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# Precipitation during anthesis reduces seed set in perennial ryegrass

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## Abstract

In perennial ryegrass seed production, the establishment of seed yield potential occurs until the point of anthesis. However, utilizing potential seed yield is predominately focused on processes after anthesis, namely seed set (%) and seed filling. In practice, seed yield is the product of the number of harvested seeds remaining after cleaning and average seed weight. For this study, the anthesis patterns and seed set were recorded in a diploid variety grown in seed production fields in three different Danish regions with contrasting weather conditions and investigated in 2013 and 2014. Increases in the total precipitation during anthesis reduced the anthesis synchrony and the seed set, which ranged from 50% to 66%. Under semi-controlled environmental conditions in which the influence of precipitation was excluded, the seed set was found to be influenced by the floret position in the spikelet and ranged from 73% in the florets in basal positions to 25% in the distal florets. It is suggested that a lower number of florets per spikelet will reduce the anthesis period. These results may provide insights for breeding programmes focused on increasing seed yield.

**KEYWORDS**
breeding, climate, flowering, rainfall, spikelet, synchrony

## 1 | INTRODUCTION

Perennial ryegrass (*Lolium perenne* L.) seed production is determined by genetics, the environment and management practices. Seed producers are able to control two of these factors by selecting and determining the best management strategy for the genetic material grown; however, they have little to no control over the environment, which influences both the development and utilization of the seed yield potential.

Seed set is an important factor in the effective utilization of the seed yield potential and the resulting seed yield. Marshall and Wilkins (2003) showed that a positive relationship occurs between the seed set and seed yield per inflorescence in a range of perennial ryegrass varieties grown under field and glasshouse conditions. However, Hampton and Hebblethwaite (1983) and Elgersma, Stephenson, and den Nijs (1989) suggested that low seed yield can be partially attributed to environmental limitations during the anthesis process, with low floret site utilization, which is defined as the percentage of florets that produce a seed, caused by low fertilization efficiency.

Anthesis, pollen dehiscence, pollen viability and stigma receptivity are influenced by a number of environmental parameters. In a comprehensive review, Hill (1980) described the environmental conditions that either promote or inhibit anthesis in a range of grass species. Temperature, light intensity and precipitation are important to anthesis and pollen dehiscence in perennial ryegrass. Hill (1980) noted that day temperatures of at least 18°C are required on the day of anthesis, night temperatures of 10°C advance both the start of anthesis and peak anthesis and day temperatures below 14°C increase the anthesis duration. However, threshold temperatures are variety specific; for example, cv. S24 requires a threshold temperature of 14°C, whereas cv. S23 requires a threshold temperature of 17°C (Emecz, 1962). The light duration at a specific intensity is an important factor that determines the flower opening time and subsequent pollen dehiscence (Hyde, 1952; Hyde & Williams, 1945). Emecz (1962) showed that different varieties of perennial ryegrass required different conditions ranging from 400 μmol $m^{-2}$ $s^{-1}$ for at least two and a half hours to 880 μmol $m^{-2}$ $s^{-1}$ for only one and a half hours. Wet weather, such as precipitation, and the soil moisture status have an influence on floret opening and anthesis (Emecz, 1962; Gregor, 1928). Precipitation during anthesis completely inhibits anthesis (Emecz, 1962), whereas the plant and soil moisture status influence pollen grain swelling and release (Matsui, Omasa, & Horie, 2000). Relative humidity has been shown to limit stigma receptivity in wheat (*Triticum* spp.) (Imrie, 1966). Stigma receptivity in perennial ryegrass is limited to 118 hr after floret opening (Gregor, 1928).

After pollen dehiscence, the most important parameter is pollen viability. The pollen of grass species tends to have a high respiratory rate; thus, this pollen is short-lived (Yang, 2009), and a high pollen count of approximately 10,000 pollen grains per floret is observed (Smart, Tuddenham, & Knox, 1979). Temperatures over 27°C during anthesis have been found to limit pollen viability in *Poa pratensis* L. (Maun, Canode, & Teare, 1969), whereas relative humidity can either promote or inhibit pollen viability (Heslop-Harrison, 1979a; Shivanna & Heslop-Harrison, 1981), with low-humidity conditions rapidly desiccating pollen grains. The pollen grain size is influenced by the floret position, which in turn may influence pollen viability (Matsui et al., 2000).

