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Nitrogen Fertility and Cultivar Effects on Potato Agronomic Properties and Acrylamide-forming Potential

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ABSTRACT

Acrylamide is a potentially harmful compound when consumed in the human diet and is formed during potato (*Solanum tuberosum* L.) processing from the precursors reducing sugars and asparagine. The objective of this study was to determine the effects of N rate (135–404 kg ha^{-1}) on tuber yield and quality and tuber reducing sugars and asparagine concentrations in newly released cultivars Easton and Dakota Russet, relative to the standard cultivar Russet Burbank. Tuber samples were collected at intervals from initial set through harvest during two growing seasons. Tuber yield of all cultivars increased quadratically with increasing N rate. Highest yield was produced by Easton, followed by Russet Burbank and Dakota Russet. Russet Burbank had more tubers per plant than the new cultivars. Specific gravity decreased with increasing N rate and was lowest in Russet Burbank both years. The new cultivars had a lower hollow heart incidence than Russet Burbank when environmental conditions were favorable for hollow heart development. Tuber-reducing sugars changed during the growing season but were related more to cultivar and growing conditions than N rate. New cultivars had lower reducing sugars than Russet Burbank. In contrast to reducing sugars, asparagine increased with increasing N rate and was less affected by environmental conditions during the growing season. Easton had slightly lower asparagine concentrations than Russet Burbank and Dakota Russet. This study indicates that cultivar and growing conditions have a dominant effect on tuber-reducing sugars, while N rate has a more consistent effect on tuber asparagine.

Core Ideas

- Agronomic practices can affect compounds involved with acrylamide formation in processed potato
- Increasing N rate increased tuber asparagine
- Tuber reducing sugars were not consistently affected by N rate
- Newly developed cultivars had lower acrylamide forming potential than Russet Burbank

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Acrylamide, a compound formed during the processing of various food products, has been identified as a neurotoxin in high concentrations and a potential carcinogen (Bethke and Bussan, 2013). The possible harmful effects of dietary acrylamide on human health have also been reconfirmed by the European Food Safety Authority (2015). In potato, acrylamide is mainly formed from reducing sugars (glucose and fructose) and asparagine when fried and is one of the largest contributors of acrylamide in the human diet. Tuber-reducing sugars are often considered the limiting factor for acrylamide formation in potato, because of their substantially lower concentrations than asparagine, and the strong correlation between reducing sugars and acrylamide (Chuda et al., 2003; Amrein et al., 2004; De Wilde et al., 2005; Elmore et al., 2015). However, a few studies have reported that under some conditions asparagine concentrations are also associated with the acrylamide formation when potato is processed (Amrein et al., 2003; Matsuura-Endo et al., 2006; Muttucumaru et al., 2014b). Therefore, concentrations of both asparagine and reducing sugars should be taken into account while assessing the potential for acrylamide formation in fried potato products.

Recent studies have shown that asparagine is synthesized in the tuber, rather than transported from leaf to tuber (Muttucumaru et al., 2014a). Asparagine accounts for 33 to 59% of the total free amino acids and is used as a N reservoir in potato tubers when N supply is sufficient and protein synthesis is limited (Eppendorfer and Bille, 1996; Gerendás et al., 2007; Lea et al., 2007). Nitrogen fertilizer application is an important and controllable agronomic practice during the growing season that affects tuber yield and quality (Bélanger et al., 2002; Zebarth et al., 2004). The N rate effect on tuber asparagine has attracted attention in the last decade because of its possible effect on acrylamide formation during processing. Muttucumaru et al. (2013) grew13 cultivars (five chip cultivars, seven French fry cultivars, and one boiling cultivar) with 0, 100, and 200 kg ha^{-1} N, and reported increased tuber asparagine at harvest with increasing N supply for all cultivars. A similar result of increased asparagine concentration with increasing N supply was observed at harvest for the French fry cultivar Agria (Gerendás et al., 2007). De Wilde et al. (2006) reported

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Abbreviations: DAP, days after planting; DNS, 3,5-dinitrosalicylic acid; FW, fresh weight; SRM, selected reaction monitoring.

increased concentrations of asparagine and total free amino acid with increasing N rate in potato cultivars Bintje, Ramos, and Saturna. The effect of N fertilizer application on reducing sugars at harvest and during storage has been shown to be cultivar dependent, and often interacted with growing and storage conditions (Kumar et al., 2004; Halford et al., 2011; Sun et al., 2017).

Growing season conditions (temperature, fertilizer amount applied, water availability, harvesting time, and growing season length) have been reported to affect tuber asparagine and reducing sugars at harvest with effects likely to continue in storage (Kooman et al., 1996; Hijmans 2003; Bethke and Bussan 2013). To have good processing quality with low reducing sugars, the recommended harvesting time is at tuber chemical maturity when sucrose drops to a minimum level, which often occurs shortly before vine desiccation (Sowokinos, 1973; Sowokinos and Preston, 1988; Kumar et al., 2003). Air and soil temperature can also affect the concentrations of reducing sugars. The optimum temperature for tuberization and growth ranges between 15 and 20°C. Temperatures below 8 to12°C or above 25 to 30°C can cause an increase in tuber sugar concentration (Kumar et al., 2004; Zommick et al., 2014).

French fry cultivars Dakota Russet and Easton were released in 2012 and 2014, respectively. Dakota Russet was selected for low reducing sugar accumulation during storage and resistance to cold-induced sweetening (North Dakota State University Research Foundation, 2012). Easton was rated as a high-yielding cultivar that produced light colored French fries (Porter et al., 2014a). The effect of N fertility on reducing sugars and asparagine concentrations for these two cultivars relative to the conventional cultivar Russet Burbank during growing season may provide insights into the factors that affect acrylamide-forming potential in processed potato.

The objectives of this study were to: (i) determine the effects of N rate on tuber yield and tuber quality of Easton and Dakota Russet, relative to the standard cultivar Russet Burbank over two growing seasons; and (ii) characterize in-season changes in tuber reducing sugars and asparagine concentrations as affected by cultivar and N rate.

MATERIALS AND METHODS

The study was conducted at the Sand Plain Research Farm in Becker, MN, on a Hubbard loamy sand (sandy, mixed, frigid Entic Hapludoll) soil in 2014 and 2015. Pre-planting soil pH (1:1 soil/water), organic matter (combustion), P (Bray P1), and K (ammonium acetate extractable) were determined in the top 15 cm soil, and the results ranged from 6.0 to 6.3, 2.0 to 2.2%, 30.8 to 35.5 mg kg^{-1}, and 94 to119 mg kg^{-1} over the 2 yr, respectively. Nitrate-N (2 M KCl extractable) in the top 60 cm soil ranged from 1.6 to 3.8 mg kg^{-1} over the 2 yr. Prior to planting, 0–0–60 at 224 kg ha^{-1} and 0–0–22–11(Mg)-18(S) at 224 kg ha^{-1} were broadcasted and incorporated with a chisel plow followed by disking.

