R. These values represent the average depth within the ensemble of decision trees that each variable was used to partition the dataset. Therefore, smaller values correlated to more significant variables, as they were used more often at shallow tree depths. In addition to the minimal depth of distribution, the individual conditional expectations (ICE) algorithm was applied to covariates of interest, and subsequent plots were created using the 'ICEbox' package in R (Goldstein et al., 2015). This allowed interpretation of how each variable was used in prediction by the RF model. Specifically, the ICE plots displayed the estimated conditional expectation curves, each of which reflected the predicted response as a function of the covariate of interest, conditional on the distribution of additional covariates. Because the curve intercepts varied, model predictions were "centered" in ICE plots for improved interpretation among the varying intercepts. In the centering process, each curve was "pinched" at the minimum observation of the given predictor variable of interest. In each plot, 10 percent of the entire training dataset was used for visualization.

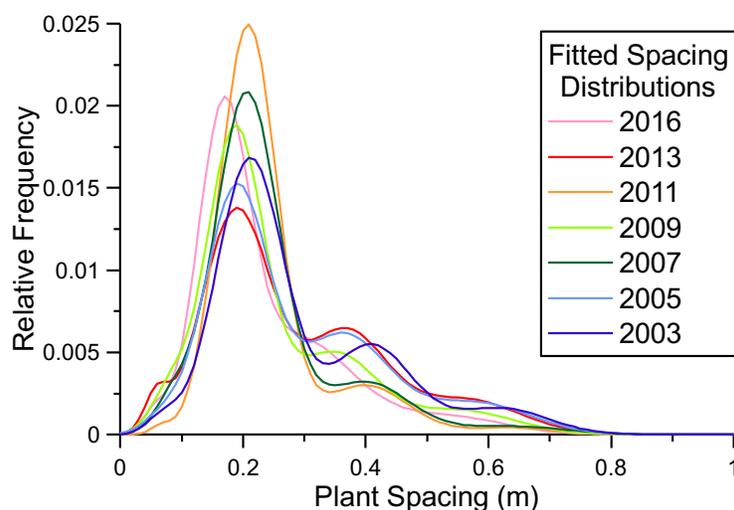
## Results and Discussion

Harvest population as measured by the mechanical counters was 20% or more lower than the target seeding rate in all years. On a percentage basis, stand loss was lowest in 2011 and highest in 2013 (Table 1). Corn grain yield was only weakly related ( $r = 0.21$ ) to stand loss.

Fitted harvest spacing distributions (Fig. 2) show that the correct spacing (i.e., spacing at the peak of the distribution) for each year was around 0.2 m and illustrate the variable fraction of total spacings that were not correct (i.e., portions away from the main peak). For the seven years where high-speed data were available, the correct plant spacing from the histogram was within 0-7% (mean = 4.4%) of the desired spacing based on target seeding rate (Table 1), providing confidence in the validity of the distribution-fitting procedure.

**Table 1. Whole-field population statistics derived from low-speed data collection.**

Year	Harvest Population plants ha <sup>-1</sup>	Target Seeding Rate plants ha <sup>-1</sup>	Stand Loss %	Fraction at Correct Spacing	Corn Yield Mg ha <sup>-1</sup>
1999	47399	61775	23.3	--	2.60
2001	50300	63011	20.2	--	6.06
2003	44347	61775	28.2	0.64	2.13
2005	46317	69188	33.1	0.60	4.52
2007	54108	69188	21.8	0.80	4.05
2009	52838	74130	28.7	0.67	9.52
2011	53692	66717	19.5	0.84	3.88
2013	46262	74130	37.6	0.57	5.71
2016	57052	79072	27.8	0.72	8.99



**Fig. 2. Fitted plant spacing distributions for the seven years where high-speed harvest population data were available.**

