Canopy Light and Tiller Mortality in Spring Barley

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ABSTRACT

Mortality of tillers in barley (*Hordeum vulgare* L.) is an important developmental event affecting spike number and yield potential of the crop. It has traditionally been thought that increased shading of young tillers by the developing canopy initiates the premature senescence of tillers. A series of field experiments were conducted in 1982, 1983, and 1984 at St. Paul, MN on a Waukegan silt loam soil (fine-silty over sandy or sandy skeletal, mixed, Typic Hapludoll) to test this hypothesis. Degree of shading within the crop canopy was measured in relation to the position of tiller leaves during the vegetative phase of development for three genotypes. The decline in rate of leaf appearance on nonsurviving primary tillers, monitored as an early indicator of tiller senescence, was noted within 3 to 4 wk after crop emergence and before appreciable shading of tillers occurred. This indicates that tiller mortality was not initiated by lack of light. However, after main stem elongation began, tillers soon became heavily shaded suggesting the possibility that shading plays an auxiliary role in the senescence of barley tillers. We discuss the possibility that changes in light quality early in the growing season may be important for initiating the senescence of tillers.

THE NUMBER of tillers produced in a barley crop community is important in establishing the yield potential of the crop. However, not all initiated tillers complete development to bear fertile spikes. The proportion of tillers that survive to produce grain depends on the genotype, N fertility, water status, plant density, and plant spatial arrangement (Thorne, 1962; Cannell, 1969; Willey and Holliday, 1971; Kirby and Faris, 1972; Masle-Meynard, 1981; Simmons et al., 1982; Simmons and Rasmusson, 1986). The sequence of developmental and physiological events resulting in premature death of tillers and their interrelationship with factors in the crop environment are poorly understood.

Both shading of tillers and shifts in shoot photoassimilate partitioning patterns have been proposed as factors causing tiller death in grasses (Spiertz and Ellen, 1972; Kays and Harper, 1974; Ong et al., 1978; Colvill and Marshall, 1984; Lauer and Simmons, 1985). Ong and Marshall (1979) hypothesized for perennial ryegrass (*Lolium perenne* L.) that reductions in the supply of photoassimilate to tillers in conjunction with increased translocation of photoassimilate to the rapidly elongating stems causes a photoassimilate limitation for young, shaded tillers resulting in their death. Simmons and Lauer (1986) confirmed for barley that the proportional allocation of photoassimilate to primary tillers in barley declined at the onset of rapid main stem elongation. The degree of shading of young tillers at the time of this shift in photoassimilate partitioning has not been previously measured.

The role of light in causing tiller mortality was investigated by Spiertz and Ellen (1972) who reported that light enrichment treatments reduced tiller mortality in perennial ryegrass. Kirby and Faris (1972) hypothesized that light was important for tiller survival based on observations that mutual shading of tillers occurred at approximately the same time as the appearance of chlorosis on nonsurviving tillers. However, specific measurements of the degree of canopy shading in relation to development of tillers have not been made. Recognizing that initiation of tiller senescence likely begins some time before the appearance of chlorosis has caused us to question the premise that

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lack of light initiates tiller mortality in barley crop communities. Knowing more precisely the degree of correspondence between the onset of tiller senescence and the development of significant tiller shading in the canopy should help to resolve this issue.

Our study was conducted with the objective of ascertaining the degree of association between canopy light conditions in field barley communities and the survival of tillers. This was approached by measuring canopy light levels in relation to the development of surviving and nonsurviving tillers in spring barley genotypes differing in tiller survival characteristics. Of particular interest was estimating the correspondence between shading and senescence of primary tillers.

MATERIALS AND METHODS

Plot culture. Similar studies were conducted in 1982, 1983, and 1984 at St. Paul, MN on a Waukegan silt loam soil fertilized in accordance with soil test recommendations for eastern Minnesota and a grain yield goal of 3.2 Mg/ha. Plots were 3 m long and 9 or 18 rows wide, depending on the year. Row spacing was 18 cm. Experimental designs in each year were randomized complete blocks with six, three, and four replicates, respectively. Crops were sown between 17 and 26 April and emerged between 3 and 7 May. Plant populations of 330 plants m^{-2} were established by overseeding and thinning. No pesticides were applied to the plots and weeds were controlled by hand.