Grasses have self-incompatibility (SI) mechanisms to avoid self-crossing and potential reductions in seed set (Studer et al., 2008). Perennial ryegrass is largely self-sterile, and viable seedlings produced via self-fertilization show a pronounced inbreeding depression (Cooper, 1959). Because grasses exhibit rapid pollen germination and pollen tube growth (Heslop-Harrison, 1979a, 1979b; Yang, Thorogood, Armstead, & Barth, 2008), the majority of self-incompatibility reactions occur on the stigma surface via abnormal pollen tube germination (Heslop-Harrison, 1979a; Yang et al., 2008). However, the extent to which SI reduces the seed set under field conditions is not known.

Compared with wheat and other agriculturally important crops (particularly grain crops), which present homogenous development and are often either self-fertile (i.e., wheat) or capable of conducting anthesis over a short duration (i.e., maize (Emberlin, Adams-Groom, & Tidmarsh, 1999)), perennial ryegrass presents inhomogeneous development in relation to its inflorescence age (Anslow, 1963) and variations in its anthesis timing (Warringa, Struik, de Visser, & Kreuzer, 1998). The aforementioned differences often lead to difficulties in determining the influence of environmental conditions on seed yield at anthesis (Elgersma, Nieboer, & Keizer, 1993). Therefore, Boelt and Studer (2010) stated that anthesis homogeneity, that is, a consolidated anthesis pattern, is an important factor for obtaining high seed yields in perennial ryegrass. In particular, the homogeneous initiation of anthesis is essential for the effective pollination of an outcrossing species, such as perennial ryegrass. At present, variations in the time of anthesis impose uneven seed ripening patterns that may reduce the seed yield by causing shattering in the field. Furthermore, uneven seed development may cause greater losses because the small light seeds are discarded during the mechanical harvesting and seed cleaning (Boelt & Studer, 2010; Elgersma & Śnieżko, 1988).

The aim of this article was to assess the influence of climatic conditions on pollen release in perennial ryegrass, with particular attention to seed set. For this study, the influence of climatic conditions on seed set in six commercial seed production fields is assessed and compared with the results of a study in which the influence of the environmental conditions was minimized. Detailed information on the floret seed set potential was used to discuss both the influence of precipitation during anthesis on seed set and breeding objectives designed to increase seed yield in perennial ryegrass.

## 2 | MATERIALS AND METHODS

The materials and methods section has been split into two sections as follows: the first is related to the field studies and the second to studies in a semi-protected environment. Data analysis was performed using the statistical software package "R version 3.1.2" (R Core Team, 2015) in connection with RStudio (version 0.98.1103).

### 2.1 | Field assessment location

A total of six commercial seed production fields (>10 hectares) located in three production regions across Denmark were selected during the production years 2013 and 2014. The selected regions were chosen based on 10 years of weather data, and climate diversity was a selection criterion. The Bornholm region was selected for its cool winters and warm summers, the West Zealand region was selected for its mild winters and warm summers and the Central Jutland region was selected for its cold winters and cool summers. All the fields had the same diploid turf variety (Esquire), which is one of the most commonly grown varieties for seed production and it is cultivated throughout Denmark. Compared with the seed yield of other diploid perennial ryegrass varieties, the seed yield of Esquire was 11 per cent above average for the 5-year period from 2011 to 2015 (SEGES, 2015). The management practices during the seed production year were performed according to the needs of each field to avoid nutrient limitation(s), disease pressure and lodging at anthesis— ensuring that management practices were not seed yield limiting.

### 2.2 | Field anthesis assessment

At each location, a Burkard volumetric spore trap (Burkard Manufacturing Co. Ltd., Hertfordshire, UK) capable of recording over 7 days and continuously sampling the aerial pollen concentrations (at a sampling orifice height of 1 m above the soil surface) at a suction rate of 10 L/min was utilized. To minimize cross-contamination, that is, pollen from other sources, spore traps were placed in the middle of the fields. Inside the spore trap, an adhesive solution was applied to a Melinex tape drum revolving at a rate of 2 mm/hr, thus allowing an analysis of daily pollen concentrations as determined by microscope inspections. The relative daily pollen intensities were used as a proxy value for the daily anthesis intensity.