### Random Forest Estimation of 2016 Harvest Population

The first RF model investigated the relationship of 2016 harvest population to landscape features, proximal soil sensor data (i.e., ECa and passive gamma), and lab-measured soil properties from 30-m grid samples. All data within the field boundary ( $n = 2485$ ) were used in this analysis to maximize the number of observations available for training the model. Test set results were very good ( $R^2 = 0.84$ ; Fig. 3). Importance of model parameters was investigated with a tree depth distribution plot (Fig. 4), which showed that elevation, hillshade (a landform parameter that incorporates slope and aspect), soil-test phosphorus, Gamma sensor total counts, and shallow ECa data were the most important variables describing variation in harvest population. Elevation

differences in this field are important for runoff and run-on of water, and therefore soil moisture. These in turn may affect germination and emergence, along with soil temperature differences represented by hillshade. Phosphorus may have been important due to its impact on seedling vigor, and passive gamma and ECa data reflect soil texture, which may affect planter performance and seed-soil contact.

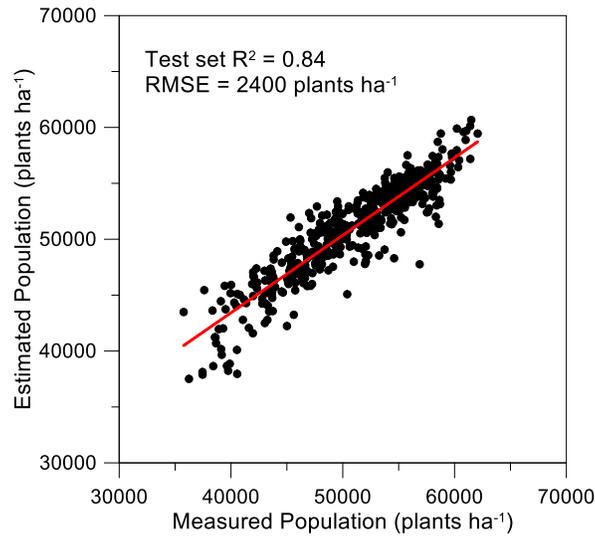


Fig.3. Results of random forest model estimating 2016 harvest population as a function of soil and landscape variables.