Three genotypes were evaluated each year of these studies; 'Dickson' and M72-269 were included in all years. They had previously been characterized as either low (Dickson) or high (M72-269) tiller survival (Simmons et al., 1982). For example, 45% of the Dickson shoots survived in 1984 compared to 62% for M72-269. 'Manker', an intermediate tiller survival genotype, was the third genotype grown in 1982. 'Morex', also with intermediate survival, replaced Manker in the 1983 and 1984 studies.

Measurements of tiller leaf production. Kirby and Riggs (1978) observed that the rate of leaf production declined for nonsurviving tillers in the initial stages of their senescence, even before they displayed visible signs such as chlorosis. We chose to use this characteristic in order to nondestructively estimate the onset of tiller senescence in the crop. Leaf numbers were counted on primary tillers of 12 randomly selected plants in each plot beginning at tiller emergence. The system of Haun (1973) was used for counting leaves in which the newest emerging leaf is expressed as a proportion of the most recently fully expanded one. This system permits repeated observations on the same tiller. The specific tillers monitored were T_1 and T_2 in the axils of the first and second main shoot leaves, respectively. Nonsurviving tillers were

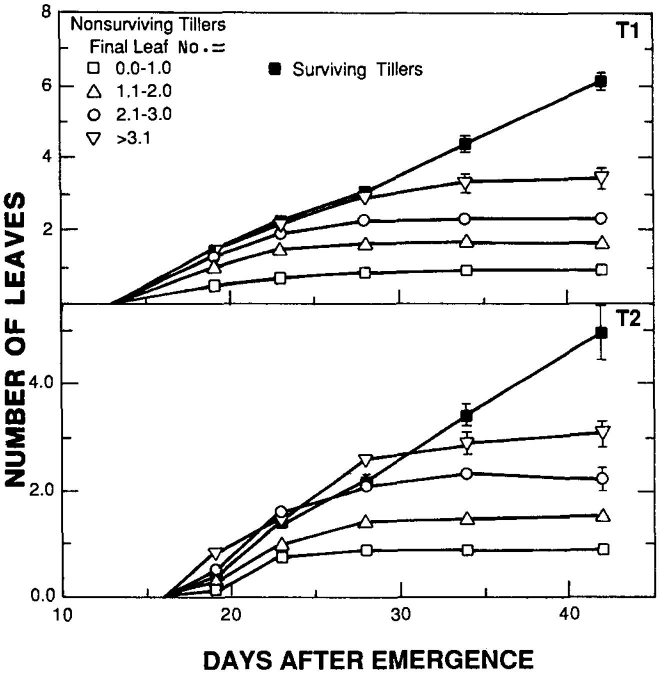

Fig. 1. Number of leaves on surviving and nonsurviving T_1 and T_2 tillers at times after crop emergence in 1984. Values are means for Dickson, Morex, and M72-269. Nonsurviving tillers are classified according to the number of fully emerged leaves present at death. Standard deviations are shown when they exceed the size of the symbol.