### 2.3 | Field climatic data

Each production field had the following environmental factors recorded hourly: the maximum, minimum and average temperatures (°C) and the precipitation (mm). In 2013, weather data were provided by DMI (Danmarks Meteorologiske Institut) weather stations located within 1 km of the study fields. In 2014, a WS-GP1 Automatic Weather Station (Delta-T Devices Ltd, Cambridge, UK) was placed alongside the spore traps to assess the same environmental conditions.

### 2.4 | Field seed set determination

Four 0.25-m$^2$ replicates of inflorescences at growth stage (GS) 92 (Zadoks, Chang, & Konzak, 1974) before seed shattering were randomly sampled within each field, excluding the headlands. Sampling was performed in consultation with regional experts on perennial ryegrass seed production. Each field was verified for uniformity. From these replicated samples, 100 randomly selected inflorescences were hand-threshed, and their seed set was determined. Hand-threshed seed samples were air-blown with a “Seedburo General Seed Blower” (Seedburo Equipment Co., Des Plaines, IL, USA). The seed and inert matter fractions were confirmed and counted as seed/inert matter via a microscope inspection. Inert matter is defined as unpollinated seeds in which only the lemma and palea were present or if the caryopsis length of the mature seed was less than one-third of the total seed length (as per ISTA (2013)). The seed set (%) was calculated as the proportion of seeds with a caryopsis length greater than one-third of the total seed length.

A nonlinear regression analysis was used to model the influence of the field climatic conditions, namely precipitation (mm) to seed set (%).

### 2.5 | Semi-protected environment: florets per spikelet and seed set

In a paired study, a total of 85 individual perennial ryegrass plants were transplanted from a seed production field experiment conducted at Flakkebjerg, Aarhus University, into 5-L pots filled with lightly cultivated field soil (Danish soil classification JB6/7, sandy clay soils). At transplanting, the plants were at GS30, prior to the onset of visible reproduction development but after their reproductive requirements were met. The plants were all between GS27 and GS29 at transfer, that is, with 7–9 tillers. The pots containing the transplanted plants were placed within an area that was protected from precipitation during the start of spring (end of March). Flakkebjerg, Aarhus University, is located in West Zealand, and weather conditions were comparable with those in the seed production field there.

Two production years were addressed. In 2013 and 2014, 40 plants and 45 were analysed, respectively, after anthesis (GS92) but before seed shattering for the total floret number per spikelet and the seed set per floret. Assessments were performed for a total of 765 spikelets that were randomly sampled from three inflorescences per plant at three positions from the inflorescence: the upper, middle and lower third positions. The seed set was analysed for each floret position over the whole spikelet from the basal to distal positions. An analysis of variance (ANOVA) was performed on the floret number per spikelet.

Probability analysis was used to determine the effective seed number per spikelet, whereby the effective seed number per spikelet is a calculated value which represents the total number of seeds a spikelet may contribute to seed yield. For any given spikelet, it is the product sum of seed set (%) for each floret position within the spikelet multiplied by the respective probability of a spikelet containing that floret position. The sum of effective seed set allowed the calculation of the critical number of florets per spikelet required to reach the 90% percentile of effective seed number for any given spikelet.

## 3 | RESULTS

For the two seed production years 2013 and 2014, weather variables were used to assess the influence of each variable on the daily and total anthesis patterns (Figure 1). The year 2013 was characterized predominately by its cool wet weather, which extended the total anthesis duration to an average of 20 days to complete anthesis. In 2014, warmer drier weather facilitated a consolidated anthesis period, which lasted an average of 17 days. A normal distribution trend for anthesis was observed in 2014, whereas the cold wet weather restricted the normal distribution patterns in 2013, particularly in Central Jutland (Figure 1a). Delayed daily anthesis can be attributed to low temperatures and/or precipitation on a given day (i.e., Figure 1c, cf. Figure 1f). In 2014, the extent to which precipitation influenced anthesis was minimal, and relatively low temperatures were found to limit anthesis.

