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Can nutrient-utilization efficiency be improved by reduced fertilizer supply to maize plants treated with the plant growth regulator paclobutrazol?

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Abstract

In previous investigations of several maize cultivars, an improvement of the harvest index was obtained by paclobutrazol (PAC) application combined with an increase in water-use efficiency. However, so far nutrient-utilization efficiencies could not be enhanced when control and PAC-treated maize plants received the same amount of fertilizers. With adjusted fertilizer supply according to the lower requirement of the smaller, PAC-treated plants, an improvement of nutrient-utilization efficiencies may be expected. Thus, in the present study, PAC was applied at growth stage V5 to two maize cultivars (*Zea mays* L. cvs. Galactus and Fabregas) grown in a container experiment. Shortly after PAC application, differential NPK fertilization was introduced in order to obtain a nutrient supply according to the requirement of control plants (100% NPK), the requirement of PAC-treated plants (85% NPK) and a further slight decrease (78% NPK). Plant height and transpiration rates were significantly reduced due to PAC treatment with stronger effects on Galactus than on Fabregas. Pollen shed, silking and the anthesis-silking interval (ASI) were unaffected by PAC application and fertilizer supply. Senescence of PAC-treated plants was delayed, whereas it was accelerated with reduced fertilizer supply. The grain yield of cultivar Galactus was significantly decreased due to PAC application by 13% to 20%, and this effect was strengthened due to reduction in NPK supply. These grain yield reductions were solely caused by decreases in kernel number, which were closely linked to reductions in cob length. On the contrary, PAC treatment did not affect grain yield of Fabregas and reductions due to less NPK supply were small. Harvest index and water-use efficiency were enhanced by PAC treatment. Plant nutrient contents were similar for control and PAC-treated plants, but strongly related to fertilizer supply with significant decreases due to reductions in NPK application. The N-, P- and K-utilization efficiencies of both cultivars were either decreased or unaffected by PAC treatments. The key constraint for improvements of nutrient-utilization efficiencies is grain yield reduction due to PAC. This problem should be addressed in further studies with avoidance of grain yield decreases by delayed application time combined with fine-tuning of cultivar-specific PAC application rates.

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KEYWORDS

gibberellin-biosynthesis inhibitor, grain yield, harvest index, kernel number, nitrogen-use efficiency, *Zea mays*

1 | INTRODUCTION

For many cereal crops, an increase in harvest index (ratio of grain yield to total above-ground biomass at physiological maturity) was achieved during the last decades, either by breeding due to the introduction of dwarfing genes, or agronomically by the application of growth regulators. A prominent example is wheat for which an increase in the harvest index by 50% was accompanied by an increase in grain yield by 59% (Hay, 1995). This improvement is in contrast to maize, where the harvest index was almost unchanged since the introduction of hybrids, and concomitant grain yield increases of 51% were mainly achieved by higher plant stand densities (Hütsch & Schubert, 2017; Russell, 1991). Yet, the huge amount of vegetative biomass, which is mostly not utilized in grain maize production, requires large amounts of nutrients and water. An increase in harvest index may thus improve resource-use efficiencies, which will be particularly important in the future as fertilizer applications have to be reduced in order to meet environmental limits and water will become an increasingly limiting factor for crop production (Davies et al., 2011; Ort & Long, 2014).

One possibility to increase maize harvest index is the reduction in vegetative shoot growth. Gibberellins (GAs) are the most important hormones for plant extension growth and thus for internode elongation in maize (Sponsel, 1995). GAs in higher plants primarily stimulate organ growth through enhancement of cell elongation and cell division (Hedden, 2020), and they promote certain developmental switches, such as between vegetative and reproductive development by induction of flowering (Evans & Poethig, 1995), and have a large impact on fertility (Hedden & Thomas, 2012). Semi-dwarf mutants with genetically inherent inhibition of gibberellin biosynthesis do exist also for maize (Fujioka et al., 1988; Harberd & Freeling, 1989), yet they are not used in commercial maize production because of negative effects on flower sexuality (Bortiri & Hake, 2007; Irish, 1996; Rood et al., 1980; Xu et al., 2004). The abnormalities in maize flowers could possibly be overcome by application of GA biosynthesis inhibitors, which allow the induction of reduced GA concentrations during selective phases of maize ontogenesis and not during the entire growth period as in the dwarf mutants. In order to decrease vegetative shoot growth of maize, the gibberellin-biosynthesis inhibitors paclobutrazol (PAC) and uniconazole (UCZ) are suitable. PAC- and UCZ-treated maize plants showed decreased plant height and thicker culms due to reduced elongation growth of the internodes (e.g., Hütsch & Schubert, 2018, 2021; Iremiren et al., 1997; Kamran et al., 2018; Schluttenhofer et al., 2011).

Nutrient-use efficiency is determined by two components: nutrient-uptake efficiency and nutrient-utilization efficiency (nutrient-UtE) (Haegele et al., 2013; Moll et al., 1982). The first parameter refers to the amount of nutrient absorbed by plants relative to the available soil N. The second parameter quantifies the amount of dry matter produced per unit of absorbed nutrient (Moll et al., 1982). In our study, we focus on nutrient UtE_{grain}, which is defined as grain dry matter / nutrient content of total above-ground biomass at physiological maturity (Hütsch & Schubert, 2017). With an improvement of nutrient UtE_{grain}, also the nutrient-use efficiency of fertilizers can indirectly be enhanced, as less fertilizer needs to be applied in order to achieve maximum grain yield (Hütsch & Schubert, 2017; Raun & Johnson, 1999). Less fertilizer application reduces the risk of losses, for example due to nitrate leaching, denitrification or phosphorus runoff. Another frequently used parameter is the nutrient-harvest index (nutrient-HI), which describes the partitioning of a specific nutrient between the total above-ground biomass and grain (Hay, 1995; nutrient-HI is defined as: grain nutrient content / nutrient content of total above-ground biomass at physiological maturity).

Most information on nutrient-use efficiency exists for nitrogen. The roles of nitrogen (N) in plant metabolism are versatile. Nitrogen is strongly associated with the source component via Rubisco in leaf tissue enabling photosynthesis, and via the stay-green capability of leaves (Ciampitti & Vyn, 2012). Nitrogen deficiency reduces leaf area index, leaf area duration and photosynthetic rate (Lemcoff & Loomis, 1986; Sinclair & Horie, 1989; Wolfe et al., 1988). Grain yield and kernel number were also reduced by suboptimal N supply (Jacobs & Pearson, 1991; Lemcoff & Loomis, 1994; Uhart & Andrade, 1995b), which could be attributed either to effects on assimilate partitioning to the maize cob during the critical period around silking (Uhart & Andrade, 1995a) or to direct effects on enzymes involved in kernel development (Below et al., 2000). In addition, N-induced alterations in hormone metabolism are closely linked to the regulation of vegetative and generative plant growth. These reports clearly demonstrate the major effect that N nutritional status exerts over maize grain yield formation during the entire growing season (Ciampitti & Vyn, 2012). Sinclair (1998) pointed out that improvements in harvest index do not only depend on the importance of carbon allocation to the grain, but that a concomitant increase in crop N accumulation is also required. As N concentration of grain is more than five times that of straw, any major shifts in the relative fraction of grain and straw require large changes in N accumulation by the plant and in allocation within the plant.

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Values for nitrogen-use efficiency strongly depend on the amount of plant-available N. With increasing N application not only a decrease in N-uptake efficiency was observed, but also a successive decline in N-utilization efficiency (Barbieri et al., 2008; Gao & Chu, 2020; Haegele et al., 2013; Liao et al., 2012; O'Neill et al., 2004; Wang et al., 2020). In contrast to nitrogen-use efficiency, information about P- and K-use efficiencies is scarce. According to Ciampitti and Vyn (2014), historical improvements in N-, P- and K-utilization efficiencies of maize were primarily achieved by reductions in nutrient contents per plant at crop maturity. The authors point to the importance of a balanced plant nutrition, as high-yield maize was associated with ratios of N:P and N:K of 5:1 and 1:1, respectively. In a modelling approach, the highest values of N-, P- and K-utilization efficiencies for a balanced nutrition were obtained, when 60%–70% of the grain yield potential had been reached (Setiyono et al., 2010). With yield approaching the yield potential, utilization efficiencies of these nutrients decreased.

For several maize cultivars, an improvement of the harvest index was obtained by PAC application (Hütsch & Schubert, 2018, 2021). Concomitantly, an increase in water-use efficiency for the time around silking was achieved. This time span is particularly important for kernel setting, as water limitation during flowering can cause kernel abortion making an efficient water use decisive to achieve high grain yields. However, no increases in nutrient-utilization efficiencies were observed after PAC application to maize plants (Hütsch & Schubert, 2018, 2021). Instead, among six tested cultivars, significant decreases in nutrient-utilization efficiencies occurred for N and K in five and three cultivars, respectively, and no effect for P was recorded due to PAC application in comparison with untreated control plants (Hütsch & Schubert, 2021). In these studies, all plants received the same amount of fertilizers, although the growth of the PAC-treated plants was strongly reduced. These smaller plants showed luxurious nutrient consumption resulting in highly significant increases in N concentrations of grain and straw, and in P and K concentrations of straw compared with the untreated control (Hütsch & Schubert, 2021). Thus, with adjusted fertilizer supply according to the lower requirement of PAC-treated plants, luxurious consumption can probably be avoided and improvements of nutrient-utilization efficiencies may be expected.