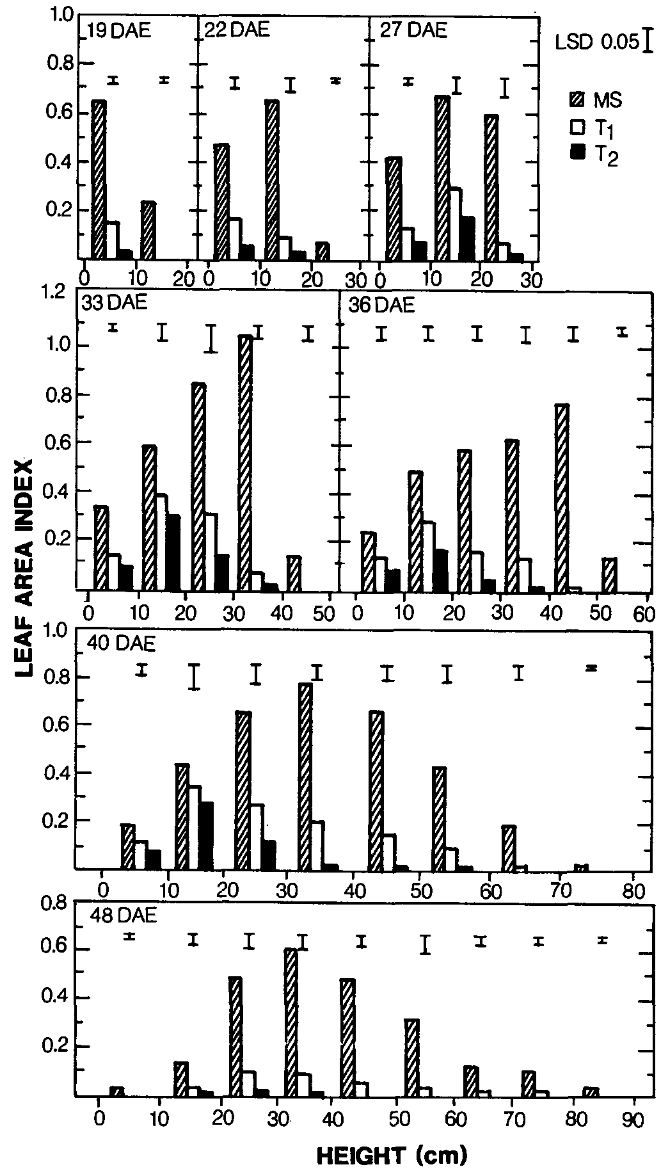

Fig. 2. Leaf area indexes for specific shoots at 10-cm increments in the canopy of barley in 1984. Values are averaged over Dickson, Morex, and M72-269 and were measured on the specified days after crop emergence (DAE). Bars represent LSD (0.05) for mean comparisons among shoots at each height.

classified according to the final number of leaves that had fully emerged before their death.

Canopy light measurements. Photosynthetic photon flux density (PPFD) was measured in the crop canopy using a LI-COR LI-190 S line quantum sensor (Li-Cor, Inc., Lincoln, NE). This instrument integrates photosynthetically active radiation along a 1 m sensor. Sensor width is 1.5 cm. Measurements were made with the sensor placed in a north-south orientation, perpendicular to the rows of the plots. The first PPFD readings were taken 2.5 and 5 cm above the soil surface and the sensor was moved upward in the canopy at 5 cm increments thereafter. Measurements were made under cloud-free sky conditions, usually between 0800 and 1100 h CST. At 26 and 47 d after emergence (DAE) in 1984, measurements were also made in early morning and/or later afternoon in order to take account of the influence of sun angle on PPFD in the canopy. All measurements for a given plot were taken within a period of 75 to 375 s, depending on the date.

Tiller leaf position and area measurements. In order to relate radiation characteristics to tiller position within the canopy, heights of leaves at their ligules and leaf areas within transects of the canopy were determined for the main shoot and tillers T_1 and T_2 every 3 to 8 d during the study period. Ten randomly selected plants were harvested from each plot, clipped in 10 cm increments starting at ground level, and the leaf and sheath areas were determined using a leaf area meter (LI-COR 3000, Li-Cor, Inc., Lincoln, NE).

RESULTS AND DISCUSSION

Crop development and canopy PPFD attenuation patterns were very similar for each year of the study. The most detailed data were collected in 1984 and are used to document the results of these studies in this paper. As expected, a higher proportion of tillers survived for M72-269 than for the other two genotypes.

Tillers T_1 and T_2 senesced at stages of development ranging from less than one to more than three leaves (Fig. 1). Kirby and Riggs (1978) previously observed that an early indicator of impending tiller death was that the rate of tiller leaf appearance declined. Such was also clearly evident in our study. The rate of leaf appearance always declined prior to development of the first visible sign of tiller nonsurvival (chlorosis of the newest emerging leaf). Leaf appearance declined between 19 and 23 DAE for tillers senescing with one or fewer leaves. For tillers that produced more leaves before senescing, the decline in leaf appearance occurred slightly later. Tillers most frequently senesced with two or less fully expanded leaves. Leaf appearance on such tillers had virtually ceased by 28 DAE (Fig. 1). Even the largest nonsurviving tillers had declined in rate of leaf appearance by 28 to 34 DAE. Thus, we estimate that the initiation of senescence for most nonsurviving tillers occurred prior to 28 DAE in our studies.