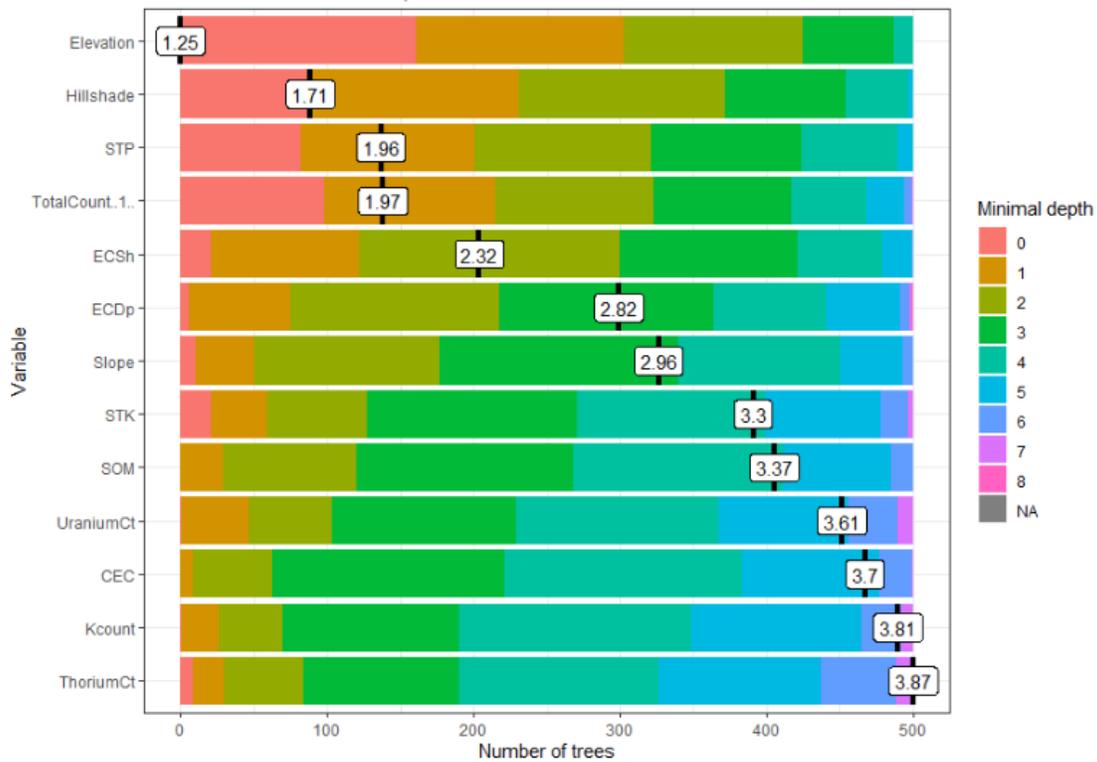


Fig. 4. Mean (in black text) and distribution of minimum depth in random forest model estimating 2016 harvest population based on soil and landscape variables. A smaller depth indicates a more influential variable.

### Random Forest Estimation of 2016 Yield Ratio

A second RF model estimated yield ratio (i.e., per-plant yield), using the same suite of predictor variables as above. Fewer observations were available in this analysis ( $n = 1483$ ) as the dataset was trimmed to eliminate edge effects due to compacted headlands and field-edge tree lines. Two nitrogen test strips were also removed because they were not managed the same as the rest of

the field. Results were good ( $R^2 = 0.65$ ; Fig. 5), although not as good as harvest population estimates. The tree depth distribution plot (Fig. 6) showed that the top two parameters were the same as for population estimates, elevation and hillshade, reinforcing the importance of soil water movement and temperature differences in affecting yield on claypan soil landscapes. Other top parameters were generally related to soil texture and depth of topsoil above the subsurface claypan layer, important factors in spatially-variable plant water availability. Texture-related parameters may have also affected planter performance; for example, poor row closure or excessive downforce requirements.

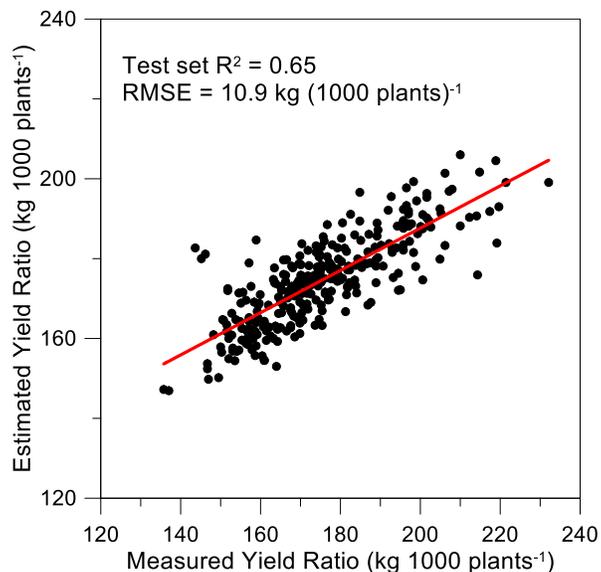


Fig. 5. Results of random forest model estimating 2016 yield ratio as a function of soil and landscape variables.

