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The reduced-tillering trait (*tin*) is not beneficial under wheat cropping systems that allow for moderate to high water-limited yields

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Reduced-tillering wheat (*Triticum aestivum* L.) lines carrying the *tin* (tiller inhibition) gene are characterized by high spike fertility and high grain weights. These traits may enable high yields under favorable climatic conditions, provided that the low tillering is offset by an adequate sowing rate. Field trials were conducted to evaluate the effect of the *tin* gene by comparing two pairs of near-isogenic lines (NILs), namely Janz ± *tin* and Kite ± *tin*, sown at a rate of 350 germinable seeds m^{-2} across six environments (two sites × three years) in Italy (Sardinia and Emilia-Romagna). Seasonal rainfall (October–May) ranged from 311 to 784 mm, corresponding to mean grain yields between 3.5 and 6.7 t ha^{-1}. On average, the *tin* lines yielded similarly to their free-tillering counterparts (4.67 vs. 4.78 t ha^{-1}, respectively), owing to their higher grain weight (45.0 vs. 42.3 mg), which compensated for a lower grain number (10408 vs. 11554 m^{-2}) resulting from fewer spikes m^{-2} (406 vs. 437), despite a similar number of grains per spike. The reduced fruiting efficiency of *tin* lines (56.0 vs. 65.6 grains g^{-1} of spike), likely due to an inefficient investment in chaff, may have constrained the expression of their typically high spike fertility. However, the lower spike number plasticity in *tin* lines was balanced by greater plasticity in grain weight, enabling comparable grain yield plasticity between NILs. Although the grain yield level and plasticity of *tin* lines were comparable to those of free-tillering lines, these results do not support their adoption in cropping systems targeting moderate to high yields. On the other hand, the findings do not rule out the potential benefits of introgressing *tin* genes into different genetic backgrounds or improving fruiting efficiency to overcome the limitations identified in this study.

KEYWORDS

low tillering, wheat, plasticity, grain weight, spike fertility

1 Introduction

Breeders have been working on the tillering capacity of cereals, and an important achievement was obtained with the introgression of the *tin* (tiller inhibition) gene (Atsmon and Jacobs, 1977) into free-tillering bread wheat lines (*Triticum aestivum* L.). By shifting part of the soil water availability from pre- to post-anthesis, the reduced-tillering trait of *tin* lines showed a small but consistent advantage in terms of yield in the most water-limited environments of Australia under current and likely future conditions (Moeller and Rebetzke, 2017; Houshmandfar et al., 2020).

Tin lines not only produce fewer tillers (Duggan et al., 2005; Mitchell et al., 2013; Sadras and Rebetzke, 2013; Hendriks et al., 2016; Moeller and Rebetzke, 2017; Motzo et al., 2004), but also generate more fertile spikes and larger, heavier grains (Richards, 1988; Duggan et al., 2005; Mitchell et al., 2012, 2013; Hendriks et al., 2016; Moeller and Rebetzke, 2017; Motzo et al., 2004). However, the extent to which these traits are expressed strongly depends on the genetic background, environmental conditions, and management strategy adopted (Moeller and Rebetzke, 2017).

This near-uniculm growth habit—characterized by a high harvest index, large spikes, high spike fertility, and heavy grains—aligns well with the ideotype proposed by Donald (1968) for highly productive environments, such as those found in Italy. These range from the Mediterranean-type climates of Southern Italy and the Italian islands to the wetter areas of Northern Italy. Such environments typically receive more than 500 mm of seasonal rainfall (October–June) and experience less severe terminal water stress compared to Australian wheat-growing regions.

In Italy, bread wheat is generally cultivated at sowing densities of 350–400 viable seeds m^{-2} and nitrogen fertilization rates of 100–150 kg ha^{-1}. Under these conditions, Giunta et al. (2019) evaluated 27 bread wheat cultivars and reported average grain yields of 6.9 t ha^{-1} (ranging from 4.7 to 9.8 t ha^{-1}). Yield variation was not markedly constrained by fluctuations in seasonal rainfall, which ranged from 297 to 592 mm across the four environments tested.

In such contexts, *tin* lines are expected to increase grain yield by enhancing the proportion of main stems, which are presumably more fertile and productive than tillers (Lin et al., 2020), and potentially capable of producing heavier grains.

However, the effectiveness of adopting a *tin* plant type depends on meeting several key conditions. First, the advantages of higher spike fertility, grain weight, and harvest index in *tin* lines must also be expressed at sowing densities of 350–400 seeds m^{-2}. Previous studies assessing the impact of sowing density on *tin* lines used lower densities (approximately 150–300 seeds m^{-2}) and found no significant effects on yield or yield-related traits (Duggan et al., 2005). Additionally, Mitchell et al. (2013) reported that *tin* lines produced heavier grains than free-tillering lines at both 100 and 200 plants m^{-2}.

Second, the inherent reduction in tiller number plasticity in *tin* lines must be offset by increased plasticity in spike fertility and/or grain weight. Although grain weight is generally considered the least plastic of the yield components (Sadras and Slafer, 2012), even small increases in grain weight can contribute to yield gains—especially when amplified by high grain number per spike in favorable seasons.

Third, potential trade-offs between yield components must be carefully considered.

The aim of this study was to compare two *tin* lines with their near-isogenic free-tillering counterparts under environmental conditions typical of Italian wheat-growing areas, using the sowing and fertilization practices commonly adopted by local farmers. The trials were designed to test whether: (i) the higher spike fertility and grain weight observed in *tin* lines relative to free-tillering lines are maintained under these conditions and result in increased grain yield; and (ii) plasticity in spike fertility and grain weight allows *tin* lines to adapt to environmental variability.