Leaf area index (LAI) for all genotypes increased slowly until the beginning of main stem elongation (approximately 25 DAE). Leaf area index then increased rapidly until flag leaf emergence (37 DAE). The main shoot had from three to six times greater total leaf area than either T_1 or T_2 (Fig. 2). At the plant populations used in our studies there was little leaf area contributed by tillers other than T_1 and T_2. Figure 2 shows that main shoot leaf area exceeded tiller leaf area at all levels within the canopy. This was especially so after the onset of stem elongation. At and after 33 DAE, the greatest leaf area for the main shoot

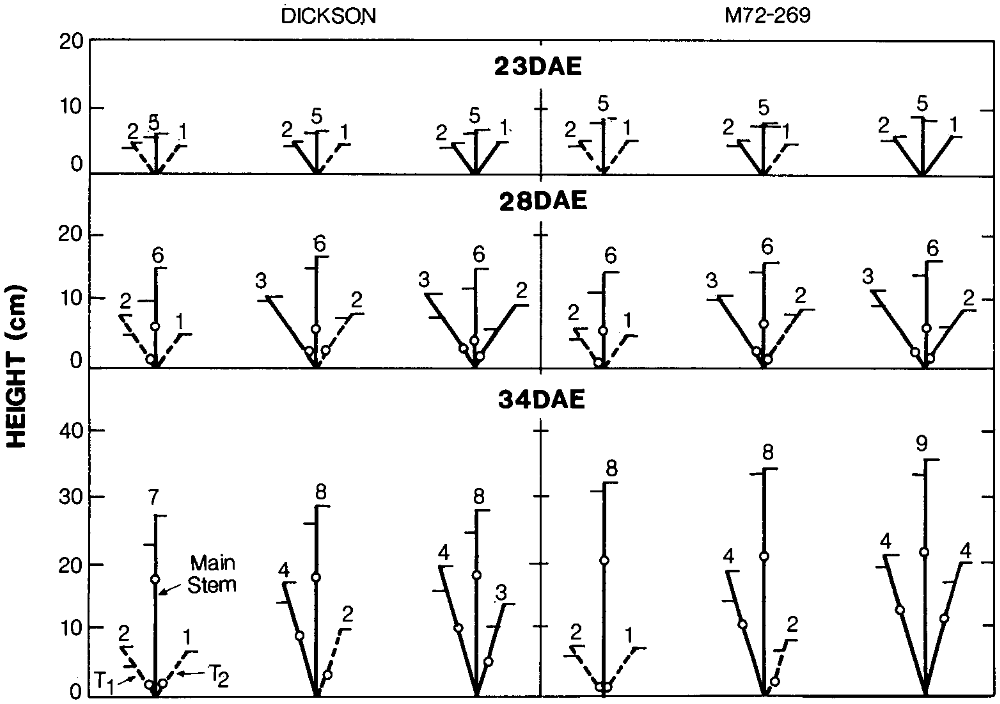

Fig. 3. Main shoot and tiller leaf heights on different days after crop emergence (DAE) in 1984 for Dickson and M72-269 barley. Each diagram schematically illustrates types of plants differentiated on the basis of their patterns of tiller survival. Tillers shown by dashed lines were nonsurviving. The numbers show how many fully emerged leaves were present on each shoot at the time of observation. Circles indicate the approximate positions of the terminal apexes after onset of stem elongation.

was 20 to 30 cm above that of the tillers. Comparing among genotypes, main shoot leaf area was greater for Dickson than for M72-269, especially in the upper canopy. Dickson also had a greater tiller leaf area early in the season, but since a higher proportion of tillers failed to survive for this genotype it had lower tiller leaf area later in the season (data not shown).

Positions of leaves on the main shoot and tillers are shown in Fig. 3. At 23 DAE, leaf heights were similar for all shoots. By 28 DAE a height differential had begun to develop between the top leaves on the main shoot and the top leaves on nonsurviving tillers. By 34 DAE leaf height differences between surviving and nonsurviving shoots were very pronounced. At this time leaves on nonsurviving tillers for either genotype were positioned at a height of no more than 10 cm above the soil surface, whereas top leaves on surviving tillers had attained a height of 20 to 25 cm. The apexes of nonsurviving tillers remained near the soil surface indicating that little stem elongation occurred for these shoots. Thus, major leaf height differences between surviving and nonsurviving shoots appeared to develop after 28 DAE, indicating that such differences were a consequence rather than a cause of tiller senescence. There were no substantive differences in development of shoot leaf heights between Dickson and M72–269 that could explain their differing tiller survival properties.

