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Abiotic Factors and Management Strategies Associated with Blueberry Replant Disorder in Northern Highbush Blueberry

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Abstract. **Northern highbush blueberry (*Vaccinium corymbosum* L.) is native to North America and an economically important fruit crop in the United States. Replanting older fields with new cultivars has become increasingly common to meet fresh market demand. However, growers frequently report poor establishment and reduced plant growth in replanted fields. We investigated this phenomenon, which is termed blueberry replant disorder (BRD), using a combination of grower surveys and field-based measurements in commercial blueberry fields. The objectives of this study were as follows: characterize the physiological symptoms associated with BRD in commercial blueberry fields using grower surveys and field measurements; quantify associations between soil chemical properties, horticultural practices, and BRD incidence; and evaluate variation in BRD incidence and severity across farms and cultivars. Fourteen replanted commercial fields across five farms in Michigan were categorized as healthy or BRD-symptomatic based on plant growth relative to planting age and evaluated over two growing seasons. Compared with healthy replanted fields, BRD-symptomatic fields exhibited 39.4%, 35.3%, and 13.0% reductions in plant height, plant width, and leaf chlorophyll index, respectively. The BRD-symptomatic fields were associated with elevated soil pH and low cation exchange capacity, which may reflect differences in nutrient availability and uptake. Cultivar choice, wider raised beds, and greater wood chip mulch use were associated with healthy replanted fields. Multivariate analyses were consistent with cultivar-specific and site-specific responses to soil and horticultural parameters. These findings provide a quantitative description of BRD and identify potential management strategies to improve blueberry establishment following replanting.**

Introduction

Blueberries (*Vaccinium* section *Cyanococcus*) are flowering shrubs endemic to North America. Blueberry cultivation began centuries ago, with records indicating that Native Americans managed the productivity of wild stands of lowbush blueberry (*Vaccinium angustifolium* and *V. myrtilloides*) through controlled burns (Strik and Yarborough 2005). Cultivation of northern highbush blueberry (*V. corymbosum*; NHB) occurred much later and was catalyzed by the research and breeding efforts of F.V. Coville and Elizabeth White throughout the early 1900s (Coville 1911; McMillan et al. 1944; Protzman 2021). In the 1920s, the first commercial blueberry orchards were established in New Jersey and Michigan, which gave rise to the US blueberry industry (Mainland 2012). Over the past century, blueberry production has expanded throughout the United States into southeastern and Pacific northwestern states (Strik and Yarborough 2005). Production has also increased globally across five continents and reached new climates and consumers (Bañados 2009; Lobos and Hancock 2015).

Blueberry is a high-maintenance crop that requires specialized management practices to accommodate distinct aspects of its physiology and ensure successful cultivation. The most widely recognized requirement for blueberry is an acidic soil (pH 4.0–5.5, depending on soil type) (Coville 1911). Recent work has shown that high soil pH damages photosynthetic and antioxidant systems within blueberry leaves, decreases dry weight of all organs, and increases berry acidity (Jiang et al. 2019; Yang et al. 2022). Together, these effects disrupt blueberry growth and development and limit yield. Beyond this, additional soil characteristics that reflect the drained bog and muckland environments in which blueberry evolved are critical for vigorous plant growth. These include high soil organic matter (SOM), adequate soil aeration during periods of active growth, relatively nutrient-depleted conditions, and ammoniacal nitrogen sources (Coville 1911; McMillan et al. 1944). To accommodate these unique requirements, blueberry growers have adopted a suite of specialized horticultural management practices. Among the most widely implemented of these are planting into raised beds and the use of organic mulches. Raised beds improve soil drainage and aeration, thereby enhancing root zone conditions and reducing the risk of waterlogging-associated diseases, including those caused by *Phytophthora* spp. (Scherm and Krewer 2008). Using wood chip mulch as a soil amendment provides plantings with weed suppression and moisture retention and also increases the soil cation exchange capacity (CEC) over time (Kuepper and Ames 2024).

Once established, perennial fruit crops, including highbush blueberries, can often be productively cultivated for decades. However, orchard replanting is an inevitable reality. The most common reason for replanting perennial fruit crops is related to a decline in productivity, which is often associated with plant age and the presence of viruses or pathogens (Teskey and Shoemaker 1978; Treder and Mika 2010). In some cases, a different cultivar is planted to reach a different market (e.g., processing vs. fresh market) or train plants to a different system to accommodate new harvesting technology (Barritt 1999; Zhang et al. 2024). In other cases, a change in consumer preferences of fruit physiochemical characteristics justifies replanting (Barritt 1999; Zhang et al. 2024). In many blueberry production regions, a shift toward producing a greater percentage of berries for the fresh market follows a trend of less consumption of processed or frozen berries (Brazelton and Strik 2007). Moreover, increasing blueberry acreage in competing countries, namely, Mexico, Peru, and Chile, is pressuring US farmers to improve yields to remain competitive in the fresh market (Yeh et al. 2023). These factors, in combination with the antiquity of many of Michigan's blueberry orchards (sometimes up to 70 years old), have led some Michigan farmers to replant older blueberry fields with new and highly productive cultivars that produce berries better suited for the fresh market.

Many fruit crops, particularly members of the Rosaceae family such as apple, cherry, peach, strawberry, rowan, and rose, have documented susceptibility to replant disease (Winkelmann et al. 2019). Replant disease is more likely to occur in field sites where the same species was previously cultivated, and it

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J.V. and M.J.H. designed the survey and experiment. A.M.K., S.S., M.J.H., and J.V. collected data. A.M.K. analyzed the data. All authors drafted the manuscript. M.J.H. and J.V. critically reviewed the manuscript.
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includes symptoms such as a reduction of aboveground and belowground biomass and growth, leaf chlorosis, root necrosis, and reduction of yield compared with unaffected plants (Mazzola 1998; Yim et al. 2014). The incidence of replant disease is not new by any means. "Don't plant pip after pip or stone after stone… " is a maxim regarding pome (pip) and drupe (stone) fruits that apple and cherry growers in England have maintained for over a century (McKenry 1999). The high variability across cases, fruit crops, and locations has muddled a myriad of potential contributing factors. Some studies indicated that abiotic factors, such as incorrect pH, soil nutrient imbalance, or weak soil structure, may be responsible for causing or modulating the severity of replant disease (Mazzola and Manici 2012; Simon et al. 2020; Spath et al. 2015; Utkhede and Smith 1994; Winkelmann et al. 2019). Others point to the consistent presence of antagonistic microorganisms in these systems, like plant parasitic nematodes, *Fusarium*, *Pythium*, or *Rhizoctonia* (Duan et al. 2022; Peter 2023; Spath et al. 2015; Traquair 1984). Fumigation and biocontrol agents have been shown to successfully alleviate replanting issues in some symptomatic fields, implying the presence of a biotic factor (Fazio et al. 2012; Mazzola et al. 2007). Currently, it is unclear whether abiotic, biotic, or a combination of both underly the symptoms reported in blueberry fields.