2 Materials and methods

2.1 Sites and experimental design

Four field trials were conducted in Ottava (SS) (40.8°N 8.5°E, 80 m above sea level) in Sardinia, Italy, in the 2016/17 ('SS17'), 2017/18 ('SS18'), 2020/21 ('SS21') and 2022/23 ('SS23') seasons, and two field trials were conducted in Fiorenzuola d'Arda (PC) (44.9°N, 9.9° E, 82 m asl) in Northern Italy, in the 2016/17 ('FI17') and 2017/18 ('FI18') seasons.

The soil in Ottava consisted of a sandy clay loam of a maximum depth of about 0.6–0.7 m overlying a limestone bedrock (Xerochrepts). The climate is typically Mediterranean, with an annual rainfall of 552 mm, mainly concentrated between October and April (with reference to the past 60 years), and a seasonal rainfall (Oct–May) of 480 mm. The annual mean temperature is 16.3°C, with minimum winter (Jan–Mar) temperatures of 6.6°C and maximum spring (Apr–Jun) temperatures of 22.5°C. The soil in Fiorenzuola d'Arda is a deep silt clay loam, mesic Udic Ustochrepts, and the climate is temperate, with an annual average rainfall of 786 mm (with reference to the past 37 years) and a seasonal rainfall (Oct-May) of 574 mm. The annual mean temperature is 12.5°C, with minimum winter (Jan–Mar) temperatures of -1.9°C and maximum spring (Apr–Jun) temperatures of 23.0°C.

In all the six environments, we compared two near-isogenic pairs of lines (NILs) (commercial cultivars and two backcross oligoculm selections containing the *tin* gene of the donor line 492) of bread wheat (*Triticum aestivum* L.), namely Janz ± *tin* and Kite ± *tin*. The two NILs, kindly provided by Dr. R.A. Richards, possess the *tin* (tiller inhibition) gene, in linkage with the *Hg* (hairy glume) gene at 10 ± 3 map units (Richards, 1988). Kite ± *tin* is awnless while Janz ± *tin* is awned.

Fields were prepared by chisel-ploughing to a depth of 0.25 m, followed by surface cultivation. Sowing was performed at the rate of 350 germinable seeds m^{-2} between 31 October and 26 November in all environments except SS23, where the unfavorable rainfall pattern moved sowing to the 3 January. The preceding crop was barley at Fiorenzuola, and faba bean or Alexandrian clover at Ottava. Plots consisted of 8 rows 8.4 m long, with a between-row distance of 0.15 m, for a total area of 10 m^2. Nitrogen fertilization only was applied in the field trials in Fiorenzuola, split between sowing and April, for a total of 177 kg N ha_{-1} in 2017 and 108 kg

N ha_{-1} in 2018. Both N and P were applied in Ottava, with the N rate varying from 49 to 119 kg ha_{-1}, and P from 13 to 40 kg ha_{-1}. Weeds, pests and diseases were chemically controlled.

Treatments were arranged in a split-plot design with four replications. Cultivars were assigned to the main plots and the presence/absence of the *tin* gene to the sub-plots.

2.2 Measurements and data analysis

Emergence, booting (DC 39, Zadoks et al., 1974), anthesis (DC 61) and physiological maturity (DC 92) were recorded by periodical inspections of the plots when more than 50% of plants in the plot had reached that phenological stage.

Two biomass samplings were carried out at the stages of anthesis and physiological maturity. Four 0.5 m long samples of uprooted plants per plot, roots excluded, were hand-cut at each stage for a total of 0.3 m^2. Anthesis and maturity samples were divided into stems plus leaves (indicated as 'stems') and spikes, and the number of stem and spikes ascertained and expressed on a square meter basis. All samples were oven-dried at 80°C for 48 hours before weighing. Spikes from the maturity samples were threshed, and grain weight, number of grains $spike^{-1}$ and moisture content determined.

Nitrogen percentage was determined on each Ottava biomass subsample by means of a Carbon/Hydrogen/Nitrogen Analyzer (628 Series, LECO Corporation, St. Joseph, MI, USA).

The number of grains m^{-2} was calculated as the product of the number of spikes m^{-2} and the number of grains $spike^{-1}$. Grain yield was obtained on a plot basis with mechanical harvesting. Grain weight and grain yield were expressed at 0% humidity.

Fruiting efficiency was calculated according to Fischer (2011) as:

Fruiting efficiency (number of grains set per unit of spike dry weight at anthesis) = (number of grains m^{-2})/(spike weight m^{-2} at anthesis)

The grain filling rate was estimated by dividing grain weight by the number of days between anthesis and maturity, considered to be roughly representative of the grain filling duration. Translocation was estimated on both a single stem basis and on a unit surface basis:

Translocation on individual stem basis (g $stem^{-1}$) = dry weight one stem at maturity – dry weight one stem at anthesis

Translocation on a surface basis (g m^{-2}) = Translocation on one stem basis x number of stems m^{-2} at physiological maturity

The maximum fraction of photosynthetically active radiation intercepted (FIPAR) by the leaves was measured at booting, i.e. once all leaves had emerged and the maximum leaf interception reached. Measurements were made at noon using a portable probe (Sun-Scan Canopy Analysis System SS1-UM-1.05. Delta-T Devices Ltd., Burwell, Cambridge, UK) allowing the simultaneous measurement of photosynthetically active radiation above (using an external sensor) and below (using the probe) the canopy. The same instrument estimated the green area index (GAI). Using these data, we calculated the KPAR (extinction coefficient for photosynthetically active radiation) of each plot according to the formula:

$$KPAR = -[LN(1-FIPAR)]/GAI$$

The daily photothermal quotient (PTQ) for the booting-anthesis period was calculated following Fisher (1985) by dividing the daily intercepted PAR (calculated by multiplying the maximum FIPAR by half the daily total solar radiation recorded at the site) by the daily mean temperature minus 4.5°C. We also calculated the mean PTQ value for the whole booting-anthesis period.