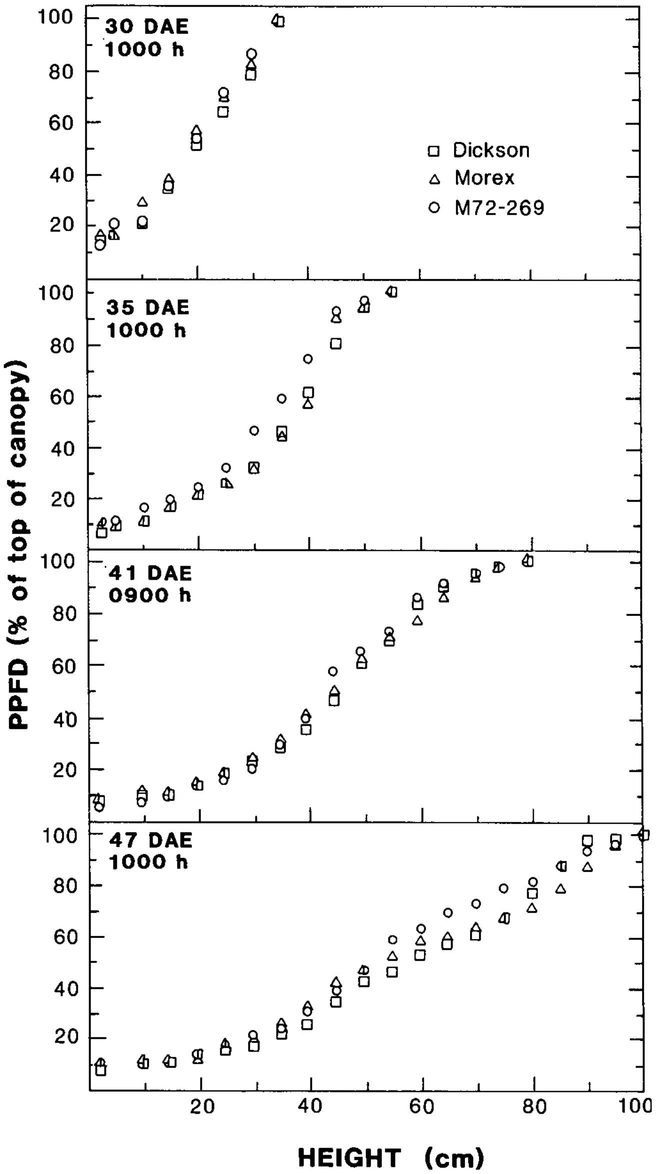

Fig. 4. Midmorning canopy light transmission profiles for Dickson, Morex, and M72–269 barley on various days after emergence (DAE) in 1984. The PPFD levels above the canopy ranged from approximately 1250 μmol m^{-2} s^{-1} on 41 DAE to 1550 μmol m^{-2} s^{-1} on the other dates. Local times are shown and can be converted to Central Standard by subtracting 1 hr.

Canopy Light Profiles

Shading of tillers caused by elongation and development of the crop canopy has traditionally been thought to cause mortality of tillers in cereals. Midmorning measurements of canopy light at 18 DAE showed little reduction in PPFD at a height of 2.5 cm, the approximate position of young tiller leaves at that time (Table 1). Even by 24 to 26 DAE, mid- to late-morning measurements indicated that young tillers received approximately one-third to one-half of the 1500 to 1850 μmol m^{-2} s^{-1} PPFD present above the canopy. Thus, these tillers were exposed to light levels above the 300 to 400 μmol m^{-2} s^{-1} estimated by Campbell and Read (1969) as necessary for sustained tiller growth in wheat (*Triticum aestivum* L.). When sun angle was greater, PPFD at 2.5 cm was less, as observed for the 1600 and 1800 h measurements on 26 DAE.

Table 1. Light transmission at a height of 2.5 cm in canopies of Dickson, Morex, and M72-269 barley on 18, 24, and 26 d after emergence in 1984.

