Tiller Initiation and its Effects on Yield and Yield Components in Winter Wheat

M. Scott Tilley,* Ronnie W. Heiniger, and Carl R. Crozier

ABSTRACT
Vegetative growth in the form of tillers is crucial to final yield in winter wheat (Triticum aestivum L.). To understand the impact management practices have on tiller initiation, a study was conducted using two seeding rates (1.9 × 10^6 vs. 6.8 × 10^6 ha⁻¹) and two N timing applications (single vs. split). Tillers initiated in the fall made up the majority of spikes compared to tillers initiated from 1 January to the start of jointing (GS 30). Tillers initiated in March at either seeding rate produced very few kernels spike⁻¹, low kernel weight, and contributed little to yield. At the high seeding rate, tillers initiated prior to 1 January were responsible for more than 87% of the grain yield. Tillers produced in January–February produced 5 to 11% of the final yield, while tillers produced in March contributed less than 2%. In contrast, at the low seeding rate tillers produced in January–February made up 80 to almost 60% of the final yield. Overall, this study shows the timing of N (single vs. split) application influences tiller size and mortality (Tilley et al., 2015). The timing of tiller initiation and management factors such as planting date (Oakes et al., 2016) that promote leaf development could also influence other yield components such as kernels spike⁻¹ and kernel weight. An understanding of when the most spikes are formed and the management factors that promote tiller formation during this critical period would help growers improve wheat yield.

Tillers can be formed at multiple nodes on the MS, and secondary and tertiary tillers can form from nodes on the tillers themselves (Klepper et al., 1982; Evers and Vos, 2013). Under glasshouse conditions Klepper et al. (1982) found that once a tiller is initiated, leaf development on the tiller proceeded at the same rate as leaf development on the MS. However, subsequent research has found that leaf development on each tiller proceeds at a slower rate than that on the MS or even on preceding tillers (Tilley et al., 2015). This indicates that tillers initiated first will always have an advantage in growth and development compared to those initiated later. This advantage will increase as time passes resulting in more leaf area. It is likely that tillers with more leaf area will produce more kernels, heavier kernels, and will be less likely to be lost to tiller mortality.

Timing of tiller initiation can also influence tiller mortality. Charles-Edwards (1984) concluded that self-thinning within plant communities is largely due to the lack of assimilate needed to continue growth and development within the individual stem which, in turn, can lead to a decrease in plant weight and eventually a decrease in plant yield. Some works have explored the purpose of tiller mortality and the effects it may have on

Core Ideas
• A marking technique was used to monitor leaf and tiller development.
• The earlier a tiller is formed the more kernels it produces.
• Seeding rate influences tiller initiation and productivity.

Published in Agron. J. 111:1–10 (2019)
doi:10.2134/agronj2018.07.0469

Copyright © 2019 by the American Society of Agronomy
5585 Guilford Road, Madison, WI 53711 USA
This is an open access article distributed under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/)


Abbreviations: BC, Beaufort County; HSR, high seeding rate; LSR, low seeding rate; MS, Mainstem; NC, North Carolina; PI, phyllochron interval; PRS, Piedmont Research Station; TRS, Tidewater Research Station.
the plant as a whole and concluded tillers that abort may have benefited the plant due to assimilate and nutrient accumulation (Lupton and Pinthus, 1969; Palfi and Dezsi, 1960). However, Langer and Dougherty (1976) concluded that dead tillers had a negative effect on grain yield due to competition for assimilates and nutrients (Sharma, 1995).

Management practices such seeding rate and N application timing can influence the timing and rate of leaf and tiller development (Bauer et al., 1984; Tilley et al., 2015) and grain yield. Tompkins et al. (1991) concluded that grain yields will decline as seeding rates decline. This in part is due to a decrease in spikes. However, it was determined that grain yield can decrease at high seeding rate (HSR) (Gooding et al., 2002) due to a decrease in kernels spike−1 and a decrease in kernel weight (Puckridge and Donald, 1967; Tompkins et al., 1991). Tilley et al. (2015) found that seeding rates influenced the rate of leaf development. Phylochon intervals (PI) were shorter for each tiller at a low seed rate (LSR) compared to the same tillers at a HSR. This resulted in more leaves on each tiller, more tillers produced and fewer tillers lost to tiller mortality.

