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# Soybean Yield Components and Seed Potassium Concentration Responses among Nodes to Potassium Fertility

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## ABSTRACT

Soybean [*Glycine max* (L.) Merr.] yield loss by K deficiency has been reported extensively, but very little research has evaluated how the yield loss is distributed among nodes. We evaluated soybean seed yield, individual seed weight, pod and seed numbers, seed abortion, and seed-K concentration among nodes of an indeterminate and determinate cultivar grown under three K fertility levels (low, medium, and high represented by 0, 75, and 150 kg K $ha^{-1}$ $yr^{-1}$, respectively). Chlorosis along upper leaf margin was observed during seed-filling period in every low K fertility plot. Soybean grown with medium and high K fertility averaged 28 and 43%, respectively, greater predicted seed yield on the top seven (of 10) node segments for the indeterminate soybean and 72 and 101% greater seed yield on the node segments 2, 3, 4, and 7 (of seven) for the determinate soybean than plants having low K fertility. Yield loss was attributed to reduced individual seed weight, fewer pod and seed numbers, and increased seed abortion. The seed-K concentration of soybean grown with low K fertility was lowest (11.6 [indeterminate] and 15.2 [determinate] g K $kg^{-1}$) for seeds located on the top nodes and increased (17.8 g K $kg^{-1}$) quadratically to the bottom of the plant. The largest proportion of seed yield and the greatest yield loss from K deficiency come from the middle and upper nodes of indeterminate plants and the combination of the bottom nodes, due to branching, plus the upper-middle nodes of determinate plants.

## Core Ideas

- The greatest proportion of soybean yield, regardless of K fertility level, was produced by nodes on the top two-thirds of the indeterminate cultivar and the combination of the bottom node, due to branching, plus the nodes on the top one-half of the determinate cultivar.
- The yield loss from K deficiency was greatest on the nodes that produced the largest proportion of seed yield for each growth habit. The yield loss on the top nodes was from reduced individual seed weight, fewer numbers of pods and seeds, and increased seed abortion.
- For K-deficient soybean there would be a large seed-K concentration gradient from the top to bottom of the plant with seed-K being greatest for seed produced on the bottom nodes and least for seed produced by the top nodes. The K concentration of seed collected from the upper nodes or the seed-K concentration gradient between the top and bottom nodes might be useful in diagnosing K deficiency at maturity in fields that showed no visible K deficiency symptoms (i.e., hidden hunger) during the growing season.

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The distribution of soybean yield and yield components among nodes is important information for modeling growth, identifying yield-limiting factors, and predicting soybean yield (Ramseur et al., 1984). Several studies have shown that soybean yield and yield components among nodes of both determinate and indeterminate cultivars vary due to the differences in water availability (Carlson et al., 1982; Ramseur et al., 1984), row spacing (Herbert and Litchfield, 1982; Ramseur et al., 1984), plant density (Dominguez and Hume, 1978; Liu et al., 2010), light interception (Liu et al., 2010), and soybean genotypes (Hansen and Shibles, 1978; Wiebold et al., 1981). The literature suggests that the differences in seed yield and yield components among treatments tends to be more evident on the upper one-half of soybean plants (Weil and Ohlrogge, 1976; Carlson et al., 1982; Herbert and Litchfield, 1982; Ramseur et al., 1984). However, seed yield and yield components of the lower nodes of determinate soybean also vary since branches originate from these lower nodes and contribute substantially to seed yield (Ramseur et al., 1984).

Soybean seed yield and yield components are reported to be influenced by K fertilization, especially on soils with low K fertility. Potassium deficiency can cause substantial yield loss in both determinate and indeterminate soybean (Coale and Grove, 1990; Mallarino et al., 1991; Slaton et al., 2010; Clover and Mallarino, 2013; Parvej et al., 2015) by decreasing the pods $plant^{-1}$, seeds $pod^{-1}$, seeds $plant^{-1}$, and individual seed weight and by increasing seed abortion (Nelson et al., 1946; Jones et al., 1977; Bharati et al., 1986; Coale and Grove, 1990; Parvej et al., 2015). Despite the large number of papers investigating soybean yield response to K fertilization, we could find no research that has evaluated whether the effects of K deficiency on yield loss and yield components are distributed uniformly across soybean plant nodes.

Based on the concept of nutrient mobility, the classical K deficiency symptoms on plant leaves should occur as an irregular yellowing (chlorosis) along the leaf margins with symptoms being worse on the lower leaves since K is mobile within the plant (Sinclair, 1993). However, during reproductive growth, K deficiency symptoms are frequently observed on the middle and upper (young) leaves of soybean (Jeffers et al., 1982; Sale and Campbell, 1986; Snyder and Ashlock, 1996) and cotton (*Gossypium hirsutum* L.; Maples et al., 1988; Oosterhuis, 2002) plants rather than the lower, older leaves. The appearance of K deficiency symptoms in the middle and upper soybean canopy during the pod set and seed-filling periods indicates the

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**Abbreviation:** MG, maturity group.

complexity of K mobilization and that source-sink relationships involving K are complex and warrants further investigation.

The actual reason of K deficiency symptoms on the upper leaves of soybean has not been clearly elucidated. The results of Wrona and Epstein (1985) showed that less than one-half of the $^{86}Rb$-labeled $K^+$ was allocated to the aboveground shoot, and <10% was recovered in leaf blades, of two tomato species [*Lycopersicon esculentum* Mill. ' Walter' and *L. cheesmanii* spp. *minor* (Hook)] suggesting impaired K translocation. Limited literature suggests that the rate of K translocation from the lower, older leaves to the upper leaves may not be sufficiently rapid to meet the high K demand during the seed-filling period resulting in K deficiency symptoms on the upper soybean leaves (Jeffers et al., 1982). Hanway and Weber (1971) showed that leaf-, petiole-, and stem-K concentrations of indeterminate soybean cultivars declined more from the top portion of the plant than from the middle and lower plant portions during the seed-filling period (R5–7; Fehr et al., 1971), which coincides with the growth period with the greatest K demand. They also showed that the K concentration of mature pods produced on the upper third of the stem was significantly lower than the K concentration of pods produced on the lower third of the stem. Sadler et al. (1991) revealed that the K concentration of mature pods (with seeds) gradually decreased with some fluctuations from the bottom to the top of the stem for a cultivar having a determinate growth habit. Collectively, the literature suggests K deficiency symptoms in the middle and upper leaves indicate the supply of K is insufficient to meet the demand of both leaves and seeds and the seed-K concentration is lowest on the upper nodes.