Consistent with previous studies that examined replant problems in perennial fruit crop systems, we first investigated potential abiotic constraints (Fazio et al. 2012; Simon et al. 2020; Utkhede and Smith 1994). Accordingly, we refer to this phenomenon as blueberry replant disorder (BRD), rather than as a replant disease, because the latter term implies the presence of a biotic causal agent, which is not currently supported by the available evidence in this study or in other studies of blueberry (Utkhede and Smith 1994). The primary objectives of this study were as follows: characterize the physiological symptoms associated with BRD in commercial blueberry fields using grower surveys and field measurements; quantify associations between soil chemical properties, horticultural practices, and BRD incidence; and evaluate variation in BRD incidence and severity across farms and cultivars. We hypothesized the following: plantings classified as BRD-symptomatic would exhibit reduced plant height and width and leaf chlorophyll index relative to healthy plantings; BRD-symptomatic and healthy plantings would differ in soil chemical and horticultural parameters, thus reflecting variation in site conditions and management practices; and BRD incidence and severity would vary among farms and cultivars, indicating site-specific and genotype-specific responses. Because of the observational nature of this study, these hypotheses were tested as associations rather than causal relationships. This study integrated a statewide grower survey with multiyear field measurements from replanted commercial blueberry fields to address these objectives to provide a framework for diagnosing BRD and guiding targeted management strategies.

Materials and Methods

Survey of commercial blueberry growers. A five-question survey was developed to assess grower experiences and practices related to replanting northern highbush blueberry fields in Michigan. Survey questions were reviewed by Michigan State University Extension specialists and key industry stakeholders before distribution, and minor revisions were made to improve clarity and relevance. Following approval by the Michigan State University Institutional Review Board (STUDY202501022), the survey was distributed at Michigan State University Extension meetings and via e-mail to commercial blueberry growers along with a brief description of the study objectives. Survey questions are provided in Supplemental Table S1.

Responses to survey questions one and two were grouped by cultivated blueberry acreage (farm size): small (<25 acres), medium (25–200 acres), or large (>200 acres). Survey questions four and five allowed respondents to select more than one response. Counts for any of the potential answers were tallied as they appeared (e.g., a response of "1 or 2 years fallowing/cover cropping" for question four was binned as a tally for 1 year and 2 years individually). Responses were collected over a 6-month period, yielding responses from 38 growers representing 7541 acres (approximately 44.5% of Michigan blueberry acreage as of 2023). Not all respondents answered every question; therefore, the sample size (n) varied slightly across questions.

Study design and field selection. The field survey was conducted during the 2023 and 2024 growing seasons and included commercial blueberry fields replanted between 2010 and 2022. Before replanting, 75% of surveyed fields were planted with 'Jersey', while the remaining fields were planted with other cultivars. Replanted cultivars included Envoy, Sensation, Aurora, and Liberty. Field assessments were conducted from 5 to 9 Jun and on 20 Jun in 2023, and on 28 and 29 May and 6 Jun in 2024. Survey field sites spanned three counties, Muskegon, Ottawa, and Van Buren, along western Michigan with high blueberry acreage (Fig. 1).

Before data collection, fields were classified as either healthy or symptomatic based on grower observations. All fields included in the study were paired, that is, each healthy field had a geographically close (often adjacent) symptomatic counterpart that contained the same cultivar and was planted the same year by the same grower using the same planting techniques. In each field, three representative plants were chosen from three randomly selected rows for measuring and sampling.

Farm 1: This site is located in Van Buren County, MI, USA. The pre-existing 'Jersey' northern highbush blueberry (NHB) field was removed in 2017 and immediately replanted with 'Sensation' NHB in 2017. The plants were established on raised beds, and wood chip mulch was incorporated into the soil before forming the raised bed as well as layered on top of raised beds. According to Web Soil Survey (WSS), this site is a Pipestone-Kingsville complex (0%–3% slopes).

Farm 2: This site is located in Van Buren County, MI, USA. The pre-existing 'Jersey' NHB fields were removed in 2018 and 2019 and replanted with 'Envoy' NHB in 2018 and 2019, respectively. The plants were established on raised beds, and wood chip mulch was incorporated into the raised beds as well as layered on top of raised beds. According to WSS, this site is a Thetford loamy sand (0%–2% slopes).

Farm 3: This site is located in Van Buren County, MI, USA. The pre-existing 'Rubel' NHB field was removed in 2017, and the land fallowed for 2 years before being replanted with 'Sensation' NHB in 2019. The plants were established on raised beds with a layer with pine wood chip mulch under black weed mat. According to WSS, this site is a Pipestone-Kingsville complex (0%–3% slopes).

Farm 4: This site is located in Ottawa County, MI, USA. The pre-existing 'Jersey' NHB fields were removed in 2011 and 2021, and immediately replanted with 'Aurora' and 'Envoy' NHB in 2011 and 2021, respectively. The plants were established on raised beds layered with pine wood chip mulch. According to WSS, this site contained both Granby loamy sand, lake plain (0%–2% slopes) and Pipestone-Covert-Saugatuck sands (0%–3% slopes).

Farm 5: This site is located in Muskegon County, MI, USA. The pre-existing 'Jersey' NHB field was removed in 2010 and immediately replanted with 'Aurora' and 'Liberty' NHB. The plants were established on raised beds layered with pine wood chip mulch. According to WSS, this site is a Roscommon and Au Gres sands.

Plant phenotype and raised bed dimensions. Plant height and width were measured at the time of sampling. The relative growth rate of height and width was calculated to normalize plant size across planting years using the following equation:

$$RGR = \frac{H2 \ or \ W2 - H1 \ or \ W1}{T2 - T1} \qquad [1]$$

where H2 and W2 represent the height and width of plants in the current year, respectively, H1 and W1 are the height and width of plants in the planting year, respectively, T2 is the current year, and T1 is the planting year. We collected H1 and W1 using representative plants of each cultivar from a nearby blueberry nursery.

Leaf chlorophyll index [soil plant analysis development (SPAD)] was measured using a SPAD-502Plus Chlorophyll Meter (Konica Minolta Sensing Inc., Osaka, Japan). Four equidistant measurements were collected from four representative leaves per plant, and the 16 measurements were averaged.

To assess raised bed dimensions, two soil probes were first inserted vertically at the

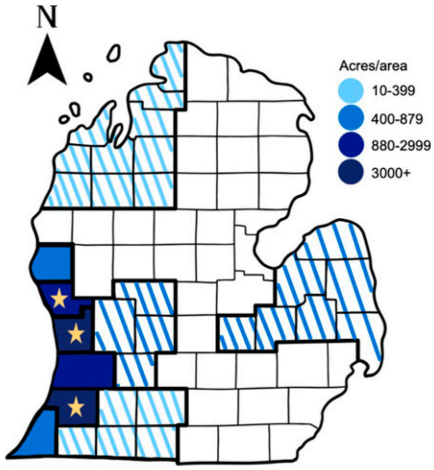

Fig. 1. A map of the state of Michigan's lower peninsula with counties representing significant blueberry acreage shaded in solid blue and geographical regions in striped blue. Stars represent counties included in the 2023–24 Blueberry Replant Survey. Source: 2018–19 US Department of Agriculture Rotational Survey.

base of either side of the raised bed. Raised bed width was measured as the horizontal distance between both probes. Raised bed height was measured using a level and yardstick to determine vertical distance from the bed apex to the adjacent soil surface.

Soil sampling and analysis. Soil samples were collected from the plants selected for measuring outlined previously. The surface layer of debris and wood chip mulch was first cleared from four equally spaced areas around the base of each plant at approximately 30 cm from the plant crown. A soil core was taken at a depth of approximately 20 cm using an AMS Regular soil probe [7/8 inches × 21 inches (2.2 cm × 53.3 cm); AMS, Inc., American Falls, ID, USA] in each area while carefully avoiding roots and rocks. The four core samples were homogenized in a 4.7-L plastic bucket, placed in a plastic bag, and kept on ice. The probe and bucket were cleaned and sterilized with a 70% ethanol solution between plants to minimize cross-sample contamination.

