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EFFECT OF NUTRIENT UPTAKE INTERACTION ON YIELD OF PEPPER IN A GREENHOUSE

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ABSTRACT

This paper reviews the effect of nutrient uptake interaction on yield of pepper (*Capsicum annuum L.*) in a greenhouse, examining how interactions among nutrients, between water and nutrients, and between the greenhouse environment and nutrient supply govern nutrient uptake and fruit yield. The review was conducted as a structured narrative synthesis of studies published between 1988 and 2026 on greenhouse pepper and comparable fruit vegetables under drip fertigation. Water and fertilizer interaction emerged as the dominant control, being statistically significant in every factorial greenhouse experiment reviewed. The best reported water-nutrient combination raised capsicum fruit yield to 60.1 t ha^{-1} against 18.9 t ha^{-1} under conventional practice, while a 20% reduction in fertilizer rate under precise water delivery caused no significant yield loss. Nutrient-nutrient effects were weaker than commonly assumed, being mediated largely through the electrical conductivity of the feed and the placement of ions within the wetting bulb rather than through fixed nutrient ratios. Maximum nutrient uptake and maximum yield did not coincide, indicating luxury consumption. The review concludes that fertilizer recommendations for greenhouse pepper should be irrigation-conditional and set at the economic rather than the uptake optimum, and that pepper-specific interaction coefficients for tropical loamy soils remain unavailable.

Keywords: *Capsicum annuum*; drip fertigation; greenhouse; nutrient interaction; nutrient uptake

1.0 INTRODUCTION

Pepper (*Capsicum spp.*) ranks among the most economically important vegetable crops cultivated worldwide for its nutritional, medicinal and industrial value (Reddy *et al*., 2017). Across the tropics and sub-tropics, including Nigeria, it is an essential source of livelihood for smallholder farmers, and the Nigerian red scotch bonnet type is valued for its color, flavor and its high capsaicin content (Sneha *et al*., 2025). Protected cultivation of such high-value vegetables has expanded rapidly, but the greenhouse does more than shelter the crop. It removes rainfall as a source of leaching, concentrates the root system into a small managed volume, and places the entire water and nutrient supply under the grower's direct control, usually through drip fertigation, which matches the fertilizer dose to the rate of plant uptake and delivers nutrients to the root zone in available forms, so that leaching losses may fall to about a tenth of those under conventional application (Thomas *et al*., 2024; Reddy *et al*., 2017; Sneha *et al*., 2025).

Fertilizer recommendations for pepper are nevertheless still expressed as independent single-nutrient rates, in kilograms of N, P_2O_5 and K_2O per hectare, applied at a nominal irrigation depth (Reddy *et al*., 2017). This formulation assumes that the response to each input is additive, that is, that the yield gain from an increment of nitrogen does not depend on how much potassium or how

much water is supplied. The assumption is not supported by the physiology of nutrient acquisition. Nutrients reach the root surface by mass flow, diffusion and root interception, all three of which are functions of soil water content (Thomas *et al.*, 2024), and they cross the root membrane through transporters for which chemically similar ions compete. Water and nutrient supply may therefore supplement or constrain one another, and the interaction may be positive or negative depending on growth stage, amounts, combinations and balances (Thomas *et al*., 2024).

Where an interaction exists, the optimum rate of one input is a function of the level of the other, so a blanket recommendation is valid only at the irrigation depth for which it was derived. This matters acutely under protected cultivation, because the same structure that permits precise control also permits precise error: salts accumulate (Ullah *et al.*, 2017), wetting patterns are non-uniform (Lao *et al.*, 2003), and the microclimate modifies nutrient demand independently of root-zone supply (Mankin and Fynn, 1996).

Despite this, the interaction literature for protected cultivation is dominated by tomato and cucumber, while pepper-specific syntheses are scarce. However, the objectives of this review are to: set out the mechanistic and statistical basis on which nutrient uptake interactions are defined and quantified; synthesize the reported effects of these interactions on nutrient uptake and fruit yield in greenhouse pepper; and lastly identify the resulting management prescriptions and research gaps, with particular attention to tropical greenhouse production.