Fertilizer Treatments

Each cultivar was subjected to five N fertilizer treatments, 135, 202, 269, 336, and 404 kg ha^{-1}. All plots received 101 kg N ha^{-1}as polymer-coated urea (Environmentally Smart Nitrogen- ESN, Agrium, Inc., Calgary, AB, Canada; 44–0–0) pre-planting, and 34 kg N ha^{-1} (31 kg ha^{-1} as monoammonium phosphate and 3 kg ha^{-1} as ammonium sulfate) at planting in a band 8 cm to the side and 5 cm below the seed tuber. In addition to the N application, all plots received 146 kg P_2O_5 ha^{-1}, 203 kg K_2O ha^{-1}, 49 kg S ha^{-1}, 22 kg Mg ha^{-1}, 0.6 kg B ha^{-1}, and 1.1 kg Zn ha^{-1}, applied as a blend of monoammonium phosphate, potassium chloride, potassium magnesium sulfate, ammonium sulfate, boric acid, and zinc sulfate at planting. At emergence, N was side-dressed at 0, 67, 134, 201, and 269 kg N ha^{-1} as ESN and then hilled in on 5 June 2014 and 21 May 2015. The coated fertilizer ESN is commonly used in the region and has be shown in previous studies to perform as well or better than conventional N sources (Wilson et al., 2009).

Plot Design and Plant Management

A randomized complete block design was adopted with four replications using a factorial arrangement of N rate and cultivar treatment combinations. Each plot consisted of seven, 7.6 m rows. The spacing between rows was 0.9 m and seed tubers were spaced 0.3 m apart within each row. Three plants of test cultivars were sampled six times in each plot during the growing season. Whole “B” seed (56–84 g) of Russet Burbank, and cut “A” seed (56–84 g) of Dakota Russet and Easton were hand planted in furrows. Weeds, diseases, and insects were controlled using standard practices from the Midwest Vegetable Production Guide for Commercial Growers (2012). Rainfall supplemented with sprinkler irrigation, which followed the checkbook method of scheduling (Wright and Bergsrud, 1991).

Sample Collection

Planting and harvesting dates were scheduled according to weather conditions. There were 139 growing days in 2014 (planted on 6 May, vine-killed on 22 September, harvested on 2 October), and 148 growing days in 2015 (planted on 21 April, vine-killed on 16 September, harvested on 28 September). Three plants of the test cultivars were dug out from second row of each plot on 69, 79, 97, 112, and 125 d after planting (DAP) in 2014, and 63, 77, 105, 118 and 133 DAP in 2015.Vines were killed at 139 DAP in 2014 and 148 DAP in 2015 with a mechanical vine beater. To allow tuber skins to suberize, final harvest was at 149 DAP in 2014 and 160 DAP in 2015. Tuber yield, specific gravity, number of tubers per plant, reducing sugars and asparagine were determined from the three bulked plant samples on each of the sampling times. Rows 5 and 6 were machine harvested and tubers were graded for total yield. Marketable yield was considered as those tubers greater than 112 g. A subsample of 25 tubers greater than 170 g from each plot was determined for hollow heart incidence. Tuber yield was assumed not to change after vine kill, so vine kill dates were considered as the last sampling day instead of the actual harvest dates for final tuber yield.

On each sampling time, tubers were collected, counted (including small tubers at early stages), washed, and weighed from the three plants in each plot. Ten tubers greater than 85 g from each plot were collected for specific gravity determination following the method of Schippers (1976). Hollow heart was determined by cutting each tuber longitudinally and recording the number affected out of the 10 tubers sampled. To determine tuber N concentration, 200 to 300 g of the sampled tubers were chopped and then oven-dried at 60°C for at least 72 h. They were then ground with a Wiley mill to pass through a 2-mm sieve followed by N determination using a combustion analyzer

(Elementar Vario EL III, Elementar Americas Inc., Mt. Laurel, NJ) using the methods of Horneck and Miller (1997).

Reducing Sugar and Asparagine Determination

At each sampling time, six tubers greater than 85 g from each plot were collected for the determination of reducing sugars and asparagine concentrations. Total tuber numbers were less than 16 for some plots at the early sampling times, and therefore, tuber quality, reducing sugars, and asparagine concentrations were determined from those tubers that were available.

Fresh tuber tissue was collected about 0.5 cm from stem and bud ends of tubers using a 7.8 mm Humboldt Brass Cork borer. Tissue samples were stored in Wheaton 20 mL HDPE Liquid Scintillation vials (DWK Life Sciences Inc., Millville, NJ) at −20°C. The extraction of reducing sugars and asparagine was modified from a previous study (Knowles et al., 2009). An IKA Ultra-Turrax disperser (T-25 digital disperser, 18 mm) was used to grind 2.5-g samples for 1 min with 6 mL of triethanolamine HCl (TEA) buffer (30 mM, pH 7, with 1 mM 1,4-Dithiothreitol), 300 μL of 85 mM Carrez I solution, 300 μL of 250 mM Carrez II solution and 500 μL 0.1 mM NaOH until no visible tuber pieces remained. The solution was transferred to a Falcon 15 mL centrifuge tube (New York), vortexed 30 s for better mixing and then centrifuged for 15 min at 1200 g. Two milliliters of the supernatant was transferred to Eppendorf tubes and centrifuged (10,000 *g*) for 10 min. Then 1.5 mL of the supernatant was transferred to a 2 mL Eppendorf snap-cap microcentrifuge safe-lock tube (Eppendorf AG, Hamburg, Germany) and stored at −20°C for the determination of reducing sugars and asparagine. All the steps were conducted on ice to reduce the enzymic browning resulting from polyphenol oxidization.

The dinitrosalicylic colorimetric method as described by Lindsay (1973) was used to determine the concentration of reducing sugars. For this method, 100 μL Sumner's reagent (44 mM 3, 5-dinitrosalicylic acid (DNS), 2 M sodium hydroxide, and 940 mM potassium sodium tartrate) were mixed with 100 μL supernatant in an Eppendorf 96-well plate. Samples were heated at 94°C for 10 min and then chilled at 4°C in the Eppendorf 5331 MasterCycler Gradient Thermal Cycler. An aliquot of 150 μL from each sample (measuring reduction of DNS to 3-amino-5-nitrosalicylic acid by glucose) was measured at A550 using Bio-Tek Instruments EL800 Universal Microplate Reader. A standard curve for quantification of reducing sugars was constructed using eight glucose concentrations ranging from 0 to 0.8 mg mL^{-1} for each plate. The amount of reducing sugars is expressed as g kg^{-1} fresh weight (FW).

Asparagine was quantified by liquid chromatography with tandem mass spectrometry (LC-MS/MS). For this method, 200 μL supernatant (described above) was deproteinized by incubating the sample at 94°C for 3 min in an Eppendorf 96-well polymerase chain reaction plate, and then centrifuged at 2000 *g* for 10 min. The supernatant was transferred to Eppendorf tubes, diluted 100-fold with the solution of two pairing ions, 0.1% heptaflourobutyric acid and 0.1% formic acid and kept at 4°C in the Agilent autosamplers. Ten microliters of diluted samples were subjected to LC-MS/MS using an Agilent Eclipse Plus C18 RP column on a Shimadzu UFLC XR coupled to an AB SCIEX– Triple Quad 5500. The sample was subjected to a linear gradient of 0 to 100% acetonitrile for 5 min at a column flow rate of 0.4 mL per minute. The retention time for asparagine was 1 min. The specific selected reaction monitoring (SRM) transitions employed for asparagine were m/z 116 > 87 transition. The data were analyzed using Multi-Quant (ABI) providing the peak area for the m/z 116, 88, and 87 transition. Asparagine concentration was determined by comparison of sample peak area to a standard curve. The amount is expressed as g asparagine kg^{-1} potato FW. All analyses were conducted by the Center for Mass Spectrometry and Proteomics at the University of Minnesota.