Nitrogen is recognized as a vital nutrient needed for growth and development (Miller, 1939; Wilhelm et al., 2002). Nitrogen application timing recommendations for winter wheat in North Carolina (NC) are based on the tiller density (Weisz et al., 2001, 2011). Winter split applications are encouraged if tiller density <550 m−2. Otherwise the standard NC recommendation is to apply N at GS 30, the time when the wheat stem begins to elongate. Maidl et al. (1998) confirms that early N application increased plant density and concluded that N fertilizer treatment applied during stem elongation not only reduced tiller mortality but also led to high grain yield in both MS and tillers.

To understand the impact of the timing of tiller initiation and management practices on kernel development and yield, a method of counting and marking leaves and tillers was created to monitor tiller growth and decline. This monitoring of individual tillers resulted in the ability to measure the number of heads, kernel number and kernel weight each tiller produced, and its contribution to final yield. The objectives of this study were to: (i) measure yield and yield components of tillers initiated at different periods during the growth of wheat and how tillers initiated at different periods contribute to overall grain yield, and (ii) determine the impact of seeding rate and timing of N applications on the productivity and sustainability of tillers initiated at different periods during the growth cycle of wheat.

**MATERIALS AND METHODS**

**Field Experiment**

Field experiments were conducted at two sites in eastern NC and one site in western NC. At the Tidewater Research Station (TRS) in Plymouth, NC, experiments were conducted in 2009, 2010, and 2011. On a private farm in Beaufort County (BC) experiments were conducted in 2009 and 2010. On the third site in western NC (Piedmont Research Station [PRS] in Salisbury, NC) a single trial was conducted in 2011. The soil at TRS was a Cape Fear loam (clayey, mixed, thermic Typic Umbraqual) soil. At the BC site in 2009 and 2010 the experiment was conducted on a Cape Fear fine sandy loam (clayey, mixed, thermic Typic Umbraqual). The 2011 experiment at PRS was conducted on a Mecklenburg clay loam (fine, mixed, thermic Urtic Hapludult).

In 2009, plots were planted on 3 November at TRS and 4 November in BC. In 2010, plots were planted on 10 November at TRS and 11 November in BC. In 2011, plots were planted on 10 November at TRS and 15 November at PRS.

At each site, Pioneer 26R12, a high yielding wheat variety in NC, was planted in 16.9-cm rows into a conventional tilled field following corn. The experimental design at all sites was a split plot design with main plots consisting of two seeding rates, 1.9 × 10^6 and 6.8 × 10^6 ha−1, and subplots consisting of 134 kg N ha−1 applied either as a single application in March or a split application with half applied in late January or early February and the remaining half applied by late March. In 2009–2010, the first N application was made on 15 February with the second split and single N application made on 22 March. In 2010–2011, the first N application was made on 4 February while the remaining split and single applications were completed on 18 March. During the 2011–2012 growing season at TRS, the first split application was applied on 19 January with the final split and single N applications applied on 12 March. Applications at the PRS were applied 1 wk later on 26 January and 19 March. All treatments were replicated five times.