For the present study, container experiments were conducted with the maize cultivars Galactus and Fabregas, which showed the best performance among six tested cultivars with respect to improvement of harvest index and water-use efficiency after PAC treatment (Hütsch & Schubert, 2021). The plant growth regulator was applied once at an early growth stage (V5), and thereafter, differential NPK fertilization was introduced in order to obtain a nutrient supply according to the requirement of control plants (100% NPK), the requirement of PAC-treated plants (85% NPK) and a further slight decrease (78% NPK). Our investigations focused on the following hypotheses: Reduced NPK fertilizer supply according to the lower requirement of smaller, PAC-treated maize plants (a) prevents luxurious nutrient consumption by the plants, (b) has no negative impact on grain yield and its components kernel number and kernel weight and (c) leads to improved N-, P- and K-utilization efficiencies.

2 | MATERIALS AND METHODS

2.1 | Plant cultivation, PAC application and measurements during growth

The experiment was conducted at the experimental station of the Institute of Plant Nutrition in Giessen (50°35´53.30´´N, 8°40´1.56´´E) during the vegetation period of 2020. Maize plants (*Zea mays* L.) were cultivated according to Hütsch and Schubert (2018, 2021) using the container technique. One hundred and twenty litre plastic containers were filled with 145 kg of a Luvisol subsoil (loamy sand: 21.2% clay, 34.5% silt, 44.3% sand; CAL-P: 8.9 mg P kg^{-1}, CAL-K: 58.3 mg K kg^{-1}; pH ($CaCl_2$) 5.9 prior to liming). The air-dry soil was mixed with $CaCO_3$ (2.5 g kg^{-1} soil; pH ($CaCl_2$) 7.5 after liming) and filled into the containers in four layers: Three layers with 30 kg soil moistened with 3 L deionized water each, and a topsoil layer (approx. 0–30 cm) which was fertilized with 40 g compound fertilizer ('Blaukorn') per container, consisting of 4.8 g N, 2.1 g P, 5.6 g K, 0.5 g Mg, 2.4 g S, 0.004 g Zn and 0.008 g B. Additionally, 0.32 g Zn, 0.16 g Cu and 0.08 g Mn were applied per container. The topsoil layer was moistened with 4.4 L deionized water.

On 13 May 2020, the maize cultivars Galactus and Fabregas were sown. Twelve days after sowing (DAS), the number of plants was reduced from nine to four per container, and water content was adjusted to 60% maximum water-holding capacity (WHC). During the whole vegetation period, water content was adjusted to this WHC by water applications at least twice daily, and water supply was recorded for each container. With this experimental setup, plant roots could exploit a rather large soil volume (120 L per container, soil depth 80 cm). The plants grew in a vegetation hall under natural light conditions. The average daily temperature during the vegetation period ranged from 12°C to 29°C with a mean of 21.7 ± 0.3°C. The containers were set up in a completely randomized design, and their position was changed at least once a week.

For each genotype, two treatments were set up (control and PAC application), which were subdivided into three fertilization regimes: 100% NPK supply with additional fertilizer application (10 g 'Blaukorn' per container) four times during the vegetation period, on June 12, June 25, July 6 and July 17. This application of in total 80 g 'Blaukorn' per container is according to the requirement of maize plants grown under control conditions. In the two other fertilization regimes, this amount was reduced to 85% NPK and 78% NPK by lowering the supply of 'Blaukorn' to 6 g and 4 g, respectively, at the three last application dates. The macronutrients Mg and S, which are also contained in this compound fertilizer, were supplemented in order to achieve a supply similar to the 100% NPK treatment. The reduction in NPK supply to 85% and 78% was calculated as optimal and suboptimal dosage to the smaller PAC-treated plants according to our previous study (Hütsch & Schubert, 2021). The different fertilization regimes were started after PAC application in order to avoid changes in synchronization in plant ontogenesis due to variation in NPK supply. As PAC is applied at a defined growth stage, the same application date for all maize plants is advantageous. Otherwise,

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varying weather conditions (temperature, solar radiation) at different dates can affect uptake and metabolism of PAC within the plants and impair results. With two maize cultivars, control and PAC treatment, three fertilization regimes and four replicates, the experiment consisted of 48 containers in total.

On June 15 (33 days after sowing, DAS) between 10 and 11 a.m., the growth regulator PAC was applied at stage V5, when the collar of the 5th leaf was visible in all plants, and 4% had already reached V6. This early growth stage was chosen in order to achieve reductions in vegetative growth and minimize effects on generative development. The cultivar-specific dosage of PAC was derived from a preliminary experiment, where five application rates (0.5, 1, 2, 3, 4 mg active ingredient (a.i.) PAC per plant) were tested for each cultivar. The lowest dosages which showed significant effects on vegetative plant growth were used for the container experiment, and which in our previous study proved to be successful with respect to increases in harvest index and WUE_{grain} (Hütsch & Schubert, 2021). These cultivar-specific PAC dosages per plant were 3 mg a.i. for Galactus and 2 mg a.i. for Fabregas. For the two dosages, 52.42 and 34.94 mg PAC (22.9% w/w) were dissolved in 1 L of deionized water and poured onto the soil surface of each container, which resulted in the desired applications of 3.0 and 2.0 mg a.i. PAC per plant, respectively. All solutions were prepared fresh in the morning of the application day. In order to ensure fast uptake of the chemicals by the plant roots, no water was applied to the containers on this day. The soil of the control treatment received 1 L deionized water only.

Growth stages were determined on the following dates: June 07, 10, 14, 15, 22 and 29 (25, 28, 32, 33, 40 and 47 DAS, respectively). Plant height (measured from the shoot base to the tip of the longest leaf) was monitored on June 15, 22, 29 and July 06, 13 and 30 (33, 40, 47, 54, 61 and 78 DAS, respectively). On 78 DAS (45 DAA, days after application of PAC), leaf areas were also determined by measuring length and maximal width of each leaf blade (leaf area = 0.5 × length × width). This date lay two weeks after the last differential fertilizer application and was chosen to indicate possible effects of NPK supply on leaf area in addition to effects of PAC treatment. For one week (41–48 DAA), transpiration rates were calculated by dividing the consumed volume of water per plant and per day during this time span by the mean leaf area. The consumed water also included evaporative water losses, which in our previous study accounted for approximately 15% of total water demand (Hütsch & Schubert, 2021).