Weather data (maximum and minimum temperature, rainfall, solar radiation, wind speed and air humidity) were recorded in meteorological stations located approx. 300 m from the fields. Reference evapostranspiration (ETo) was calculated from those data according to the Penman-Monteith equation (Allen et al., 1998). Cumulative growing degree days (°Cd) from sowing were calculated assuming a base temperature of 0 °C (Ritchie, 1991).

Linear regressions were used to explore the relationships between different agronomic traits, and to analyze trait plasticity (Finlay and Wilkinson, 1963; Lin et al., 1986; Becker and Leon, 1988). Plasticity was quantified separately for *tin* and free-tillering lines as the slope of the regression relating the line means of the two groups to the environment means (i.e. a response is non-plastic if it is in parallel to the mean environment response, as indicated by a regression coefficient of zero). We calculated plasticity for each group of lines using the 12 'environment x cultivar' means. We used t-tests to calculate the probability that differences in the slopes for *tin* and free-tillering lines occurred by chance.

After assessing the homogeneity of variances by means of the Bartlett Test, we performed a combined analysis of variance (ANOVA) by superimposing the year as the main plot factor on the original design. The resulting split-split-plot design is an extension of the split-plot design, and can be adopted to accommodate a third factor (Gomez and Gomez, 1984; Quinn and Keough, 2002). Year was the whole plot factor (A), cultivar was the sub plot factor (B), and +/- *tin* the sub-sub plot factor (C). Error (a) (Block x A) was used to test the significance of A; error (b) (Block x B(A)) was used to test A and A x B; error (c) (Block x C x (A X B)) was used to test C, A x C, B x C and A x B x C. Statistical analyses were conducted using R software (R Core Team, 2017), package 'agricolae', ssp.plot procedure. Following a significant F test, means were compared through the least significant difference (LSD) test, considering a probability level of 0.05, calculated using the appropriate standard errors of the mean and t values (Gomez and Gomez, 1984).

3 Results

3.1 Weather

Temperatures. From October to March, Fiorenzuola recorded lower temperatures than Ottava, with December showing the greatest difference: maximum temperatures averaged 16.8°C at Ottava and only 6.6°C at Fiorenzuola, and minimum temperatures

10.3389/fagro.2025.1636711

averaged 8.5°C at Ottava and -1.8°C at Fiorenzuola (Figure 1). Mean monthly minimum temperatures at Fiorenzuola dropped to around or below 0°C between December and January in both the 17/18 and 18/19 seasons. During this early part of the growing cycle, Ottava in 22/23 experienced the warmest temperatures between October and January.

In contrast, during the final three months of the growing cycle, both sites experienced similarly increasing temperatures. SS23 was the coolest environment during this period, particularly in terms of maximum temperatures, averaging 18.2°C compared with 24.4°C in the other environments. In April and May, the grain filling phase, maximum temperatures ranged from 18.7°C in SS23 to 22.6°C in FI17.

Evapotranspiration. Reference evapotranspiration (ETo) was also lower at Fiorenzuola than at Ottava during the October–March period, with values ranging from 0.3 to 1.9 mm d^{-1} at Fiorenzuola and 1.2 to 2.7 mm d^{-1} at Ottava. At Ottava, SS17 showed the highest ETo throughout the season, peaking at 6.5 mm d^{-1} in June, while SS23 recorded the lowest values, with 3.7 mm d^{-1} in May and 5.4 mm d^{-1} in June.

Rainfall. SS18 recorded the highest total seasonal rainfall (784 mm from October to June), partly due to an exceptional 200 mm in May. SS23, the second-wettest environment (649 mm), received most rainfall during winter, with 200 mm in December, 180 mm in January, and 150 mm in February. The driest season was 2017, with totals of 311 mm at Ottava and 329 mm at Fiorenzuola, although spring rainfall was higher at Fiorenzuola (117 mm from March to May) than at Ottava (25 mm). Total rainfall in FI18 was 518 mm, including a notable 136 mm in May.

The overall performance of *tin* and free-tillering lines across these environmental conditions was assessed at both anthesis and maturity.

3.2 Anthesis

Depending on the environment and sowing date, anthesis occurred between 9 April (SS18) and 16 May (FI18). In terms of cumulative growing degree days from sowing, anthesis ranged from 1318°Cd (FI18) to 1718°Cd (SS21). All lines flowered at approximately the same time, indicating that the *tin* gene did not affect developmental rate. Compared with the Italian commercial cultivar Bologna, grown in an adjacent field and sown on the same day in 2017 and 2018 at both SS and FI, the Australian lines flowered 8 days earlier at FI and 17 days earlier at SS. Cultivar Bologna can be considered representative of the leading Italian bread wheat cultivars, as it ranked among the top five Italian cultivars in 2018 based on certified seed production (https://www.crea.gov.it/web/difesa-e-certificazione/-/statistiche).

A wide variation in total biomass at anthesis (558–1174 g m^{-2}) and related traits was observed across environments (Table 1). The presence of the *tin* gene led to greater biomass, heavier stems, and higher spike dry weight per unit area, without affecting the proportion of fertile stems (about 0.90, regardless of *tin* presence) or the spike-to-total dry weight ratio (about 0.20). Cultivar Kite exhibited lower spike dry weight than Janz, both in absolute terms and relative to total dry weight.