Disease pressure was minimum across all three site years and did not reach current threshold recommendations (Weisz et al., 2011). However, weed and insect control practices were applied. In 2009–2010 at TRS, thifensulfuron-methyl/tribenuron-methyl was applied POST at 0.04 kg a.i. ha−1 on 8 Mar. 2010. The BC location received the same application on 9 Mar. 2010. In 2010–2011 at both TRS and BC, thifensulfuron-methyl/tribenuron-methyl was applied POST at 0.04 kg a.i. ha−1 on 14 Mar. 2011. In 2011–2012 at TRS, mesosulfuron-methyl was applied POST at 0.33 kg a.i. ha−1 on 6 Dec. 2011 and thifensulfuron-methyl/tribenuron-methyl applied POST at 0.05 kg a.i. ha−1 on 1 Jan. 2012. At the PRS, cloransulfuron/metsulfuron-methyl was applied PPE at 0.03 kg a.i. ha−1 on 3 Nov. 2011 and thifensulfuron-methyl/tribenuron-methyl was applied POST at 0.05 kg a.i. ha−1 on 28 Feb. 2012.

Individual plots were 24.4-m long and 1.98-m wide equaling a total of 48.31 m². Each plot was divided into three sections. The first 18.01 m² section was designated for grain yield and grain sampling. This section of the plot was harvested using a Gleaner K2 combine with a Harvestmaster Grainage (Juniper Systems, Logan, UT) that recorded moisture, grain weight, and test weight. The TRS in 2010–2011 was harvested on 20 June and on 22 June during 2011–2012. Beaufort County in 2010–2011 was harvested on 23 June and PRS was harvested on 29 June during the 2011–2012 season. Grain weight was adjusted to 15.5% moisture before calculating yield.

The second section equaling 9.12 m² was designated for marked samples. Five plants from each plot were marked and the number of full and partial leaves on each MS and tiller were recorded along with the total number of tillers at current growth stage. This was done once a month from planting to harvest. Throughout the 2009–2010 growing season, observations were made at TRS and BC on 22 December, 28 January, 1 March, 19 March, 7 April, and 26 April. During the 2010–2011 growing season, observations were made on 7 December, 31 January, 4 March, 2 April, and 30 April. During the 2011 growing season, leaf and tiller counts were recorded on 9 December, 2 January, 11 February, and 3 April at TRS and 15 December, 9 January, 24 February, and 13...
April at PRS. Each new and existing tiller was noted using either a black, silver, or red permanent marker to mark leaf number. Black markings represented tillers that were initiated from planting through the end of December. Silver markings represented early winter tillers that developed from the first of January to the beginning of March. Red markings represented late spring tillers produced from March till growth stage GS30. The three colors used to track tillers helped categorize each individual tiller and determined whether or not they initiated in the fall, winter, or spring. Furthermore, tillers were marked on each subsequent leaf to track the number of leaves produced throughout the growing season. Harvest samples were taken in 2010–2011 and 2011–2012 at TRS, BC, and PRS on the same dates that the larger plots were harvested. At harvest, each of these five plants were clipped and placed in individual bags. For each plant, the MS and tillers were separated by color markings (black, silver, red) counted and hand threshed to determine the number of spikes and grain weight spike$^{-1}$ for each tiller initiation period. The data for all five plants were averaged to represent values for each plot.

The last 21.18 m$^2$ of each plot was reserved for destructive sampling. Method for destructive sampling consisted of a 2-m stick and a garden shovel. A trench, encamping an area of 0.33 m$^2$, was carefully dug around plants to a depth of 15 cm and the plants were then excavated from the destructive sampling area. Samples were taken on 17 June 2010, at TRS and BC. On 15 and 20 June 2011, destructive samples were taken at TRS and BC. Destructive samples were taken at TRS and PRS in 3012 but were destroyed before they could be processed. Leaf counts were taken from each individual stem and recorded. Leaf numbers were determined by counting the nodes on the plant. This was done by splitting the plant at the base and finding the small (0.6–1.25 cm) gap between the compressed nodes and the first separated node. The first separated node was counted as the fifth node (fifth leaf) and subsequent nodes (leaves) were counted in ascending order. Plants were separated into classes corresponding to the periods of tiller initiation (black, silver, and red) based on leaf number and the ratio of stems found in each initiation period in the marked samples. This ratio was determined by counting the number of MS or tillers from each category (black, silver, and red) in the five marked plants described above and dividing that number by the total number of MS or tillers produced in these same plants. Using the ratio of MS or tillers that were initiated from planting to the end of December (Black), the same ratio of plants with the highest leaf numbers in the destructive sample were designated as having been initiated during this period. Plants with the next highest leaf number were considered initiated during the period from 1 January to the end of February; and plants with the fewest leaves were considered initiated after 1 March. Spikes from samples representing each initiation period were hand threshed and grain weight, kernel number and 100 kernel seed weight were measured.

