Getting to the roots of aeroponic indoor farming

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Keywords: Vertical farming, plant factory, aeroponics, plant physiology, surface interactions, plant-microbe interactions

Word counts: Abstract: 108; Main text: 3359.

Summary

- Vertical farming is a type of indoor agriculture where plants are cultivated in stacked systems. It forms a rapidly growing sector with new emerging technologies. Indoor farms often use soil-free techniques such as hydroponics and aeroponics.
- Aeroponics involves the application to roots of a nutrient aerosol, which can lead to greater plant productivity than hydroponic cultivation. Aeroponics is thought to resolve a variety of plant physiological constraints that occur within hydroponic systems.
- We synthesize existing studies of the physiology and development of crops cultivated under aeroponic conditions and identify key knowledge gaps.
- We identify future research areas to accelerate the sustainable intensification of vertical farming using aeroponic systems.

Introduction

A period of rapid development in agricultural technology is underway, with precision dosing, machine learning, process automation, robotics, gene editing, and indoor farming paving a revolution in agricultural productivity (Rose & Chilvers, 2018; Klerkx & Rose, 2020). Indoor farming has expanded quickly within the horticultural sector due to yield consistency and environmental control capabilities (Benke & Tomkins, 2017). Indoor farming divides into two broad sectors: greenhouse and vertical farming. Vertical farming has emerged as an increasingly economic strategy within horticulture, enabling improvements in resource- and land-use efficiency.

Vertical farming involves plant cultivation in vertically stacked irrigation systems, using artificial or natural light (Fig. 1). This commonly uses soil-free growing environments and hydroponic or aeroponic irrigation technology (Benke & Tomkins, 2017). Benefits include urban food production, fewer food miles, seasonal independence of crop production, price stabilization, product consistency, isolation from pathogen pressures, cultivation at latitudes incompatible with certain crops (e.g. desert and arctic areas), and utilization of space including disused buildings or tunnels (Despommier, 2011; Specht *et al.*, 2014; Benke & Tomkins, 2017). Further benefits include crop production without impacting soil health, and nutrient recapture and recycling (Benke & Tomkins, 2017). This makes vertical farming land- and water-use efficient (Despommier, 2011). One commercial forecast suggests that the vertical farming industry will have annual compound growth of 21.3% to reach an estimated value of $9.96 billion by 2025 (Grand View Research, 2019). The potential benefits and value of indoor vertical farming has caused the proliferation of cultivation technologies (Benke & Tomkins, 2017; Shamshiri *et al.*, 2018).

A driver of technological innovation for vertical farms is minimizing operational costs whilst maximising productivity. One such expanding technology is aeroponics (Fig. 1). For example, the number of “aeroponic” patents filed increased from 320 between 1975 and

2010 to over 1000 in the last decade (Google Patents, 2020). Aeroponics is thought to resolve several plant physiological constraints occurring during hydroponic cultivation. This can include greater oxygen availability within the root bed and enhanced water use efficiency (Jackson, 1985; Mobini *et al.*, 2015). However, the variety of aeroponic technologies, species cultivated, and growth conditions makes systematic comparisons of technologies and growth conditions challenging. Whilst aeroponics can provide advantages for plant performance, it also requires more extensive farm infrastructure and control technology compared with the more mature technologies of hydroponics. Therefore, aeroponics might be less compatible with certain economics, crops, or locations with intermittent electricity supply. To refine the commercial implementation of aeroponic horticulture, we examine the effects of aeroponic cultivation upon several aspects of plant physiology, development and productivity. We identify knowledge gaps and areas for future plant sciences research to advance this field.

What is aeroponic cultivation?