Soil samples were stored at 4 °C until all samples had been collected; thereafter, they were sieved using a 4-mm mesh to remove wood chip mulch and particulates and small root fragments. Sieved soil samples were sent to A&L Great Lakes (Fort Wayne, IN, USA), where they were dried overnight at 40 °C, sieved using a US no. 10 sieve (2 mm), and suspended in a 2:1 ratio of distilled water to soil before analyzing organic matter, available phosphorus, exchangeable potassium, magnesium, calcium, soil pH, soil buffer pH, and CEC (Brown 1998). The percentage of wood chip mulch in soil samples was estimated as the ratio of the mass of wood chip mulch to the mass of the original soil sample.

Base saturation was calculated from the soil data by first converting the nutrient values from ppm to meq/100 g and then using the following formula excluding sodium because it was not measured:

$$Base\ Saturation\ (\%\ BS) = \frac{Ca^{2+} + Mg^{2+} + K^{+}}{Total\ CEC}\, meq/100\ g \qquad [2]$$

Data processing and statistical analysis. All statistical analyses were conducted using R version 4.4.0 (R Core Team 2016). Mixed linear models were assessed using the Bayesian Index Criterion. The best-fitting model with the lowest relative Bayesian Index Criterion value was used for the analysis of variance (ANOVA). The chosen model included the BRD status and year as fixed effects and farm as a random effect. Both the main effects and BRD status × year interaction were assessed. Assumptions were checked and validated using Shapiro-Wilk's and Levene's tests and residual plots. A type III ANOVA table was generated using the "car" package version 3.1.3 to account for the unbalanced sample number within "BRD status" and "year." Marginal means for the BRD status and year were calculated using statistically significant ($P \leq 0.05$) factor(s)/interaction(s) using the emmeans package (Lenth and Piaskowski 2025). Parameters significantly altered by the BRD status were subjected to a post hoc analysis using Tukey's honestly significant difference adjusted pairwise t tests. A principal component analysis (PCA) was conducted using 14 parameters of 69 individuals as well as individual cultivars using the "prcomp" function. The PCA results were visualized using the "FactoMineR" version 2.11 and "factoextra" version 1.0.7 packages, with 95% confidence ellipses displayed from a minimum of three datapoints (Kassambara 2016; Lê et al. 2008).

Results

Insights from a grower survey of blueberry replanting efforts. To establish the groundwork for this study and gain a better understanding of growers' issues with replanting blueberry fields, a five-question survey was distributed to commercial blueberry growers in Michigan. We first asked about the blueberry acreage that each respondent produces and the acreage that they intend to replant during the next 5 years. Small farms (<25 acres) reported their intention to replant the highest percentage of their acreage (38%), while medium (25 to <200 acres) and large (<200 acres) farms planned to replant 18% and 17% of their acreage, respectively (Fig. 2A). Regardless of farm size, this equated to an industry-wide average of 18% of acreage being replanted from 2023 to 2028. Next, we asked about their methods for removing plants in established fields, and 83.3% of respondents reported "stump grinding" as their method of choice compared with "stump pulling" (Fig. 2B). Before replanting fields, the majority (58.5%) of respondents reported that they intended to fallow or cover crop their fields for 1 year, while 36.6% intended to fallow for 2 years, and 4.9% did not intend to fallow at all but intended to replant in the same year (Fig. 2C). Finally, growers were asked whether they had observed any "replant disease" symptoms in replanted fields they had observed, if any, at the time of taking the survey. The most frequently reported symptoms were poor growth/stunting (66.7%), followed by leaf chlorosis (15.0%), root rot (4.0%), and total plant death (4.0% each) (Fig. 2D).

Effect of BRD on plant growth and physiology. With the knowledge that many replanted fields were experiencing "poor growth/stunting," we sought to characterize the physiological effect of BRD in replanted commercial blueberry fields. To accomplish this, we measured plant growth rate and estimated chlorophyll content in fields that commercial growers deemed as "healthy" or "symptomatic" based on the visual appearance of the plants. The plant growth rate [vertical plant growth rate (plant height) and lateral plant growth rate (plant width)] were significantly different between healthy and BRD symptomatic plantings. Symptomatic plants were shorter and narrower, representing a slower annual vertical growth rate (9.50 ± 1.97 vs. 15.7 ± 2.05 cm; $P = 0.0240$) and lateral growth rate (9.92 ± 1.68 vs. 15.3 ± 1.72 cm; $P < 0.001$) than those of healthy plants (Table 1). This equated to decreases of 39.4% and 35.5% in plant height and width, respectively (Fig. 3A, 3B). Leaf SPAD was significant by the interaction term (BRD status × year; $P = 0.005$). Symptomatic plants exhibited a lower average leaf SPAD value compared with healthy plants in both years, but the magnitude of this difference varied. More specifically, in 2023, symptomatic plants (41.8 ± 1.06) had 3.91% lower leaf SPAD values than those of healthy plants (43.5 ± 1.16); however, in 2024, symptomatic plants (40.2 ± 0.933) had 13.0% lower SPAD values than those of healthy plants (46.2 ± 0.933). A post hoc analysis revealed that only the 2024 contrast between BRD statuses was statistically significant (Fig. 3C).

The role of soil chemistry and horticultural management in BRD. Among the soil chemistry parameters, soil pH, soil buffer pH, CEC, and percent base saturation showed significant differences by BRD status. Healthy replanted fields had a mean soil pH values of 5.03 ± 0.268 (2023) and 4.71 ± 0.254 (2024), whereas those of symptomatic plantings were 5.64 ± 0.262 and 4.85 ± 0.254, respectively (Table 1, Fig. 4A). Soil buffer pH, however, was not significant according to the BRD status ($P = 0.085$) (Supplemental Fig. S1). In 2023, the symptomatic plantings had notably high (alkaline) soil pH compared with that of the other BRD status–year combinations; additionally, it was the only group with a mean that was statistically distinguishable. Symptomatic plantings also exhibited a greater range of pH values compared with healthy plantings. The pH range of healthy replanted fields was 0.600 (2023) to 1.30 (2024). In contrast, the pH range of symptomatic plantings was 2.10 (2023) to 2.20 (2024), indicating a 2.26-fold difference across years. Regarding CEC, healthy replant fields had a mean value of 11.6 ± 1.44 meq/100 g, whereas symptomatic

