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Key staff:	Paul Challinor, May Barn Consultancy Barry Mulholland, ADAS Tim O'Neill, ADAS
Location of project:	ADAS Boxworth
Industry Representative:	Philip Morley, TGA Technical Officer Nigel Bartle, North Bank Growers
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AUTHENTICATION

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

Sarah Mayne
Plant Pathologist
ADAS

Signature Date 30.06.2014

Report authorised by:

Barry Mulholland
Head of Horticulture
ADAS

Signature Date 30.06.2014

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GROWER SUMMARY

Headline

- Modulation of nutrition (e.g. N, Ca, Si) can produce plants that are more resistant to pathogen attack.
- Increased plant resistance will potentially reduce the use of pesticides, improve efficiency of production, optimise product quality and increase the potential for effective use of biological controls.
- Yield and fruit quality must be considered in novel recipes.
- As well as increasing concentrations, active uptake by the plant must be encouraged.
- Targeted information for growers remains scant; further R&D is required to provide new insights and develop robust strategies of nutrient management for increased resistance to diseases that are consistent and effective.

Background

Plant nutrient management has been primarily targeted at achieving high crop yield and quality, with relatively little work carried out to enhance disease resistance. On a commercial basis, any improved resistance that can be achieved with targeted mineral nutrition must be balanced against optimum yields, fruit quality, taste and flavour.

Targeted and accurate nutrient management is beneficial for numerous reasons. Firstly, the cost of fertiliser is kept low and waste is minimised. Successful cropping is becoming increasingly challenged by the need for water use efficiency (Water Framework Directive, 2000/60/EC) and less reliance on harsh chemicals (Sustainable Use Directive, 2009/128/EC) at the EU level. This has hastened the need to recycle water and nutrients, with the target of emitting as little drain water as possible. Systems that allow greater accuracy may further facilitate manipulation of the crop with beneficial effects, not only on yield, but also on disease susceptibility. Currently, numerous growing systems exist within UK tomato production sites, which involve a range of substrates and fertigation techniques.

There has been little research over the last 10 years evaluating the role of nutrition in disease management in protected edible crops. This literature review and critical examination of the latest research findings was therefore undertaken to identify links between nutrient management and disease.

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The commercial objective of this project was to evaluate the potential of targeted nutrient management as a cost effective and sustainable approach to enhance crop pathogen resistance. Application of this approach would enhance the reputation of the industry, and will help to meet the expectations of the retailers and consumers in the purchase and consumption of safe and nutritious food. The project aim was to clarify the role of individual nutrients for plant disease resistance, tolerance and reduced disease development in tomato. Specific objectives were:

1. To summarise current and potential future practices in nutrition of hydroponic tomato crops;
2. To review current literature on the impact of crop nutrition on the occurrence and severity of plant diseases in protected edible crops and identify knowledge gaps;
3. To identify potential nutrient management strategies for use in hydroponic tomato which have a high probability of conferring improved disease control to long season tomato crops;
4. To propose research and development areas where there appears to be significant potential to develop crop nutrition management strategies to assist sustainable disease control in tomato.

Summary and main conclusions

Objective 1 – Nutrition practices in hydroponic tomato crops

Current practices

Crop fertiliser application systems in hydroponic crops are usually based on two tanks of stock solution (to prevent precipitation of phosphates) which continually dose the irrigation solution applied to the crop. UK crops are most commonly grown in rockwool, coir or by Nutrient Film Technique (NFT), though other substrates are available. NFT is less popular compared to rockwool or coir because it has a lower buffering capacity, necessitating more active nutrient management and ensuring no leaks, blockages or pools exist in the system. Measurements of pH and EC values are regularly recorded by growers, and it is possible to make alterations to the nutrient solution based on these. However, in order to monitor the concentration of individual nutrients and the balance between them, it is necessary to take samples of the hydroponic system solution for laboratory analysis; ideally taken on a fortnightly basis.

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Solution target values were collected via a questionnaire to growers. There was some variability around the 'optimum' concentration for each nutrient supplied. Growers take account of environmental variables and varietal differences and work to slightly different product specifications. Most recipes used in hydroponics are many years old and based on original empirical nutrient recipes for starter solutions (dependent on the different hydroponic systems and influencing conditions) and refill solutions (accounting for daily uptake conditions). Improved and more targeted recipes have, over the years, resulted in higher yields, but water and nutrient losses to the environment remain a problem. Nutrient losses occur through flushing of the system, denitrification, leaks (to groundwater), but mainly through surplus nutrients added to open systems, which is usually around 30% of the total.

Future practices – A move towards nutrient recirculation systems

Initially hydroponic systems were all 'run-to-waste', whereby fertiliser stock solutions were used to dose the irrigation water, which was sent through the crop only once before being disposed of, usually by release into the environment. Whilst open run to waste systems are simple, cheap and relatively easy to manage, compared with closed systems such practices are in the long term unsustainable. Currently, a number of growers are using at least partially 'closed' or recirculating systems, whereby nutrient solution is collected, stored, re-dosed to appropriate levels and sent around the crop multiple times. In a fully recirculating system, a small amount of solution may still have to be discharged, for example if chloride or sodium levels climb too high and the system requires flushing. Ultimately, this system provides the perfect opportunity to optimise nutrient and water efficiency, and results in release of fewer nutrients to the environment. This is becoming increasingly regulated because of the harmful effects high nutrient levels can have on natural ecosystems, and a growing system that has minimal environmental impacts is more attractive to retailers and consumers. Importantly, recirculating systems also save on fertiliser and water costs, and as they require more active management, they also facilitate a more controlled and targeted nutrient regime that could result in higher fruit quality or yields. Savings made could encourage the move away from cheaper chloride based fertiliser products that can result in chloride build up in solution, and towards higher quality nitrate based products that also contribute nitrates to the solution and may render solution nitrogen levels to be manipulated more easily.

A fully recirculating system may also render growing with NFT a more attractive option, as greater care and attention will need to be paid to consistently achieving target nutrient

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levels. Due to the EU legislation noted above, it is becoming increasingly likely that all UK growers will have to make the shift to recirculating systems, as has occurred in The Netherlands. Furthermore, it is likely that restrictive legislation will be implemented regarding water abstraction, adding further incentive to use water efficiently. Installing a more cost-effective and technologically advanced system now, will better prepare nurseries for these future challenges. A hydroponic system that is easily manipulated will mean that future research and development can quickly be implemented at a commercial scale, including the implementation of models based upon growth and transpiration, and which involve feedback based on climatic changes and rootzone environment. There is also the potential to introduce the management of diseases and to incorporate fruit quality. The introduction of ion selective electrodes (ISEs), represents a way to continually monitor and dose a nutrient solution in line with these ideals. In future hydroponic growing, nutrient demand and nutrient supply could be synchronized, and nutrient and water losses would be minimised by the move from open to closed recirculating systems.

Objective 2 – Review of current literature

Over 190 scientific papers were identified and reviewed. Plant mineral nutrient impacts on pathogen function were classified in relation to pathogen identity and lifestyle, for example whether vascular, foliar, or root infecting; fungal, bacterial or viral; biotroph, nectrotroph or hemibiotroph. The degree of control reported and the potential to apply to commercial crops for disease control were evaluated and synthesised. Whilst this work focused on hydroponic crops, soil grown crop data were also used to provide insights on the potential for disease-suppressing nutrient management. The likely extent to which selected nutrient management could control disease was evaluated and factors influencing how widely applicable techniques would be in a commercial production environment are discussed. The main conclusions are listed below.

- The effect of over 15 nutrients on a variety of diseases on various crops have been researched and are discussed in the Science Section (Tables 8 & 9);
- Many studies have used tomato as a model crop, but methods are not standardised;
- Effects observed in one crop cannot be easily transferred to another;
- Results include successful applications of silicon and manganese when the crops are deficient, use of silicon in glasshouse crops, use of metals to improve biocontrol efficacy and the promising use of calcium and nitrogen in tomato;

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- The nutrient elements known to have the largest potential effect on disease resistance/tolerance outside the deficiency range are nitrogen, calcium, silicon, boron and phosphorus as phosphite;
- A number of interesting interactions of nutrients with biocontrols were noted;
- There has been a considerable amount of research on hydroponic nutrition overseas in recent years and it appears to be a topical research area currently;
- Nutrition in soilless tomato production presents a number of conflicts between crop yields, produce quality, microorganisms, consumer and retailer demands and environmental concerns and ideally, an optimal strategy will incorporate as much of the production process as possible.

Objective 3 – Identifying potential strategies

Problem diseases identified by UK tomato growers include Botrytis, powdery mildew and a variety of viruses, especially *Pepino mosaic virus*. Maintaining nutrient levels at the 'optimum' for plant growth still appears to be the best general strategy, though the nutrient levels considered 'optimum' in hydroponics vary and there are no universally agreed values. One example in current use is illustrated in Table 1. Recirculating systems are becoming more widely used, and as more growers may move to recirculation it is important that newly developed strategies consider this. If a specific disease threat is identified, or an epidemic occurs, there may be more targeted strategies that could have beneficial effects, on top of this general guide. However, although supplementation with additional nutrition has been found to reduce some diseases, the presence of excessive fertiliser, especially nitrogenous fertilisers, may also make the severity of other diseases worse. This may be linked to the different nutrition requirements of different pathogens, or to the type of plant growth produced. Currently, this approach may not be cost effective and further research and development is required.

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Table 1. Optimum nutrient concentrations for hydroponic tomato plants (as supplied by May Barn Consultancy Ltd and used as part of nutrient solution lab analysis)

Slab Sample	Minimum	Optimum	High	Comments
RAG Chart: Tomato	Amber: Likely to result in nutrient deficiency	Green: at or near the optimum concentration	Red: Likely to result in plant damage	
pH	< 5.5	6.0	> 6.5	Target range: 5.8-6.2
EC (µS / cm nutrients)	< 2,500	4,000	> 6,000*	*Early season growth control
Major (mg / litre)				
NH_4-N	0	2	> 10	As low as possible
NO_3-N	150	250	> 300	
P	20	30-40	> 50**	**Induced Zn+Cu deficiency likely
K	< 400	500	1,000	Toxicity: rare
Ca	150	250	> 300	
Mg	< 65	80	> 100	High K inhibits Mg absorption
Na	< 100	200	> 400	High Na inhibits uptake of K, Ca, Mg
Cl	< 100	200	> 400*	*Early season growth control
SO4-S	< 50	100	> 200	
Trace (mg / litre)				
Fe	< 2.0	3.0-4.0	> 5.0	
Mn	< 0.4	0.5-0.6	> 1.0***	***Toxicity risk higher
B	< 0.3	0.4-0.6	> 1.0	
Zn	< 0.5	1.0	> 1.5	Link with P and Mn
Cu	< 0.05	0.1	> 0.2	
Mo	< 0.03	0.05	> 0.1	
Ratios				
K:N	> 3.0	2.0	< 1.6	
K:Ca	> 3.0	2.0	< 1.6	
K:Mg	> 8.0	6.0	< 5.0	
K:Na	> 5.0	2.5	< 1.25	Important in recirc.

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Slab Sample	Minimum	Optimum	High	Comments
K:Cl	> 5.0	2.5	< 1.25	Important in recirc.

Information gathered in the review shows that altering the basic nutrient recipe could have advantages at certain points in the season, at certain environmental conditions, or under certain disease pressures. A nutrient regime that is frequently adjusted for variables such as crop health and fruit quality may not always be consistent with the highest yield. As the crops in the UK are largely specialist, high quality varieties, it makes sense that a forward thinking nutrient regime should account for consequences on fruit appearance, structure, taste and nutritional content.

The ratios contained in the above optimum regime are the most important aspect, and must be maintained whatever absolute values may change. An important ratio in terms of pathogen attack is the ammonium to nitrate ratio. This is generally always kept low due to numerous other factors. Too much ammonium can cause issues of pH falling too low and of calcium deficiency, whereas nitrates tend to be more beneficial in terms of yield as they are mobile, non-volatile and their assimilation is a more energy efficient process. This ratio's impact on the ability of different types of pathogen to cause damage is notable with effects in both directions. However the potential to manipulate it may be limited, as it is advised (with good reason) that ammonium is not supplied at above 15 % of total nitrogen supply. These recommended nutrient ratios attempt to account for the abiotic effects of pH and EC, synergistic relationships between nutrients, climate, and biotic variables such as pathogens, beneficial microorganisms and plant growth and transpiration.

Using the example recipe as a base, alterations could be made in light of our findings to increase the resistance/decrease the susceptibility of the crop to certain diseases, or to make the nutrient solution less hospitable to specific pathogens (Table 2). Regardless of impacts on disease, nutrient elements must not be allowed to climb to concentrations likely to result in phytotoxicity. Focus is on those diseases that are commonly a problem in UK growing. Many of the diseases where control with nutrition appears most promising are not problems in the UK at present (see Science Section). It is unlikely that these suggested changes to nutrient regimes would remain in place throughout the growing season, but may be useful at times of heightened risk or when infection occurs. It is clear that nutrition is not an equally applicable solution to all disease problems, but may be a useful part of IPM against some.

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Table 2. Hydroponic tomato nutrition 'toolkit' for managing disease

Disease	First usual occurrence	Suggested change to optimum	Risks	Benefits
Botrytis cinerea	April onwards	Consider increasing N to strengthen plant against attack. Additional Ca has also been found to reduce *Botrytis* severity. In sweet basil, a regime using half the N but double the Ca to maintain appropriate nutrient balance was utilised successfully against *Botrytis.* Control of humidity is important in encouraging uptake and movement of Ca into the plant.	May encourage infection by obligate diseases. May also result in vigorous plants that require more pruning.	Significant reductions in disease have been demonstrated experimentally. Additional Ca may protect against BER and increase shelf life. Humidity control benefits both nutrition and disease control.
Oidium neolycopersici	March - September	Reduce N, especially in nitrate form as this obligate pathogen is favoured by factors that encourage plant growth. Si has also been shown to reduce powdery mildew experimentally. Disease levels were lowest at moderate EC (approx. 4 mS).	Reducing N may encourage more opportunistic pathogens. Adding Si to the nutrient solution may cause problems by precipitating out of solution and blocking the irrigation system. It may also necessitate an additional fertiliser dosing tank.	Significant reductions in disease have been demonstrated experimentally, and some fertiliser costs are saved.
Viruses E.g. PepMV, ToMV	February onwards	A study involving Ca sprays may be promising. It is beneficial to provide the plant with supraoptimal nitrate N to allow the plants to grow through the initially strong symptoms of viral infection. Using a vigorous rootstock may promote a similar growth effect as higher N. Elevated CO_2 may also help reduce severity of viruses such as TYLVC. Additional B may also have potential to prevent spread of some viruses.	Nutrient management of infected plants is already practiced in UK growing successfully. CO_2 supply may be limited.	Ca nutrition will avoid BER and may also have other disease targets.
Verticillium wilt	May onwards	Promising effects of sulphur nutrition in limiting the spread of *Verticillium dahliae* by 'sulphur enhanced defence'. It may be worth exploring if Verticillium wilt becomes problematic on grafted crops, and allowing sulphate to accumulate in solution to supraoptimal concentrations.	Sulphate is traditionally seen as an unwanted ion. Though there is a relatively large range of acceptable sulphate values in solution, allowing sulphate concentrations to climb too high will have deleterious effects.	The threshold of acceptable sulphur may be higher than previously thought, and it may offer some defence against vascular disease, though this is unlikely if disease is severe.

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Pythium and Phytophthora root rots	April-June	If a threat of Oomycete root rot is present, extra care should be taken to avoid salinity stress and high EC values, which predispose crops to infection. A degree of tolerance may be initiated with elevated (700 ppm) glasshouse CO_2. Copper ion water treatment has also shown efficacy in the ornamental sector.	None, it is generally beneficial to limit salinity and EC regardless of pathogens.	Somewhat limited information.
Clavibacter michiganensis pv. *michiganensis*	July onwards	Resistance of some cultivars is dependent on adequate Ca, and higher Ca supplies reduced disease severity in both a resistant and susceptible cultivar. Survival and spread in hydroponics is encouraged by higher pH. Potential to reduce pH of drain water overnight. Higher leaf concentrations of Mg correlated with lower disease level.	Further tweaks required to nutrient solution if changes to calcium are made (N, K etc.). pH changes may alter uptake of other nutrients.	Potential to reduce disease severity in commercial cropping. Suggested lowering of pH at night. Likely a promising area of research due to aggressiveness of disease and lack of PPPs.
Agrobacterium spp. (crown gall and root mat)	April onwards	Disease requires nutrition as plant does, and excluding N, P and Ca limited tumour size. However, this would be impossible in a commercial crop.	Loss of crop, loss of productivity.	Disorders such as crown gall and root matt are not generally widespread enough in the crop to warrant a large scale change to nutrition.
Passalora fulva	May/June onwards	*In vitro* tomato cells produced a calcium dependent defence protein, so it may be prudent to ensure Ca is supplied at sufficient concentrations. Many of the pathogens effector genes are triggered by N starvation.	Maintaining sufficient Ca should be part of any successful nutrient regime, and avoiding supra-optimal N.	Though *in planta* links between nutrition and leaf mould severity are untested, supplying adequate calcium will benefit overall plant health and limiting N is cost effective.

For sources of information and more detail, see the Science Section.

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Costs of implementation

Reductions in the severity, sporulation and pathogenicity of *Botrytis cinerea* have been illustrated by numerous studies supplying plants with additional nitrogen. The cost of Botrytis control is estimated at £2,500 per hectare, and a reduction in these costs would represent a significant saving, compared with the cost of raising nitrate to 500 mg/L, estimated at approx. £1600 per season. However, this does not account for other required changes to the recipe, for example increased potassium, and more frequent nutrient solution analysis.

This example shows there is potential for a reduction in disease due to modified nutrient strategies, and this could confer cost benefits to growers. However, it is unlikely that these could be realised in commercial cropping without further research into plant nutrition due to the high number of variables present in UK tomato growing.

Objective 4 – Proposed research and development priorities

Nutrition delivered to the root-zone has the potential to affect almost every aspect of cropping, including disease resistance. It is in turn affected by a variety of environmental variables and is unlikely to have a constant effect in changing conditions. Even different strains of the same pathogen were found to react differently to changes in plant nutrition, and variables such as substrate, water supply and quality, climate, variety and fertilisers used may all affect nutrient uptake by the crop. Knowledge of how this can be manipulated in a commercial setting would be invaluable. From the findings of Objective 2 and analysis undertaken in Objective 3, a series of proposed research and development priorities is proposed (Table 3). This is based on the perceived benefit to the tomato growing industry and the probability of successful research as well as the likely time period for promising results. Further research specifically on commercial tomato is required as many of the effects identified are crop and disease specific.

The interactions between nutrient, crop and disease are highly complex and as yet not fully understood. Further research in a variety of areas that may be promising but not immediately beneficial to the UK industry are summarised in Table 4. Increasing the efficiency of systems, especially drain water nutrient recirculation systems to allow greater accuracy of dose application, maintenance of slab targets and monitoring of pH, EC and nutrients in the system will ensure optimum growing conditions are achieved. Further

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determination of what ‘optimum’ concentrations are, and how far ranges can be pushed will also contribute to this.

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Table 3. Proposed R & D priorities to improve the use of nutrient management for disease management

Potential R & D priorities	Description	Impact	Cost	Likelihood of success	Time until uptake	Rank
Re-evaluate optimum nutrition concs for recirculation systems	Likely that recirculation will play a major role in future growing. Quantify the savings in nutrient & water.	Increased yields, greater disease resistance/tolerance. More cost effective, environmentally friendly fertiliser and water use.	May save money in terms of fertiliser and disease control programmes and may also increase yields.	High. Optimums have not been evaluated in the UK in years, and it is likely beneficial changes can be made to regimes.	Possible to start now.	**1**
Improved nutrient technology	Work ongoing in Canada and China on ISEs and modelling software.	Potential to match nutrient supply with plant demand closely, optimising nutrition.	Cost of new technology is generally high, but savings and improved profits would also be facilitated.	Medium. If can be shown to work effectively in practice they would be very attractive to growers if the price was acceptable.	In development for over 10 years, but not yet adopted. These systems do seem like the future, but time to market is uncertain.	**2**
Large, commercial scale nutrition experiments	Many promising interactions that warrant further exploration e.g. use of silicon (as a silicic acid spray, slow release slab, or potassium silicate + acid).	Possible reductions in pesticide use, improvements in plants tolerance to stress. Possible impacts on yield and quality should be included.	Large commercial trials are more expensive than smaller trials, but the latter have already shown promise, and commercial trials will show if a technique will be effective.	High. Will succeed in generating further data on which to base decisions on future nutrition strategies.	Potential to develop new recipes for use in specific situations is present currently, and is performed by growers to differing degrees.	**3**
Production of grower guide on hydroponic nutrition	No singular source of comprehensive information on growing hydroponic tomato exists. Also potential for further KT.	This would recap growers on the basic rules of crop nutrition, & inform on recent and future developments. It may also stimulate open discussions on the topic.	Bringing together information would make tomato nutrition more accessible to industry professionals, saving time & money.	High.	Could be started at any time.	**4**
Effect of nutrition on PepMV	Limited information was found, though it is known that growers manage crop nitrogen following infection so that the crop can outgrow symptoms.	PepMV can cause considerable reductions in yield and fruit quality, appearance and flavour. Control options are currently very limited.	If a cost effective solution can be found based on crop nutrition that is more effective than methods currently in use, savings could be made. E.g. Boron	Uncertain. Could improve control, but may not be effective or practical in a commercial setting.	This control method for PepMV is already utilised, but it would be useful to establish If this could be taken further.	**5**
Nutrition's use within IDM	Nutrition interactions with microorganisms in the root zone, be they natural, introduced, pathogen, beneficial or saprophytic.	Reduction in pesticide use, improved efficacy and uptake of biocontrols, interaction with elicitors, cultural controls & forecasting risk.	Laboratory and glasshouse trials could result in savings on pesticides and spray applications.	Medium. Would require extensive monitoring and for the appropriate microbes to be detected effectively (as in PC 281a).	There is grower interest, but success of biocontrols has been limited. IDM is preferred over harsh pesticides, & if efficacy is improved they may be used.	**6**
Water treatment technology with nutritive effects	Cu electrodes ionise and disinfect water & provide plants with copper nutrition. Electrolysed water also promising – does this affect nutrition?	An effective method of reasonable cost that also provides some crop nutrition would be beneficial.	Many different methods available, differ in cost. The AquaHort method provides copper nutrition and keeps the irrigation system clean.	This method is already used effectively by many in the bedding plant industry. Heat, UV and biofilters are generally in use within Protected Edibles.	Technology already in use in Protected Ornamentals.	**7**
Effects of substrate	A variety of substrates with different properties, & NFT growing are in use in the UK	Substrates are known to affect nutrient uptake. Information would be useful to growers.	Many substrates are used, would require trials and monitoring of rootzone solutions.	High.	Numerous different substrates are currently available to UK growers.	**8**

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Table 4. Potential longer term R&D topics on crop nutrition

Point raised by review	No. studies (approx.)	Description	Pros	Cons
Impact on human health/nutrition	10+	Incorporation of beneficial compounds in produce, as well as nutrition targeted at human malnutrition problems.	Currently the area of health foods is fashionable, so there is a potential market for produce	Potentially more applicable in developing countries
Novel active ingredients	3+	Novel technology has shown new active ingredients such as lactoferrin to be effective in controlling some diseases. Potential to send elicitors through hydroponic system.	Potential for new active ingredients with novel modes of action against disease	New substances may meet specific regulatory problems, or may not be found to be cost effective
Large-scale monitoring of UK tomato crops	0	Monitoring of multiple crops nutrition and disease incidence over a growing season	May highlight key risk areas or particularly effective strategies, and the effects of recent developments in growing (e.g. dawn temperature drop's effect on calcium uptake and sinks)	So much variability may just serve to confuse matters and mask any trends present
Differing varietal/rootstock requirements	5+	Whilst some studies have focused on the response of varietal resistance to differing nutrition, further work on the requirements of different varieties may be useful	Prior knowledge of a varieties preferences or weaknesses may make for a smoother growing season and improved yields/quality	Generally, growers come to their own valid conclusions on how to differently manage varieties, and many new varieties are introduced or moved away from constantly, meaning this work may have limited use.
Changes to EC	5+	A higher EC may also reduce susceptibility to certain diseases	High EC results in smaller, more flavoursome fruits but lower yields and new, vigorous rootstocks may have the potential to tolerate higher ECs in the rootzone	Allowing EC to climb has many potential deleterious effects (e.g. BER, impaired water uptake) and has been consistently lowered by growers over the last 10 years
Effect of type of fertiliser	5+	There are numerous different fertilisers on the market, compound or single element, chemical or organic, liquid or solid form. Fertiliser choice is dependent on many different factors.	Organic fertilisers may offer some protection from soil-borne disease. Single element fertilisers, though not always available, may be more easily managed	Fertilisers differ in cost depending on the source and form, the production process and demand. Cheaper fertilisers, may be less effective, and vice versa. Organic fertilisers may also be variable in formulation.
Foliar sprays	10+	Use of foliar feed e.g. calcium, silicon to combat both disease and nutrition disorders as is done currently to some degree.	Could improve shelf life and act to top up rootzone nutrition	Application incurs higher costs to the grower, so it would have to be highly effective.

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SCIENCE SECTION

Introduction

The ability of some plant species to resist some pathogens is altered when plant tissue nutrient concentrations change above or below a critical threshold. Tissue nutrient concentrations in the rhizosphere can be rapidly modulated in hydroponic culture and there is therefore potential opportunity to provide nutrient feed regimes that not only optimise growth and yield but can have a positive impact on pathogen infection control.

A recent analysis across a range of crops, focussing on N fertilisation, found that fungal pathogen identity and lifestyle were the main significant regulators affecting the extent of the modification of plant disease resistance (Veresoglu *et al*., 2013). Results varied with plant species. In most cases increased N fertilisation increased disease severity, while for certain plant species and fungal pathogens, disease severity declined with increasing N. It was concluded that fertilisation does modify plant disease severity of fungal pathogen induced diseases and this should be considered on a cost-benefit basis before deciding the rate of fertiliser to add to a crop. Currently, to ensure high yielding crops large amounts of expensive nitrogenous fertilisers are used and improving Nitrogen Use Efficiency (NUE) is of high importance. It has been proposed that integration of data from a variety of sources and studies with knowledge of whole plant behaviour and commercial agriculture will aid better understanding of NUE (Masclaux-Daubresse *et al*., 2010).

Investigations with tomato plants suggest that nitrogen does affect susceptibility to fungal pathogens (Lecompte *et al*., 2010). Other work has demonstrated that optimal nutrient concentrations can reduce sporulation of *Botrytis* and the production of secondary inoculum (Abro *et al*., 2013). Calcium is a key component of cell walls; the occurrence of blossom end rot has been studied extensively and has been linked to localised tissue calcium deficiency. Adequate concentrations of calcium in plants also aid in the plant’s ability to isolate an infection. There may be potential to reduce occurrence and / or severity of *Botrytis cinerea* and other necrotrophic fungi through increased calcium nutrition (Elad *et al.,* 1993) which may also serve to combat blossom end rot (BER). Having optimum environmental control is required to prevent many diseases but also to prevent BER as plant transpiration needs to be encouraged so sufficient calcium and boron are taken up at the roots. The role of nutrients in plant health and defence are complex and results are variable. Magnesium nutrition may have a variable effect on disease severity as it is known to complement or antagonize other nutrients (Huber & Jones, 2013).

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There is evidence to suggest that micronutrients may also enhance plant defences. For example, silicon is a component of plant cell walls and an important facilitator of calcium utilisation (Currie & Perry, 2007). In hydroponic cucumbers, increased silicon nutrition applied as potassium metasilicate was shown to reduce powdery mildew and stem rot (*Didymella bryoniae*) (O'Neill, 1991). The role of metals in plant nutrition is also hypothesised to play an important role in plant defence in plants that hyperaccumulate them by stimulating biotic defences (Poschenrieder *et al*., 2006). However metals are also utilised by fungal and bacterial pathogens in a variety of infection processes, for example zinc is required in formation of appressoria in many fungi and iron is withdrawn from the environment by bacterial siderophores (Poschenrieder *et al.,* 2011).

Commercial tomato crops are susceptible to a wide range of fungal, bacterial and viral diseases. Some diseases, including Botrytis and powdery mildew, thrive under high humidity and humidity is often controlled through a combination of venting, heating and fans. As mentioned above, environmental conditions will also exert a strong effect on uptake efficiency of nutrients such as calcium and boron. This is an energy intensive control measure which is becoming increasingly expensive to implement as energy prices rise. In addition to these cultural controls, fungicides are often applied. There is increasing interest from retailers and consumers in the production of residue-free food.

In hydroponic tomato crop production, there is opportunity to apply varying nutrient concentrations to specific target ranges in order to modify plant growth and composition. Adjusting the crop nutrition with the aim of reducing disease development has not been thoroughly examined in tomato. There is therefore an opportunity to supply key nutrients such as nitrogen, phosphorus and potassium at known and effective concentrations, in addition to micronutrients such as selenium and iron, at strategic points in the crop production cycle; this approach could be used by growers to reduce both the incidence and severity of diseases, and provide an additional tool for sustainable disease management.

Prior to the review, the major disease problems of those crops are summarized in this report in order to aid interpretation and potential application of research results obtained from the literature review. General comments on the effect of nutrition on individual diseases are highlighted.