Statistical Procedures

For the marked plant samples the data taken from TRS in 2010–2011 and 2011–2012 at BC in 2010–2011 and PRS in 2011–2012 were analyzed using a repeated measures design with the Proc Mixed procedure in SAS (SAS Institute, Inc., Cary, NC) to determine if there were differences in the number of spikes plant$^{-1}$ and grain weight spike$^{-1}$ among site-year, tiller initiation periods (planting to 31 December, 1 January to 28 February, and after 1 March) seeding rate, and N application timing. In all cases, site-year, seeding rate and N timing were treated as fixed effects, while blocks and the interactions with blocks were treated as random. When differences were detected, Fisher’s Protected LSD was used to separate means.

In the destructive sample plots some samples were lost in 2011–2012. Therefore, only samples taken in 2009–2010 and 2010–2011 at TRS and BC were used in the analysis. The Proc Mixed procedure in SAS (SAS Institute, Inc.) was used to determine if there were differences in spikes m$^{-2}$, kernels spike$^{-1}$, weight per 100 kernels, and grain yield among site-years, tiller initiation period, seeding rate and N application timing. As with previous analysis, site-year, seeding rate, and N timing were treated as fixed effects; while blocks and the interactions with blocks were treated as random. When differences were detected, Fisher’s Protected LSD was used to separate means.

Grain yield from the large 18.01 m$^2$ section of each plot for the 2010–2011 and 2011–2012 seasons at TRS and BC were analyzed using the Proc Mixed procedure in SAS (SAS Institute, Inc.) to determine if there were differences in grain yield among site-years, seeding rate, and N application timing. These site-years were chosen so that the grain yield from the large samples could be compared with that calculated from the small 2-m samples.

RESULTS AND DISCUSSION

Analysis of Tracked Plants

Environmental conditions among the various sites and across the three seasons of this study represent the variation in temperature and precipitation commonly found in the southeastern United States (Table 1). Results showed a three-way interaction between site-year, seeding rate, and tiller initiation period for the number of spikes produced per plant along with two-way interactions between site-year and seeding rate and tiller initiation period and seeding rate. In addition, the tiller initiation period and seeding rate main effects were significant at $p < 0.05$ (Table 2). Across the 4 site-years more spikes plant$^{-1}$ were developed in the fall period at the two sites in 2011–2012 than in the same growing period at the two sites in 2010–2011 (Fig. 1). This was an indication of the warm fall and early winter weather in 2011–2012 (Table 1). In both HSR and LSR, a greater number of harvestable spikes were generated per plant during the fall growing season compared with any of the other growing periods. In the HSR, the MS and first leaf tiller made up the majority of fall tillers, while at the LSR the MS, tiller one, and second leaf tiller made up the majority of heads. The key difference between the seeding rates was the number of spikes plant$^{-1}$ produced during the January–February growing period. In 3 of 4 site-years significantly more spikes plant$^{-1}$ were produced at the LSR during January compared to the HSR. Regardless of seeding rate, across all site-years most of the spikes were produced in the growing period from planting through the end of December with fewer spikes initiated in January–February and almost no spikes initiated in the March period. The vast majority of spikes in this study were either MS or tillers initiated in the fall. It should be noted that no January–February tillers developed at the PRS at the HSR and no March tillers developed at either PRS or TRS during the 2011–2012 season. Likewise, no March tillers developed at BC or TRS at the HSR when a split N application was made in 2010–2011.
These same trends among growing periods and seeding rates were found in the amount of grain produced per spike. There was a four-way interaction for grain weight spike$^{-1}$ among site-year, seeding rate, N application timing, and tiller initiation period (Table 2). There was a significant three-way interaction among site-year, seeding rate, and N application timing and two-way interactions between seeding rate and N application timing, tiller initiation period and seeding rate, site-year and seeding rate, and site-year and tiller initiation period. Site-year, tiller initiation period, and seeding rate main effects were also significant at $p < 0.05$. Regardless of site-year, seeding rate and N application timing, MS or tillers initiated prior to 1 Jan often had more grain weight spike$^{-1}$ (averaging 1.0–1.6 g spike$^{-1}$) than tillers initiated after 1 January (0.09–1.4 g spike$^{-1}$) (Fig. 2). The only exception to this trend occurred at the TRS location in 2010–2011 under a single N application, grain weight spike$^{-1}$ was similar between tillers produced after 1 January and those