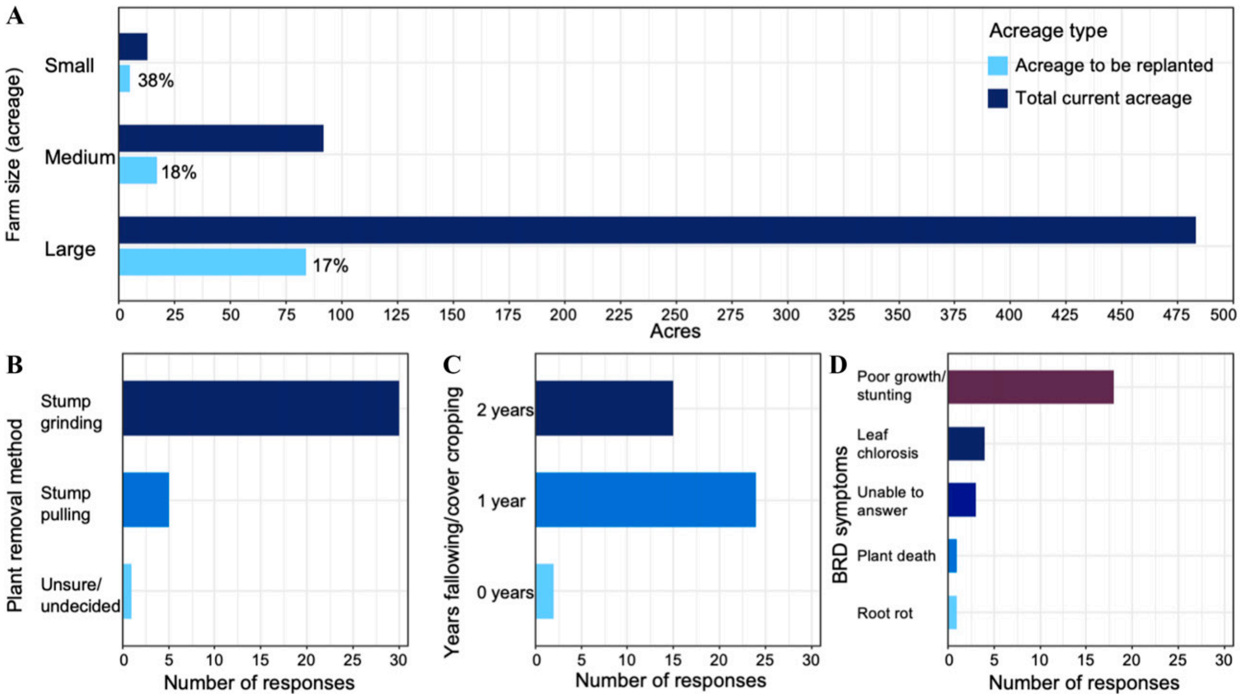

Fig. 2. Responses to a survey inquiring about the process of replanting northern highbush blueberry fields in Michigan. For questions 1 and 2, responses were grouped by blueberry acreage cultivated (farm size): small (<25 acres), medium (25–200 acres), and large (>200 acres). Not all respondents answered every question. Questions 1 and 2, $n = 31$; question 3, $n = 36$; question 4, $n = 35$; question 5, $n = 27$.

plantings had a mean value of 8.54 ± 1.40 meq/100 g ($P < 0.001$) (Fig. 4B). Of the calculated CEC, percent base saturation values for healthy replant fields were 30.0 ± 3.7% and 44.9 ± 3.5% for symptomatic fields ($P < 0.01$).

Considering horticultural management parameters, a significant effect of the BRD status was found for raised bed width, but not for raised bed height. The raised bed width of healthy replanted fields was 147 ± 18.3 cm, while that of symptomatic plantings was significantly ($P = 0.004$) lower at 136 ± 18.2 cm, corresponding to an 8.01% difference in width (Table 1, Fig. 4C). Wood chip mulch did not differ across BRD status in either year.

Variables associated with BRD incidence and initial trends by farm and plant cultivar. Because BRD is a poorly understood but multifaceted issue, we characterized relationships between plant, horticultural, and soil chemistry parameters through a PCA. Using 14 parameters, we were able to resolve 85% of the variation within the data frame with six principal components (Supplemental Table S2). The first principal component accounted for 28.8% of the variation. The second principal component accounted for 20.5% of the variation. The top contributing loadings for the first principal component were calcium, magnesium, and soil pH (Supplemental Table S3). The top contributing loadings for the second principal component were buffer pH, CEC, organic matter, and raised bed width.

In the PCA, plant height and width aligned with soil wood chip mulch percentage and opposed increasing values of measured soil nutrients, raised bed height, and raised bed width (Fig. 4). The third plant parameter, leaf SPAD, was positively associated with CEC and negatively associated with soil pH and buffer pH. Furthermore, leaf SPAD was associated orthogonally with plant height and width.

When color-coded for BRD status, healthy replanted fields exhibited more peripheral values across most parameters compared with

Table 1. Physiological, horticultural, and soil chemistry parameters in healthy and BRD symptomatic replanted commercial blueberry fields in Michigan. Values represent the estimated marginal means and corresponding standard errors. Treatment P values were calculated using a type III analysis of variance (ANOVA) table to account for unbalanced design and considered significant when $P < 0.05$.

	BRD status			Year			BRD status × year
Parameter	Healthy	Symptomatic	P value	2023	2024	P value	P value
Physiological parameters							
Plant height (cm·yr^{-1})	15.7 ± 2.05	9.50 ± 1.97	0.024	12.1 ± 2.21	13.1 ± 1.86	0.963	0.651
Plant width (cm·yr^{-1})	15.3 ± 1.72	9.92 ± 1.68	<0.001	12.5 ± 1.80	12.8 ± 1.62	0.338	0.088
Leaf SPAD	44.8 ± 0.868	41.0 ± 0.838	0.170	42.7 ± 0.927	43.2 ± 0.798	0.024	0.005
Horticultural parameters							
Raised bed height (cm)	21.2 ± 2.58	20.0 ± 2.51	0.920	20.7 ± 2.72	20.6 ± 2.41	0.789	0.650
Raised bed width (cm)	147 ± 18.3	136 ± 18.2	0.004	138 ± 18.3	145 ± 18.2	0.996	0.057
Soil wood chip mulch (%)	2.70 ± 0.500	2.60 ± 0.500	0.728	1.70 ± 0.600	3.50 ± 0.500	0.053	0.709
Soil chemistry							
Soil pH	4.84 ± 0.251	5.24 ± 0.248	<0.001	5.29 ± 0.261	4.79 ± 0.239	0.032	0.018
Soil buffer pH	6.30 ± 0.147	6.52 ± 0.145	0.085	6.61 ± 0.153	6.22 ± 0.141	0.018	0.686
SOM (%)	3.81 ± 0.619	3.21 ± 0.604	0.531	3.48 ± 0.651	3.55 ± 0.582	0.781	0.787
CEC (meq/100 g)	11.6 ± 1.44	8.54 ± 1.40	0.037	8.12 ± 1.52	12.0 ± 1.34	0.089	0.483
Phosphorus (ppm)	92.8 ± 22.1	104 ± 21.8	0.963	115 ± 22.9	82.2 ± 21.3	0.042	0.455
Potassium (ppm)	43.8 ± 6.69	43.2 ± 6.61	0.832	43.3 ± 6.86	43.7 ± 6.50	0.983	0.883
Magnesium (ppm)	90.9 ± 17.0	91.2 ± 16.8	0.421	116 ± 17.4	66.4 ± 16.5	0.006	0.217
Calcium (ppm)	477 ± 79.2	505 ± 78.4	0.441	609 ± 80.8	374 ± 77.3	<0.001	0.631
Base saturation (%)	30.0 ± 3.70	44.9 ± 0.035	<0.01	0.478 ± 0.040	0.272 ± 0.032	0.126	0.080

BRD = blueberry replant disorder; CEC = cation exchange capacity; SPAD = soil plant analysis development.