Figure 1 sets out the conceptual framework guiding this review, linking the three interaction domains addressed above (water × nutrient, nutrient-nutrient, and environment × nutrient) to nutrient uptake, fruit yield and resource-use efficiency in greenhouse pepper; the evidence supporting each linkage is presented in Section 4.

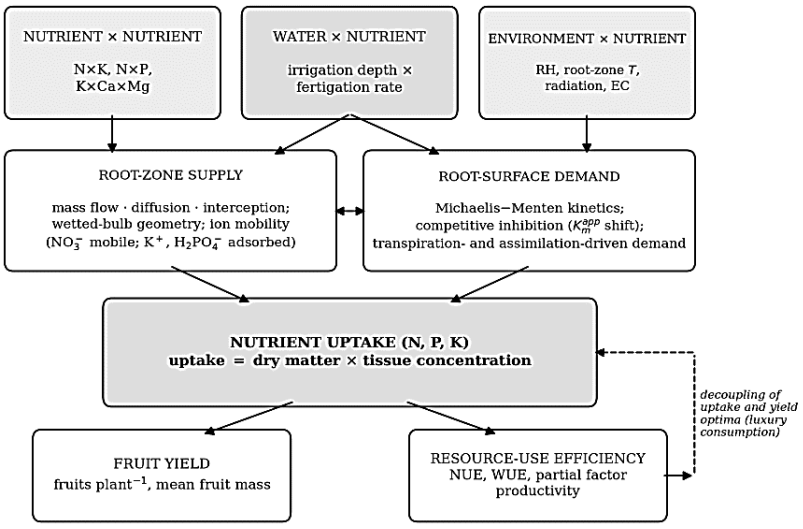


Figure 1: Conceptual framework linking the three domains of nutrient uptake interaction to nutrient uptake, fruit yield and resource-use efficiency in greenhouse pepper.

2.0 THEORETICAL ANALYSIS

2.1 Transport of nutrients to the root and uptake at the root surface

Nutrients reach the root surface by three mechanisms. Mass flow carries ions moving with the transpiration stream, principally calcium, magnesium, nitrate-nitrogen and sulphate. Diffusion moves ions down the concentration gradient created by root absorption and governs the supply of potassium and phosphorus. Root interception accounts for the remainder and dominates for several micronutrients (Thomas *et al.*, 2024). Soil water content enters uptake twice over: it sets the convective flux driving mass flow, and it sets the cross-sectional area and tortuosity of the diffusion path. This dual dependence is the physical origin of the water and nutrient interaction. Solute movement in the root zone is described by the convection–dispersion equation, which for one-dimensional vertical flow may be written as

$$\partial(\theta C)/\partial t = \partial/\partial z\,[\theta D\,(\partial C/\partial z)] - \partial(qC)/\partial z - S \qquad (1)$$

where θ is volumetric water content ($cm^3\ cm^{-3}$), C is solute concentration in the soil solution ($mg\ cm^{-3}$), D is the dispersion coefficient ($cm^2\ d^{-1}$), q is water flux density ($cm\ d^{-1}$), S is the root uptake sink term ($mg\ cm^{-3}\ d^{-1}$), z is depth (cm) and t is time (d). The convective term contains q, so any change in irrigation alters solute distribution even when the fertilizer rate is held constant. Uptake at the root surface follows saturable kinetics of the Michaelis–Menten form,

$$I = I_{max}\,C\,/\,(K_m + C) \qquad (2)$$

in which I is net influx per unit root surface area, I_{max} is the maximum influx and K_m is the concentration at which half of I_{max} is attained. When two ions compete for the same transporter, the apparent Michaelis constant becomes

$$K_m(app) = K_m\,(1 + C_j\,/\,K_i) \qquad (3)$$

where C_j is the concentration of the competing ion and K_i its inhibition constant. Equation (3) is the formal statement of ionic antagonism: the competing ion does not lower the maximum attainable influx but raises the concentration at which half of it is realized. Antagonism is therefore most damaging where the target ion is already dilute, the condition prevailing at the periphery of a drip wetting bulb.