Statistical Analysis

In-season tuber yield, specific gravity, reducing sugars and asparagine concentrations were combined over 2014 and 2015 and analyzed using PROC MIXED with the SAS 9.4 statistical software package (SAS Institute Inc., Cary NC). Tuber number per plant was also determined over the growing season and presented in supplementary data. Repeated measures were used for sampling time. To assess the effects of N rate and cultivar on agronomic properties, total tuber yield, marketable yield, hollow heart incidence and tuber N at harvest, and tuber number per plant (data collected 125 DAP in 2014 and 133 DAP in 2015) were combined over the 2 yr and analyzed using PROC MIXED in SAS. A square root transformation was used when necessary to account for the heterogeneity of variance.

Linear or quadratic regressions between N rate and tuber yield, specific gravity, asparagine, and tuber N were determined using PROC MIXED and CONTRAST statements in SAS. Probability levels £ 0.05 were considered significant for the linear or quadratic trends, and the quadratic trend was selected over the linear trend when both were significant.

RESULTS AND DISCUSSION

Weather Conditions

The monthly average temperature from May to August in 2014 and 2015 was compared with the average temperatures over the past 30 yr (Table 1). A cold spring occurred with a monthly average temperature of 3.4°C in April 2014 compared to 7.8 and 7.6°C in 2015 and the average of past 30 yr, respectively. The colder temperatures in 2014 resulted in a late planting on 6 May. September 2015 with a monthly average temperature of 18.2°C was warmer than September 2014 and the average of the past 30 yr (15.6 and 15.7°C, respectively). Before tuber harvest on 2 Oct. 2014, a period of cold weather occurred from 10 to 15 September and 17 to 18 September with the minimum temperature each day ranging from −1.1 to 6.7°C, while the daily minimum temperatures during the same period in 2015 ranged from 3.3 to 17.2°C. In 2014, precipitation above the 30-yr average occurred in April, May, June, and August. Precipitation was above the 30-yr average during May, July, and August in 2015.

Tuber Yield

For both years, tuber yields were estimated throughout the growing season and at harvest. Tuber yield of all cultivars increased quadratically during the growing season (Fig. 1). No yield differences among cultivars were observed at the first sampling time (up to 66 DAP), suggesting a similar initial tuber bulking rate for the three cultivars. After that, tuber-bulking rates differed among the cultivars and yield differences became significant. At the last sampling time, Easton was still bulking

Table 1. Monthly weather conditions during the growing season at Becker, MN, in 2014 and 2015.†

	Temperature			Precipitation		
Month	2014	2015	Avg (1985–2015)	2014	2015	Avg (1985–2015)
	°C			cm		
April	3.4	7.8	7.6	17.8	3.7	7.5
May	13.4	13.4	14.4	18.4	14.9	9.4
June	19.6	19.4	19.1	16.0	11.3	11.2
July	20.3	21.7	21.5	8.8	16.6	10.1
Aug.	21.0	19.6	20.0	11.2	22.2	10.7
Sept.	15.6	18.2	15.7	6.0	5.4	7.6

† The monthly average temperature and precipitation data from 1985 to 2015 were recorded in the Santiago, MN, weather station (approximately 19 km from the research site in Becker) and retrieved from the Minnesota Department of Natural Resources website (http://www.dnr.state.mn.us/climate/historical/acis_stn_meta.html).

(yield increase of 13.3% compared to the fifth sampling time), while tuber yields of Russet Burbank and Dakota Russet did not increase significantly during this same sampling period. The high tuber-bulking rate of Easton late in the growing season resulted in higher tuber yields than the other two cultivars at harvest.

The interaction of N rate and sampling time was significant for tuber yield during the growing season in 2014 and 2015 (Table 2, Fig. 2). Tuber yield across the three cultivars did not respond to N rate at sampling times up to 101 DAP. After that, the effect of N rate on tuber yield became significant. At the final sampling time, tuber yield increased quadratically with increasing N rate. When averaged over sampling time and N rate, the cultivar and year interaction was significant (Table 2); however, the effect was due to a change in magnitude rather than direction. In both years, Russet Burbank and Easton had higher tuber yield than Dakota Russet (Supplemental Fig. S1). The sampling time by year effect was also significant (Table 2). In both years, tuber yield averaged over N rate and cultivar increased quadratically during the growing seasons, with a higher tuber bulking rate in 2015 during the mid-growing season (approximately between 78 and 115 DAP, Supplemental Fig. S2).

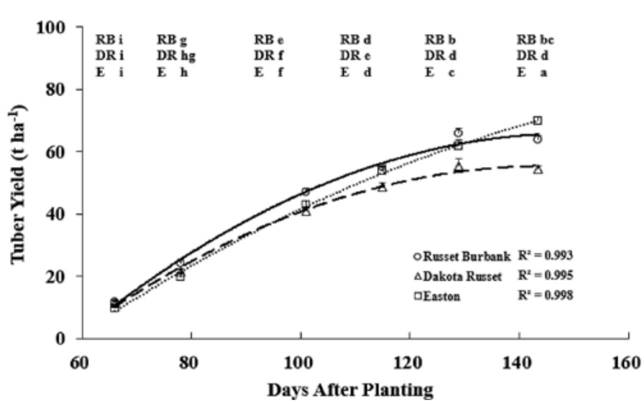

Fig. 1. Russet Burbank, Dakota Russet, and Easton tuber yield during the 2014 and 2015 growing seasons averaged over N rate (cultivar × sampling time interaction). Means with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard errors. Each sampling time is the average sampling time over the 2 yr. Equations:
RB (Russet Burbank): $y = -2.15\ x^2 + 26.30\ x - 14.89$
DR (Dakota Russet): $y = -1.94\ x^2 + 22.84\ x - 11.86$
E (Easton): $y = -1.26\ x^2 + 21.30\ x - 12.60$

The main effects of cultivar, year, and N rate were significant for total and marketable yields at harvest (Table 3, Fig. 3A–C). The cultivar effect was consistent for total and marketable yields at harvest both years, with Easton > Russet Burbank > Dakota Russet. In 2015, total and marketable yields at harvest were significantly higher than those yields in 2014. Previous studies have reported that air temperature ranging from 15 to 24°C is optimum for foliar expansion, tuber initiation, and tuber growth during the growing season (Kooman and Haverkort, 1995). In this study, weather conditions in 2015 (warm weather early and late in the growing season) caused more favorable conditions for tuber bulking, which resulted in higher total yield in 2015 than in 2014.Combined over years and cultivar, total and marketable yields increased quadratically with increasing N rate (Fig. 3C). The agronomic optimum N rates were 385 kg ha^{-1} N and 360 kg $ha^{-1}$for total and marketable yield, respectively. This yield response to N is higher than that reported at this site by Wilson et al. (2009), but comparable to responses reported by Sun et al. (2017) when conditions were favorable for tuber bulking.