Any effect of reduced tillering or cultivar on radiation interception by anthesis was ruled out based on data for the fraction of intercepted PAR (Supplementary Table S1), which ranged from a minimum of 0.55 at SS23—where late sowing limited GAI to 1.42—to a maximum of 0.96 at SS18, where GAI reached 6.31, but were not different between NILs (0.82 and 0.81 on average, se= 0.01). This fraction of intercepted radiation was used to calculate the mean daily photothermal quotient (PTQ) for the period between booting and anthesis. We observed a

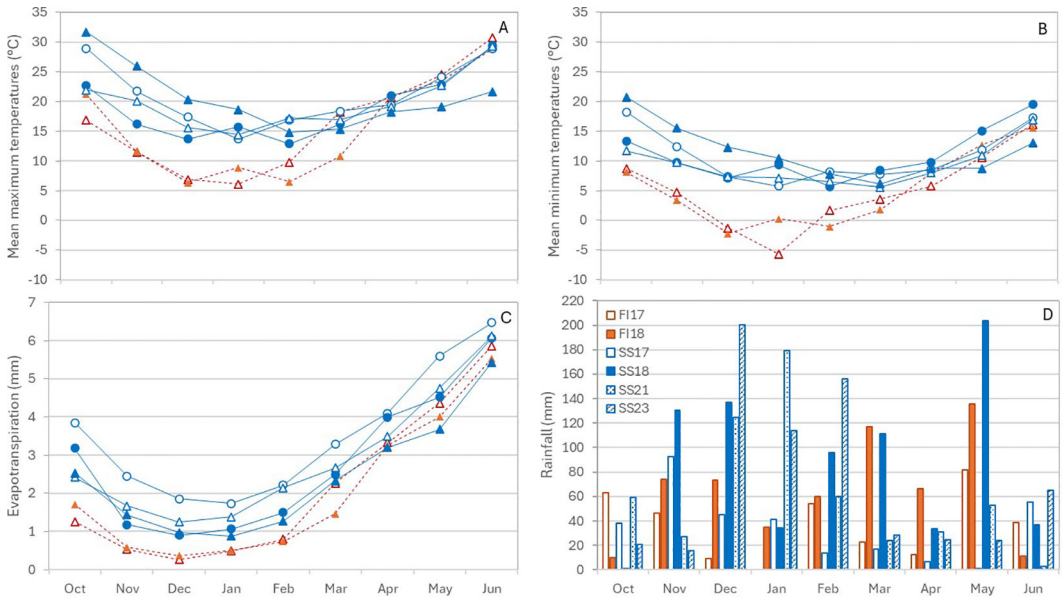

FIGURE 1
Average maximum monthly temperatures **(A)**, average minimum monthly temperatures **(B)**, mean monthly evapotranspiration **(C)**, and mean monthly rainfall **(D)** during the studied growing seasons. (FI17, orange empty triangles; FI18, orange full triangles; SS17, blue empty circles; SS18; blue full circles; SS21 blue empty triangles; SS23 blue full triangles).

10.3389/fagro.2025.1636711

TABLE 1 Anthesis sampling: treatment means of the measured traits and results of the ANOVA.

Source of variation	Total biomass	Spike biomass	Weight 1 'stem'	Spike weight/ total weight	Fertile stem number/ Total stem number
	(g m^{-2})	(g m^{-2})	(g)		
Environment	***	***	***	*ns*	***
FI17	906 bc	217 b	1.45 a	0.24	0.85 d
FI18	560 d	137 d	1.65 a	0.25	0.94 a
SS17	1174 a	242 a	1.55 a	0.2	0.88 c
SS18	993 b	245 a	1.46 a	0.25	0.91 b
SS21	827 c	163 c	1.63 a	0.19	0.95 a
SS23	558 d	129 d	0.81 b	0.22	0.95 a
Cultivar	*ns*	***	*ns*	***	*
Kite	829	169 b	1.45	0.18 b	0.91 b
Janz	851	210 a	1.38	0.23 a	0.93 a
TIN	**	**	***	ns	ns
Free-tillering	808 b	181 b	1.25 b	0.20	0.91
Tin	873 a	199 a	1.58 a	0.21	0.92
TIN x ENV	*ns*	*	**	*	*ns*
TIN x CULT	*ns*	*ns*	*ns*	***	**
ENV x CULT	**	**	ns	***	*ns*
TIN x ENV xCULT	ns	***	**	**	*ns*

ns, not significant at the ANOVA F-test; *significant for P ≤ 0.05; **significant for P ≤ 0.01; ***significant for P ≤ 0.001.
Means with the same letter are not significantly different at the LSD-test for P ≤ 0.05.

wide variation in mean PTQ across environments, ranging from 0.6 MJ °C^{-1} in SS23 (late sowing) to 1.4 MJ°C^{-1} in FI17, along with inconsistent and difficult-to-interpret differences between *tin* and free-tillering lines. As a result, NILs did not differ significantly in mean PTQ values.

Data on nitrogen uptake at anthesis and its partitioning between the spike and vegetative tissues ("stems") were available only for the four Ottava environments. These data showed no significant effect of the *tin* gene on N uptake or partitioning (Supplementary Table S2), despite large variation in these traits across environments. Cultivar Janz exhibited greater N uptake than Kite.

3.3 Maturity: grain yield and yield components

The presence of the *tin* gene had no effect on grain yield, and no interaction was detected between the *tin* gene and either the environment or parental cultivar for this trait (Table 2). Grain yield ranged from 3.5 ± 0.22 t ha^{-1} at SS23, likely due to late sowing, to 6.7 ± 0.22 t ha^{-1} at FI17. Yields were comparable to that of the Italian commercial cultivar Bologna, which produced 5.2 ± 0.7 t ha^{-1} when grown in adjacent fields and sown on the same day in 2017 and 2018 at both sites.

3.3.1 Grain number

Grain yield was more strongly associated with grain number per unit area (GNO; r = 0.83, P ≤ 0.001, n = 24) than with grain weight (r = 0.42, P ≤ 0.04). In turn, GNO correlated more closely with spikes m^{-2} (r = 0.64, P ≤ 0.001) than with grains $spike^{-1}$ (r = 0.41, P ≤ 0.04). However, no differences in these relationships were observed between *tin* and free-tillering lines.