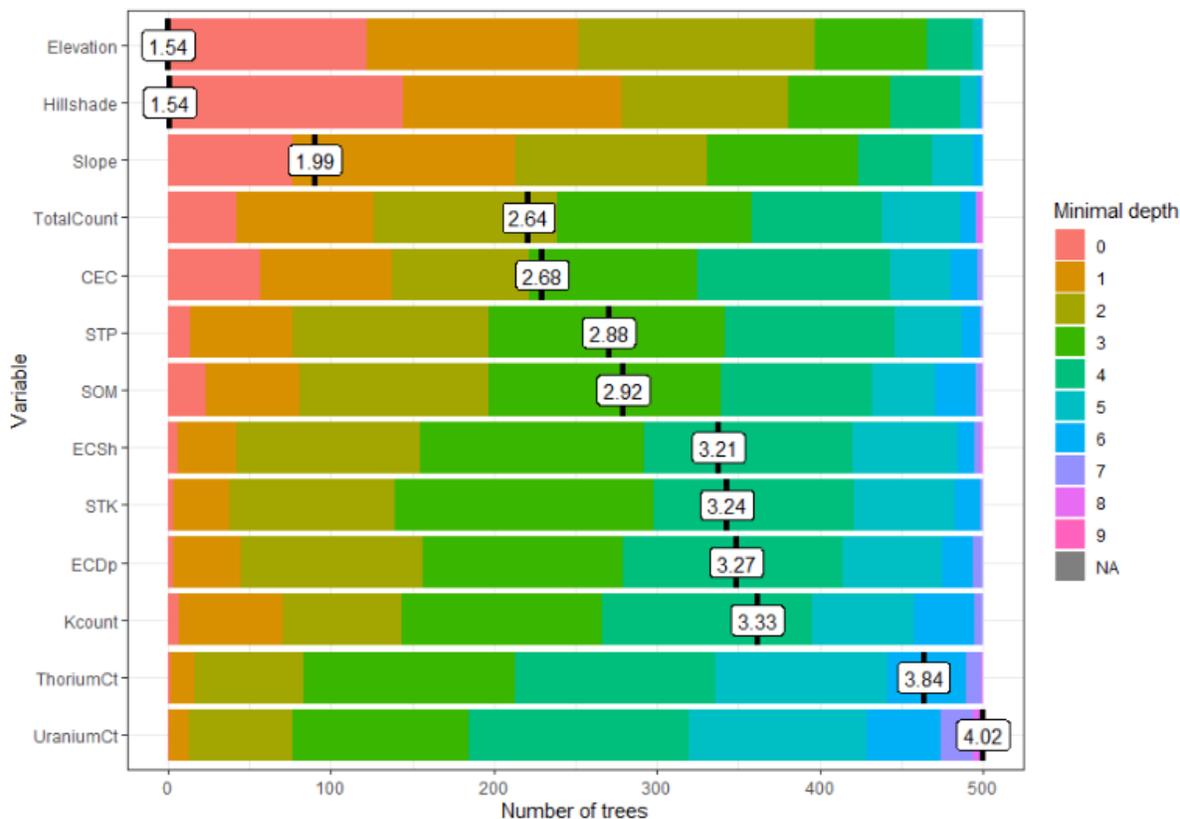
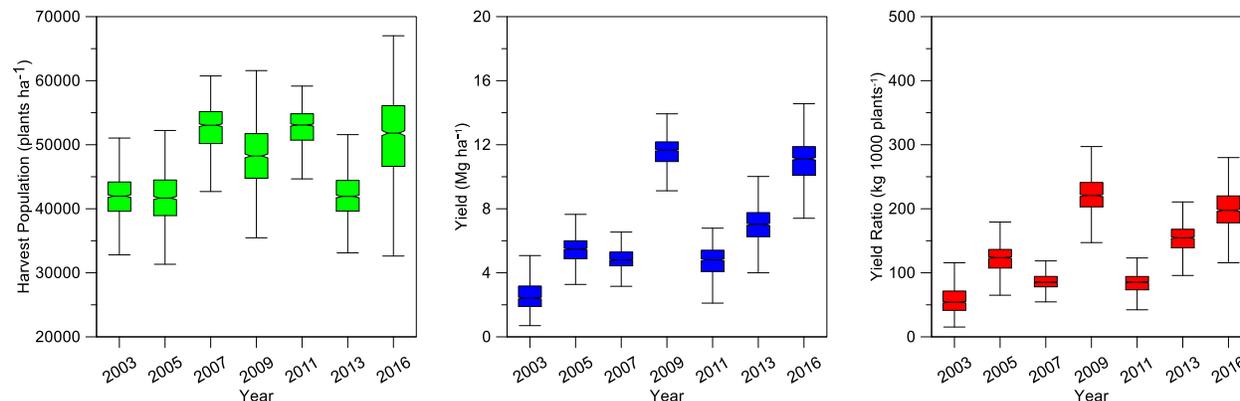


Fig. 6. Mean (in black text) and distribution of minimum depth in random forest model estimating 2016 yield ratio (i.e., per-plant yield) based on soil and landscape variables. A smaller depth indicates a more influential variable.