Tuber Quality

Tuber specific gravity during the growing season was significantly affected by the interaction of cultivar by sampling time (Table 2, Fig. 4). During the growing season, specific gravity increased up to101 DAP for Dakota Russet and Easton, and 115 DAP for Russet Burbank. After then, the specific gravity of all three cultivars had a tendency of decreasing. During the growing season, new cultivars Dakota Russet and Easton had a significantly higher or comparable level of specific gravity compared with Russet Burbank. At harvest, specific gravity of three cultivars ranked as Easton (1.082) > Dakota Russet (1.079) = Russet Burbank (1.078).

Specific gravity averaged over three cultivars decreased linearly with increasing N rate (Fig. 5) during the growing season. However, the effect of N rate was not as pronounced toward the end of the season. Averaged over sampling dates the year × cultivar and the N rate × year interactions were significant. New cultivars Dakota Russet and Easton had consistently higher specific gravity than Russet Burbank over the 2 yr (Supplemental Fig. S3), but specific gravity of Easton was higher than Dakota Russet in 2014 while the reverse was found in 2015. The N rate × year interaction effect on specific gravity was significant. Specific gravity averaged over three cultivars decreased linearly with increasing N rate in 2014, but quadratically in 2015 (Supplemental Fig. S4). However, it then decreased both years by the end of the season. Overall, specific gravity was higher in 2014 than in 2015 (Supplemental Fig. S5).

The effect of N rate on specific gravity has been reported in a number of previous studies with variable results. These include a linear decrease as N rate increased (Westermann et al., 1994; Bélanger et al., 2002; Zebarth et al., 2004), a linear or quadratic increase with increasing N rate (Sun et al., 2017), a decrease followed by an increase above the optimum N rate for yield (Long et al., 2004), and not affected by N rate treatment (Sun et al., 2017). At tuber harvest, specific gravity of all three cultivars decreased linearly with increasing N rate in this study. The N rate effect on new cultivars Dakota Russet and Easton has not been previously reported. In a previous study at the same location, specific gravity of Russet Burbank increased quadratically

Table 2. Analysis of variance for total yield, tuber quality, reducing sugars, and asparagine concentrations during the growing season in 2014 and 2015.

Source	Tuber yield	Specific gravity	Reducing sugars		Asparagine	
			Stem end	Bud end	Stem end	Bud end
Cultivar	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
N Rate	0.002	<0.001	0.177	0.887	<0.001	<0.001
Sampling time (S. time)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Year	<0.001	<0.001	<0.001	<0.001	<0.001	0.032
Cultivar × S. time	<0.001	<0.001	<0.001	<0.001	0.120	<0.001
N Rate × S. time	0.003	<0.001	0.105	0.330	0.301	0.122
Cultivar × Year	0.014	0.002	0.003	0.020	0.369	0.384
N Rate × Year	0.061	<0.001	0.282	0.744	0.005	0.317
S. time × Year	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Cultivar × N Rate	0.652	0.254	0.943	0.006	0.612	0.759
Cultivar × N Rate × Year	0.844	0.490	0.683	0.163	0.139	0.089
Cultivar × S. time × Year	0.437	0.053	<0.001	0.023	0.344	0.056
N Rate × S. time× Year	0.849	0.803	0.864	0.892	0.409	0.892
Cultivar × N Rate × S. time	0.915	0.909	0.198	0.001	0.691	0.908
Cultivar × N Rate ×S. time × Year	0.570	0.984	0.795	0.363	0.600	0.999

from 34 to 242 kg N ha^{-1} and then decreased at the 336 kg ha^{-1} N rate) the first year, but was not affected by N rate in the second year (Sun et al., 2017), suggesting a significant impact of growing conditions. In North Dakota State University trials, Dakota Russet was reported to have an average specific gravity of 1.085, which is higher than the average value 1.079 at tuber harvest, in this study (North Dakota State University Research Foundation, 2012). Easton was reported to have an average specific gravity of 1.081 in 17 trials at Maine state from 2007 to 2013 (Porter et al., 2014b). An average specific gravity of 1.082 at tuber harvest was found in this study, which is consistent with values reported in Maine. A specific gravity ranging from 1.080 to 1.089 is recommended for frozen French fry processing (Wang et al., 2016). Therefore, Easton had a specific gravity that was generally ideal for French fry processing. Dakota Russet tubers had a lower specific gravity but it was still in a range suitable for French fry processing.

Hollow heart incidence (data combined over 2 yr) was determined and analyzed at tuber harvest (Table 3). Nitrogen supply did not significantly affect hollow heart incidence in either year. This is in contrast to other studies showing that N rate can have an effect on increasing hollow heart incidence in some years (Sun et al., 2017). Reasons for this variable effect are likely due to other environmental factors affecting the disorder as discussed below. The cultivar effect was significant and differed by year (Table 3). In 2014, 27.0% of Russet Burbank tubers had hollow heart, which was significantly higher than Dakota Russet (13.5%) and Easton (3.5%). However, the incidence of hollow heart in all three cultivars was lower than 5.0%, with no significant differences in 2015. This indicates that environmental conditions affecting tuber growth in 2014 were favorable for the formation of hollow heart (Nelson et al., 1979; Rex and Mazza1989), especially in susceptible cultivars like Dakota Russet and Russet Burbank. Similar results have been reported

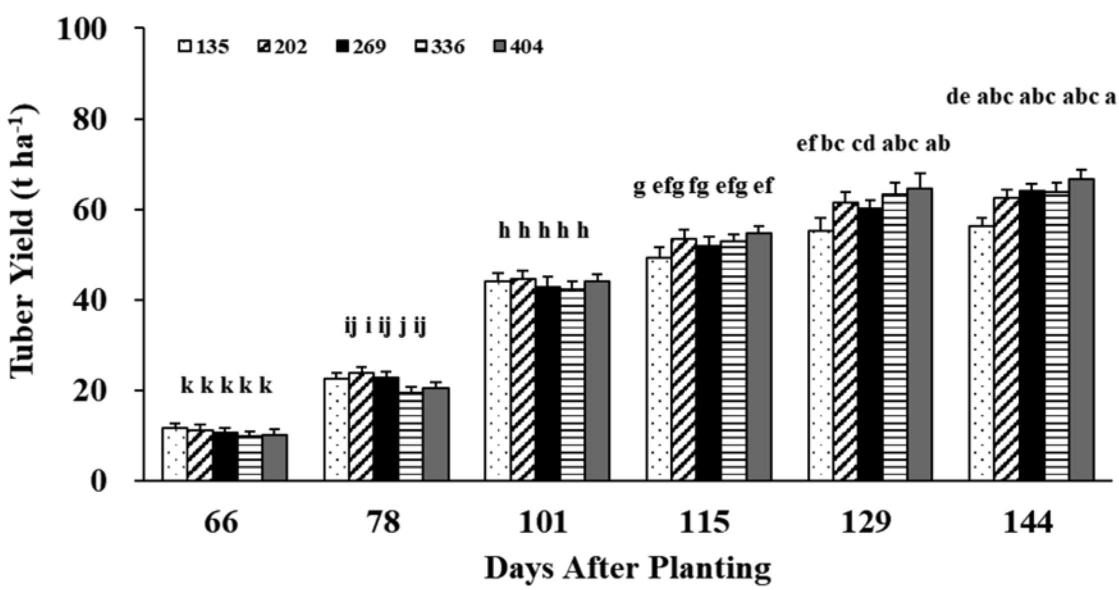

Fig. 2. Effects of N rate on tuber yield during the 2014 and 2015 growing season averaged over cultivar (N rate × sampling time interaction). Means with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard errors. Each sampling time is the average sampling time over the 2 yr. Equation: 144 DAP: $y = -0.63\ x^2 + 5.96\ x + 51.68$, $R^2 = 0.89$

Table 3. Analysis of variance for total yield and marketable yield, hollow heart incidence and tuber N at harvest in 2014 and 2015.