Nutrient removal by harvested grain is important information for fertilizer recommendations. Many fertilization recommendations follow the "build and maintain" philosophy that includes a nutrient replacement component in the rate equation (Vitosh et al., 1996; Hochmuth et al., 2014). The variation of pod (with or without seed) K concentration among nodes (Hanway and Weber, 1971; Sadler et al., 1991) suggests that the amount of K removed from a particular soybean field could vary with the K concentration of seeds collected from different portions of the plant. A better understanding of how K is allocated among seeds at different node positions may help develop more efficient fertilization practices or lead to improved methods for monitoring plant K nutrition and yield potential.

Our primary objective was to evaluate soybean seed yield, individual seed weight, pod and seed numbers, seed abortion, and seed-K concentration among nodes of an indeterminate and determinate cultivar grown under different K fertility levels. We hypothesized that when K availability was low K deficiency would increase in severity during seed filling and at nodal positions with the largest number of pods due to limited active K uptake and mobilization from vegetative tissues to seeds. Hence, we predicted that (i) K deficiency would decrease soybean yield, individual seed weight, and pod and seed numbers and increase seed abortion on the middle to the upper portions of the indeterminate plants and lower and upper portions of the branching determinate plants and (ii) regardless of soybean growth habit, seed-K concentration at each node segment would increase with each increase in K fertility level and would be greatest for seed produced on the lower nodes of the plant and decrease gradually toward the upper nodes of the plant.

## MATERIALS AND METHODS

The response of soybean yield components and seed-K concentration among nodes to K fertilization was evaluated on a Calhoun silt loam (fine-silty, mixed, active, thermic Typic Glossaqualf) at the Pine Tree Research Station near Colt, AR, (35°07′17.19″ N, 90°57′30.05″ W) in 2012 and 2013. A detailed description of the experimental sites, treatment structure, soil sampling and analysis methods, crop management, and plant sampling and analysis was published by Parvej et al. (2015). Briefly, two glyphosate [N-(phosphonomethyl) glycine]-resistant soybean cultivars, Armor 48-R40 [indeterminate growth habit and maturity group (MG) 4.7] and Armor 53-R15 (determinate growth habit and MG 5.3) were strip planted across three annual-K fertilization rates (0, 75, and 150 kg K $ha^{-1}$ $yr^{-1}$ representing low, medium, and high K fertility levels, respectively). The terms low, medium, and high K fertility represent the cumulative soil-K availability to plants by annual-K fertilization and soil-test K index (Parvej et al., 2015). The experiment was a strip-plot with five blocks where K fertilization rate was the main plot and soybean cultivar was the strip-plot that contained 10, 38-cm wide rows of each cultivar. Soybean was planted into an untilled seedbed on 26 April in 2012 and 16 May in 2013. The seeding rate (73 kg $ha^{-1}$ i.e., 417,600 seeds $ha^{-1}$), irrigation, and pest management closely followed recommendations provided by the University of Arkansas Cooperative Extension Service (University of Arkansas, 2000).

Four plants of each cultivar were collected from each plot at maturity to evaluate seed yield, selected yield components, and seed-K concentration as affected by main-stem and branch node locations and K fertility levels. The nodes of the sampled plants were numbered from the topmost node (node 1) to the bottom node. The four sampled plants were dissected from the top of the plant to the bottom and tissues from the four plants were composited into a single sample. The indeterminate cultivar had an upright growth habit, no lateral branches, and 18 (2013) to 20 (2012) main-stem nodes $plant^{-1}$ at maturity. The determinate plant was a bushy plant, had 12 (2013) to 14 (2012) main-stem nodes $plant^{-1}$ at maturity, and contained multiple branches that also contained pods. Nodes on the lower one-half of the determinate cultivar contained at least one primary branch that had five to six nodes. Each plant was dissected by cutting immediately above the main-stem nodes (from top to bottom) 3, 5, 7, 9, 11, 13, 15, 17, and 19 so that each sample (node segment) consisted of two nodes and two internodes. Tissues from each dissected node segment were separated into (i) stem internodes, (ii) pods, and (iii) seeds to evaluate soybean seed yield, selected yield components such as individual seed weight, pod and seed numbers, and seed abortion, and seed-K concentration responses among nodes to K fertility. Branches were dissected by node with nodes counted from the top of the branch toward the main-stem node and separated into the same plant components as described for the main stem.

Each pod from each node segment was also examined and categorized by the number of filled and unfilled seed cavities (one-, two-, three-, or four-cavity pods) to calculate the total percentage of seed abortion from the 2013 study (Parvej et al., 2015). The distribution of the total percentage of seed abortion among node segments [(total number of unfilled cavities $node^{-1}$ segment/total number of cavities plant) × 100] was also evaluated. The seeds were counted and weighed from each node segment after discarding the aborted and/or malformed seeds. For evaluating seed-K concentration at different main-stem and branch node segments, a subsample of three whole seeds from each main-stem and branch node segment was weighed, digested (Jones and Case, 1990), and analyzed by inductively coupled plasma atomic emission spectroscopy (ICP–AES). For the determinate cultivar, some lower main-stem node segments did not contain any seed, but did contain a branch. The seed-K concentration for main-stem node segments that produced no pods was replaced by the seed-K concentration of the branch node segment closest to the main-stem node segment.

### Statistical Analysis

Data for the determinate and indeterminate cultivars were analyzed separately because of their different growth habits (e.g., branches vs. no branches). Replicate data of each variable was regressed across node segments using a statistical model (MIXED procedure of SAS v9.4, SAS Inst., Cary, NC) that included the linear, quadratic, and cubic node segment terms and their interaction with K fertility level as fixed effects. Block and year were included as random effects. The model was refined for each variable by eliminating the most complex nonsignificant ($P > 0.10$) model term in a stepwise fashion until the simplest model with all significant model terms was obtained. The studentized residuals distribution was examined for possible outliers (studentized residual > ±2.5) and the model was refit by omitting the outliers when appropriate. When a significant $F$ test was obtained for any variable, the means were separated by LSMEANS and DIFF statements at each node segment at the 0.05 probability level.

## RESULTS AND DISCUSSION

### Potassium Deficiency Symptom

Chlorosis along the margins of lower soybean leaves was observed on only a few plants shortly before the R1 (flowering) stage for both the indeterminate and determinate cultivars grown in soil having low K fertility. The leaf-K deficiency symptoms within the low K fertility treatments became more common on the upper leaves as the season progressed. During the seed-filling period (R5–7), the yellowing of leaf margins was observed on the upper leaves of soybean plants grown in every low K fertility plot, and the visual symptoms were more severe for the early-maturing indeterminate growth habit than the late-maturing determinate growth habit. Although we could not find any information for soybean, Halevy (1976) found more frequent K deficiency symptoms on an early-maturing cotton cultivar than on a late-maturing cultivar. No K deficiency symptoms were visible at any time during the growing season on soybean grown in the medium and high K fertility soil in either year.