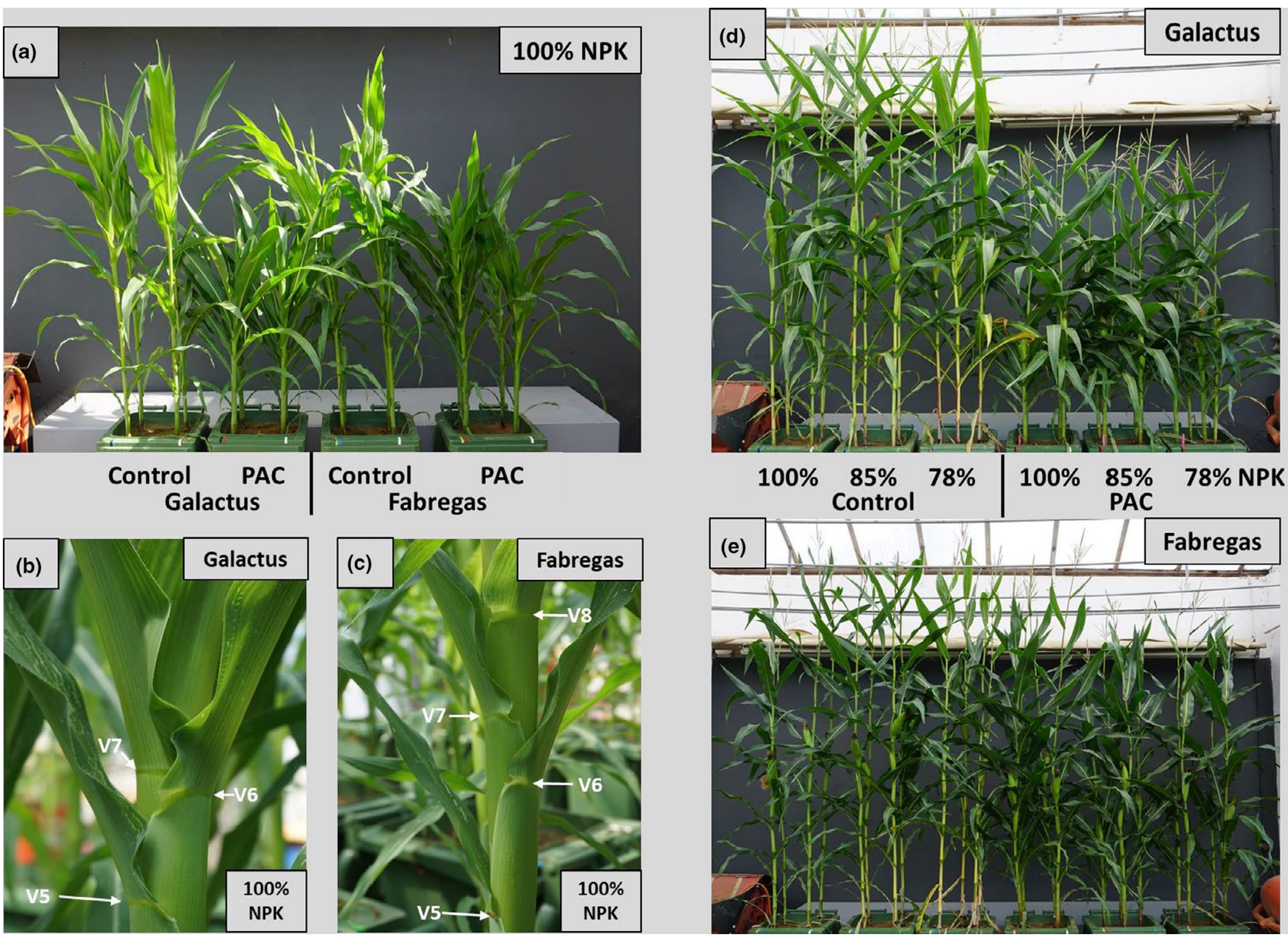

FIGURE 1 Effect of the plant growth regulator paclobutrazol (PAC) on the development of maize cultivars Galactus and Fabregas with 100% NPK fertilizer supply: (a) at 51 days after sowing (DAS) and 18 days after PAC application (DAA), (b) and (c) at 47 DAS (14 DAA); and at 83 DAS (50 DAA) with 100%, 85% and 78% NPK supply to (d) Galactus and (e) Fabregas; PAC dosage per plant: Galactus 3 mg a.i., Fabregas 2 mg a.i. [Colour figure can be viewed at wileyonlinelibrary.com]

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Starting with July 12, production of fresh pollen and start of silking was recorded for each plant daily in the morning until July 23. From these data, the duration of pollen production and the anthesis-silking interval ASI (start silking minus start pollen production) were determined. For better comparisons of grain yield per plant and of yield components, such as kernel weight and kernel number per cob, tillers had been removed immediately after appearance. Axillary branches were not produced. Additional cobs on the main culm were not removed, as the effect of PAC application on this trait was evaluated. Start of senescence (yellowing of older leaves, appearance of red-coloured culms) was also recorded. Pesticides against European corn borer and aphids were applied when required.

2.2 | Harvest and analyses of plant material

For each maize cultivar, treatment and fertilization rate four containers with four plants each were harvested at physiological maturity 138 and 139 DAS (September 28 and 29). Plant height, straw dry mass per container, cob dry mass per plant, cob length, maximal cob diameter (measured at cob base), number of kernel rows per cob, kernel dry mass (80°C drying), kernel number per cob and individual kernel weight were determined after harvest. Barren cobs were added to the straw material, which also included the rachis. The dried straw and grain material were milled to fine powder and dry-ashed. Potassium concentrations were determined using atomic absorption spectrometry, and P concentrations were determined colorimetrically. Total N concentrations were measured using an elementar analyser (Unicube® trace, Elementar Analysensysteme GmbH, Langenselbold, Germany). Sample digestion was carried out via catalytic combustion at a temperature of 950°C, with the nitrogen-containing components in the sample forming N_2, which was measured with thermal conductivity detection.

The nutrient concentrations are given as mg nutrient g^{-1} dry matter. For the determination of the nutrient content per plant, which reflects net nutrient uptake of the above-ground biomass, the concentrations were multiplied by the corresponding plant dry weights.

2.3 | Calculation of efficiency parameters and statistical analysis

Harvest index (HI), water-use efficiency of grain (WUE_{grain}), nutrient-utilization efficiency of grain (nutrient UtE_{grain}) and nutrient-harvest index (nutrient-HI) were calculated according to the following equations:

$$\mathrm{HI} = \text{Grain yield/Total above} - \text{ground biomass at physiological maturity} \quad (1)$$

$$\mathrm{WUE}_{\mathrm{grain}} = \text{Grain dry matter/Total water consumption} \quad (2)$$

$$\mathrm{WUE}_{\mathrm{grain}}\,\text{during silking} = \text{Grain dry matter/water consumption during 4 weeks around silking (silking} \pm 2\text{ weeks)} \quad (3)$$

$$\text{Nutrient UtE}_{\mathrm{grain}} = \text{Grain dry matter/Nutrient content of total above} - \text{ground biomass at physiological maturity} \quad (4)$$

$$\text{Nutrient} - \mathrm{HI} = \text{Grain nutrient content/Nutrient cotent of total above} - \text{ground biomass at physiological maturity.} \quad (5)$$

Means ±standard errors (*SE*) were calculated from four replicates per growth regulator treatment, fertilizer supply and maize cultivar. After two-way ANOVA (factors: growth regulator treatment and fertilizer supply) using *Rstudio*, multiple comparisons of means were conducted following adjustment with the *Tukey* test. Statistically significant differences are indicated with different letters ($p \le 5\%$). Differences between the two cultivars were not statistically evaluated, as they had received different amounts of the plant growth regulator.

3 | RESULTS

For each cultivar, firstly, the effects of PAC treatment in comparison with the untreated control are described, and secondly, differences due to reduced fertilizer supply are evaluated for control and PAC treatment, respectively. Individual effects of fertilization rates on control or PAC-treated plants of one cultivar are named as follows: for example Galactus-PAC-100%NPK, which means the 100% NPK supply to PAC treatment of cultivar Galactus. Occasionally observed significant differences between control and PAC treatment with different fertilizer rates are not explicitly mentioned in the text.

3.1 | Vegetative plant growth and development, and time of flowering

Culm elongation growth of the two maize cultivars was considerably decreased at 18 days after application (18 DAA) of PAC with stronger effects on Galactus than on Fabregas, mainly resulting from the higher PAC dosage to Galactus (Figure 1a). At 14 DAA, plant development was significantly retarded due to PAC treatment, which can be demonstrated with the lower growth stage and reduced plant height in comparison with the control plants (Table 1). The different intensity of growth retardation of the two cultivars can also be seen in Figure 1b and 1c: Galactus showed a stronger decrease in internode length between the 5th and 7th leaf (V5 and V7) in comparison with Fabregas, and in Galactus the collar of the 8th leaf was not yet visible, whereas this growth stage had already been reached by

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TABLE 1 Plant growth stage at 14 DAA (days after application of the plant growth regulator paclobutrazol, PAC), plant height at 14, 21, 28 and 45 DAA, leaf area at 45 DAA, and transpiration rate (calculated for the timespan 41 to 48 DAA) of two maize cultivars under control conditions and after application of PAC, with decreasing fertilizer supply

			Growth stage (V-stage)	Plant height (cm)				Leaf area (cm^2 $plant^{-1}$)	Transpiration rate ($mL\ cm^{-2}\ d^{-1}$)
Maize cultivar	Fertilizer supply	Treatment	14 DAA	14 DAA	21 DAA	28 DAA	45 DAA	45 DAA	41 to 48 DAA
Galactus	100% NPK	Control	8.6 ± 0.2 a	176 ± 3 a	220 ± 4 a	257 ± 5 a	296 ± 2 a	4,039 ± 124 a	0.219 ± 0.006 a
		PAC	7.3 ± 0.2 c	138 ± 2 b	151 ± 3 b	174 ± 5 b	223 ± 5 b	4,272 ± 78 a	0.149 ± 0.008 c
	85% NPK	Control	8.5 ± 0.2 a	179 ± 5 a	221 ± 6 a	259 ± 7 a	295 ± 3 a	3,985 ± 33 a	0.203 ± 0.011 a
		PAC	7.5 ± 0.2 bc	139 ± 2 b	152 ± 3 b	177 ± 5 b	223 ± 4 b	4,043 ± 152 a	0.159 ± 0.004 bc
	78% NPK	Control	8.4 ± 0.1 ab	177 ± 6 a	217 ± 4 a	254 ± 3 a	300 ± 2 a	3,880 ± 121 a	0.192 ± 0.012 ab
		PAC	7.2 ± 0.3 c	134 ± 3 b	145 ± 3 b	166 ± 5 b	212 ± 5 b	4,066 ± 123 a	0.159 ± 0.008 bc
Fabregas	100% NPK	Control	8.3 ± 0.0 ABC	173 ± 1 A	216 ± 5 A	264 ± 3 A	304 ± 4 A	3,364 ± 90 A	0.217 ± 0.004 ABC
		PAC	8.0 ± 0.1 BC	148 ± 1 B	185 ± 2 B	221 ± 2 B	273 ± 5 B	3,702 ± 160 A	0.196 ± 0.007 BC
	85% NPK	Control	8.6 ± 0.3 A	178 ± 2 A	228 ± 4 A	270 ± 4 A	313 ± 6 A	3,671 ± 54 A	0.229 ± 0.013 A
		PAC	7.9 ± 0.1 C	151 ± 4 B	186 ± 5 B	224 ± 7 B	269 ± 8 B	3,628 ± 64 A	0.188 ± 0.003 C
	78% NPK	Control	8.5 ± 0.1 AB	185 ± 4 A	232 ± 2 A	271 ± 4 A	310 ± 3 A	3,671 ± 44 A	0.224 ± 0.005 AB
		PAC	7.9 ± 0.1 C	145 ± 3 B	183 ± 3 B	225 ± 4 B	273 ± 4 B	3,670 ± 71 A	0.205 ± 0.007 ABC

Note: Data show means of four replicates ±SE; significant differences ($p \leq 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

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Fabregas at 14 DAA (Figure 1b and 1c). Fertilizer supply had no significant effect on growth stage and plant height (Table 1; Figure 1d and 1e). The strongest reduction in plant height was obtained at 14 DAA for Fabregas (17% on average), and one week later at 21 DAA for Galactus (32% on average). Shortly after flowering, at 45 DAA, the final plant height was reached, and the growth reduction due to PAC application in comparison with the control had become smaller (12% and 26% on average for Fabregas and Galactus, respectively), pointing to an alleviated inhibition by PAC (Table 1). In addition, the height of cob insertion was also significantly affected by PAC treatment with average reductions of 23% and 53% for Fabregas and Galactus, respectively (not shown), and was thus stronger than maximal decreases in plant height.