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Current key diseases of tomato in the UK

UK tomato crops suffer from a variety of fungal and bacterial diseases, as well as several viruses causing both foliar and root symptoms (Blancard, 2009). Some diseases are more important than others, due to factors such as frequency of epidemics, effect on yield, cost of treatment and whether or not an effective treatment is available. Taking these factors into account, the key diseases of UK tomatoes are detailed below and as such this list is not exhaustive. It should also be noted that though these diseases have been classified according to their primary symptoms, some may spread to infect other parts of the plant in certain circumstances. Some diseases subsequently found in the literature review were not listed here, as they are not common problems for UK growers. A good understanding of pathogenesis of problem diseases can illuminate potential control options at points where their lifecycle can be interrupted and inhibited, whether this be through nutrient management or through other methods.

Foliar diseases

Grey mould (*Botrytis cinerea)*

Figure 1. Botrytis stem lesion from leaf scar

This ascomycete fungus has an extremely broad host range, and is a problem on a variety of crops, both indoor and outdoor. In tomatoes the severity of disease is generally greater in a glasshouse setting (the main growing situation in the UK) due to high relative humidities, soft growth and frequent creation of wounds (compared to outdoor crops), often resulting in stem lesions which progress to cankers and girdle the stem. There is some variability between strains of Botrytis, with some strains possessing resistance to iprodione and fenhexamid fungicides, and others having transposons additional to their basic genome. It is

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thought that glasshouse strains of Botrytis show some degree of specialisation to this lifestyle (Decognet *et al.,* 2009).

Botrytis infections are commonplace in UK growing, and occur on all aerial parts of the plant, at all ages. It can cause problems with irrigation due to missing plants, and may also spread to the fruit to cause ghost spotting or post-harvest rots if environmental conditions are favourable. Ghost spotting occurs on fruit where a *B. cinerea* spore has landed and germinated, but infection has been unsuccessful. Botrytis is also favoured by pruning wounds on the plant, made necessary by the indeterminate varieties grown, and by the long growing season which allows inoculum to build up in the glasshouse. Botrytis is also more common towards the end of cropping because it easily colonises older, senescing tissue as a rich source of nutrition. Lesions appear wet at first, but dry with age, leaving brown coloured lesions with well-defined margins. Eventually, distal leaves exhibit yellowing, wilting, and may die and if conditions are favourable, fuzzy, grey sporulation can be seen on affected tissue. Hard sclerotia 2-5 mm in diameter may also be formed, but these are rarely visible on lesions. Botrytis may survive on seeds, organic matter and on other susceptible hosts in the environment. Spores (conidia) are easily spread by the wind, by water and by movement of staff and keeping infection out is impossible due to its ubiquitous nature. Spores germinate at humidities above 95%, but are inhibited at temperatures above 30°C. Sporulation may begin again 3 days after initial contamination of the glasshouse.

Traditionally, control of *B. cinerea* was largely dependent on protective fungicide sprays, especially when glasshouse conditions are favourable for infection (e.g. during wet weather) or after pruning. Botrytis has been seen to evolve fungicide resistance, and dependence on a dwindling pool of active ingredients means that other control methods are becoming increasingly important. Glasshouse environmental monitoring, venting and heating ensure effective humidity control, and effective pruning improves air circulation in the crop. Pruning is performed carefully and in the mornings for optimum protection and doing so in humid conditions is to be avoided. Young lesions found in a crop are usually removed and the susceptible area may be covered with a clay paste and it is prudent to remove infected crop debris.

- It is generally known that nitrogen fertilisation should be controlled to avoid highly vegetative plants which may be susceptible to subsequent physical damage, leading to creation of entry points for disease.
- High concentrations of calcium nutrition in tissues is also known to reduce infection (Blancard, 2009).

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Powdery mildew (*Oidium neolycopersici*)

Figure 2. A severe outbreak of *Oidium neolycopersici* in a tomato crop

Tomato in the UK is affected by two types of powdery mildew. *Oidium neolycopersici* is the most common cause of outbreaks, and *Leveillula taurica* a rarer species of the disease on tomato, though occasional on pepper. It is thought that *L. taurica* may be an aggregate species.

O. neolycopersici appeared in the UK in 1987 and can spread quickly and cause considerable damage if control is absent, necessitating intensive preventative treatments. It causes spots on the upper sides of leaves, which are typical of a powdery mildew, being covered in powdery, white mycelium and conidiophores. Spots become chlorotic and eventually necrotic, and whole leaves can be affected. Tomato stems can also be affected. This fungus invades the cell with use of an appressorium to penetrate epidermal cells. Warm temperatures and humidities of 80% or below favour the fungus.

L. taurica causes symptoms distinct from *O. neolycopersici*, causing pale green spots to gradually appear on the upper sides of leaves which are delimited by leaf veins. These spots turn yellow over time and discrete spots of white sporulation can be seen on the lower side of the spots. Sporulation may also occur on the upper leaf surface in wet conditions. Eventually, spots become necrotic and complete yellowing and death of leaves and leaflets may occur. Conidia germinate at humidities higher than 40% to invade directly through the cuticle or through the stomata to occupy the spaces between mesophyll cells in the leaf. Conditions involving temperatures around 26°C and humidities of 70-80% encourage disease development, as does leaf wetness and warm days with cool, humid nights.

Both fungi may be spread by wind, water splash and by crop workers. Control methods are similar for both powdery mildews. Infected leaves and crop debris should be carefully

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removed, and careful application of protectant fungicides performed. It can be difficult to eradicate these diseases once established, but usual hygiene methods should also be followed, as well as control of environmental conditions to avoid favouring the fungi. Several varieties containing a resistance gene to *L. taurica* are available, and the use of commodity substances and biocontrols may also be an option. Resistance to *O. neolycopersici* has been found in wild tomato species and has been used by breeders. Disinfection and removal of susceptible weeds such as nightshade between crops will also help remove spores and mycelium of the fungi.

- Solanaceous powdery mildew (*O. neolycopersici)* is exacerbated by high nitrogen content of leaves (Blancard, 2009).

<u>Tomato leaf mould *(Passalora fulva)*</u>

Figure 3. Lower surface of tomato leaf showing distinctive olive brown sporulation of *P. fulva*

Previously known as a Cladosporium species, this disease has a gene for gene relationship that governs cultivar resistance (See AHDB Horticulture Factsheet 09/13). The fungus evolves quickly, and though many cultivars are grown that possess resistance to a number of strains of *P. fulva* new strains are evolving all the time. Some strains are also known to be resistant to the fungicide azoxystrobin (e.g. Amistar). Leaves infected with leaf mould develop leaf spots that appear yellow from above, and have olivaceous to purple-brown sporulation on the lower leaf surface. As with most fungal diseases in glasshouses, it is encouraged by high humidity and poorly ventilated or poorly heated glasshouses. Leaf mould almost exclusively attacks leaves, starting with the lower leaves first, eventually

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resulting in necrotic and dry tissue appearing in the leaves, which start to curl. When conditions are very favourable, sporulation also begins to occur on the upper leaf surface. Very occasionally, flowers and fruit may also be attacked.

Mycelium, sclerotia and conidia can survive in glasshouses between crops, and so disinfection after an outbreak is crucial as conidia can remain viable for over a year. Condia require a film of moisture to germinate, and *P. fulva* enters leaves via the stomata, in just 24-48 hours in favourable conditions. The fungus has a long incubation period of about 10-15 days before sporulation occurs. Spores are easily spread by wind, water, workers and tools, as well as some insects.

Reducing the humidity, avoiding leaf wetness, removing infected lower leaves and maintaining the glasshouse temperatures at night are effective control methods should infection occur. Fungicide sprays must be regularly applied, and good coverage on the lower surface of leaves is important. As well as azoxystrobin resistance observed in the UK, strains resistant to many other fungicides have been recorded in China (Yan *et al*., 2008). Temperatures of 20-25°C favour development and disease is also favoured by low light conditions.

- Excessive nitrogen fertiliser may also favour leaf mould (*P.fulva*) (Blancard, 2009).

<u>Late blight *(Phytophthora infestans)*</u>

Figure 4. Symptoms of late blight observed in a glass house

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Famously also affecting potato, nearby potato crops serve as an inoculum reservoir for disease in tomato crops. Long lasting oospores may also be formed in field soil, which are extremely persistent and constitute permanent inoculum. A glasshouse located near prominent potato growing areas is therefore at greater risk. Late blight has the potential to cause extensive damage to crops and their fruit if a severe epidemic occurs. The disease is favoured by damp, humid conditions and so is usually observed late in the season (as its name suggests) only in glasshouses with poor climate control. It is not normally a problem in modern, heated glasshouses unless heating is off temporarily or the system fails. Multiple strains of the disease exist, of two sexual types, which facilitates high genetic diversity, and increased virulence. The disease can complete its full life cycle on tomato, and there are thought to be strains specialised for tomato infection that survive year to year.

All aerial parts of tomato are affected, but the disease usually begins with formation of wet, brown spots on leaflets. Leaflets may quickly become necrotic, and a white down is sometimes observed on the underside of spot margins. Leaves or even complete plants may eventually become necrotic, and brown cankerous lesions may form on stems and petioles. Flowers may be infected and fall, and fruits exhibit brown mottling. If fruit are infected quite late, brown patches, often with concentric circles form, which may be confused with other *Phytophthora* species symptoms, such as *P. nicotianae*. Optimal growth temperature is 23°C, and sporulation requires relative humidities of at least 90%. In glasshouse tomatoes, control can generally be achieved by the avoidance of high humidities, and quick treatment with a blight effective fungicide if infection does occur. If a small number of plants are affected, it may be plausible to remove these. Glasshouse ventilation may ensure that moisture is reduced, but may also allow in potentially contaminated soil and dust. Several decision support systems for late blight are in existence and may guide growers as to when high risk periods occur, for example Blightcast (http://www3.syngenta.com/country/uk/en/agronomytools/.../blightcast.aspx).

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Viruses

Pepino mosaic virus (PepMV)

Figure 5. Common fruit symptoms of PepMV

Pepino mosaic virus was detected for the first time in 1974 in Peru and has caused outbreaks in the UK every year since its arrival in Europe in 1999, in the Netherlands. Several strains of the virus are known, but UK infections mainly consist of strains EU and CH2. Generally, infected plants will take on a blotchy, mottled appearance and usually exhibit stunted growth. Flavour of fruit and plant vigour are also affected. The most characteristic symptom of this virus is yellow spotting. Leaves may also curl and blister in low light conditions. Brown and corky ridges may appear on the stem, and leaves may take on a nettle-like appearance that may look similar to herbicide damage. Flowers may brown and abort and fruits will show blotchy ripening of varying severity, more obvious on ripe fruit. Fruit symptoms are often the only visible symptom, and symptoms are highly variable, depending on virus isolate, cultivar, environmental conditions and plant age.

The virus spreads rapidly and yield losses are estimated at between 5 and 15%, but losses of 40% have been recorded in Spain and Canada. The virus is very stable and may survive in glasshouses and for more than 90 days in plant debris and 14 days on clothing. It may also be spread via the nutrient solution and by glasshouse bees and is often observed along rows, at least initially. Currently the only effective control is the avoidance of initial infection through intensive hygiene measures. Workers should not be permitted to consume tomatoes, especially those of unknown origin, on site. Once a crop is infected, it is difficult to limit spread and the usual practice is to manage the crop through the period of severe symptoms. At the end of the season, intensive disinfection should be performed. In the Netherlands, work on the use of a mild strain of the virus to confer resistance to the more

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damaging strains has resulted in this potential treatment, not currently permitted on UK crops.

Tomato mosaic virus (ToMV)

Figure 6. ToMV affected truss showing advanced necrotic symptoms (Image courtesy of May Barn Consultancy Ltd)

Tomato mosaic virus is considered to be a specialised strain of Tobacco Mosaic Virus (TMV), and at least six pathotypes have been identified. Symptoms are varied, but include slowing plant growth and leaf distortion and discolouration. This can include vein clearing, mottling, mosaic with patches of green, yellow or white. Leaves may become fern-like in low light and flower drop may occur. Fruit produced are small and often bumpy, and may show yellow discolouration on the outside, and necrotic vascular tissue inside. Impacts on yield are greater if infection occurs early in the season. Spread of the virus is often in lines, or related to cultural operations. Symptoms vary depending on tomato cultivar and environmental conditions. For example high temperatures generally reduce symptom severity, but if the tomato has the resistance gene Tm2, high temperatures may result in a necrotic reaction to the virus. Symptoms increase in severity if plants are also infected with another virus. ToMV may survive in substrates and debris for several years and is easily spread by contact and through hydroponic systems. This virus cannot be eradicated once present in the crop, and control methods are as for PepMV. Resistant varieties of tomato have greatly reduced the impact of this virus, but it may still cause problems if newer, non-resistant varieties are grown.

- ToMV may be influenced by nitrogen and boron nutrition (Blancard, 2009).

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Root and stem diseases

Pythium and Phytophthora root rots

Figure 7. Roots infected with a *Pythium* sp. showing characteristic rot

Pythium and *Phytophthora* spp. are members of the Oomycete family, and have similar biology, symptoms, favourable conditions and control measures. Phytophthora diseases are commonly seen as more severe, but *Pythium* sp. are common and also capable of causing severe root disease, especially in soil-less crops. These pathogens have a somewhat aquatic lifestyle, and thus their survival, infection and spread is favoured by the hydroponic growing environment.

Pathogenic *Pythium* spp. are found throughout tomato production at all stages, causing symptoms on the roots and stem base, but also capable of affecting fruit, especially if carried close to, or in contact with the ground or occasionally aerial blights. *Pythium* spp. are a main cause of damping off in seedlings, but different species and isolates vary considerably in their pathogenicity. Typical root symptoms on adult plants include browning, decay and loss of rootlets and smaller roots. Vascular tissues turn brown and the cortex of the root rots away. It is quite common for Pythium root rot to occur in UK soil-less systems (see PC 281a), however their presence is not always damaging to the crop due to the variation in pathogenicity, unfavourable conditions for disease and the use of rootstocks resistant to root disease.

Phytophthora species are less common, though some may thrive in poorly heated glasshouses. Occasionally, Phytophthora root rot has resulted in severe disease in UK hydroponic crops where water is recycled with nil or inadequate water treatment. *P. nicotianae* is a common pathogen of soil grown crops, but does not generally cause severe

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damage in hydroponics. *P. cryptogea* is also known to cause a disease on seedlings similar to Pythium damping off. On adult plants, the symptoms of Phythopthora foot and root rot are similar to those described for *Pythium* spp. but are more severe. Generally, a plant with root rot will be less able to absorb water and nutrients and may exhibit reversible wilting, stunting, leaf yellowing, or if fruiting blossom end rot may develop on some trusses. Tomatoes are quite tolerant to root disease and may undergo considerable root rot before aerial symptoms appear. *Phytophthora* spp. may also infect fruit held close to the ground, resulting in firm brown lesions, often with concentric rings.

These pathogens have a variety of spore types that allow them to survive in the absence of hosts, and may also colonise organic matter in the substrate. Host range is generally very broad, and they may be present in irrigation water or glasshouse dust. Optimum temperatures vary from species to species, and their spread is favoured by damp conditions as many species are capable of producing motile zoospores attracted to root exudates. Young and stressed plants are generally more susceptible. They may also be spread by water splash, insects and staff. Control methods include the use of specific anti-oomycete fungicides, at the base of plants or in the nutrient solution, though consideration of fungicide resistance is key as these species may reproduce sexually and evolve quickly. Diseased plants, and most especially their root systems, should be carefully removed from the crop and disposed of.

- It has been found that some *Phytophthora* species are favoured by excess nitrogen, but that severity is reduced with the addition of potash (Blancard, 2009).

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Bacterial canker *(Clavibacter michiganensis* subsp. *michiganensis)*

Figure 8. Leaf lesions and wilting caused by bacterial canker in a UK glasshouse

This disease is not currently established in the UK, but isolated cases have been reported and it is known to be extremely damaging to crops. *Clavibacter michiganensis* subsp. *michiganensis* (Cmm) mainly affects the Solanaceae and its spread and development is encouraged by soil-less glasshouse production systems. This disease has the potential to spread rapidly, affecting the majority of a susceptible crop, and may greatly reduce yields. As such, growers are concerned about the potential of this disease to be introduced and establish in UK nurseries. Under certain conditions the disease can go undetected, but early recognition of symptoms is key to control. Initially, subtle, pale green or water soaked tissue at the edges of leaves or between the veins of some leaflets. These dry out and become necrotic, and significant portions of the leaves can be destroyed. Overnight plants may wilt as the bacteria affects the vascular system. Discrete yellowing or browning of vascular and surrounding tissue occurs and severely affected plants produce small fruits with poor colour. Air-borne (e.g. water splash) bacteria may cause cankerous white to beige spots on leaves and fruit.

Cmm is favoured by wet conditions and humidities above 80%, with an optimum temperature of between 24 and 27°C. Bacteria are resistant to dry conditions and low light, poor nutrition and excessive nitrate nitrogen may exacerbate disease. It can survive several months to over a year once introduced to the glasshouse and may spread through the nutrient solution. It may also be spread as a result of water splash and pesticide sprays, and by staff. There are no effective control methods so prevention of initial infection is key. Infected plants should be carefully removed, intensive hygiene measures implemented and

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a thorough clean up performed at the end of cropping with specific focus on elimination of Cmm inoculum.

Root mat/Crown gall (*Agrobacterium* sp. with plasmid)

Root mat, is caused by a plasmid (Ri=root inducing) vectored by *Agrobacterium* spp. and is occasional, sometimes severe, in soil-less systems in the UK. The similar disease, crown gall, is caused by the Ti (tumour inducing) plasmid vectored by *A. tumefaciens.* The *A. tumefaciens* group is also being utilised in genetic modification of plants due to its unusual infection mechanism. To infect, the bacteria must integrate part of its genome, the plasmid, into the plant genome, resulting in overproduction of growth regulators. Infected plants are usually sporadically spread throughout the glasshouse, and are identifiable by the massive overproduction of roots. This 'root mat' makes irrigation impossible, and plants deteriorate as their roots can no longer supple water and nutrients effectively. Many plant species can be affected, and the bacteria can survive in substrates and nutrient solutions, where they are chemically attracted to susceptible root systems. It is favoured by high temperatures and the only control methods are good hygiene practices and the removal of affected plants.

Verticillium wilt *(V. dahliae & V. albo-atrum)*

Figure 9. Wilting plants due to *Verticillium* sp. Infection

Both *Verticillium dahliae* and *Verticillium albo-atrum* attack tomatoes in the UK, but in recent outbreaks *V. albo-atrum* is more common. *V. albo-atrum* does not form microsclerotia and has a lower optimum temperature. In the past, Verticillium wilt has had much greater impacts on tomato growing but its impact is less now resistant rootstocks are used, though

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certain growing situations and varieties may be vulnerable. The lower leaflets of infected plants begin to wilt in the heat of the day, and eventually lose turgidity and begin to yellow. This progresses to browning and necrosis. The vascular tissue, when cut, shows slight browning (much less pronounced than is the case with Fusarium wilt). *Verticillium* sp. survive in the soil as mycelial fragments or microsclerotia for up to 15 years. On its invasion of the xylem the plant attempts to stop the progress of the invading mycelial by laying down tyloses or gum which may further contribute to wilting. Infected soil may be dispersed by air currents, water splashes and soil insects. For control, hygiene methods must be utilised between infected and uninfected crop, as there are limited control options once the disease is established. Fungicide delivery through drip irrigation may slow disease progress, and a number of biocontrol agents with activity against *Verticillium* sp. have been discovered. Generally the use of resistant varieties and rootstocks is the most effective measure.

Fusarium wilt and Fusarium crown and root rot (*Fusarium oxysporum* f. sp. *lycopersici &* *Fusarium oxysporum* f. sp. *radicis-lycopersici*)

Figure 10. Fusarium crown rot observed on an imported tomato plant

The causal agent of Fusarium wilt is *Fusarium oxysporum* f. sp. *lycopersici* and results in a characteristic wilt by blocking the vascular tissue. The causal agent of Fusarium crown and root rot is *Fusarium oxysporum* f. sp. *radicis-lycopersici*, and results in a severe root rot and stem cankers. Soilless crops are susceptible, but the development of resistant root stocks has rendered these diseases relatively rare in the UK.

Fusarium wilt is a vascular disease known to cause variable, but often severe damage in non-resistant crops, and 3 races are known. The primary symptoms of *F. oxysporum* f. sp. *lycopersici* are wilting and unilateral leaf yellowing. Eventually leaves dry out totally, but do not fall from the plant. Lesions form on one side of the stem and adventitious roots may form. This disease primarily affects the vascular system, causing vascular browning, but

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leaving the pith unaffected. As the fungus invades the xylem vessels, the plant may form gum or tyloses to slow its progress, but also contributing to wilting. Spread by staff, on the wind, in water and in dust spores can be disseminated over long distances.

Fusarium crown and root rot was a later addition to the UK and usually occurs very quickly but impacts vary depending on the plant and environmental conditions. Wilting may occur suddenly, followed by necrosis and drying of leaves, culminating in plant death. However, as well as wilting, the main symptoms of this pathogen are at the root and stem base. On roots, reddish brown, moist lesions appear. Roots rot and rapidly decompose, starting with small feeder roots which are more numerous in soil-less crops. A dark, sometimes recessed, canker frequently develops at the stem base, and sporulation may occur at its centre. Though not a vascular disease as Fusarium wilt above, some vascular browning may also be noted, and as a result adventitious roots may form on the stem. Fruit is often flaccid and dull from a diseased plant. *F. oxysporum* f. sp. *radicis-lycopersici* may be found in the dust of glasshouses, and may survive saprophytically on organic material. As such, it is capable of survival in the nutrient solution recycling system, and in water storage tanks. It may also be spread by water splash, air currents and glasshouse staff. If the disease does establish, there are very limited control options.

Control methods for both diseases are similar. An effective fungicide must be administered as soon as symptoms are noticed to keep affected plants alive as long as possible, though no fungicides have high efficacy. Removal of affected plants, and disinfection between infected and healthy plants, and subsequent crops also required. Trichoderma or Pseudomonas biocontrol agents are also effective against Fusarium species, but success in commercial situation has been limited. As stated, the introduction of resistant varieties and rootstocks has made a huge difference to the status of this disease in the UK.

Bacterial wilt *(Ralstonia solanacearum)*

There have been occasional outbreaks of this notifiable disease in the UK where irrigation water was abstracted from rivers infested with the causal bacterium. *Ralstonia solanacearum*, can be classified into five races, each with different geographical origins, and this dictates its severity and ability to infect. Rapid wilting of young leaves occurs at the hottest times of the day, but subsequently becomes permanent. Following this, leaves become necrotic, dry out and many plants eventually die. Plants may also exhibit stunted growth, leaf epinasty, adventitious rooting and lower leaf yellowing. These symptoms are more likely to be seen where plants are infected, but conditions are not favourable to

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disease development. Roots can also be affected and may rot. A longitudinal section of the roots and stems shows yellowish to dark brown vascular tissue, and later the pith and cortex may also brown.

Many different crops are susceptible and the bacteria may be present in irrigation water. Outbreaks have occurred in UK potato crops as rivers have become infested downstream of potato processing plants handling imported (Egyptian) potatoes. Bacteria may be released from the roots of infected plants allowing spread in hydroponic systems, and may also be spread by contaminated tools and staff. This pathogen is favoured by high temperatures between 25 and 35°C, wet conditions, neutral pH and the presence of gall nematodes. Once this disease is present, there are no effective control measures other than hygiene measures to prevent the disease infecting, and careful removal of infected plants.

- Excessive nitrogenous fertilisers are known to increase severity of bacterial wilt (*R. solanacearum*) (Blancard, 2009).

Didymella stem canker (*Didymella lycopersici* (syn. *Phoma lycopersici*))

This ascomycete fungus causes stem canker in tomato crops, and sometimes also a fruit rot. There are several *Phoma* species known to infect Solanaceous crops, and differentiation is often difficult. When it does occur in the UK disease is often severe, but infections are sporadic. Cankers with slightly recessed tissues appear on the stem, and are moist and dark brown. Xylem tissue also turns brown after the epidermis and cortex decompose. Eventually cankers surround the stem and sap flow is disrupted, causing yellowing, wilting and even whole plant death. Fruit most often become infected at the peduncular scar, and this results in large spots with concentric rings covering the fruit. Similar symptoms may also manifest on fruit as a post-harvest rot. Brown, wet spots also occur on the leaves, generally at leaf edges and eventually becoming necrotic and drying up. Flowers may also be attacked and destroyed. Brown to black globular structures known as pycnidia that can be seen with the naked eye are formed on the damaged tissues, most commonly on infected fruit. Perithecia which look similar and produce sexual spores are rarely observed in nature.

D. lycopersici survives on plant debris and may persist in a glasshouse and on equipment after diseased plants have been present. Conidia are dispersed by water splash and on tools and workers and the fungus may also survive on seed. Ascospores from perithecia may be spread on the wind. Removal of infected material is prudent, as is thoroughly

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disinfecting a nursery that has experienced an epidemic, followed by buying seeds from a known clean source. The fungus is encouraged by high humidities and temperatures between 13 and 29°C. There are resistant root stocks available that would avoid infections occurring at the stem base, and fungicides may be applied both protectively and after infection. Didymella was relatively common when UK tomato crops were grown in soil, but the disease is relatively rare in hydroponic crops.

- Didymella stem canker is more virulent on plants that have received reduced nitrogen or reduced potassium nutrient regimes (Blancard, 2009).

Corky root rot *(Pyrenochaeta lycopersici*)

Figure 11. Characteristic corky root rot symptoms of tomato

Caused by *Pyrenochaeta lycopersici*, this disease is only generally a problem in soil grown crops, though it has been reported in soil-less systems. Strain groups are defined according to optimum temperature, and in soil crops losses as high as 40-70% have been reported, especially where tomatoes have been repeatedly grown. When an outbreak occurs, fine roots turn brown and rapidly deteriorate, and larger roots exhibit superficial corky lesions of the cortex that may encircle roots. Eventually the root system becomes limited and vulnerable to a number of secondary root pathogens, such as *Colletotrichum coccodes* (black dot) and *Rhizoctonia solani*. Root damage results in stunted plants prone to wilt and yellowing during warm periods of the day. Once established, control options are limited, but irrigation should be controlled and plants drenched in the heat of the day to avoid wilting or overwatering. Infected plants should be removed, though infection is very rare in hydroponic systems.

Diseases in the UK

Based on a grower survey undertaken as part of this project, and additional consultation, it was concluded the ‘priority’ UK diseases of hydroponic tomato are *Botrytis cinerea, Oidium*

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neolycopersici powdery mildew and viral diseases such as *Pepino mosaic virus*. Evaluation was based on frequency and severity of outbreaks in UK hydroponic crops. Problems experienced in main season crops were given more weight than those in propagation.

Table 5. Summary of key diseases in UK hydroponics based on industry consultation - 2013

Disease	How common (1-5)	How severe (1-5)	Overall rank (1-5)
Fungi/Oomycete			
Pythium root rot	3	3	1
Phytophthora root rot	1	2.5	1
Late blight	2	3.5	2
Verticillium wilt	1.5	2.5	1.5
Fusarium wilt	1.5	3	2
Sclerotinia stem rot	1	2	1
Colletotrichum (black dot)	1.5	2.5	1.5
Alternaria (early blight)	1	2	1
Didymella stem rot	1	4	1.5
Calyptella root rot	1	2	1
Thielaviopsis black root rot	1	2	1
Leaf mould	2	4.5	4
Corky root rot	2	3.5	2.5
Botrytis	4.5	4.5	5
Rhizoctonia stem base rot	1	2	1
Powdery mildew	5	2	4
Bacteria			
Bacterial wilt	1	2	1
Bacterial canker	2	4.5	2
Root mat	3.5	3.5	3.5
Virus/Viroid			
PepMV	5	3	4.5
ToMV	2	4.5	4.5
PSTVd	2	4.5	4.5
CLVd	2	4.5	4.5

Summary points – Current key diseases in the UK

- **A variety of foliar, vascular and root diseases can infect UK tomato**
- **Diseases differ in their incidence, with some occurring every year and others only appearing rarely**
- **Diseases also differ in their severity, and control options for some of the more severe are limited**
- **As well as good nutrition, chemical sprays, aerial crop management, environmental management and effective hygiene measures are all key to a healthy crop**
- **It was concluded the 'priority' UK diseases of hydroponic tomato are *Botrytis cinerea, Oidium neolycopersici* powdery mildew and viral diseases such as *Pepino mosaic virus***

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Review methods

The review itself was carried out using a variety of on-line tools (e.g. Google-scholar, Scopus, Google, Web of Science). Literature searches were performed using a range of initially broad search terms, becoming more focused on research in tomato crops and on specific tomato diseases over time. Each set of returns from these searches was limited to those sources on agricultural and biological sciences, and searched through by sorting by date, relevance and number of citations. A number of paper references held by ADAS were also utilised, as were webpages and consultation with growers and industry experts.

Initial grower contact was made with the use of a questionnaire (Appendix 1) sent out via both the Tomato Growers Association (TGA) and AHDB Horticulture. This was to establish current grower practices and the importance of tomato diseases in the UK as summarised above to give the review a baseline on which to build. The uptake, return and completeness of these questionnaires were limited but consultation with Paul Challinor, an independent consultant with expertise on tomato nutrition, and use of current literature also contributed to this. Attendance at a grower study group, held by the Hampshire and Isle of Wight group, and attending meetings of the Tomato Working Party also contributed to gaining information and grower opinion regarding plant nutrition.

Following literature searches information was analysed to give a number of nutrition strategies applicable to tomato-pathogen systems, using data from tomato crops as results of altered nutrition were not found to be consistent across different crops. From this summary, which can be seen in Tables 10, 11 and 12 below, the gaps in knowledge of nutrition's potential to contribute to disease management in tomato were elucidated. For the most common and/or severe diseases in UK crops, a simple cost benefit analysis was performed in order to establish their applicability in a commercial setting.