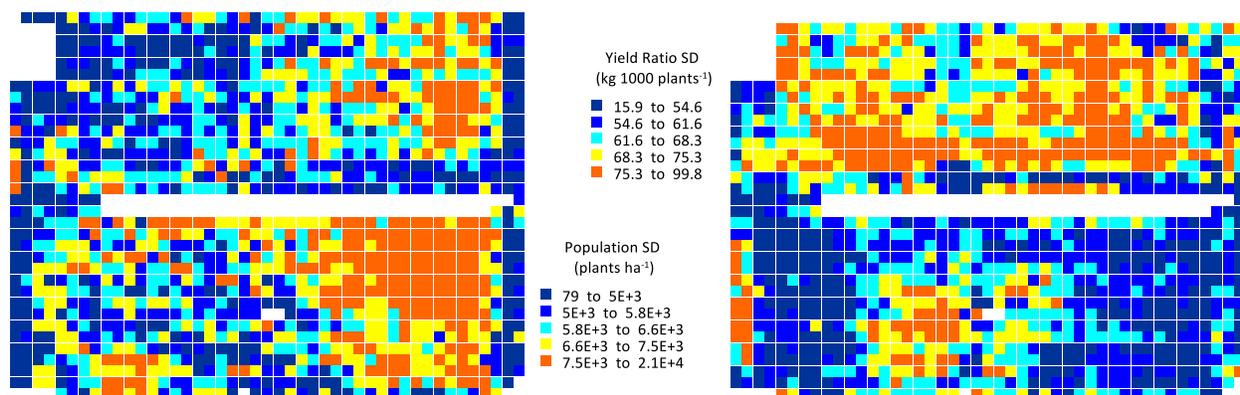
## Random Forest Analysis Across Multiple Years

Temporal variation in harvest population, yield, and yield ratio were examined for the south 15-ha of the field where seven years of data were available: 2003, 2005, 2007, 2009, 2011, 2013, and 2016. Particularly for yield and yield ratio, between-year variability was large in comparison to within-year spatial variability (Fig. 7). Assuming that between-year variability was primarily due to weather differences, we attempted to fit RF models across years including growing-season precipitation data, with poor results (data not shown). We hypothesized that a primary reason for the poor fit was likely the small number of observations in the temporal domain ( $n = 7$ ).