Table 2. Analysis of variance table for marked samples for each dependent variable for all locations during the 2010–2011 and 2011–2012 growing seasons.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Number of spikes (loc)</th>
<th>Total grain weight (seedrt)</th>
<th>Grain weight per spike (loc&lt;seedrt)</th>
<th>Max. temperature (loc×seedrt)</th>
<th>Min. temperature (loc×seedrt)</th>
<th>Rainfall (loc×seedrt)</th>
<th>Max. temperature (loc×seedrt×tillinti)</th>
<th>Min. temperature (loc×seedrt×tillinti)</th>
<th>Rainfall (loc×seedrt×tillinti)</th>
<th>Max. temperature (loc×seedrt×splitN)</th>
<th>Min. temperature (loc×seedrt×splitN)</th>
<th>Rainfall (loc×seedrt×splitN)</th>
<th>Max. temperature (loc×seedrt×splitN×tillinti)</th>
<th>Min. temperature (loc×seedrt×splitN×tillinti)</th>
<th>Rainfall (loc×seedrt×splitN×tillinti)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site-year (loc)</td>
<td>3</td>
<td>ns†</td>
<td>***</td>
<td>***</td>
<td>4.0</td>
<td>5.8</td>
<td>40.3</td>
<td>4.0</td>
<td>5.8</td>
<td>40.3</td>
<td>4.0</td>
<td>5.8</td>
<td>40.3</td>
<td>4.0</td>
<td>5.8</td>
<td>40.3</td>
</tr>
<tr>
<td>Seeding rate (seedrt)</td>
<td>1</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc&lt;seedrt</td>
<td>3</td>
<td>*</td>
<td>***</td>
<td>***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N timing (splitN)</td>
<td>1</td>
<td>ns‡</td>
<td>ns</td>
<td>ns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc&lt;splitN</td>
<td>3</td>
<td>ns‡</td>
<td>ns</td>
<td>ns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>seedrt×splitN</td>
<td>1</td>
<td>ns‡</td>
<td>ns</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc&lt;seedrt×splitN</td>
<td>3</td>
<td>ns‡</td>
<td>ns</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tiller initiation period (tillinti)</td>
<td>2</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc×tillinti</td>
<td>6</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>seedrt×tillinti</td>
<td>2</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc&lt;seedrt×tillinti</td>
<td>6</td>
<td>*</td>
<td>*</td>
<td>ns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>splitN×tillinti</td>
<td>2</td>
<td>ns‡</td>
<td>ns</td>
<td>ns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc&lt;splitN×tillinti</td>
<td>6</td>
<td>ns‡</td>
<td>ns</td>
<td>ns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>seedrt×splitN×tillinti</td>
<td>2</td>
<td>ns‡</td>
<td>ns</td>
<td>ns</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loc&lt;seedrt×splitN×tillinti</td>
<td>6</td>
<td>ns‡</td>
<td>ns</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Significance at the 0.05 significance level.
*** Significance at the 0.001 significance level.
† ns, not significant.
initiated after 1 March (Fig. 3) contributing to a higher final yield at the TRS 2010–2011 location for the HSR.