A review meeting with Philip Morley of the TGA, Paul Challinor and the AHDB Horticulture Research Manager allowed these different strategies to be discussed, and their practical, environmental and economic limitations and benefits considered. The final output of this project, recommended future research and development objectives, were formulated using the most promising strategies identified through the literature review and grower liaison. Gaps in knowledge identified also contributed, as these areas may reveal insights in future and warrant further research.

In this review, a nutrient is considered as a mineral element deemed essential for healthy

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plant growth, but also includes beneficial elements. Effects of CO_2 added to glasshouses on disease is also mentioned, as providing the crop with an additional source of carbon could be counted as nutrition, and it is widely used in the UK. The effects of elicitors such as fosetyl-aluminium (Grote & Busci, 1998) or natural defence compounds of salicylic acid or jasmonate, that could feasibly be added to a nutrient solution and exert effects on a crops natural defence systems, are not generally included, though interactions with nutrition are to be expected.

As work was undertaken it became evident that a summary of current UK practices in nutrient management would aid interpretation of the review findings. This was therefore added as an extra objective. The objectives of the project were therefore:

1. To summarise current practices in nutrient management
2. To review literature on crop nutrition and disease
3. To propose potential nutrient management strategies for improved disease control
4. To propose R & D priorities

Objective 1 – Summary of current practices in nutrient management

Nutrient management in hydroponic glasshouse tomato is performed via a nutrient solution made to a specific recipe, and delivered through an irrigation/fertigation system. The systems in use vary from grower to grower, in terms of substrate and in terms of water recirculation, and there are many different solid and liquid fertilisers on the market currently that growers use to mix their nutrient stock solutions. Typically an 'A' and a 'B' stock solution is produced, which allows effective mixing and subsequent dilution so that the correct amounts can be delivered to the crop. Two stock solutions are made up to prevent calcium mixing with phosphates, which would cause the phosphate to precipitate out of solution.

The correct concentrations of macro- and micro- nutrients in solution are very dynamic and dependent on the variety grown, the time of year, crop load and age and on environmental factors which may be more or less stringently controlled within a glasshouse. If concentrations of specific nutrients drop too low, growth and yield will be compromised, but if allowed to climb too high the crop may be damaged, money is wasted and excessive loss to the surrounding environment may occur. As well as specific nutrients, with which this review is directly concerned, pH and conductivity (EC) levels must be stringently controlled in a tomato crop's nutrient solution to facilitate appropriate uptake of nutrients by the crop.

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The best conductivity level at any point also depends on the conditions mentioned above, and is dependent on numerous variables. A crop's nutrient management is therefore a highly complex process, as addition of a single nutrient/fertiliser to the solution influences pH, EC and the relative concentrations of other nutrients available in the solution.

In the UK, working hydroponic systems include rockwool (stonewool), coir and nutrient film technique (NFT). Although the majority of the substrate systems do not collect and recirculate drainwater, there is an increasing trend towards capture and re-use of the waste-water and diluted nutrient solution.

Nutrient Film Technique (NFT)

A well-designed NFT system allows for total recirculation of water and nutrients.

The NFT system consists of a series of closed polythene troughs in which the plant root system is encouraged to develop. The nutrient solution is introduced at one end of each trough and it is allowed to flow over the root system, providing the plant roots with water, nutrients and oxygen. The unused nutrient solution is collected at the lower end of the trough and is recirculated back to the crop. Following collection of the solution, the pH values and EC concentrations are monitored and then adjusted by the addition of dilute acid solution and nutrients in liquid form. Constant aeration of the solution is essential to maintaining a good oxygen supply for the root system and a fast flow rate (up to 6 litres per minute) in the channels also ensures continuous oxygenation.

In terms of early growth control, it may be necessary to use a lower nitrate-nitrogen concentration in NFT systems.

Rockwool (Stonewool)

Rockwool is made from basalt volcanic rock, which has been heated to 1500°C in a factory-based process. The rock fibres are then spun and formed into blocks and slabs. Approximately one cubic metre of basalt can produce fifty cubic metres of rockwool.

The slabs are versatile and contain a high proportion of air spaces for root development.

Depending on the slab type, rockwool may be re-used for crop production but there is an associated risk of plant disease carry-over. Slabs may be steam sterilised but there are attendant costs of handling and energy use. One method of disposal involves the collection and transfer of the waste material to a brick-manufacturing factory.

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Coir (Cocopeat)

Coir is a natural fibre, which is extracted from the waste husk of the coconut. It has a good air-filled porosity percentage and is reliably easy to re-wet. The raw material contains high concentrations of sodium, chloride and potassium. Most coir supplies are washed, to reduce the salt concentration, and also buffered, prior to delivery. The post-crop coir material may be re-used several times and its final disposal is comparatively easy.

The move to nutrient recirculation systems

Nutrient recirculation involves a closed system of water, nutrients and plants, in which the water draining from the plant rootzone is collected and recirculated back to the plants. Recirculation systems may save considerable water and fertiliser, and though run-off water must occasionally be stored and released, it is possible in theory to one day have a totally closed system with no drainage to the environment. These systems represent the most up to date commercially available method to accurately control the nutrients and water delivered to the crop, which will allow growers to adapt more quickly and effectively in the light of new technology and knowledge in the area of hydroponic nutrition. Additionally, as well as lower costs for the grower, improved nutrient control and more active management may improve the quality and yield of produce, and will also contribute to growing in a sustainable and environmentally conscious manner, which is becoming increasingly important to retailers and end consumers of high quality fruit and vegetables.

One of the main concerns regarding drainwater recirculation systems is the introduction and potentially easy spread of pathogens. Water treatment with heat, UV light, chemicals or by use of a biological or slow sand filter is often performed to reduce the risk of introducing and spreading pathogens throughout the glasshouse, though the practice of implementing no water treatment is becoming increasingly common (grower communication). Additionally, since the adoption of grafting onto rootstocks with increased vigour and pathogen resistance the situation has improved. This is discussed in AHDB Horticulture project PC 281a. There may also be a role in recirculation systems for beneficial microorganisms, whether they be artificially introduced or naturally colonising the root zone. For example, recycled substrate has been found to supress Fusarium crown rot in tomato when inoculated, compared to never before used substrate (Minuto *et al.,* 2008). However, one of the main problems is in the identification of the main microorganisms involved.

Nutrient losses may still occur in recycling systems, due to dumping of solution, but they are considerably lower than in run to waste systems (by approximately 40%). Denitrifying

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bacteria may also cause N losses of up to 30% from closed systems (Schwarz *et al*., 1997). The achievement and maintenance of the correct nutrient balance in the hydroponic system will add to the longevity of the batch of liquid nutrients and should also make the final disposal (via another crop, for example) easier and more environmentally acceptable.

The preferred water source for a recirculation system is that with the lowest salinity (expressed as electrical conductivity, EC) and with minimal content of ions, especially those absorbed in minimal quantity by plants such as Na and Cl. High concentrations of sodium and chloride ions in recirculation systems should be avoided, to prevent saline conditions in the rootzone and subsequent crop damage. EC, pH and nutrient concentration measurement devices are installed at various points in the system to monitor and alter inputs of water, fertilisers and acids, and samples of nutrient solution (preferably taken from within the crop, and not from the drainage) are regularly sent to laboratories for analysis. A recirculation system requires more capital investment in equipment and active nutrient management, however, there is good potential for savings in water and fertilisers. Certain nutrients, such as potassium and nitrogen, may deplete quickly from the recirculation solution and undesirable ions may accumulate rapidly, adversely affecting plant development and fruit quality.

The EU's Water Framework Directive has stated that water use efficiency should be greatly increased. Therefore, nurseries should aim to have no drainwater, which may mean that growers have little choice but to move towards a recirculation system. Reducing the volume of irrigation water will save money, and provides motivation to improve irrigation accuracy with the ultimate aim of running systems that do not require bleeding, and lose no water or nutrients. As recirculation systems become more widely used, there is scope for new systems not only based on growth and transpiration models (Van Noordwijk, 1990), but environmental conditions, plant/microorganism interactions and the changes nutrient availability can have on fruit taste and quality, as well as yield, to be developed. The development of these integrated systems presents a huge challenge to soilless tomato production, but would result in cost effective, low waste, environmentally friendly and profitable growing (Schwarz *et al*., 2009).

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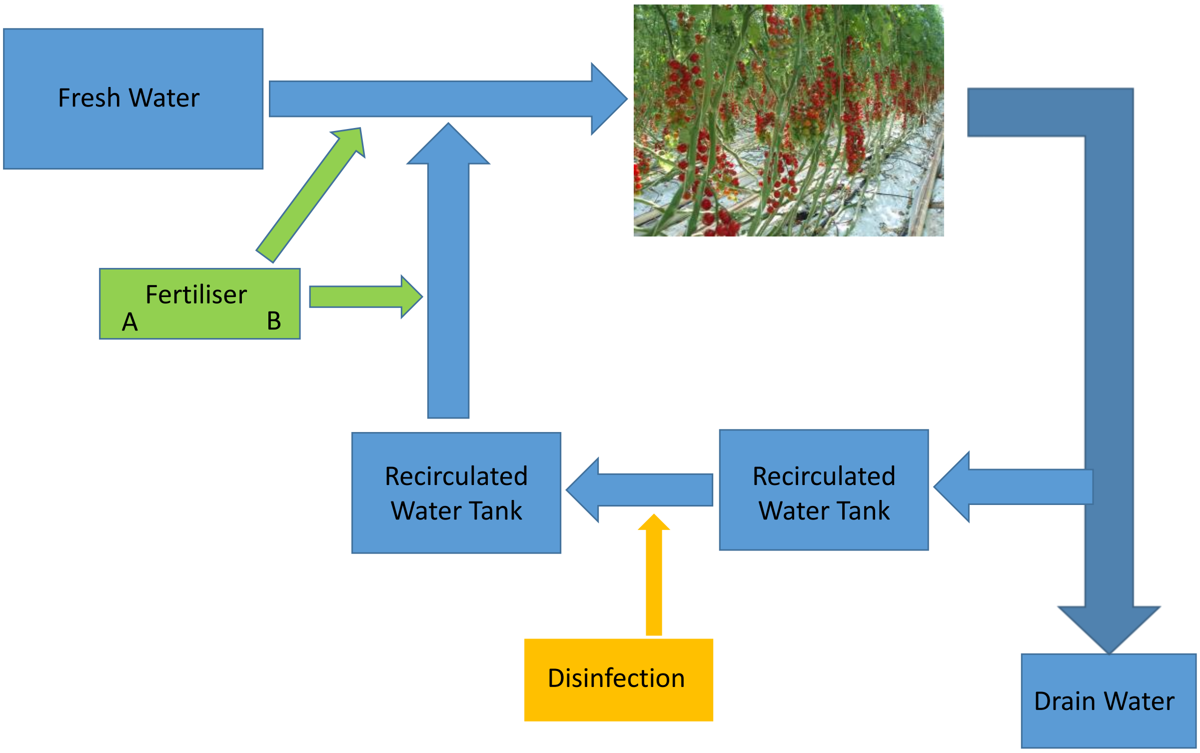

Figure 12. Simplified example of a recirculating nutrient delivery system

A variety of fertilisers are available on the market in both liquid and solid forms. Many elements are available in their pure forms, which tend to make nutrient management easier. Premixed fertilisers and fertiliser compounds are also available, which may each contribute multiple ions to the solution. In either case, the nutrient balance of the solution is key. Cost is a major consideration in the choice of fertiliser used, for example nitrate compounds are more expensive than chloride compounds, as these contribute nitrogen to the solution rather than potentially increasing the EC due to too many chloride ions. In a run to waste system cheaper alternatives are more likely to be used as management of nutrient balance is less involved, however a recirculating system where EC must be kept stable is more likely to utilise more expensive fertiliser products. However, as a well set up and managed recirculating system produces minimal water and nutrient losses and it facilitates the use of higher quality fertiliser through savings elsewhere. This also makes a recirculating system suitable for manipulation according to the presence of numerous biotic and abiotic variables, with a reduced risk of build-up of sodium and chlorides. The change to a recirculating system requires large initial investment and more attention to be paid to nutrient recipes so that large amounts of used solution do not have to be stored and dumped. Specifically, growers need to reconsider why they use the recipes they do, and what impacts the alterations they make have. If the solution moves significantly away from what is considered optimum for a crop, it is no longer viable to dump the solution and mix a new one, and well thought out action plan must be in place to bring the solution back to optimum.

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Specific nutrient concentrations in use in the UK

Summarising current grower practices proved challenging due to the high levels of variation from nursery to nursery in growing system, environmental conditions and individual grower preference. The field of tomato growing is also continually developing and new technology is being implemented by growers each year. An overall summary is attempted, though it is appreciated there are variations which have proved effective or are used for specific purposes.

<u>Measurements</u>

Most growers have hand held meters to check EC and pH in the crop. The frequency of sampling is important in order to help maintain an optimum nutrient balance and this is usually undertaken every two weeks. In recirculation systems, nutrient changes may occur more quickly, for example close to first harvest when the plant demand for potassium is high. Therefore, it is important to track the nutrient changes and react more quickly; this may necessitate more frequent sampling and fertiliser recipe adjustment.

Leaf analysis is also a useful method of monitoring actual nutrient uptake and partitioning of nutrients in the plant. One reliable method of taking leaf samples from a tomato crop is to harvest a total of 20 to 25 fully-expanded, new leaves from under a random selection of plant heads.

<u>Quantity and timing of irrigation</u>

Irrigation varies from nursery to nursery, largely depending on individual grower preference and dependent on substrate, for example rockwool crops will require greater irrigation volumes to flush the system. NFT crops are, by nature, continually irrigated, and so irrigation control cannot be used to balance generative and vegetative growth. As such, NFT crops are often more vegetative and early season growth is controlled by nitrogen management. Generally, rockwool and coir crops are irrigated from the start of plant activity in the morning and receive a number of irrigation pulses over time and in line with solar radiation received. Prevention of substrate waterlogging over the night period is also important in the prevention of fruit blossom-end rot and splitting.

Irrigating at higher volumes ensures the plants have sufficient water in high temperatures and light intensities and that the system is flushed through. It also prevents the EC climbing too high due to undesirable chloride or sulphite ions accumulating. Fresh water is generally

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abstracted from rivers or boreholes, but rainwater is also harvested for glasshouse production (see AHDB Horticulture soft fruit grower guide on water harvesting for more information). Rainwater is an ideal base for hydroponic growing, containing no added nutrients and being of very low salinity. Due to the Water Framework Directive growers are increasingly required to reduce their drainage and water use, with targets in the Netherlands already stipulating zero drainage targets. As nitrate-nitrogen loss to the environment also becomes more strictly controlled it is likely that recirculating systems, which are more challenging to manage than traditional run to waste systems, will be necessary. Water and fertiliser waste can be dramatically reduced by the use of technologically advanced recirculating systems, as well as being able to provide the crop with nutrient concentrations as close to targets as possible.

Nutrient concentrations

Studies of tomato nutrition have been going on for over 20 years, both officially undertaken by research institutions and as part of grower experimentation to obtain the best crop possible. Many growers also employ the services of crop advisors who have specialist expertise in tomato nutrition. The nutrients currently added to hydroponic solutions, their importance to the crop and the concentrations generally in use are detailed below. For further information on deficiency and toxicity symptoms in tomato crops, The AHDB Horticulture Crop Walkers' Guide, Protected Edibles II is a useful resource.

The nutrient concentrations mentioned apply to the main growing season, and not for plants during propagation. Details for optimal nutrient concentrations are provided as mg/L in the nutrient solution. Slab values and dry plant weight values may also be used in practice and these are closely linked. Current grower practice, in terms of what concentration is viewed as the optimum, is summarised in Table 6. Slab values, as received from laboratory analysis, will not always reflect the targets aimed for, and will differ depending on the position in the crop. However, ultimately as much synchronicity between inputted feed and uptake in the slab as possible is the aim.

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Table 6. Nutrient targets in the applied hydroponic solution, averaged across returned surveys – 2013 (n=4)

Nutrient (mg/L)	Early season	Mid-season	Late season
Nitrate nitrogen	147.50	196.67	180.00
Ammonium nitrogen	5.00	7.83	5.50
Potassium	370.00	395.00	367.50
Phosphorus	32.50	27.67	27.50
Zinc	0.70	0.87	0.80
Calcium	180.00	210.00	190.00
Manganese	0.58	0.52	0.58
Magnesium	52.50	56.67	55.00
Iron	2.25	2.00	2.00
Copper	0.10	0.10	0.10
Sulphur	150.00	150.00	150.00
Molybdenum	0.08	0.07	0.08
Boron	0.45	0.48	0.50
Sodium	108.50	108.50	108.50
Chloride	242.50	267.50	267.50
HCO3 (used to regulate pH)	25.00	50.00	50.00
pH	5.50	5.75	5.50
EC	4.00	3.13	3.20

Variation in these values exists due to differences in variety grown (cherry will be different to plum), growing system (for example, higher iron targets in NFT crops) and individual grower or consultant preference. Point in the season is an important variable, hence why this was split into early, mid and late on the grower survey. Changes in potassium are common throughout the season due to fruit development, and high EC may be useful for growth control early in the season. Sampling hydroponic system nutrient concentrations fortnightly is what is recommended, and this was found to be adhered to by UK growers.

There were notable differences in nutrient delivery for crops in propagation. Most notably, ammonium-nitrogen in propagation is much lower, with nitrate kept at the higher end of the range as for main season crops. Potassium, phosphorus, copper and boron were also at the higher end of the ranges, and magnesium supplied at higher concentrations. Calcium and molybdenum targets were similar to main season crops, and tolerable ranges of zinc lower. Greater pH control is required in propagation as a buffer is lacking between the solution and root zone.

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Conductivity and pH

The best conductivity in a nutrient solution is dependent on crop age, season and crop load, and EC in the input solution should be adjusted according to conditions to achieve the correct value in the rootzone. Tomato crops require a higher conductivity in the rootzone than many other hydroponically grown crops. Generally, a minimum value is that of 2.0 mS/cm, and cherry tomatoes may require up to 6.0 mS/cm. EC is generally kept low at the start of the growing season to avoid root damage, but increased subsequently. An optimum conductivity level is usually considered as 3.5 mS/cm. EC levels of 3.5-9.0 mS/cm have been observed to improve tomato fruit quality (Dorais *et al*., 2001) and in the past higher ECs were utilised in UK growing than currently. However, this is likely because crops were planted a few months earlier, and levels would still be dropped prior to picking. It is important to monitor light levels a crop is receiving, as well as the number of times solution is drained from the system, in order to ensure EC is kept relatively stable throughout cropping. EC is linked with light levels, as well as inputs of ions. A stable EC helps maintain fruit quality and avoids blossom end rot. A high EC introduces a restriction on water uptake at the roots, resulting in a smaller fruit size but better flavour.

The tolerable pH range is relatively narrow, and is usually considered to be between 5.5 and 6.5, though slightly lower values were returned by growers, as these referred to the input feed. If pH is allowed to climb too high, as well as damage to plants, precipitation of calcium phosphate may occur within the system resulting in phosphorus deficiency as well as an increased need to flush the system through after cropping.

The interaction of nutrient elements delivered to the tomato rootzone with pH, EC and humidity is summarised below (Table 7). Trace elements do not affect EC as much as the man elements.

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Table 7. The interaction of pH, EC and humidity with hydroponic nutrient concentrations - summary

Nutrient	Uptake efficiency*	Uptake affected by pH	Affects pH	Uptake affected by EC	Affects EC	Affected by humidity
Nitrate nitrogen	1			✓	✓	
Ammonium nitrogen	1		✓		✓	
Potassium	1		✓	✓	✓	
Phosphorus	1	✓			✓	
Zinc	2	✓			✓	
Calcium	3			✓	✓	✓
Manganese	1	✓			✓	
Magnesium	2				✓	✓
Iron	2	✓			✓	✓
Copper	2	✓			✓	
Sulphur	2		✓		✓	
Molybdenum	2				✓	
Boron	3			✓	✓	✓
Sodium	-		✓		✓	
Chloride	-		✓		✓	

*In relation to water, as from Bugbee, 1996, where Group 1 nutrients are taken up and removed from solution quickly, Group 2 nutrients are removed at intermediate speed by plants, and Group 3 are removed slowly and more passively taken up.

Macronutrients

Nitrogen is the key macronutrient to the growth of any plant, and nitrate and ammonium taken up by tomato contribute to plant growth, yield, quality and flavour. Ammonium is largely incorporated into organic compounds in the roots, whereas nitrate is more mobile and may travel in the xylem and accumulate in plant cell vacuoles where it impacts plant quality, before being reduced to ammonia and assimilated into leaf tissue. It is also thought that nitrogen reduction in plant leaves may play a role in reducing high light stress. Additionally, there may be a role for nitrate in a variety of signalling roles, whereby it exerts an effect on the multitude of chemical reactions within cells. For example, in carbon partitioning as it has been shown that competition for carbon skeletons occurs between

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sucrose and amino acid synthesis in tomato leaves (Hucklesby and Blanke, 1992) and that this may be mediated by nitrate.

Due to its vital role in growth, young tomato crops generally require more nitrogen nutrition than older plants, and its concentration can be reduced around picking. Nitrogen concentration is closely linked to vegetative growth and health of the crop and as a result it may be increased again towards the end of cropping if there is an unwanted decline. At low nitrate concentrations much is assimilated in the roots of the plant, whereas as nitrate concentrations increase more is translocated to the plant's shoots. Generally, more nitrogen is required in summer than winter as the proportion of nitrate reduced to nitrite in the roots increases with temperature and plant age. Maximum activity occurs in leaves when the rate of leaf expansion is highest. Nitrogen deficiency causes protein synthesis to become inhibited, meaning growth slows and plants may exhibit chlorosis. Too much nitrogen may lead to plants with excessive vegetative growth, poor flowering or excessively large fruit. Ammonium nitrogen is kept very low compared to nitrate nitrogen, in order to prevent root damage and drops in pH. An ammonium:nitrate ratio that is too high may also inhibit root uptake of other nutrients, such as magnesium, calcium and potassium, resulting in deficiency symptoms even if sufficient concentrations are present in solution. Currently, growers are recommended to aim for ammonium values no higher than 10 mg/l, a maximum the growers consulted adhered to. Nitrate nitrogen is supplied at much higher concentrations, but may be limited to help control growth. The recommended lower limit in the main season is 150 mg/l (AHDB Horticulture Project PC55a, HRI), as limited nitrogen may affect early fruit flavour, with a normal range seen as 3.5-5 % plant dry matter.

Phosphorus is also key to the growth of any plant, and is used as a structural element in nucleic acids and phospholipids and has a key role in energy transfer as part of the adenosine tri-phosphate molecule. Concentrations in a tomato crop's nutrient solution are less dependent on EC and the concentrations of other nutrients than many as its removal from the solution by plants is very efficient. As such, after the first high growth period, low concentrations of phosphorus in solution are sufficient (Bugbee, 1996). Very high concentrations of phosphate may impede on fruit quality, and additionally, supplying a crop with too much phosphorus increases costs unnecessarily. Deficiency commonly manifests itself in plants with purple to red colouration on older leaves, and suppression of growth and maturity. Excess phosphorus may result in zinc or copper deficiencies. Plant dry matter should generally contain 0.3-0.5% phosphorus, and a recommended range of phosphorus in hydroponic solution is 30-40 mg/L, though it is apparent that some growers supply their

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crops with lower concentrations of phosphorus than this. Phosphorus availability is affected by rootzone pH.

Potassium, another key nutrient, is required in high quantities for tomatoes with set fruit because it is a key nutrient in plant water relations and the process of osmosis. Deficiency symptoms include flaccid leaves, chlorosis and necrosis, and delayed fruit ripening known as 'greenback' that may be confused with viral infection. EC levels must be taken into account when calculating potassium required as it plays an important role in cation-anion balance within the plant, being taken in at the roots and acting as a counter-ion for long distance transport of nitrate. As such its uptake is selective, and strongly linked to metabolic activity. Potassium itself is not metabolised, but stabilises the pH at a level favourable for most other enzyme reactions that occur in plant cells. Toxicity is rare and a range of 2-5% plant dry weight is desirable, though some may see <2.5% as deficient. Rootzone recommendations are 400-600 mg/L; it was noted that growers seem to cluster at the lower end of this range (input solution). Potassium concentrations may deplete quite quickly, especially in recirculating systems, and the aim of a balanced nutrient solution is to maintain potassium to nitrogen ratios of 2 to 3, depending on the growth stage.

Magnesium fulfils both a structural and metabolic role in tomato, through ionic bonding and as a bridging element and in forming complexes with enzymes to facilitate metabolic reactions. Magnesium contributes to the chlorophyll molecule and is also involved in pH regulation and cation-anion balance within cells. Its uptake by plants is dependent on the level of other cations in solution, and thus on concentrations of potassium, calcium, and sodium. Deficiency is seen as interveinal chlorosis, and older leaves are affected first. As increased potassium availability inhibits magnesium absorption, deficiency symptoms are often seen during high fruit loads, or if irrigation is irregular. High humidity levels in April and May can also limit absorption of magnesium. Dry plant weight of 0.15-0.35% magnesium is considered healthy, and values supplied in the AHDB Horticulture Crop Walker's Guide state 0.35-0.8% as normal. Concentrations in solution are desirable between 65 and 100 mg/L, with a target of 80 mg/L. Some growers supplied their crops with lower values than this, which brought the average values down. In a balanced nutrient solution, a potassium to magnesium ratio of 6 is desirable.

Calcium is an integral component of the cell wall, acts as an intracellular messenger and also makes up part of many macromolecules. Importantly, calcium acts as a second messenger in signal conduction between the environment and plant responses. In deficient plants the upper parts of shoots become yellow-green, and Ca is also essential for the

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growth of pollen tubes. Blossom end rot is a well-known result of calcium deficiency, caused by calcium in the transpiration stream moving preferentially to the leaves. An excess of calcium may lead to 'goldspot', caused by the deposition of calcium oxalate crystals under the skin of the fruit. Values of 0.1-<5% of dry plant weight of calcium are considered healthy, and the AHDB Horticulture Crop Walkers Guide states levels between 2 and 4 % as normal. Generally, the calcium concentration in solution needs to be around 50% of the potassium concentration. Calcium concentrations may reach relatively high levels before toxicity is caused to the plant. A recommended target is 250 mg/L, which growers returning the survey generally conformed with, though some supplied their crops with more and some less. There may be a tendency to supply higher concentrations of calcium if a blossom end rot sensitive variety is being grown. Control of EC and encouragement of plant uptake and movement to fruit sinks is the key to calcium nutrition. Temperature changes also affect calcium uptake as night temperature drops increase root pressure, encouraging movement of calcium into fruit sinks.

Sulphur is required by plants to form specific organic compounds including the amino acids cysteine and methionine and as a result many plant proteins. Sulphur is also utilised in polysaccharides, sulpholipids and coenzymes both structurally and as a functional group. It plays an important role in the tri-peptide antioxidant glutathione, preventing cell damage. Though SO_2 may also be taken up from the atmosphere, the most important uptake pathway is of sulphate via the nutrient solution. Although lower concentrations are usually sufficient, higher concentrations often have to be pumped into nutrient solution to allow high concentrations of potassium and magnesium to be achieved without nitrogen concentrations becoming excessive. However, sulphate is generally viewed as an unwanted ion, as it builds up in a recirculated system. If sulphate concentration is allowed to remain high for too long a period, fruit quality may be compromised. If plants become sulphur deficient, protein synthesis is inhibited and shoot growth is compromised, net photosynthesis is reduced due to reduced chlorophyll in leaves and chlorosis may occur. It is recommended that sulphate concentrations are kept below 200 mg/L. In recirculating systems, the concentrations may often rise above 200 mg/L with minimal problems.

Micronutrients

Iron is utilised in a variety of metabolic proteins and enzymes, and is required for protein synthesis. In iron deficient plants, chlorophyll content of leaves is reduced due to iron's integral role in the chloroplast. Iron also contributes to healthy root growth. Generally, higher concentrations of iron are required for a crop in winter than in summer. In recent years, it

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has been noted that lower concentrations of iron in solution than previously thought are tolerable. Optimum concentrations notably differ between rockwool and NFT crops, with NFT crops generally requiring higher iron concentrations between 1.5 and 5 mg/L with an optimum of 3, whilst in rockwool the optimum is generally considered as around 2, and must be kept between 1 and 3. Notably, UV sterilization will reduce iron EDTA concentrations in the solution, and must be accounted for. pH control is vital for optimum uptake, as is root health.

Manganese plays an important role in metabolic processes within the plant and can substitute itself or compete with calcium or magnesium ions in chemical reactions. Manganese is part of many important enzymes, including RNA polymerase. It is also often the metal component of the superoxide dismutase enzyme, which protects cells from free radical damage. Manganese deficiency disrupts protein, lipid and carbohydrate metabolism, photosynthesis and uptake of iron and may result in interveinal chlorosis, and tomatoes are known to be particularly susceptible. Manganese is immobile within the plant, and is less available at high pH. Tomatoes are, however, relatively tolerant to a high manganese level compared to many other species. Higher concentrations of manganese in a solution compete with iron for uptake. This would generally be undesirable, but there may be situations where manganese uptake takes priority where this can be manipulated. Optimum concentrations are between 0.5 and 0.6 mg/L. pH control is vital for optimum uptake, as is root health.

