

Corn Era Hybrid Macronutrient and Dry Matter Accumulation in Plant Components

Krishna P. Woli,* John E. Sawyer, Matthew J. Boyer, Lori J. Abendroth, and Roger W. Elmore*

ABSTRACT

As corn (*Zea mays* L.) hybrids change over time, and with increased use of different plant components for feed, bedding, and energy production, it is important to know macronutrient distribution within plants and how nutrient concentration and accumulation varies during plant development. This field study was conducted in 2007 and 2008 to evaluate dry matter (DM) biomass, macronutrient concentration, and macronutrient content in corn plant fractions (stalk, leaf, tassel, ear shoot, cob, and grain) across developmental stages with two hybrids from 1960 and 2000 eras. Concentrations of N, P, and K were generally lower in all plant fractions for the 2000 compared to 1960 era hybrids, except P concentration in stalks and grain and K concentration in leaves and ear shoots. In contrast, N, P, and K content was consistently higher in 2000 era hybrids for whole plants, leaves, and grain; a reflection of greater DM production. Nitrogen, P, K, and DM content in tassels was lower for 2000 than 1960 era hybrids. From the 1960s to 2000s, hybrid development brought about an increase in plant biomass and grain yield resulting in greater total nutrient content. However, macronutrient concentrations in vegetative plant fractions and grain decreased, thus moderating increase in plant total and grain nutrient content. This research shows the importance for analysis of newer hybrid vegetative and grain biomass on an ongoing basis to provide reliable estimates of macronutrient uptake patterns and removal with harvest of specific vegetative material and grain.

Core Ideas

- We compared 1960 and 2000 era hybrid DM and macronutrient partitioning.
- Similar DM, N, P, and K accumulation patterns occurred for 1960 and 2000 era hybrids.
- Nutrient concentrations (g kg^{-1}) were lower for 2000 than 1960 era hybrids.
- Plant component N, P, and K contents (kg ha^{-1}) were greatest for 2000 era hybrids.
- Greater modern hybrid nutrient uptake was mainly due to greater DM and yield.

CONTINUOUS ADVANCEMENT in biotechnology, plant breeding, and crop management practices have resulted in increased corn grain yield worldwide. Corn grain yields in the United States started to rise in the late 1930s, associated with introduction of hybrids and improved cultural methods (Duvick, 2005). The United States yield gains averaged $63 \text{ kg}^{-1} \text{ ha}^{-1} \text{ yr}^{-1}$ from 1930 to 1960 and $110 \text{ kg}^{-1} \text{ ha}^{-1} \text{ yr}^{-1}$ during the next 40 yr (Troyer, 2000). Approximately 50 to 60% of yield gains may be attributed to genetic improvement and the remainder attributed to climate change and improvement in cultural practices such as weed and pest control, timeliness of planting, and increased efficiency of harvest equipment (Russell, 1974; Duvick, 1977; Cardwell, 1982; Edmeades and Tollenaar, 1990; Duvick, 1992; Osteen, 2000; Tollenaar and Lee, 2002; Assefa et al., 2012). There is a close interaction between genetic improvement and cultural practices, and neither could have resulted in such progress alone.

Maintaining optimal soil test levels and appropriate fertilization are essential for hybrid yield potential to be realized, but nutrient applications must use sustainable financial and environmental approaches (Shapiro and Wortmann, 2006). Effective nutrient management includes an accurate accounting of nutrient removal from soils in harvested portions of crops (Heckman et al., 2003). Hybrid developments can influence accumulation and partitioning of nutrients (Bender et al., 2013). For example, improvement in corn grain yield has been accompanied by a decline in grain N concentration (Duvick, 1997; Ciampitti and Vyn, 2013). Increased understanding of macronutrient uptake in newer hybrids may be gained by determining nutrient concentration and partitioning in plant fractions including grain, cobs, and vegetative components at different crop development stages. Furthermore, crop nutrient management programs may need to take into account nutrient partitioning and uptake requirements at different development stages in the growing season (Jordan et al., 1950); they must certainly account for removal with harvest of different plant fractions.

The harvest of corn stover components and cobs for cellulosic ethanol production is an example where there would be differences in nutrient removal, and compared to grain only harvest, could increase removal and accelerate depletion of soil nutrients if not properly accounted for (Sindelar et al., 2013). There

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K.P. Woli, Kathmandu, Nepal; J.E. Sawyer, L.J. Abendroth, Dep. of Agronomy, Iowa State Univ., Ames, IA 50011; M.J. Boyer, Helena Chemical Company, Guthrie Center, IA 50115; R.W. Elmore, Dep. of Agronomy and Horticulture, Univ. of Nebraska, Lincoln, NE 68583. Received 11 Jan. 2018. Accepted 7 Apr. 2018. *Corresponding authors (krishnawoli@hotmail.com; roger.elmore@unl.edu).

Abbreviations: DM, dry matter; GDD, growing degree days.

are relatively few studies that document corn nutrient uptake throughout the growing season. Studies of this nature define not only the total amount of nutrients that corn utilizes, but also when the plant requires a specific nutrient and where it is being allocated in the plant. The pattern of nutrient assimilation in corn can be nutrient specific and vary in time, rate, and duration of uptake; as well as the tissues to which nutrients are partitioned (Bender et al., 2013). For deficiency diagnosis, concentration of macronutrients in specific tissues can be important. Woli et al. (2017) evaluated the accumulation of DM and macronutrients at the whole-plant level during development stages for different era hybrids. However, they did not report the accumulation of DM and plant nutrients at the plant-fraction level.

Research on historical hybrids (1960s) in Iowa identified the allocation of DM, N, P, and K into different plant components (Hanway, 1962a, 1962b) during the vegetative and reproductive development phases. However, modern hybrids and new management practices have potentially altered corn nutrient uptake and allocation patterns. It is imperative to understand potential changes with modern hybrids as differences could affect nutrient recommendations for rate and timing, relationship of N and P uptake with water quality impacts, and especially important for understanding nutrient removal with increasing harvest of specific corn plant components for feed, fiber, and fuel uses. Therefore, the objectives of this study were to evaluate the partitioning of macronutrients and dry matter across vegetative and reproductive stages for historical to modern era hybrids.

MATERIALS AND METHODS

This study was conducted at the Iowa State University Agricultural Engineering and Agronomy Research Farm near Ames, IA (42°0'41" N, 93°44'32" W in 2007 and 41°59'17" N, 93°40'46" W in 2008). Soil characteristics and soil test information are described in detail by Woli et al. (2016). The previous crop was soybean [*Glycine max* (L.) Merr.] each year. Corn was planted on 15 May each year.

The study used four DuPont Pioneer (Pioneer Hi-Bred International Inc., Johnston, IA) hybrids (3206 and 3618 from the 1960 era and 33D11 and 34A15 from the 2000 era). These were popular commercial hybrids and considered representative of the respective decade, and were recommended by Dr. Donald Duvick (Pioneer Hi-bred) and Dr. Garren Benson (Iowa State University) for the study (personal communication, 2006 and 2007). Corn relative maturity ratings for the hybrids ranged from 108 to 114 d, which are appropriate for central Iowa. For the purpose of achieving high yields, modern hybrids are population dependent (Tokatlidis and Koutroubas, 2004). Therefore, modern hybrids need to be planted at higher plant densities than hybrids from previous eras to achieve optimum yields, while older hybrids do not have the same population tolerance and therefore need to be at a lower population and at the population appropriate for the respective era (Duvick et al., 2004). Therefore, the hybrids were planted with 5% more seed than the approximate final stand for the respective era; 39,000 and 84,000 plants ha⁻¹ for 1960 and 2000 eras, respectively. Plots were 6.1 m wide (8 rows, 0.76 m row spacing) and 16.5 m long.