Aeroponics exposes plant roots to nutrient-containing aerosol droplets (Fig. 1). This contrasts hydroponics, which includes partial or complete root immersion in a nutrient solution, and drip irrigation involving application of nutrient solution to the rhizosphere (Fig. 1) (Keeratiurai, 2013; Benke & Tomkins, 2017; Lakhiar *et al.*, 2018). Within the context of aeroponics, an aerosol is an ensemble of solid particles or liquid droplets suspended in a gas phase (Hinds, 1999). In nature, plants including epiphytic orchids and bromeliads absorb naturally occurring aerosols such as mist through leaves and aerial roots (Zotz & Winkler, 2013). In horticulture, the most commonly used aerosol generation technology is high pressure atomisation, where high pressure liquids are forced through a small orifice, breaking the liquid stream into droplets. This typically generates aerosol droplets of 10-100 μm (Lakhiar *et al.*, 2018). Other atomization methods include inkjet printer droplet ondemand generators, low pressure atomisation, and ultrasonic atomisation, which generate varied droplet size distributions (Reis *et al.*, 2005; Lakhiar *et al.*, 2018).

Aerosol deposition, capture and nutrient uptake on the root surface

We propose that aeroponic cultivation involves a cycle of aerosol deposition and capture (Fig. 2a, b). We reason that aerosol droplets become deposited on the root surface, and coalesce to form a thin, nutrient-dense aqueous film (Fig. 2a). The mechanisms of nutrient and water uptake during hydroponic and aeroponic cultivation might be similar, because both involve interaction between an aqueous nutrient solution and plant root. We predict that root surface thin-film formation is likely governed by aerosol composition, plant root architecture and environmental properties (Table 1).

The thickness of known biological thin-films, such as bacterial biofilms and alveolar surfactants, range from micrometres to millimetres (Murga *et al.*, 1995; Adams & McLean, 1999; Siebert & Rugonyi, 2008). Therefore, we reason that root surface thin-films might occupy this range. However, root surface aerosol droplet capture and thin-film formation is likely to be dynamic and have spatiotemporal heterogeneity (Fig. 2a, b**).** Mathematical modelling and experimentation with *Artemisia annua* hairy root cultures predicts that aerosol droplet size, root architectural properties and root hairs influence droplet deposition and aerosol capture efficiency (Wyslouzil *et al.*, 1997). Aerosol droplets < 2 μm are thought unlikely to deposit on the root surface, whilst the deposition efficiency of droplets > 2 μm increases with greater droplet size (Wyslouzil *et al.*, 1997). Root hairs increase droplet capture efficiency compared with hairless roots (Wyslouzil *et al.*, 1997).

Investigation of the formation, thickness, composition and residency times of aeroponically-produced root surface thin-films could allow aeroponic cultivation systems to be tuned for the optimal performance of specific crops (Table 1). It would be informative to assess the interplay between these parameters during root surface thin-film formation and retention for different crops. This might inform aerosol delivery regimes and characteristics for specific crops at defined developmental stages to ensure water, nutrient and oxygen uptake supports optimal plant performance.

Productivity within aeroponic cultivation

Yields from aeroponic cultivation can exceed compost or hydroponic cultivation for certain crops (Wyslouzil *et al.*, 1997; Souret & Weathers, 2000; Ritter *et al.*, 2001; Hayden *et al.*, 2004; Kratsch *et al.*, 2006; Chandra *et al.*, 2014). One study reported that yields of aeroponically cultivated basil, parsley, cherry tomato, squash, bell pepper and red kale increased by 19%, 21%, 35%, 50%, 53% and 65% compared to soil culture, respectively (Chandra *et al.*, 2014). Greater saffron bulb growth and unaltered saffron yield has also been reported under aeroponic horticulture (Souret & Weathers, 2000). Aeroponic cultivation was also reported to achieve greater tomato fruit mass when aeroponic and hydroponic cultivation was compared directly (1.95 g/fruit from aeroponics; 1.56 g/fruit from hydroponics) (Wang *et al.*, 2019).