Copper shares iron's qualities of easy electron transfer and formation of stable complexes, and as such it plays an important enzymatic role in redox reactions. Copper is an integral part of multiple enzymes in the electron transport chain within the chloroplast, and may also be part of superoxide dismutase like manganese. Copper deficient plants may exhibit distortion as lignification of the cell wall is disrupted. It also has a large effect on fruit formation as pollen from copper deficient plants is non-viable. Rosetting, necrotic spotting, leaf distortion and terminal die back may also occur. Toxicity can occur at high concentrations, at around 20-30 ug g^{-1} dry weight. Copper concentrations are kept between 0.05 mg/l and 0.5 mg/l, with an optimum level of 0.1 mg/l.

Zinc plays a functional and structural role in enzyme reactions as it has a high tendency to form tetrahedral complexes with nitrogen, oxygen and sulphur ligands. As a result, metabolic changes due to zinc deficiency are complex, but include inhibition of many enzymatic reactions (zinc may also form part of the important superoxide dismutase enzyme, as well as RNA polymerase and alcohol dehydrogenase), inhibition of protein

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synthesis and carbohydrate metabolism. Zinc is also important for biomembrane integrity. It is possible to induce zinc deficiency by delivering too high a phosphorus supply, which decreases the availability of zinc to the plant. Zinc deficiency presents itself in plants with shortening of internodes and notably small leaves, with symptoms intensified under high light intensities (Boardman & MacGuire, 1990). Zinc is less available at higher pH. Deficiency may occasionally be confused with viral infection. Concentrations of zinc that are too high may also cause induced iron or magnesium deficiency, and resultant leaf chlorosis. An optimum level in tomato nutrient solution is considered to be around 1 mg/l, with a minimum of 0.5 mg/l and a maximum of 2 mg/l.

Boron is part of the metalloid group of elements, as is silicon, and so has intermediate properties between metals and non-metals. Uptake of boron is highly pH dependent, and the margin between boron deficiency and toxicity is narrow. In fact, yield and quality could be affected before visible phytotoxicity is evident in the crop, necessitating careful checks on boron concentrations. Boron is thought to be important in sugar transport, cell wall synthesis, lignification, membrane integrity and in the metabolism. Due to the key role it plays in cell wall formation, boron is integral to root elongation and pollen germination. Plants are more sensitive to boron deficiency under high light intensity and symptoms are more obvious in younger plants and young leaves. Interveinal chlorosis may appear on older leaves, followed by discolouration, which often spreads a third of the way up the leaves from the tip. Internodes may be shorter giving plants a bushy appearance, but importantly in tomato boron deficiency may also lead to brittle leaves and stems, and splitting and misshapen fruit. Boron is less available at low pH and interruption of the water supply may also cause insufficiencies as uptake is via the transpiration pathway. It should be kept between 0.3 and 1.5 mg/l, with an optimum of 0.4 mg/L. More sensitive varieties, such as those of baby plum type, will benefit from slightly higher boron concentrations, up to 0.8 mg/L. As with calcium, control of EC and encouragement of plant uptake and movement to fruit sinks is key to boron nutrition.

Molybdenum is a transition element and is contained within many plant enzymes, where it performs both structural and catalytic roles. Its requirement by plants is lower than other essential mineral nutrients, apart from nickel. Only a small number of enzymes contain molybdenum and its functions are closely related to nitrogen metabolism, being important in the assimilation of nitrogen into plant organic compounds, and therefore in plant growth. As such molybdenum requirement strongly depends on nitrogen supply, but in hydroponic tomato concentrations are usually kept between 0.01 and 1 mg/l, with an optimum of 0.05 mg/l. Deficiency in molybdenum manifests itself as nitrogen deficiency, and chlorosis and

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disrupted leaf development is an obvious symptom. Plants can generally tolerate quite high concentrations of molybdenum before toxicity occurs, though cattle fed on high molybdenum feed crops may suffer from molybdenum induced copper deficiency as a result (Gupta *et al*., 2011).

Sodium and **chloride** concentrations in a crop are acceptable in the nutrient solution at a wide range so long as adequate amounts for the plants are present. Additionally, concentrations may be allowed to reach relatively high levels so long as they are monitored and EC and pH are adjusted to compensate for their respective contributions. If chloride levels get too high, some leaf scorch may occur. The specific roles of chlorine in plants has not been fully elucidated, but it is known to be important for photosynthetic oxygen evolution from water molecules, for stimulation of ATPase and in stomatal regulation. Sodium ions are used to maintain turgidity and build osmotic potential in plant cells, and tomato is known to respond positively to additional sodium, but high salinity will cause toxicity (Subbarao *et al*., 2003). Excessive sodium inhibits the uptake of potassium, calcium and magnesium, and can be used in their places in many plant processes, though this is less efficient. Calcium deficiency or a high sodium to calcium ratio results in enhanced sodium uptake. Excess salinity may also interfere with N metabolism and uptake of nitrogen. Chlorine deficiency is rare, as the chloride ion is ubiquitous in the environment but results in wilting, curling and necrosis. Salinities higher than 2.3-5.1 mS/cm result in an undesirable yield reduction (Dorais *et al*., 2001). Sodium and chloride concentrations were the most variable in the grower survey, but so long as concentrations are sufficient and not toxic, a wide range is acceptable. Chloride may also facilitate calcium uptake and decrease the risk of blossom end rot (De Kreij, 1995). Target values returned in the survey ranged from 17 to 200 and varying irrigation levels used to control concentrations. It is recommended that sodium and chloride concentrations be kept below 400 mg/L in the main season, and concentrations of both should not be allowed to climb too high in recirculation systems.

Beneficial nutrients

There are micronutrients considered ‘non-essential’, but which are beneficial for plant growth and sodium is thought by many to fall into this category. There are other beneficial nutrients not currently added to tomato nutrient solutions as their beneficial effect has not been sufficiently demonstrated. Additions to the standard recipe also introduce challenges in terms of cation-anion balance. The actual amounts of chemical that is put into the system varies dependent on irrigation supply, and the ratios of potassium to calcium, magnesium and nitrate can often be more important than their absolute concentrations.

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For example, **Nickel** is not usually included in standard recipes but is considered an essential micronutrient for plant growth. It is contained in a number of enzymes and is involved in nitrogen metabolism. No visible damage can be seen in tomatoes at 67-77 mg/kg dry matter (Challinor, 2014). **Silicon** is not included in standard recipes and is only considered essential for a few plant species. However, an abundance of research points to silicon as a key player in plant defensive pathways. It has also been suggested that omission of silicon from nutrient solutions may impose stress on plants due to an atypical environment, given the abundance of silicon in the natural environment (Epstein, 1994). Silicon is deposited in cell walls adding stabilisation in the epidermal layers of leaves which prevents self-shading and aids photosynthesis, increases tolerance to metal toxicity and protects against pathogens such as powdery mildew (Miyaki & Takahashi, 1983). This study showed essentiality in tomato by excluding silicon, and there has previously been experimentation on its addition to nutrient solutions (Wooley, 1957). However, in the past when added, deposits in the irrigation system caused it to clog and the practice was discontinued, even in cucumbers where it was relatively common practice 10-15 years ago.

It would be interesting to look into the effects of nutrients not yet added, though care clearly needs to be taken to avoid changes being detrimental to the crop. **Selenium** is another beneficial nutrient not yet included in standard recipes, as tomato can be seen as a selenium non-accumulator (Shrift, 1969) meaning toxicity can occur at low levels. High concentrations of selenium in plants can also lead to toxicity in animals that consume them, but it also has health benefits in animals. Selenium has many features in common with sulphur, and may cause problems to non-selenium tolerant plants by replacing it in enzyme complexes, making them less effective. **Cobalt** and **chromium** also fulfil roles in plant metabolism and can be tolerated up to 0.05-0.3 mg kg^{-1} and 112-124 mg/kg dm respectively (Challinor, 2014).

Summary points – Objective 1

- **A variety of growing systems are used in UK tomato crops**
- **Irrigation as a tool for generally good nutrient management and generative vs. vegetative growth strategies**
- **Aerial management utilises the impact of humidity and temperature differentials on fruit**
- **Majority of UK crop still on run-to-waste, but potential future need for moving towards recirculating systems**
- **Changes in schedules including returning to earlier planting date and move to year round growing impact nutrient strategies**
- **Nutrient management in the UK is effective and aims to achieve optimum concentrations of key nutrients in the rootzone**
- **There may be scope for improvement, especially if other variables, such as disease, are incorporated into nutrient recipes and delivery strategy**

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Objective 2 - Review of current literature on crop nutrition and disease

A summary of information found in the literature review illustrating a link between disease tolerance/susceptibility and nutrient inputs is given here. This includes sources and research covering many crops as well as tomato and is followed by an evaluation of the potential for application of this information in commercial tomato growing. It should be noted that effects of nutrients not currently added to nutrient solutions in the UK have been found in this review, and so potential effects on the crop in these cases are partially speculative. The implementation of nutrition and its effect on disease have been in place in arable crops for some time, but in horticulture where the crops are more varied and grown on smaller scales, the application of nutritional disease control is more difficult. The mobility of the nutrient in question will also have an impact, as delivery via the nutrient solution will mean only mobile nutrients reach the foliar parts of the plant to have an effect. Where found effective, delivery of nutrients for the purpose of disease resistance via the nutrient solution will have advantages over foliar spraying, requiring less labour, time and avoiding the increases in humidity and leaf wetness in the crop which favour foliar diseases. It is also suggested that the mode of action of nutrients, such as silicon, differs according to its method of application (Belanger *et al*., 1995).

Optimum nutrition

Well-nourished, healthy plants are likely to be less stressed and more resistant to pathogen infection. Additionally, by altering plant morphology, chemical composition, or up-regulating or down-regulating processes resistance or tolerance of pathogens may be increased or decreased. Resistance can be viewed as the ability of the host plant to limit invasion, development and reproduction of a pathogen, whereas tolerance can be viewed as the ability of a host plant to maintain its own growth despite pathogen attack (Marschner, 2011). Maintaining a crop at its nutritional optimum avoids the added susceptibility to disease often observed with nutrient deficiencies, and allows the plant to more effectively compensate for losses due to infection. Numerous reviews have been written on the roles of individual nutrients in plant defence, and on the topic as a whole (Huber & Haneklaus, 2007; Walters & Bingham, 2007; Dordas, 2008; Schwarz *et al*., 2009; Veresoglou *et al*., 2013).

It is important to note that manipulation of a plant’s nutrient balance could also impact negatively on disease resistance if the optimal nutritional balance is moved away from. The composition of the nutrient solution supplying the crop has obvious impacts on the composition of plant tissue and exudates. For fungal diseases, the flow of plant exudates

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often stimulates spore germination and the composition of these exudates may dictate whether the infection attempt is successful or not. The relative supplies of nutrients exert changes on the composition on all parts of the plant, for example sugar and amino acid concentration in leaves is high when potassium is deficient. The concentration of photosynthates at the leaf and root surface and in the apoplast depends on the permeability of the plasma membrane and rise considerably with calcium or boron deficiency (Hancock & Huisman, 1981). The effect of make-up of exudates versus make-up of the plant tissue itself depends on the type of pathogen that is attempting to infect, as only a few pathogens are truly intracellular and the nutrition source accessed varies from pathogen to pathogen. Improved knowledge of the nutrient requirements of pathogenic fungi could enable strategies to be developed that are not only beneficial to plant resistance, but that target weaknesses in fungal metabolism (Solomon *et al*., 2003).

Although the resistance and tolerance of plants is largely genetic, and has been a focus of varietal breeding for years, the environment a plant grows in may exert considerable influence, and may be manipulated by growers. Generally, the role of nutrition is relatively small in highly susceptible or highly resistant cultivars, but can be substantial in moderately resistant or susceptible cultivars. This could have importance in new varieties where disease resistance is unclear, or for newly emerging or re-emerging diseases, such as tomato leaf mould, where resistance may break down easily. Breeding for resistance largely focuses on the addition of physical barriers to invasion and the production of antimicrobial compounds such as phytoalexins. For example, the resistance of tomato cultivars tested against bacterial wilt was found to be dependent on adequate calcium supply (Berry *et al*., 1988) whereas when resistant and susceptible cultivars of cucumber were tested against downy mildew their differential resistances were not found to be closely related to nitrogen supply (Tanaka *et al*., 2000). As detailed above, many nutrients make up structural or metabolic elements in plants and play roles in their defence pathways so maintaining a crop with an optimal nutritional status is likely to foster disease resistance in numerous ways.

Carbon nutrition

The effects of carbon nutrition, as supplied to glasshouse tomatoes through atmospheric carbon dioxide, also has implications for disease susceptibility as well as general crop growth. This shall not receive as much focus as it is already widely practiced and hydroponic solutions are the main focus of this review. Elevated carbon dioxide (363 or 758 ppm in 2009 and either 372 or 746 ppm in 2010) has been found to decrease incidence and severity of tomato yellow leaf curl virus (TYLCV) by modulating salicylic and jasmonic acid

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(Huang *et al*., 2012). Elevated CO_2 has also been seen to improve tolerance of tomato to *Phytophthora parasitica* (Jwa & Walling, 2001) though CO_2 supply is becoming increasingly limited in glasshouses.

Fertiliser type

As well as the amount of a mineral nutrient added to a solution, the type of fertiliser has repercussions for disease management. For example, phosphate is uptaken far more easily than phosphite, mureate of potash (KCl) was found to reduce disease where sulphate of potash (K_2SO_4) did not (Ehsan Akhtar *et al*., 2010), and certain organic fertilisers were found to be more effective than chemical fertilisation in controlling *Phytophthora infestans* in a soil grown tomato crop (Wang *et al*., 2000; Sharmer *et al*., 2012). The form in which calcium is delivered may also make nutrition in terms of nutrient management more or less effective, with calcium dihydrogen phosphate and calcium sulphate both decreasing *B. cinerea* severity on soil grown tomato, but calcium chloride and calcium nitrate increased fungal growth in vitro (Elad & Volpin, 1993).

Viral and bacterial diseases

The effect of nutrition on viral diseases is not clear, and there is more limited literature on this topic. In mineral deficient plants, increasing the nutrient supply may lead the plants to 'outgrow' the disease and cease to show symptoms, despite a link being known between increasing nutrient supply, increasing plant growth and increasing viral replication. The effect of nutrition on viral diseases is further complicated because of the presence of vectors, mainly fungi and insects which spread viruses and viroids from one plant to another. Plant nutritional status strongly impacts the success of insect attack, and if infection with a virus is a particular issue on a nursery, supplying supraoptimal concentrations of zinc (Tomlinson & Hunt, 1987) or other heavy metals to deter aphids or vectoring fungi may be worth exploring (Poschenrieder *et al*., 2011). *Agrobacterium tumefaciens*, the tumorigenic agent of crown gall disease in tomato, is similarly encouraged by high nutrient concentrations in the host. It has been found that limiting nitrogen, as well as phosphorus and calcium were effective in reducing tumour proliferation (Swain & Rier, Jr, 1968).

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Interactions

The use of mycorrhizae is an expanding area of study within horticulture, and implementing nutrition that encourages colonisation of the roots by beneficial fungi which effectively excludes root pathogens from the rhizosphere (Pozo *et al*., 2002). This may have particular application to control Fusarium and Verticillium wilts in tomato. A nutritional regime that would favour one fungus, and disadvantage another may be difficult to achieve. More recently, the success of various species of *Pseudomonas fluorescens* as biocontrols has also been linked to the nutrition delivered to the rhizosphere (Duffy & Defago, 1997). These biocontrol agents are thought to compete with pathogens for iron due to their production of siderphores, produce toxic cyanide and are likely favoured by ammonium nitrogen and a higher pH (Sarniguet *et al*., 1992). The presence of fertiliser may also enhance the effects of biological fungicides, for example cassia oil action against *Alternaria alternata* was enhanced by both potassium chloride and sodium chloride (Feng & Zheng, 2006).

Though the links have been long established between plant nutrition and disease, their interaction is highly complex and further study is required. Some diseases may be closely correlated with supply of certain nutrients, but others may be suppressed, and these relationships are not constant between different nutrients, crops or pathogens. The relative concentrations of nutrients are key, and it is often hard to separate the effect of one nutrient from another. It is also important to note that though disease may be supressed by supply of certain nutrients, this may be at the cost of yield or severe phytotoxicity. Integrative plant nutrition is an essential component to a successful hydroponic system, and could be a cost-effective and environmentally friendly way to complement disease control with pesticides. The various direct and indirect effects on disease of altering a crops nutritional environment found in this literature review are detailed below, and are categorised according to nutrient as far as is possible. Key results and general findings for each nutrient are shown in bold.

1. Nitrogen

There is long standing knowledge of linkages between nitrogen supply and disease in numerous crops, but this relationship is not universal. Largely, the effect of nitrogen depends on the pathogen in question and more specifically if an obligate or a facultative pathogen is trying to infect. **A high nitrogen supply is known to increase the severity of disease by obligate pathogens, but has the opposite effect on facultative pathogens** such as *Alternaria* and *Fusarium*, and most bacterial diseases (Snoeijers *et al*., 2000). This is because the different types of pathogen have different nutritional requirements

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themselves. Facultative parasites prefer senescing tissue or release toxins to damage or kill host cells, and so generally all factors which support the metabolic activities of host cells will also increase resistance or tolerance to facultative parasites. Infection with a key pathogen of UK tomato crops, *Botrytis cinerea*, drops in sweet basil as nitrogen nutrition increases (with a standard concentration considered 7.2 mM, or approximately 100 mg/L), and it has also been found to decrease sporulation (Yermiyahu *et al*., 2006). Pathogenicity of spores to tomato was found to be lowest at intermediate concentrations of applied nitrogen, and highest at very low (0.5 mM NO_3, approx. 30 mg/L) or very high (30 mM NO_3, 1860 mg/L) (Abro *et al*., 2013) concentrations. **The response of *Botrytis cinerea* to nitrogen fertilisation appears to vary between hosts, and on tomato the response in disease progression and severity has been found to depend on the specific isolate** (Lecompte *et al.,* 2010). The relatively uncommon Alternaria blight of tomato was also found to be inhibited by increasing nitrogen compound concentration in the lab but not in the field (Blachinski *et al*., 1996) though for *Alternaria brassicae* this relationship held in field brassicas (Veromann *et al*., 2013). This backs up an earlier study where nitrogen regime was found to have no direct effect on *Alternaria tomatophila* in tomato (Sharma & Kumar, 1998).

Susceptibility to the facultative pathogen *Botrytis cinerea* decreased as nitrogen increased and carbon to nitrogen ratio decreased (Hoffland *et al*., 1999). Generally, the carbon to nitrogen ratio is regarded as a good indicator of growth and quality, and can be considered a good indicator of secondary compounds, especially those used in defence (Royer *et al*., 2013) but this is clearly only the case for certain pathogen-host relationships.

In Arabidopsis, when treated with an elicitor, reaction time and production of resistance compounds such as chitinase were positively correlated with the nitrogen conditions the plants were cultivated under (Dietrich *et al*., 2004). A plant grown under a limiting nutrient regime will not have the same resources to invest in defence, should a pathogen challenge arise. A trade-off between growth and defence has been observed in tomato under nitrate limitation with significant differences occurring between 9 hydroponically grown cultivars. This response was organ dependent, with roots being more responsive to limited nitrogen supply than the aerial parts of the plants. Nitrogen limitation did not change the phenolic content in shoots, whereas it stimulated accumulation in roots (Larbat *et al*., 2012).

Obligate pathogens require assimilates supplied by living cells, and young tissue favoured by high nitrogen regimes are more susceptible to infection. Additionally, increased amino acid content, more so than increased sugar content, at the leaf surface and in the apoplast

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influences germination and growth of conidia. When nitrogen supply to a plant is too large, the number and antifungal activity of phenolics may also decrease, which may have knock-on effects for disease resistance as is the case for powdery mildew in wheat (Sander & Heitefuss, 1998). A reduction in phenolics may also lead to a reduction in lignin. A negative relationship has been shown in grapevine resistance to downy mildew, dependent on the leaf content of the phytoalexin stilbene under increasing nitrogen supply (Bavaresco & Eibach, 1987). A further response to increasing nitrogen supply in plants is usually a decrease in silicon, an element used by plants extensively in pathogen defence, due to dilution. However, obligate parasites largely gain the advantage due to the increase of low molecular weight organic nitrogen compounds, which they can easily utilise as a substrate, in combination with the various biochemical changes that occur within the plant. Increasing nitrogen nutrition has been shown to increase cucumber's susceptibility to external fruit rot (Van Steekelenburg, 1982). **Viral diseases are also likely to be favoured by high nitrogen**, as nutritional factors that favour plant growth also favour viral multiplication. This has been illustrated for tomato spotted wilt virus in tomato (Stavisky *et al*., 2002) and tobacco mosaic virus (Spencer, 1939). Hemibiotrophic pathogens infect as a biotroph would, but switch their lifestyle to that of a necrotroph through disease development. Expression of the Avr9 gene, key to infection, in the hemibiotrophic tomato pathogen *Passalora fulva* is induced by nitrogen starvation in host, but many other effectors are not (Thomma *et al.,* 2006).

In arable crops, timing of nitrogen has been shown to be a key factor in disease control (Macnish, 1988). As the grower survey illustrates, nutrient delivery to a tomato crop also differs throughout the season, largely dependent on the factors of plant age and fruit load. However, a glasshouse environment is not subject to the same variables as a field, though it could be prudent to avoid application of nitrate nitrogen if a high risk of facultative pathogen infection is identified at that time. In hydroponic, closed systems populations of microorganisms present have been observed to fluctuate according to both nitrogen concentration and EC (Schwarz *et al*., 1997).

Depending on the disease, ammonium or nitrate nitrogen should be favoured to avoid supplying the pathogen with easily accessible nutrients. Specific examples of the effect of nitrate to ammonium ratio include the **lower disease index of corky root rot (*Pyrenochaeta lycopersici*) observed with ammonium dominated fertiliser in soil grown crops** (Knopp & Martensson, 2010). **Conversely, in a recirculated system nitrogen concentration and ammonium to nitrate ratio were varied and *Pythium* associated mortality was seen to increase as ammonium did**. However, it is generally

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recommended for plant health that ammonium:nitrate ratio be kept low. It was found that if ammonium was replaced with urea mortality dropped by 22%. Increased mortality was thought to be due to nitrite accumulation in solution, reduction of solution pH and reduction of plant calcium concentration (Bar-Yosef *et al*., 2008). **Increasing the ammonium to nitrate ratio in hydroponically grown tomato plants was found to reduce disease severity caused by Fusarium crown and root rot by improving the efficacy of the biological control agent *Trichoderma asperellum* strain T34.** This may also favour the development of other pathogens, but may also be useful for growers in attenuating ill effects if high ammonium concentrations are required but **in a large scale glasshouse experiment where tomato plants were inoculated with Fusarium crown and root rot, ammonium nitrogen significantly increased disease severity** (Duffy & Defago, 1999). In tomato, the ammonium:nitrate ratio is generally kept low, as if allowed to climb too high plants may struggle to uptake enough magnesium, calcium and potassium.

However, the obligate or facultative pathogen relationship with nitrogen is not absolute. Disease severity of *Colletotrichum gloeosporioides* in strawberry increased with increasing nitrogen in the nutrient solution, regardless of ammonium to nitrate ratio (Nam *et al*., 2006). Similarly, disease severity of *Phytophthora nicotianae* in tomato increased with increasing nutrient concentrations (Grote & Claussen, 2001), despite being facultative, showing this relationship is far from absolute, but linked with each pathogen's identity and lifestyle and nutritional requirements (Veresoglou *et al*., 2013). The relationship between whether a pathogen is obligate or facultative and it's response to increased plant nitrogen has been illustrated in glasshouse tomato. **Response to nitrogen supply is highly pathogen dependent**, and in one experiment under increasing nitrogen supply susceptibility to *Fusarium oxysporum* was unaltered, but *Pseudomonas syringae* and *Oidium lycopersicum* susceptibility increased significantly (Hoffland *et al*., 2000). For disease severity of *Xanthomonas campestris* pv. *campestris* on broccoli (Seabra Junior *et al*., 2013), plant optimal nitrogen was observed to be the best regime, with disease severity being worse if nitrogen was lacking or in excess. Overall, improved nitrogen use efficiency could contribute to reducing the impacts of crop disease, reduce the cost of nitrogenous fertilisers and losses to the environment (Masclaux-Daubresse *et al*., 2010). Actively managing nitrogen also controls crop growth.

2. Potassium

Potassium has an easily illustrated role in disease resistance and, unlike nitrogen, elicits uniform responses. The effects of nitrogen and potassium nutrition are often examined

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together, and they are known to interact. **High concentrations of potassium increase host plant resistance to both obligate and facultative pathogens.** For anthracnose in corn, a high dose of potassium (1000 mg/L) combined with a lower dose of nitrogen (75 mg/L) was found to be most effective in reducing disease severity (Carvalho *et al*., 2013). In cucumber, when nitrate concentrations were low, adding potassium significantly reduced *Botrytis cinerea* on fruit by up to 33% (Elad *et al.,* 1993). When a parasitic fungus or bacterium releases pectic enzymes, potassium ion efflux from cells is increased, triggering a defence-related hypersensitive response (Atkinson *et al*., 1986). Some pathogens, such as leaf spot in cereals (*Helminthosporium cynodontis*) have fungal toxins which induce this and deplete cells of potassium. It then follows that disease symptoms can be effectively reduced in severity with increased potassium content in leaves (Richardson & Croughan, 1989). The role of potassium in diseases has been reviewed multiple times, in both textbooks (Perrenoud, 1990) and scientific papers (Wang, M., *et al*., 2013).

High potassium nutrition increasing plant resistance to disease has been illustrated for banana plantlets grown on a medium of increasing potassium having a greater resistance to Xanthomonas wilt (Atim *et al*., 2013), Xanthomonas black rot in broccoli (Seabra Junior *et al*., 2013) and for tomato infected with bacterial canker (Berry *et al*., 1988) and tomato pith necrosis (Ustun *et al*., 2009). Alternaria blight of tomato was found to be inhibited by both potassium and nitrogen compounds in lab studies, but when this was translated to the field no effect was observed (Blachinski *et al.,* 1996). Potassium supplementation was also found to reduce disease incidence in cotton infected with cotton leaf curl virus (CLCUV) (Zafar & Athar, 2013).

In fact, on review of over 2000 references it was estimated that potassium nutrition decreased the incidence of fungal diseases by 70% and bacteria by 69%. This translated to yield increases in infected plants of 42% and 57% respectively (Perrenoud, 1990). For most plant-pathogen relationships, the effect of potassium on disease is confined to the deficiency range. **Potassium deficient plants are more susceptible to disease and if the plant is maintained at its nutritional optimum and is still exhibiting disease symptoms, further application of potassium will have no effect** (Dordas, 2008). This relationship occurs because in deficient plants the synthesis of high molecular weight compounds is impaired and low molecular weight compounds accumulate. Therefore, for a plant in the deficiency range, an increase in potassium supply leads to an increase in growth and an increase in the content of low molecular weight compounds until growth is maximal. Further increases in potassium supply would have little effect on the organic constituents of the plant. The increased growth caused by potassium when the plant is

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deficient also lead to dilutions by growth of other mineral elements, and beyond maximal growth there may also be a slight decrease in cations such as calcium and magnesium due to competition at uptake sites. Elevated potassium caused disease severity of *Colletotrichum gloeosporioides* in strawberry to increase (Nam *et al*., 2006). *Colletotrichum* sp. are generally more of a problem in organic tomatoes. Maintaining an optimum potassium status and controlling plant growth by manipulating nitrogen and phosphorus concentrations is also vital to maintain good fruit flavour. Rootstocks have been found to enhance tomato growth and quality characteristics under low potassium supply, and the effect of rootstocks on nutrition and the subsequent effect on disease development in tomato (Schwarz *et al*., 2013).

If the plant is receiving a suboptimal calcium supply whilst this potassium nutrition is ongoing, there may be a risk of calcium deficiency related disorders, and increased disease susceptibility. This is especially important in tomatoes in order to avoid blossom end rot, and an obvious nutrient management strategy that growers already follow would be to keep as many elements as possible at optimum supply level, which is difficult in practice. Potassium also has strong bearing on tomato production as during fruiting the potassium content of fruit is important to minimise fruit disorders, and as detailed above. Potassium has been observed to mitigate the ill effects of cold chilling in cherry tomatoes when potassium chloride was supplied at 0.2 mg/L by reducing oxidative stress (Constán-Aguilar *et al*., 2014). Crops are generally supplied with higher concentrations of potassium during fruiting to combat this, and avoid fruit skin micro-splitting and cracking which could allow disease in. Though data on nutrition’s effect on viral diseases is limited, there is evidence that potassium supply has an effect on viral replication, with viral diseases becoming worse as potassium supply is increased (Perrenoud, 1990). The form in which potassium is delivered to the crop may also have an impact, as in tomato (*Solanum lycopersicum*) potassium supplied as muriate of potash significantly reduced incidence of leaf blight (*Alternaria alternata*) compared to sulphate of potash (Ehsan Akhtar, *et al*., 2010).

3. Phosphorus

Phosphorus nutrition has varying effects on plant resistance, and results are inconsistent. There is potential to impact on viral diseases, as nutritional factors which favour the growth of the host plant also favour viral multiplication (Huber & Haneklaus, 2007). Similarly with fungal and bacterial diseases, ensuring the crop is supplied with sufficient phosphorus will allow the plants to tolerate disease, and grow through it. This is in comparison to other nutrients such as copper and manganese, which have direct effects on the biosynthesis of

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lignin, and hence on disease resistance. Elevated phosphorus in a non-circulated nutrient solution supplied to strawberry infected with *Colletotrichum gloeosporioides* was shown to reduce disease severity, and also increased the dry weight of the strawberry plants (Nam *et al*., 2006). Further evidence for phosphorus nutrition in maintaining resistance was identified in a study where Arabidopsis was grown under prolonged phosphate starvation, transcription of a gene (PAP5) required for basal resistance to certain pathogens is induced (Ravichandran *et al*., 2013). Despite all this, mycorrhizal fungi may be encouraged by limiting the phosphorus supply (Schwarz *et al*., 2009).