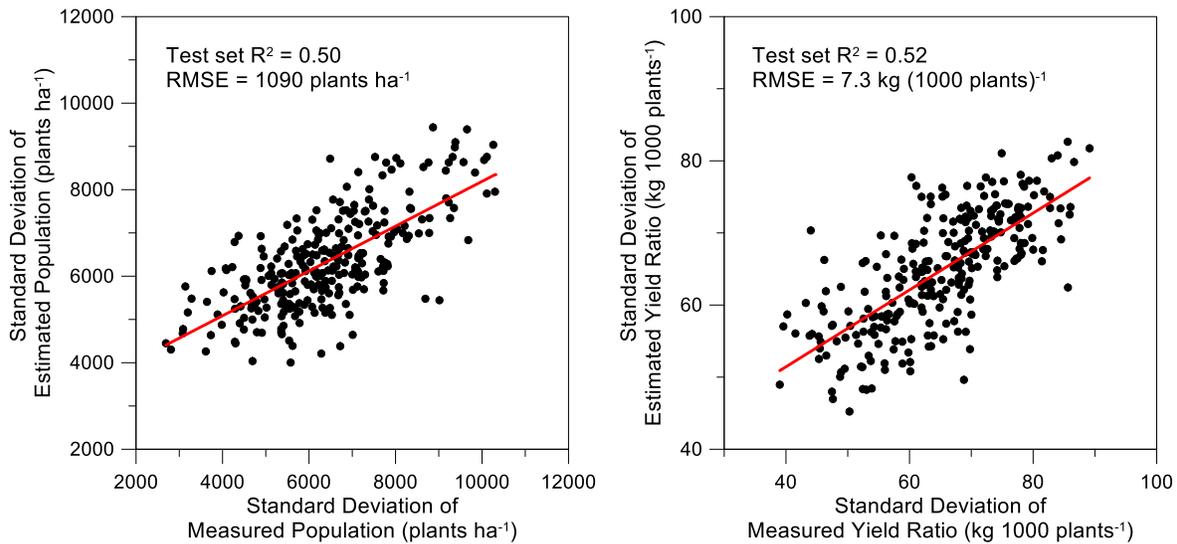


**Fig. 7. Variability in harvest population, corn yield, and yield ratio across seven years and, as represented by individual box-and-whisker plots, across 1432 10-m grids in the south 15-ha of the experimental field.**

In another approach to examining temporal variation, mapped across-year standard deviations (SD) in yield, population, and yield ratio provided strong evidence of spatial patterns. For each variable, SD were  $> 50\%$  higher in relatively large ( $> 1000 \text{ m}^2$ ) field areas than in other areas of similar size (Fig. 8). We constructed RF models to investigate the relationship of population SD and yield ratio SD to soil and landscape variables. Predictors included ECa, gamma sensor, and landscape data, along with lab-measured parameters that were expected to be more temporally stable, CEC and OM. Results were of moderate accuracy ( $R^2 = 0.50 - 0.52$ ; Fig. 9), indicating a potential for identifying field areas with higher or lower temporal variability based on relatively static soil and landscape variables. Based on the minimum depth distribution plots, the important predictors included landscape variables, ECa, SOM, and CEC. In both cases, the top two predictors represented landscape variation (hillshade or elevation) and indicators of near-surface soil texture (ECsh or CEC).



**Fig. 8. Standard deviation (SD) of harvest population (left) and SD of yield ratio (right) for the south 15 ha of the case-study field, calculated across seven corn years from 2003 to 2016.**



**Fig. 9. Results of random forest models estimating 2003-2016 standard deviation in population (left) and standard deviation in yield ratio (right) as a function of soil and landscape variables.**

The ICE plots for population SD and yield ratio SD provided further insight into the relative effects of top predictors. Fig. 10 (top) shows the effect of hillshade and ECsh on population SD. Higher population SD values were found at high hillshade values, or the west-facing areas of the field. This could indicate that the importance of solar warming in germination varied from year to year depending on temperature and/or soil moisture conditions at the time of planting. Lower ECsh values tended to increase population SD. Perhaps the inter-annual variation in soil water content, creating variable emergence issues due to slotting or surface crusting was higher in these areas. Areas of higher ECsh might experience these problems on a more regular basis, and therefore exhibit a relatively lower SD. Fig. 10 (bottom) shows the combined effect of elevation and ECsh on yield ratio SD. Yield ratio was less variable across years in the higher-elevation areas, likely due to less variation in soil water than in the lowest part of the landscape where runoff could tend to collect. At higher elevations, higher yield ratio SD was generally associated with higher ECsh. Areas of claypan soil fields with higher ECsh can vary greatly in yield depending on the timeliness of rainfall, due to the lower plant-available water holding capacity associated with high clay.

## Conclusion

Yield, harvest population, and soil and landscape data were collected for nine corn production years on a central Missouri, USA research field from 1999 to 2016. For seven years, high-speed data collection enabled measurement of individual plant spacing. Spatial population variability was large in all site-years, and harvest populations were between 20 and 40% lower than seeding rate. The fraction of plants at correct spacing (i.e., not doubles or skips) ranged from 57 to 84%.