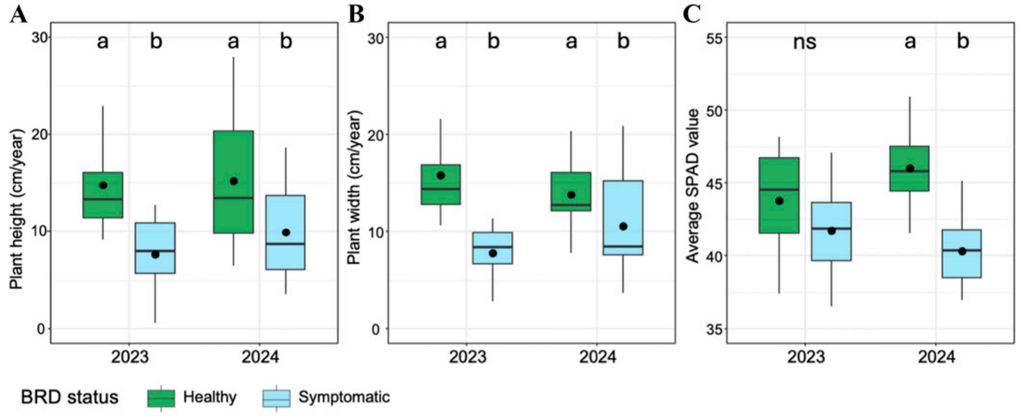

Fig. 3. Boxplots of (**A**) plant height, (**B**) plant width, and (**C**) leaf soil plant analysis development (SPAD) between healthy and blueberry replant disorder (BRD) symptomatic fields in Michigan. The mean value for each box is represented by a black dot. Data were analyzed with an analysis of variance (ANOVA) generalized across BRD status as the fixed factor. A two-way ANOVA was conducted when the status × year interaction term was significant ($P < 0.05$). Post-hoc analysis using Tukey's honestly significant difference adjusted pairwise *t* tests. ns = not statistically significant.

symptomatic fields, appearing at the peripheries of the biplot (Fig. 5A). In contrast, symptomatic fields tended to cluster near the origin, with higher soil pH, buffer pH, magnesium, and calcium being associated with their distribution.

The PCA also revealed clustering by both farm site and plant cultivar (Fig. 5B, 5C). For example, plants at farm 5 (cultivars Aurora and Liberty) were strongly associated with variables including SOM, raised bed dimensions, and soil nutrients, while plants at farm 2 ('Envoy' only) were strongly associated with soil buffer pH. This pattern may indicate cultivar-specific and location-specific responses, although the confounding of farm and cultivar in this study prevented the identification of a definitive source for these differences.

Differential response of farm and plant cultivar to BRD. To better characterize the effects of cultivar and farm management in our study, the four cultivars were analyzed individually. In the cultivar-specific PCAs, a separation between healthy and symptomatic plants was observed (Fig. 6). However, the primary variables associated with this separation differed among cultivars.

In the 'Aurora' PCA, dimensions 1 and 2 captured 37.4% and 28.4% of the variance, respectively (Fig. 6A, 6B). Plant parameters exhibited strong positive correlations with SOM and raised bed width, but no association with buffer pH, calcium, or phosphorus. Weaker positive relationships emerged with raised bed height, magnesium, potassium, CEC, and wood chip mulch, while a weak negative association was found with soil pH. Both BRD status and farm differentiated along the first dimension: healthy plants and farm 5 specimens clustered toward negative x-values, whereas symptomatic plants and farm 4 specimens occupied positive x-values.

In the 'Sensation' PCA, dimensions 1 and 2 captured 34.8% and 31.1% of the variance, respectively (Fig. 6C, 6D). Plant parameters exhibited a strong positive relationship with raised bed height, strong negative relationships with soil nutrient concentrations, SOM, and wood chip mulch; however, they were not associated with soil pH, buffer pH, and CEC. Both BRD status and farm were differentiated along dimension 1. Within each farm, plant status separated along dimension 1, such that symptomatic plants shifted left in comparison with healthy plants.

In the 'Liberty' PCA, dimensions 1 and 2 captured 51% and 26.9% of the variance, respectively (Fig. 6E, 6F). Plant parameters exhibited strong positive correlations with raised bed height, CEC, SOM, potassium, and raised bed width, while there were strong negative correlations with buffer pH, soil pH, phosphorus, and wood chip mulch. No association with magnesium or calcium emerged. 'Liberty' was only found at farm 5; therefore, the differentiation between the data, which occurred on the x-axis, is associated with BRD status.

The 'Envoy' PCA exhibited distinct patterns (Fig. 6G, 6H). First, dimensions 1 and 2 captured 58.3% and 22.2% of the variance, respectively, which were the highest proportions of variance among the four cultivars. Unlike other cultivars, the plant parameters did not cluster together. Leaf SPAD and plant width were negatively associated with wood chip mulch and weak positive relationships with potassium and magnesium. Conversely, plant height showed a positive correlation with CEC and SOM and a weak negative

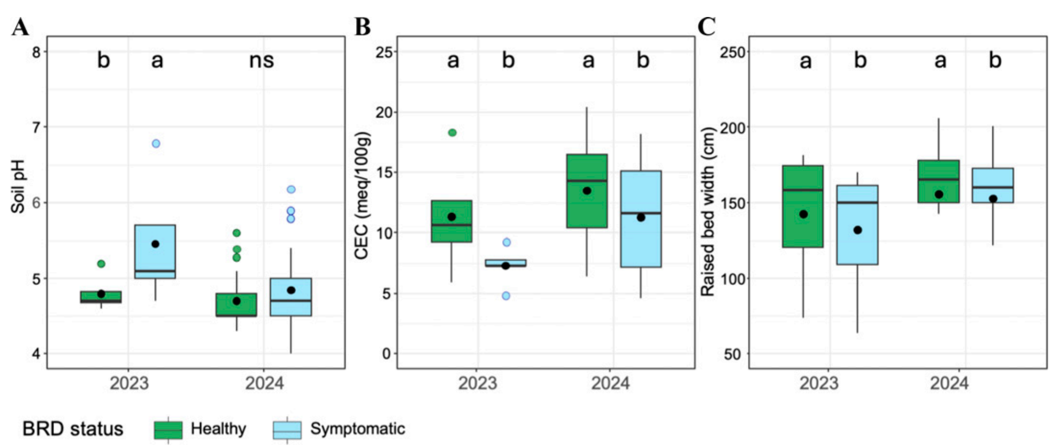

Fig. 4. Boxplots of soil chemistry parameters. (**A**) Soil pH. (**B**) Soil cation exchange capacity (CEC). (**C**) Raised bed width between healthy and blueberry replant disorder (BRD) symptomatic fields in Michigan. The mean value for each box is represented by a black dot. Data were analyzed using an analysis of variance (ANOVA) generalized across status as the fixed factor. A two-way ANOVA was conducted when the status × year interaction term was significant ($P < 0.05$). Post hoc analysis using Tukey's honestly significant difference adjusted pairwise *t* tests. ns = not statistically significant.