The fungicidal effects of phosphite are well known, especially against Oomycete diseases such as *Phytophthora* spp.. It is widely marketed as a fungicide or as a fertiliser and is considered a 'grey area' product in terms of registration. However, phosphate is preferentially uptaken by plants for nutritional purposes, and phosphite treated plants with no alternative source of phosphorus may exhibit deficiency symptoms (Forster *et al*.,1998). Phosphite is not thought to provide tomato plants with sufficient phosphorus nutrition and under phosphate limited regimes may even be deleterious. As such when supplied at too high a rate as a foliar feed has also been observed to result in phytotoxicity in some plants. Substituting phosphate for phosphite, even if oxidation by microbes occurs, is an inefficient way to deliver phosphorus to the crop (Thao & Yamakawa, 2009a), however a balance of phosphate (94.97 mg/L) and phosphite (42.28 mg/L) may be an efficient way to both limit disease, and provide phosphorus nutrition as has been shown in pepper crops infected with *Phytophthora capsici* (Forster et al., 1998). Delivery of phosphite via a hydroponic system has been demonstrated but risks of root damage and resultant decreased uptake of nutrients were present at even low concentrations of phosphite (as low as 0.2mM) (Thao & Yamakawa, 2009b). Phosphorus concentrations may also be manipulated to control early growth.

4. Calcium

There is a strong link between calcium content of tissues and resistance to fungal and bacterial diseases. Most parasitic fungi and bacteria invade the apoplasm by producing enzymes which dissolve the middle lamella, and these enzymes are strongly inhibited by Ca^{2+} (Bateman & Lumsden, 1965). Calcium is also essential for the stability of biomembranes, and so low calcium content enhances the efflux of low molecular weight compounds such as sugars into the apoplasm. A suboptimal calcium supply, due to insufficient inputs or through competition with potassium or magnesium cations, will

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increase disease susceptibility. In fact, it has been found that so long as calcium content of plants is kept at a high level, increasing the potassium content past the optimum does not necessarily lead to an increase in infection as described above.

Increasing the calcium supply to tomato is known to avoid blossom end rot, and this nutrition disorder commonly allows secondary fungal infection in. Tomato cell cultures exposed to tomato leaf mould, *Passalora fulva*, were found to produce a calcium-dependent protein kinase that was found to be produced systemically in glasshouse tomato plants when mechanically wounded (Chico *et al*., 2002) (i.e. calcium is required for the plant's protein modulated response to mechanical wounding, an entry method commonly used by pathogens). Also in tomato**, increasing calcium supply was shown to suppress Fusarium wilt** that occurs when *Fusarium oxysporum* grows to plug the plants xylem vessels. Plants were severely infected with *F. oxysporum* when fed with a low external calcium supply, resulting in low concentrations of calcium in the xylem, but nearly all plants were healthy when the calcium concentration in the xylem was raised (Corden, 1965). **Increased calcium was also shown to reduce corky root disease (*Pyrenochaeta lycopersici*)** in glasshouse experiments (Hasna *et al*., 2009), though the crop was grown in compost and the pathogen is largely only a problem in soil grown crops. Calcium applied as both a basal fertiliser and a spray was effective against *Erwinia carotovora* subsp. *carotovora* in *Zantedeschia aethiopica* (Cho *et al*., 2013). Calcium nutrition has also been found to influence *Botrytis cinerea* in tomato (Elad *et al*., 1993; Elad & Volpin, 1993) and sweet basil (Yermiyahu *et al*., 2006), *Colletotrichum gloeosporioides* in strawberry (Nam et al, 2006), downy mildew in cucumber (Elad *et al*., 1993) and Phytophthora pink spot in potato (Benson *et al*., 2009), with reduced disease at higher calcium nutrition.

Multiplication and severity of bacterial leaf spot diseases are also generally enhanced under deficient calcium conditions, partly because of the inhibition of polygalacturonase enzymes as detailed above. In small banana plantlets, increased calcium supply was found to reduce incidence and increase incubation period of *Xanthomonas capestris* pv. *musacearum*, as did increased potassium and nitrogen (Atim *et al*., 2013). **Disease severity of tomato pith necrosis caused by numerous bacteria was reduced at a higher calcium regime** (Ustun *et al*., 2009).

Bacterial canker in tomato is inversely correlated with calcium content in tomato shoot tissue and experimentally symptoms can be effectively treated with calcium nutrition in both susceptible and resistant cultivars. This indicates that genetic resistance of a cultivar is dependent on adequate calcium supply. At each level of calcium, the more resistant

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cultivar had higher calcium and magnesium contents, but lower potassium content (Berry *et al*., 1988). It should be noted, therefore, that selection of cultivars for potassium uptake efficiency may bear risks of negative effects on disease resistance to certain bacterial and fungal diseases (Marschner, 2011). However, calcium uptake efficiency was found to have no effect on bacterial wilt (*Ralstonia solanacearum*) severity when a calcium efficient and a calcium inefficient genotype were grown under sufficient calcium conditions (Hacisalihoglu *et al.,* 2010). Further studies explored effects under varying calcium supply and found increasing calcium nutrition decreased disease severity of bacterial wilt (Jiang *et al.*, 2013; Yamazaki & Hoshina, 1995). As well as calcium's importance to the middle lamella, and it's inhibition of pathogen enzymes, it also plays a role in a plant's hypersensitive response to bacterial infection. Tobacco, another solanaceous crop, requires calcium ions to be taken into the cytoplasm from the apoplasm through Ca^{2+} channels for its hypersensitive response against *Pseudomonas syringae*. This leads to cell acidification and death of host cells at the infection site (Atkinson *et al*., 1990). Calcium supply also improves resistance to bacterial spot (*Xanthomonas*) of tomato (Huber & Jones, 2013). For *Tomato mosaic virus* (ToMV) it also appears that calcium could have some beneficial effects, as sprays of 0.3% calcium prepared from four different calcium sources were shown to decrease virus concentration in plants (Eraslan *et al.,* 2007) and visible symptoms (Tu, 1986).

Fleshy fruits like tomato typically have a relatively low calcium content compared to many others, but fruits high in calcium are more resistant to both physiological disorders and rotting by storage pathogens. In peanut, postharvest rots are caused by *Rhizoctonia solani* and *Pythium myriotylum*, both also pathogens of tomato. The incidence of disease in peanuts is closely related to calcium content of the pod tissue, and it was shown to reduce when calcium was applied (Hallock & Garren, 1968).

The pathogen refuge hypothesis (Kruckeberg, 1992) speculates that plants grown in inhospitable environments, such as on low calcium serpentine soil, may be less susceptible to pathogen attack. However, plants from this environment grown in a low calcium soil have been shown to be highly susceptible to the rust fungus *Melampsora lini* (Springer *et al*., 2007) and for non-specialist species in a commercial cropping environment this theory is especially unlikely.

5. Magnesium

Magnesium can have both direct and indirect effects on disease and there is less information available in the literature as its effects are often complex, and specific disease

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related functions are hard to elucidate. Plant defence responses to magnesium supply are not generally conserved, as magnesium can complement or antagonize other minerals. As such, there are fewer studies performed on magnesium, and it is rarely studied alone due to its close relationship with other nutrients, which makes it difficult to assign the changes in disease levels specifically to changes in magnesium concentrations. For instance, a strain of wheat more resistant to Fusarium ear blight was found to have higher magnesium content than common wheat varieties, along with zinc, potassium and others (Wiwart *et al*., 2013), however this could be coincidental and no causal link may exist. Similarly, magnesium content of soil was found to contribute significantly to the separation of different communities of *Pythium* in soil (Dorrance *et al*., 2009; Lewis *et al*., 1992) and the efficacy of biocontrol agent *Trichoderma koningii* against take-all in wheat (Duffy *et al*., 1997). Fusarium wilt tends to be less severe when adequate magnesium is available, and the resistance of plant tissue to the pectolytic enzymes produced by macerating and soft rotting pathogens may increase (Huber & Jones, 2013). There is definitely potential for magnesium to reduce the impact of some diseases, but information is limited. Concentrations of magnesium supplied to rice plants ranging from approximately 6 mg/L (0.25 mM) to approximately 97 mg/L (4mM) resulted in higher foliar concentrations of magnesium in plants given a greater supply, which in turn resulted in lower severity of brown spot (*Bipolaris oryzae*) (Moreira *et al*., 2013). Lower levels of bacterial canker correlated with higher concentrations of magnesium in tomato shoots in a resistant cultivar (Berry *et al*., 1988). Alternatively, magnesium may interfere with calcium uptake and so may make the diseases improved by calcium supply detailed above, such as bacterial spot (*Xanthomonas*) of tomato, worse (Huber & Jones, 2013).

6. Sulphur

Sulphur has the potential to enhance plant defence across a variety of crops, a relationship that has become apparent due to the increase in disease now that coal fired power stations are decreasing. In arable farming, relative abundances of pathogen DNA are closely correlated with UK emissions of oxidised sulphur over the past 160 years. To prove a causal link, sulphur nutrition was implemented on 3 varieties of wheat. Sulphate and sulphurous acid were found to alter the susceptibility of wheat to *Phaeosphaeria nodorum* and *Mycosphaerella graminicola* (Chandramohan & Shaw, 2013). Sulphur is also one of the world’s oldest antifungals, but when delivered as a feed rather than as a fungicide it can be assimilated to perform a variety of defensive roles. Elemental sulphur acts as an inorganic phytoalexin in tomato (and a variety of other crops) and is produced in response to xylem invading fungi and bacteria. It was found to be highly toxic to fungal pathogens representing

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ascomycetes, basidiomycetes and deuteromycetes, but not to a *Phytophthora* species exposed, or to bacteria. It is thought this reaction may be xylem specific as sulphur was not found in leaves of six plant species undergoing a hypersensitive reaction to *Pseudomonas syringae*. This study found sulphur to be present in tomato at sites appropriate to counter *Verticillium dahliae* attack, and it is thought to be a highly localized reaction (Cooper & Williams, 2004). **In tomato plants infected with *Verticillium dahliae*, high sulphur nutrition significantly reduced fungal spread in both susceptible and resistant genotypes** (Bollig *et al*., 2013). Rates of photosynthesis were also impeded by the fungus in both genotypes, especially under low sulphur supply and an increase in the anti-oxidant glutathione was observed under high sulphur nutrition in response to fungal colonisation. However, plant shoot growth and infected root growth did not exhibit an improvement due to higher sulphur supply.

7. Boron

Boron has some important defensive roles as discussed earlier, and is especially active in phenol metabolism. Phenolic compounds play an important role in early stages of infection, both chemically and in the inducement of defence structures, as phytoalexins or as precursors of lignin and suberin biosynthesis. Wheat plants that are boron deficient exhibited a higher rate of infection with powdery mildew than in boron sufficient plants, and the fungus was able to spread more rapidly (Schutte, 1967). Boron supplementation has also been shown to reduce development of clubroot in oilseed rape, at both primary and secondary infection stages. In this study, phytotoxicity to OSR seedlings occurred at rates higher than 2 kg/ha in controlled conditions, but in a field experiment rates of 4 kg/ha provided effective disease control and resulted in no phytotoxicity (Deora *et al*.. 2011). **Control of a tomato pathogen, late blight (*Phytophthora infestans*), has also been illustrated with boron at sub-phytotoxic concentrations via a nutritional effect** rather than being directly inhibitory to the pathogen (Frenkel *et al*., 2010). Boron may also have positive effects on viral pathogens, with plants grown in boron deficient conditions containing lower concentration of Tobacco Mosaic Virus (Shepherd & Pound, 1960). As the use of recirculating systems increases in tomato crops, the boron concentrations present may increase and have beneficial effects (Frenkel *et al*., 2010).

8. Iron

Iron, as well as many other metal elements, plays a role in generating and detoxifying oxygen radicals and hydrogen peroxide, large amounts of which are produced in plant

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responses to pathogen infection. However, it should be noted that many pathogens, especially those infecting plant roots, also require iron and increasing it to supra-optimal concentrations may inadvertently favour pathogens whilst offering no real advantages to the crop. The use of Pseudomonas biocontrol species that play a role in competing with pathogens for iron in the rhizosphere could potentially negate this. The biocontrol agent T34 (*Trichoderma asperellum*, strain T34) has also been found to compete with *Fusarium oxysporum* for iron in a tomato soilless culture. T34 may also protect tomato plants from iron toxicity at high concentrations of the nutrient (Segarra *et al*., 2010). The plant pathogen *Dickeya dadantii*, to which tomato is susceptible (bacterial soft rot), has been shown to require its siderophore mediated iron uptake system for systemic disease progression on several host plants. The effect of plant iron status on *D. dadantii* was investigated and it was observed that iron starved tomato plants showed a reduction in disease. A reduction in infection with *B. cinerea* was also observed (Kieu *et al*., 2012). Iron limiting conditions have also been found to increase resistant tomatoes' sensitivity to *Verticillium dahliae* (Macur *et al*., 1991). Ferrelitic soils, which are low in silicon but high in aluminium and iron have been found to sustain *R. solanacearum* better than other soils, suggesting it is favoured by these nutrient conditions (Stefanova, 1998).

A great deal of recent research has focused on the iron-binding milk protein lactoferrin, which contributes to plant nutrition and exerts a broad spectrum defence in mammals. Transgenic tobacco, Arabidopsis and wheat containing mammalian lactoferrin were shown to have high levels of resistance to *Rhizoctonia solani* and *Fusarium graminearum*. Transgenic tomato plants also received resistance to *Ralstonia solanacearum* (Lakshman *et al*., 2013). This resistance has also been acquired via foliar applications where it was thought to induce resistance and stimulate the salicylic acid pathway (Wang et al., 2013b), and further research into its delivery hydroponically would be of interest.

9. Manganese

Manganese nutrition influences plant resistance surrounding plant-pathogen interactions by having a role in both detoxification and generation of oxygen radicals and hydrogen peroxide. It also plays an active role in phenol metabolism and lignin biosynthesis. Manganese can control numerous diseases due to these roles, and broccoli plants overexpressing a manganese superoxide dismutase gene were found to be totally downy mildew resistant (Jiang *et al*., 2012). The symptoms of viral diseases appear very similar to manganese deficiency, and application of manganese has the potential to mask the symptoms of these viruses. Manganese supplementation has also been found to impact

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numerous soil-borne diseases of crops, for example, directly inhibiting the growth of common potato scab after application (Mortvedt *et al*., 1963). In the nutrient solution, manganese availability may be decreased due to increases in pH or nitrate, which may impact the formation of lignin and ease of hyphal penetration of the roots. In wheat, additional manganese is added to the soil, but in a hydroponic system the impacts on other nutrient concentrations would have to be considered. Foliar application would have little worth as manganese is not highly mobile within the plant. Many soil-born pathogenic fungi also have the ability to oxidise manganese in the root environment, and at higher pH levels manganese is less available, so a supra-optimal supply may be necessary.

Manganese has been effectively used on golf courses to control *Gaeumannomyces graminis* (Heckman *et al*., 2003) and found to reduce Rhizoctonia in clusterbean (Wadwha *et al*., 2013). Manganese nutrition is also known to interact with silicon nutrition in the control of rice blast (Cacique *et al*., 2012) and to induce protective mechanisms in grapevine against powdery mildew (Yao *et al*., 2012). At supra-optimal but sub-toxic concentrations it has been supplied to tomato plants to control of *Pseudocercospora fuligena* (black leaf mould), a problem on tomato in South East Asia. Plant peroxidases were significantly increased, especially at point of inoculation in treated plants, and when inoculated defence proteins were also produced (Heine *et al.,* 2011). This disease is not present in the UK, but this could apply to other diseases.

10. Zinc

Zinc plays a role in detoxification and generation of oxygen radicals and hydrogen peroxide, which play an active role in plant defence. The response of disease to zinc supply is variable, and increases, decreases and no effects have all been observed (Dordas, 2008). Rubber trees deficient in zinc were found to be more susceptible to *Oidium*, due to a leakage of sugars onto the leaf surface (Bolle-Jones and Hilton, 1956) providing the fungus with a more suitable feeding substrate. *Oidium lycopersicum* powdery mildew commonly infects tomato crops, and so zinc deficiency could be linked to outbreaks of this pathogen. Zinc application is also utilised in wheat crops to supress Rhizoctonia root rot, though this is only effective where zinc is limiting to plant growth (Thongbai *et al*., 1993). However, brown spot inoculated rice grown in hydroponic culture amended with zinc was shown to become more susceptible to disease as foliar zinc concentration increased (Moreira *et al*., 2013). **Specifically in tomato, zinc nutrition has been found to improve the biological control of Fusarium crown and root rot by *Pseudomonas fluorescens*** (Duffy & Defago, 1997). Similarly in both the laboratory and a glasshouse experiment on soil grown tomato addition

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of zinc was found to improve the control of charcoal rot, *Macrophomina phaseolina* by *Pseudomonas aeruginosa* and *P. fluorescens* species (Shaukat & Siddiqui, 2003). When used both alone and with rhizobacteria zinc was shown to supress *Rhizoctonia solani* in tomato, and also had suppressive effects on root knot nematode (Siddiqui *et al*., 2012). The biocontrol agent alone can only provide moderate disease control, but following a one-time amendment of zinc (33 mg/L) disease was reduced by 25%. This improvement was due to zinc suppressing the pathogen's antibacterial metabolism. The mycorrhizal fungus *Glomus intraradices* has also been shown to be influenced by zinc in the control of Phytophthora blight of pepper. Both zinc application and application of the mycorrhizae alone reduced *Phytophthora capsici* infection, and disease severity was reduced by combined applications (Kucukyumuk *et al*., 2013).

11. Copper

Copper also plays a key role in phenol metabolism, and the plant's nutritional status will likely have a strong influence on the plants defence responses if sub-optimal. Copper is commonly used as a commodity substance and is applied to a large number of crops due to its antimicrobial properties. This can also confer yield increases due to improvement of plant nutritional status and by suppression of disease. Copper is routinely applied to numerous horticultural crops as a foliar spray, however its use is largely as a fungicide at the high rates it is used at. Applying copper as a foliar feed, despite its motility in the plant, may not ensure high enough levels of protection are reached at the roots, and so in terms of root disease resistance application via the nutrient system is likely to be beneficial so long as concentrations high enough to cause toxicity are not reached. Applying copper at 5 and 10 mg/L (converted from ppm) resulted in reduction of Rhizoctonia root rot (Wadwha *et al*., 2013). In vitro, copper amendment reduced the growth of Fusarium crown and root rot, and also increased the biocontrol activity of a *Pseudomonas fluorescens* strain (Duffy & Defago, 1997).

Supplying plants with too much copper at the roots may reduce plant phosphorus contents, and the ability of plants to uptake other nutrients such as potassium, phosphorus, calcium, iron and zinc (Kaplan *et al*., 2010). However, it has been observed that exposing pepper plants to stress inducing concentrations of copper (as 50uM copper sulphate, approx.. 8 mg/L) induces a defence response that offers cross protection against a *V. dahliae*, with reduced disease severity observed (Chmielowska *et al*., 2010). Relatively new disinfection technology used widely in pot and bedding plants and in cut flower production makes use of highly charged copper ions supplied by electrodes to both deliver the appropriate amount of

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copper to the solution for plant nutrition, but also to combat waterborne diseases such as *Phytophthora* root rots. The 'AquaHort' system is also reported to keep irrigation pipes clean. Similarly, new developments in fertilisers where copper is formulated to be uptaken systemically may have a beneficial effect on disease resistance in future by improving the plants redox state (De Lassen & Buhr, 2001).

12. Molybdenum

Molybdenum is required only in small amounts by plants, and its role in plant defence is not yet fully understood. Amendment with molybdenum was found to have no effect on production of fusaric acid or microconidia of Fusarium crown and root rot in vitro (Duffy & Defago, 1997). However, a variety of wheat more resistant to Fusarium ear blight was found to contain more molybdenum (Wiwart *et al*., 2013) though this could be purely coincidental. Lentil seeds were soaked in 2 or 5 ppm molybdenum solution, and were found to be less susceptible to Rhizoctonia damping off and Fusarium wilt when planted with 2 ppm being more effective (El-Hersh *et al*., 2011). Ammonium molybdate has also been found to be effective in controlling post-harvest rots of peach (Cao *et al*., 2010) and apple (Nunes *et al*., 2001).

13. Sodium and Chlorine

Sodium can often cause problems in a hydroponic system and water may have to be bled from closed systems to lower the EC and salinity of the circulating water. EC management is key in glasshouse tomato to ensure stress to plants is minimal, especially at key points in the growing system due to this increased disease susceptibility and potential yield losses. However, increasing the electrical conductivity with sodium chloride was found to reduce titratable acids, potassium and nitrogen in fruit, increase their sodium content and improve their overall flavour (Dorais *et al*., 2001). **Exposure to salinity stress (11,688 mg/L NaCl or 2,220 mg/L $CaCl_2$) even for brief periods was found to increase severity of disease on tomato plants grown in hydroponic culture when inoculated with *Phytophthora* spp.** This is thought to be due to induced production of abscisic acid, which is also produced when plants are grown under drought conditions (Dileo *et al*., 2010). However, in a **hydroponic tomato crop infected with powdery mildew, *Oidium neolycopersici*, the addition of sodium chloride (up to 1.74 g/L) to the nutrient solution generally reduced the incidence and severity of disease** (Garibaldi *et al*., 2011). Silicon has been found to increase plants tolerance to salt stress and could make strategies utilising high EC for its beneficial effect on disease less damaging to the plant (Saqib *et al*., 2008). Overall, though

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there may be several management regimes that could improve cropping, the composition and proper ratios of the nutrient solution must be maintained to avoid the risk of root disease.

The use of chloride fertilisers is linked to reductions in disease in arable crops such as wheat (Christensen *et al*., 1987) and barley (Timm *et al*., 1986). This action could be direct by improving the plants water balance, or indirect due to changes exerted in the rhizosphere. It is now thought that chlorine application enhances host plants' resistance to disease (Dordas, 2008). Chlorine is a common component of many disinfectants and is used by growers of a variety of horticultural crops to treat their water e.g. as chlorine dioxide. Tomato transplants grown in NFT recycled solution that was chlorinated showed reduction in growth observed for treatments chlorinated at over 40 mg/L. Plants grown in solution chlorinated at 5 mg/L exhibited better than normal growth. The threshold for normal tomato transplants was 20 mg/L, which was also an effective rate to eliminate *Pythium* sp. and *Phytophthora* sp. (Saha *et al*., 2011).

14. Silicon

Silicon has long been known to play an important role in plant defence, historically viewed as mostly structural, but increasingly silicon's other roles in plant defence are becoming apparent. Additional silicon is rarely added to nutrient solutions, despite its benefits to plant growth (Epstein, 1999). **As well as pathogen defence, silicon may also defend against salt stress, metal toxicity, drought stress, radiation damage, nutrient imbalance, high temperature and freezing** (Ma, 2004). It is thought that silicon has a relatively small role in unstressed plants, though recent research shows it to be involved in amino acid remobilization in unstressed rice (Detmann *et al*., 2013).

Especially in terms of fungal pathogens, accumulation and deposition of silicon in epidermal cell layers may form an effective physical barrier to hyphal penetration in both roots and shoots. Plants which are classified as 'silicon accumulators' exhibit a corresponding rise in silicon content of leaves when the silicon supply increases, conferring increased tolerance to fungal diseases. This has been extensively documented in rice (Datnoff *et al.*, 1997; Kim *et al*., 2002; Dallagnol *et al*., 2013) where resistance is conferred to invasive fungal pathogens such as rice blast. However, silicon is preferentially translocated in the xylem to mature leaves, whereas rice blast, and many other foliar fungal pathogens, preferentially infect young leaves. This means that once rice is sufficiently old enough, silicon ceases to have an effect as resistance is almost complete regardless. However, when high

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concentrations of nitrogen result in rice with increased susceptibility to rice blast, silicon application can effectively eliminate this. Studies in wheat have also found silicon to have an active role in defence against powdery mildew (Belanger *et al*., 2003), and fertilisation with silicon has been shown to decrease brown rust in sugarcane (Camargo *et al*., 2013). 'Silicon non-accumulators', such as tomato, also exhibit increased protection against pathogen invasion (Garibaldi *et al*., 2011). Protection against powdery mildew results in cucumber, a silicon accumulator (Miyake & Takahashi, 1983) and grapevine (Bowen *et al*., 1992). Powdery mildew incidence in plants decreases as silicon content increases, and depends to some extent on the form of nitrogen given to the crop.

As well as forming physical barriers, at infection silicon is also preferentially accumulated at the point of pathogen penetration, and this requires a continual supply of silicon from the roots (Samuels *et al*., 1991). This indicates that after deposition in the leaves the silicon cannot be remobilized. This has been shown to be associated with sites of unsuccessful infection in Barley (Carver *et al*., 1987). Silicon inhibits fungal infection at these sites by increasing the phenolic content, and facilitating their synthesis and mobility (Menzies *et al*., 1991). The role of silicon in plant defence as more than structural is thought to be due to its ability to act as a modulator of plant defence, be involved in signal transduction and its ability to interfere with enzyme cofactors (Fateux, *et al*., 2005). It has also been shown to induce defence related genes (Gaeo *et al*., 2010).

The anti-fungal action of silicon has been illustrated for *Penicillium digitatum* (Liu *et al*., 2010), Sorghum anthracnose (Resende *et al*., 2013), Pythium root rots (Cherif *et al*., 1994), Blast of wheat (Sousa *et al*., 2013), *Didymella bryoniae* and to some extent *Botrytis cinerea* (O'Neill, 1991) in cucumber crops. Tomato powdery mildew, *Oidium neolycopersici*, was found to be reduced, though this was also dependent on the EC of the nutrient solution, and a significant effect was only observed between 3.9-4.0 mS/cm, slightly higher than recommended for tomato crops (Garibaldi *et al.,* 2011). Notably in this experiment, drip or sub-irrigation methods were ineffective, but addition to the nutrient solution was effective. Tomato seedlings grown in sand culture amended with silicon showed reduced severity of Fusarium crown and root rot compared to seedlings grown on sand unamended with silicon. This is thought to be due increased silicon present in plant roots slowing the progress of initial infection after inoculation (Huang *et al*., 2011).

The effective control of gummy stem blight was summarised in AHDB Horticulture project PE 001 and links with silicon supply noted. These observations have been taken further, and altered silicon concentrations have been supplied to a cucumber crop grown in a

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recirculating nutrient system. 10 mg/L were already present in the water supply, and for the high silicon treatment a further 100 mg/L were added. Silicate was depleted when cucumbers were grown and leaves were more rigid and exhibited delayed senescence. Mature leaves acquired the beneficial characteristics of leaves grown in higher light intensity, and though final leaf area was unaffected, increased silicon resulted in greater root fresh and dry weights. Importantly, it was noted that outbreaks of the powdery mildew *Sphaerotheca fuliginea* occurred regularly on the low silicon plants, whilst the high silicon plants remained almost completely free of symptoms (Adatia & Besford, 1986). The growing system of cucumbers is very similar to that of tomatoes, however the same study established that **when tomatoes are grown with supplemental silicon, it is not depleted from the system, but accumulates**. This was also observed by Heine *et al*., 2005 who concluded tomato was a silicon excluder. This has been seen in practice by forward thinking growers, who noted that **addition of silicon to their nutrient solution caused deposition in the irrigation system which caused blockages and was difficult to clean**. This makes the application of additional silicon nutrition difficult in tomato growing, despite its benefits to disease resistance, difficult. Further work on how silicon uptake in tomatoes could be encouraged or deposition in the system prevented would undoubtedly be valuable. The use of slow release silicon slabs as were produced for the cucumber industry in the past could have value, as could silicic acid sprays or the modulation of solution acidity to prevent silicon deposition.

In terms of bacterial disease, silicon nutrition has been found to reduce bacterial speck development (Andrade, 2013). This study involved soil grown crops, and added silicon both by soil incorporation and by foliar sprays. Foliar additions of silicon may be the solution to the problem encountered with irrigation systems in the past. However, as the spray was the most effective treatment it is likely that the spray was acting directly on *Pseudomonas syringae* pv*. tomato*, rather than having an effect on host defences. Silicon amendment has also been found effective against bacterial wilt development (*Ralstonia solanacearum*) (Wang *et al*., 2013a). However, the genotype of plants was also found to strongly affect wilt development, with some genotypes succumbing to wilt totally despite increased silicon supply. Resistant genotypes, however, exhibited increased tolerance with silicon nutrition (Dannon & Wydra, 2004). Silicon application reduced bacterial wilt incidence by 50.7% in the moderately resistant genotype King Kong 2 and by 31.3% in the susceptible genotype L390. Combined application of silicon with biocontrol *Bacillus pumilis* failed to result in any disease reduction (Krabachew & Wydra, 2014). The effect of silicon on the microbial community has been found to counteract the reduction in soil microbe diversity and shift in fungi to bacteria ratio caused by *R. solanacearum* (Wang, L., et al., 2013). In practice, it

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must be ensured multiple disease control options do not have antagonistic effects, and that a beneficial rhizosphere community is encouraged.

Compared to silicon's effects on plants in protecting them from environmental stress, bacterial and fungal infection, relatively little is known of its effects on viral pathogens. Tobacco plants grown in elevated silicon showed a delay in symptoms and lowered disease severity of tobacco ringspot virus (TRSV) but had no effect on tobacco mosaic virus (TMV) (Zellner *et al.*, 2011).

