### 4.3 Integrated effects of planting density and sowing date adjustment

Planting density and sowing date jointly shape yield by balancing spike number, grains per spike, and grain weight. In northeastern Poland, increasing sowing density from 200 to 400 live grains $m^{-2}$ raised spikes·$m^{-2}$ and grain yield, while delaying sowing by 14-28 days slightly reduced grains per spike but increased thousand-grain weight, with maximum yields achieved under mid-September to early October sowing and higher densities (Lachutta and Jankowski, 2024). A broader multi-genotype study found sowing date had a stronger impact on yield components than plant density, though density strongly correlated with heading time and tillering pattern (Kiss et al., 2018).

Fine-tuning density with N and sowing time can mitigate yield loss in sub-optimal windows. Under rice-wheat rotation, late sowing reduced spikes and kernels, but higher planting densities combined with a 25% N increase (300 kg·N·$ha^{-1}$) restored yield, with optimal densities depending on whether sowing was delayed 10 or 20 days (Tian et al., 2024). Other semi-winter wheat trials report that sowing around early-mid October at densities near $450 \times 10^4$ plants $ha^{-1}$ maximizes yield, with higher densities mainly increasing spike number and lower densities favoring thousand-grain weight (Chen et al., 2021).

## 5 Coupling Relationships among Yield Components

### 5.1 Trade-off between spike number and grains per spike

The relationship between spike number per unit area and grains per spike is typically antagonistic, reflecting resource limitations during pre-anthesis development. Large multi-environment analyses show that increases in grains per·$m^2$ are usually achieved either via more spikes per·$m^2$ or more grains per spike, but simultaneous maximization of both components is rare (Xie and Sparkes, 2021). Compensation between these two routes appears as a hierarchy of plasticity, where spike number acts as a coarse regulator of grains per·$m^2$ and grains per spike fine-tune the response when resources or genotypes change.

Long-term trial data in winter wheat confirm that the strongest negative correlation among yield components often occurs between spike number and grains per spike, illustrating a robust trade-off in many environments. Yet cultivars differ in how strictly they follow this relationship; some lines deviate positively, combining relatively high spike number with high grains per spike and thus partially escaping compensation (Mandea et al., 2019). Recent work on grain number plasticity further suggests that overlapping developmental periods for tiller and floret mortality can generate feedback between spike number and grains per spike, so that resource shifts during stem elongation alter both components simultaneously (Bicego et al., 2024).

### 5.2 Synergistic and compensatory effects between grain number and grain weight

Across studies, grain yield is more tightly related to grains per·$m^2$ than to average grain weight, and negative correlations between grain number components and thousand-grain weight (TGW) are frequently reported. Genome-wide association in tetraploid wheat indicates that many loci for kernel number per spike (KNS) and TGW show opposing phenotypic effects, so gains in one component are often partially offset by losses in the other (Mangini et al., 2018). This genetic antagonism underpins the classic trade-off where increases in grain number reduce average grain size, limiting yield progress.

Nonetheless, both physiological and genetic evidence show that the trade-off is not absolute and can be mitigated. Doubled haploid populations derived from parents contrasting in grain number and weight have produced transgressive segregants with high grain number and relatively large grains, achieving very high yields and reducing the usual compensation. At the molecular level, some manipulations of expansin expression increased grain size without reducing grain number, boosting yield per spike and demonstrating that targeted modification of grain growth can overcome the typical negative association between grain number and grain weight in specific backgrounds (Calderini et al., 2020; Vicentin et al., 2024).

### 5.3 Mechanisms of multi-factor interactions affecting final yield

Final yield reflects not only pairwise trade-offs among components but also multi-factor interactions among management variables such as nitrogen, water, and density. Drip-fertigation experiments show that irrigation and