	Days after emergence				
	18	24	26		
Genotype	Time of day				
	0900 h	0900 h	1100 h	1500 h	1700 h
	% of PPFD above canopy				
Dickson	87	46	30	15	13
Morex	84	51	39	27	10
M72-269	87	47	45	28	13
LSD (0.05)	NS	NS	10	10	NS

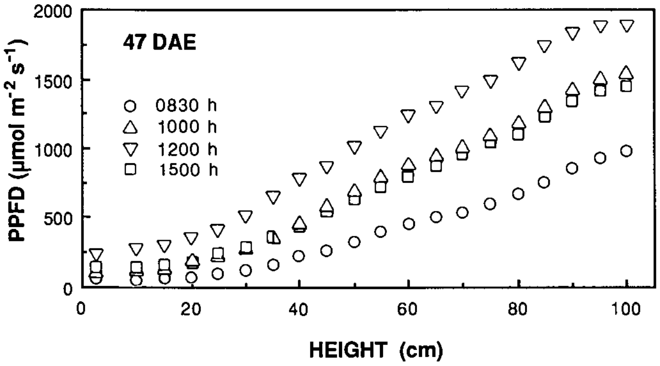

Fig. 5. Early, midmorning, late morning, and midafternoon photosynthetic photon flux density (PPFD) profiles in canopies of barley on 47 d after crop emergence (DAE) in 1984. Local times are shown and can be converted to Central Standard by subtracting 1 h. Values are averages for genotypes Dickson, Morex, and M72–269.

Several factors should be kept in mind when interpreting these canopy light data. The quantum line sensor used to make these measurements integrated PPFD over both the row and interrow area. Thus, on the earlier measurement dates before canopy closure, light levels in the rows where the tillers were positioned would have been slightly lower than those shown in Table 1. Also, measurements reported in Table 1 were made on cloud-free days, meaning that tillers would also have experienced lower radiation levels on overcast days. Nevertheless we feel that the data in Table 1 taken together with the leaf area and leaf position information in Fig. 2 and 3 indicate that mutual shading of tillers was likely not the factor initiating tiller mortality in the barley crops monitored in these studies. The leaf appearance data in Fig. 1 suggest that the nonsurviving tillers began senescing before canopy development and associated shading were sufficient to have induced such senescence. Reduction in leaf appearance rate, even on the largest nonsurviving tillers, usually took place by 28 DAE, whereas most canopy development and stem elongation took place after that time. Prior to 28 DAE, tillers were exposed to relatively high PPFD regimes on cloud-free days.

After 28 DAE, tillers with leaf area only in the lower level of the canopy became increasingly shaded. Fig. 4 shows midmorning canopy light profiles during the period of rapid stem elongation between 30 and 47 DAE. After 30 DAE, PPFD in the lower canopy was consistently below 400 μmol m^{-2} s^{-1}. By early grain filling (47 DAE), the height in the canopy at which PPFD was below 400 μmol m^{-2} s^{-1} ranged from 60 cm in early morning to 20 cm in late morning (Fig. 5). By the time nonsurviving tillers showed visible signs of senescence (i.e. chlorosis), they were positioned where PPFD was quite low and likely insufficient to support growth. Although our data led us to conclude that shading was not the factor initiating tiller senescence in our experiments, it is not our contention that it played no role in the mortality of tillers. It may well have hastened the senescence process once it had been initiated.

In conclusion, our tiller leaf appearance results cause us to conclude that the onset of senescence for nonsurviving tillers in barley occurs much earlier in development than traditionally recognized, and certainly much earlier than the first expression of chlorosis. We think that it is plausible that tiller senescence began as early as 19 DAE or before for some tillers. This was just a few days after the initial emergence of the tiller from the subtending leaf sheath and much before the establishment of appreciable mutual shading within the canopy. A less recognized environmental factor that might conceivably influence tiller growth in a barley community at such early growth stages is light quality. This is an attractive hypothesis since changes in light quality have recently been shown to modify tillering in other grasses and cereals (Deregibus et al., 1985; Casal et al., 1986; Kasperbauer and Karlen, 1986; Casal, 1988). The hypothesis has been advanced by Casal et al. (1986) that tillering is influenced through a photomorphogenic response to shifts in light quality before limitations in radiant energy become a factor. These previous studies suggest a scheme involving red: far red light ratio as the photomorphogenic feature modifying tillering. This possibility of an association between early season changes in light quality and tillering needs to be a topic for future investigation. Other environmental factors such as nutrient and water status are also known to modify tiller production and survival. We are only beginning to appreciate the mechanistic complexity that likely exists to account for regulation of tiller production and survival in cereal plants.

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