Source	Yield		Hollow heart	Tuber N
	Total	Marketable	tubers	
			%	
Cultivar	<0.001	<0.001	<0.001	<0.001
N Rate	<0.001	<0.001	0.834	<0.001
Year	<0.001	<0.001	<0.001	<0.001
Cultivar × N Rate	0.361	0.742	0.455	0.021
Cultivar × Year	0.558	0.913	<0.001	0.092
N Rate × Year	0.097	0.155	0.955	0.497
Cultivar × N Rate × Year	0.614	0.732	0.659	0.178

in a previous study for Russet Burbank, which had up to 19.0% hollow heart in 1 yr and only 3.1% in the following year (Sun et al., 2017). Easton was highly resistant to hollow heart formation even under favorable environmental conditions for development of the disorder.

Tuber number per plant data were analyzed on the second to last sampling time, 125 DAP in 2014 and 133 DAP in 2015 (Table 4, Fig. 6). The main effects of cultivar and year were significant, with no effect due to N rate. Dakota Russet (nine tubers per plant) and Easton (nine tubers per plant) had significantly less tubers per plant than the standard cultivar Russet Burbank (12 tubers per plant). The higher yield of Easton relative to Russet Burbank (Fig. 1) indicates that Easton had on average a higher tuber weight than Russet Burbank. Tuber number per plant was higher in 2015 (11 tubers per plant) than in 2014 (nine tubers per plant) across three cultivars, which contributed to the higher yield in 2015 compared to 2014 (Fig. 1 and 3). The number of tubers per plant was also measured though the growing season each year (data not presented). A significant year × cultivar × sampling time interaction was recorded (Supplemental Fig. S6). In 2014, tubers per plant decreased through the season for Russet Burbank while for the other two cultivars tubers per plant increased. In 2015, tubers per plant increased in all three cultivars though the season. The phenomenon of tuber resorption through the growing season is common in some cultivars; although, the exact causes and mechanisms are unclear (Ewing, 1997).

Tuber Bud and Stem End Reducing Sugars and Asparagine

The three-way interaction of cultivar, sampling time, and year was significant for stem end- reducing sugars (Table 2). In 2014, concentrations of stem end-reducing sugars increased (69–79 DAP), decreased (79–112 DAP) and then increased again from 112 to 149 DAP for all three cultivars, although the increase was much higher for Russet Burbank than for Easton or Dakota Russet (Fig. 7A and 7B). Reducing sugars concentrations averaged over N rate in Russet Burbank (6.83 g kg^{-1} FW) were significantly higher than those in Dakota Russet (2.35 g kg^{-1} FW) and Easton (2.94 g kg^{-1} FW) at harvest. Russet Burbank was susceptible to weather conditions favorable for reducing sugars accumulation during the growing season, but the new cultivars were bred for low reducing sugar levels over varied environments. In 2015, stem end- reducing sugars concentrations decreased from 63 to 105 DAP for all cultivars, and then

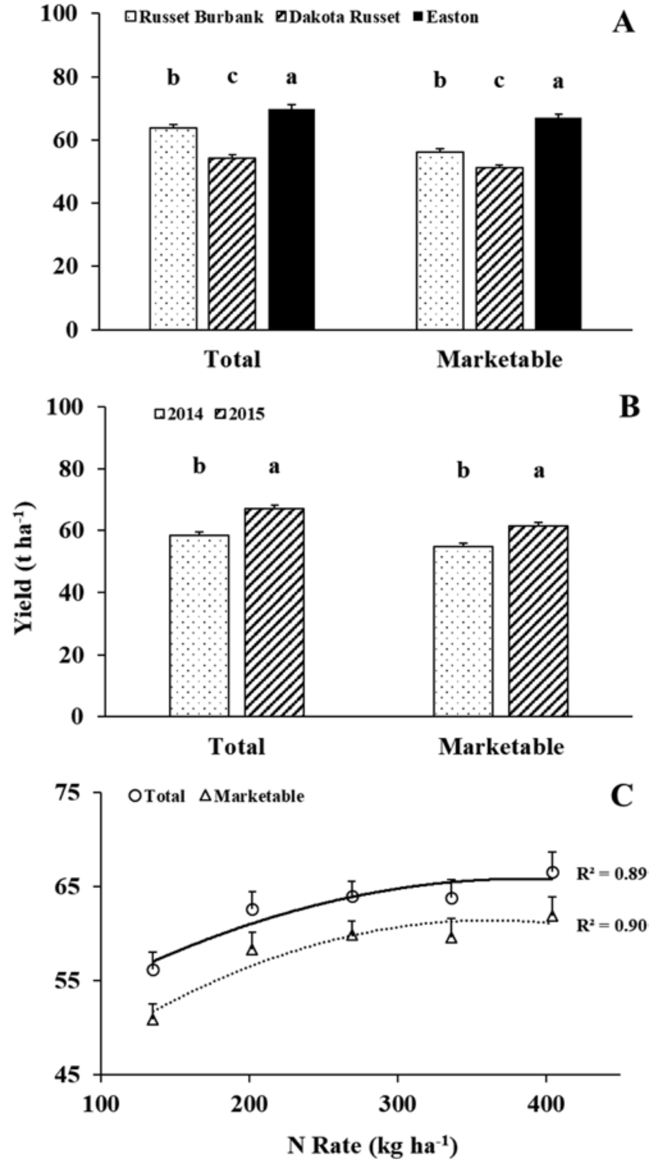

Fig. 3. Main effects of (A) cultivar, (B) year, and (C) N rate on total and marketable yield at harvest over the 2-yr study. Error bars indicate standard errors. Equations:
Total yield: $y = -0.14 \times 10^{-3} x^2 + 0.11 x + 45.02$
Marketable yield: $y = -0.19 \times 10^{-3} x^2 + 0.14 x + 36.70$

increased for Russet Burbank or leveled off for Dakota Russet and Easton. By the end of the season, stem end reducing sugars in 2015 were much lower with concentrations of 1.48, 0.50, and 0.67 g kg^{-1} FW for Russet Burbank, Dakota Russet and Easton, respectively. The lower reducing sugar concentrations of the same cultivars in 2015 relative to 2014 indicates that variation in weather conditions, especially temperature is an important factor affecting reducing sugar concentrations across different years as noted by others (Kumar et al., 2004; Bethke and Bussan, 2013; Sun et al., 2017).