### 3.1 | Precipitation reduced anthesis consolidation

Increases in the total precipitation were found to increase the duration of anthesis. For both years, the anthesis process was never shorter than 16 days (Figure 2). The maximum duration of anthesis for the years and fields studied was less than or equal to 21 days. A logarithmic model was fitted, and the resulting model explained 60% of the variation observed in the anthesis consolidation. In 2014 (Fields D, E and F; Figure 2), the duration of anthesis was more consolidated than the duration in 2013 (Fields A, B and

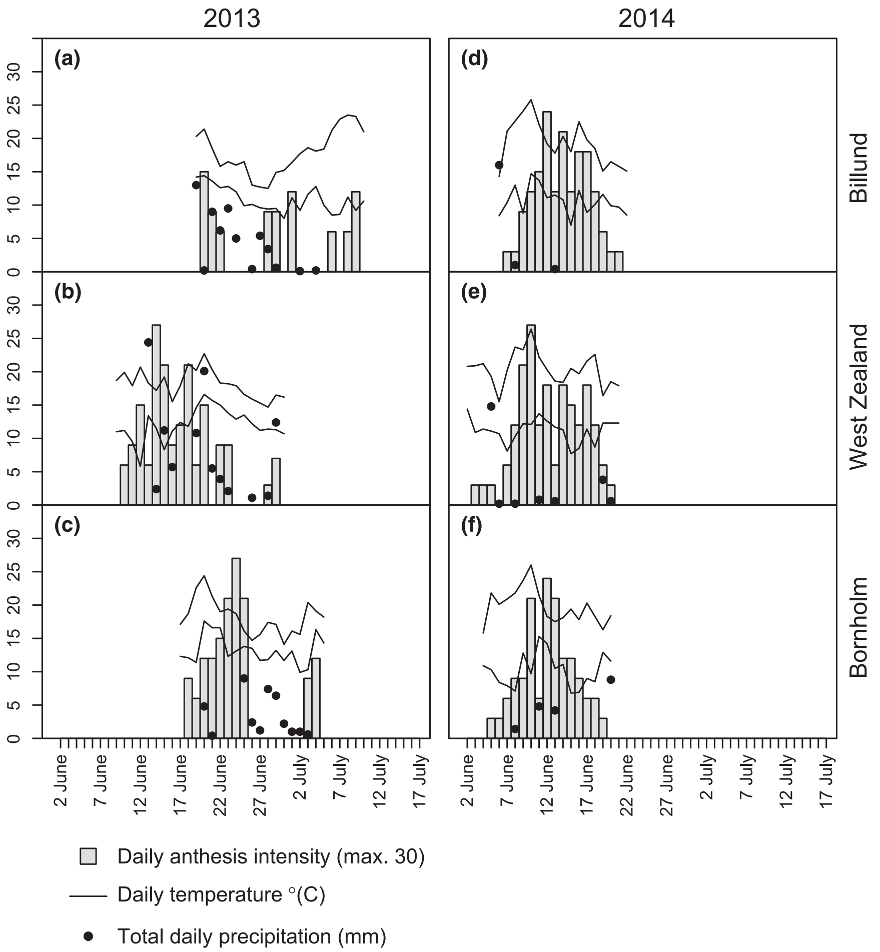


**FIGURE 1** Daily anthesis intensities (grey bars; max. 30) of perennial ryegrass (*Lolium perenne* L.) under the influence of the predominant daily temperature range (upper and lower lines) and total daily precipitation (dark circles) for 2013 (a–c) and 2014 (d–f) in three regions of Denmark: Central Jutland (a, d), West Zealand (b, e) and Bornholm (c, f)