15. Selenium

Selenium accumulation has been shown to protect Indian mustard (*Brassica juncea*) from invertebrate herbivory and fungal infection. Leaves of plants supplied with selenium were less susceptible to both *Alternaria brassicicola* and a *Fusarium* sp. (Hanson *et al*., 2003). Selenium is not commonly added to nutrient solutions in tomato, but in a Mexican study (Companioni *et al.,* 2012) application of sodium selenite reduced damage inflicted by Fusarium wilt. Additionally, total protein content and antioxidant activity increased in both susceptible and resistant cultivars of tomato. Recent work has been carried out by the University of Agriculture in Krakow, looking into biofortication of hydroponically grown lettuce with selenium and iodine additions (Smoleń *et al*., 2014).

16. Nickel and other heavy metals

The protective effects of heavy metals against feeding herbivores and pathogens when hyperaccumulated are well studied (Poschenrieder *et al.,* 2011). It is also thought that this relationship results in trade-offs, where a reduced investment in induced disease resistance accounts for the cost of metal hyperaccumulation (Fones & Preston, 2013). This relationship has also been studied for the viral pathogen, *Turnip mosaic virus* (TuMV). In this case it was shown that a nickel hyperaccumulator became more susceptible to viral disease with increasing nickel supply (Davis *et al*., 2001). A similar non-hyperaccumulator was less susceptible to the virus, but this was largely unaffected by nickel supply. Tomato is a non-hyperaccumulator, and it seems that addition of nickel to nutrient solutions in order to protect against viral infection would be ineffective. The effect of nickel on proliferation of potato virus X in tomato was investigated and it was found that increased nickel increased vegetative plant growth, but also viral multiplication and spread, and nitrogen and free amino acid content (Singh & Singh, 1974). Studies carried out in the 10 km Chernobyl zone have demonstrated a decrease in plant disease resistance due to the high amount of heavy

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metals there, as well as a greater diversity of pathogens and would advise against the use of high concentrations of heavy metals in plant nutrition (Dmitriev *et al*., 2009). Further studies specifically in hydroponic tomato, and using lower concentrations of heavy metals may elucidate useful effects, but as tomato is a non-accumulator this is unlikely.

The heavy metal cadmium is highly toxic at even low concentrations in the environment, but it has been discovered that below the toxicity threshold cadmium triggers defence gene expression in Arabidopsis (Cabot *et al*., 2013). When inoculated with *Botrytis cinerea*, those plants treated with low level Cadmium showed a reduction in growth of Botrytis, thought to be due to the activation of the salicylic acid and jasmonate mediated defence pathways. When cadmium was supplied at non-toxic concentrations to tobacco plants, turnip vein clearing virus symptoms were completely blocked, and it may be more promising than nickel. Cadmium caused the systemic movement of the virus to be inhibited, preventing virions from exiting the vascular tissue (Ghoshroy *et al*., 1998). Species diffier significantly in their tolerance to heavy metal ion toxicity, but it is known glutathione and phenolics play a role in defence against this, potentially allowing cross talk between pathogen and metal ion defence (Llugany *et al*., 2013). There is also evidence that silicon supplied to the root zone can mitigate cadmium toxicity (Liu *et al*., 2013; Lukačová *et al*., 2013).

In hydroponically grown tea, treatment with 0.3 mM (approx. 8 mg/L) aluminium resulted in more than a threefold increase in root biomass, and the activation of antioxidant defence enzymes. Treated plants had a higher proportion of soluble phenolics, but lower phenolic and lignin concentrations in the cell wall (Hajiboland *et al*., 2013). The added defence provided by aluminium treatment would likely be ineffective against many invasive pathogens. Additionally, aluminium is known to have a negative effect on plant growth when pH is low. These effects are not likely to be true for all heavy metals, crops and pathogens. For example, the effect of arsenic on cucumber mosaic virus (CMV) infection in tomatoes was explored, but no synergistic effect was observed with both arsenic and virus limiting plant growth (Miteva *et al*., 2005). Lentil seeds soaked in both 2 and 5 mg/L Cobalt were more resistant to Fusarium wilt and Rhizoctonia when planted out (El-Hersh *et al*., 2011)

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Summary points – Objective 2

- **The nutrient elements known to have the largest potential effect on disease resistance/tolerance are nitrogen, calcium, silicon, manganese, boron and phosphorus as phosphite**
- **Effects can be via nutrition or because substances are directly inhibitive to pathogens**
- **Phosphite is directly inhibitory to some pathogens, as are copper and sulphur compounds**
- **A high nitrogen supply is known to increase the severity of disease by obligate pathogens, but has the opposite effect on facultative pathogens**
- **Viral diseases are also likely to be favoured by high nitrogen**
- **Boron and cadmium may have potential to limit viral spread, though this has not been effectively illustrated in a tomato crop**
- **Calcium has the potential to boost host defences against pathogens**
- **Some nutrients, such as potassium, only have positive effects on disease when the plants are deficient, and giving a supra-optimal supply will have no beneficial effects**
- **Ammonium to nitrate ratio can effect disease severity**
- **The carbon to nitrogen ratio of plant tissue may also affect some pathogens**
- **The specific host and pathogen isolate also effects response of disease severity to nutrition**
- **Type of fertiliser may also affect disease severity, e.g. organic or chemical**
- **Nutrients such as zinc, copper and iron have the potential to improve efficacy of certain biocontrol agents**
- **EC and pH exert differing effects on different pathogens, but a high EC or high salinities are generally considered inhibitory**
- **As well as pathogen defence, silicon may also defend against salt stress, metal toxicity, drought stress, radiation damage, nutrient imbalance, high temperature and freezing**
- **When tomatoes are grown with supplemental silicon, it is not depleted from the system, but accumulates. Addition to irrigation systems is likely to cause blockages and make them difficult to clean**
- **Summary points, emboldened in text are repeated in more detail in Appendix 2**

Objective 3 – Potential nutrient management strategies for improved disease control

The mechanisms by which nutrients impact on disease (Table 8) and the most promising potential nutrient treatment for disease control (Table 9) are summarised below.

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Table 8. The roles and mechanisms by which essential and beneficial plant nutrients may exert a positive impact on disease infection, incidence and severity, if known

Nutrient	**Mechanism that may decrease disease**	**Role in defence**
Nitrogen	May 'outgrow' facultative disease and aid production of defence metabolites. May encourage obligate disease by diluting silicon in the plant, or decreasing production of phytoalexins Can depend on whether ammonium or nitrate nitrogen (pathogens differing nutritional requirements or a response to changing pH)	Facilitates plant growth
Potassium	Deficient plants are less able to defend themselves and sufficient supply may improve shelf life	Osmotic
Phosphorus	Phosphite directly inhibitive to pathogens phosphate facilitates growth	Metabolic and directly inhibitory to some pathogens
Calcium	Key to some forms of cultivar resistance and production of peroxides and defence proteins	Structural and metabolic
Magnesium	Difficult to elucidate fully, very complex. May interfere with Ca uptake, can complement or antagonize other minerals effects.	Structural and metabolic
Sulphur	Required for specific defence compounds e.g. phytoalexins, glutathione, but is unwanted in high concentrations in nutrient solution May be key in resistance to vascular disease	Structural and metabolic
Boron	Phenol metabolism, lignin biosynthesis - pH dependent	Structural and metabolic
Iron	Necessary for many plant pathogens but makes up numerous defensive compounds. NFT and winter crops require more.	Metabolic
Manganese	Involved in HPO production, lignin biosynthesis, phenol metabolism and production of peroxidases.	Metabolic
Zinc	Role in generation of oxygen radicals, hydrogen peroxide. Encourages some microorganisms	Metabolic
Copper	Phenol metabolism	Metabolic
Molybdenum	Metabolic - stress response	Structural and metabolic
Sodium	Salinity stress, climbing EC may damage pathogens directly, or prime plant defences	Osmotic
Chlorine	May illicit a stress response, primes for further attack	Metabolic and directly inhibitory to pathogens
Silicon	Laid down as a physical barrier but also has roles in metabolism, and in the plant stress response	Structural and metabolic
Selenium	Defence hypothesis for accumulating plants - unattractive to herbivory etc.	Metabolic and directly inhibitory to some pathogens
Cadmium	Triggers defence	Metabolic
Cobalt	Triggers defence	Metabolic

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Table 9. Promising nutrient effects on disease, exemplified by specific references, with quantitative data where possible, across crops

Nutrient	Crop	Concentrations of nutrition recorded
N	Sweet basil	Standard level of approx. 100 mg/L, increasing reduced disease (Yermiyahu *et al.*, 2006)
	Tomato	Susceptibility to Botrytis differed over a range of 30 - 2790 mg/L, Severity decreased up to 1860 mg/L (Abro *et al*., 2013)
	Tomato	Leaves with C:N ratio of 21 more susceptible to Botrytis than leaves with C:N ratio of 11 (Hoffland et al., 1999)
	Tobacco	10 - 2000 mg/L N increased conc. and severity of TMV. (Spencer, 1939)
	Tomato	Replacing NH_4 with urea decreased mortality due to Pythium root rot by 22%. Mortality was lowest with a NH_4:NO_3 ratio of 20:80 than of 80:20
K	Corn	Anthracnose lowest at 1000 mg/L K (Carvalho *et al.*, 2013)
	Cucumber	Botrytis reduced by 33% when N:P:K was 7:3:7 (Elad *et al*., 1993)
	Banana	Potassium supplied at 78-3913 mg/L, increasing K reduced Xanthomonas wilt (Atim *et al*., 2013)
P	Pepper	A balance of phosphate (94.97 mg/L) and phosphite (42.28 mg/L) may be an efficient way to both limit disease, and provide phosphorus nutrition as has been shown in pepper crops infected with *P. capsici* (Forster *et al.,* 1998).
	Strawberry	Reduced *C. gloeosporioides* severity with increasing P, 0- 92.9 mg/L (Nam *et al*., 2006)
Ca	Tomato	Fertilisation with Ca resulted in 30% more Ca in the leaves and reduced grey mould by 35-50% (Elad et al., 1993)
	Banana	Ca supplied at 12-603 mg/L, increasing Ca reduced Xanthomonas wilt (Atim *et al*., 2013)
	Sweet basil	53 mg/L in standard, increasing reduced disease (Yermiyahu *et al.*, 2006)
	Potato	Increasing Ca 3-343 mg/L decreased Phytophthora pink spot (Benson *et al*., 2009)
	Tomato	Increasing Ca 20.4-1,020 mg/L reduced severity of R. solanacearum (Jiang *et al*., 2013)
Mg	Rice	ranging from approximately 6 mg/L (0.25 mM) to approximately 97 mg/L (4mM)
S	Wheat	*Mycosphaerella graminicola* and *Phaeosphaeria nodorum* infected less at higher sulphate (approx. 48 mg/L or 240 mg/L) (Chandramohan & Shaw, 2013)
B	Tobacco	0 to 0.5 mg/L, initially boron deficient plants contained lower concs. of TMV
	Potato	Foliar sprays of Boron at 700 mg/L with or without fungus reduced *P.infestans* infection (Frenkel *et al*., 2010)
	OSR	0 - 32 kg/Ha applied, 4kg/ha supressed *Plasmodiophora brassicae* with no phytotox (Deora *et al*., 2011)
Fe	Tomato	Iron deficient (basic FeEDTA, 20 mg/L, plus iron depleting conditions) tomato was less susceptible to *V. dahliae* than iron replete (basic plus 30 mg/L) (Macur *et al*., 1991)
	Tobacco	Lactoferin and esterified lactoferin as a foliar spray inhibited TMV infection and multiplication over 0-100 mg/L (Wang *et al*., 2013b)

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Mn	Clusterbean Rice	Applying at 5 and 10 mg/L (converted from ppm) resulted in disease reduction (Wadwha *et al*., 2013) Applied with Si, Mn decreased blast with increasing concentrations. From approx. 27.5 mg/L to 550 mg/L (Cacique *et al*., 2012)
Zn	Tomato Sweet pepper	Following a one-time amendment of zinc (33 mg/L) disease caused by *R. solani* was reduced by 25% in the presence of a biocontrol (Siddiqui *et al*., 2012) 0, 5 and 10 mg/Kg applied to soil grown peppers, reduced *Phytophthora capsici* infection (Kucukyumuk *et al*., 2013)
Cu	Clusterbean	Applying at 5 and 10 mg/L (converted from ppm) resulted in reduction of Rhizoctonia root rot (Wadwha *et al.,* 2013) Applied at 33 mg/L reduced Fusarium crown and root rot by improving biocontrol (Duffy & Defago, 1997)
Mb	Apple Lentil	Ammonium molybdate applied at 15 mM (approx. 17460 mg/L) was effective in reducting *Rhizopus* and *Penicillium* spp. and *B. cinerea* in post-harvest apple (Nunes *et al*., 2001) Seeds soaked in 2 mg/L molybdenum were more resistant to Fusarium wilt and Rhizoctonia (El-Hersh *et al*., 2011)
Na	Tomato	NaCl up to 1740 mg/L reduced incidence and severity of *Oidium neolycopersici* (Garibaldi *et al*., 2011)
Cl	Tomato	Normal transplants were grown at 20 mg/L chlorinated solution, a rate at which *Pythium* and *Phytophthora* spp. would be eliminated (Saha *et al*., 2011)
Si	Rice Tomato Tomato Cucumber	Applied with Mn, Si decreased blast when applied at approx. 56 mg/L compared with no Si application (Cacique *et al*., 2012) Bacterial speck was reduced with a silicon spray at 2 ml/L (Andrade *et al*., 2013) *R. solanacearum* reduced with treatment with Si at approx. 56 mg/L (Wang *et al*., 2013a) Silicon was applied at 10 or 100 mg/L and induced resistance to powdery mildew (Adatia *et al*., 1986)
Se	Mustard	Leaves with 0.1% Se dry weight were more susceptible to fungal infection (Hanson *et al*., 2003)
Cd	Arabidopsis	Plants supplied with increasing Cd (0- approx. 1.12 mg/L) were less susceptible to *B.cinerea* at the highest concentration (Cabot *et al*., 2013)
Co	Lentil	Seeds soaked in 2 mg/L Cobalt were more resistant to Fusarium wilt and Rhizoctonia (El-Hersh *et al*., 2011)

Table 9 focusses on the clearest, positive results gained through research discovered in the review, however there have also been studies where no effects or negative effects were found. Those studies on crops related to, or grown similarly to tomato, or on diseases that also infect tomato, or have close relatives that do, may provide guidance for what may be effective. However, the effects of nutrients seem to be highly crop and pathogen specific, so results in other crops may not directly translate. As such, a summary of the effects of altering nutrient concentrations delivered to the root environment specifically in tomato is given below (Table 10 and 11). Based on the information found, pathogen lifestyle appears to contribute most variability towards the effect of each nutrient on disease incidence and

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severity and so three tables have been produced which split pathogens according to these characteristics. Tables 10, 11 and 12 show the potential for disease management across the necrotrophs, hemibiotrophs, and biotrophs respectively (Oliver & Ipcho, 2004). Table 13 also illustrates the effects plant and rhizosphere nutrition have been found to have on biocontrols and their efficacy. It must be noted that in many cases the study at hand has been simplified in order to state the result as simply an increase or a decrease in disease. It can also be seen that, despite making an obvious difference to the effect of a nutrient, pathogens with the same lifestyle may still show variation in their responses to the same nutrient. This could be because there is no standardised way to test this, and each experiment differed considerably in its methodology. It also remains to be seen if these nutrient regimes would work in practice, or if the changes suggested by the review in order to mitigate disease symptoms would be compatible with each other and with current systems.

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Table 10. Summarised effects of plant nutrition on necrotrophic diseases found in this literature review

Pathogen type	Pathogen	Nutrient (increased)	Effect on disease	Comment	Reference
Fungi Foliar	*Alternaria tomatophila (*prev. *Alternaria solani)*	Nitrogen (Ammonium)	Decrease	Urea had affect in vitro on spore germination + mycelial growth, not in field	Blachinski *et al*., 1996
		Nitrogen	No effect	In either rainy or winter season	Sharma & Kumar, 1998
		Potassium	Decrease	Effect in vitro, on detached leaves but not in field	Blachinski *et al*., 1996
		Potassium muriate	Decrease	In field using mureate of potash. Yield was also increased	Ehsan Akhtar *et al*., 2010
	Alternaria alternata	Potassium Sodium	Decrease Decrease	As chlorides, in combination with cassia oil in vitro and on cherry toms	Feng & Zheng, 2006
	Botrytis cinerea	Calcium	Decrease	In perlite (70% reduction) + soil (80% reduction), disease severity + ghost spotting decreased. In vitro some compounds ceased to be inhibitive at rates above 0.1mM	Elad & Volpin, 1993
		Nitrogen	Decrease	Sporulation and 2° inoculum pathogenicity (highest for spores produced on v. high or v. low N plant)	Abro *et al*., 2013
		Nitrogen	Decrease	6 isolates, overall delayed disease development and reduced severity in vitro + on plant. Isolates different on plant.	Lecompte *et al*., 2010
		Nitrogen	Decrease	Hydroponic. Due to altered C:N ratio, high ratio = more susceptible to 1° lesions.	Hoffland *et al*., 1999
	Pseudocercospora fuligena	Manganese	Decrease	In Thai nethouse, applied supraoptimal but below toxic supply to substrate.	Heine *et al*., 2011
Root	*Verticillium dahliae*	Sulphur	Decrease	Reduction in infected vascular cells, reduced fungal spread with supraoptimal supply but limited impact on plant growth.	Bollig *et a*l., 2013
		Sulphur	Decrease	Inhibitory to pathogens in vitro and present in xylem walls, but no *in planta* study or link.	Cooper & Williams 2013
		Iron	Increase	Hydroponic. Fe deficiency made more susceptible.	Macur *et al*., 1991
	Macrophomina phaseolina	Zinc Zinc	Decrease Decrease	Improved biocontrol in vitro and in soil grown GH crop Also improved plant growth, but without biocontrol resulted in toxicity.	Shaukat & Siddiqui, 2003 Siddiqui *et al*, 2002

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	Rhizoctonia solani	Zinc	Decrease	Improved biocontrol (fluorescent pseudomonad).	Siddiqui *et al,* 2002
	Colletotrichum gloeosporioides (prev. *phomoides*)	Nitrogen	Increase	Disease stimulated.	Williams, 1965
	Pyrenochaeta lycopersici (brown and corky root rot)	Ammonium nitrogen Calcium	Increase Decrease	GH experiments on organic tomato.	Hasna *et al*., 2009
		Ammonium nitrogen pH	Decrease Increase	In vitro and in GH soil, organic tomato. Highest disease with balanced nitrogen, lowest with ammonium dominated but no treatment achieved satisfactory control.	Knopp & Martensson, 2010
Stem	*Fusarium oxysporum* f. sp. *lycopersici* (Fol)	Ammonium Nitrogen	Decrease	Hydroponic. Improved biocontrol (T34). Leaf Fe + N content high.	Borrero *et al.,* 2012
		pH	Increase	Soil grown with suppressive biological composts.	Borrero *et al*., 2004
		Selenium	Decrease	Sodium selenite on tomato plantlets.	Companioni *et al*., 2012
		Nitrate Nitrogen	No effect	Hydroponic.	Hoffland *et al*., 2000
		Iron	Decrease	Hydroponic. Improved biocontrol (T34) which competes for Fe. Reduction in Fol at 10 uM above which T34 siderophore inhibited.	Segarra *et al*., 2010
	Fusarium oxysporum f. sp. *radicis lycopersici* (Forl)	Zinc Copper	Decrease Decrease	Hydroponic rockwool culture. Improved biocontrol (fluorescent pseudomonad), 1 time amendment reduced by 25%. Similar effect in vitro.	Duffy & Defago, 1997
		Ammonium Nitrogen Sodium Iron Manganese Molybdenum Zinc Nitrate Nitrogen Copper	Increase Increase Increase Increase Increase Increase Decrease Decrease	Hydroponic rockwool using compound fertilisers. Fertilisers used included phosphites, sulphates and chlorides.	Duffy & Defago, 1999

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		Calcium	Decrease		
		Silicon	Decrease	Seedlings into Hoaglands nutrient ±Si. Reduced severity on stem 4 weeks after inoculation.	Huang *et al*., 2011
	Fusarium solani	Zinc	Decrease	Improved biocontrol (fluorescent pseudomonad).	Siddiqui *et al*, 2002
Oomycete Root	*Phytophthora* sp.	Sulphur	No effect	Inhibitory to other pathogens in vitro.	Cooper & Williams, 2004
	Phytophthora sp.	Sodium chloride	Increase	Short period of very high salinity stress.	DiLeo *et al.,* 2010
	Phytophthora nicotianae	EC	Increase	Hydroponic, increased all nutrients.	Grote & Claussen, 2001
	Phytophthora parasitica	CO_2	Decrease	Plants showed degree of tolerance in elevated (700 ppm) but pathogenesis not significantly affected.	Jwa & Walling, 2001
Bacteria Foliar	*Pseudomonas syringae* pv. *tomato* (Bacterial speck)	Silicon	Decrease	In soil ±calcium silicate, ±silica spray (x 3). Lesions per plant decreased with sprays. Negative effect on Ps in vitro so thought to be directly inhibitory.	Andrade *et al.,* 2013
		Nitrate nitrogen	Increase	More susceptible.	Hoffland *et al*., 2000
Bacteria Stem	*Clavibacter michiganensis* (Bacterial canker)	Calcium	Decrease	Resistant + susceptible cv. Rapid disease development if plants given no Ca. 100 ppm or higher reduced severity. Resistance dependent on sufficient Ca.	Berry *et al*., 1988
		Magnesium	Decrease	Lower level of disease when % Mg in tissue was higher.	Berry *et al*., 1988
		pH	Increase	Survival and spread in solution impeded at lower pH. More plants developed canker at pH 6.5 than pH 5.	Huang *et al.,* 2001
	Pith necrosis (*Pseudomonas* sp.)	Calcium	Decrease	Three potassium (100 ppm, 200 ppm & 400 ppm) and two calcium (60 ppm and 120 ppm) concentrations. Four different bacteria (*P. corrugata*, *P. cichorii*, *P. viridiflava* and *E. carotovora* subsp. *carotovora*). Highest concentrations reduced disease and led to highest yields.	Ustun *et al.,* 2009
		Potassium	Decrease		
	Ralstonia solanacearum (Bacterial wilt)	Silicon	Decrease	Reduced incidence but not consistently, just slowed disease development.	Dannon & Wydra, 2004
		Silicon	Decrease	Si stronger elicitor than biocontrol (*B. pumilis*), had antagonistic effects when applied together.	Kurbachew & Wydra, 2014
		Silicon	Decrease	Pot experiment. Pathogen increased Fungi:bacteria ratio of soil, Si reduced it.	Wang, L., *et al*., 2013
		Calcium	No effect	A cv.'s Ca use efficiency can dictate resistance, Ca	Hacisalihoglu *et*

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				inefficient cv. was more resistant when supplied with sufficient calcium.	*al*., 2010
		Calcium	Decrease	Disease severity reduced, plant growth increased.	Jiang *et al*., 2013
	Referred to here as *Pseudomonas solanacearum*	Calcium	Decrease	Seedlings of 3 cv.s with differing resistance. In moderately and highly resistant cv.'s Ca decreased disease.	Yamazaki & Hoshina, 1995

Table 11. Summarised effects of plant nutrition on hemibiotrophic diseases found in this literature review

Pathogen type	Pathogen	Nutrient (increased)	Effect on disease	Comment	Reference
Fungi Foliar	*Passalora fulva* (Tomato leaf mould)	Calcium	Decrease	In vitro, no link with disease severity. Tomato cells produced calcium dependent defence protein when challenged with *P. fulva.*	Chico et al., 2012
		Nitrogen	Increase	Expression of some genes (including Avr9) and subsequent transcription of effector proteins necessary for pathogenesis are triggered by nitrogen starvation in the host.	Thomma *et al.,* 2006
Oomycete Foliar	*Phytopthora infestans* (Late blight)	Boron	Decrease	In GH tomato both leaves treated with Boron and untreated distant leaves showed reduced severity – systemic reaction?	Frenkel et al., 2010
		Organic fertilisers	Decrease	Organic tomato, soil grown. BioILSA + Biofeed Basis better than chemical fertilisers.	Sharma et al., 2012
		Organic fertilisers	Decrease	Organic tomato, soil grown. More disease in chemically fertilised plots, higher nitrate in soil and more nitrogenous compounds in leaves.	Wang et al., 2000

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Table 12. Summarised effects of plant nutrition on biotrophic diseases found in this literature review

Pathogen type	**Pathogen**	**Nutrient (increased)**	**Effect on disease**	**Comment**	**Reference**
Fungi Foliar	*Oidium neolycopersici* (Powdery mildew)	Silicon EC	Decrease at moderate EC Decrease	Moderate EC = 3.9-4.0 mS , applicable to UK growing. Used NaCl.	Garibaldi et al., 2011
		Nitrate nitrogen	Increase	Hydroponic.	Hoffland *et al*., 2000
Bacterial Root	*Agrobacterium tumefaciens* (crown gall)	Nitrogen Phosphorus Calcium	Decrease Decrease Decrease	Nutrients excluded totally from solution. Nitrogen had biggest effect on tumour size.	Swain & Rier Jr, 1968
Viral Foliar	Potato virus X	Nickel	Increase	Also increased plant growth at low concentrations.	Singh & Singh, 1974
	TYLCV	CO_2	Decrease	Open top chambers in field for 2 years.Increased tomato C:N ratio, interaction with JA and SA pathways.	Huang *et al*., 2012
	CMV	Arsenic	Increase	Young tomato plants, both virus and As stressed them. Though 100 mg/Kg inhibited viral infection it was also toxic to the plant.	Miteva *et al.,* 2005
	TSWV	Nitrogen	Increase	Field grown, more disease in N fertilised plots.	Stavisky *et al*., 2002
	ToMV	Calcium	Decrease	x 3 foliar sprays, decreased viral concs.	Eraslan *et al*., 2007

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Table 13. Summarised effects of plant nutrition on biocontrols found in this literature review

Type	Biocontrol	Nutrient	Efficacy	Comment	Reference
Fungal Root	T34	Ammonia nitrogen	Increase	Increased activity against Fol. Fol severity was reduced at high leaf N concs.	Borrero et al., 2012
	T34	Iron	Increase	Competes with Fol for Fe	Segarra et al., 2010
Bacterial Root	*P. fluorescens*	Zinc Copper	Increase	Copper in vitro and Zinc both *in vitro* and *in planta*, helped inhibition of Forl.	Duffy and Defago, 1997
	P. fluorescens *P. aueruginosa*	Zinc Copper Zinc	Increase Increase	Aids inhibition of *M. phaseolina.*	Shaukat & Siddiqui, 2003
	Bacillus pumilis	Silicon	Decrease	Inhibition of *R. solanacearum* by biocontrol reduced by Si.	Kurbachew & Wydra, 2014

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Knowledge gaps identified

The table below (Table 14) illustrates the areas where no or limited information has been found, specifically for tomato. However, further study in all areas of nutrient management for disease control would be beneficial. As the results of studies vary according to the nutrient in question, the crop, growing system etc. it is thought that the most valuable research for this review's commercial objectives to be met would be performed on hydroponic tomato crops. Research on other crops is useful as a broad guide with which to focus research in tomato, but much of the methodology and empirical data cannot be directly translated. Additionally, studies in vitro may fail to translate to the field (as was the case in Blachinski *et al*., 1996) and this requires further investigation. With improvements in molecular techniques, plant defence responses can be illustrated better than before, however, causal links between production of phytoalexins or defence proteins at infection sites and a reduction in disease severity are sometimes lacking, and it is merely assumed that this would be the case. Similarly, effects on yield are often unknown, despite being highly important. The limitations of the research uncovered by this review are discussed further in the next sections of this report.

Table 14. Summary of knowledge gaps identified by the review, illustrated by shading

Nutrient		**Increase (↑) or decrease (↓) in disease**	
		Obligate	**Facultative**
Nitrogen	Ammonium	↓	↓
	Nitrate	↑	↓
Potassium			↓
Phosphorus			
Zinc			↓
Calcium		↓	↓
Manganese			↓
Magnesium			
Iron			
Silicon		↓	↓
Cadmium			
Nickel		↑	
Molybdenum			
Boron		↓	
EC		↓	
CO_2		↓	↓
Sodium			↓
Sulphur			↓

*N.B. when results conflicted, the most common result was included. It should also be noted that the concentrations used vary between studies, and variations in efficacy and phytotoxicity could be due to this.

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Costs of implementation

Three simple cost-benefit analyses have been performed to illustrate the potential savings that could be made should effective disease management be performed. As the gap analysis above identified, data is limited for the majority of diseases, and where available may not have been performed in a manner relatable to current commercial practice. Additionally, it is thought that focus on implementation should be on those diseases identified by growers as problematic in UK tomato growing. This excludes the majority of root diseases, especially those associated with soil grown crops, though these still have implications for organic growers.

As such, and with use of the questionnaire sent to growers on what diseases they considered key, the three examples that have been chosen are *Botrytis cinerea, Oidium* powdery mildew and viruses such as PepMV and ToMV. It should be noted that as data is somewhat limited at this point, a number of assumptions have been made. Yields have not been reported in the majority of studies, and so exact effects are largely unknown. Yields have been averaged across all varieties and a reduction in disease severity has been interpreted as an increase in yield of comparable/probable magnitude as informed by research and grower experience. On review of over 2000 references it was estimated that potassium nutrition decreased the incidence of fungal diseases by 70% and bacteria by 69%. This translated to yield increases in infected plants of 42% and 57% respectively (Perrenoud, 1990) so it is known that altered nutrition has the potential to both decrease disease and increase yield. However, achieving this in practice may prove difficult and variable. Aspects of cropping that would not be likely to change in light of novel nutrient strategies have not had their costs considered in this review. Additionally, the effects of resistant varieties have been neglected from these costings as commonly grown varieties differ in their resistances to a variety of diseases. Notably, costs will also differ between long season and all year round crops.