### Soybean Seed Yield

We previously reported that seed yield plant$^{-1}$ was 40 to 60% greater for soybean grown with medium and high K fertility levels, respectively, compared to the seed yield plant$^{-1}$ of soybean grown with low K fertility (Parvej et al., 2015). The primary research objective reported in this paper was to determine how K availability influenced the yield at each node segment. Regression analysis showed that soybean seed yields were different among node segments and were significantly affected by K fertility level for both the indeterminate and determinate cultivars (Table 1; Fig. 1a, 1b). For the indeterminate cultivar, seed yield was a cubic function of node segment that differed among K fertility levels. Seed yield on the top seven node segments (1–7) was affected by K fertility level where soybean grown with medium and high K fertility produced, on average, 28 and 43%, respectively, greater predicted seed yield than soybean grown with low K fertility (Fig. 1a). The predicted seed yield on node segments 1 through 5 averaged 13% greater in the high K fertility compared to soybean grown with medium K fertility. Regardless of K fertility level, the largest proportion (55–60%) of the seed yield was produced on the middle four node segments (4–7) where seed yield was increased, on average, 18 to 27% by the medium and high K fertility levels.

For the determinate cultivar, seed yield was a cubic function of main-stem node segment that differed among K fertility levels (Table 1). The predicted soybean seed yield was different among

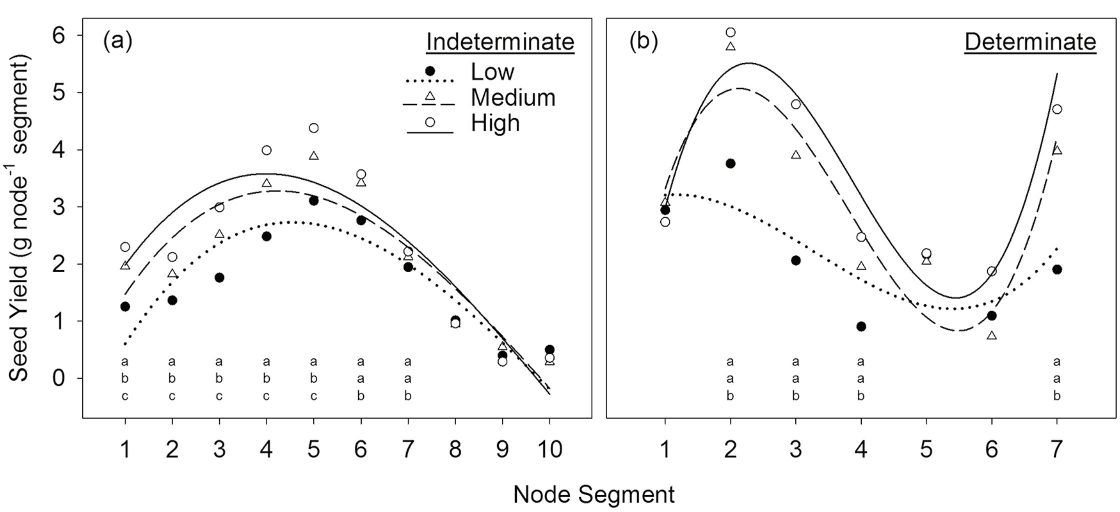


Fig. 1. Seed yield across node segments of an (a) indeterminate and (b) determinate soybean cultivar as affected by K fertility level and predicted with a polynomial model for research conducted at the Pine Tree Research Station in 2012 and 2013. Node segment '1' is the top two consecutive nodes and '7' (determinate) or '10' (indeterminate) is the bottom two consecutive nodes. Different letters within the same node segment represent significant predicted seed yield differences among K fertility levels at the 0.05 probability level. Top letter for each node segment represents the top trend line. Predicted seed yield was not significant among K fertility levels at the 0.05 probability level (a) on node segments 8, 9, and 10 for the indeterminate cultivar and (b) on node segments 1, 5, and 6 for the determinate cultivar. Coefficient values are listed in Table 1.

Table 1. Coefficients of polynomial models used for predicting seed yield, individual seed weight, seed and pod numbers, seed abortion, and seed-K concentration among main-stem node segments of indeterminate and determinate soybean cultivars from research conducted at the Pine Tree Research Station in 2012 and 2013.