2.2 Statistical definition of an interaction

For a two-factor factorial experiment the response is modelled as

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk} \qquad (4)$$

in which μ is the general mean, α_i and β_j the main effects of irrigation and fertigation, $(\alpha\beta)_{ij}$ the interaction and ε_{ijk} the residual. An interaction exists when $(\alpha\beta)_{ij}$ differs significantly from zero, that is, when the effect of one factor is not constant across levels of the other. For quantitative factors the response is more usefully fitted as a second-order surface,

$$Y = b_0 + b_1X_1 + b_2X_2 + b_{11}X_1^2 + b_{22}X_2^2 + b_{12}X_1X_2 \qquad (5)$$

where X_1 and X_2 are irrigation depth and fertilizer rate. The cross-product coefficient b_{12} carries the interaction, being positive under synergism, negative under antagonism and zero when effects are additive. Setting the partial derivatives of Equation (5) to zero shows that the optimum level of either factor contains a term in the other whenever $b_{12} \neq 0$. This is why a fixed recommended dose cannot be transferred between irrigation regimes.

Uptake itself is quantified as $U = \Sigma (DM_p \times C_p)$, the dry matter of each plant part multiplied by its nutrient concentration and summed over parts, and efficiency as partial factor productivity, $PFP = Y / F_a$; agronomic efficiency, $AE = (Y - Y_0) / F_a$; apparent recovery efficiency, $RE = (U - U_0) / F_a$; and water use efficiency, $WUE = Y / ET$, where Y is yield, Y_0 and U_0 those of an unfertilized control, F_a the nutrient applied and ET seasonal evapotranspiration. Because U and Y enter different indices, the combination maximizing uptake need not maximize yield (Section 4.4).

Interactions of this kind are representable at two scales. At field scale the response surface of Equation (5) suffices for deriving irrigation-conditional fertilizer recommendations. At root-zone scale, coupling Richards' equation with the convection–dispersion equation and a Michaelis–Menten sink term, as in models of the HYDRUS family, reproduces the placement effects reported by Nijamudeen *et al*. (2013b). Feed-forward control combining crop models with plant sensors, demonstrated for greenhouse tomato (Marcelis *et al*., 2000; Elings *et al*., 2004), is the logical endpoint of this work.

Four gaps constrain application to pepper. Values of I_{max} and K_m for nitrogen, phosphorus and potassium in *Capsicum spp.* under tropical conditions are essentially unreported, so mechanistic models must borrow tomato parameters. Almost all factorial greenhouse pepper experiments cross irrigation with total fertilizer as a single factor, so three-way factorial designs combining water, nitrogen and potassium are rare and second-order interactions unquantified. The corpus is dominated by temperate, subtropical Asian and Mediterranean conditions, with greenhouse studies on the loamy soils of humid tropical West Africa absent. Finally, interaction effects on quality are seldom reported, although ascorbic acid in capsicum fruit rose from 91.1 and 94.3 to 100.0 and 103.4 mg per 100 g fresh weight when water-soluble rather than conventional fertilizers were fertigated (Muralidhar, 1998), indicating that quality responds to fertilizer source independently of yield.

3.0 MATERIALS AND METHODS

3.1 Literature corpus and inclusion criteria

This review addresses the research problem that fertilizer recommendations for greenhouse pepper are conventionally derived by treating nitrogen, phosphorus and potassium as independent inputs, without accounting for interactions among nutrients, between water and nutrients, and between the greenhouse environment and nutrient supply. It is conducted as a structured narrative review rather than a systematic review or meta-analysis, because the heterogeneity of crops, structures,