The lower mean GNO in *tin* lines (11235 ± 182) compared to free-tillering ones (10741 ± 182) (Table 2) was attributed to the reduced number of spikes m^{-2} in *tin* lines (406 ± 7 vs 467 ± 7) across all environments except FI18 and SS21, which had the lowest spike densities. Spike fertility was higher in *tin* lines in only two out of six environments, and the average difference in spike fertility between NIL groups was not significant. Cultivar Kite exhibited fewer spikes m^{-2} than Janz.

The presence of the *tin* gene was also associated with lower fruiting efficiency (56.0 ± 1.4 vs 65.6 ± 1.4 grains g^{-1} of spike weight at anthesis), with no significant interaction with environment.

To assess the effect of environmental conditions around anthesis on GNO, values were regressed against the PTQ between booting and anthesis. Two distinct relationships emerged for *tin* and free-tillering lines (Figure 2), but comparison of intercepts and slopes revealed no significant differences.

10.3389/fagro.2025.1636711

TABLE 2 Yield and yield components.

Source of variation		Grain yield	Grain weight	GNO	Grains spike^{-1}	Spikes m^{-2}	Grain filling rate	Fruiting efficiency
		(t ha^{-1})	(mg)	(no m^{-2})	(no)	(no)	(mg °Cd^{-1})	(no grains g^{-1} of spike)
Environment		***	***	***	***	***	***	**
FI17		6.73 a	50.3 a	13431 ab	27.3 ab	500 ab	0.20 c	63.3 b
FI18		4.05 c	49.0 a	8335 c	25.5 bc	332 d	0.19 cd	62.3 b
SS17		4.99 b	41.4 b	12110 b	22.9 cd	542 a	0.29 a	53.7 c
SS18		5.46 b	40.5 b	13751 a	30.1 a	463 bc	0.14 e	57.0 bc
SS21		3.60 c	40.7 b	9449 c	29.8 a	320 d	0.27 b	58.1 bc
SS23		3.54 c	40.1 b	8884 c	19.7 d	452 c	0.19 d	71.1 a
Cultivar		*ns*	***	*ns*	*ns*	**	***	**
Kite		4.82	44.6 a	10741	25.7	420 b	0.22 a	65.1 a
Janz		4.64	42.8 b	11235	25.9	454 a	0.21 b	56.9 b
TIN		*ns*	***	***	*ns*	***	***	***
Free-tillering		4.78	42.3 b	11554 a	25.5	467 a	0.21 b	65.6 a
Tin		4.67	45.0 a	10408 b	26.2	406 b	0.22 a	56.0 b
TIN x ENV		*ns*	***	*ns*	**	***	***	*ns*
FI17	Free-tillering	6.32	48.6	13097	25.4	519	0.20	63.6
	Tin	6.80	52.5	12982	29.2	478	0.21	63.1
FI18	Free-tillering	4.08	46.0	8918	27.6	325	0.18	68.5
	Tin	4.08	51.8	7885	23.3	346	0.21	55.3
SS17	Free-tillering	5.10	38.6	13151	21.4	624	0.27	62.7
	Tin	4.88	44.3	11068	24.5	461	0.32	44.6
SS18	Free-tillering	5.50	40.1	14228	28.1	508	0.14	60.7
	Tin	5.43	40.9	13275	32.1	419	0.14	53.3
SS21	Free-tillering	3.80	40.0	10408	31.0	337	0.26	63.5
	Tin	3.40	41.3	8490	28.6	303	0.27	52.8
SS23	Free-tillering	3.70	39.9	9332	19.5	482	0.18	75.2
	Tin	3.38	40.2	8436	18.9	422	0.19	66.9
$LSD_{0.05}$		*0.04*	*1.5*	*1110*	*3.3*	*40*	*0.01*	*8.6*
TIN x CULT		*ns*	***	*ns*	*ns*	*ns*	**	*ns*
ENV x CULT		*ns*	***	*	***	*ns*	*ns*	*ns*
TIN x ENV x CULT		***	*	***	**	***	*ns*	*ns*

Treatment means of the measured traits and results of the ANOVA.
ns, not significant at the ANOVA F-test; *significant for P ≤ 0.05; **significant for P ≤ 0.01; ***significant for P ≤ 0.001;
Means with the same letter are not significantly different at the LSD-test for P ≤ 0.05.
$LSD_{0.05}$, Least Significant Difference for the comparison of *tin* and free-tillering lines within the same environment at P ≤ 0.05.

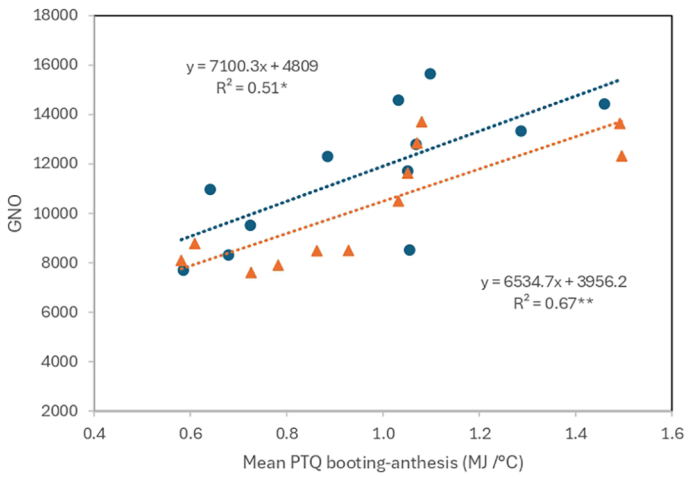

FIGURE 2
The relationship between mean photothermal quotient (PTQ, MJ°C^{-1}) between DC39 and DC61 and the grain number (GNO, grains m^{-2}). Data are tin x cultivar x environment means. Blu circles= free-tillering; Orange triangles= tin.