| | Polynomial model‡ coefficients | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Indeterminate | | | | | Determinate | | | | |
| K fertility level† | Intercept | Linear | Quadratic | Cubic | $R^2$ | Intercept | Linear | Quadratic | Cubic | $R^2$ |
| | | | | | Seed yield, g node$^{-1}$ segment | | | | | |
| Low | –0.937 | 1.7807 | –0.2505 | 0.0080 | 0.64 | 2.697§ | 0.9725§ | –0.5118§ | 0.0520§ | 0.48 |
| Medium | 0.031§ | 1.6851 | –0.2505 | 0.0080 | | –2.203§ | 7.8609 | –2.5653 | 0.2248 | |
| High | 0.606§ | 1.6177 | –0.2505 | 0.0080 | | –3.878 | 9.5913 | –2.9875 | 0.2579 | |
| SE¶ | 0.325 | 0.2319 | 0.0497 | 0.0031 | | 1.414 | 1.4073 | 0.4062 | 0.0347 | |
| | | | | | Individual seed weight, g seed$^{-1}$ | | | | | |
| Low | 0.083 | 0.0194 | –0.0027 | 0.00013 | 0.33 | 0.143 | –0.0235 | 0.0051 | –0.00029§ | 0.40 |
| Medium | 0.107 | 0.0160 | –0.0027 | 0.00013 | | 0.164 | –0.0254 | 0.0051 | –0.00029§ | |
| High | 0.117 | 0.0141 | –0.0027 | 0.00013 | | 0.172 | –0.0269 | 0.0051 | –0.00029§ | |
| SE | 0.006 | 0.0031 | 0.0007 | 0.00004 | | 0.007 | 0.0069 | 0.0020 | 0.00017 | |
| | | | | | Seed number, seeds node$^{-1}$ segment | | | | | |
| Low | –2.857§ | 11.4539 | –1.5242 | 0.0382§ | 0.65 | 18.974§ | 11.2350§ | –4.9111§ | 0.4689§ | 0.48 |
| Medium | 2.825§ | 10.9176 | –1.5242 | 0.0382§ | | –20.790§ | 63.1974 | –20.1629 | 1.7424 | |
| High | 6.722 | 10.4996 | –1.5242 | 0.0382§ | | –36.513 | 78.5162 | –24.1804 | 2.0899 | |
| SE | 2.326 | 1.5667 | 0.3290 | 0.0203 | | 10.637 | 10.6559 | 3.0532 | 0.2585 | |
| | | | | | Pod number, pods node$^{-1}$ segment | | | | | |
| Low | 0.008§ | 4.3430 | –0.5865 | 0.0145§ | 0.65 | 9.654§ | 7.4932§ | –3.1321§ | 0.2963 | 0.51 |
| Medium | 1.440§ | 4.2036 | –0.5865 | 0.0145§ | | –12.149 | 35.4082 | –11.2446 | 0.9683 | |
| High | 3.162 | 4.0138 | –0.5865 | 0.0145§ | | –19.900 | 42.5146 | –13.0351 | 1.1209 | |
| SE | 0.912 | 0.6214 | 0.1306 | 0.0081 | | 5.548 | 5.6766 | 1.6361 | 0.1358 | |
| | | | | | Seed abortion, % | | | | | |
| Low | 0.374§ | 1.1196 | –0.1305 | ns# | 0.54 | –4.746 | 9.0247 | –2.7349 | 0.2281 | 0.68 |
| Medium | 0.477§ | 0.5697 | –0.0660 | ns | | –2.044§ | 3.7224 | –1.0416 | 0.0799§ | |
| High | 0.706§ | 0.2782§ | –0.0378 | ns | | –1.017§ | 2.6393§ | –0.6931§ | 0.0479§ | |
| SE | 0.392 | 0.1831 | 0.0179 | | | 1.364 | 1.5550 | 0.4976 | 0.0470 | |
| | | | | | Seed-K concentration, g K kg$^{-1}$ | | | | | |
| Low | 10.222 | 1.4293 | –0.0676 | ns | 0.68 | 13.579 | 1.8261 | –0.1742 | ns | 0.57 |
| Medium | 16.605 | 0.7295 | –0.0402 | ns | | 18.516 | 0.5609§ | –0.0514§ | ns | |
| High | 19.869 | 0.0200§ | 0.0213§ | ns | | 20.348 | 0.1606§ | 0.0065§ | ns | |
| SE | 1.448 | 0.1941 | 0.0179 | | | 1.298 | 0.3338 | 0.0436 | | |

† The terms low, medium, and high K fertility represent the cumulative soil-K availability to plants by annual-K fertilization of 0, 75, and 150 kg K ha$^{-1}$ yr$^{-1}$, respectively and soil-test K index.

‡ Quadratic model equation, $y = z + ax + bx^2$ and cubic model equation, $y = z + ax + bx^2 + cx^3$; where $y$, independent variable; $x$, main-stem node segment; $z$, intercept; $a$, linear coefficient; $b$, quadratic coefficient; and $c$, cubic coefficient.

§ Coefficients are not significantly different from zero at the 0.05 probability level.

¶ SE, Standard error of the model coefficients.

# Cubic coefficients are not significant at the 0.10 probability level.

Table 2. Coefficients of the polynomial models used for predicting branch seed yield and seed-K concentration across branch node segments of a determinate soybean cultivar from research conducted at the Pine Tree Research Station in 2012 and 2013.

| K fertility level† | Polynomial model‡ coefficients: Intercept | Linear | Quadratic | $R^2$ |
|---|---|---|---|---|
| | | Branch seed yield, g node$^{-1}$ segment | | |
| Low | 0.368§ | 0.0286§ | –0.0131§ | 0.18 |
| Medium | 0.180§ | 0.3276 | –0.0551 | |
| High | –0.063§ | 0.4977 | –0.0739 | |
| SE¶ | 0.254 | 0.1363 | 0.0207 | |
| | | Branch seed-K concentration, g K kg$^{-1}$ | | |
| Low | 16.418 | 0.2099 | ns# | 0.58 |
| Medium | 19.164 | 0.2099 | ns | |
| High | 20.624 | 0.2099 | ns | |
| SE | 0.373 | 0.0901 | | |

† The terms low, medium, and high K fertility represent the cumulative soil-K availability to plants by annual-K fertilization of 0, 75, and 150 kg K ha$^{-1}$ yr$^{-1}$, respectively and soil-test K index.

‡ Quadratic model equation, $y = z + ax + bx^2$; where $y$, independent variable; $x$, branch node segment; $z$, intercept; $a$, linear coefficient; and $b$, quadratic coefficient.

§ Coefficients are not significantly different from zero at the 0.05 probability level.

¶ SE, Standard error of the model coefficients.

# Quadratic coefficients are not significant at the 0.10 probability level.

K fertility levels on node segments 2, 3, 4, and 7 (bottommost) on which plants grown with medium and high K fertility produced similar yields that were, on average, 72 and 101%, respectively, greater than the seed yield produced by soybean grown with low K fertility (Fig. 1b). Regardless of K fertility level, the greatest proportion (51–63%) of seed yield came from node segments 2, 3, and 7 (bottom) where seed yield averaged 77 to 104% greater for soybean grown with medium and high K fertility than low K fertility.

The determinate soybean cultivar produced branches from the bottom two main-stem node segments with each branch having five to six nodes. Branches contributed 25 to 32% of the total seed yield. The seed yield of branches showed a quadratic relationship across node segments that differed among K fertility levels (Table 2). The predicted branch seed yield averaged 99 and 133% greater on the middle portion of the branches (node segments 2 through 5) for soybean grown with medium and high K fertility, respectively, compared to soybean grown with low K fertility (Fig. 2a). There was no difference in predicted seed yield between the medium and high K fertility treatments for the same node segment across branch node segments.