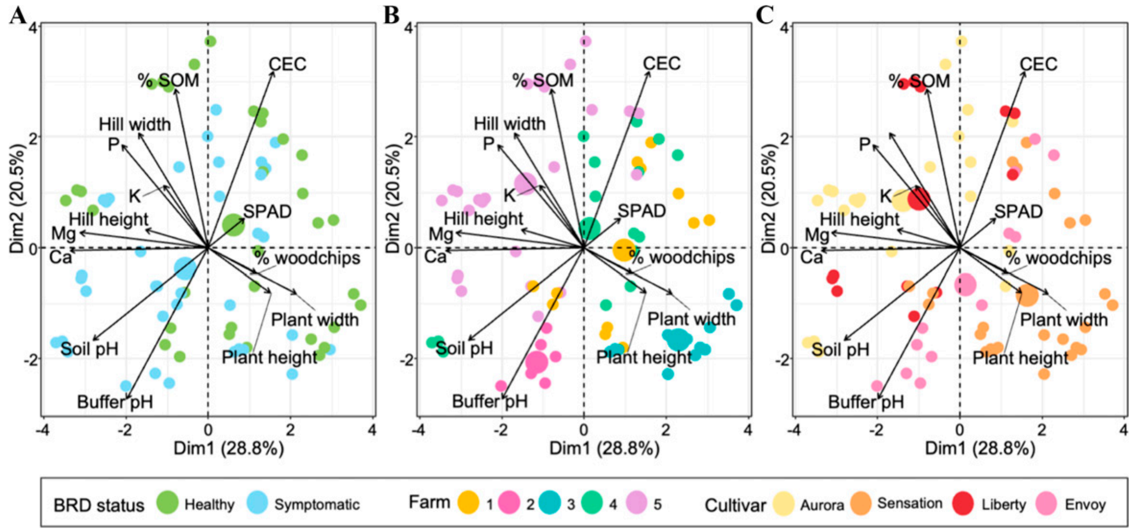

Fig. 5. Principal component analysis (PCA) with clustering by blueberry replant disorder (BRD) status, farm site, and plant cultivar. The PCA was grouped by (**A**) BRD status, (**B**) farm site, and (**C**) plant cultivar for replant fields in Michigan. The PCAs were generated from 14 parameters, resolving 85% of the variation in the dataset within six principal components. Data were visualized using FactoMineR and factoextra packages in R.

correlation with both soil and buffer pH. Furthermore, 'Envoy' displayed unique axis separation: BRD status divided along dimension 2 and was primarily influenced by leaf SPAD and wood chip mulch, while farm divided along dimension 1 and was influenced by all other measured parameters.

Discussion

Survey of commercial blueberry growers highlighted replanting efforts and issues. Blueberry production and consumption are experiencing significant growth in the United States and globally (Brazelton and Strik 2007). To keep pace with fresh market consumption, some growers are establishing large plantings of new cultivars in soil-based or alternative production systems (Fang et al. 2020) or through replanting existing fields. This study aimed to assess acreage replanting efforts in Michigan, which has historically been a leading contributor to the US supply of fresh and processed blueberries, and investigate growers' standard replanting practices to better understand reports of establishment issues faced by some growers during this process.

Surveyed growers stated their intentions to replant approximately 18% of total industry acreage over a 5-year span from 2023 to 2028. This percentage was higher for farms smaller than 25 acres (35%), but it was similar for farms larger than 25 and 200 acres (17% and 18%, respectively). The survey also inquired about methods of removing existing plants. The majority of respondents (83.3%) said they would use "stump grinding" rather than "stump pulling." Two studies of almond demonstrated that the practice of whole tree grinding, as opposed to pulling and discarding or burning, provides numerous benefits (Holtz et al. 2016, 2004). Stump grinding led to an increase in *Basidiomycetes* populations, which aid in nutrient recycling and soil aggregation, add soil nutrients, organic matter, and organic carbon to the soil, and acidify the soil (Holtz et al. 2016, 2004). At 2, 3, and 4 years after whole tree grinding, these changes resulted in higher levels of nitrogen, potassium, phosphorus, manganese, and iron in leaves and improved yields in new plants (Holtz et al. 2004, 2016). Because blueberries require acidic soil with high SOM, grinding could offer benefits to replanted fields other than time-savings. While grinding plant material infected with pathogens is a potential concern, there is currently no evidence to support negative effects in replanted fields (Browne et al. 2026).

The survey indicated that 58.5% and 36.6% of growers intend to fallow or cover crop (planted fallow) for 1 or 2 years before replanting, respectively. As opposed to bare fallows that promote soil erosion and compaction (Havlin et al. 2021), planted fallows or regrowth of natural vegetation are well-documented methods of enhancing soil fertility, reducing erosion, rebuilding soil nutrients, and reducing pests, diseases, and weeds (Ahn 1979; Soropa et al. 2022; Styger and Fernandes 2006; Tian et al. 2005). Traditionally, the regenerative effects of fallowing are attributed to decades-long efforts; however, recent works demonstrated that short-term fallowing (1–5 years) may catalyze positive physiochemical changes to the soil by altering the soil microbiome (Li et al. 2018; Lin et al. 2023). Cover cropping, specifically interrow cover cropping, is a related practice with increasing benefits for woody perennial systems such as blueberry. Historically, cover cropping has been restricted to annual systems (Castellano-Hinojosa and Strauss 2020), but recent studies of peach and apple demonstrated that interrow cover cropping increases water status and leaf nitrogen content of the primary crop as well as improves overall soil fertility across a number of metrics (Ciacci et al. 2023; Ma et al. 2024).

The primary goal of this survey was to identify the symptoms of plants that did not establish well. Nearly 66.7% of surveyed growers stated that "poor growth/stunting" was the main symptom. Only 15% of surveyed growers mentioned that symptomatic plantings exhibited "leaf chlorosis," indicating that most plants appear healthy but were simply not growing as vigorously as expected. This issue was further investigated through a soil sampling survey.

BRD is represented by decreased plant growth rate and leaf chlorosis. Replanting-related disorders diminish plant growth, leading to obvious differences in plant size, canopy density, and leaf color. This disorder has been highlighted in many economically important fruit and nut crops, including apple, cherry, strawberry, peach, and almond (Browne et al. 2006; Hoestra 1968; Munro 2018; Singh and Dhiman 2003; Winkelmann et al. 2019). Replanting disorder has yet to be defined in blueberry, although several works have highlighted tangential problems associated with new planting establishment, such as the presence of parasitic nematodes or *Phytophthora root rot* (Bryla et al. 2008; Jagdale et al. 2013; Noe et al. 2013; Zydlik et al. 2019). The primary objective of this study was to characterize the physiological symptoms associated with BRD in commercial blueberry fields using grower surveys and field measurements. Therefore, a critical first step was to characterize the apparent differences in plant growth rate and leaf color. Our data revealed that, compared with healthy replanted fields, BRD symptomatic fields exhibited 39.4% and 35.3% reductions in plant height and width, respectively. In other fruit crops known to suffer from replant disorder, growth reduction of effected plants can be substantial. Mountain and Boyce (1958) indicated reductions in plant height of approximately 50% in peach, whereas Hoestra (1968) reported reductions of nearly 90% under some circumstances in apple. In our study, symptomatic plants also showed 13% lower leaf SPAD values compared with healthy plants in the first year of the study. Studies of multiple crops noted that leaf chlorosis was a common