Using random forest machine learning models to examine the effects of soil and landscape properties on the dependent variables of harvest population and yield ratio, we found that:

- Single-year (2016) population was very well-estimated ( $R^2 = 0.84$ ), with the most important predictors in the model being landscape and proximal sensor variables as well as soil-test phosphorus.
- Single-year (2016) yield ratio was well-estimated ( $R^2 = 0.65$ ), with the most important predictors being landscape variables.
- Multiple-year models incorporating precipitation information in the predictor dataset were not successful in modeling population or harvest ratio. Additional weather variables and/or model structures that better deal with variables with a small number of observations (i.e., by year) should be evaluated.

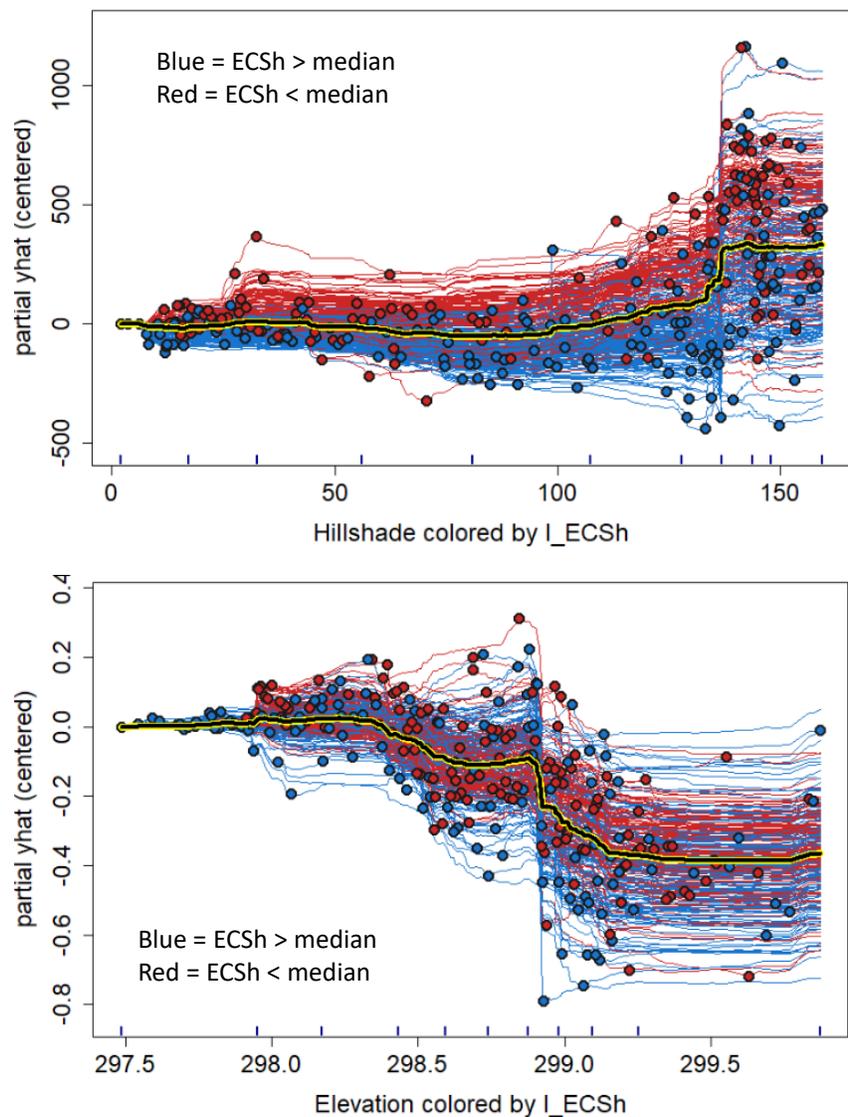


Fig. 10. Individual conditional expectation (ICE) plots for standard deviation (SD) of population (top) and SD of yield ratio (bottom). The top plot shows expected variation in population SD as a function of variation in hillshade (horizontal axis) and ECsh (red vs. blue colors). The bottom plot shows expected variation in yield ratio SD as a function of variation in elevation (horizontal axis) and ECsh (red vs. blue).