Fertilizer N was applied by hand at the V3–V4 corn development stages both years as a post emergence application of ammonium nitrate at a rate of 168 kg N ha⁻¹. The N rate of

168 kg N ha⁻¹ was used for both eras and their population densities as that rate is within the recommended range in Iowa for corn following soybean and a rate being optimal for the soybean–corn rotation across a long period of time (Sawyer et al., 2006). Because the spring 2007 soil test results (Woli et al., 2016) indicated high soil test levels for P and K, no additional P and K fertilizer was applied in 2007. The soil test results in 2008 indicated that the site had a soil P test in the Low category and a K test in the Optimum category (Sawyer et al., 2002). Therefore, granular triple super phosphate (0–46–0) was applied 13 May 2008 at a rate of 38 kg P ha⁻¹ before tillage.

Ten corn plant sampling dates were targeted for the following development stages: V6 (sixth collar), V10 (10th collar), V14 (14th collar), VT (tasseling), R1 (silking), R2 (blister), R3 (milk), R4 (dough), R5 (dent), and R6 (physiological maturity), as described in Abendroth et al. (2011). Plant fractions for the development stages from VE (emergence) through V5 (fifth collar) could not be separated, and therefore the study focuses on the mid- to late-vegetative and reproductive stages. Details of the sampling by corn development stage and calendar dates are given in Woli et al. (2016). The R6 sampling date was after all hybrids had reached physiological maturity. To remain consistent, sampling was based on the staging of a single hybrid, 33D11, a modern hybrid with a relative maturity of 112 d.

For each sampling date, three consecutive plants located within two adjacent rows (total of six plants) were cut off at the ground level. Each sampling location was randomized within each plot and bordered on both sides by two rows that were not previously sampled. The plant sampling area was calculated by determining the average plant spacing per plot and then calculating the average area that the six plants occupied. The resulting area was used to calculate the DM biomass and nutrient content on a per ha basis.

At the V6 and V10 stages, plants were collected and analyzed as whole plants. At the V14 stage, plants were separated into three fractions and reported as stalks (stalk + leaf sheaths + ear shoots), leaf blades, and tassel. From VT to R2, plants were separated into four fractions: stalks (stalk + leaf sheaths), leaf blades, tassel, and ear shoots (shank + husk + cob + grain). Tassels were clipped off from the stalks directly below the lowest tassel branch. Ear shoots, when present, were pulled away from the stalk and clipped from their respective stalk nodes. Any ear shoot visible above the leaf sheath attached to the same node was counted as an ear shoot and cut from the stalk. Beginning at R3 and continuing until R5, plants were separated into five fractions: stalks (stalk + leaf sheaths), leaf blades, tassel, ear shoots (shank + husk + cob), and grain. At the R6 stage, plant fractionation was similar to the R3–R5 stages except the cobs were separated from the shank and husk fractions of the ear shoots and analyzed separately.

Dissection of plants took place in the field before any artificial drying except for the ear shoots, which were partially dried before separating the grain and cobs from the shank and husk. All plant fractions were oven-dried at 60°C until they reached a point where weight loss ceased. Biomass dry weights were then determined for all fractionated components.

After drying, samples were ground to obtain a subsample for nutrient analysis. Fractioned samples were ground in a Wiley

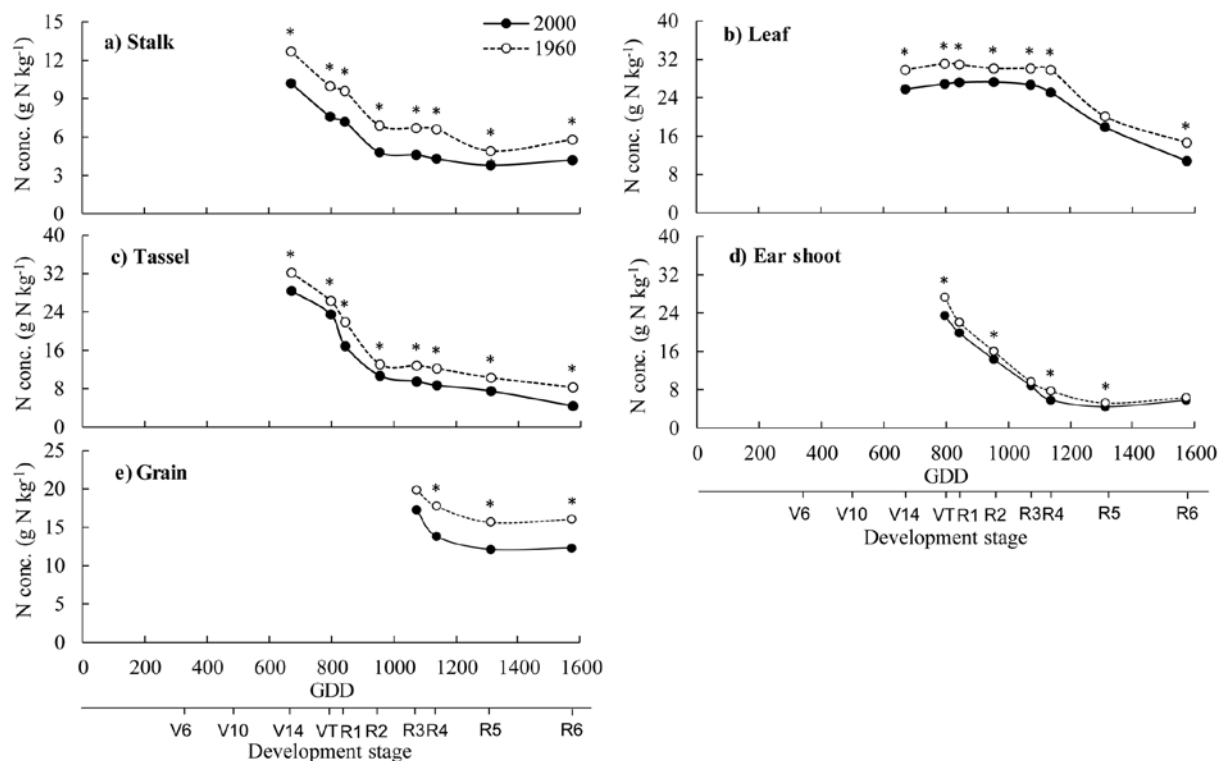


Fig. 1. Era hybrid N concentration for plant fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

mill (Arthur H. Thomas Co., Philadelphia, PA) until the sample would pass through a 2-mm sieve. The only exception was grain which was ground through a flour mill (WonderMill Company, Pocatello, ID). After grinding, the samples were thoroughly mixed, and a small subsample sent to a commercial lab for nutrient analysis.

The daily Celsius-based growing degree days (GDD) were calculated using a maximum temperature threshold of 30°C and a minimum base temperature of 10°C (Dwyer et al., 1999). The average daily temperature was calculated from the high and low temperature obtained from the Iowa Environmental Mesonet (2016).

The era hybrids whole plant DM and nutrient accumulation rates per cumulative GDD were evaluated for whole plant in the vegetative (V6–R1) and reproductive (R1–R6) periods, and for grain in the reproductive (R1–R6) period. Grain DM and nutrient accumulation rates for the R1–R6 period were calculated assuming no grain amount at R1.

Remobilized nutrients from the vegetative to reproductive components were calculated by the content difference between R1 and R6 vegetative fractions, as in Mueller et al. (2017). Specific components combined for R1 were leaf blades + tassel + stalk + leaf sheaths + ear shoots and combined for R6 were leaf blades + tassel + stalk + leaf sheaths + shank + husk.