treatments and reporting units across the available studies precluded a pooled quantitative synthesis. Literature was searched in Google Scholar, Scopus and Web of Science, using combinations of the search terms “pepper” OR “Capsicum”, “greenhouse” OR “protected cultivation”, “fertigation” OR “drip irrigation”, and “nutrient interaction” OR “nutrient uptake”. A corpus of peer-reviewed articles, postgraduate thesis, conference papers and book chapters published between 1988 and 2026 was assembled from the greenhouse horticulture, drip fertigation and plant nutrition literature. A study was retained where the crop was grown under a protected structure, or under drip fertigation in the open where the mechanism was transferable; where fruit yield, nutrient uptake or both were reported; and where two or more production factors were varied so that an interaction term could be estimated or reasonably inferred. Studies on *Capsicum spp.* were given precedence, and because the pepper-specific literature remains thin, corroborating evidence was drawn from greenhouse tomato and cucumber, which share an indeterminate growth habit, an extended harvest window and comparable nutrient demand patterns. Extracted records were then synthesized qualitatively, as described in Section 3.2.

3.2 Data extraction and synthesis

Crop and cultivar, structure type, soil or substrate, experimental design, factors and levels tested, fruit yield, N, P and K uptake, water and nutrient use efficiencies, and the reported significance of interaction terms were extracted from each study. Because reference doses, units and structures were heterogeneous, formal meta-analysis was not attempted; the synthesis is qualitative, with quantitative anchors given in the units of the original studies. Two limitations follow: reporting is biased towards interactions that reached significance, and few studies report the full response surface required to estimate b_{12} in Equation (5), so most interactions can be described only through treatment contrasts.

4.0 RESULTS AND DISCUSSION

4.1 Water and nutrient interaction is the dominant control on yield

Every factorial greenhouse experiment reviewed reported a significant interaction between water and fertilizer supply, and in each case its magnitude exceeded that of any nutrient-nutrient effect (Table 1).

Table 1: Reported interaction effects of water and nutrient supply on yield and nutrient uptake in greenhouse pepper and comparable fruit vegetables.

Crop	Method (factors tested)	Standard/control practice	Recommended dosage	Outcome & remark	Source
Capsicum annuum L. (greenhouse)	Sensor-based irrigation (75, 50, 25% ASM) × fertigation (75, 100, 125, 150% RDF)	100% RDF under conventional surface irrigation (recommended practice)	75% ASM × 125% RDF	60.1 t ha^{-1}; 217.9% above surface-irrigated control (18.9 t ha^{-1}). I × F significant for yield and for N, P and K uptake. **Remark:** Deficit irrigation with elevated fertigation far exceeded the recommended standard; the irrigation × fertigation interaction drives the gain.	Ningoji *et al.* (2023)

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Crop	Method (factors tested)	Standard/control practice	Recommended dosage	Outcome & remark	Source
Capsicum annuum L. (naturally ventilated greenhouse)	Mulch color (silver, yellow, black) × irrigation (100, 80, 60% ETc)	Black mulch (or no mulch) at 100% ETc (conventional practice)	Silver mulch × 100% ETc	63.9 t ha^{-1}; yield at 80% ETc comparable to 100% ETc; water productivity highest at 60% ETc (35.53 kg m^{-3}). **Remark:** Silver mulch conserved water without a yield penalty at 20% deficit irrigation, relative to the conventional standard.	Kumari (2014)

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Crop	Method (factors tested)	Standard/control practice	Recommended dosage	Outcome & remark	Source
Capsicum annuum L. (field, drip)	Application method (fertigation, drip, furrow) × fertilizer rate (100, 80% RDF)	Furrow irrigation at 100% RDF (conventional practice)	Fertigation × 80% RDF	9.39 and 9.25 t ha^{-1} against 7.64 and 7.70 t ha^{-1} under furrow; 80% RDF at par with 100% RDF. **Remark:** Fertigation and irrigation precision act as partial substitutes; a fertilizer saving is possible without yield loss relative to furrow irrigation.	Muralidhar (1998)