The interaction of cultivar × sampling time × year for bud end-reducing sugars is presented in Fig. 7C and 7D. In 2014, bud end-reducing sugars of all cultivars increased from 69 to 79 DAP, decreased to low concentrations 112 DAP (ranging from 0.50–0.69 g kg^{-1} FW), then slightly increased at harvest (0.64 to 1.29 g kg^{-1} FW). At the later sampling times, bud end-reducing sugars concentrations in Russet Burbank were not

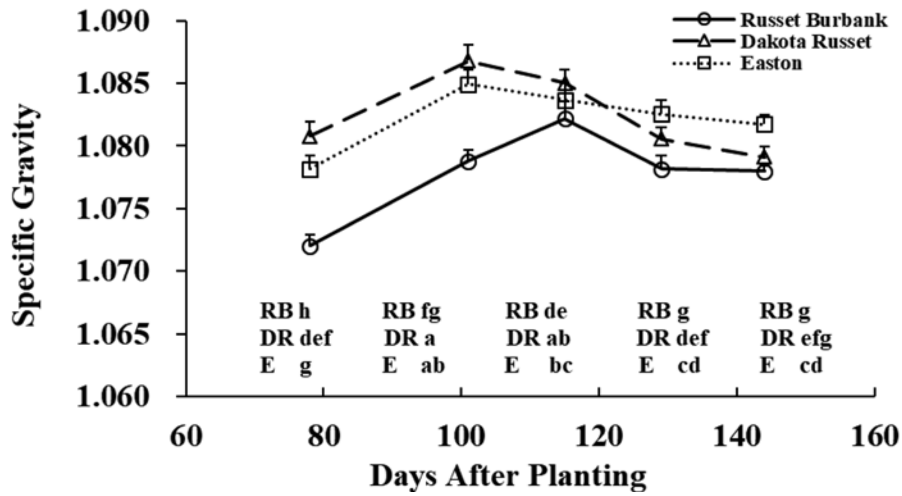

Fig. 4. Cultivar × sampling time interaction effects on specific gravity averaged over N rate and year. Means with the same letter are not significantly different at $P = 0.05$. Error bars indicate standard errors. Each sampling time is the average sampling time over the 2 yr.

significantly different from those in the new cultivars, except for at harvest with Russet Burbank higher than Easton. In 2015, bud end-reducing sugar concentrations of all three cultivars were the highest at 63 DAP, gradually decreased to low levels 118 DAP (0.29–0.42 g kg^{-1} FW), and then leveled off for all three cultivars. In both years, the cultivar effect on bud end-reducing sugars was significant at the earlier sampling times, but then gradually attenuated to low levels at harvest.

The three-way interaction of cultivar by N rate by sampling time was significant for bud end- reducing sugars (Table 2). However, bud end-reducing sugars in 2015 were only affected by N rate on the first two sampling times for all cultivars with no clear patterns (data not presented).

Asparagine concentrations in the stem and bud ends were affected by the interaction of sampling time × year (Table 2, Fig. 8A and 8B). Concentrations in both ends tended to increase and then decrease during the growing season. Stem end asparagine concentrations were higher or comparable in 2014 than in 2015. However, bud end asparagine generally started out higher in 2015 than in 2014, but by the end of the growing season concentrations were higher in 2014 than in 2015 and similar to end of season asparagine concentrations in the stem end. At harvest, stem end asparagine concentrations averaged over the three cultivars were 1.44 g kg^{-1} in 2014 and 0.94 g kg^{-1} in 2015, while the bud end asparagine concentrations were 1.09 g kg^{-1} in 2014 and 0.76 g kg^{-1} in 2015.

The effect of N rate on stem end asparagine was significant but depended on year (Table 2, Fig. 9A). In 2014, asparagine concentrations increased linearly, but in 2015, increased in a quadratic manner with a peak at 370 kg N ha^{-1}. Bud end asparagine concentration also responded to N rate and increased linearly with increasing N rate both years (Fig. 9B). These results are consistent with those reported in previous studies showing an increase in asparagine concentration with elevated N supply (Gerendás et al., 2007; Lea et al., 2007; Muttucumaru et al., 2013). Asparagine concentrations in the stem end in 2014 were significantly higher than in 2015, which may have been due to a higher N demand for higher tuber yield in 2015 that in turn resulted in a lower proportion of N contributing to free asparagine as an N reservoir. In the bud end, asparagine concentration was significantly higher in Dakota Russet than in Easton during the growing season, suggesting a consistent cultivar effect. Russet Burbank bud end asparagine concentrations were significantly lower than Dakota Russet before 115 DAP, but comparable with or slightly lower than Dakota Russet after that time (Supplemental Fig. S7). Similarly, stem end asparagine concentrations in Easton (1.08 g kg^{-1} FW) were lower ($P = 0.05$) than those in Russet Burbank (1.48 mg g^{-1} FW) and Dakota Russet (1.51 g kg^{-1} FW).

Table 4. Analysis of variance for number of tubers per plant on 125 d after planting (DAP) in 2014 and on 133 DAP in 2015.

Source	Number of tubers per plant
Cultivar	<0.001
N Rate	0.450
Year	<0.001
Cultivar × N Rate	0.150
Cultivar × Year	0.295
N Rate × Year	0.798
Cultivar × N Rate × Year	0.839

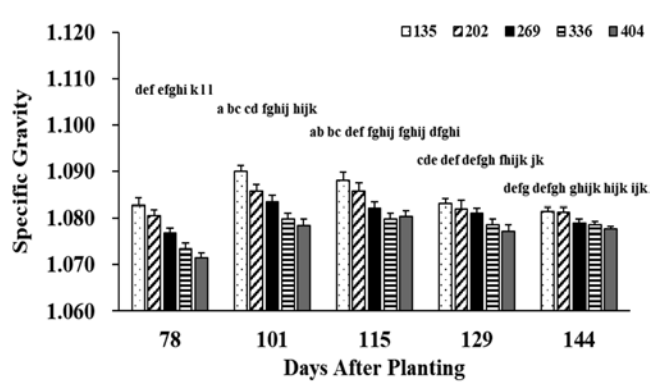

Fig. 5. Nitrogen rate effects on specific gravity averaged over cultivar in 2014 and 2015 (N rate × sampling time interaction). Error bars indicate standard errors. Each sampling time is the average sampling time over the 2 yr. Equations:
78 DAP: $y = -2.95 \times 10^{-3}\,x + 1.09$, $R^2 = 0.99$
101 DAP: $y = -2.92 \times 10^{-3}\,x + 1.09$, $R^2 = 0.98$
115 DAP: $y = -2.12 \times 10^{-3}\,x + 1.09$, $R^2 = 0.90$
129 DAP: $y = -1.54 \times 10^{-3}\,x + 1.09$, $R^2 = 0.97$
144 DAP: $y = -1.00 \times 10^{-3}\,x + 1.08$, $R^2 = 0.93$