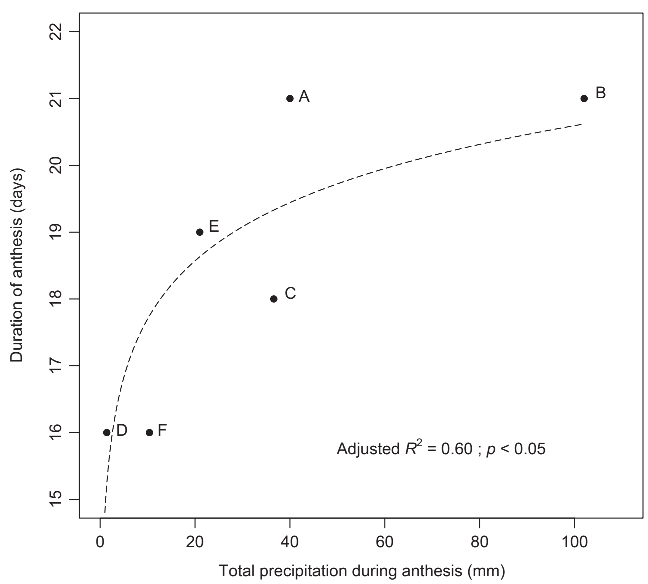


**FIGURE 2** Influence of total precipitation (mm) during the consolidation of anthesis (days) in perennial ryegrass (*Lolium perenne* L.) seed crops grown in 2013 (A–C) and 2014 (D–F) in three regions of Denmark: Central Jutland (A, D), West Zealand (B, E) and Bornholm (C, F)

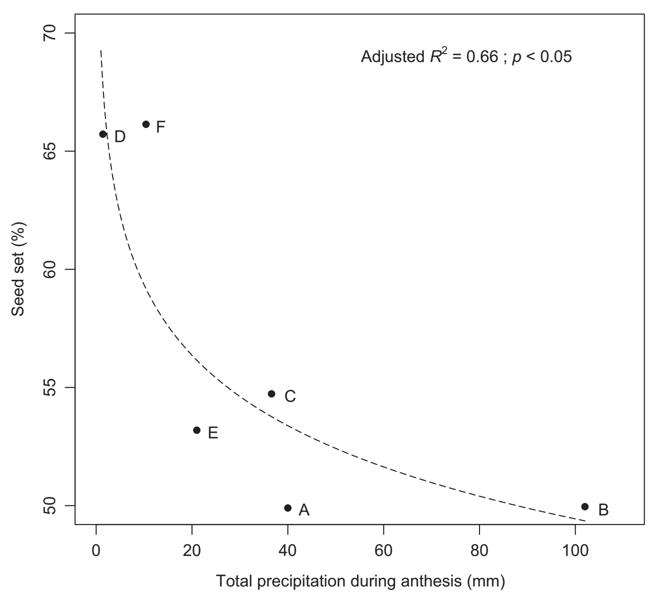


**FIGURE 3** Influence of the total precipitation (in mm) during anthesis on the seed set (%) in perennial ryegrass (*Lolium perenne* L.) seed crops grown in 2013 (A–C) and 2014 (D–F) in the following three regions in Denmark: Central Jutland (A, D), West Zealand (B, E) and Bornholm (C, F).