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Crop	Method (factors tested)	Standard/control practice	Recommended dosage	Outcome & remark	Source
Sweet pepper (greenhouse)	N (3 rates, urea) × K (3 rates, MOP), 32 weekly splits	Recommended dose: 320 kg N + 360 kg K ha^{-1}	400 kg N + 360 kg K ha^{-1}	62.2 t ha^{-1}; 11, 26 and 104% above recommended dose, ready-mix fertilizer and control; K response plateaued once N was corrected. **Remark:** Nitrogen, not potassium, was limiting at the recommended rate; further potassium beyond the plateau gave no gain.	Nijamudeen *et al.* (2013a)

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Crop	Method (factors tested)	Standard/control practice	Recommended dosage	Outcome & remark	Source
Solanum lycopersicum L. (greenhouse)	Irrigation (100, 80, 60% ET_o) × N (240, 180, 120 kg ha^{-1})	Deficit irrigation (60% ET_o) with high nitrogen (240 kg N ha^{-1})	100% ET_o × 180 kg N ha^{-1}	54.1–78.7 t ha^{-1}; W1 exceeded W3 by 17.8 and 21.4%; root weight density lower at 240 than at 180 kg N ha^{-1}. **Remark:** Excess nitrogen under deficit irrigation suppressed root growth relative to the better-performing, moderate-input combination.	Wang et al. (2019)

ASM = available soil moisture; RDF = recommended dose of fertilizers; ETc = crop evapotranspiration; ET_o = reference evapotranspiration; Ep = pan evaporation; MOP = muriate of potash; EC = electrical conductivity.

Ningoji *et al*. (2023) recorded 60.1 t ha^{-1} at 75% available soil moisture with 125% of the recommended dose, 217.9% above a surface-irrigated control at the recommended dose (Table 1). The interaction was significant for fruit yield and for N, P and K uptake, and the same combination gave the highest net return and benefit–cost ratio.

Kumari (2014) obtained a comparable result for capsicum in a naturally ventilated greenhouse, where mulch color and irrigation level interacted significantly and water productivity peaked below the yield optimum (Table 1). Mulching also lowered summer surface soil temperature by 2 to 3 °C and raised winter temperature by 3 to 5 °C, which matters because root-zone temperature governs uptake kinetics through I_{max} in Equation (2).

Muralidhar (1998) separated the effect of delivery method from that of rate (Table 1). The fertigation advantage arose from more fruits per plant (6.91 to 6.75 against 5.7 to 5.6) and greater fruit weight per plant (438 to 430 g against 314 to 317 g), and reducing the fertilizer dose to 80% of the recommended rate did not significantly depress yield. The interaction here takes a practically important form: improving the precision of water delivery lowers the marginal product of fertilizer, so the two inputs behave as partial substitutes rather than as complements.

The pattern recurs in closely related fruit vegetables. In greenhouse tomato, full evapotranspiration replacement out yielded the 60% treatment by 17.8 and 21.4% in successive seasons, yet root weight density was lower at 240 than at 180 kg N ha^{-1}, indicating that excess nitrogen suppressed root proliferation and hence the crop's own capacity to acquire nutrients (Wang *et al*., 2019). In cucumber, yield rose with irrigation depth while water use efficiency peaked at an intermediate depth and nitrogen use efficiency fell significantly as nitrogen rate increased (Zhang *et al*., 2011). These observations follow from the transport relations of Section 2.1. Under deficit irrigation the diffusive path lengthens and convective flux falls, so delivery becomes the limiting step even where the soil nutrient stock is adequate; under excess irrigation, nitrate is displaced beyond the rooted volume by the convective term of Equation (1). The optimum irrigation depth is therefore that which maximizes nutrient residence time in the rooted volume rather than soil water content, a principle established for nitrogen uptake efficiency by Scholberg *et al*. (2002).

4.2 Nutrient-nutrient interaction is real but weaker than commonly assumed

The nutrient-nutrient interactions reported for greenhouse pepper and comparable fruit vegetables, together with their mechanisms, are summarized in Table 2.

Table 2: Reported nutrient-nutrient interaction effects on yield and nutrient uptake in greenhouse pepper and comparable fruit vegetables.