At 45 DAA, no effect of PAC treatment or fertilizer supply on total leaf area was observed (Table 1). In all treatments, Galactus had higher leaf areas than Fabregas. Shortly after flowering, during kernel setting (41–48 DAA), the transpiration rates were significantly reduced due to PAC treatment, namely for Galactus with 100% and 85% NPK supply, and for Fabregas with 85% NPK supply (Table 1). These smaller transpiration rates were solely caused by significant reductions in water consumption of the PAC-treated plants, which ranged between 19% and 28% during the considered time period (not shown). The different fertilizer supply showed no significant effects on transpiration rates (Table 1).

Tillers were only produced by three plants of cultivar Galactus. They occurred prior to PAC treatment at 25 DAS and were immediately removed after detection.

For both maize cultivars, pollen production started between 63 and 64 DAS and was unaffected by PAC treatment and fertilizer supply (Table 2). The duration of pollen production ranged between 5 and 7 days and also showed no significant differences. Start of silking was delayed by only 1–2 days (anthesis-silking interval, ASI) with no significant effects of PAC application and fertilizer supply. The ASI values were calculated with the four replicates, then means and *SE* were determined; thus, in some instances, these values slightly deviate from the differences between the means of start of silking and pollen production, respectively (Table 2).

3.2 | Senescence, yield determinants and harvest index

Two weeks after anthesis, in both cultivars, older leaves of the control treatment with 78% NPK supply showed chloroses and starting necroses, and the culm basis of Galactus began to turn red (83 DAS, Figure 1d and 1e). Similar but less pronounced effects were observed in the control plants with 85% NPK supply. The first symptoms of senescence on PAC-treated plants were observed about one week later. At harvest (physiological maturity), a few PAC-treated Galactus plants still showed some greenish colour of the youngest leaves, yet the cobs had already reached maturity.

At maturity, almost all plants had produced only one kernel-carrying cob (Figure 2). An exception occurred in the PAC treatment of Galactus-85%NPK, where one plant had developed seven cobs at one node, and apart from one barren cob, they were infested by corn smut and had to be removed six weeks before harvest. Multiple cobs at one node were also produced on a plant of Galactus-PAC-100%NPK (three with cob smut) and of Fabregas-Control-100%NPK (no cob smut), respectively, although only one cob each set kernels. These two cobs were not included in further

TABLE 2 Start and duration of pollen production, start of silking and anthesis-silking interval (ASI; start silking minus start pollen production) of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply; DAS = days after sowing

			Pollen production		Silking	Anthesis-Silking Interval
Maize cultivar	Fertilizer supply	Treatment	Start (DAS)	Duration (d)	Start (DAS)	ASI (d)
Galactus	100% NPK	Control	63.0 ± 0.2 a	5.8 ± 0.4 a	64.3 ± 0.2 a	1.3 ± 0.2 a
		PAC	63.0 ± 0.6 a	6.3 ± 0.3 a	64.0 ± 0.6 a	1.0 ± 0.2 a
	85% NPK	Control	63.3 ± 0.4 a	5.5 ± 0.3 a	64.3 ± 0.3 a	1.0 ± 0.2 a
		PAC	63.0 ± 0.5 a	6.7 ± 0.4 a	64.0 ± 0.5 a	0.9 ± 0.2 a
	78% NPK	Control	63.8 ± 0.8 a	5.3 ± 0.4 a	65.1 ± 0.5 a	1.4 ± 0.5 a
		PAC	62.6 ± 0.8 a	6.5 ± 0.3 a	63.7 ± 0.9 a	1.1 ± 0.3 a
Fabregas	100% NPK	Control	63.2 ± 0.4 A	6.1 ± 0.4 A	63.9 ± 0.4 A	0.7 ± 0.1 A
		PAC	63.3 ± 0.5 A	5.4 ± 0.4 A	64.9 ± 0.5 A	1.6 ± 0.4 A
	85% NPK	Control	63.5 ± 0.6 A	5.4 ± 0.2 A	63.9 ± 0.6 A	0.4 ± 0.2 A
		PAC	63.3 ± 0.4 A	6.2 ± 0.4 A	64.4 ± 0.1 A	1.1 ± 0.4 A
	78% NPK	Control	63.4 ± 0.8 A	5.7 ± 0.6 A	64.5 ± 0.8 A	1.1 ± 0.2 A
		PAC	64.2 ± 0.1 A	5.3 ± 0.4 A	65.0 ± 0.3 A	0.8 ± 0.2 A

Note: Data show means of four replicates ±SE; significant differences ($p \leq 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

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FIGURE 2 Effect of the plant growth regulator paclobutrazol (PAC) and differential fertilizer supply (100%, 85%, 78% NPK) on cob development of maize cultivars Galactus and Fabregas at maturity (at 138/139 days after sowing (DAS) and 105/106 days after PAC application (DAA); PAC dosage per plant: Galactus 3 mg a.i., Fabregas 2 mg a.i. [Colour figure can be viewed at wileyonlinelibrary.com]

analyses, as their grain yield lay well below the other three treatment replicates. Galactus control plants with 100% NPK generally showed good kernel development over the entire cob (Figure 2). With reduced fertilizer supply, however, kernel abortion in the apical part of the cobs occurred more frequently. In the PAC treatment, the cobs were shorter and distinct kernel abortion was observed with 78% NPK supply. In Fabregas, the best cob development obviously occurred in the control plants with 85% NPK, whereas the cobs with 100% and 78% NPK supply showed kernel abortion at their tips. In the PAC treatment, reduction in cob length was only visible with 85% NPK, whereas apical kernel abortion was more pronounced in all fertilization rates in comparison with control plants (Figure 2).

The grain yield of cultivar Galactus was significantly decreased due to PAC application with reductions between 13% and 20% in comparison with the control (Figure 3a). In addition, gradual grain yield decreases in Galactus in control and PAC-treated plants were caused by stepwise reduction in NPK supply. For cultivar Fabregas, the picture is different: PAC treatment showed no effect on grain yield, and significant reductions due to less NPK supply were only observed between 100% NPK and 78% NPK of PAC-treated plants (Figure 3a). The straw yield of Galactus was significantly reduced by 27–32% in the PAC treatment, whereas fertilizer supply showed no effect on straw yield (Figure 3b). For Fabregas, a significant reduction in straw yield by 20% was observed due to PAC treatment only with 85% NPK application, and the different fertilization had also no effect on straw yield (Figure 3b). The harvest index could be improved due to PAC treatment in all NPK rates of both cultivars, although the difference to the control was only significant for Galactus-85%NPK, where an increase of 10% was obtained (Figure 3c). In addition, with *t* test for each fertilizer step separately, significant increases in harvest index by PAC application were also obtained in Galactus-100%NPK and Fabregas-85%NPK. Different fertilizer supply had no impact on the harvest index (Figure 3c).

For cultivar Galactus, PAC treatment caused significant decreases in kernel number, which lay in the range of 16–21% (Figure 4a). A significant smaller kernel number due to less fertilizer supply was only observed between 100% NPK and 78% NPK of the Galactus control treatment. For cultivar Fabregas, only for 85% NPK a significant decrease in kernel number was observed due to PAC treatment, whereas reduced fertilizer supply had no effect (Figure 4a). Kernel weight of Galactus was affected neither by PAC treatment nor by different fertilizer supply, which was also true for Fabregas with one exception (significant decrease in kernel weight between 100% NPK and 78% NPK of the PAC treatment; Figure 4b). The cobs of the Galactus control plants with 100% NPK were characterized by a higher kernel number and rather small kernels as compared to Fabregas (Figure 4a and 4b). Effects of PAC treatment and fertilizer supply on cob length were closely related to variations in kernel number (Figure 4c versus Figure 4a). For Galactus, cobs were significantly shorter due to PAC treatment and due to the reduction in fertilizer supply to 78% NPK (Figure 4c). For Fabregas, a significant