- Multiple year models estimating the temporal SD of population and yield ratio were moderately successful (set  $R^2 = 0.50-0.52$ ), with the most important predictors being landscape variables, soil apparent electrical conductivity, soil organic matter, and CEC.

Overall, this case-study analysis showed the potential for explanatory modeling of spatial variability in harvest population and yield ratio, as well as their across-year temporal variability. Further research should investigate extending this analysis to other field-years and incorporate additional population metrics (e.g., fraction at correct spacing) into the machine learning analysis.

### Acknowledgements

We acknowledge the contributions of Stuart Birrell, Michael Krumpelman and Scott Drummond to population sensor development, system implementation, and data analysis. We also acknowledge Matt Volkman, Kurt Holiman, and many other USDA and University of Missouri employees who contributed to collection of the data used in this research.

This research was funded by the USDA Agricultural Research Service through Project 5070-12610-005. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by USDA or the University of Missouri. USDA is an equal opportunity provider and employer.

## References

- Barnhisel, R.I., Bitzer, M.J., Grove, J.H., & Shearer, S.A. (1996). Agronomic benefits of varying corn seed populations: A central Kentucky study. In P.C. Robert, R.H. Rust, and W.E. Larson (Eds.), *Proceedings of the 3rd International Conference on Precision Agriculture* (pp. 957-965). ASA/CSSA/SSSA, Madison, WI, USA.
- Bauer, M.G., Davis, J.G., Sudduth, K.A., & Drummond, S.T. (2000). Agronomic and economic evaluation of variable-rate corn seeding on Missouri soils. In P.C. Robert, R.H. Rust, and W.E. Larson (Eds.), *Proceedings of the 5th International Conference on Precision Agriculture*. ASA/CSSA/SSSA, Madison, WI, USA.
- Birrell, S.J. & Sudduth, K.A. (1995). Corn population sensor for precision farming. Paper No. 951334. American Society of Agricultural and Biological Engineers, St. Joseph, MI, USA.
- Bullock, D.G., Bullock, D.S., Nafziger, E.D., Doerge, T.A., Paszkiewicz, S.R., Carter, P.R., & Peterson, T.A. (1998). Does variable rate seeding of corn pay? *Agronomy Journal*, 90: 830-836.
- Nafziger, E.D. (1996). Effects of missing and two-plant hills on corn grain yield. *Journal of Production Agriculture*, 9(2): 238-240.
- Nielsen, R.L. (1995). Planting speed effects on stand establishment and grain yield of corn. *Journal of Production Agriculture*, 8(3): 391-393.
- Sudduth, K.A., Birrell, S.J., & Krumpelman, M.J. (2000). Field evaluation of a corn population sensor. In P.C. Robert, R.H. Rust, and W.E. Larson (Eds.), *Proceedings of the 5th International Conference on Precision Agriculture*. ASA/CSSA/SSSA, Madison, WI, USA.
- Sudduth, K.A., Birrell, S.J., Bollero, G.A., Bullock, D.G., Hummel, J.W., & Kitchen, N.R. (2005). Site-specific relationships between corn population and yield. In *Proceedings of the 7th International Conference on Precision Agriculture*. University of Minnesota, St. Paul, MN, USA.
- Sudduth, K.A. & Drummond, S.T. (2007). Yield editor: Software for removing errors from crop yield maps. *Agronomy Journal*, 99:1471-1482.
- Sudduth, K.A., Drummond, S.T., & Myers, D.B. (2012). Yield Editor 2.0: Software for automated removal of yield map errors. Paper No. 121338243. American Society of Agricultural and Biological Engineers, St. Joseph, MI, USA.
- Yost, M.A., Kitchen, N.R., Sudduth, K.A., Sadler, E.J., Drummond, S.T., & Volkmann, M.R. (2017). Long-term impact of a precision agriculture system on grain crop production. *Precision Agriculture*, 18(5):823-842.