Study / crop	Method (factors tested)	Standard/control practice	Recommended dosage / best treatment	Outcome	Remark
Nijamudeen *et al.* (2013a) — Sweet pepper (greenhouse)	N (3 rates) × K (3 rates), 32 weekly splits	Recommended dose: 320 kg N + 360 kg K ha^{-1}	400 kg N + 360 kg K ha^{-1}	62.2 t ha^{-1} (maximum two-year mean yield)	Response is a plateau, not a synergy — nitrogen was the limiting factor.
Nijamudeen *et al.* (2013b) — Sweet pepper (greenhouse)	Soil-profile N and K distribution mapping under drip fertigation	n/a (descriptive/mechanistic study)	n/a	Ammonium-N and K concentrated near the dripper; nitrate at the root-zone boundary	N × K interaction is largely a placement effect within the wetting bulb, not a ratio effect.

Study / crop	Method (factors tested)	Standard/control practice	Recommended dosage / best treatment	Outcome	Remark
Papadopoulos and Khosla (1993) — Greenhouse tomato	K:N ratio varied 14:1 to 2:1 in the fertigation solution across five crops	Conventional fixed K:N ratio	Ratio-independent, provided EC is maintained	No significant effect of ratio on yield or fruit quality	Ionic strength (EC), not ratio, controls the interaction.
Xu *et al.* (2022) — Summer tomato	Foliar potassium silicate, potassium fulvate and betaine under heat stress	No foliar supplementation (heat-stressed control)	Foliar application as tested	Raised N and K uptake and summer yield	Genuine synergism where a real co-limitation (heat stress) is relieved.
Pan *et al.* (2011) — Banana seedlings, acid soil	Phosphorus fertigation vs conventional placement	Conventional P placement	Fertigated P in small, frequent doses	Available P +108%; P sorption index −31%	Fertigation keeps P in solution, outcompeting sorption on P-fixing soils — relevant to humid-tropical loams.
Rigby (1988) — Bell pepper, Quebec	Trickle fertigation; nitrogen form and potassium rate varied	n/a (mechanistic/observational study)	Nitrate-dominant feed, moderate potassium	Ammonium-dominant feed and high potassium depress Ca uptake; nitrate favors Ca uptake	Blossom-end rot risk reflects a nitrogen-form × potassium × water interaction, not simple calcium deficiency.

Pepper's nutrient requirement is not constant through the season: nitrogen and phosphorus dominate at the seedling stage, nitrogen and potassium during vegetative growth, and potassium and calcium during fruiting, with uptake of nitrogen and potassium peaking during fruit development (Ramanjaneya *et al*., 2016). A feed of fixed composition therefore creates a period

of relative excess in one element and relative deficit in another, so part of what is measured as a nutrient-nutrient interaction is a scheduling phenomenon rather than a chemical one; Nijamudeen *et al*. (2013a) applied nitrogen and potassium in 32 equal weekly splits for this reason.

Those authors tested eleven nitrogen and potassium combinations on greenhouse sweet pepper over two seasons. The maximum two-year mean yield of 62.2 t ha^{-1} at 400 kg N and 360 kg K ha^{-1} was significantly above the 56.1 t ha^{-1} recorded at the recommended 320 kg N with the same potassium rate, and at par with 400 kg N and 450 kg K ha^{-1} (Table 2). Nitrogen was thus limiting at the recommended rate, and once it had been corrected, further potassium produced no additional gain. The response is a plateau rather than a synergy. A spatial explanation emerges from the companion study. Nijamudeen *et al.* (2013b) found ammonium-nitrogen and potassium accumulating close to the dripper while nitrate accumulated at the boundary of the root zone. The two nutrients therefore occupy different positions within a single wetting bulb, and the nitrogen to potassium ratio the crop realizes is set by root distribution relative to those zones rather than by the ratio in the feed. Much of what presents as an N × K interaction in drip-fertigated pepper is a placement problem.