The key differences in grain weight spike$^{-1}$ between a single and split N application were found at the HSR at BC 2010–2011 and at the LSR at TRS in 2011–2012. At BC the split N application produced more grain weight in the tillers produced in January–February (0.5 g spike$^{-1}$) compared to a single N application (0.09 g spike$^{-1}$) (Fig. 3). At TRS the split N application resulted in more grain weight in the tillers produced in January–February (0.78 g spike$^{-1}$) compared to a single N application (0.48 g spike$^{-1}$).

Analysis of Destructive Samples

Analysis of plants harvested from the 2-m plots found a three-way interaction among site-year, seeding rate, and tiller initiation period for heads m$^{-2}$ (Table 3). The two-way interactions between tiller initiation period and seeding rate and site-year and seeding rate were also significant along with the main effects of site-year, seeding rate, and tiller initiation period. The patterns in spikes m$^{-2}$ in these larger samples were similar to those found in spikes plant$^{-1}$ in the marked plant samples. Over all locations in 2009 through 2011, MS and tillers initiated in the fall made up 88 to 97% of all spikes harvested in the HSR treatments and 50 to 80% of spikes in the LSR treatments (Fig. 4). Tillers initiated in January–February only contributed from 3 to 10% of the spikes at the HSR but were a significant factor in yield at the LSR contributing 19 to 42% of the spikes.

Mar tillers were the least important, contributing less than 4% of the spikes at the HSR and 1 to 14% of the spikes at the LSR.

Regardless of seeding rate, the number of tillers initiated in the fall were significantly higher than those initiated in January–February or March periods. The only exception to this occurred at TRS 2010–2011 were the number of spikes produced in January–February was not significantly less than those produced in the fall. At the HSR, there were few significant differences in the low number of spikes m$^{-2}$ from tillers produced in January–February and those initiated in the March period. While at the LSR there often were significant differences in spikes m$^{-2}$ produced with more January–February tillers resulting in spikes compared with the low numbers of March tillers producing spikes.

As with spikes m$^{-2}$, analysis of the number of kernels spike$^{-1}$ from the 2-m plots found a significant three-way interaction among site-year, seeding rate, and tiller initiation period; significant two-way interactions between tiller initiation period and seeding rate and site-year; and significant main effects of site-year, seeding rate, and tiller initiation period (Table 3). Mainstem and tillers established in the fall at the HSR resulted in a greater number of kernels spike$^{-1}$, ranging from 24 to 28 kernels spike$^{-1}$ compared to the tillers established in the winter and spring which produced only 8 kernels spike$^{-1}$ or less (Fig. 5). At the LSR the MS and fall tillers had significantly more kernels spike$^{-1}$ (37–43 kernels spike$^{-1}$) compared to the January–February tillers which produced 19 to 32 kernels spike$^{-1}$ and the January–February tillers had significantly more
kernels spike\(^{-1}\) than the March tillers which only produced 3 to 18 kernels spike\(^{-1}\). Within each tiller initiation period the LSR treatment often had more kernels spike\(^{-1}\) compared with the HSR treatment. The only exception to this pattern was found at TRS 2009–10 where the number of kernels spike\(^{-1}\) in the HSR and LSR treatments were similar in tillers initiated in the March period. It is interesting to point out that the January–February tillers within the LSR matched the number of kernels spike\(^{-1}\) found in fall tillers under HSR treatments. January–February tillers at LSR clearly contributed to final grain yield in a significant manner.