3.3.2 Grain weight

The *tin* gene had a positive effect on grain weight, with *tin* lines averaging 1.8 mg more than free-tillering lines. This difference resulted from a significant *tin* × environment interaction, driven by large differences of 5.7 mg at SS17 and 5.9 mg at FI18. Notably, in the driest environment (SS17), grain weight was more negatively affected in free-tillering lines than in *tin* lines.

Grain weight variation was significantly associated with the rate of grain filling in both NIL groups. A higher rate was observed in *tin* lines (0.22 ± 0.001 mg °Cd^{-1}) compared to free-tillering ones (0.21 ± 0.001 mg °Cd^{-1}), with the largest differences between NILs being 0.05 and 0.03 mg °Cd^{-1} at SS17 and FI18, respectively.

The greater grain weight of *tin* lines was also linked to their greater capacity to translocate assimilates to developing grains between anthesis and maturity. This was evident both on a single stem basis (0.4 ± 0.02 g stem^{-1} vs 0.2 ± 0.02 g stem^{-1}) and per unit area (25 ± 1.4 g m^{-2} vs 13 ± 1.4 g m^{-2}) (Table 3). For *tin* lines, translocation represented 25% of stem dry matter at anthesis when expressed per unit surface, and 16% on a per-stem basis.

The extent of translocation varied with environment, reaching a maximum in SS18, but it was not associated with post-anthesis water stress, as the most stressful grain filling conditions occurred in SS17, not SS18.

3.3.3 Nitrogen

Nitrogen data were available only for the four Ottava environments (Table 4). Grain protein content ranged from 9.9 ± 0.1% in SS21 to 16.1 ± 0.1% in SS18. Among these environments, SS18 consistently showed the highest total N uptake and N content in all plant organs, and, in terms of cultivars, Kite absorbed more nitrogen than Janz.

As observed at anthesis, the *tin* gene did not affect nitrogen-related traits, with the only exception being grain N per unit area (g m^{-2}), likely due to the higher GNO in free-tillering lines.

3.4 Plasticity

Plasticity in yield and related traits was assessed by calculating the slope of the regression between trait values and a gradient of environmental conditions ranging from 'unfavorable' to 'favorable', separately for the two groups of NILs. According to the determination coefficients R^2, the environmental indexes explained from 76 to 96% of the trait variation. The plasticity of spikes m^{-2} was significantly greater in free-tillering lines, indicating that this trait was less responsive (i.e., less plastic) in *tin*-containing genotypes (Table 5). Conversely, *tin* lines exhibited greater plasticity for grain weight.

No other traits showed significant differences in plasticity due to the presence of the *tin* gene, although the difference in spike dry matter at anthesis approached significance (P ≤ 0.055).

4 Discussion

The target environment of this experiment is not as water-limited as the Australian-type environments for which *tin* lines were proposed as a way of coping with severe terminal water stress (Duggan et al., 2005; Moeller and Rebetzke, 2017; Houshmandfar et al., 2020), as demonstrated by its high potential yield (Fischer, 2015), estimated in about 10 t ha^{-1}on a plot basis (Giunta et al., 2019). The sowing rate commonly adopted for wheat in these situations is 350–400 seeds m^{-2}, much higher than the 100–150 seeds m^{-2} typical of the Australian cropping systems (Kirkegaard and Hunt, 2010).

Under these conditions, reduced-tillering lines may be used, not to save water early in the season, but to increase the proportion of main stems and hence mean spike fertility, grain weight and, ultimately, grain yield, consistent with Donald's (1968) ideotype for high yields in favorable environments. Although *tin* lines generally performed less well than their free-tillering counterparts in the more favorable situations of Australia (with grain yields

10.3389/fagro.2025.1636711

TABLE 3 Translocation to the growing grains, roughly estimated as the decrease in stem dry matter (DM) between anthesis and maturity (data from FI18 are missing).

Source of variation		DM decrease anthesis-maturity	
		(g m^{-2})	(g $stem^{-1}$)
Environment		***	**
FI17		127 b	0.25 b
SS17		222 a	0.38 a
SS18		122 b	0.25 b
SS21		146 b	0.45 a
SS23		54 c	0.14 c
Cultivar		**	*
Kite		107 b	0.24 b
Janz		162 a	0.35 a
TIN		***	***
Free-tillering		107 b	0.20 b
Tin		162 a	0.38 a
TIN x ENV		**	***
FI17	Free-tillering	125	0.23
	Tin	128	0.27
SS17	Free-tillering	180	0.26
	Tin	263	0.50
SS18	Free-tillering	59	0.07
	Tin	186	0.44
SS21	Free-tillering	104	0.31
	Tin	188	0.58
SS23	Free-tillering	65	0.15
	Tin	43	0.12
$LSD_{0.05}$		48	0.1
TIN x CULT		ns	ns
ENV x CULT		***	***
TIN x ENV x CULT		***	***

Means and ANOVA results.
ns, not significant at the ANOVA F-test; *significant for P ≤ 0.05; **significant for P ≤ 0.01; ***significant for P ≤ 0.001.
Means with the same letter are not significantly different at the LSD-test for P ≤ 0.05.
$LSD_{0.05}$, Least Significant Difference for the comparison of *tin* and *non-tin* lines within the same environment at P ≤ 0.05.

exceeding 2 t ha^{-1}, Moeller and Rebetzke, 2017), the difference in sowing rate might be expected to have an impact on the relative performance of *tin* vs free-tillering lines, as shown by the *tin* x sowing rate interaction for yield described by Duggan et al. (2005), with *tin* lines yielding more than the freely tillering lines at the higher but not at the lower sowing rates.