Standard spray and fertiliser programmes have been used to discern costs (as advised by grower consultants). Yield losses have been estimated by combination of research data, past experience of ADAS and other advisers and growers. It is noted that the products and amounts used by growers vary, much dependent on the nutrient system they have in place. The effects of staff time and labour have also been considered, including time saved should fungicide sprays be avoided, and extra time spent sampling and interpreting the nutrient solution. This may also require additional outside consultation.

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Application of this research data is likely to be more costly in the beginning while it is fine-tuned, and as further research is done, and technology devised costs will reduce. A good example of this is the Netherlands, where nutrient and water management is the subject of ongoing research, and where savings in water and nutrients are notably higher than in the UK. Overall, it is envisioned that reliable reductions in disease severity and the associated increases in yield could be achieved by intensive nutrient management in this way, without dependence on fungicide controls. These are costly, use high volumes of water, and are increasingly limited by the EU. Chemical pesticides are also unattractive to the consumer, so it is envisioned that as well as saving direct costs, produce will be more attractive if grown under an IDM strategy. Though unlikely to completely replace chemical control methods, especially in these early stages, nutrient management certainly has the potential to contribute to keeping disease down to a tolerable level.

The cost of an average nutrient regime, in terms of fertiliser and effective nutrient management per season has been summarised below (Table 15). This table also illustrates the direct benefits to the grower of a recirculation system.

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Table 15. Estimated total nutrient use in a long season hydroponic tomato crop (including recirculation: saving 40% water and nutrients). As supplied by May Barn Consultancy Ltd.

Element	Optimum Conc. (mg/L)	Use per Season (mg/m^2)*	Use per Season (kg/m^2)	Use per season (Kg/ha)	
				RTW	Recirc.
	PFC targets	X 850 litres per m^2	X 0.000001	X10,000	X 0.6
NO_3-N	250	212,500	0.2125	2,125	1,275
P	30-40	25,500-34,000	0.0255-0.034	255-340	153-204
K	500	425,000	0.425	4,250	2,550
Ca	250	212,500	0.2125	2,125	1,275
Mg	80	68,000	0.068	680	408
SO4-S	100	85,000	0.085	850	510
Na	200	170,000	0.17	1,700	1,020
Cl	200	170,000	0.17	1,700	1,020
Fe	3.0-4.0	2,550-3,400	0.00255-0.0034	25.50-34.00	15.3-20.4
Mn	0.5-0.6	425-510	0.000425-0.00051	4.25-5.10	2.55-3.06
B	0.4-0.6	340-510	0.00034-0.00051	3.40-5.10	2.04-3.06
Zn	1.0	850	0.00085	8.50	5.1
Cu	0.1	85	0.000085	0.85	0.51
Mo	0.05	42.5	0.0000425	0.425	0.255

*Average UK Tomato Working Party Data

Notes on costings

- If we assume that the complexity of crop nutrition is set to increase, frequency of analysis must increase for some growers.
- Most growers currently test their solution fortnightly, this equates to analysis costs of approximately £20 per sample. Additional costs of taking and sending the samples could increase this.
- Costs in time of making up the nutrient solution every 1-2 days would likely not increase or decrease, unless new technology were introduced.
- The hygiene measures utilised in UK tomato growing to guard against introduction of diseases would likely remain in place, regardless of the capabilities of nutrition to regulate disease severity.

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- Notably, costs are considerably lowered by recirculation by approximately 40%, though fertiliser costs listed below are for run to waste systems.
- Increasing plant uptake of certain nutrients may also serve the same purpose as supplying additional nutrition, and would likely cost considerably less.

Strategy 1 – *Botrytis cinerea*

- Currently, a spray regime is generally implemented to prevent Botrytis epidemics, and a cost of **£200** per hectare has been assumed in application costs per spray
- A typical spray programme has been considered as including sprays of Switch, Serenade, fenhexamid, Rovral and Scala.
- Costs of PPPs and cost of application for an average regime equate to approx. **£2,500**.
- Scaniavital Silica paste is available for wound dressing, and utilises the ability of silicon to effectively form physical barriers. This costs **£295** for 10 litres.

From the review

- Fertilisation with calcium nitrate reduced severity of Botrytis, and ghost spotting on tomato grown in perlite at approx. 164 mg/L and 492 mg/L.
- The lower level is generally supplied in the UK, and increasing calcium concentrations in hydroponics to around 500 mg/L, and the associated increase in nitrogen, would also require much higher concentrations of potassium in solution (approx. 1000 mg/L). This could have negative knock on effects, for example high EC concentrations and a different main element balance in solution.
- Calcium nitrate is approximately **£0.38** per kg, and doubling the amount used would mean an increase in fertiliser costs of approx. **£1615** per hectare per season, not accounting for increased potassium or other related alterations.
- Leaves treated with calcium were also observed to produce less ethylene than untreated leaves, which could have other potential benefits.
- This effect was also observed in tomatoes grown in soil with $Ca(H_2PO_4)_2$ and $CaSO_4$ at 1 and 3 g/kg soil respectively, applied once reducing Botrytis by 80% (Elad & Volpin, 1993).
- At these concentrations in soil, it is assumed that Ca would be sufficiently available in UK hydroponic growing to emulate these concentrations under normal circumstances. This study illustrates that different forms of calcium fertiliser were more or less effective in different situations, and this could be further explored.

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- Grey mould of pepper was reduced by 50-60% by adding calcium, as sulphate or with calcium dihydrogen phosphate, but pepper yield was not increased. (Elad *et al*., 1993).
- It may be possible to reduce sprays, especially toward the end of the season (earlier sprays are more important for Botrytis control). If 1 spray was dropped from the end of a programme, a saving of **£250** per hectare per season could be made, but accounting for additional fertiliser costs, larger savings than this would be required to be worthwhile.
- Plant nutrition can not only be improved by increasing nutrient concentrations, but also by improving nutrient uptake. By improving control of glasshouse humidity, which will also contribute towards effective management of Botrytis, boron and calcium nutrition may be improved.

Strategy 2 – *Oidium lycopersici*

- A cost of **£200** per hectare has been assumed for application.
- 4 sprays of Thiovit (sulphur to directly inhibit the pathogen) over season to control powdery mildew would give a product cost of approximately **£80**, and increases in yield may be associated.

From the review

- Silicon was found to reduce powdery mildew by approx. 20-40% on 2 cultivars of tomato grown in hydroponic systems when added at 100 mg/L, though its efficacy was linked with the EC of solution (Garibaldi *et al*., 2011).
- As discussed at various points in this report, adding silicon to the nutrient solution has a history of causing problems with the irrigation system, though much mains water already contains silicon at around 10 mg/L, though this was not sufficient to induce resistance to powdery mildew in cucumber (Adatia & Besford, 1986).
- The crops grown by Garibaldi *et al*., 2011 were grown in solution for over 90 days and no problems were reported, with treatment estimated to cost 0.09 Euro **(£0.08**) per 100 L of nutrient solution. On average a grower uses 850 litres per m^2/per season, equating to an increased cost per season of approximately **£0.68** per m^2.
- Silicon (silicic acid) was sprayed at 2 ml/L by Andrade *et al*., 2013 and a reduction in bacterial speck (*Pseudomonas syringae*) observed, so spraying could be a viable option if the product cost is reasonable, though the associated costs of spraying would be incurred.

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Strategy 3 – Viral disease

Plant protection products are ineffective against viral diseases and so currently costs of control generally focus on hygiene measures and strategic management once infection has occurred. Generally, removal of infected plants is the only control option, and in terms of profitability it is most often less practical than effectively managing infected plants. Cost of hygiene measures may be justified as an extra protection regardless of any added benefit nutrition can provide. Here, information on many different viruses have been included, as information was relatively limited, and especially lacking was nutrition's experimental effects on Pepino mosaic virus.

- Pepino as a new crop infected with *Tomato mosaic virus* has been affected severely, affecting total and marketable yield, fruit weight, length-width ratio and soluble solids content. It was recorded to depress total yield by 43.1% in 'Sweet Long' but had no effect in 'Sweet Round'. Marketable yield was depressed by 94% in Sweet Long and 100% in Sweet Round, showing fruit quality is also affected by this virus (Pérez-Benlloch *et al*., 2001).
- If no control measures are in place e.g. resistant varieties, effects on yield can also be sizeable in tomato, as high as 25% (Eraslan *et al*., 2007).
- Pepino mosaic infected tomatoes had overall yield loss of 4% (Isolate 1066) with class 1 fruit yield reduced by 14% (Peters *et al*., 2011). Losses have been recorded as high as 40%. Though less topical currently, the potential for ToMV to exert significant yield effects is what influenced its inclusion in this simple cost-benefit analysis.
- Once infected, the crop is usually managed to mask symptoms and outgrow the disease, and the cost of this has been assumed to match any additional nutrient management strategy that may be implemented, resulting in no overall change.

From the review

- 3 sprays of 0.3% Ca have been shown to reduce ToMV concentrations in tissues, with minimal effects on magnesium, nitrogen or potassium concentrations in plants. Plants remained infected, but there could be a potential decrease in yield loss, and some forms of calcium decreased fresh and dry weights (Eraslan *et al*., 2007).
- A spray of 0.3% Ca would likely cost approximately **£1.20** per hectare, with an application cost of **£200**. There may also be potential to tank mix calcium products with other sprays to save on application costs.

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- The virus infected plants treated with water were found to have greater fresh weights than those treated with calcium. Though no correlation with yield was made, if we assume that data on fresh weight can be extended to yield, no saving would be made.
- Improving calcium uptake from the rootzone by management of glasshouse conditions may be more cost effective than increasing concentrations in the nutrient solution or applying sprays.
- Chant & Gbaja, 1985 found the presence or absence of Fol to be a greater determinant of ToMV viral replication than plant nutrition.
- Silicon was found to have no effect on TMV, and concluded nutritional effects to be very virus specific, as an effect was observed on Cotton Leaf Curl Virus (Zellner *et al*., 2011). The cost of silicon fertiliser is assumed to be as above.

Future potential scenarios for viral disease

- Lactoferrin, when sprayed on plants at 25 – 100 mg/L, significantly inhibited viral infection, and had both protective and curative action (Wang et al., 2013b). However, this study was performed on detached leaves, the cost of lactoferrin is unknown and most other research in this area focuses on transgenic plants that can produce their own lactoferrin.
- In plants infected with Cucumber Mosaic Virus, using N fixing bacteria increased the yield by approx. 40% where mild strain CMV had reduced it by approx. 20% (Dashti *et al*., 2007) giving an overall increase of 20% and also possibly contributing to fruit quality.
- Plant Growth Promoting Rhizobacteria (PGPRs) that play a large role in fixing N are not yet commercially available, but Serenade (*Bacillus subtilis*) is roughly **£150** per hectare (10 L).
- This could represent a viable option to boost yields should plants become infected by viral pathogens, without altering the nutrient solution though it should be noted this occurred with use of a protective strain of CMV, not an aggressive one, and that amount of virus was not decreased.
- However, AHDB Horticulture Project PC 281a could not detect PGPRs added via irrigation lines on the tomato microarray developed for the project.

Overall, a reduction in nutrition from the plants optimum of such key mineral nutrients is likely to leave the crop open to invasion by other diseases or open to nutrient deficiency. In

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the case of viruses, though increased nutrition generally leads to increased viral replication and spread, it also allows the plant to out-grow disease and masks symptoms. With current knowledge, and the reductions observed, this is very much still the sensible option for growers. A reduction in yield and quality could occur as a result of a nutrient regime deviating from the plant optimum that would not be covered by reductions in fertiliser or spraying costs or labour through plant/debris removal. Where improvements in disease severity due to changes in nutrient regime have been illustrated, the absolute effects on yield are largely unknown as studies have rarely been taken to harvest or performed on a full size tomato crop for the length of a season. Additionally, fruit quality or problems due to unbalanced nutrient regimes have not been considered.

For the full potential of nutrient management to be realised, the information summarised in this review must be used to inform development of new, balanced nutrient regimes so that yields do not suffer. Until the effects of fine tuning nutrient regimes to negate the effects of disease have been fully elucidated for commercial crops, it is unlikely that implementation will convey significant savings. It needs to be established that, where identified to be beneficial, changes are worth their increased cost in terms of yield increases, or decreases in other control methods. Potential for these techniques in future is undoubtedly present, as can be seen by some studies.

Potential problems of implementation

Effect on crop growth

The research carried out to date looks promising, and a definitive link between nutrient delivery to a crop and it’s susceptibility to disease has been illustrated. However, any changes to a nutrient regime, especially in hydroponic cropping, can have fast and noticeable effects on the crop and the yield it provides. It is envisioned that the main problem of implementation of this research would be limited grower uptake, as moving away from a proven system and towards something new with potentially high risks involved would not be attractive to most growers. As such, many more crop specific trials in commercial growing environments, guided by commercial objectives must be performed before growers are likely to have sufficient faith in disease management through nutrient regime. Even then, it is unlikely that nutrient management will be able to totally replace fungicide use in commercial monoculture, but significant reductions in chemical use could be made.

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Precise nutrition technology

Especially in recirculating systems, towards which the industry is likely to shift, the appropriate measurement and maintenance of optimum concentrations of nutrients in the system is already a difficult process requiring regular testing and often the help of an outside consultant. This is perhaps the next largest limitation to the application of these ideas, as until the technology to enable nutrient management to be performed at such a fine level is devised, there is only so much control available to a grower. Where growers' profit margins are often so small there is little room for error, and the time and effort that may be required with current systems to fine tune a nutrient regime to such a high degree may not be balanced by savings on PPPs or reflected in yield. Optimization of fertiliser application has applications for both economic and environmental sustainability and may also help to make a more nutritious product for the end consumer (White & Brown, 2010). There is ongoing research into the development of improved nutrient delivery systems, but should an effective system be devised the roll out across the industry would still take time (Elings *et al*., 2004). The end goal of recirculation systems is improved management of drainwater, so that any reservoir of liquid nutrients at the end of a specific crop may be used as a starter solution for the following crop, or may be transferred to another crop system.

The application of these methods has definite potential in recirculated, regularly monitored and analysed systems, but may be less worthwhile for growers who perform limited checks, practice poor system maintenance or who have a less flexible system in place. New nutrient recirculating systems using commercially available ion selective electrodes (ISEs) and controlled via computer that can both detect concentrations and make appropriate alterations have been in development for some time, and this would reduce the time and money spent by the grower ensuring targets are met (Jung *et al*., 2013; Thompson *et al*., 2013). One potential problem is that these systems, made up of many individual electrodes, are likely to be expensive and take up a lot of space in an area where space is valuable. Of the tomato specific research found, multiple different delivery systems were used, and nutrients added at different concentrations in different units. This makes comparison between the studies difficult, and comparison between some studies and commercial practice nearly impossible. Accurate nutrient probes are available, but are generally reserved for scientific use due to their high cost.

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Testing in commercial crops

The insufficiency/incompleteness of research data also makes it difficult to apply to the real world. There is lack of information on the impact of running the hydroponic system to waste or recirculating it, or of the effect of substrate. Additionally, though more complex studies are more relatable to real world crops, it is often difficult to know which part of compound fertilisers are having the effect on disease levels when these are applied. In practice balancing the respective parts of compound fertilisers to optimum concentrations may be counter-productive if previously 'unwanted' ions such as sulphates, or high EC levels are actually having positive effects. Where many studies utilised different cultivars, these were often near isogenic and were used to elucidate the differential effects between resistant and susceptible plants.

The use of a range of commercially grown varieties would be beneficial to the practical application of these techniques, for example the EC concentration tolerance for medium and large fruited varieties is likely to be lower than for smaller-fruited baby plum and cherry tomatoes. Similar growing systems to where the disease is most of a problem is also important, for example many of the studies found in this review were on young plants grown in nutrient solution, and more akin to tomato propagation than fruiting plants grown in a hydroponic system (e.g. Jiang *et al*., 2013). Though small scale laboratory studies are cost effective and illuminating, it must also be noted that results from lab tests and results from field tests may not always be complimentary (Knopp & Martensson, 2010). Many experiments use NFT, or a much simplified hydroponic growing system. Effects of substrates like coir or rockwool were rarely dealt with, though in cucumbers (O'Neill, 1991) rockwool cucumber crops were shown to contain less silicon in their shoot and leave tissues than those grown on straw beds. As such, the most effective strategy may differ between growing systems. Furthermore, many studies illustrated beneficial disease effects of nutrient concentrations that are similar to those already supplied to commercial tomato crops. As such, no improvement can be made based on these studies, though the beneficial role of optimum nutrition has been illustrated. An improved knowledge of commercial practice would benefit researchers and allow more targeted research and development.

It should also be noted that smaller scale and laboratory studies do not take plants to harvest, and so any yield effects (which are key to the uptake of new methods) are not known. As is to be expected, there is more information available on macronutrients such as nitrogen than there are many micronutrients, whose effects in general plant nutrition are less well known, whose effects are not conserved and that are more difficult to study in

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practice. It may be useful to focus on these nutrients, as beneficial effects may be as yet unknown, whereas for key elements, benefits and crop optimums are well understood.

Strength of evidence

The reliability of the references used in this review is extremely high, as the majority of sources are from respected, peer reviewed journals. Established textbooks and industry knowledge have also been utilised, and backed up by primary research where possible. There is variation in the perceived quality of journal, and this has been taken into account. For example, a paper from a lesser known journal was viewed more critically than an established journal like Plant Pathology. As discussed above, however, the robustness of studies included vary considerably as there are no standardised methods for studying the effect of hydroponic nutrition on disease.

Adaptation to season/risk

An additional limitation of this in practice is that ultimately, maintaining a crop at its optimum nutrition is still the best general strategy for overall crop health and resistance to a wide range of diseases. Maintaining a crop throughout the growing season with the appropriate nutrients at the appropriate times is what growers already strive for, and no doubt this is already bringing beneficial knock on effects to the crop in terms of disease resistance. Additionally, the beneficial effects of many mineral nutrients on disease severity occur only when the plant is deficient, and cease when the nutrient is delivered supra-optimally, as is known to be the case with potassium nutrition. Minimising stress to the crop also avoids fruit disorders such as blossom end rot and maintaining the nutrient balance, especially in wholly or partially recirculating systems, is key to this. In order for altering the nutrient regime to a strategy found to be effective against a certain disease may only have value at a time when it is known that that disease is a serious threat. As such, disease focused nutrient management may only be worth applying in a crop known to have a disease problem season on season. There is potential to combine changes in nutrient management to increase a crop's disease resistance with environmental monitoring and forecasting, so that a crop can be primed and protected before and during a period of high disease risk. This is dependent on forecasting systems becoming more efficient, as moving the nutrient concentrations, pH or conductivity away from plant optimum may have associated growth and yield reductions should disease fail to establish. There must also be the consideration that in most disease epidemics, only a small amount of crop is infected in the early stages. In a hydroponic system, nutrition cannot be targeted towards individual plants. Therefore

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moving the nutrient concentrations away from the optimum may help the plants currently infected, and potentially offer protection for the rest, but it may also serve to make the rest of the crop more susceptible.

Specificity of nutritional effects

A limitation of these strategies in the UK are that a lot of the diseases thrown up as promising targets are not problems here. Much of the research into nutrition's effect on disease, especially in tomato, has been carried out in the wider world where specific disease priorities are different. For example, much literature focuses on Fusarium and bacterial wilts which are a problem in tomato growing areas of the southern United States. Many diseases are opportunistic, e.g. pith necrosis, which will often appear in a crop which is fast growing and well supplied with nitrate-nitrogen in April/May. Additionally, some of the diseases under study are not traditionally problems for hydroponic growing e.g. Fusarium wilt or brown and corky root rot. The overseas nature of much of this research also makes it likely that in inoculated experiments involving diseases also common in the UK, the strains used are not those dominant in the European population. It was also rare for studies to look at the effects on multiple isolates, and in those that did variable effects of plant nutrition were found (Lecompte *et al*., 2010). A significant reduction in problem diseases must be consistently possible in order to make this management technique attractive to growers and worthwhile for the tomato industry as a whole. However, it should be noted that information on diseases not currently large issues in the UK should be maintained in case changing conditions and markets mean they are problems in the future. Similarly, experimental data on the advantages of organic fertilisers may have limited applications for UK hydroponic growing, as soilless production in the UK may not be organically certified. However, there is potential for their use in hydroponics, regardless of organic certification, if they confer benefits in yield and disease susceptibility.

Mechanism of action

Where a mineral element exerts an effect on disease development or severity, care must be taken with interpretation as substances such as sulphur, copper and phosphites may have direct biocidal effects on pathogens, rather than influencing them indirectly through plant nutrition. Mineral nutrients used in this way are currently referred to as 'commodity substances', but this is under review by the Chemicals Regulation Directorate. The mechanism of action of supplied nutrients in suppressing disease are often hard to elucidate, and effects observed *in vitro* may not be the same as occur in the plant.

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Identifying the mechanism by which disease symptoms are reduced is becoming increasingly common in molecular studies, and is necessary so that the nutrition technique can be used at its highest efficacy, and at an appropriate dose so that it is not damaging to other microbes in the rhizosphere, and does not meet regulatory problems.

Knowledge gaps

Overall, there are currently too many gaps to make this disease management technique instantly applicable, but this scoping study has effectively identified those areas requiring more research. Laboratory and smaller scale testing is of value, as the individual role of each mineral nutrient and their molecular interactions with plant and pathogen need to be further elucidated to direct and target larger scale, applied fieldwork. Similarly, studies on the effects of fertiliser without the presence of a pathogen, such as Kaplan *et al*., 2010 will also continue to be useful and addition of a mineral that is damaging to the crop is unlikely to confer benefits in disease resistance. Further experiments that are crop and situation specific need to be carried out, as commercial trial work is imperative to knowing whether a technique can be effectively applied by the industry. For example, on paper the effects of silicon on numerous diseases look highly promising, but unfortunately this failed to work in glasshouse crops in practice.

Summary points – Objective 3

- **A variety of studies in hydroponic tomato have been identified that have shown promising results**
- **Potential impacts must be considered to ensure adoption of new nutrient strategies is practical with minimal negative impact on yields and fruit quality**
- **Irrigation regime & aerial management as well as nutrient management may be used to encourage nutrient uptake and achieve cropping targets (e.g. reducing BER, reducing disease)**
- **Cropping history or forecasting tools could be used to focus targeted nutrient management**
- **May be dependent on improved nutrient delivery technology to synchronise supply and plant demand**
- **Potential savings in PPPs, staff time and fertiliser if targeted nutrient management can be achieved**
- **Research effort differs between diseases, dependent on the host country and the specific disease problems present there**
- **Knowledge gaps also exist regarding commercial applicability, yield and fruit quality impacts**

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Objective 4 – Proposed R & D priorities

Prospects for use in tomato

As this review attests, much of this information has been known for some time, although not rigorously tested, or the mechanisms explored. Hopefully if the information presented above is validated for commercial tomato crops the potential applications of nutrient management with regards to disease resistance will expand. Additionally, growers will begin to have more faith in increasingly technical nutrient systems and the beneficial effects they can have on all aspects of cropping. The limitations above illustrate that not all research can be directly applied to UK tomato crops, or that it would not be cost-effective to do so, at least without further study.

As discussed above, moving away from optimum nutrition carries with it risks for yield, fruit disorders or increased disease susceptibility. Before large changes are made to current empirical recipes it must be ensured that the consequences have been well explored and understood. NFT crops have very little buffering of nutrients, so other substrates like coir or rockwool may be more appropriate for studies until techniques have been fine tuned.

Disease targets

Currently, there is only limited need for additional control of root diseases due to widespread adoption of rootstocks which provide vigorous root systems and resistance to some common root pathogens. As such, the majority of problem diseases in the UK are foliar, causing problems via a reduction in green leaf area or by damage to the fruit. As hydroponic nutrition is delivered to the rhizosphere, it is therefore important that nutrients are able to move systemically through the vascular system, which is not the case for all mineral nutrients, in order to have an effect on foliar disease. It is important to note that beneficial effects on root disease summarised in this review may be of use in future cropping, despite not being required currently, and that the same goes for pathogens only causing problems overseas. Plant pathogens are continually evolving over defences put in place by newly developed fungicides and varieties, for example a new race of *Fusarium oxysporum* f. sp. *lycopersici* (Race 3) present in the USA, Asia and Middle East could enter UK crops (Choi *et al*., 2013). In this case it would be beneficial to limit ammonium-nitrogen and potassium, and supply lower concentrations of phosphorus and calcium. The increasing tolerance of rootstocks also brings about potential tolerance to higher EC and pH levels than have been tolerated in the past (Garibaldi *et al*., 2011), as well as better growth when nutrients are limiting (Schwarz *et al*., 2013), which may also have beneficial impacts on

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plant disease. Rootstocks differ in their disease resistance, and their resistance has also been found to differ with age (Gilardi *et al*., 2011) so there may be scope to use nutrition to supplement their beneficial effects.

Elements with large effect on disease

The nutrient elements known to have the largest potential effect on disease resistance/tolerance are nitrogen, calcium, silicon, manganese, boron and phosphorus as phosphite**.** Potassium may have large effects when in the deficiency range, or on crop aspects aside from disease resistance. Copper and sulphur have historical uses as fungicides, though these effects are often only evident when applied at levels far exceeding those for fertilisation, with the exception of electrolytic fertilisation with copper ions. Cropping practices in a variety of crops also confirm this, as the majority are used, or have been used in the past, to combat disease. Though it appears some nutrients may not be easily applied to hydroponic tomato, for example silicon, it is worth exploring the effects of those nutrients where benefits are known. Additionally, there may be beneficial effects of other nutrients whose mechanisms and roles in plants are not as fully understood and on which a smaller amount of research has been carried out. The effects of these also need to be fully explored in tomato in a commercial situation. This is especially valid where relatively few control options currently exist, as is the case for the viral diseases of tomato present in the UK. For example cadmium nutrition has been found to block symptoms and spread of turnip vein clearing virus in tobacco (Ghoshroy *et al*., 1998) and there are potential effects of boron on ToMV (Shepherd & Pound, 1960). The ability to implement a poorly growing crop barrier using heavy metal nutrition to prevent viral spread could save time and money spent avoiding initial infection and managing the crop once infection has occurred.

Though some effects are nutrient specific, for example silicon is commonly found to have positive effects, others are pathogen specific, for example the different reactions of obligate and facultative pathogens to nitrogen (Hoffland *et al*., 2000). There may be scope to apply the reactions of related diseases on other crops to nutrition in tomato crops, however there is no guarantee that these reactions will be conserved. For example, different glasshouse strains of *B. cinerea* were found to react differently (Lecompte *et al*., 2010). However, this is also true to pathogen reactions to most other control methods, and should not preclude efficacy in tomato crops.

As mentioned, silicon seems very promising for incorporation into nutrient recipes in hydroponic tomato, and this has successfully been done in the past in cucumber to combat pathogens such as powdery mildew. However, resistant varieties and the adoption of

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multiple cropping in cucumber have largely removed the need for this, and as it was high in cost it is no longer economically viable for cucumber growers. The use and applicability of silicon for glasshouse crops was summarised by Bélanger *et al*., 1995, and focuses on cucumber, eggplant and muskmelon, not on tomato. Tomato crops are in the glasshouse for far longer than cucumber, and partial control gained may be of more value, but as tomato does not accumulate silicon it is likely that problems with irrigation blockages would make this technique unusable. Even in cucumber, its addition to the nutrient solution required a third fertiliser tank to avoid precipitation. Silicon is already present in the water of some areas at base concentrations of around 10 mg/L, and it would be interesting to monitor its natural occurrence in systems alongside occurrence of diseases where it is known to have an effect. There is potential for use of silicon as a foliar spray, which was found to confer some tolerance to bacterial speck in soil grown tomato (Andrade *et al*., 2013). However, this would negate the benefits of the relatively low input nutrient delivery system, requiring the extra labour costs, increased environmental loss of nutrients and increased water use associated with spraying and potentially leaving unwanted residues. The review of silicon use in glasshouse crops agrees that the mode of action of silicon differs between foliar spray, where it is likely directly inhibitory, and root uptake, where it is more likely the plants defences are being stimulated (Bélanger et al., 1995). Magnesium is already sprayed commonly in spring to avoid nutrient deficiency occurring during fruit production. Potassium and magnesium are antagonistic and insufficient magnesium is generally taken up by the plant, in favour of potassium. The increased growth caused by potassium when the plant is deficient can lead to dilutions by growth of other mineral elements, and beyond maximal growth there may also be a slight decrease in cations like calcium and magnesium due to competition at uptake sites. This shows that foliar sprays of fertiliser may be possible in UK tomato growing, if their beneficial effects are strong enough to outweigh the extra cost. Spraying tomatoes with calcium pre-harvest could have the potential to extend shelf life and calcium sprays in crop have also been shown to reduce ethylene (Elad & Volpin, 1993). Phosphite is commonly sprayed on ornamental crops as a foliar feed, but also has beneficial effects on foliar disease. However, toxicity can occur if over used and it may be more efficient to incorporate phosphite into the nutrient solution in balance with phosphate to ensure appropriate nutrition and protection from root diseases such as Phytophthora root rot (Forster *et al*., 2008). Silicon is currently available as a spray, in the form of silicic acid (as used successfully against bacterial wilt by Heine *et al*., 2005) but there may also be other options for its effective delivery. Slabs containing slow release silicon as previously used in cucumbers could be a potential option, and positive results combining potassium silicate with additional acid have been observed in both cucumbers and more recently, tomatoes.