The experimental design for both years was a randomized complete block with four replications. Hybrid era was treated as fixed and year and block (year) as random. Plant DM, nutrient concentration, nutrient content, remobilized nutrient, and nutrient accumulation rate data were analyzed using the MIXED procedure in SAS (SAS Institute, 2012). Dry matter, nutrient concentration, and content data were analyzed

separately for each sampling date due to range of variances across the sampling dates. Differences considered significant at $P \leq 0.05$.

RESULTS AND DISCUSSION

Nutrient Concentration

Nitrogen

Nitrogen concentration in corn plant fractions changed considerably across the development stages (Fig. 1). Except for leaves, there was a decrease across stages until approximately R3–R4. For leaves, N concentration remained constant until R4, and then decreased to R5 and R6 (Fig. 1b). The pattern of N concentration across stages was similar for the 1960 and 2000 era hybrids. However, N concentrations were different in all plant fractions between the 1960 and 2000 era hybrids at most development stages (Fig. 1), except cobs (Table 1); N concentrations were lower in the 2000 era hybrids compared to 1960 era hybrids. Cob N concentrations were not different between 1960 and 2000 era hybrids.

Phosphorus

Phosphorus concentration in corn plant fractions changed considerably across the development stages, except for grain (Fig. 2). The pattern of P concentration change was similar to that for N with most plant fractions. Tassel and ear shoot P concentrations decreased continuously to R6 (Fig. 2c, 2d) while stalk P concentration did not change from R5 to R6 (Fig. 2a). Like N concentration, leaf P concentration was constant until R4, and then decreased to R6 (Fig. 2b). Grain P concentration had an opposite pattern to the vegetative fractions, with a

Table 1. Cob dry matter (DM) and nutrient composition at physiological maturity for the 1960 and 2000 era hybrids. Means significant at $P < 0.05$.

Era	DM	N		P		K	
		Concentration g kg ⁻¹	Content kg ha ⁻¹	Concentration g kg ⁻¹	Content kg ha ⁻¹	Concentration g kg ⁻¹	Content kg ha ⁻¹
1960	1268	3.59	4.5	0.30	0.37	6.17	7.8
2000	1639	3.45	5.6	0.23	0.35	5.76	9.4
$P > F$	< 0.001	0.373	<0.001	0.004	0.514	0.199	0.003

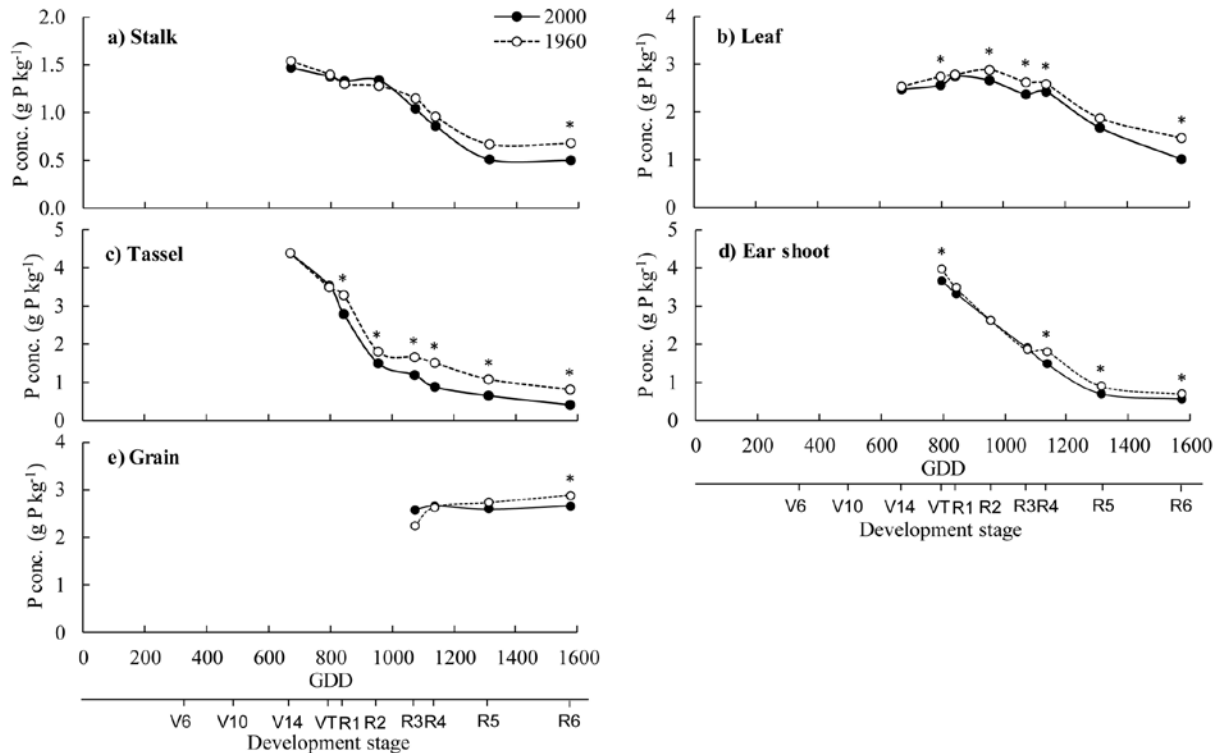


Fig. 2. Era hybrid P concentration for plant fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

concentration increase to R6 for the 1960 era hybrids but not the 2000 era hybrids (Fig. 2e).

Compared to era hybrid differences for N concentration, differences in P concentration between the 1960 and 2000 era hybrids were less frequent. For stalk and grain, there were differences only at R6 (Fig. 2a, 2e). For leaf, tassel, and ear shoot (Fig. 2b, 2c, 2d) most development stages had differences in P concentration. For all plant fractions, P concentration was lower for the 2000 era hybrids compared to the 1960 era hybrids, and lower at R6 for all plant fractions, including cobs (Table 1).

Potassium

Potassium concentration changes across plant development stages had different patterns than for N and P. For leaf and tassel, K concentration decreased throughout plant development (Fig. 3b, 3c), for stalk and ear shoot, K concentration decreased until the R3 stage and then increased or remained constant (Fig. 3a, 3d), and for grain, K concentration decreased to the R5 stage and then remained the same to R6 (Fig. 3e). The continual decrease in K concentration for the leaf and tassel could be related to K remobilization or leaching from degraded tissue exposed to precipitation.

Potassium concentrations were lower for the 2000 era hybrids than the 1960 era hybrids in the stalk, tassel, and grain (Fig. 3a, 3c, 3e). There was little or no difference between era hybrids in the other plant fractions (Fig. 3b, 3d, Table 1).

Discussion of Nutrient Concentrations

Nitrogen concentrations in the various plant fractions had specific patterns throughout the growing season. Until R4, leaves had high and consistent N concentrations, above 25 g N kg⁻¹, and then decreased to R6. Despite the decline in N concentration at later grain filling stages, at R6 leaves ranked with grain in terms of N concentration level. An N concentration decline occurred in vegetative tissues beginning at V14, with a rapid N loss from the leaves during grain fill, coinciding with the ear development; this leads to the assumption of translocation from vegetative to fruiting organs as discussed by Jordan et al. (1950) and Hanway (1962b). Jordan et al. (1950) found that N concentrations in stalks, although never as high as in leaves, exceeded 10 g N kg⁻¹ in young corn plants and then dropped abruptly after tassels appeared. In our study, stalk N concentrations were 12.7 g N kg⁻¹ and 10.2 g N kg⁻¹ in 1960 and 2000 era hybrids at V14, respectively, with a rapid decrease until R2.