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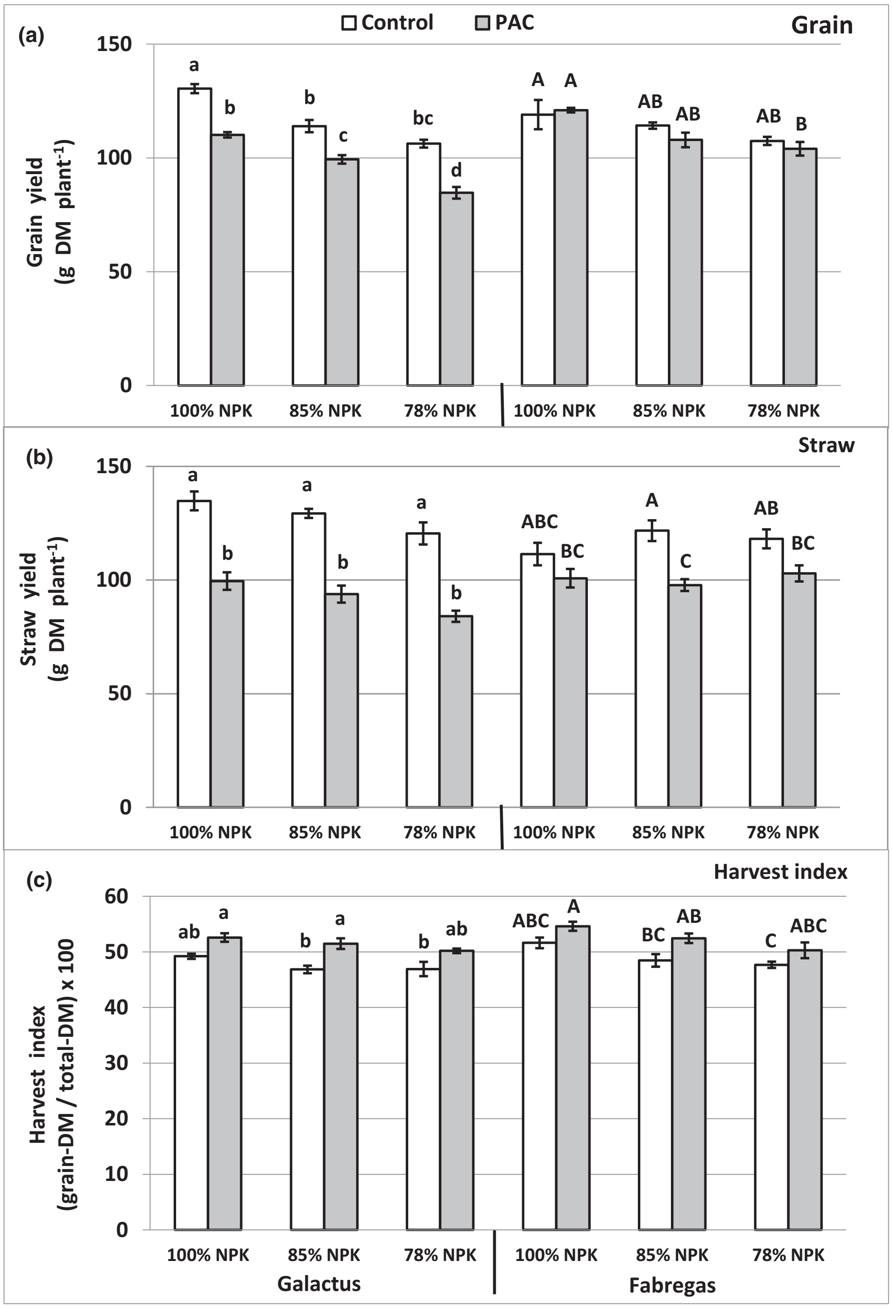

FIGURE 3 Grain dry matter yield (a), straw dry matter yield (b) and harvest index (c) of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply; data show means of four replicates ±SE; significant differences ($p \le 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

difference in cob length was only observed after PAC treatment combined with 85% NPK supply (Figure 4c). Galactus showed significant decreases also in cob diameter, which were caused by PAC treatment and fertilizer supply, whereas no effects on cob diameter were observed for Fabregas (Figure 4d). In both cultivars, the number of kernel rows per cob was 15.9 ± 0.1 (*SE*) on average and unaffected by PAC treatment and fertilizer supply (not shown).

3.3 | Water consumption and water-use efficiency (WUE)

For cultivar Galactus, PAC treatment significantly reduced total water consumption by 15% to 17% in comparison with the control plants (Table 3). In addition, maize plants with 78% NPK supply consumed significantly less water than with 100% NPK. A significant decrease in water consumption of PAC-treated Fabregas plants was only observed with 85% NPK supply. The reduced fertilizer application did not affect total water consumption of Fabregas (Table 3).

When WUE_{grain} was calculated with the total amount of consumed water, no significant changes were observed after PAC application to Galactus and Fabregas (Table 3). In contrast, WUE_{grain} decreased significantly with reduced fertilizer supply to both cultivars. If the grain yield was related to water consumption during four weeks around silking, positive effects of PAC were observed in both cultivars with significant increases of 16% in the two highest fertilization rates of Galactus (100% and 85% NPK). For Galactus-PAC, WUE_{grain} during silking was significantly decreased

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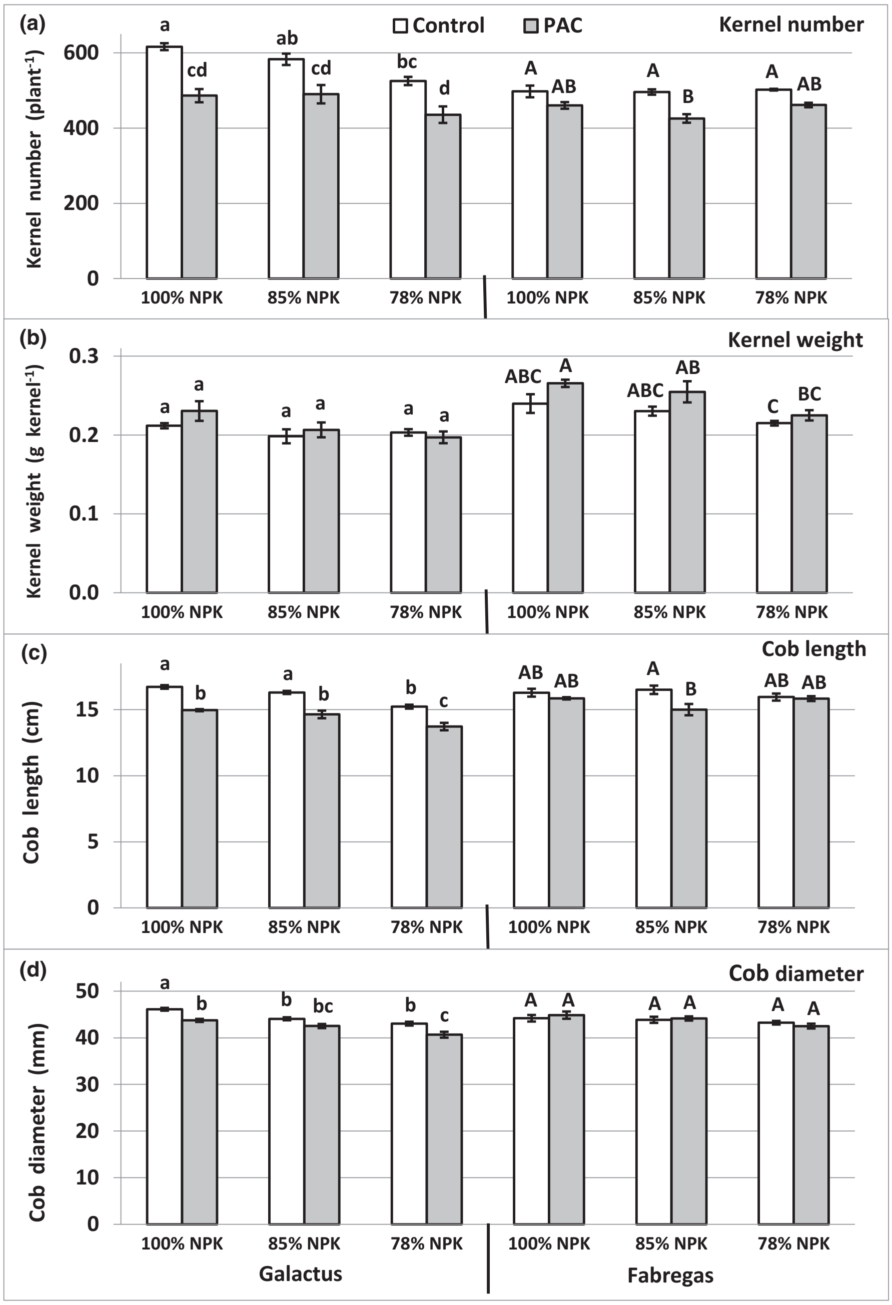

FIGURE 4 Kernel number (a), single kernel weight (b), cob length (c) and cob diameter (d) of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply; data show means of four replicates ±SE; significant differences ($p \le 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

in 78% NPK in comparison to 100% NPK, and in Fabregas, this was true for control and PAC treatment (Table 3).

3.4 | Nutrient concentrations, contents and utilization efficiencies

In the present growth regulator experiment, the maize plants were supplied with various amounts of NPK fertilizer. In Figure 5, the N, P and K concentrations in grain and straw dry matter are combined for cultivars Galactus and Fabregas, grown under control conditions or after PAC treatment with three fertilization rates each. PAC application to Galactus caused significant increases in N concentrations of grain and straw with stronger effects in straw than in grain (on average 24% increase in grain and 47% in straw; Figure 5a and 5b). In Galactus, effects of fertilizer supply were only observed on grain N concentrations in the PAC treatment with a significant decrease in 85% NPK in comparison to 100% NPK (Figure 5a). The grain N concentrations of Fabregas were unaffected by PAC treatment, whereas in straw a significant increase in 85% NPK was observed. Reduced fertilizer supply to Fabregas plants caused significant decreases in N concentrations of grain and straw in control and PAC treatment (Figure 5a and 5b).