The distribution of soybean seed yield across node segments of both the indeterminate and determinate cultivars was similar to the seed yield distribution across nodes reported by Carlson et al. (1982), Herbert and Litchfield (1982), Scott et al. (1983), Ramseur et al. (1984), and Sadler et al. (1991). We could find no other research showing soybean seed yield variation among nodes due to K fertilization in the literature, but our results agree with other research showing the effects of stand density, row spacing, and irrigation on seed yield across nodes. For example, seed yield of an indeterminate soybean cultivar varied by 24 to 31% on the lower-middle nodes and 13 to 38% on the middle to upper nodes due to

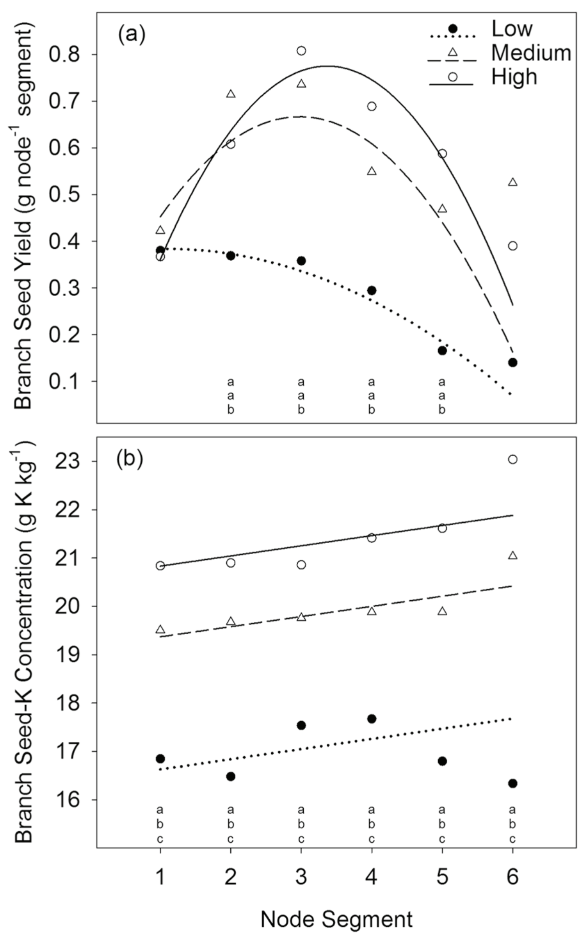


Fig. 2. (a) Seed yield and (b) seed-K concentration across branch node segments of a determinate soybean cultivar as affected by K fertility level and predicted with a polynomial model for research conducted at the Pine Tree Research Station in 2012 and 2013. Variables were measured from branches produced from the fifth (2013) and seventh (2012) main-stem node segments. Branch node segment '1' is the topmost node and '6' is the bottommost node close to the main-stem node segment. Different letters within the same node segment represent significant predicted seed yield and seed-K concentration differences among K fertility levels at the 0.05 probability level. Top letter for each node segment represents the top trend line. Predicted seed yield (a) was not significant among K fertility levels at the 0.05 probability level on branch node segments 1 and 6. Coefficient values are listed in Table 2.

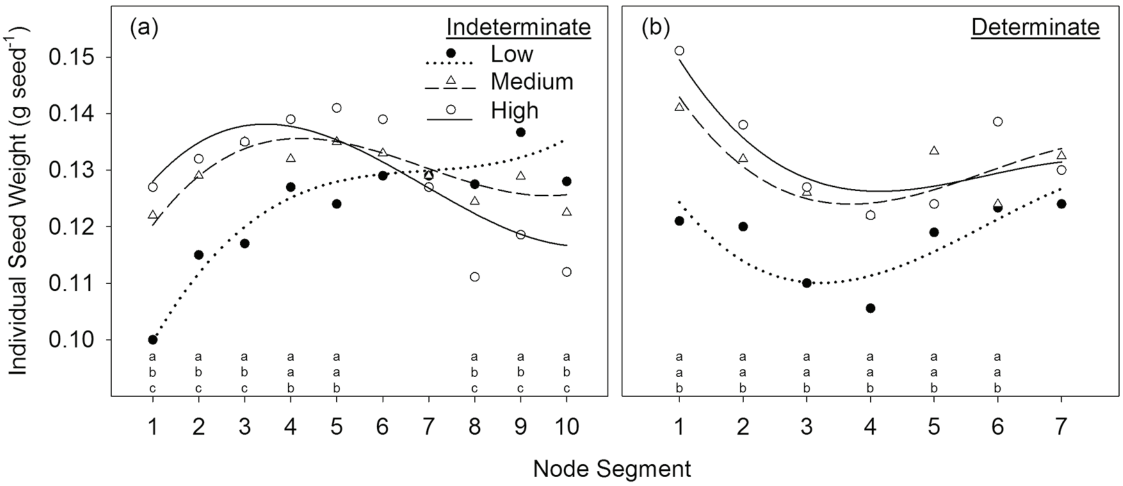


Fig. 3. Individual seed weight across node segments of an (a) indeterminate and (b) determinate soybean cultivar as affected by K fertility level and predicted with a polynomial model for research conducted at the Pine Tree Research Station in 2012 and 2013. Node segment '1' is the top two consecutive nodes and '7' (determinate) or '10' (indeterminate) is the bottom two consecutive nodes. Different letters within the same node segment represent significant predicted individual seed weight differences among K fertility levels at the 0.05 probability level. Top letter for each node segment represents the top trend line. Predicted individual seed weight was not significant among K fertility levels at the 0.05 probability level (a) on node segments 6 and 7 for the indeterminate cultivar and (b) on node segment 7 for the determinate cultivar. Coefficient values are listed in Table 1.