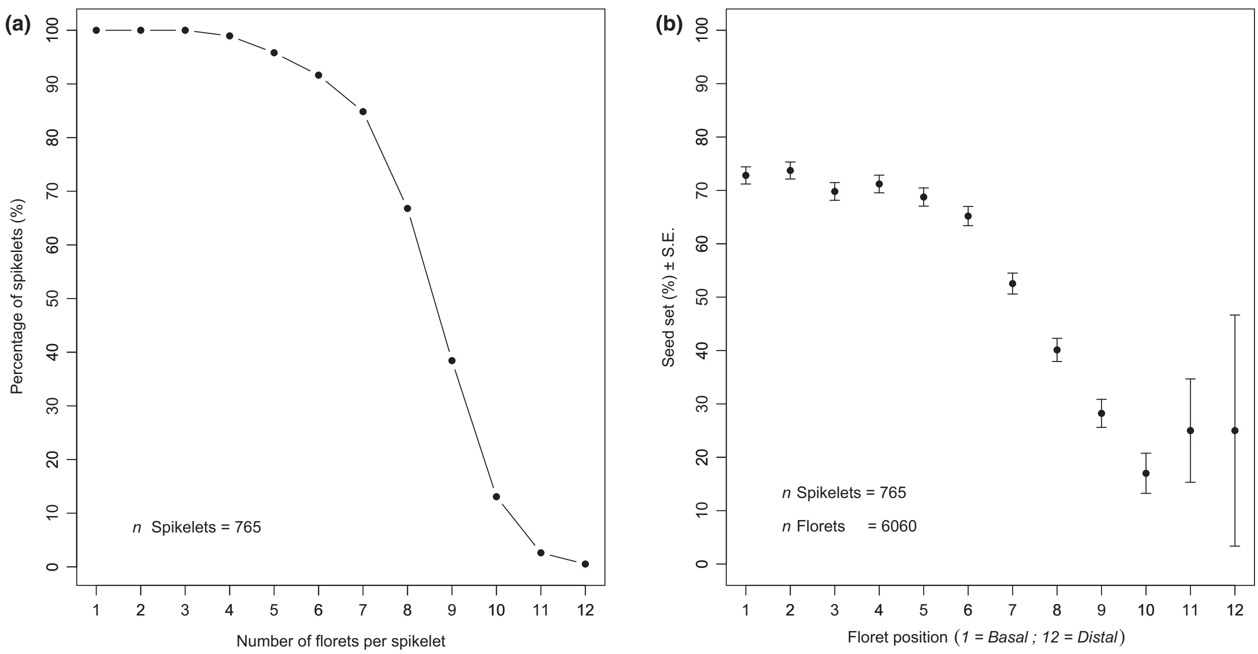


**FIGURE 4** (a) Florets per spikelet distribution in perennial ryegrass (*Lolium perenne* L.) and (b) influence of floret position within the spikelet on the seed set (%) for a total of 6,060 perennial ryegrass (*Lolium perenne* L.) florets assessed over 2 years, 2013 and 2014, and grown in a semi-protected environment at Flakkebjerg Research Centre, Aarhus University

C; Figure 2). Bornholm (Fields C and F; Figure 2) presented consolidated anthesis, which was reduced to 16 days, whereas West Zealand (Fields B and E; Figure 2) presented the least consolidated anthesis at 21 days.

## 3.2 | Precipitation reduced seed set

Increases in the total precipitation during anthesis significantly reduced the seed set ($p < .05$), and the nonlinear model accounted for 66% of the observed variations. The field seed set ranged between 50% and 66% for both years. The lowest percentage seed set was observed when the precipitation during anthesis was greater than 40 mm total (Figure 3).

The seed set in 2014 (Fields D, E and F; Figure 3) was 61.6% on average, whereas the seed set in 2013 (Fields A, B and C; Figure 3) was 51.5% on average, with all the fields expressing the same trend. Additionally, regional differences were observed in the reduced seed set (%). The seed set in West Zealand was 3.2 units lower in 2013 (Field B, Figure 3) than that in 2014 (Field E, Figure 3), and the seed set in Central Jutland and Bornholm was 13.6 units lower on average in 2013 (Fields A and C; Figure 3) than in 2014 (Fields D and F; Figure 3).

## 3.3 | Seed set within the spikelet

Variations in floret numbers for a population of inflorescences are shown in Figure 4a. The results for 2013 showed a significantly ($F_{(1,755)} = 4.378$; MSE = 10.96; $p = .03$) greater number of florets per spikelet at 8.07 ± 0.01 (mean ± *SE*) than the results for 2014, which showed 7.82 ± 0.01 florets per spikelet. The differences between years can most likely be attributed to the cooler spring conditions in 2013 (average spring temperature of 6.0°C in 2013 and 8.5°C in 2014 (data from DMI)). The data sets were pooled for the following analysis, which indicated that regardless of the year 85% of the population had seven or fewer florets per spikelet, and a large reduction of florets per spikelet was observed after this point.