The P concentrations in grain and straw of cultivar Galactus were unaffected by PAC treatment with one exception (increase in straw with 100% NPK; Figure 5c and 5d). Fertilizer supply did not affect P concentrations in grain and straw of Galactus. In Fabregas, growth regulator application showed differential effects on grain P

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TABLE 3 Total water consumption, water-use efficiency WUE_{grain} calculated with total water consumed, WUE_{grain} calculated with water consumed during silking (± 2 weeks) of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply

Maize cultivar	Fertilizer supply	Treatment	Total water consumption (L plant^{-1})	WUE_{grain} (g L^{-1}) (Grain-DM/ Total water consumption)	WUE_{grain} (g L^{-1}) (Grain-DM/ Water consumption silking)
Galactus	100% NPK	Control	46.4 ± 0.5 a	2.81 ± 0.01 a	7.24 ± 0.13 bc
		PAC	39.7 ± 0.8 cd	2.78 ± 0.04 ab	8.41 ± 0.18 a
	85% NPK	Control	44.1 ± 0.3 ab	2.58 ± 0.06 bcd	6.61 ± 0.30 c
		PAC	37.4 ± 1.0 de	2.66 ± 0.05 abc	7.69 ± 0.21 ab
	78% NPK	Control	42.4 ± 0.8 bc	2.51 ± 0.06 cd	6.41 ± 0.17 c
		PAC	35.2 ± 0.7 e	2.40 ± 0.03 d	6.84 ± 0.09 bc
Fabregas	100% NPK	Control	42.8 ± 0.9 AB	2.78 ± 0.11 AB	7.57 ± 0.43 AB
		PAC	43.3 ± 0.9 AB	2.80 ± 0.05 A	7.84 ± 0.25 A
	85% NPK	Control	46.0 ± 0.5 A	2.48 ± 0.05 BC	6.39 ± 0.17 BC
		PAC	42.2 ± 0.7 B	2.55 ± 0.05 ABC	7.11 ± 0.34 ABC
	78% NPK	Control	44.7 ± 0.8 AB	2.40 ± 0.01 C	5.79 ± 0.17 C
		PAC	42.1 ± 0.4 B	2.47 ± 0.09 C	6.26 ± 0.38 BC

Note: Data show means of four replicates ±SE; significant differences ($p \leq 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

concentrations, depending on NPK supply: In 100% NPK, a significant decrease was observed; in 85% NPK, no change occurred; and in 78% NPK, grain P concentrations increased significantly due to PAC treatment (Figure 5c). P concentrations in straw of Fabregas plants were unaffected by PAC application (Figure 5d). In the control plants of Fabregas, P concentrations in grain and straw decreased significantly from the highest to the lowest fertilization rate, whereas in grain and straw of PAC-treated plants, fertilizer supply had no effect on P concentrations (Figure 5c and 5d).

For Galactus and Fabregas, PAC application and fertilizer supply caused only small changes in K concentrations of grain, yet in straw, they were strongly increased by 21% to 61% due to growth regulator treatment (Figure 5e and 5f). With reduced fertilizer supply, the straw K concentration significantly decreased in the control of Fabregas and in the PAC treatment of both cultivars (Figure 5f).

Overall, increases in N, P and K concentrations caused by PAC application were much more pronounced in straw than in grain. In Fabregas, in most cases, a clear trend of decreasing nutrient concentrations with declining fertilizer supply was observed, whereas in Galactus, this was rarely true (Figure 5).

The N, P and K contents per total above-ground biomass of one plant are shown in Table 4 for both maize cultivars. The contents of all three nutrients were mostly unaffected by application of PAC. Only, Galactus-85%NPK and Fabregas-100%NPK showed a significant decrease in P content after PAC treatment. However, the total nutrient contents were strongly related to fertilizer supply with mostly significant decreases due to reductions in NPK application. Particularly, the total N content in control and PAC treatment of both cultivars mirrored the stepwise declining N fertilization rate very well (Table 4). Because in Galactus the N concentrations in grain and straw were mostly unaffected by fertilizer rate (Figure 5a and 5b), decreases in N content are caused by declining grain and straw yields (Figure 3a and 3b). Yield reductions in the PAC treatment resulted in higher N concentrations, leading to similar N contents and thus N uptake of the shoot in comparison with the control plants (Table 4). In Fabregas, decreasing shoot N uptake due to reduced fertilizer supply relies on both, decreasing N concentrations in grain and straw (Figure 5a and 5b) and decreasing grain yields (Figure 3a).

The N-, P- and K-utilization efficiencies of grain of both cultivars were not improved by PAC application (one exception: $PUtE_{grain}$, Fabregas-100%NPK; Figure 6a, 6c, 6e). Instead, Galactus showed significant reductions in $NUtE_{grain}$ and $KUtE_{grain}$ and no effect in $PUtE_{grain}$ due to PAC treatment, and effects of reduced fertilizer supply on nutrient-utilization efficiencies were rarely observed. In contrast, PAC application to Fabregas had no effect on N-, P- and K-utilization efficiencies in most cases, whereas with reduced fertilization rate, an increase in $NUtE_{grain}$ and $PUtE_{grain}$ of control plants and in $NUtE_{grain}$ of PAC-treated plants was obtained (Figure 6a and 6c). In Fabregas, $KUtE_{grain}$ was unaffected by PAC treatment and fertilizer supply (Figure 6e).

The nutrient-harvest indices, which give the percentage of nutrient content in grain to total nutrient content of the above-ground biomass, are shown in Figure 6 as well. In Galactus and Fabregas, NHI and PHI were unaffected by PAC treatment and fertilizer supply (one exception: PHI, Fabregas-78%NPK; Figure 6b and 6d). KHI was significantly decreased due to PAC application, namely in all fertilization rates of Galactus and in Fabregas-100%NPK (Figure 6f). Thus, as the total K content was similar in control and PAC-treated plants (Table 4), at maturity less K had been retained in grain after PAC application in comparison with the control. In both cultivars, the fertilizer rate itself showed no significant effect on KHI (Figure 6f).

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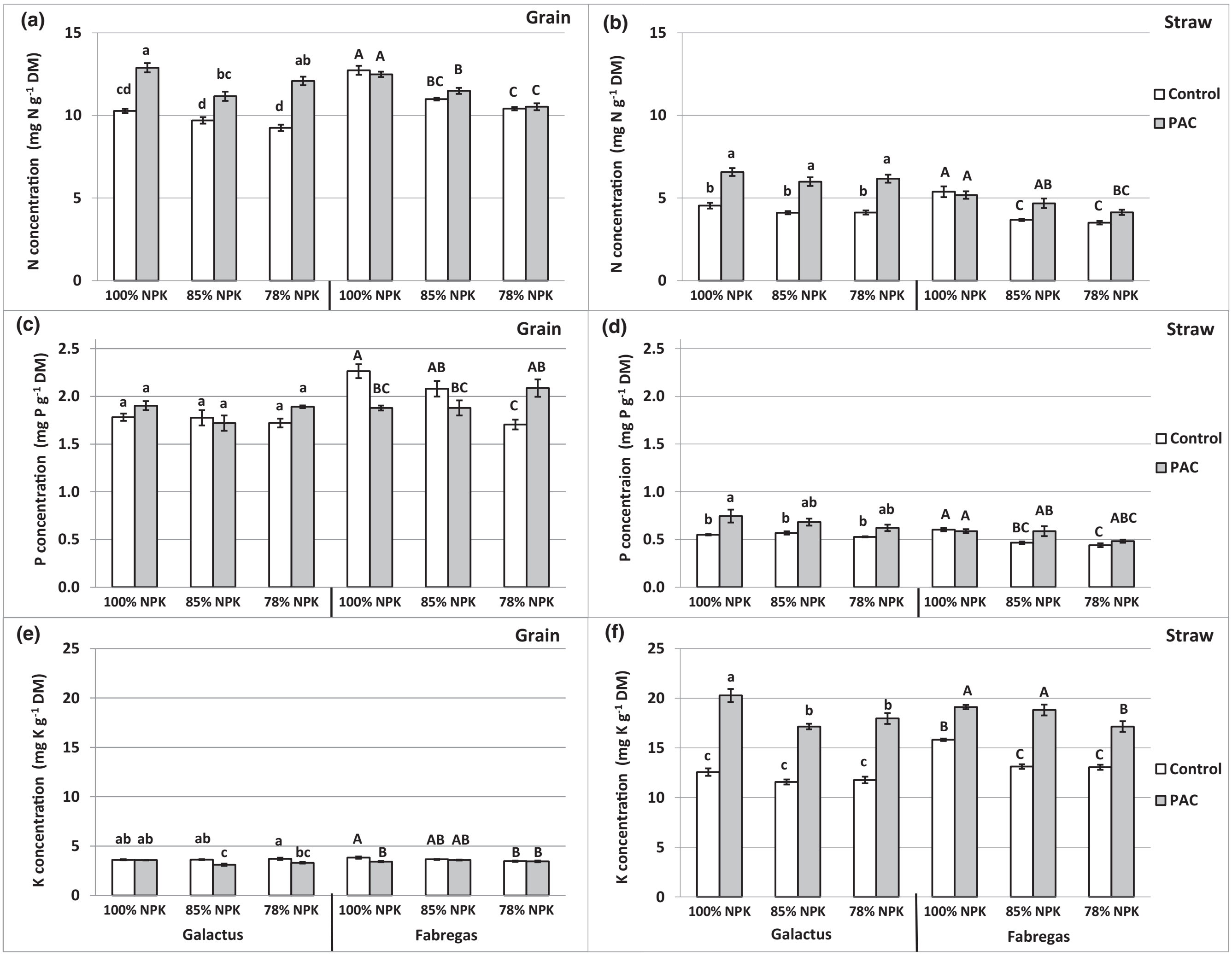