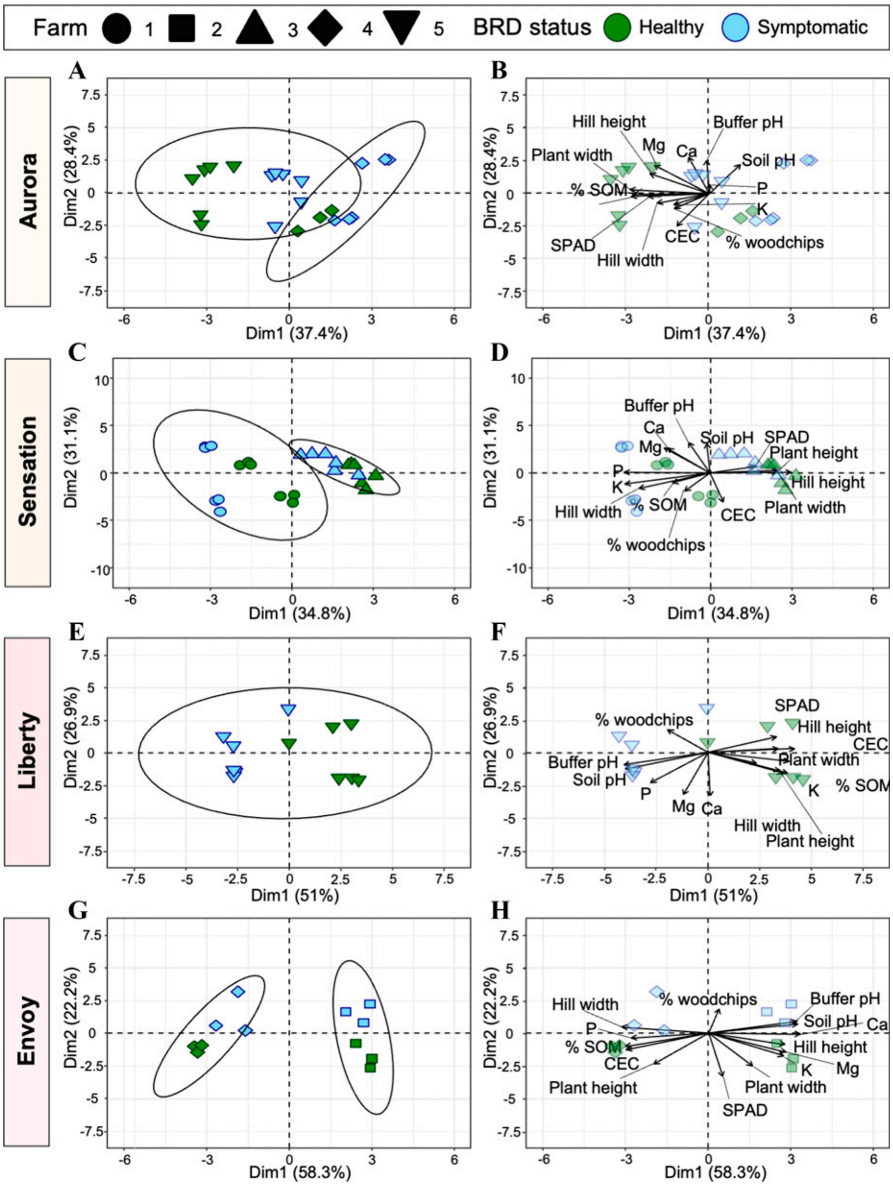

Fig. 6. The impacts of horticultural and soil chemistry parameters on the incidence of blueberry replant disorder by plant genotype for replant fields in Michigan. Principal component analyses (PCAs) were sorted by cumulative variance explained in two dimensions from least to greatest. Ellipses represent 95% confidence intervals as generated by farm site from a minimum of three data points. Data were visualized using FactoMineR and factoextra packages in R.

symptom in symptomatic replanted fields; however, this symptom has not been previously quantified through leaf SPAD or chlorophyll concentration measurements (Browne et al. 2006; Singh and Dhiman 2003; Traquair 1984). Given this complexity, many factors could limit plant growth rate and leaf chlorophyll concentration, including abiotic factors, such as horticultural and soil chemistry conditions, or biotic conditions. To address this diagnostic challenge, the study first investigated differences in horticultural management and soil chemistry factors in replanted commercial blueberry fields.

Soil chemistry parameters were strongly associated with differences in BRD among replanted fields. Blueberries belong to the *Vaccinium* genus, which are classified as acidophilic plants. At the onset of commercial blueberry production in the early 20th century, it was established that blueberries require soils with a pH in the range of 4.0 to 5.5 for optimal growth (Coville 1911). As a crop that lacks fine root hairs (Zhu et al. 2025), blueberry is more dependent on sufficiently acidic soil conditions to facilitate adequate nutrient solubility and uptake compared with most crops (Gilroy and Jones 2000; Holmes 1960; Payá-Milans et al. 2017). The results revealed that BRD symptomatic fields had significantly higher soil pH values compared with healthy fields. Symptomatic fields also had both greater variability in pH and more frequent deviations from the optimal pH range for blueberries. The consequences of elevated soil pH on plant growth and development are particularly severe for acidophilic crops such as blueberries and cranberries (Devi et al. 2025).

In addition to its negative effects on blueberry growth, deviations in soil pH have direct implications for soil nutrient dynamics, particularly CEC and base saturation. The CEC of topsoils mainly comprised the negatively charged sites of clay minerals and SOM (Kaiser et al. 2008), although this charge is not static (Helling et al. 1964). The SOM fraction of CEC is highly pH-dependent and can become more negative because of the deprotonation of functional groups of organic molecules in elevated soil pH, thus increasing the soil's net capacity for retaining base cations (Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}) (Sparks 1995). Therefore, pH is a modulator of what is sometimes referred to as the effective CEC (CEC_e) and the corresponding base saturation, which is the percentage of exchange sites occupied by base cations (Albuquerque et al. 2024; Ngewoh et al. 1989; Ross and Ketterings 1986).

This study found that symptomatic fields exhibited a lower CEC than that of healthy fields (8.54 meq/100 g vs. 11.6 meq/100 g) despite having higher soil pH (5.24 vs. 4.84) and a corresponding higher base saturation (44.9% vs. 30.0%). Based on WSS data, we found no differences in the clay content between healthy and symptomatic fields at any site. This discrepancy may be explained by subtle differences in SOM quality or material. Nevertheless, when CEC is diminished, a higher base saturation is insufficient to ensure adequate nutrient availability for plants. In fact, low CEC can cause nutrient deficiencies from leaching as well as antagonism between nutrients (Fang et al. 2020; Rietra et al. 2017). Soil composition, including but not limited to the presence of phytotoxins, nutrient imbalances, pH, and soil type and structure, has been identified in other crop species as a variable that modulates replant disorder severity or directly contributes to its onset (Mazzola and Manici 2012; Utkhede and Smith 1994; Winkelmann et al. 2019).

Soil pH and CEC influence the ability of plants to uptake nutrients from the soil (Hodges 2010; Neina 2019). Soil pH has also been shown to modulate the activity of important soilborne microorganisms that contribute positively to nutrient solubilization and acquisition in blueberry (Che et al. 2025; Read 1983). Previous studies of replant disease in apple and cherry described the weakened ability of symptomatic plants to uptake nutrients (Munro 2018; Simon et al. 2020). Physiochemical soil conditions may have limited nutrient uptake, but the plant tissue nutrient status was not assessed. The PCA in our study demonstrated an inverse association between most measured soil nutrients and plant growth parameters, which may reflect differences in nutrient availability and uptake, which were likely influenced by soil chemistry parameters such as high soil pH and low soil CEC. Although we did not analyze the nutrient composition of leaf tissue in this study, we speculated that BRD-symptomatic plants likely would have had lower leaf concentrations of some nutrients compared with healthy plants, consistent with the literature (Simon et al. 2020). This may have contributed to the estimated chlorophyll content of the lower leaf.