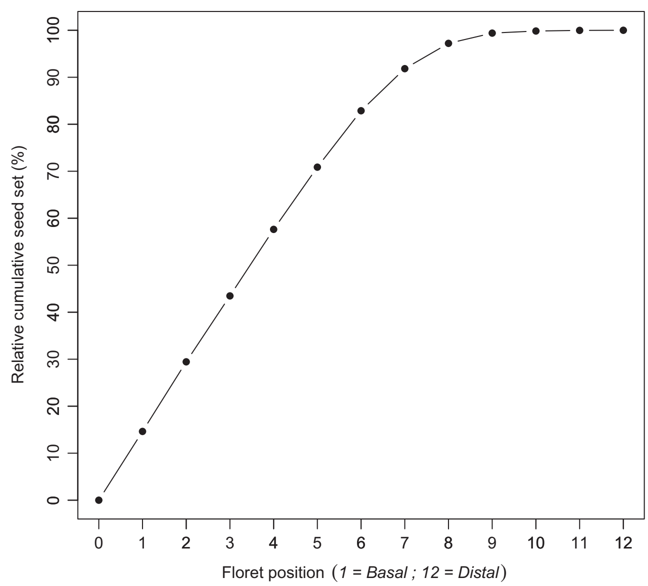


**FIGURE 5** Relative cumulative seed set (%) offered by each floret position to the total effective seed number per spikelet (100% = 5 seeds) of perennial ryegrass (*Lolium perenne* L.) assessed over 2 years, 2013 and 2014, and grown in a semi-protected environment at Flakkebjerg Research Centre, Aarhus University

Twelve florets per spikelet were observed in less than 0.5% of the total population of assessed spikelets.

In a semi-controlled environment protected from the effects of precipitation, a large variation in the average seed set levels was observed for each floret position throughout the spikelet (Figure 4b). The seed set ranged from 73.7% in the basal florets to 17% in the distal florets. Floret position two, that is, the second floret from the rachis, had the highest seed set rate at 73.7% ± 1.6%, whereas floret position ten (a distal floret position) had the lowest seed set at 17.0% ± 3.8% (Figure 4b). Compared with the maximum observed seed set, the florets located after position six had a seed set level of less than 60%. Significant year effects were not observed for the seed set between 2013 and 2014 when assessed via ANOVA ($F_{(1,755)} = 2.498$; MSE = 998; $p > .05$).

Because a population distribution was observed for the florets per spikelet (Figure 4a), with each of these floret positions having a different seed set (Figure 4b), the effective seed number per spikelet calculated here is five seeds. For example, 14% of the total effective seed number was derived from floret position one, whereas only 2% of the total effective seed number should be derived from floret position nine (Figure 5). Our calculations indicated that a critical floret per spikelet number of seven was required to generate five effective seeds.

## 4 | DISCUSSION

A consolidated anthesis pattern and seed set are both important factors in obtaining a high utilization of the potential seed yield. An increase in the total amount of precipitation over the anthesis period was found to increase the duration of anthesis (Figure 2), which was consistent with Emecz (1962) and Hill (1980), who noted that anthesis was inhibited under low temperatures and precipitation.

The field study sites were identified to highlight the climatic variability across Denmark. During 2013, our results identified a trend in anthesis in the order West Zealand > Bornholm > Central Jutland (Figure 1). However, the mild winter and spring period in 2014 advanced anthesis, with all fields entering anthesis within a few days of the others. Furthermore, Bornholm had the shortest duration of anthesis at 17 days (Figure 2), which most likely occurred because of the warm summers, whereas West Zealand was the least consolidated. Although a regional influence on anthesis was observed, the seed set was highest in 2014 because of the consolidated anthesis period (Figure 3).

The results presented here show that precipitation reduced the consolidation of anthesis (Figure 2) and seed set (Figure 3). To assess the influence of precipitation on the seed set, the average floret number per spikelet from the field and the relationship formed in Figure 4b are required. For example, during 2013, Central Jutland had an average floret per spikelet count of 7.8, whereas in 2014, this value was 6.9 (data not presented), and the maximum expected seed set for these numbers of florets per spikelet (from Figure 4b) was 64% and 67% respectively. However, in 2013 (a wet year), the seed set was reduced by approximately 22% compared with the calculated expected value (64% seed set calculated; 50% recorded), whereas in 2014 (a dry year), the calculated (67% seed set) and recorded (66% seed set) results were comparable. Overall, under field conditions in which less than 15 mm of precipitation falls during anthesis, the seed set was not influenced by precipitation, rather it was limited by the seed set variability within the spikelet (Figure 4b). Precipitation greater than approximately 20 mm limited the seed set under field conditions. Chastain, King, Garbacik, Young, and Wysocki (2015) reported a similar trend, with precipitation during anthesis reducing the seed set; however, they did not quantify this effect.