The most direct test of ratio effects remains that of Papadopoulos and Khosla (1993), who varied the potassium to nitrogen ratio in the fertigation solution from 14:1 to 2:1 across five greenhouse tomato crops. No significant effect was detected on early or total marketable yield or on fruit quality, provided the osmotic effect of the solution, measured as electrical conductivity, was maintained. Their conclusion that fertilizers may be selected on cost without concern for an undesirable K:N ratio indicates that the nutrient-nutrient interaction in fertigated fruit vegetables operates predominantly through total ionic strength rather than through the ratio of individual ions. On this basis electrical conductivity has become the controlling variable in automated fertigation, for which Wu *et al.* (2019) developed proportional–integral–derivative and combined fuzzy control algorithms.

Genuine synergism appears where a second input relieves a real co-limitation, as when foliar potassium silicate, potassium fulvate and betaine raised both nitrogen and potassium uptake and summer tomato yield by alleviating heat stress (Xu *et al.*, 2022). Phosphorus follows a different route: fertigation raised available phosphate by 108% and lowered the phosphorus sorption index by 31% in the surface layer of an acid soil relative to conventional placement (Pan *et al.*, 2011), because holding phosphorus in solution within a small, frequently replenished volume outcompetes sorption kinetics. This is directly relevant to the moderately phosphorus-fixing loams of the humid tropics.

The clearest antagonisms in pepper involve calcium. Rigby (1988) noted that increasing nitrate uptake enhances the absorption of accompanying cations such as calcium and so reduces the likelihood of blossom-end rot, whereas ammonium-dominant feeds and high potassium rates depress calcium uptake through the competitive mechanism of Equation (3). Since calcium is delivered almost exclusively by mass flow and is not appreciably remobilized within the plant, it

is the element most sensitive to the water and nutrient interaction. Blossom-end rot in greenhouse pepper is therefore best understood as the joint outcome of irrigation regime, nitrogen form and potassium rate rather than as a simple deficiency of calcium supply. The principal interactions and their management implications are summarized in Table 3.

Table 3: Observed or reviewed principal nutrient interactions relevant to greenhouse pepper, their mechanisms and management implications.

Interaction	Type	Mechanism	Implication for greenhouse pepper
Water × N	Synergistic below, antagonistic above the optimum	Nitrate reaches the root by mass flow; excess irrigation displaces it beyond the rooted volume, deficit irrigation lengthens the diffusive path	Schedule irrigation to maximize nutrient residence time in the rooted volume rather than to maximize soil water content
Water × Ca	Synergistic	Calcium moves almost exclusively by mass flow in the transpiration stream and is not appreciably remobilized in the plant	Sustain transpiration during fruit set; prolonged high humidity or water deficit precipitates blossom-end rot even at adequate Ca supply
N × K	Largely additive at constant electrical conductivity	Both are absorbed as counter-ions; the yield effect is expressed through total ionic strength of the feed rather than through their ratio	Control the feed by electrical conductivity; select fertilizer sources on cost and solubility rather than to meet a prescribed K:N ratio
$NH_4^+ \times Ca^{2+}$ and $K^+ \times Ca^{2+}$	Antagonistic	Competition among cations for uptake sites raises the apparent Michaelis constant for calcium (Equation 3)	Restrict the ammonium fraction and avoid excessive K during fruit set; nitrate-dominant feed supports calcium status
N × P	Synergistic, form-dependent	Ammonium nutrition acidifies the rhizosphere and raises P solubility; fertigation holds P in solution and lowers the P sorption index	Apply P through fertigation in small frequent doses on the P-fixing loamy soils typical of the humid tropics

Taken together, Table 3 indicates that management of pepper nutrition is better directed at total ionic strength and irrigation scheduling than at fixed nutrient ratios, because the interactions of greatest practical consequence act through the convective term of Equation (1) and the competitive term of Equation (3) rather than through feed composition as such.