To investigate this possibility, we studied the effects of the tiller-inhibition gene in wheat grown in six different field environments, characterized by large differences in seasonal (Oct-May) rainfall, varying from 311 to 784 mm, and a wide range of grain yield (3.5–6.7 t ha^{-1}), considering two genetic backgrounds (Kite and Janz), which differ in most of the traits recorded at anthesis and in their yield components, but which are similar in terms of overall grain yield and flowering time. It is noteworthy that, despite the wide range of environmental conditions, no environment-by-line interaction was detected for grain yield. This result can be attributed to the similar and early anthesis dates of the NIL lines, which makes these findings applicable to a wide range of environments. Based on the available data for cultivar Bologna, which is representative of the best Italian bread wheat cultivars, the productivity of the Australian cultivars evaluated in this experiment falls within the range of Italian commercial cultivars.

The lower mean number of spikes m^{-2} recorded for the *tin* lines compared with their free-tillering counterparts was not an obvious result, considering the negative relationship between tiller number and plant population density (Darwinkel, 1978). On average, *tin* lines produced 13% fewer spikes m^{-2} than their free-tillering counterparts, lying in-between the 11% (Duggan et al., 2005) and 16% (Moeller and Rebetzke, 2017) quoted in the literature with respect to lower sowing densities. The sowing rate adopted here did not prevent *tin* lines from producing a certain number of fertile tillers, which was nonetheless smaller than in the free-tillering lines and insufficient to guarantee a value of plasticity in spikes m^{-2} comparable to that expressed by free-tillering lines. This lower number and degree of plasticity in spikes m^{-2} is an obvious and proven consequence of the reduced-tillering habit (Moeller and Rebetzke, 2017; Duggan et al., 2005).

Despite the reduction in spikes m^{-2}, *tin* lines assured a grain yield and a level of plasticity in grain yield comparable to the free-tillering lines in all the environmental conditions and genetic backgrounds. This result contrasts with what was observed in the Australian context and suggests a difference in how *tin* altered the balances and trade-offs, i.e. the compensation, between GNO and grain weight.

4.1 The effect of *tin* gene on the grain number

GNO was the main determinant of grain yield, and the generally lower GNOs produced by *tin* lines derived from the inability of their spike fertility to compensate for the lower number of spikes m^{-2}. But in contrast with previous studies reporting a variable but significantly greater grain number $spike^{-1}$ in *tin* vs free-tillering lines at lower plant population densities (Duggan et al., 2005; Mitchell et al., 2012), we observed no difference in the average grain number $spike^{-1}$, signalling that the sowing rate adopted did not allow the full expression of the '*gigas*' phenotype, i.e. limited tillering plus large and proliferous spikes and robust and vigorous vegetative parts (Atsmon and Jacobs, 1977). Duncan et al. (2005) similarly observed a decrease in *tin* spike fertility at higher sowing densities.

Analyzing GNO through the Fischer's (2011) approach (GNO = spike weight m^{-2} at anthesis x number of grains g of $spike^{-1}$ or 'fruiting

10.3389/fagro.2025.1636711

TABLE 4 Nitrogen (N) uptake and partitioning at harvest.

Source of variation	Grain protein	Grain N	Stem N	Chaff N	N in grains	N in stems	Total N
	(%)	(mg grain^{-1})	(%)	(%)	(g m^{-2})	(g m^{-2})	(g m^{-2})
Environment	***	***	*	ns	***	***	***
SS17	10.7 c	0.78 c	0.76 b	1.04	9.4 b	4.8 b	16.8 b
SS18	16.1 a	1.14 a	1.03 a	0.91	15.4 a	6.5 a	23.5 a
SS21	9.9 d	0.71 d	0.73 b	0.91	6.3 c	2.5 c	9.7 d
SS23	13.2 b	0.93 b	0.88 ab	1.06	8.1 b	3.0 c	14.3 c
Cultivar	***	***	ns	**	**	*	**
Kite	13.1 a	0.97 a	0.86	1.09 a	10.4 a	4.7 a	17.4 a
Janz	11.8 b	0.81 b	0.84	0.88 b	9.2b	3.7 b	14.7 b
TIN	*ns*	*ns*	*ns*	*ns*	*	*ns*	*ns*
Free tillering	12.5	0.88	0.90	0.96	10.1 a	4.5	16.6
Tin	12.4	0.90	0.81	1.01	9.5 b	3.9	15.5
TIN x ENV	*ns*	*ns*	*ns*	*	*ns*	*ns*	*ns*
TIN x CULT	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
ENV x CULT	*	**	*ns*	*ns*	*	*ns*	*ns*
TIN x ENV x CULT	*ns*	*ns*	*ns*	*ns*	*	*ns*	*

Means and ANOVA results. Fiorenzuola environments were not available.
ns, not significant at the ANOVA F-test;
*significant for P ≤ 0.05;
**significant for P ≤ 0.01.
Means with the same letter are not significantly different at the LSD-test for P ≤ 0.05.

TABLE 5 Plasticity of *tin* and *free-tillering* lines for the main measured traits, quantified as the slope of the regression between line means and environment means.

Source of variation	Free-tillering		*Tin*		Probability T-test
	Plasticity (b ± s.e.)	R^2	Plasticity (b ± s.e.)	R^2	*tin vs* free-tillering
Grain yield (t ha^{-1})	0.95 ± *0.07*	0.95	1.05 ± *0.07*	0.96	0.389
Grain weight (mg)	0.83 ± *0.09*	0.90	1.17 ± *0.09*	0.94	0.026
Grain number m^{-2}	1.07 ± *0.10*	0.92	0.93 ± *0.1*	0.9	0.376
Number of grains spike^{-1}	1.00 ± *0.18*	0.76	1.00 ± *0.18*	0.76	0.978
Number of spikes m^{-2}	1.25 ± *0.10*	0.94	0.75 ± *0.1*	0.84	0.007
Fruiting efficiency	1.01 ± *0.12*	0.87	0.99 ± *0.12*	0.87	0.899
Spike DM at anthesis (g m^{-2})	0.87 ± *0.08*	0.91	1.13 ± *0.08*	0.95	0.055

