from tillers initiated early (from three-leaf stage to jointing), whereas late-initiated tillers produce few kernels and contribute minimally to yield (Tilley et al., 2019). The timing of tiller initiation and cessation, together with tiller mortality between jointing and anthesis, governs final spike density and explains large genotypic differences in spike number. Genetic variation in traits such as tillering onset, duration, and survival indicates substantial scope to manipulate these temporal patterns for yield improvement (Xie et al., 2015).

Temporal dynamics of tillering interact with canopy signals and resource competition. Low red:far-red light ratios arising as canopies close tend to accelerate the end of tillering and promote tiller abortion, thereby fixing spike number earlier in genotypes that are more sensitive to shading (Xie et al., 2015). Management and environment modify these dynamics by altering water status, radiation interception, and assimilate availability during the tillering window. Under post-jointing drought, ear-bearing capacity and seed setting of specific tiller positions are highly sensitive to the exact spike developmental stage at which stress occurs, with tillers at intermediate positions showing the greatest reductions in kernels per spike and grain yield per spike (Lin et al., 2020). These findings highlight that both the calendar time and developmental time at which stresses or inputs occur are critical in determining final spike number.

3.2 Limiting factors in grain number formation

Grain number per unit area is jointly determined by spike number and grains per spike, and both components follow a similar pattern of over-production of reproductive structures followed by intense abortion. Detailed observations of tiller and floret primordia show that survival, rather than initiation, is the primary driver of variation in spike number per area and grains per spike, especially during the late reproductive phase when degeneration is most intense (Bicego et al., 2024). Resource availability around stem elongation and heading strongly affects the survival of initiated tillers and florets, making grain number highly plastic in response to shading, thinning, and other changes in assimilate supply.

Within spikes, floret fertility and grain set are constrained by floral degradation and developmental timing. In hexaploid wheat, visible floral degradation from green-anther stage to anthesis strongly influences maximum floret primordia, fertile florets, and final grain number per spikelet, while detillering delays this degradation and increases the number of fertile florets and grains. The spatial gradient along the spike also reflects developmental limitations; basal spikelets are developmentally delayed and therefore exhibit higher floret abortion and more rudimentary spikelets, even when assimilate distribution along the spike is relatively uniform (Backhaus et al., 2023). Ovary size at anthesis emerges as a key integrative trait: larger ovaries, especially in distal florets, are associated with higher floret and grain survival, linking pre-anthesis growth with post-anthesis grain set (Guo et al., 2016).

3.3 Environmental response mechanisms of thousand-grain weight formation

Thousand-grain weight (TGW) is mainly determined during the grain filling period through the interplay between grain filling rate and duration. Field experiments manipulating post-anthesis night temperature show that warming of about 4 °C from 10 days after anthesis to maturity shortens the effective grain filling period, reducing TGW by roughly 3% per degree while leaving grain filling rate largely unchanged (Garcia et al., 2016). Similar work under controlled heat stress indicates that high temperatures hasten physiological maturity and decrease final grain weight, with genotypic differences in heat tolerance closely associated with the capacity to sustain a high grain filling rate (Dias and Lidon, 2009). These responses reflect sink-limited grain growth where accelerated development truncates the time over which potential grain size can be realized.

Broader analyses of climate-related factors confirm that elevated temperature and drought generally reduce grain yield of C3 cereals by depressing TGW. Meta-analysis shows that thousand-grain weight is particularly sensitive to warming, whereas drought and heat together can substantially reduce grain filling and starch accumulation even when grain number is less affected (Mariem et al., 2021). At the crop scale, variation in TGW can be explained by differences in post-anthesis thermal regime and radiation, as well as water availability that maintains photosynthesis and nitrogen metabolism during grain filling (Ru et al., 2023). New remote-sensing approaches, such as UAV-based estimation of grain filling rate and TGW from canopy traits, emphasize that TGW integrates