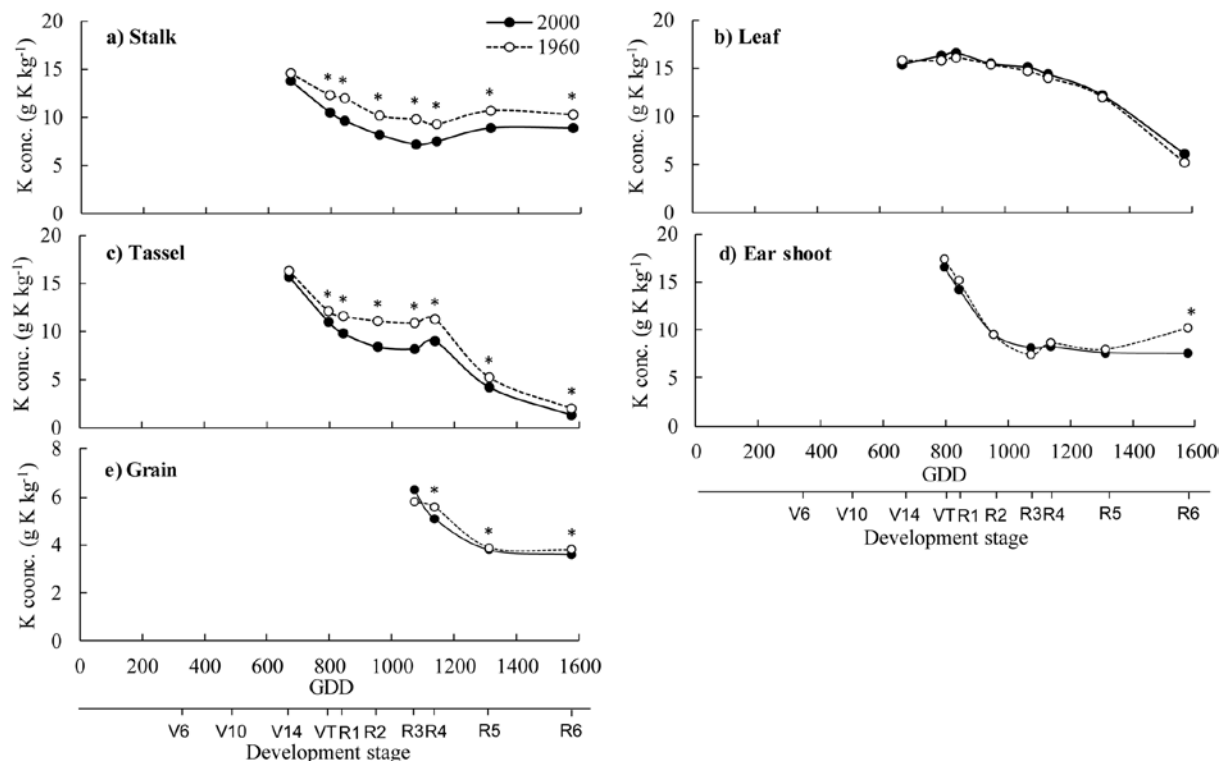


Fig. 3. Era hybrid K concentration for plant fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

Researchers who conducted a 2010 study in Illinois reported grain N, P, and K concentrations to be 13.8 g N kg^{-1} , 3.3 g P kg^{-1} , and 4.4 g K kg^{-1} , averaged over six hybrids grown at two locations (Bender et al., 2013). The reported average N concentration was lower than that from our 1960 era hybrids and slightly higher than the 2000 era hybrids. Based on 100 published reports, Ciampitti and Vyn (2013) investigated N partitioning to grain and stover for two time periods (research conducted from 1940 to 1990 [“Old Era”] and research conducted from 1991 to 2011 [“New Era”]), and reported that one of the most remarkable results was the decrease in grain N concentration over time. The compiled mean grain N concentrations for the old and new eras were 13.3 and 11.9 g N kg^{-1} , respectively. Our grain N concentrations for 1960 and 2000 era hybrids were 16.1 and 12.3 g N kg^{-1} , respectively, which are similar to those reported by Ciampitti and Vyn (2013). Grain N concentration for our 1960 era hybrid was lower than that reported for the hybrids in mid 1940s, which was 16.6 g N kg^{-1} (Hay et al., 1953), and is higher than that reported for the hybrids in 1980s, which was 15.4 g N kg^{-1} (Boone et al., 1984). Haegele et al. (2013) reported a reduction of grain N concentration from 13.6 g N kg^{-1} for 1970 hybrids to 12.6 g N kg^{-1} for 1990 and 2000 era hybrids. Duvick and Cassman (1999) compared the hybrids from 1930s and 1990s and reported a 15% decline in grain N concentration (16.0 and 13.6 g N kg^{-1} , respectively). Comparing the hybrids released in 1930s and 2010s, DeBruin et al. (2017) reported up to a 23% decline in grain N concentration (16.4 and 12.7 g N kg^{-1} , respectively). There is agreement among these studies of a decline in corn grain N concentration over time.

Across 23 site-years in the late 1990s in the Mid-Atlantic region of the United States, Heckman et al. (2003) found higher grain N (13 g N kg^{-1}), P (4.0 g P kg^{-1}), and K (4.8 g K kg^{-1}) concentrations at maturity than our study. Lower grain N concentration in 2000 era hybrids used in our study is consistent with the results reported in a recent study (DeBruin et al., 2017) using a set of DuPont Pioneer hybrids released between the era decades of 1930 to 2010. Johnson et al. (2010) reported N, P, and K concentrations in cobs to be 5.5 , 0.50 , and 6.2 g kg^{-1} , respectively, which were higher than the N (3.6 and 3.4 g N kg^{-1}) and P (0.30 and 0.20 g P kg^{-1}) concentrations and similar to the K concentration (6.2 and 5.8 g K kg^{-1}) for our 1960 and 2000 era hybrids, respectively.

For N, P, and K, the 1960-era hybrids consistently had higher tissue and grain concentrations than the 2000 era hybrids. The decline in grain nutrient concentration over time was greater for N (24%) compared to P (7%) and K (5%); 16.1 and 12.3 g N kg^{-1} for N, 2.9 and 2.7 g P kg^{-1} for P, and 3.8 and 3.6 g K kg^{-1} for K in 1960 and 2000 era hybrids, respectively. A number of studies reported corn grain N concentrations for specific times during the growing season (Jordan et al., 1950; Hay et al., 1953; Boone et al., 1984; Liang et al., 1996; Heckman et al., 2003; Bender et al., 2013; Haegele et al., 2013; DeBruin et al., 2017), however, such differences in N, P, and K concentrations for two different eras separated by a 40-yr period have rarely been reported. The difference in concentration between the two eras has important implications, not only for total nutrient demand, but also removal with harvest of various plant fractions; especially for the most common removal in corn grain. When calculating removal for mass balance determination or the increasing practice of harvesting