As with spikes m\(^{-2}\) and kernels spike\(^{-1}\) there was a significant three-way interaction among site-year, seeding rate, and tiller initiation period for kernel weight (Table 3). The two-way interaction between seeding rate and tiller initiation period was also significant as were the main effects of site-year, seeding rate, and tiller initiation period. Within the HSR, MS and tillers initiated during the fall had higher kernel weights compared to tillers initiated in January-February or in the March period (Fig. 6). Likewise, the kernel weights in tillers initiated in January-February at LSR clearly contributed to final grain yield in a significant manner.

As with spikes m\(^{-2}\) and kernels spike\(^{-1}\) there was a significant three-way interaction among site-year, seeding rate, and tiller initiation period for kernel weight (Table 3). The two-way interaction between seeding rate and tiller initiation period was also significant as were the main effects of site-year, seeding rate, and tiller initiation period. Within the HSR, MS and tillers initiated during the fall had higher kernel weights compared to tillers initiated in January-February or in the March period (Fig. 6). Likewise, the kernel weights in tillers initiated in January-February were often higher than the weights of kernels in tillers initiated in March with the only exception found at TRS 2009–10. However, within the LSR, there were no significant differences in kernel weights between MS and tillers initiated in the fall and those initiated in January–February. Seed weight among January–February tillers contributed significantly to final yield compared to the January–February tillers.
within the HSR. The largest differences in kernel weight at the LSR were between the tillers initiated in January–February and those initiated in March, with the March tillers having significantly lower kernel weights. Comparisons between the seeding rate treatments found that the fall tillers in the HSR and LSR and the January–February tillers at the LSR had similar kernel weights (3 and 4 g per 100 kernels). Kernels produced in the March period generally had kernel weights below 1 g per 100 kernels and did not contribute much to yield. This was especially true at the HSR. March tillers within the LSR measured between 0.65 g to 2.58 g per 100 seeds compared to March tillers within the HSR ranging from 0 to 0.63 g per 100 seeds.

The significant interactions among site-year, seeding rate, and tiller initiation period for spikes m$^{-2}$, kernels spike$^{-1}$, and weight kernel$^{-1}$ were ultimately reflected in yield (Table 3). There was a significant three-way interaction among site-year, seeding rate, and tiller initiation period for yield along with two-way interactions between seeding rate and tiller initiation period and site-year and tiller initiation period. There were also significant main effects of site-year and tiller initiation period. In both the HSR and LSR treatments the MS and tillers produced in the fall were responsible for most of the yield (Fig. 7). In fact, the yield response at each location to seeding rate and tiller initiation period match the pattern in spikes m$^{-2}$ found in the marked plant and 2-m samples. The only difference in the pattern between spikes m$^{-2}$ and yield was found at the TRS 2010–2011 site-year where the yield from the fall tillers was significantly greater than the yield from either the January–February or March tillers. This change in significance was due to the greater kernel number and kernel weight in the fall tillers in this site-year. At the HSR tillers produced in January–February and the March period contributed very little to overall yield, often less than 0.25 t ha$^{-1}$. At the LSR the January–February tillers did contribute significantly to yield (0.5–2.5 t ha$^{-1}$) but the March tillers did not (0–0.25 t ha$^{-1}$). It is clear from these data that the keys to greater wheat yield are the MS and early tillers developing in the period from planting to 1 January. The HSR produced more yield from the MS and fall tillers. However, the January–February tillers at the LSR produced significantly more yield than the January–February tillers at the HSR.