The reduced seed set resulting from increased precipitation may be limited by stigma receptivity and pollen longevity. Precipitation and humidity are highly correlated environmental factors, with increasing precipitation resulting in higher canopy humidity. Imrie (1966) showed that the stigma receptivity of male-sterile wheat (which is measured as a percentage of the seed set) was reduced by 40% under high relative humidity, thus indicating the importance of pollen hydration by the stigma. At dehiscence (low water contents), pollen grains tend to have a high osmotic potential. During times of high humidity, pollen grains may swell uncontrollably, which would effectively render the pollen defective in terms of normal stigma–pollen interactions as described by Heslop-Harrison (1979a) and Shivanna and Heslop-Harrison (1981).

In regions where precipitation did not limit anthesis, a maximum seed set of 73% was observed (Figure 4b). Under controlled glasshouse conditions, Warringa et al. (1998) found a similar level of seed set. The remaining 27% of florets that failed to produce a true seed (as defined by ISTA (2013)) can be a result of numerous factors including anthesis patterns within the spikelet. Warringa et al. (1998) reported that anthesis may occur 13 days later in distal florets than it does in basal florets within the same spikelet. Under field conditions, this delay will result in different environmental conditions during anthesis and seed development for distal florets. Moreover, the results of Yang et al. (2000) for rice (*Oryza sativa* L.) showed that asynchronous anthesis resulted in large variations in grain filling rates and produced a low overall grain filling percentage. The plant hormone cytokinin is believed to be an important regulating factor (Yang et al., 2000). Similarly, in perennial ryegrass, an increased duration of anthesis resulted in a reduced seed set, although other factors may have been responsible for the reduced seed set, including the pollen size/viability as influenced by floret position, which has been observed in barley (Matsui et al., 2000), or genetic/cytological mechanisms (Elgersma & Śnieżko, 1988). Recent findings on seed set patterns throughout the spikelet are consistent with Anslow (1963), Elgersma and Śnieżko (1988) and Warringa et al. (1998).

In the 50 years between the first seed yield study (i.e., Anslow, 1963) and this study, seed yield increases have been attributed to changes in agronomic practices rather than plant breeding/genetic increases (Chynoweth, Pyke, Rolston, & Kelly, 2015). Breeding for seed yield is often referred to in the current literature as representing the next step towards increasing seed yields in perennial ryegrass (Boelt & Studer, 2010; Stewart, 2015). The environmental conditions during the reproductive phase may alter the floret number. Work by Ryle (1965) showed that low light intensity and temperatures increased the floret numbers because of the extended duration of the reproductive development phase. Moreover, the floret number per spikelet is reported to be highly heritable (Bugge, 1987; Elgersma, 1990), although the floret number is reduced for later forming tillers (Ryle, 1964) with similar results observed for the spikelet number. Therefore, management practices have little influence on the floret number unless they alter tiller formation.

To date, few targeted seed yield breeding objectives have been established within perennial ryegrass breeding programmes. Both Marshall and Wilkins (2003) and Bugge (1987) indicated the importance of indirectly selecting for the seed number per inflorescence that results in increased seed yield, and the results presented here identify a direct breeding objective. Thus, it is recommended that plant breeders reduce the maximum floret number per spikelet to seven to achieve increased seed yields because more than seven florets per spikelet result in minimal increases in seed numbers per spikelet (Figure 5).

Breeding seven or fewer florets per spikelet should provide additional benefits in terms of reducing the anthesis period. Based on the spikelet anthesis data from Warringa et al. (1998), a reduced floret number per spikelet would reduce the anthesis period from 15 days to approximately 8 days for a mid-inflorescence-positioned spikelet. Currently, an unconsolidated anthesis period is believed to be a seed yield-limiting factor because anthesis variations lead to uneven seed development and/or a greater risk of seed shattering (Boelt & Studer, 2010). Although this study cannot fully confirm the hypothesis of Boelt and Studer (2010), our results suggest that an increase in the seed yield would be feasible by reducing the floret number per spikelet and consolidating anthesis; however, this hypothesis warrants further investigation.

## 5 | CONCLUSIONS

According to seed set studies conducted under both field conditions and in a semi-controlled environment, increases in precipitation were found to reduce the consolidation of anthesis and the rate of seed set. The seed set distribution declined throughout the spikelet from the basal to the distal florets, and more than seven florets per spikelet resulted in minimal increases in the seed number per spikelet. It is recommended that plant breeders should restrict the spikelet size to seven florets.

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