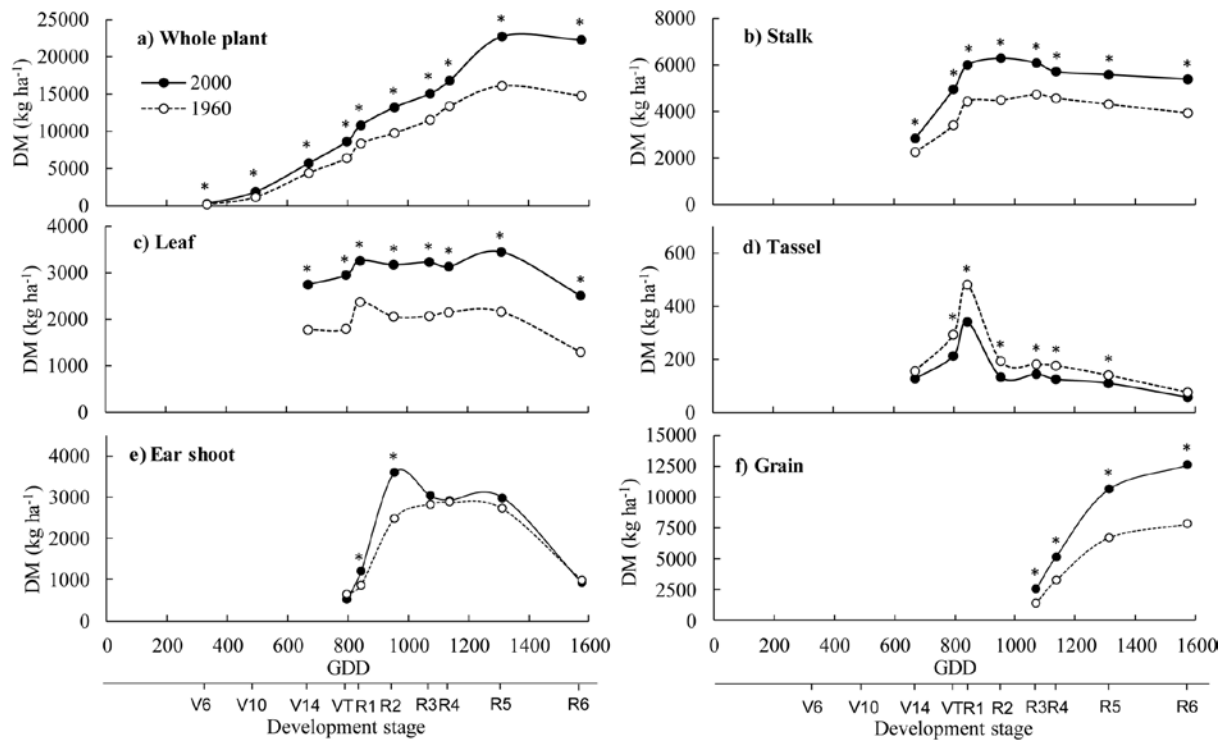


Fig. 4. Era hybrid plant dry matter (DM) for whole plant and fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

Table 2. 1960 and 2000 era hybrid dry matter (DM) and nutrient accumulation rates per cumulative Celsius-based growing degree days (GDD) for whole plant vegetative (V6–R1) and reproductive (R1–R6) periods, and for the grain fill period (R1–R6). Means significant at $P < 0.05$.

Era	Whole plant		Grain
	V6–R1	R1–R6	R1–R6
kg ha ⁻¹ GDD ⁻¹			
	DM		
1960	16	9	11
2000	21	16	18
$P > F$	<0.001	<0.001	<0.001
	N		
1960	0.279	0.045	0.179
2000	0.298	0.077	0.221
$P > F$	0.407	0.137	<0.001
	P		
1960	0.033	0.016	0.032
2000	0.041	0.025	0.047
$P > F$	0.012	0.006	<0.001
	K		
1960	0.217	-0.030	0.042
2000	0.245	-0.014	0.065
$P > F$	0.169	0.358	<0.001

of corn stover, appropriate nutrient concentrations are needed otherwise estimated removal amounts will be incorrect.

DRY MATTER BIOMASS

For both the 1960 and 2000 era hybrids, whole plant biomass DM increased until the R5 development stage and then decreased slightly at R6 (Fig. 4a). The maximum DM was 16,114 kg DM

ha⁻¹ for 1960 era hybrids and 22,727 kg DM ha⁻¹ for 2000 era hybrids, a 41% increase in biomass for the 2000 era hybrids.

For stalks, DM increased gradually from V14 to R2 in 2000 era hybrids (maximum 6288 kg DM ha⁻¹) and from V14 to R3 in 1960 era hybrids (maximum 4732 kg DM ha⁻¹), and then decreased to R6 for hybrids of both eras (Fig. 4b). For leaves, DM remained relatively constant from V14 to R5 in both era hybrids and then decreased at R6 (Fig. 4c). For grain, DM increased from R3 to R6, with 7840 and 12,611 kg DM ha⁻¹ in the 1960 and 2000 era hybrids, respectively (Fig. 4f).

Unlike the whole plant and other plant fractions, the DM pattern across development stages was different for tassels and ear shoots (Fig. 4d, 4e). For tassels, DM peaked at R1, decreased considerably at R2, and then gradually decreased to 68 kg DM ha⁻¹ at R6 for both era hybrids (Fig. 4d). For ear shoots, DM peaked at R2 in 2000 era hybrids (3592 kg DM ha⁻¹) and at R4 in 1960 era hybrids (2870 kg DM ha⁻¹), remained constant until R5, with a decrease to 949 kg DM ha⁻¹ at R6 for both era hybrids (Fig. 4e), with that decrease mainly because grain was not included at R6 in the ear shoots.

Dry matter in whole plants and plant fractions were different between the 1960 and 2000 era hybrids at nearly all development stages (Fig. 4, Table 1). Throughout the growing season, DM was highest in the 2000 era hybrids for the entire plant (with 78% greater DM accumulation rate during the reproductive stages, Table 2) and all plant fractions except for tassels where the 2000 era hybrids had lowest tassel DM. The relative greatest difference in DM for the 2000 era hybrids compared to the 1960 era hybrids was for grain; which of course also influenced the higher total plant DM for the 2000 era hybrids, and resulted in a 64% greater grain DM accumulation rate for 2000 era hybrids compared to 1960 era hybrids (Table 2). Both 1960 and 2000 era hybrids accumulated DM in the grain fraction with the same