**Yield from Large Plot Sections**

The increase in yield from later tillers at the LSR helped overcome the advantage that the HSR had in early development resulting in similar overall yield (Fig. 8). Results showed a significant site-year by seeding rate interaction for yield along
with significant site-year and seeding rate main effects. At the 2 site-years that are matched with the 2-m samples (BC 2010–2011 and TRS 2010–2011), the large plot yield showed no difference in grain yield between seeding rates at the BC 2010–2011 site-year (7.7 vs. 8.1 t ha\(^{-1}\)). For comparison, the small 2-m plot data indicated an overall yield of 6.01 t ha\(^{-1}\) at the HSR and 6.2 t ha\(^{-1}\) at the LSR. Likewise, at TRS 2010–2011 where the large plot yield found a significant yield advantage at the HSR (6.4 vs. 4.6 t ha\(^{-1}\)), the small 2-m plot data indicated a small advantage to the HSR of 6.3 t ha\(^{-1}\) compared with 6.1 t ha\(^{-1}\) at the LSR. In the other 2 site-years in the large plot analysis both the HSR and LSR yielded the same. Clearly at LSR, January–February tillers can help overcome the advantage that the MS and fall tillers have at the HSR.

**Nitrogen Application Timing**

There were no significant differences among the N application timing treatments (Schulz et al., 2015) in the 2-m plots in any of the 4 site-years nor was there any significant yield differences due to N application timing in the larger plots. This contrasts with the differences found when analyzing the grain weight from the spikes of the marked plant samples. Clearly the effect of N timing in increasing grain weight in the January–February tillers is very small and given the small contribution of these tillers to overall yield results in an overall yield impact that was too small to produce significant differences. As described by Scharf and Alley (1993) the yield impact of a split N application will only be significant when plant densities are low enough to allow the January–February and/or March tillers to have a significant contribution to yield. Applying a split N application in January or February to a field with high plant densities will not help increase yield as much as a split N application applied at low plant density since the late tillers produced in this situation will not have sufficient kernels spike\(^{-1}\) or weight kernel\(^{-1}\) to make much of a contribution.

**CONCLUSION**

To understand the mechanisms that lead to spikes and final yield, this study examined the impact of management practices on tillers produced during the fall, winter, and spring seasons and their contribution to spike number, kernel number, kernel weight, and final yield. Results from the marked plant samples and 2-m samples both indicate that the combination of MS or tillers initiated in the fall (planting to 1 January) made up the majority of plants that produced spikes (especially at HSR), had...
more kernels spike$^{-1}$ and kernel weight, and contributed the most to yield compared with tillers that are initiated from 1 Jan to the start of jointing (GS 30). While the January–February tillers did make a significant contribution to yield at the LSR, tillers initiated in March at either seeding rate produced very few kernels spike$^{-1}$, low kernel weight, and contributed very little to yield. Therefore, it can be concluded, the earlier a tiller is formed the higher the kernel number and weight and the more it will contribute to yield at harvest.

The key management factor that influences the number of tillers produced at different periods during the growing season and the contribution that tillers initiated at different periods make to yield is seeding rate. At the HSR, MS and tillers initiated prior to 1 January were responsible for more than 87% of the grain yield. Tillers produced in January–February produced from 5 to 11% of the final yield, while tillers produced in March contributed less than 2% of the yield. In contrast, at the LSR tillers produced in January–February made up 20% to almost 60% of the final yield. Furthermore, kernels spike$^{-1}$ and kernel weights in these tillers were almost as high as those found at the HSR. Clearly, depending on the environmental conditions the period from January–February can be important in developing spikes.

In this study, a split application of N had very little effect on spike number, kernel number, kernel weight or grain yield. While a split application of N did increase grain weight in spikes during the January–February period that allows the plant to develop larger spikes, more kernels spike$^{-1}$, and heavier kernels. This is the reason that under field conditions the number of productive plants at harvest is often independent of seeding rate. If stress during the period from emergence to GS30 could be reduced as it was at both locations in 2011–2012 it is feasible that the rate of leaf development in each tiller would become similar to that in the MS (as observed by Klepper under glasshouse conditions) and that HSR would result in more productive tillers per unit area. This would help increase grain yield and productivity.

**ACKNOWLEDGMENTS**

We thank the NC Small Grain Association for funding and support.

**REFERENCES**


**Fig. 8. Impact of seeding rate on yield combined from large plots across all 4 site-years. Error bars represent LSD = 0.53 t ha$^{-1}$.**