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Interaction with biocontrols

One interesting prospect for targeted nutrient management in hydroponic tomato is the potential for interaction with biocontrols. As a glasshouse crop, biocontrols have been available to tomatoes for quite some time, and beneficial microbes can also occur naturally, as discussed in AHDB Horticulture project PC 281a, and due to biofilters. The effect of altered nutrition and presence of a biocontrol together were found to be better than each used alone in numerous studies (Borrero *et al*., 2012; Shaukat & Siddiqui, 2003; Duffy & Defago, 1997) though there is also potential for no effect, or antagonistic effects (Kurbachew *et al*., 2014). These complementary effects have the potential to provide effective controls without the reliance on chemical fungicides as part of Integrated Disease Management (IDM) programmes, for example *Fusarium oxysporum* f. sp. *lycopersici* was reduced by 25% by combined application of zinc and a *P. fluorescens* biocontrol. The resistance of some tomato cultivars to disease may also be interlinked with the nutrition they receive (Hacisalihoglu *et al*., 2010). It should be noted that whilst levels of control achieved by biocontrols has often been observed to be poor in tomato, as the number of active ingredients available to tomato growers decreases, options that did not seem valid in the past may become more attractive (Borrero *et al*., 2004). However, as beneficial microbes can be favoured over pathogens by certain environmental conditions, the same must also be true if conditions tip in the pathogen's favour. Some diseases may also be favoured by certain nutrient conditions directly as they require more or less specific nutrition for their own metabolisms (Apparao, 1969). Additionally, if a biocontrol or mycorrhizal fungus is favoured by limited nutrition, this conflicts with the overarching aim of tomato growers to produce a high yield of high quality and flavoursome fruit. Further research into what nutrients favour pathogens and where these thresholds lie will help to inform which strategies carry with them risks of pathogen development. For example, trace metals play a very important role in the health of plants but iron, zinc, manganese, copper and molybdenum are essential to all fungi. Boron is not shown to be essential for fungi (Apparao, 1969), so may be a 'safer' option to include in nutrient regimes at supra-optimal concentrations.

Need for new technology

As discussed above, improved technology will be key to the application and uptake of targeted nutrient management in hydroponic tomato. Improvements in nutrient systems themselves will allow more accurate targeting of nutrients, and potentially require analysis less regularly. The prospects discussed may require altered concentrations and ratios of nutrients to be present in the nutrient solution, which may cause problems in terms of

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balanced uptake by plants or in terms of precipitation in the system. These are all problems that the systems of the future will have to take account of. As well as improved technology of the nutrient system, improved forecasting of disease risk periods would enable further targeting of nutrient regimes, so that the problems associated with moving away from optimum nutrient concentrations can be negated. There is even potential in future for a system that links nutrient delivery with a calculated risk of each disease, so that specifically tailored nutrition is being delivered to the plant at all times to suit both its biotic and abiotic environment. As technology improves, new equipment will emerge onto the market and it is important that the systems put forward are realistic, cost effective and fit with commercial settings. Again, as mentioned above, there are prospects for this improved technology to work with increasingly complex nutrition models, which account for light levels, climate, transpiration and growth rates in an attempt to continually tailor the nutrients received by the crop to the ever changing biotic and abiotic conditions in the glasshouse that affect the balance of nutrients in the root zone (Bugbee, 1996; Schwarz *et al.,* 2009).

Risk and reward

Finally, the prospects for use of targeted nutrient management for disease control in hydroponic tomato is dependent on the UK tomato industry. As discussed, development of technology is imperative to being able to accurately control the inputs and outputs of the system. As well as this, tomato growers must feel able to put their faith in changing a recipe that has always worked well for them. As such, further research has to be done to illustrate that any changes made can improve disease control and yields, and can do so cost effectively, before growers can be expected to make any changes. There is undoubtedly a balance to be struck between high concentrations of fertiliser which may have consequences for disease and for the environment, and low concentrations of fertiliser which may negatively impact plant growth.

Growers would also require a large amount of faith not to spray a crop protectively, and it is unclear at this point if disease control with the use of nutrition can be comparable to control achieved with chemical fungicides. Large scale trials in commercial crops are key to ensuring research and development is applicable in practical growing situations and a supportive growing community will be key to this. Effective two way knowledge transfer will likely be key to the development of commercially useful research with good prospects of uptake, as UK tomato growers are highly knowledgeable in the field of crop nutrition. Some prospective treatments would likely sound unattractive to growers, for example treatment with heavy metals, and keeping these at sub-toxic concentrations would be dependent on

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accurate delivery systems as detailed above.

Evidently all the potential consequences of implementation of these prospects need properly exploring. Plant nutrition in hydroponics is highly complex and altering concentrations of one nutrient will have knock-on effects on others, on pathogens, on microbes in the biosphere and on plant growth and yield. For example, rather than the concentration of nitrogen or calcium, the ratio (Ca+Mg)/(Na+K) correlated better with reduced severity of bacterial canker (Berry *et al*., 1988). So long as key ratios in the nutrient solution are kept within recommended ranges new recipes can be developed that also take account of the information summarised in this review. In order to address the multitude of variables in this growing system, the promising information found has been used to propose some priority areas of research and development. This will help contribute to the ongoing development of our understanding of the relationships between nutrients, plants and pathogens and our ability to harness them for improved crop production.

Proposed Research & Development priorities

The research and development priorities listed below are based on the knowledge gaps identified in the literature review, as well as the pursuit of further information on promising areas found through the review. Additionally, through grower consultation the impacts of the potential costs and practicalities of disease control through disease management in this way have been considered. It was the aim that through consultation at the TGA Technical Committee the majority of opinions and viewpoints within the UK tomato industry would be heard and accounted for. However, in some cases, where it may have proven difficult to reach a consensus, the conflict in opinion and constructive points generated in discussion are stated. It is envisaged that cost-benefit analyses will play a key role in future commercially focused R & D, and that interactions between different areas of research will be present.

Areas where no or limited data were found, but a need in the grower community has been identified also warrant further work. Only limited research was found for some diseases on the effect of differing nutrients on their severity. Also, nutrients such as magnesium, whose effects on disease are complex, generally lack study across all crops compared to some other nutrients, and more general research and development into plant nutrition is necessary to better understand the roles individual nutrients play in plant defence. Though some studies included effects of their altered nutrient regimes on yield, the majority did not, and this must be included in future hydroponic nutrition research to attempt to alleviate the

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concerns and conflicts surrounding moving away from more traditional recipes.

Specific R & D priorities that are likely to have applicability and potential in UK tomato growing in the near future are listed below and prioritised in Table 16. Interesting points raised are also included separately (and summarised in Table 17) as they may warrant further thought and study in future, but may not be practical at this time.

1. Further explore 'optimum' nutrition, especially in recirculating systems

- Focus on recirculation as it seems to be the most accurate way to deliver and monitor nutrients supplied to the crop so long as the correct management practices are in place
- Recirculating systems are becoming increasingly more common/necessary in UK growing
- Are current nutrient 'optimums' really 'optimum'?

2. Improved technology

- Improved disease forecasting models and software to aid nutrient regimes targeted at glasshouse diseases
- Improved nutrient delivery technology, moving towards fully recirculating, zero drain systems.
- Ideally, an effective and targeted nutrition strategy should take into account the interactions between fertilisers, compound fertiliser choices, EC and cation-anion balances, climate, microorganisms and more.
- Ion Selective Electrodes (ISEs) have been researched for use in hydroponics for many years, but a number of recent overseas studies have been developing systems combining these with software and dosing systems that aim to produce a nutrient solution that is kept continually at optimum (Thompson *et al.,* 2013).

3. Novel nutrition strategies & large scale commercial experiments

- Many conclusions drawn are based on a few or a single study, repetition is needed to back these up especially when so much variation exists in these situations.
- Potential beneficial effects of almost all plant mineral nutrients need to be further explored.
- Large scale trials using nutrient systems and crop husbandry similar to in industry are required, as lab or small scale trial effects do not always translate.

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- Development of models/adaptation of recipes and models already in use.
- Making changes to nutrient regimes to combat disease has the potential to be rewarding, but data is extremely limited on how this would affect fruit yield and quality. Until this is quantified, the true potential of this approach cannot be realised.
- New balanced strategies need to be devised and tested so that disease control can occur via nutrition without negative effects on growth.
- Exploration of rate at which silicon becomes problematic, programmes combining silicon, calcium and boron to get synergistic effects, or silicon's ability to increase plant tolerance to stressors
- More research into costs of specific nutrient regime changes to the grower

4. Future KT

- Grower liaison is key to ensure research and development is targeted in a way that will most benefit UK growers.
- Growers and industry professionals are extremely knowledgeable regarding crop nutrition, and this knowledge should be utilised to ensure the best use of resources.
- Becoming increasingly more topical as research is ongoing overseas e.g. 6th International Conference on silicon in agriculture, Nutrihort Conference, 2013 and the future BOPP seminar.
- Any future research with prospects for use in commercial tomato will have to be effectively communicated to UK growers, as uptake of novel strategies would require a lot of faith.
- There is no single, comprehensive resource available currently on hydroponic tomato nutrition and numerous sources must be consulted. It may be useful for this document to be produced so that all information is easily accessible and industry professionals can easily re-cap their knowledge and have their questions easily answered.

5. Nutrition's effect on PepMV

- Limited information on nutrition's effect on PepMV
- As a disease that can lower yield, affect fruit appearance, quality and flavour novel control options are valuable
- Viral diseases are commonly managed via nutrition to reduce the visible symptoms and allow plants to outgrow the often more severe initial stages of

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infection

- If this could be quantified and built upon, and the effect of other promising nutrients or regimes extended, potential management strategies could improve
- Could you apply data on other viral diseases to the management of PepMV?

6. Applications within IDM

- Antagonistic and complimentary relationships with biocontrols have been observed
- There may be further interactions and applications to discover that may have value in UK hydroponic tomato?
- Quantification of reductions in pesticide use (reduction of MRLs) for experimental IDM nutrition strategies.
- Potential interactions with the Salicylic and Jasmonic Acid defence pathways and with varietal resistance

7. Exploring the effects of water treatment

- Copper ions used as disinfection, irrigation system cleaner and as fertiliser (AquaHort) in bedding plants
- The effects of different disinfection treatments on nutrient uptake may warrant investigation
- Other novel techniques such as the use of electrolysed water are likely to have a distinct effect on the nutrient solution and on plant uptake

8. Exploring effect of substrate

- There are many variables in hydroponic growing, and in responses to nutrition and disease
- Crop and disease specific effects observed, even down to strain or isolate of pathogen, though information from other crops could help to target research in tomato, but may not be directly applicable.
- There are differences in how nutrition must be managed between substrates and growing systems, and in how different substrates facilitate or inhibit nutrient uptake
- It may be valuable to further study and quantify the effect of substrate on nutrition, disease and the interactions between the two

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Summary points – Objective 4

- **Application of targeted nutrient management for disease control has potential as part of an integrated disease management strategy if limitations are addressed**
- **Of the experimental evidence detailed in this review, the most promising, practical solutions have been put forward for further R&D (Table 16)**
- **Proposed targets require further experimental study to fully evaluate their use in commercial cropping in the UK**
- **Many strategies could have associated benefits, encouraging a regularly monitored, tightly controlled nutrient management system and encouraging further integration of aerial, environmental and rootzone crop management**
- **Further potential targets for future R&D have been included as points of interest (Table 17)**

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Table 16. Proposed R & D priorities to improve the use of nutrient management for disease management

Potential R & D priorities	Description	Impact	Cost	Likelihood of success	Time until uptake	Potential R & D priorities
Re-evaluate optimum nutrition concs for recirculation systems	Likely that recirculation will play a major role in future growing. Quantify the savings in nutrient & water.	Increased yields, greater disease resistance/tolerance. More cost effective, environmentally friendly fertiliser and water use.	May save money in terms of fertiliser and disease control programmes and may also increase yields.	High. Optimums have not been evaluated in the UK in years, and it is likely beneficial changes can be made to regimes.	Possible to start now.	**Re-evaluate optimum nutrition concs for recirculation systems**
Improved nutrient technology	Work ongoing in Canada and China on ISEs and modelling software.	Potential to match nutrient supply with plant demand closely, optimising nutrition.	Cost of new technology is generally high, but savings and improved profits would also be facilitated.	Medium. If can be shown to work effectively in practice they would be very attractive to growers if the price was acceptable.	In development for over 10 years, but not yet adopted. These systems do seem like the future, but time to market is uncertain.	**Improved nutrient technology**
Large, commercial scale nutrition experiments	Many promising interactions that warrant further exploration e.g. use of silicon (as a silicic acid spray, slow release slab, or potassium silicate + acid).	Possible reductions in pesticide use, improvements in plants tolerance to stress. Possible impacts on yield and quality should be included.	Large commercial trials are more expensive than smaller trials, but the latter have already shown promise, and commercial trials will show if a technique will be effective.	High. Will succeed in generating further data on which to base decisions on future nutrition strategies.	Potential to develop new recipes for use in specific situations is present currently, and is performed by growers to differing degrees.	**Large, commercial scale nutrition experiments**
Production of grower guide on hydroponic nutrition	No singular source of comprehensive information on growing hydroponic tomato exists. Also potential for further KT.	This would recap growers on the basic rules of crop nutrition, & inform on recent and future developments. It may also stimulate open discussions on the topic.	Bringing together information would make tomato nutrition more accessible to industry professionals, saving time & money.	High.	Could be started at any time.	**Production of grower guide on hydroponic nutrition**
Effect of nutrition on PepMV	Limited information was found, though it is known that growers manage crop nitrogen following infection so that the crop can outgrow symptoms.	PepMV can cause considerable reductions in yield and fruit quality, appearance and flavour. Control options are currently very limited.	If a cost effective solution can be found based on crop nutrition that is more effective than methods currently in use, savings could be made. E.g. Boron	Uncertain. Could improve control, but may not be effective or practical in a commercial setting.	This control method for PepMV is already utilised, but it would be useful to establish If this could be taken further.	**Effect of nutrition on PepMV**
Nutrition's use within IDM	Nutrition interactions with microorganisms in the root zone, be they natural, introduced, pathogen, beneficial or saprophytic.	Reduction in pesticide use, improved efficacy and uptake of biocontrols, interaction with elicitors, cultural controls & forecasting risk.	Laboratory and glasshouse trials could result in savings on pesticides and spray applications.	Medium. Would require extensive monitoring and for the appropriate microbes to be detected effectively (as in PC 281a).	There is grower interest, but success of biocontrols has been limited. IDM is preferred over harsh pesticides, & if efficacy is improved they may be used.	**Nutrition's use within IDM**
Water treatment technology with nutritive effects	Cu electrodes ionise and disinfect water & provide plants with copper nutrition. Electrolysed water also promising – does this affect nutrition?	An effective method of reasonable cost that also provides some crop nutrition would be beneficial.	Many different methods available, differ in cost. The AquaHort method provides copper nutrition and keeps the irrigation system clean.	This method is already used effectively by many in the bedding plant industry. Heat, UV and biofilters are generally in use within Protected Edibles.	Technology already in use in Protected Ornamentals.	**Water treatment technology with nutritive effects**
Effects of substrate	A variety of substrates with different properties, & NFT growing are in use in the UK	Substrates are known to affect nutrient uptake. Information would be useful to growers.	Many substrates are used, would require trials and monitoring of rootzone solutions.	High.	Numerous different substrates are currently available to UK growers.	**Effects of substrate**

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Interesting longer term prospects

Though not a primary focus of this review, notable research that may have applications in future tomato growing are summarised below. Though not immediately applicable to commercial practice or able to feed directly into imminent research and development, they have definite potential for the future and raise some interesting ideas.

Impact on human health/nutrition

- Greater consideration of human health in variety selection and nutrition. This has been on the increase in recent years with the discovery of numerous antioxidants in tomato fruit, including lycopene, lutein and anthocyanins. It has been proposed that crop varieties with enhanced accumulation of certain nutrients that are lacking in human diets be favoured in future. This includes boron and molybdenum (Gupta *et al*., 2011), iodine (Landini *et al*., 2011) and selenium (Broadly *et al*., 2006).
- A few potential control methods summarised in this review do not sound immediately attractive, for example treatment with heavy metals against viral infection, and any potential effects on fruit from a human nutrition point of view will have to be proven harmless to consumers and end users before it is permitted.
- Subsequent effects on the nutritional profiles of resultant tomatoes of novel nutrition strategies are an important to consider
- A lot of this work is going on currently, and though it was beyond the scope of this review it is an area of consumer and retailer interest.

Novel active ingredients

- Though not strictly plant nutrition, the potential applications of mammalian lactoferrin in plant defence has potential, though much of this work has been carried out overseas and is GMO focussed
- Potential to send elicitors such as fosetyl aluminium through hydroponic systems (Grote & Busci, 1998). There may also be a role for stimulating plant defence pathways, using salicylic or jasmonic acid, via hydroponic solutions.

Monitoring of UK tomato crops

- Given the variability of nutrition already delivered to UK crops, it would be very interesting to carry out a comprehensive survey of current grower practices, so that

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baseline concentrations of nutrition are accurate.

- Inclusion of slab values would enable crop uptake and its impacts to be considered, as well as the determination of what growers consider optimum (as in Objective 1 in this project).
- If both the nutrients delivered over a season and the disease problems experienced at each nursery over a season were monitored, there would be potential to link differences from one nursery to another in nutrient delivery to differences in disease levels observed, provided other variables can be minimised (e.g. variety, glasshouse environment, crop management).
- Exploring the effects of new practices on nutrition e.g. dawn temperature drop on calcium and boron uptake. Growers want calcium and boron to move into the fruit, and this may be encouraged by this new practice. At night humidity rises, resulting in lower levels of transpiration and increased root pressure. Therefore a short period of cold at dawn could encourage high uptake, and these nutrients would subsequently move into fruit.
- Such large scale monitoring may not be possible due to the high levels of cooperation required, and the high levels of variability that could not be accounted for would make drawing substantial conclusions difficult.

Differing varietal/rootstock requirements

- Whilst varieties are often bred for their different disease resistance traits, some experimental studies have found varietal resistance to be dependent on the nutrition delivered
- It may therefore be possible to provide supra-optimal nutrition to a non-resistant variety to induce greater tolerance, or for the resistance of a variety to break down if certain nutrients are lacking
- Different rootstocks may also have different responses to nutrition or uptake nutrients differently
- Evaluating each rootstock and variety under experimental conditions would be extremely labour intensive and the benefits may not prove worth the time, cost and work

Changes to EC or pH

- A higher EC may reduce susceptibility to certain diseases and also convey benefits in terms of fruit flavour and quality

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- Potential to investigate how new vigorous rootstocks respond to higher ECs
- However, this may be a risky strategy as high salinities can damage root systems and make plants more susceptible to attack, there are increased risks of BER and also impaired water uptake
- There are conflicting opinions on this topic and it may not warrant further research currently, especially as there has been a trend in UK growing for a lower EC over time
- A lower pH may reduce survival and spread of diseases in the hydroponic system, but may also affect nutrient uptake and general root health

Effect of fertiliser type

- There are many different types of fertiliser available which each have their own advantages and disadvantages, usually in terms of cost and in having more of a tendency to cause build-up of undesirable ions in solution
- There is evidence organic fertilisers may increase plant tolerance to soil-borne disease than chemical
- It would be interesting to examine the different effects on nutrition and disease that formulations of fertilisers currently on the market have, regardless of the absolute values of nutrient elements in solution

Foliar sprays

- Foliar feed sprays are sometimes used in UK growing to supplement hydroponic nutrition at times of high plant stress to avoid deficiencies
- Calcium sprays and sprays containing silicon have been found to be effective against some fungal and bacterial diseases
- May also have potential benefits in stopping BER development, or improving shelf life but would have to be very effective to warrant cost and effort of application

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Table 17. Potential longer term R&D topics on crop nutrition

Point raised by research	Approx. No. studies	Description	Pros	Cons
Impact on human health/nutrition	10+	Incorporation of beneficial compounds in produce, as well as nutrition targeted at human malnutrition problems.	Currently the area of health foods is fashionable, so there is a potential market for produce	Potentially more applicable in developing countries
Novel active ingredients	3+	Novel technology has shown new active ingredients such as lactoferrin to be effective in controlling some diseases. Potential to send elicitors through hydroponic system.	Potential for new active ingredients with novel modes of action against disease	Many new substances may meet specific regulatory problems, or may not be found to be cost effective
Large-scale monitoring of UK tomato crops	0	Monitoring of multiple crops nutrition and disease incidence over a growing season, including both feed and slab values.	May highlight key risk areas or particularly effective strategies, and the effects of recent developments in growing (e.g. dawn temperature drop's effect on calcium uptake and sinks)	So much variability may just serve to confuse matters and mask any trends present
Differing varietal/root stock requirements	5+	Whilst some studies have focused on the response of varietal resistance to nutrition, further work on the differing requirements of different varieties may be useful	Prior knowledge of a varieties preferences or weaknesses may make for a smoother growing season and improved yields/quality	Generally, growers come to their own valid conclusions on how to differently manage varieties, and many new varieties are introduced or moved away from constantly, meaning this work may have limited use.
Changes to EC/pH	5+	Changes to EC and pH may also reduce susceptibility to certain diseases	High EC results in smaller, more flavoursome fruits but lower yields. New, vigorous rootstocks may have the potential to tolerate higher ECs and pHs in the rootzone	Allowing EC to climb has many potential deleterious effects (e.g. BER, impaired water uptake) and has been consistently lowered by growers over the last 10 years. pH changes may also affect uptake, and could potentially damage roots.
Effect of type of fertiliser	5+	There are numerous different fertilisers on the market, compound or single element, chemical or organic, liquid or solid form. Fertiliser choice is dependent on many different factors.	Organic fertilisers may offer some protection from soil-borne disease. Single element fertilisers, though not always available, may be more easily managed	Fertilisers differ in cost depending on the source and form, the production process and demand. Cheaper fertilisers, may be less effective, and vice versa. Organic fertilisers may also be variable in formulation.
Foliar sprays	10+	Use of foliar feed e.g. calcium, silicon to combat both disease and nutrition disorders as is done currently to some degree.	Could improve shelf life and act to top up rootzone nutrition	Application incurs higher costs to the grower, so it would have to be highly effective.

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Knowledge and Technology Transfer

Project review meeting held 18th March, 2014, AHDB, Stoneleigh.
Presentation at the TGA Technical held 4th June to enable an extended grower consultation.
An AHDB Grower article will follow.

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Glossary

Appressorium: A fungal infection structure formed to build up pressure that enables fungal hyphae to penetrate the host epidermis.
Ascomycete: A family of fungi, known commonly as the sac fungi, including many plant pathogens that reproduce via the production of spores inside an asci (sac).
Basidiomycete: A family of fungi whose spores develop inside a basidia, including the majority of mushrooms and toadstools.
Biotroph: obligate plant pathogens that must gain their nutrition from a living host, facilitated by complex biological interactions between plant and pathogen.
Conidiophores: Spore (conidia) bearing structures held within fungal mycelium.
Deuteromycete: Also known as the fungi imperfecti, these fungi have only been observed to reproduce asexually and so cannot be classified in traditional taxonomic groups
Hemibiotroph: as the name suggests, pathogens in this group begin with biological interactions with their host, and then switch to a necrotrophic lifestyle.
Hypersensitive response: This is a defence response by resistant plants where, when a pathogen is recognized, tissue surrounding an invading microbe rapidly dies to stop its spread.

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Necrotroph: facultative pathogens that gain their nutrition from dead and dying tissue produced during pathogenesis.

Oomycete: A family including many plant pathogens, including Pythium and Phytophthora species, and the downy mildews, similar in appearance to fungi but genetically distinct.

Oospores: A type of sexual spore produced by the Oomycetes that are extremely long lived.

Pathogenesis: The mechanism by which a pathogen proceeds to cause disease.

Perithecia: A flask like structure found in ascomycetes, containing asci and possessing an opening at its top through which ascospores are released.

Pycnidia: A flask shaped fungal structure containing asexual spores that ooze out when mature. These can often be seen as small dots with the naked eye.

Transposon: A type of mobile genetic element, a fragment of DNA that is capable of changing its position within the genome.

Vacuoles: A membrane bound organelle found in cells, containing water and compounds such as enzymes.

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Appendices

Appendix 1 - Questionnaire

Please rank these diseases of UK tomato in order of importance to you using an index of 1-5 where 1=not important and 5=very important.
Space has been provided at the bottom of the form to add any diseases that have been omitted, but that you feel are notable.

Disease	How common (1-5)	How severe (1-5)	Overall rank (1-5)
Fungi/Oomycete			
Pythium root rot			
Phytophthora root rot			
Late blight			
Verticillium wilt			
Fusarium wilt			
Sclerotinia stem rot			
Colletotrichum (black dot)			
Alternaria (early blight)			
Didymella stem rot			
Calyptella root rot			
Thielaviopsis black root rot			
Leaf mould			
Corky root rot			
Botrytis			
Rhizoctonia stem base rot			
Powdery mildew			
Bacteria			
Bacterial wilt			
Bacterial canker			
Root mat			
Virus/Viroid			
PepMV			
ToMV			
PSTVd			
CLVd			
Additional			

Nursery	
Nutrient system	
Substrate	

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Variety (Plum/Cherry)					
Nutrient	**Units**	**Early season**	**Mid-season**	**Late season**	**Tolerable range**
N (NO_3)					
N (NH_4)					
P					
K					
S					
Ca					
Fe					
Mg					
B					
Mn					
Cu					
Zn					
Mo					
Cl					
Na					
HCO3					
Irrigation level					
pH					
EC					
Comments					

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Appendix 2 – Key points from Objective 2

- The nutrient elements known to have the largest potential effect on disease resistance/tolerance are nitrogen, calcium, silicon, manganese, boron and phosphorus as phosphite;
- A high nitrogen supply is known to increase the severity of disease by obligate pathogens, but has the opposite effect on facultative pathogens;
- Solanaceous powdery mildew (*Oidium neolycopersici*) is exacerbated by high nitrogen content of leaves;
- Excessive nitrogen fertiliser may also favour leaf mould (*P. fulva*)
- The response of *Botrytis cinerea* to nitrogen fertilisation appears to vary between hosts, and for tomato the response in disease progression and severity has been found to depend on the specific fungal isolate;
- It has been found that some *Phytophthora* spp. are favoured by excess nitrogen, but that severity is reduced with the addition of potash;
- Excessive nitrogenous fertilisers are known to increase the severity of bacterial wilt (*Ralstonia solanacearum*);
- Viral diseases are also likely to be favoured by high nitrogen;
- Lower disease index of corky root rot (*Pyrenochaeta lycopersici*) observed with ammonium dominated fertiliser in soil grown crops;
- In a recirculated system nitrogen concentration and ammonium to nitrate ratio were varied and *Pythium* associated mortality was seen to increase as ammonium did;
- Increasing the ammonium to nitrate ratio in hydroponically grown tomato plants was found to reduce disease severity caused by Fusarium crown and root rot by improving the efficacy of the biological control agent *Trichoderma asperellum* strain T34;
- But in a large scale glasshouse experiment where tomato plants were inoculated with Fusarium crown and root rot, ammonium nitrogen significantly increased disease severity;
- The carbon to nitrogen ratio of plant tissue may also affect some pathogens;
- Some nutrients, such as potassium, only have positive effects on disease when the plants are deficient, and giving a supra-optimal supply will have no beneficial effects;
- Didymella stem canker is more virulent on plants that have received reduced nitrogen or reduced potassium regimes;
- Phosphite is directly inhibitory to some pathogens, as are copper and sulphur compounds;
- Zinc, copper and iron have the potential to improve efficacy of certain biocontrol agents;
- High concentrations of potassium increase host plant resistance to both obligate and facultative pathogens;
- Calcium has the potential to boost host defences against pathogens such as *B.cinerea*, and reduce secondary inoculum production;
- Increasing calcium supply was shown to suppress Fusarium wilt;
- Increased calcium was also shown to reduce corky root disease (*Pyrenochaeta lycopersici*);
- Disease severity of tomato pith necrosis caused by numerous bacteria was reduced at a higher calcium regime;
- Bacterial canker in tomato is inversely correlated with calcium content in tomato shoot tissue;
- Control of late blight (*Phytophthora infestans*), has also been illustrated with boron at sub-phytotoxic concentrations via a nutritional effect;
- Boron and cadmium may have potential to limit viral spread, though this has not been effectively illustrated in a tomato crop;
- In tomato plants infected with *Verticillium dahliae*, high sulphur nutrition significantly reduced fungal spread in both susceptible and resistant genotypes;

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- Specifically in tomato, zinc nutrition has been found to improve the bioco0ntrol of Fusarium crown and root rot by *Pseudomonas fluorescens*;
- EC and pH exert differing effects on different pathogens, but a high EC or high salinities are generally considered inhibitory;
- Exposure to salinity stress even for brief periods was found to increase severity of disease on tomato plants grown in hydroponic culture when inoculated with *Phytophthora* spp;
- However, in a hydroponic tomato crop infected with powdery mildew, *Oidium neolycopersici*, the addition of sodium chloride to the nutrient solution generally reduced the incidence and severity of disease;
- As well as pathogen defence, silicon may also defend against salt stress, metal toxicity, drought stress, radiation damage, nutrient imbalance, high temperature and freezing;
- When tomatoes are grown with supplemental silicon, it is not depleted from the system, but accumulates. Addition to irrigation systems is likely to cause blockages and make them difficult to clean.

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