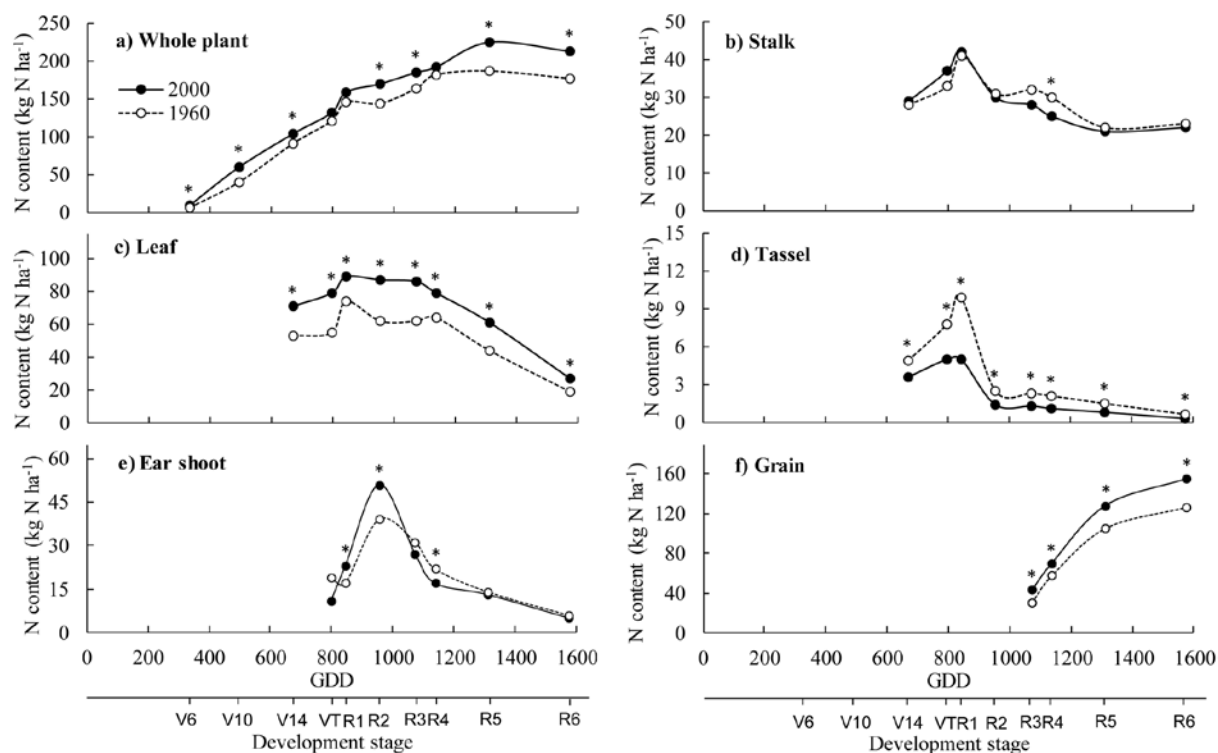


Fig. 5. Era hybrid plant N content for whole plant and fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

pattern; mean of 19%, 41%, and 85% of the total grain DM at R6 being present by the R3, R4, and R5 stages, respectively.

Discussion of Dry Matter Biomass

There was a steady increase in whole plant DM biomass, with maximum accumulation at R5, not R6, for both era hybrids. Hanway (1962a) and Karlen et al. (1988) found similar decline of whole plant DM from R5 to R6. The decrease in plant DM between R5 and R6 was in the vegetative material, not grain. At R1, the 2000 era hybrids had accumulated 5994 and 3262 kg DM ha⁻¹ in stalks and leaves, while the 1960 era hybrids accumulated 4432 and 2374 kg DM ha⁻¹, respectively. With tassels added in at R1, the total DM of stalks, leaves, and tassels for the 1960 and 2000 era hybrids were 7287 and 9598 kg DM ha⁻¹, respectively. The fraction of total R6 plant DM accumulated at the R1 stage was 57% for the 1960 era hybrids and lower at 48% for the 2000 era hybrids.

After R1, DM began to steadily accumulate in the ear shoot fraction and grain. Grain harvest index was similar for both era hybrids, with 0.54 for the 1960 and 0.57 for the 2000 era hybrids. Grain DM accumulated at R6 by our 1960 era hybrids (7840 kg DM ha⁻¹) was comparable with the 7200 kg DM ha⁻¹ reported by Hanway (1962a).

The 2000 era hybrids had higher DM accumulation rates during both vegetative and reproductive periods, with the DM amount greater in the 2000 era hybrids at all development stages. The whole plant accumulation rates were highest during the vegetative period (Table 2). The 2000 era hybrids were higher yielding (grain) than the 1960 era hybrids, and with more overall comparative DM allocation (between eras) to grain fill than vegetative development. The 2000 era hybrids accumulated more DM in stalks, leaves, and ear shoots during the VT to R2 stages,

as well as cobs and grain than the 1960 era hybrids. However, the ear shoot biomass was not different between era hybrids during later grain fill. Unlike the other plant fractions, 2000 era hybrids accumulated less DM in tassels. Duvick et al. (2004) also observed a decrease in tassel size of newer hybrids.

Nutrient Accumulation

Nitrogen

Whole plant N gradually increased and peaked at R5 (187 and 225 kg N ha⁻¹, respectively, for 1960 and 2000 era hybrids), followed by a small decrease at R6 in both era hybrids (Fig. 5a). The stalk N content peaked at R1 (average 42 kg N ha⁻¹) and then decreased gradually to R5 and remained the same at R6 (Fig. 5b). Similar peaks at R1 were found in leaves and tassels for both era hybrids, and at R2 in ear shoots, followed by a large decrease in all three fractions (Fig. 5c, 5d, 5e). In grain, N accumulation continued to plant R6, with an increasing difference between era hybrids as development continued (Fig. 5f). The N accumulation in cobs was small for both eras (Table 1).

Although there was no difference in whole plant N accumulation rates on a GDD basis between 1960 and 2000 era hybrids at both vegetative and reproductive periods (Table 2), differences in total N accumulation were significant at most development stages (Fig. 5). The pattern of N accumulation was not consistent, however, for all plant fractions. Nitrogen content at R6 was greater in the 2000 than 1960 era hybrids for whole plant, leaves, tassel, ear shoots, cobs, and grain; but generally not stalks or ear shoots (Fig. 5, Table 1). The difference between era hybrids was most pronounced in later reproductive stages for whole plant and grain. The greatest difference in N content between era hybrids by development stage was for leaves until R5, tassel at R1, grain

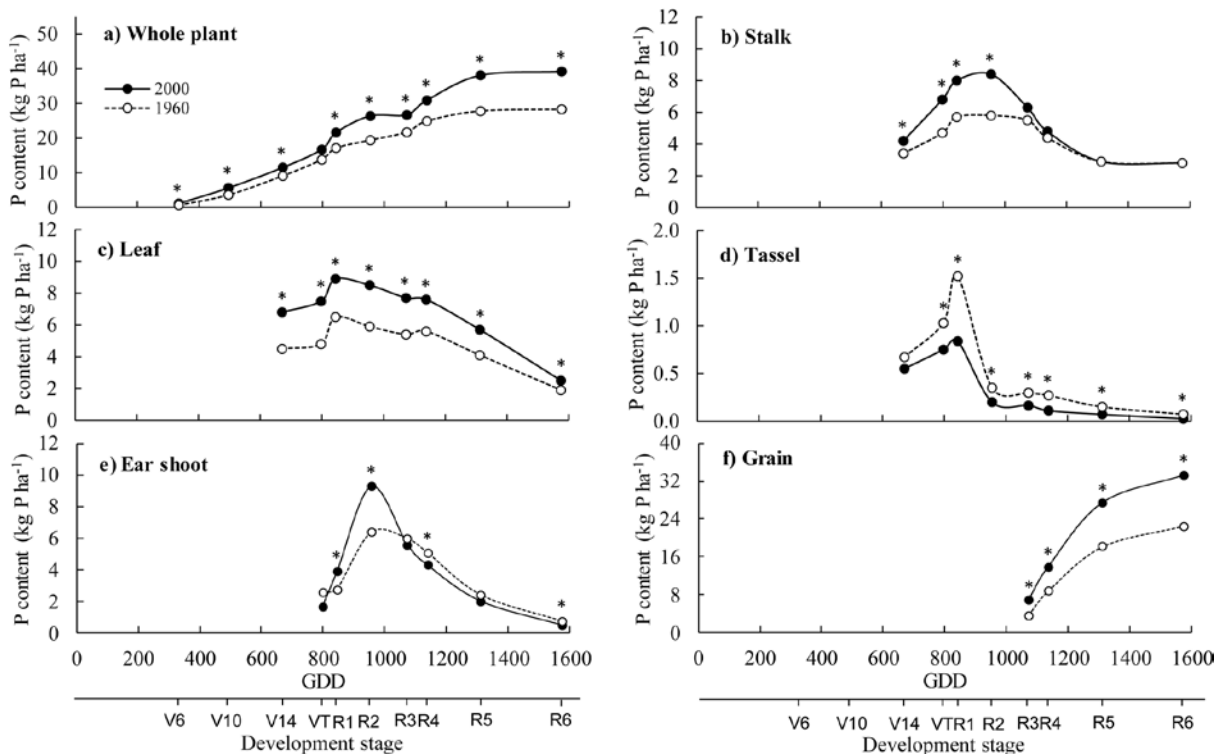


Fig. 6. Era hybrid plant P content for whole plant and fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

at R6, and whole plant at R5 and R6. Whole plant N at R1 was 82% and 75% of the total at R6, respectively, for the 1960 and 2000 era hybrids. Whole plant N accumulation rates per GDD were higher during the vegetative compared to the reproductive period in both 1960 and 2000 era hybrids (Table 2).