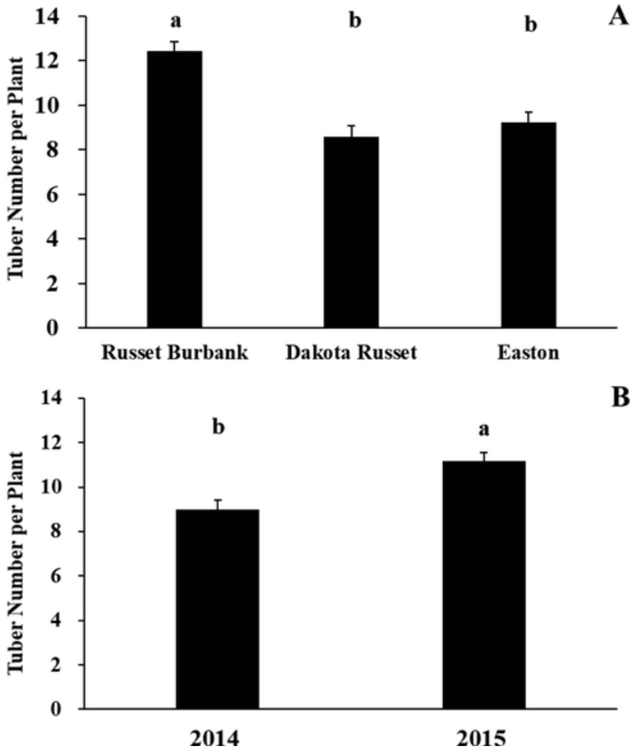

Fig. 6. (A) Cultivar and (B) year effects on tuber number per plant at 125 d after planting (DAP) in 2014 and on 133 DAP in 2015. Means with the same letter are not significantly different at P = 0.05. Error bars indicate standard errors.

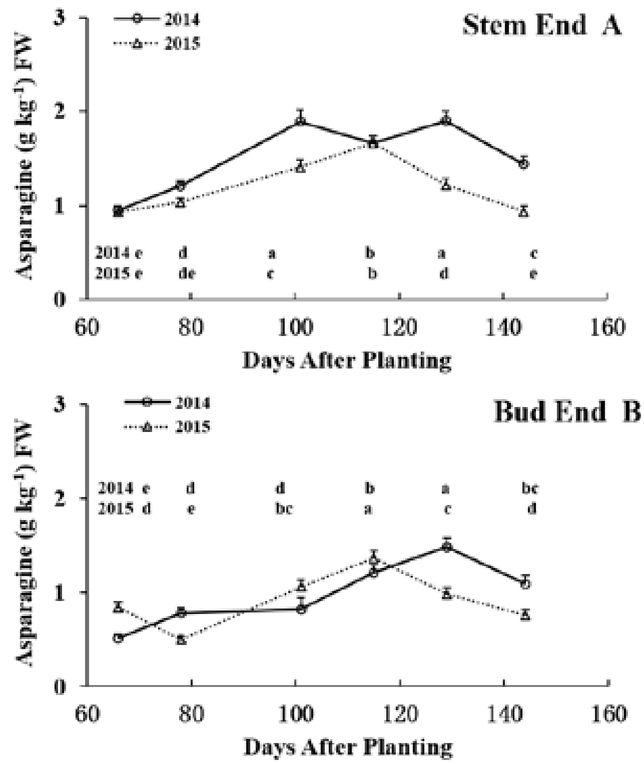

Fig. 8. Sampling time by year effects on asparagine concentrations (A) in the stem and (B) bud end. Error bars indicate standard errors. Means with the same letter are not significantly different at P = 0.05. Each sampling time is the average sampling time over the 2 yr.

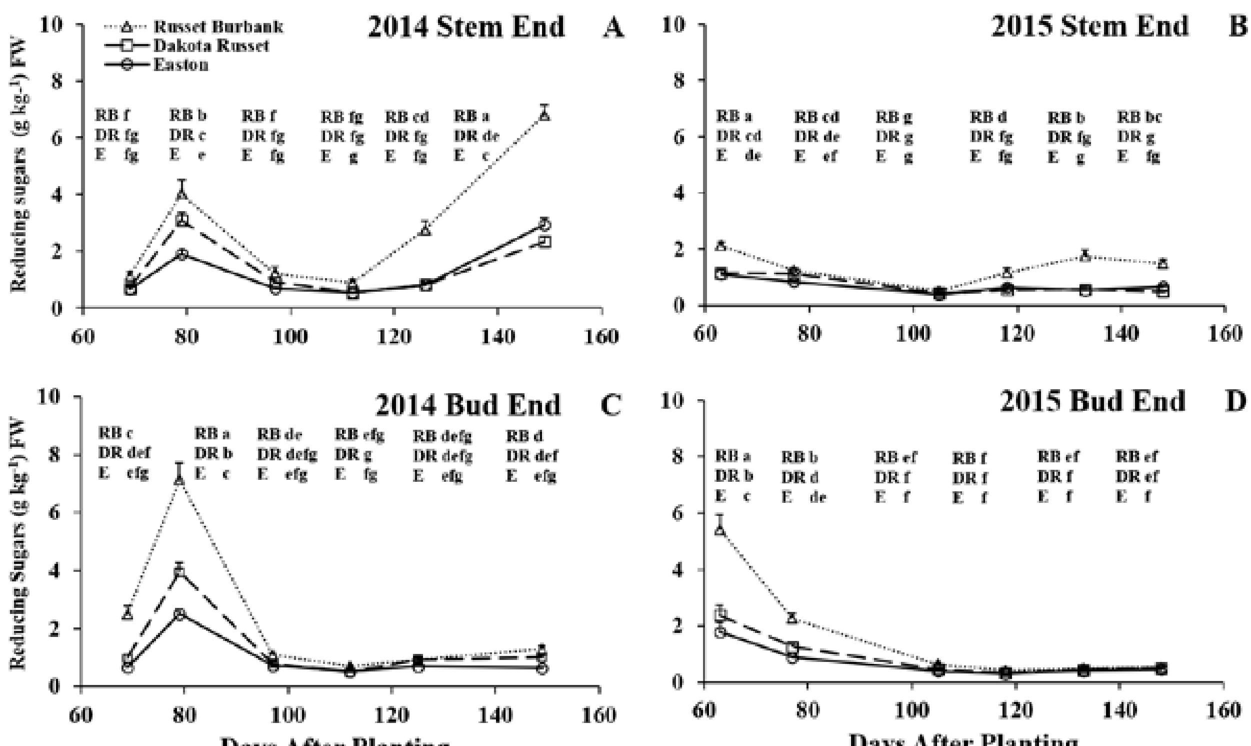

Fig. 7. Cultivar by sampling time by year effects on concentrations (A and B) of stem and (C and D) bud end-reducing sugars. Means with the same letter are not significantly different at P = 0.05. Error bars indicate standard errors. Each sampling time is the average sampling time over the 2 yr.