Soil and rhizosphere microbial communities were analyzed in this study and will be the focus of future work.

Raised bed shape and soil amendment use may partially mitigate BRD. Raised beds are an important component of highbush blueberry production systems because they play a role in reducing soil compaction, improving soil drainage, and enhancing mechanical harvesting efficiency (Strik et al. 2017). Multiple studies have demonstrated that raised beds promote faster plant growth during establishment, with plants exhibiting increased shoot-to-root ratios (Larco 2011), greater root proliferation (Valenzuela-Estrada et al. 2011), and higher yields in the years immediately following planting (Larco et al. 2013). The results revealed that the width of raised beds was statistically significant by BRD status, but the raised bed height was not. This difference may be attributed to a wider raised bed providing a larger space for lateral root expansion into untapped resource zones (Bryla et al. 2016).

Mulch use is also a common practice in contemporary highbush blueberry production systems, although the preferred mulching material varies greatly between farms and growing regions. Different mulch materials confer unique benefits to blueberry production systems. Plastic mulches, for example, provide superior weed suppression compared with organic mulch alone (Sciarappa et al. 2008). In contrast, organic mulches (e.g., sawdust, wood chips, and pine bark) help to maintain soil moisture levels, buffer soil pH through an increase in the CEC, and provide long-term SOM through the gradual decomposition of the organic substrate (Coville 1911; Kuepper and Ames 2024; Li et al. 2024). No significant difference was found in wood chip mulch or SOM between healthy and symptomatic plantings; this result may have originated from the wide range of planting ages across plantings. However, a significant positive correlation was found between SOM and leaf SPAD (Supplemental Fig. S2). This correlation may have resulted from the mineralization of SOM contributing significant nitrogen to plants in addition to nitrogen from fertilizer (Sloan et al. 2024). The SOM originating from wood chip mulch applications contains significant macronutrients important for building chlorophyll molecules (Johnson and Mirza 2020; Pickering and Shepherd 2000).

BRD severity and mitigation strategies were influenced by cultivar The PCA revealed associations between cultivar, horticultural, and soil chemistry parameters that may have implications for mitigating BRD incidence. Healthy replanted fields tended to occupy extreme values in the PCA that were more distinctly associated with CEC and SOM. This pattern suggests that CEC and SOM may be key parameters in BRD incidence and should be investigated further. Second, multiple associations between plant growth parameters and horticultural or soil chemistry parameters were significantly correlated in further analyses. Plant height and width were negatively associated with soil cation concentrations and positively associated with soil wood chip mulch content in the PCA. However, these variables were not found to be significantly negatively correlated according to Pearson's correlation coefficient analysis. Leaf SPAD was negatively associated with soil pH and buffer pH in the PCA, but they were not significantly correlated. Finally, leaf SPAD was orthogonally associated with plant height and width, which may indicate that soil pH and CEC influence leaf greenness more strongly than they influence plant morphology. Collectively, these results highlight relationships among measured variables that are associated with the BRD status. The multifaceted nature of replant disease in tree fruit and nut crops is a distinguishing feature, and unique biotic and abiotic factors interact with variable effects on disease incidence and severity (Leinfelder and Merwin 2006; Traquair 1984; Utkhede and Smith 1994). This lack of consistency leads to issues in diagnosis and treatment, which explains why replant issues have plagued fruit crop cultivation for decades.

The BRD and farm effects were inseparable in our analyses for all cultivars except Envoy. In the 'Envoy' PCA, there was distinct clustering by farm on the y-axis and separately distinct clustering by BRD status on the y-axis, suggesting that 'Envoy' may respond differently to the abiotic parameters associated with BRD in other cultivars. The Envoy cultivar was released more recently (2019) than the other cultivars (Aurora and Liberty were co-released in 2004 and Sensation was released in 2014). Additionally, 'Envoy' has a more diverse genetic background, which may contribute to differential responses to parameters associated with BRD. 'Aurora', 'Liberty', and 'Sensation' have ancestry largely based on *V. corymbosum*, with little or no genetic background from *V. angustifolium* (Hancock 2004a, 2004b; Wheeler, 2014). In contrast, 'Envoy' has a more complex ancestry based largely on *V. corymbosum*, with small contributions of *V. darrowii, V. angustifolium, V. tenellum*, and *V. ashei* (Wheeler and Hancock 2019). This observation suggests that certain cultivars may be more suitable for establishment in replanted fields than others, and that breeding could be a feasible avenue for improving NHB blueberry establishment.

Differences in root physiology and architecture as result of cultivar may more specifically address the discrepancies in the cultivar response to BRD. In other perennial systems, rootstock genotype dictated both establishment success and general plant growth in replant soils (Browne et al. 2006; Fazio et al. 2012; Massai and Loreti 2002). For example, Browne et al. (2006) found that tree height, trunk diameter, and replant disease severity in almond were all significantly affected by rootstock genotype, with Lovell (*P. persica*) and Nemaguard (*P. persica*) rootstocks performing better than Marianna 2624 (*P. cerasifera*). Similarly, (Remorini, 2015) found that rootstocks Barrier 1 (*P. persica* × *P. davidiana*), GF 677 (*P. persica* × *P. dulcis*), and Cadaman (*P. persica* × *P. davidiana*) had lower mortality rates and greater vegetative growth in peach trees planted in replant soils compared with six other rootstocks. Similar results have been found in apple (Fazio et al. 2012; Leinfelder and Merwin 2006), cherry (Sewell and Wilson 1975; Webster et al. 2000), plum (Sewell and Wilson 1975), and pear (Webster 2003). While grafting onto rootstocks is not a common practice for northern highbush blueberry, some work involving southern highbush blueberry highlighted rootstocks as a potential strategy to produce this crop under elevated soil pH conditions (Casamali et al. 2016). Future studies that examine the role of roots in establishment would likely reveal additional insight regarding BRD.

Conclusion

This study investigated reports from commercial blueberry growers about an emerging threat to blueberry cultivation, specifically during the field replanting process. A survey of commercial growers revealed that over half of replanted fields exhibited stunted growth, which is reminiscent of "replanting disease" in other fruit crops. To identify potential abiotic factors associated with this issue, we compared plant growth rate, leaf SPAD, soil chemistry, and horticultural practices in 14 commercial fields across five farms in Michigan that were designated by growers as either healthy or symptomatic. Consistent with replanting issues in other perennial fruit and nut crops, we reported that BRD led to decreased plant growth rate as well as greater leaf chlorosis. This phenomenon was designated as BRD according to nomenclature commonly used in other fruit crops. This decrease in growth was most prominently associated with elevated pH and low CEC in symptomatic fields, which may be associated with differences in plant nutrient status. Healthy replanted fields were associated with specific cultivars, wider raised beds, and increased wood chip mulch application. The PCA revealed patterns consistent with genotypic differences in response to BRD, indicating that some cultivars may be more susceptible than others. Horticultural practices such as lowering soil pH (4.4–5.3), amending soil with wood chip mulch, and designing raised bed dimensions to allow for adequate lateral root expansion may mitigate BRD. Future research will evaluate potential biotic factors associated with BRD in northern highbush blueberry.

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