FIGURE 5 Nitrogen (N) concentrations in grain (a) and straw (b), phosphorus (P) concentrations in grain (c) and straw (d) and potassium (K) concentrations in grain (e) and straw (f) of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply; data show means of four replicates ±SE; significant differences ($p \leq 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

4 | DISCUSSION

Although in the present study, which was conducted in 2020, Galactus and Fabregas received the same PAC dosages as in 2019 (3 mg a.i. and 2 mg a.i. PAC, respectively; Hütsch & Schubert, 2021), Galactus showed stronger and Fabregas weaker PAC effects than in 2019. Thus, for several parameters, the effects of PAC and in some cases also of fertilizer supply have to be discussed separately for the two maize cultivars.

4.1 | Reduced fertilizer supply did not prevent luxurious nutrient consumption of PAC-treated Galactus plants resulting in increased concentrations in straw and grain

For both cultivars, the N, P and K contents and thus uptake of the total above-ground biomass were in most cases similar in control and PAC-treated plants and decreased stepwise with reduced fertilizer supply (Table 4). In Galactus, this resulted in significant increases in grain N concentrations and in N and K concentrations of straw, which were mainly caused by PAC application and not by fertilizer supply (Figure 5a, 5b, 5f). Even, reduction to 78% NPK did not affect nutritional status of Galactus plants at maturity. Thus, the PAC-treated plants showed again luxurious nutrient consumption resulting in a nutritional status above the control plants. The increases in N and K concentrations of straw mirror very well the reduced straw yield after PAC treatment (Figure 3b), where the same amount of nutrients is allocated to a smaller biomass. In addition, for Galactus also the grain yield decreased significantly due to PAC application in comparison with the control (Figure 3a), leading to significantly increased grain N concentrations (Figure 5a). The grain yield reductions in PAC-treated Galactus plants were solely due to significant decreases in kernel number, whereas kernel weight was unaffected (Figure 4a and 4b).

According to Jacobs & Pearson (1991), maize kernel number is a function of (1) rate and duration of differentiation of spikelets with

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TABLE 4 Nitrogen (N), phosphorus (P) and potassium (K) contents in grain plus straw of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply

			Total nutrient content (grain +straw) (mg plant^{-1})		
Maize cultivar	**Fertilizer supply**	**Treatment**	***N***	**P**	**K**
Galactus	100% NPK	Control	1,914 ± 18 a	304.2 ± 9.3 a	2,168 ± 23 ab
		PAC	2,027 ± 57 a	280.0 ± 9.5 ab	2,236 ± 53 a
	85% NPK	Control	1,618 ± 22 b	274.0 ± 5.4 ab	1,999 ± 9 bc
		PAC	1,633 ± 18 b	232.4 ± 11.0 c	1,879 ± 59 cd
	78% NPK	Control	1,456 ± 23 c	244.5 ± 5.5 bc	1,864 ± 40 cd
		PAC	1,512 ± 16 bc	209.3 ± 5.9 c	1,758 ± 41 d
Fabregas	100% NPK	Control	2,035 ± 34 A	346.5 ± 13.1 A	2,085 ± 73 A
		PAC	1,988 ± 31 A	279.5 ± 5.2 B	2,097 ± 65 A
	85% NPK	Control	1,684 ± 18 B	289.9 ± 10.4 B	1,973 ± 18 AB
		PAC	1,657 ± 9 B	253.4 ± 10.3 BC	1,988 ± 58 AB
	78% NPK	Control	1,516 ± 24 C	220.0 ± 12.9 C	1,834 ± 33 B
		PAC	1,493 ± 53 C	261.4 ± 5.2 BC	1,942 ± 42 AB

Note: Data show means of four replicates ±SE; significant differences ($p \le 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

florets, (2) fertilization of the florets, which requires synchronization of pollen shed and silking, and (3) kernel abortion after floret fertilization. Spikelet primordia (potential kernels) are formed following floral initiation. The number of spikelets formed on an ear is the primary determinant of potential yield as it sets the upper limit for the number of kernels per plant (Jacobs & Pearson, 1992). Floret initiations start at the 9-leaf stage (approximately V5), during early vegetative growth, and last for about 5–10 days (Zhao et al., 2021). Thus, start of floret initiation coincided with the time of PAC application in our study. According to Zhao et al. (2021), after application of plant growth retardants, frequently observed reductions in cob size and kernel number and thus grain yield, are related to application time. In their investigations, ethephon applied at the floret initiation period suppressed floret development and reduced cob size and potential kernel number. With delayed application time, floret initiation was protected and grain yield increased compared with the untreated control, mainly due to an increased kernel number per cob (Zhao et al., 2021). Because PAC and ethylene, the active ingredient of ethephon, both hamper culm elongation growth, effects of ethylene on maize plants are possibly applicable to PAC. However, in order to prove this assumption, further investigations are necessary.

In both maize cultivars, PAC treatment did not diminish synchronization of pollen shed and appearance of silks and, therefore, showed no difference in ASI (anthesis-silking interval) in all NPK dosages (Table 2). Also in our previous study, ASI was not extended by PAC and proper pollination and floret fertilization were assumed (Hütsch & Schubert, 2021). Thus, impeded fertilization of developing kernels as second reason for decreased kernel number can be excluded. Thirdly, after pollination and fertilization enhanced kernel abortion was frequently observed, particularly in the apical part of the maize cob in response to stress factors such as water deficits and salinity (Hütsch et al., 2015; Jung et al., 2017; Mueller et al., 2019; Oury et al., 2016; Schubert et al., 2009; Setter & Parra, 2010; Turc & Tardieu, 2018). Even under optimal growth conditions, only approximately 80% of initiated florets finally develop into kernels at maturity (Jacobs & Pearson, 1991). PAC treatment favoured kernel abortion at the cob tip of Fabregas, and for Galactus, this was observed with 78% NPK (Figure 2). Therefore, the main reason for the significantly reduced grain yield of Galactus after PAC application was presumably a diminished floret initiation resulting in smaller numbers of potential kernels.

In contrast to Galactus, for Fabregas, no significant effect of PAC on grain N concentrations was observed in comparison with the control (Figure 5a). Similarly, no significant differences in grain yield and kernel number (one exception: 85% NPK) occurred between control and PAC treatment (Figures 3a, 4a). Thus, similar N uptake (Table 4) combined with no changes in grain yield resulted in similar grain N concentrations and no luxurious nutrient consumption in PAC-treated Fabregas plants.

4.2 | Reduced fertilizer supply negatively affected grain yield of both, control and PAC-treated maize plants

Decreases in grain yield of control plants due to NPK supply below the optimal dosage, namely with 85% and 78% NPK, were observed for both cultivars and had to be expected (Figure 3a). In Galactus control plants, cob length, cob diameter and kernel number were significantly decreased with 78% NPK in comparison to 100% and 85% NPK supply, whereas kernel weight was unchanged (Figure 4a–4d). N deficiency during the production of spikelet primordia or during kernel setting could have contributed to the reduced kernel number