Phosphorus

In the vegetative tissues, P content peaked at the R1–R2 stages, and then declined to plant maturity (Fig. 6). Whole plant and grain accumulated P continuously to maturity, and the P content in cobs was small with no difference between era hybrids (Table 1).

Phosphorus accumulation in the 2000 era hybrids was greater than the 1960 era hybrids in whole plant, leaves, and grain at all development stages (Fig. 6a, 6c, 6f). The whole plant P uptake rate was higher for the 2000 era hybrids than the 1960 era hybrids across vegetative and reproductive development (Table 2). There was also a 47% greater grain P uptake rate in 2000 era hybrids compared to 1960 era hybrids (Table 2). Whole plant P at R1 was 60% and 55% of the total at R6, respectively, for the 1960 and 2000 era hybrids. In stalks, there was a difference in P content between 1960 and 2000 era hybrids only for the V14–R1 development stages (Fig. 6b). At all development stages, unlike in the whole plant and with all other plant fractions, the P content in tassels was lower in the 2000 than 1960 era hybrids (Fig. 6d). With the ear shoots, the pattern of difference in P content in 1960 and 2000 era hybrids was not consistent. Although ear shoot P content was higher in 2000 era hybrids at R1 and R2, the 1960 era hybrids had slightly more P in ear shoots from R4–R6 (Fig. 6e).

Potassium

As with whole plant DM, N, and P content, whole plant K content gradually increased to R1, but there was little to no increase in K accumulation during grain fill. Whole plant K at R1 for the 1960 and 2000 era hybrids was 93 and 86% of the total at R5, but was 123 and 107% of the total at R6, respectively, indicating the lack of K increase during grain fill and the plant K content decrease from R5 to R6. As found in N and P, there was a peak in K content of the ear shoot at R2 and tassel at R1, and then a large decrease to the next development stage (Fig. 7d, 7e). Peaks of the ear shoot at R2 in both 1960 and 2000 era hybrids were because the ear shoot contained grain at this stage that was not removed. Similar large peaks were not present for the other plant fractions. However, all vegetative plant fractions had a decline in K content after the R1–R2 stages. The grain K content increased through grain development in both era hybrids (Fig. 7f). As the total plant K content changed little after R1–R2 stages, it appears that K moved from the vegetative tissues to the developing grain; and as evidenced by the negative whole plant K accumulation rate for the R1–R6 period with both era hybrids (Table 2). Although not a large amount, the K content was greater than N or P in cobs (Table 1).

There was no difference in whole plant K accumulation rates between the 1960 and 2000 era hybrids for both the vegetative and reproductive periods (Table 2). However, K content in 2000 era hybrids was higher in whole plants, leaves, and grain at all development stages (Fig. 7a, 7c, 7f) and in cobs at maturity (Table 1). The stalk K content was different between 1960 and 2000 era hybrids only at three development stages; with the 2000 era hybrids having more K during the earlier stages (V14 and VT) and at R6 (Fig. 7b). As with N and P content, K content in tassels was lower in 2000 than 1960 era hybrids at all development stages (Fig. 7d). The ear shoot K content was

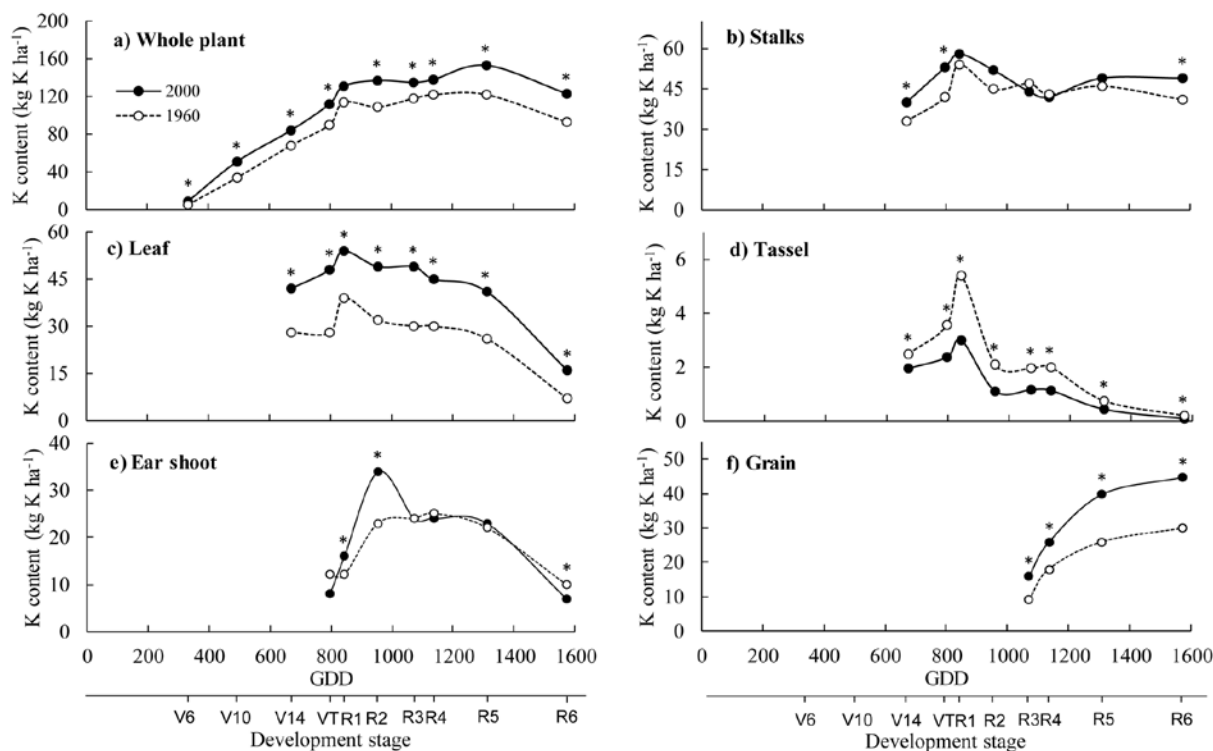


Fig. 7. Era hybrid plant K content for whole plant and fractions across corn development stages. At each development stage, * indicates significant difference ($P \leq 0.05$) between eras.

similar for 1960 and 2000 era hybrids at most stages, except at R2 where it was higher for the 2000 era hybrids (Fig. 7e). There was a negative whole plant K accumulation rate during the reproductive period (R1–R6) (Table 2), indicating that K accumulated in early vegetative development stages in the leaf, tassel, and ear shoot was either translocated to the developing grain or lost from the plant. This negative trend did not occur with the stalk tissue, with the K either not going to developing grain or protected from loss. With K as the ionic form within plant material, it is possible that some K leached from the leaf, tassel, and ear shoot tissues, but not stalks. However, the increase in grain K content could also account for the decrease in vegetative plant fractions and overall lack of increase in total plant K after R1–R2. In grain, there was a 55% higher grain K uptake rate in 2000 era hybrids compared to 1960 era hybrids (Table 2). The K accumulation pattern in the proportion of grain at R3, R4, and R5 compared to that at R6, was similar in both 1960 and 2000 era hybrids, with a mean of 33, 59, and 88%, respectively.