efficiency') revealed that *tin* lines were able to build a greater biomass by anthesis thanks to their heavier stems, more than compensating for their lower number of spikes m^{-2}, and to translate this greater biomass into a greater spike weight at anthesis. The reduced tillering did not compromise their ability to intercept radiation in the critical period for grain number determination (here, roughly considered to coincide with the booting to anthesis period). In fact, although Moeller et al. (2014) observed both a lower leaf area index and lower radiation interception in *tin* lines compared with free-tillering lines, the relationship between tillering, leaf area index and radiation interception is not straightforward (Duggan et al., 2005; Sadras and Rebetzke, 2013). Therefore, what limited the production of higher grain numbers in *tin* lines was their lower fruiting efficiency, which prevented any advantage being gained from the greater biomass and spike weight at anthesis. As already observed (Gaju et al., 2009; Motzo et al., 2004), the increase in chaff weight induced by the *tin* gene is disproportionately

greater than the increase in grains spike^{-1}, resulting in lower fruiting efficiencies. The earlier cessation of bud outgrowth associated with the *tin* gene during the transition of the shoot apex from the vegetative to the reproductive stage (Kebrom et al., 2012) likely favored the allocation of the diverted assimilates to organs that were growing in that period, while also lengthening the duration of their growth. Rachis and glumes start growing before the florets (McMaster et al., 1992); hence, this earlier availability of resources may have resulted in a greater growth and weight of the spike's structural tissues and, in turn, a heavier chaff weight, but not necessarily in more fertile florets. A possible avenue to overcome this limitation could be an increase in the number of competent florets per spike weight, and/or in the proportion of competent florets that progress through pollination, fertilization and early grain survival to bear grains at maturity (Fischer, 2011). The association between floral abortion and the 7Ag.7DL translocation in wheat (Reynolds et al., 2005) could be useful in breeding for a higher fruiting efficiency.

4.2 The effect of *tin* gene on the grain weight and protein percentage

The greater grain weight of *tin* lines was the yield component accounting for both the similar grain yields of *tin* and free-tillering lines, despite the lower number of grains m^{-2} in the former, and the lack of any decrease in grain yield plasticity in *tin* compared with free-tillering lines.

The mean grain weight recorded here for *tin* lines (45 mg) was significantly higher than the values reported for most of the Australian environments at lower plant population densities, despite the negative effect of an increase in plant population density on the grain weight in *tin* lines observed by Mitchell et al. (2013). Moeller and Rebetzke (2017) quoted a mean grain weight of 38 mg for *tin* lines grown across different water stress environments, whereas the higher grain weight recorded by Mitchell et al. (2013), for their higher plant density treatment (about 200 plants m^{-2}) cultivated under irrigation, was 31 mg.

The greater anthesis biomass, translocation and grain filling rate associated with the higher grain weight of *tin* lines was in line with previous observations (Mitchell et al., 2013). Higher rates of grain filling and greater translocation are both important for environments with terminal water stress (Mitchell et al., 2013; Asseng et al., 2019). That is why the SS17 environment, characterized by the most severe water stress, was the one in which the greatest difference between the two NIL groups was observed. On the other hand, the lack of any increase in spike fertility meant that the potentially higher amount of water-soluble carbohydrates present in the denser stems by anthesis (Motzo et al., 2004; Dreccer et al., 2013) were shared between a lower number of grains per spike, allowing them to grow at a higher rate, resulting in higher final grain weights also in the more favorable environments with abundant spring rainfall (FI18, SS18).

Therefore, we can at least partly attribute the higher plasticity in grain weight observed in the *tin* lines to the exploitation of greater quantities of assimilates and resources per spike in the more favorable environments, which compensated for their lower plasticity in spikes m^{-2}, as shown by the similar levels of grain yield plasticity in *tin* and free tillering lines, in contrast with what was observed under Australian agricultural systems (Moeller and Rebetzke, 2017).

Grain protein percentage is the most important component of wheat grain quality, and low protein grains are better suited for feed and not for human consumption (Shewry, 2009). The range in grain protein percentage recorded in the four environments for which nitrogen traits were available lay within those reported by Duggan et al. (2005). Interestingly, the increase in grain weight did not cause a 'dilution effect' on grain protein content, and by consequence did not result in a decrease in grain protein percentage, confirming the findings of Duggan et al. (2005). GNO is generally considered the sink for grain nitrogen (Martre et al., 2006). In this sense, the lower GNO of *tin* lines meant that the similar amounts of nitrogen taken up by anthesis by *tin* and free-tillering lines were shared by a lower, although heavier, number of grains at maturity.

5 Conclusions

The expected advantages arising from a greater proportion of main stems in *tin* lines were only partly achieved, as the unfruitful investment in chaff weight prevented the expression of their characteristic higher spike fertility at the sowing densities analyzed. The limited plasticity in the number of spikes m^{-2}, together with the reduced fruiting efficiency, compromised the yield potential under favorable environmental conditions. On the other hand, we must be careful not to rule out the possibility that the notable increase in grain weight and grain weight plasticity was, at least partly, a consequence of the lack of any increase in spike fertility. This is why the grain yield level and grain yield plasticity of *tin* lines, although comparable to free-tillering ones, do not justify their use for increasing wheat productivity in the target bread wheat cropping systems in Italy. On the other hand, the observed cultivar effect does not allow us to exclude the possibility that the limits highlighted here cannot be overcome by the introgression of the *tin* genes in other genetic backgrounds, or by genetic improvement of fruiting efficiency.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

FM: Formal Analysis, Writing – original draft, Data curation, Investigation. RM: Writing – original draft, Supervision, Conceptualization, Writing – review & editing. F-WB: Investigation, Formal Analysis, Writing – review & editing, Data curation. FR: Data curation, Investigation, Formal Analysis, Writing – original draft. FG: Writing – review & editing, Conceptualization, Methodology, Supervision, Formal Analysis, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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