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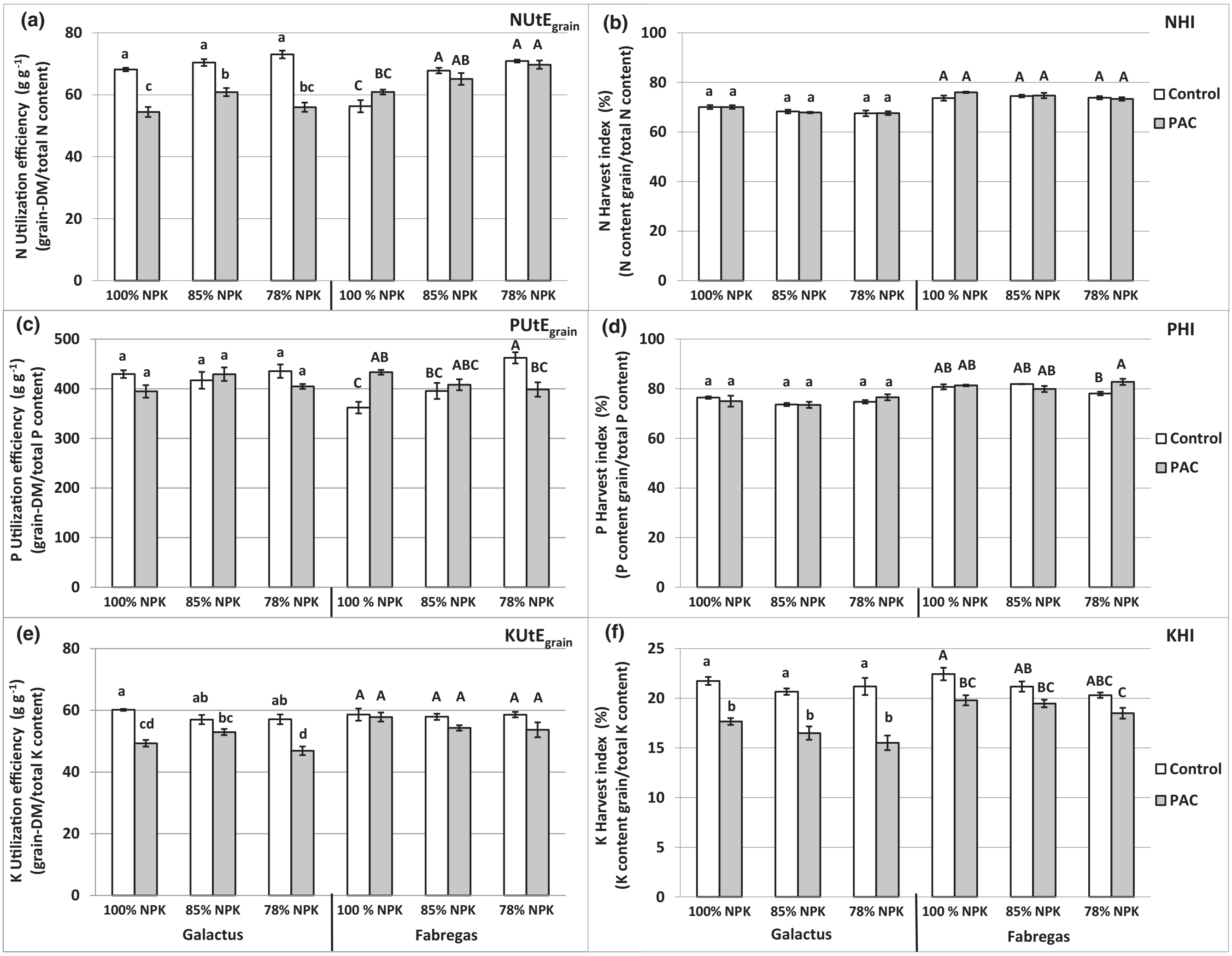

FIGURE 6 Nitrogen-utilization efficiency NUtE$_{grain}$ (a), nitrogen-harvest index NHI (b), phosphorus-utilization efficiency PUtE$_{grain}$ (c), phosphorus-harvest index PHI (d), potassium-utilization efficiency KUtE$_{grain}$ (e) and potassium-harvest index KHI (f) of two maize cultivars under control conditions and after application of the plant growth regulator paclobutrazol (PAC), with decreasing fertilizer supply; data show means of four replicates ±SE; significant differences ($p \leq 5\%$) within each cultivar are indicated by small (Galactus) or capital letters (Fabregas). PAC dosage per plant: Galactus 3 mg a.i.; Fabregas 2 mg a.i.

per plant with the lowest fertilizer application rate. Aborted kernels at the cob tips occurred more frequently with 78% NPK than with the two higher fertilizer dosages (Figure 2). These results are in agreement with studies of Jacobs & Pearson (1991, 1992), who found that an increase in grain yield per plant with increased N fertilizer was mainly due to a rise in kernel number with no change in individual kernel weight. In contrast to Galactus, the control plants of Fabregas showed only small reductions in grain yield due to decreased NPK supply (Figure 3a).

However, also in the PAC treatment, a stepwise decrease in grain yield occurred with reduced fertilizer supply, which was particularly pronounced for Galactus (Figure 3a). This fertilizer effect on grain yield was not related to kernel number or kernel weight, as in Galactus-PAC both yield components were unaffected by NPK supply (Figure 4a and 4b). However, between 100% and 78% NPK, cob length and cob diameter of Galactus decreased significantly (Figure 4c and 4d). Like potential kernel number, cob length is also determined during early vegetative growth (Zhao et al., 2021). Considering the grain nutrient concentrations at maturity, particularly not only N deficiency but also P deficiency of PAC-treated Galactus plants seem to be unlikely. However, it has to be considered that decreases in total NPK supply by 15% and 22% were brought about by reductions in NPK application by 40% and 60%, respectively, in the three last dosages during vegetation, starting with differential NPK supply 10 days after PAC application. At this growth stage, competition between the exponentially-growing young leaves, which are large sinks for carbon and nitrogen assimilates, and the developing ears could temporarily occur. This is different to the time around flowering, when almost all leaves have reached their maximum size and function as assimilate sources, resulting in no source limitation, even under stress conditions (Hütsch et al., 2015; Jung et al., 2017).

In the PAC treatment of Fabregas, a significant decrease in grain yield was observed between 100% and 78% NPK (Figure 3a),

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which was accompanied by a significant decrease in kernel weight and no effect on kernel number (Figure 4a and 4b). A lack of N can limit starch deposition in the endosperm of maize kernels, primarily through an influence on the synthesis of metabolic enzymes needed for starch production followed by decreased activities (Singletary & Below, 1990; Singletary et al., 1990). Mueller et al. (2019) also found a strong impact of N treatment on kernel growth and thus on final kernel weight.

Apart from these possibilities of N limitation of assimilation during early cob development and grain filling, N also functions as a signal, triggering widespread modifications in gene expression, enzyme activities and metabolite contents (Sakakibara et al., 2006). One signalling route depends on nitrate itself and one uses cytokinin as a messenger. The nitrate-specific signal regulates a wide variety of metabolic processes including cytokinin biosynthesis. Among all plant nutrients, N has the most prominent influence on the production of cytokinins in roots and export to the shoots. The synthesis and export of cytokinins are also affected by P and K supply, although this effect is somewhat less prominent than in the case of *N* (Horgan & Wareing, 1980; Salama & Wareing, 1979). Cytokinins primarily enhance cell division and cell expansion, both are prerequisites for ear development and floral initiation early in plant ontogenesis. Levels of gibberellins can also be modulated by N nutrition, whereby the effects of N are presumably indirect. Main sites of GA synthesis are the shoot apex and the expanding leaves. N supply favours growth rate of shoots and thus indirectly also GA synthesis (Marschner, 1995). Low N conditions suppressed the production of gibberellins as compared to sufficient *N* (Wang et al., 2020). Thus, in the PAC treatment, the inhibition of GA biosynthesis could have been strengthened with reduced N application in the 85% and 78% NPK supply.

4.3 | With reduced fertilizer supply, the N-, P- and K-utilization efficiencies of PAC-treated maize plants could not be improved

After PAC treatment, nutrient-utilization efficiencies were either unchanged or significantly decreased in comparison with control plants (one exception: increase in $PUtE_{grain}$ of Fabregas-100% NPK). As the total nutrient contents of control and PAC-treated plants were similar in most cases (Table 4), the significant reductions in $NUtE_{grain}$ and $KUtE_{grain}$ of Galactus (Figure 6a and 6e) resulted only from the significantly decreased grain yields after PAC application (Figure 3a). Because for Fabregas, PAC had no impact on both, grain yield and nutrient content (Figure 3a, Table 4), this resulted in similar nutrient-utilization efficiencies of control and PAC treatment (Figure 6a, 6c, 6e). This is in contrast to the effect of reduced fertilizer supply to Fabregas, which caused significant enhancements of $NUtE_{grain}$ in control and PAC treatment and of $PUtE_{grain}$ in control plants (Figure 6a and 6c). In these cases, the decreases in grain yield were less strong than the decreases in total nutrient content due to reduced fertilizer supply (Figure 3a, Table 4). In contrast, the unchanged $PUtE_{grain}$ of Fabregas-PAC plants and of $KUtE_{grain}$ of all Fabregas plants (Figure 6c and 6e) were accompanied by similar total P and K contents in all fertilizer dosages (Table 4).

5 | CONCLUSIONS AND PERSPECTIVES

With reduced fertilizer supply, luxurious nutrient consumption was not prevented in PAC-treated plants resulting in increased concentrations in straw and grain. As control and PAC-treated plants took up similar amounts of nutrients, the concentrations were enhanced due to the allocation to a smaller straw and grain biomass. The main constraint for improvement of nutrient-utilization efficiencies were grain yield decreases, caused by PAC treatment and further strengthened by reduced fertilizer supply. Thus, further research should focus on the avoidance of grain yield depressions after PAC treatment, frequently observed in no-stress environments. In this regard, not only the optimum PAC application rate for individual maize cultivars is decisive, but also the application time has profound impacts on potential kernel numbers and thus grain yield at maturity. Delayed application time (e.g., V7 instead of V5), when floret initiation has almost terminated, could probably avoid damage of florets and increase potential kernel number per cob, eventually increasing kernel number at maturity. However, PAC application at a later growth stage could cause negative impacts on flowering such as later silking due to reduced silk elongation rates leading to higher values of ASI, which could decrease the rate of successful fertilization of developing kernels. In order to evaluate these possible impacts, further studies are needed. Avoidance of reduction in kernel number after PAC treatment is the key to minimize grain yield decreases and to provide the opportunity for improvement of nutrient-utilization efficiencies and further enhancement of water-use efficiency, which also relies on grain yields.

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