4.3 Environment and nutrient interaction is specific to protected cultivation

This review found that the greenhouse alters the boundary conditions of uptake in ways with no counterpart in the open field. Because calcium and other mass-flow-borne ions arrive with the

transpiration stream, suppressing vapour pressure deficit suppresses their delivery even when solution concentration is unchanged (Suzuki *et al*., 2015), while Mankin and Fynn (1996) modelled nutrient uptake as a demand set by photosynthetic rate and driven by photon flux density, independent of water uptake. The environment therefore sets nutrient demand while the root zone sets supply, and yield responds to whichever is the more limiting.

This review identified root-zone temperature as a second modifier. Bonachela *et al*. (2025) recorded mean daily substrate temperatures 0.9 to 3.0 °C below those of the surrounding soil in passive Mediterranean greenhouses, often near 15 °C in cold periods and generally regarded as suboptimal. Since I_{max} in Equation (2) is temperature dependent, an identical feed produces different uptake at different root-zone temperatures. In the tropics the thermal risk runs the other way, and the mulch effects reported by Kumari (2014) are the corresponding management lever.

The review further highlighted two features of the protected root zone that deserve emphasis. Salts accumulate where rainfall no longer leaches the profile, so the optimum becomes a compromise surface rather than a single agronomic maximum (Ullah *et al*., 2017); and the soil solution is spatially heterogeneous (Lao *et al*., 2003), so a composite sample may misrepresent the concentration roots actually experience.

4.4 Maximum uptake and maximum yield do not coincide

The most consequential finding of this review is a decoupling. In the capsicum experiment of Ningoji *et al.* (2023) fruit yield was maximized at 125% of the recommended dose, whereas nitrogen, phosphorus and potassium uptake continued rising to 150%. Nutrient absorbed beyond the yield plateau is stored without conversion into harvestable product, the classical signature of luxury consumption. The same pattern appears as declining nutrient use efficiency with rising nitrogen rate in cucumber (Zhang *et al.*, 2011) and as the absence of any yield penalty from a 20% fertilizer reduction in capsicum (Muralidhar, 1998). Three optima therefore exist and they are ordered: the uptake maximum highest, the agronomic yield maximum below it, and the economic optimum lowest. Recommendations derived from uptake data alone will systematically over-fertilize. Nutrient not converted into yield also remains at risk of loss, so the leaching advantage of fertigation, which can cut fertilizer losses to about 10% against some 50% under traditional application (Thomas *et al.*, 2024), is forfeited where rates are set at the uptake maximum. This decoupling of the uptake and yield optima is represented by the feedback path shown in Figure 1.

5.0 CONCLUSION

Nutrient uptake in greenhouse pepper is not additive, and recommendations treating nitrogen, phosphorus and potassium as independent inputs applied at a nominal irrigation depth misrepresent the crop's response. The water and fertilizer interaction is the dominant control on both uptake and yield, and was significant in every factorial greenhouse experiment reviewed; pairing moderate deficit irrigation with a moderately elevated fertigation rate, near 75% available soil moisture with 125% of the recommended dose, more than tripled capsicum fruit yield relative to surface irrigation at the recommended dose.

Interactions among the nutrients themselves proved weaker than commonly assumed. In drip-fertigated pepper the nitrogen–potassium relationship operates principally through the total ionic strength of the feed and the placement of ions within the wetting bulb rather than through any prescribed ratio, and blossom-end rot is better treated as a joint outcome of irrigation regime, nitrogen form and potassium rate than as a calcium deficiency.

Because maximum uptake occurs at a higher fertilizer rate than maximum yield, recommendations derived from uptake data alone will over-fertilize. Three prescriptions follow: blanket single-nutrient recommendations should give way to irrigation-conditional fertigation schedules; electrical conductivity rather than a fixed nutrient ratio should be the primary control variable for feed composition; and rates should be set at the economic rather than the uptake optimum, where reductions of about 20% appear achievable without significant yield loss. The principal research requirement is the determination of pepper-specific uptake kinetic parameters and three-way factorial experiments combining water, nitrogen and potassium on tropical loamy soils.

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