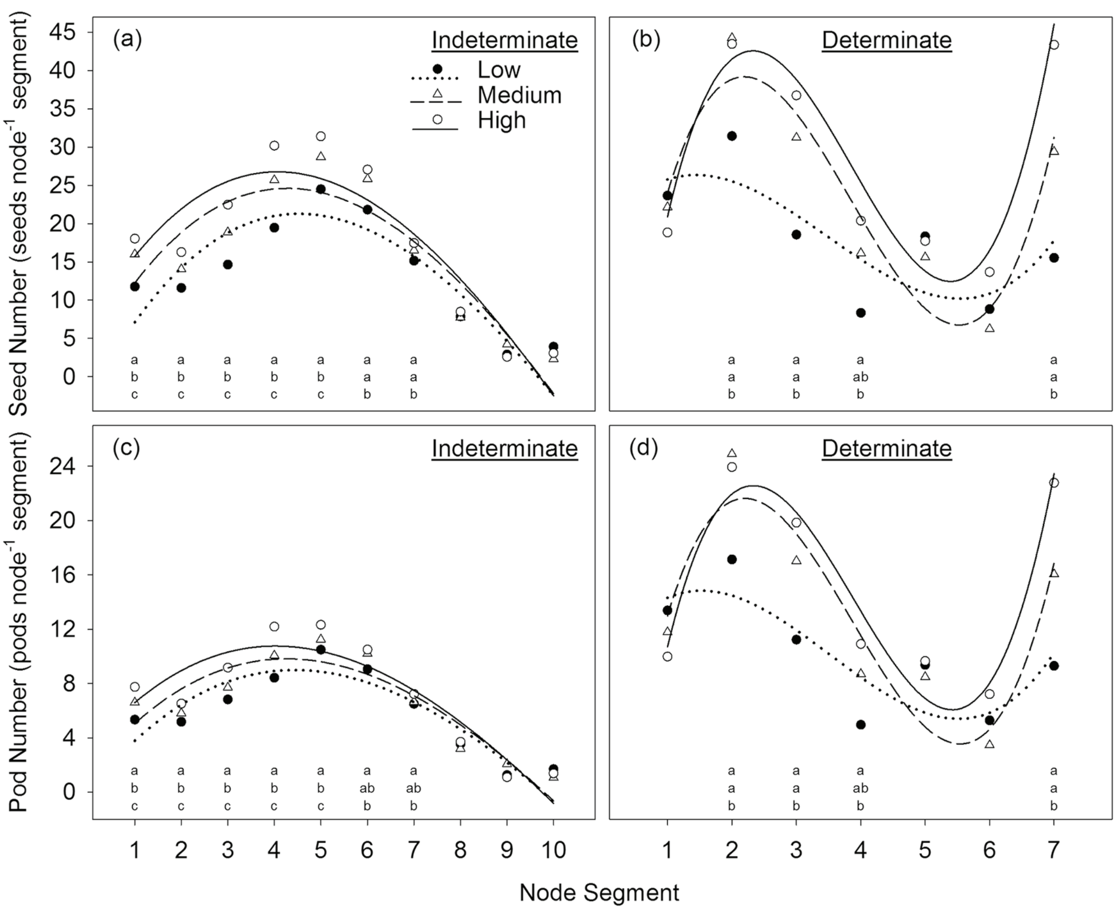


Fig. 4. (a–b) Seed and (c–d) pod numbers across node segments of an indeterminate and determinate soybean cultivar as affected by K fertility level and predicted with a polynomial model for research conducted at the Pine Tree Research Station in 2012 and 2013. Node segment '1' is the top two consecutive nodes and '7' (determinate) or '10' (indeterminate) is the bottom two consecutive nodes. Different letters within the same node segment represent significant predicted seed and pod number differences among K fertility levels at the 0.05 probability level. Top letter for each node segment represents the top trend line. Predicted seed and pod numbers were not significant among K fertility levels at the 0.05 probability level (a, c) on node segments 8, 9, and 10 for the indeterminate cultivar and (b, d) on node segments 1, 5, and 6 for the determinate cultivar. Coefficient values are listed in Table 1.

differences in plant density and row spacing (Weil and Ohlrogge, 1976; Herbert and Litchfield, 1982) and 24 to 36% on the lower-middle to upper-middle nodes due to soil-moisture stress (Carlson et al., 1982). Ramseur et al. (1984) reported that the overall seed yield of a determinate cultivar was increased 170 to 199% by irrigation, but the largest difference in seed yield (228–344%) occurred on the upper nodes. The literature coupled with our findings indicate that the largest proportion of seed yield plant$^{-1}$ comes from the middle and upper-middle nodes of the indeterminate plants and the combination of the bottom node, due to branching, plus the nodes on the top one-half of the determinate plants. Nodes that produce the greatest proportion of seed yield are also the nodes most affected by stress resulting from nutrient deficiencies, drought, and perhaps other stresses.

## Individual Seed Weight

Individual seed weight was a cubic function of node segment, which depended on K fertility level for both the indeterminate and determinate cultivars (Table 1; Fig. 3a, 3b). The indeterminate soybean cultivar grown with medium and high K fertility had, on average, 12 and 15%, respectively, greater predicted individual seed weights on the top five node segments and 5 and 10% lower individual seed weights on the bottom three node segments compared to plants with low K control (Fig. 3a). The predicted individual seed weight averaged 4% greater on the top three node segments and 5% lower on the bottom three node segments under high K fertility than medium K fertility. Individual seed weights were similar among K fertility levels for node segments 6 and 7.

The determinate soybean cultivar grown with medium and high K fertility had similar predicted individual seed weights on the top six node segments that averaged 12 and 14%, respectively, greater than the seed weight of soybean grown with low K fertility (Fig. 3b). Regardless of growth habit, the individual seed weight of soybean is known to vary among nodes, differ among cultivars, and be affected by crop management and stress conditions (Weil and Ohlrogge, 1976; Carlson et al., 1982; Ramseur et al., 1984). Nelson et al. (1946) and Sale and Campbell (1987) reported individual seed weight reduction by K deficiency, but their research lacks in showing how the individual seed weight reduction is distributed among nodes.

## Seed and Pod Numbers

Soybean seed and pod numbers were cubic function of node segment for both the indeterminate and determinate cultivars, respectively (Table 1; Fig. 4a–4d). On the top five node segments of the indeterminate cultivar, the predicted seed number increased, on average, 13% as fertility level increased from medium to high fertility and 25% as fertility increased from low to medium fertility (Fig. 4a) and pod number increased by 14% with each increase in K fertility level (Fig. 4c). On node segments 6 and 7, the number of seeds was statistically similar for plants grown with medium and high K fertility, but averaged 13 and 19%, respectively greater than plants grown with low K fertility (Fig. 4a). The number of pods on node segments 6 and 7 averaged 14% greater for plants grown with high K compared to low K fertility (Fig. 4c). Like soybean seed yield, the largest proportion (54–59%) of predicted seed and pod numbers came from the middle four node segments (4–7) of the indeterminate plants where seed and pod numbers were increased, on average, 14 to 22% and 8 to 17%, respectively, due to medium and high K fertilization.

For the determinate cultivar, the predicted seed and pod numbers were influenced by K fertility on node segments 2 through 4 and 7 (the bottommost node segments; Fig. 4b, 4d). The greatest percentage (51–63%) of seeds and pods were produced on node segments 2, 3, and 7 where plants grown with medium and high K fertility had statistically similar values that averaged 62 and 91%, respectively, more seeds and 56 and 80% more pods than soybean grown with low K fertility. On node segment 4, plants grown with high K fertility produced 59% more seeds and 57% more pods than soybean having low K fertility.

The literature clearly shows that the numbers of seeds and pods vary among nodes, are affected by a number of factors, and the trends across nodes are different for cultivars having indeterminate and determinate growth habits. For soybean with an indeterminate growth habit, Carlson et al. (1982) showed that the major differences exhibited between irrigated and non-irrigated plants occurred on nodes located on the middle to the upper-middle portion of the plant. For the determinate soybean, Ramseur et al. (1984) showed irrigation resulted in seed and pod number differences on the upper one-half of the main-stem nodes as well as on the lower nodes only when seeds and pods of lower main-stem nodes and branch nodes were combined. Regardless of soybean growth habit, K fertilization, irrigation, and perhaps other factors influence seed and pod numbers on those node locations where the largest number of seeds and pods are produced and seed yield differences occurred. Our research did not address the dynamics of fewer seeds and pods plant$^{-1}$ to know whether flowers or pods were aborted at a higher rate or never formed. Such information would be useful in developing effective strategies for managing in-season K deficiency (e.g., how K fertilizer timing influences yield).