Discussion of Nutrient Accumulation

Between VT and R1, both 1960 and 2000 era hybrids continued to accumulate N in all vegetative fractions except the ear shoot for the 1960 era hybrids. This result was in contrast with the N loss that Karlen et al. (1988) observed during the same period. There was a decline in accumulated N in stalks, leaves, tassels after R1 in our study, and after R2 for ear shoots. Hanway (1962b) and Karlen et al. (1988) reported similar results of declining accumulated N after R1 and to maturity in those plant fractions. Presumably, this was N translocating into the developing ear shoot and then to the grain. The decline in N content found in stalks, leaves, and tassels was more pronounced and started earlier after R1 than the decline in DM.

Calculated remobilized N from vegetative to reproductive components were 93 and 104 kg N ha⁻¹ for the 1960 and 2000 era hybrids, respectively, without significant difference (data not shown). These values are larger compared to those reported in Indiana by Mueller et al. (2017), 79 and 90 kg N ha⁻¹ for hybrids released in 1990s and 2010s, respectively.

At R6, the 2000 era hybrids accumulated 155 kg N ha⁻¹ in grain, while 1960 era hybrids accumulated only 126 kg N ha⁻¹. Our 1960 era hybrid results were similar to the grain N at maturity in the study reported by Hanway (1962b) and our 2000 era hybrid results were similar to a study conducted in 2010 that reported 166 kg N ha⁻¹ (Bender et al., 2013). At maturity, grain contained about two-thirds of the total N in the plant (Sayre, 1948; Hanway, 1962b), and approximately the calculated amount of N remobilized. Jordan et al. (1950) reported that vegetative components gained N until the tassel stage; subsequently a part of this N was translocated to the developing grain. Nelson (1956) also reported that N moved from cobs, leaves, and stalks, and a considerable amount from the husks. Whitehead et al. (1948) reported that the N content of leaves, sheaths, shanks, and tassels reached a maximum and then decreased, the net loss being attributable to gains in the ears. As found with DM, the 1960 and 2000 era hybrids accumulated N in the grain with a similar pattern; at development stages R3, R4, and R5, accumulation averaged across both era hybrids was 26, 46, and 83% of plant total N at R6, respectively.

Unlike with N where there was no difference between era hybrids, there was more P accumulation in stalks of 2000 era hybrids (through R2) than 1960 era hybrids. Our 1960 era hybrids had 12 kg P ha⁻¹ in stalks, leaves, and tassels at R1, which was the same content reported by Hanway (1962b). After R2, accumulation of P gradually declined in stalks, leaves, tassels,

and ear shoots. Similar results were found by Hanway (1962b) and Karlen et al. (1988). Calculated remobilized P was higher at 16 kg P ha⁻¹ for 2000 era hybrids than 11 kg P ha⁻¹ for 1960 era hybrids. Our grain P content at R6 in 2000 era hybrids was similar to that reported by Bender et al. (2013), which was 39 kg P ha⁻¹. As with DM biomass and N content, hybrids from both eras accumulated P in grain at a similar pattern, with a mean across era hybrids at 19, 41, and 82% of grain total (R6) for development stages R3, R4, and R5, respectively. Grain P content at maturity in the 1960 and 2000 era hybrids were 80 and 85% of the whole plant total P, respectively. These proportions are comparable with those reported by Hanway (1962b), which was 75% and that reported by Karlen et al. (1988), which was 85%.

As we observed, several studies showed that P accumulation in corn plants followed a nearly steady rate of uptake from V6 through R6 (Sayre, 1948; Jordan et al., 1950; Hanway, 1962b; Karlen et al., 1988). As found with N, from VT to R1 both the 1960 and 2000 era hybrids accumulated P in all fractions, except the ear shoot for the 1960 era hybrids. The decrease of vegetative P from R1–R2 to plant maturity is consistent with that reported in other studies (Jordan et al., 1950; Hanway, 1962b; Karlen et al., 1988).

Although the pattern was not the same as that for N or P, K content decreased in stalks, leaves, and tassels starting around the R2 stage. In the 1960 and 2000 era hybrids, at R6 approximately 44 and 40% of K was in stalks and 32 and 37% of K in grain, respectively; indicating that only about one-third of the total plant K was in grain at R6, compared to much higher percentages of N (71 and 73%) and P (80 and 85%). Hanway (1962b) and Karlen et al. (1988) also reported that the grain fractions were as low as 26 and 19% in K, respectively. A recent study reported the grain fraction to be 33% in K (Bender et al., 2013), which is higher than the Hanway (1962b) and Karlen et al. (1988) results but lower than our 2000 era hybrids. The calculated K remobilization from vegetative to grain was 51 and 60 kg K ha⁻¹ for the 1960 and 2000 era hybrids, respectively, with no significant difference. However, with the negative whole plant K accumulation rate for the R1–R6 period (Table 2), and as noted earlier, it is possible part of the calculated remobilized K was lost from the vegetative leaf and tassel tissues through leaching and not accumulated in the grain.

Accumulation of N, P, and K in whole plant, leaves, and grain at most development stages followed a similar pattern as for DM biomass, and was consistently higher in 2000 era hybrids compared to 1960 era hybrids. Interestingly, N, P, and K content in tassels were lower in 2000 era hybrids compared to that in 1960 era hybrids. There has been a report of decreasing tassel DM biomass in newer hybrids (Duvick et al., 2004), but this is the first study that reports declined macronutrient contents in tassels over a four-decade period. In stalks, although DM was greatest in 2000 era hybrids at most development stages, there were few differences in N and K content between 1960 and 2000 era hybrids while P content was higher in 2000 era hybrids through the R2 stage. In ear shoots, DM and content of N, P, and K were higher in the 2000 era hybrids only at the R1 and R2 stages. Cob DM, N, and K content were higher in 2000 era hybrids, with no difference in P content. There is a growing potential for use of cobs as a cellulose material for bioenergy production, and this study is one of the few that reports cob macronutrient content with modern hybrids.

Nitrogen, P, and K content of stalks, leaves, tassels, and ear shoots all decreased after approximately the R1 stage, with the pattern similar between nutrients. However, the pattern was not the same for each plant fraction or the total change in content from vegetative fractions to grain. Our 1960 and 2000 era hybrids had 71 and 73% of total plant N in grain at R6, similar to the older study by Hanway (1962b). However, our 2000 era hybrid results are much higher compared to the 58% reported by Bender et al. (2013). Hanway (1962b) also reported approximately 75% of total plant P in grain at R6, whereas our results were 80 and 85% in the 1960 and 2000 era hybrids, which were both higher than the 78% reported by Bender et al. (2013).

CONCLUSIONS

The results of this study indicate that while DM, N, P, and K accumulation patterns with respect to corn development stages were similar in the 1960 and 2000 era hybrids, nutrient concentrations decreased but DM, N, P, and K accumulations were higher with the newer 2000 era hybrids. Because of this, nutrient uptake is greater in newer hybrids than older hybrids, and will likely continue to increase with hybrid improvements in the future. Results also indicate that higher nutrient content in newer hybrids was driven mainly by increases in DM and associated nutrient uptake rates, but those higher nutrient amounts were moderated due to generally lower nutrient concentrations in the 2000 era hybrids. Nutrient concentrations in the fractioned plant parts are useful in determining nutrient partitioning during the growing season and removal rates when different plant fractions are harvested other than just the whole plant or grain. Having access to newer hybrid plant component macronutrient concentrations is also important for estimating current global corn nutrient use, effects on nutrient cycling and stover nutrient return to soil, N, and P uptake and recycling relationships with water quality, and soil nutrient budget estimations.

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