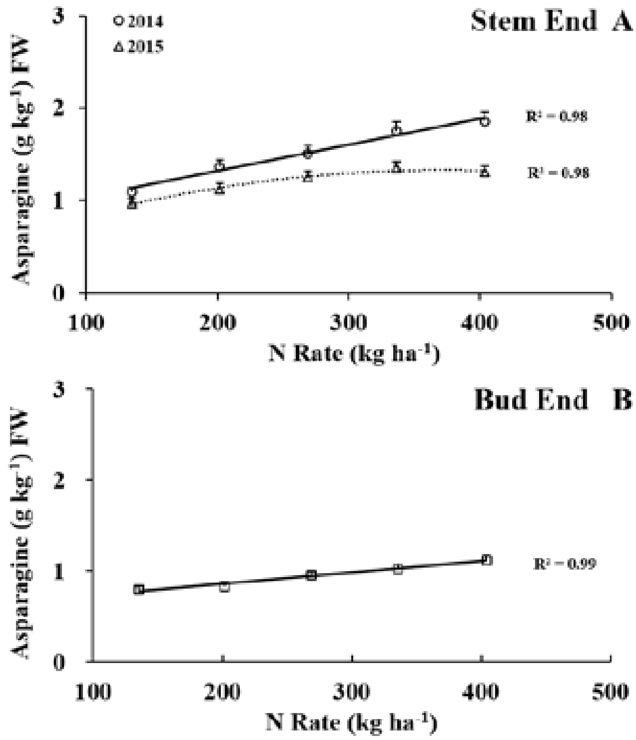

Fig. 9. Nitrogen rate effects on asparagine concentration (A) in the stem end (interacted with year) and (B) in the bud end. Error bars indicate standard errors. Equations:
Stem end: 2014 $y = 2.83 \times 10^{-3} x + 0.75$, 2015 $y = 0.01 \times 10^{-3} x^2 + 4.93 \times 10^{-3}x + 0.42$
Bud end: $y = 1.26 \times 10^{-3} x + 0.61$

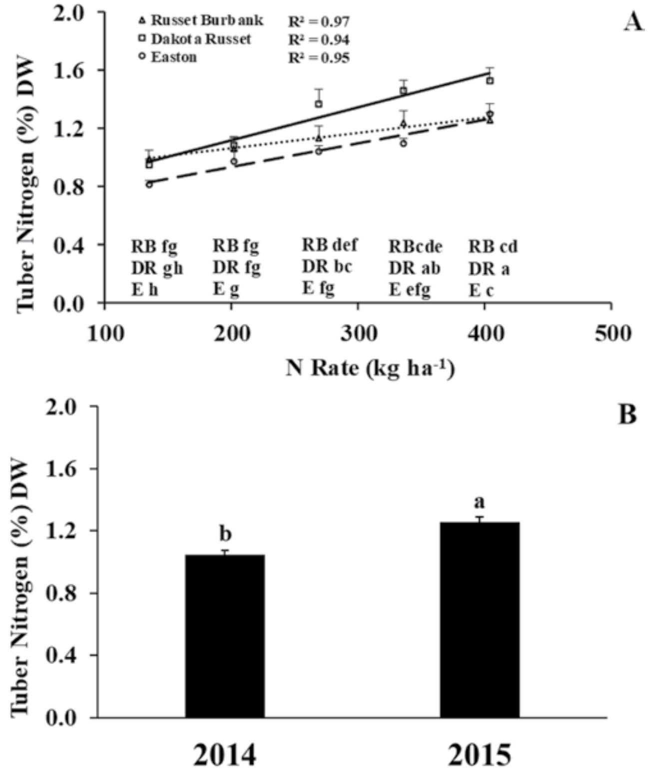

Fig. 10. (A) Cultivar by N rate effects, and (B) main effect of year on tuber N concentration at harvest. Error bars indicated standard errors. Means with the same letter are not significantly different at $P = 0.05$. Equations:
Russet Burbank: $y = 1.10 \times 10^{-3} x + 0.85$
Dakota Russet: $y = 2.30 \times 10^{-3} x + 0.67$
Easton: $y = 1.60 \times 10^{-3} x + 0.61$

In contrast to the large differences between concentrations of stem and bud end-reducing sugars at the end of growing season, the concentrations of asparagine at stem and bud ends were similar, and in a relatively narrow range (from 0.45–2.23 g kg^{-1} in 2014, and 0.43–1.86 g kg^{-1} in 2015 including both ends). In other studies, Bethke and Bussan (2013) reported a range of 4 to 25 g kg^{-1} dry weight basis for asparagine and 0.04 to 4.8 g kg^{-1} dry weight for reducing sugars (approximately 0.8–5 g kg^{-1} fresh weight for asparagine and 0.01–0.96 g kg^{-1} fresh weight for reducing sugars, assuming a tuber dry matter content of 20%).

Tuber Nitrogen Concentration

The cultivar by N rate effect on tuber N concentration was significant and consistent in both years (Table 3, Fig. 10A). Tuber N concentration linearly increased with increasing N rate for all three cultivars, but increased at different rates within cultivars (Dakota Russet > Easton > Russet Burbank). Previous studies reported similar results of increasing tuber N concentration with increasing N application in tuber and the whole plant (Joern and Vitosh, 1995; Jamaati-e-Somarin et al., 2009; Badr et al., 2012). When averaged over cultivar and N rate, tuber N concentration was higher in 2015 than in 2014, showing a significant year effect (Fig. 10B). The higher tuber N concentration (Fig. 10B), together with lower free asparagine (Fig. 9B) in 2015, suggest that favorable growing conditions can result in a stronger N sink by the potato tubers.

CONCLUSIONS

The new cultivars, Dakota Russet and Easton, had higher or comparable specific gravity, less hollow heart incidence, fewer tubers per plant regardless of N rate (indicating larger tuber size), lower concentrations of reducing sugars, and lower or comparable concentrations of asparagine than the standard cultivar Russet Burbank. Easton demonstrated continuous tuber bulking until vine kill, which resulted in higher total yield than Russet Burbank and Dakota Russet at harvest. As expected, tuber yield increased with increasing N rate, but overall N response was found to be similar among the three cultivars tested.

Stem and bud end-reducing sugars concentrations changed over the growing season, but were not consistently affected by N rate. Stem end-reducing sugars concentrations of Russet Burbank were significantly higher than Dakota Russet and Easton both years, which were also affected by different growing conditions. Weather conditions in 2014 caused greater accumulation of reducing sugars later in the growing season than in 2015, especially for the susceptible cultivar Russet Burbank. Compared to Russet Burbank, the new cultivars Dakota Russet and Easton demonstrated better resistance to reducing sugar accumulation, which lowers the potential for acrylamide formation.

In contrast to reducing sugars, stem and bud end asparagine generally increased with increasing N rate. Asparagine concentrations were highest during the bulking period but then generally decreased by harvest, suggesting a dilution effect as tuber size increased. The cultivar Easton had lower asparagine concentrations than the other two cultivars. Overall, this study has shown that N fertility and cultivar had significant effects on agronomic properties such as tuber yield and specific gravity as well as tuber asparagine; however, concentrations of reducing sugars largely depended on cultivar and growing conditions and less on N fertility.

SUPPLEMENTAL MATERIAL

Due to limited space, not all figures with significant treatments effects on tuber yield and tuber quality are shown in the text. Effects of cultivar × year and sampling time × year Interactions on tuber yield, effects of cultivar × year, N rate × year and sampling time × year interactions on specific gravity, effects of sampling time × cultivar interaction and sampling time on number of tubers per plant, and effects of sampling time × cultivar interaction on asparagine concentration are shown in the supplementary material.

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