## Seed Abortion

The percentage of seed abortion was a quadratic function of node segment for the indeterminate cultivar and a cubic function of node segment for the determinate cultivar and, like most other variables, seed abortion was affected by K fertility level (Table 1; Fig. 5a, 5b). Significant differences in predicted seed abortion among K fertility levels occurred at node segments 2 to 7 of the indeterminate cultivar (Fig. 5a) and node segments 1 to 4 of the determinate cultivar (Fig. 5b). Nodes that experienced the greatest abortion rate (nodes 2 and 3 for the determinate and nodes 4, 5, and 6 for the indeterminate cultivar) were also the greatest yielding node segments (Fig. 1) suggesting the competition for K and other nutrients among developing seed is likely to occur where the demand is greatest. There were no differences in abortion (Fig. 5) or yield (Fig. 1) on the lowest nodes of each cultivar (e.g., growth habit) perhaps because the nodes are located on the lowest part of the stem where they receive preferential access to K. We did not find any research that has investigated the effect of K deficiency or any other stress on soybean flower, pod, or seed abortion across nodes. Research has demonstrated that soybean flower, pod, or seed abortion increases due to stress resulting from K deficiency (Nelson et al., 1946), drought (Westgate and Peterson, 1993), and increased plant density (Weil and Ohlrogge, 1976).

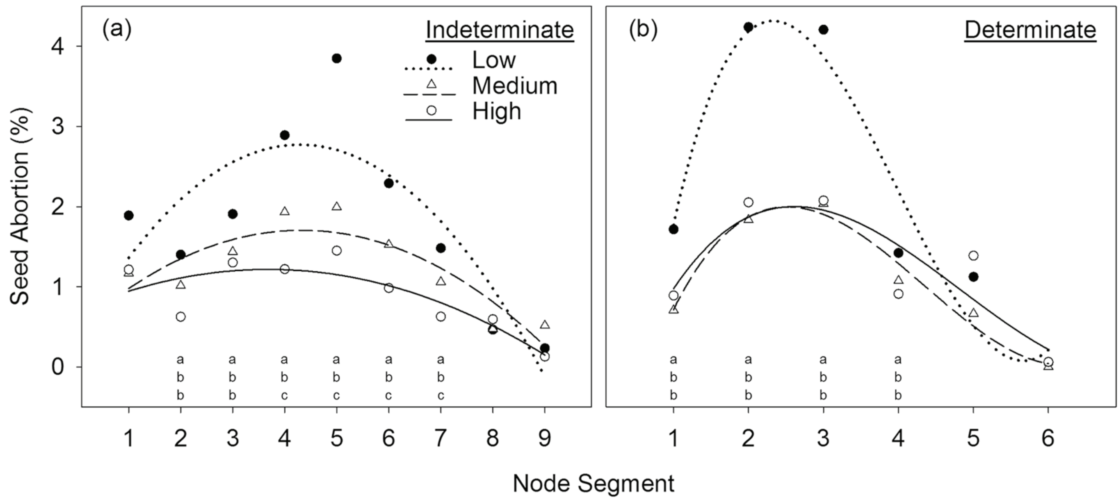


Fig. 5. Seed abortion across node segments of an (a) indeterminate and (b) determinate soybean cultivar as affected by K fertility level and predicted with a polynomial model for research conducted at the Pine Tree Research Station in 2013. Node segment '1' is the top two consecutive nodes and '6' (determinate) or '9' (indeterminate) is the bottom two consecutive nodes. Different letters within the same node segment represent significant predicted seed abortion differences among K fertility levels at the 0.05 probability level. Top letter for each node segment represents the top trend line. Predicted seed abortion was not significant among K fertility levels at the 0.05 probability level (a) on node segments 1, 8, and 9 for the indeterminate cultivar and (b) on node segments 5 and 6 for the determinate cultivar. Coefficient values are listed in Table 1.

## Seed Potassium Concentration

Soybean seed-K concentrations for each cultivar (growth habit) was a quadratic function of node segment that depended on K fertility level (Table 1; Fig. 6a, 6b). Regardless of soybean growth habit, seed-K concentration increased with each increase in K fertility level, and the predicted seed-K concentration at each node segment was different among K fertility levels. Seed-K concentrations increased quadratically from the top to the bottom nodes of the plant for the determinate soybean grown with low K fertility and for the indeterminate soybean grown with low and medium K fertility. The linear and quadratic slope coefficients for seed-K concentrations of the indeterminate soybean grown with high K fertility and determinate soybean grown with medium and high K fertility were not different from zero indicating that seed-K concentration was uniform among node segments with mean concentrations (intercept values) of 18.5 to 20.4 g K $kg^{-1}$ (Table 1). For soybean grown with low K fertility, the predicted seed-K concentrations from the top to bottom node segments ranged from 11.6 to 17.8 g K $kg^{-1}$ for the indeterminate cultivar (Fig. 6a) and 15.2 to 17.8 g K $kg^{-1}$ for the determinate cultivar (Fig. 6b). Although the two soybean growth habits were not statistically compared, the numerical values suggest that seed-K concentration is more variable in the indeterminate cultivar. The results for each growth habit clearly indicate the seed-K concentrations among nodes are more variable when K availability is limiting.

Seed-K concentrations of the branches of the determinate soybean also increased linearly for each K fertility level from the top to bottom branch node segments (Table 2; Fig. 2b). Regardless of K fertility level, seed-K concentration increased at the same linear rate (0.210 g K $kg^{-1}$ $node^{-1}$ segment) from the top (branch node

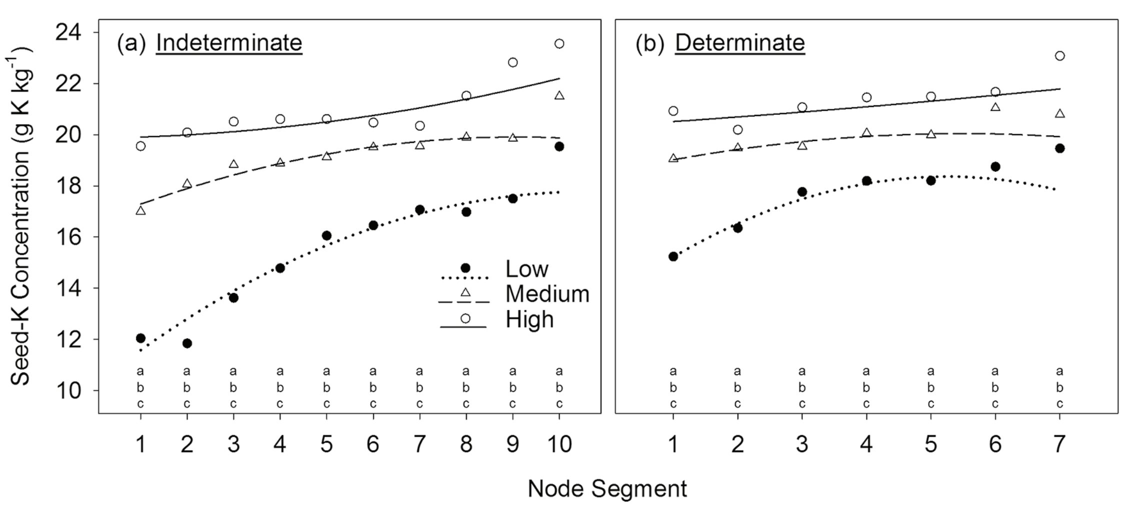


Fig. 6. Seed-K concentration across node segments of an (a) indeterminate and (b) determinate soybean cultivar as affected by K fertility level and predicted with a polynomial model for research conducted at the Pine Tree Research Station in 2012 and 2013. Node segment '1' is the top two consecutive nodes and '7' (determinate) or '10' (indeterminate) is the bottom two consecutive nodes. Different letters within the same node segment represent significant predicted seed-K concentration differences among K fertility levels at the 0.05 probability level. Top letter for each node segment represents the top trend line. Coefficient values are listed in Table 1.

1) to the bottom (branch node 6) of the branch but the intercept values increased with each increase in K fertility level.

The decline of seed-K concentration from the bottom toward the top of the main-stem or branch node segment agree with the findings of Hanway and Weber (1971; indeterminate soybean) and Sadler et al. (1991; determinate soybean). Our results support these findings and indicate that the range of seed-K concentrations on soybean plants can be decreased or eliminated by increasing K availability. Results from the literature and the low and medium K fertility levels in our research indicate that soybean seeds produced on the lower nodes receive K preferentially over seed produced on the middle and upper nodes of main-stems and branches. Foliar feeding of K during the pod set and fill stages may be useful in minimizing seed-K concentration differences from the top to bottom of the plant, but the amount of K needed to equalize seed-K concentrations among nodes may be impractical to apply to plant leaves, especially if the yield response to foliar K is minimal or if ample pre-plant-applied K can maximize yield (Nelson et al., 2005). Aside from providing ample K to prevent K deficiency and maximize yield, other benefits of minimizing seed-K concentrations differences among nodes are currently unknown and warrants further research. Seed-K concentrations have been shown to be positively correlated with seed oil ($r = 0.48–0.64$) and total isoflavone concentrations ($r = 0.57–0.76$) and negatively correlated with seed protein concentration ($r = 0.67–0.78$; Vyn et al., 2002; Yin and Vyn, 2003).

The rapid decline of seed-K concentration toward the upper canopy under low K fertility helps explain why K deficiency symptoms commonly appear on the middle and upper canopy during reproductive growth. The developing seed is a strong sink for K and other nutrients. For example, Vasilas et al. (1980) showed that mature soybean seeds contained about 94% of the $^{15}N$ applied at the R5 to R7 growth stages. Several researchers have noted that during reproductive growth, N and K concentrations decrease from all soybean plant parts except the seed (Hanway and Weber, 1971; Barber, 1978; Batchelor et al., 1984; Sallam et al., 1985), suggesting active accumulation, mobilization of K from vegetative structures, or both to soybean seed, the dominant sink. Hanway and Weber (1971) showed that late in the growing season, soybean leaf-K concentration declined more from nodes located on the top one-third of the stem than from nodes located on the middle and lower one-third of the stem for an indeterminate soybean. A similar observation was made by Drossopoulos et al. (1994), who noted that K mobilizes mainly from the middle and upper leaves rather than the lower leaves to the reproductive sinks. Ohlrogge (1960) and Jeffers et al. (1982) hypothesized that the rate of K translocation from the lower, older leaves to the upper leaves may be impaired or may not be sufficiently rapid to meet the high K demand during the seed-filling period (R5–7). Soybean uptake of K from the soil is most rapid during reproductive growth and peaks at the R6 growth stage (Bender et al., 2015). The large seed-K concentration range among nodes is likely from the combination of active K uptake and transport to the strongest sinks plus mobilization of K from vegetative plant structures to the developing seeds. Egli and Leggett (1973) showed that the flowering to pod set period (R1–4) of an indeterminate MG IV soybean cultivar was 6 to 8 d longer than that of a determinate cultivar having the same MG rating. The early initiation of pod and seed set of indeterminate cultivars from the lowest nodes may give the seed on the lower nodes a competitive advantage for K and other nutrients in the early season, but be a disadvantage for seed set on the middle and upper nodes later in the growing season, especially when K is limited.

## CONCLUSIONS

Our primary research goal was to determine how K deficiency influences the distribution of seed yield among nodes of determinate and indeterminate soybean cultivars. The greatest proportion of soybean yield, regardless of K fertility level, was produced by nodes on the top two-thirds of the indeterminate cultivar and the combination of the bottom node, due to branching, plus the nodes on the top one-half of the determinate cultivar. The yield loss from K deficiency was greatest on the nodes that produced the largest proportion of seed yield for each growth habit. Previous research has shown this for other plant stresses (e.g., drought), but our research is the first to show the node positions where yield loss from K deficiency occurs. Thus, our results were consistent with our first prediction that K deficiency would affect yield components to a greater extent in the middle to upper portion of an indeterminate cultivar and the lower and upper portions of a determinate cultivar. The yield loss on the top nodes was from reduced individual seed weight, fewer number of pods and seeds, and increased seed abortion.

Our results were also consistent with our second prediction that for K-deficient soybean there would be a large seed-K concentration gradient from the top to bottom of the plant with seed-K being greatest for seed produced on the bottom nodes and least for seed produced by the top nodes. The K concentration of seed collected from the upper nodes or the seed-K concentration gradient between the top and bottom nodes might be useful in diagnosing K deficiency at maturity in fields that showed no visible K deficiency symptoms (i.e., hidden hunger) or K deficiency symptoms were not observed because the field was not scouted thoroughly during the season. Maintaining moderate to high K fertility in soil minimizes the seed-K gradient among nodes and increases seed-K concentration. Maintaining high soil K fertility may minimize the seed-K gradient but it may also lead to seed-K accumulation and greater crop K removal without a corresponding yield increase.


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