The effectiveness of root crop cultivation by aeroponics depends upon crop variety and method of cultivation. One study reported a mean root storage increase of more than 20 g dry weight for cassava cultivated aeroponically compared with drip hydroponic cultivation (Selvaraj *et al.*, 2019). Another reported potato tuberization to occur 6-8 days earlier than during aeroponic cultivation (Chang *et al.*, 2012). On the other hand, a separate study identified that whilst potato minituber yield increased by 70% compared with hydroponic cultivation, the mean tuber weight was 33% lower (Ritter *et al.*, 2001). In that study, delayed tuberization only allowed one productive cycle over a year, compared with two productive cycles for hydroponically grown potatoes (Ritter *et al.*, 2001). Furthermore, whilst aeroponic-cultivated burdock was reported to accumulate 49% more aerial biomass compared with soil cultivation, the harvestable root biomass was unaltered (Hayden et al., 2004). We speculate that differences between these studies might arise from differing cultivation platforms and environmental- and genotypic variability. For example, (Ritter *et al.*, 2001) attributed delayed tuber formation to enhanced vegetative growth caused by an unlimited nitrogen supply, whilst (Chang *et al.*, 2012) and (Tokunaga *et al.*, 2020) identified variation between tuber yield of distinct potato and cassava cultivars during aeroponic cultivation. Therefore, it would be informative in future to compare and understand the performance of different varieties of specific crops cultivated aeroponically, under various environmental conditions, to identify traits compatible with aeroponic cultivation in particular climates.

Root zone oxygen, plant productivity and aeroponic cultivation

Root zone aeration supports plant productivity by allowing root respiration (Fig. 3a) (Armstrong, 1980; Soffer *et al.*, 1991). Reduced root zone oxygen decreases yield, growth rates, mineral and water uptake (Rosen & Carlson, 1984; Tachibana, 1988; Soffer *et al.*, 1991). In closed growing systems, aeration also prevents the release of gaseous hormones such as ethylene that can inhibit growth (Weathers & Zobel, 1992; Raviv *et al.*, 2008). Aeroponic systems provide the advantage that roots can, theoretically, access all available root zone oxygen, whereas in hydroponic culture, the low water solubility of oxygen means that dissolved oxygen concentrations may need to be closely monitored when cultivating certain plant species to ensure that dissolved oxygen concentrations do not become limiting for plant growth (Jackson, 1985; Goto *et al.*, 1996; Ritter *et al.*, 2001; Wang & Qi, 2010; Mobini *et al.*, 2015; Gopinath *et al.*, 2017). This can be optimized during hydroponics through regular nutrient solution cycling, or bubbling oxygen into the nutrient solution (Fig. 1).

Aeroponics allows artificial elevation of root zone O_2 to enhance yield. One study identified in tomato and cucumber a positive linear relationship between root zone O_2 concentration and growth rates, when root zone gaseous O_2 increased between 5% (v/v) and 30% (v/v), plateauing above ~35% O_2 (v/v) (Nichols *et al.*, 2002). However, to evaluate the viability of this strategy it would be helpful to gain better understanding of the relationship between O_2 concentration and growth rate for other aeroponic-cultivated species.

Relationship between root zone temperature and CO_2 within aeroponic cultivation

In vertical farms, high root zone temperatures inhibit root growth and cause nutrient deficiency, reducing photosynthetic efficiency (Tan *et al.*, 2002; He *et al.*, 2007; He *et al.*, 2010; He *et al.*, 2013; Choong *et al.*, 2016). This inhibition can be reversed in aeroponic horticulture by root zone cooling or CO_2 supplementation (Tan *et al.*, 2002; He *et al.*, 2010; He *et al.*, 2013). For example, cooling the root zone of aeroponic-cultivated lettuce to 20°C increased root surface area and root/shoot mineral content compared with plants grown at tropical temperatures (23 - 38°C) (Tan *et al.*, 2002), and similar root-zone cooling in tropical greenhouses increased lettuce shoot yields (Choong *et al.*, 2016). Furthermore, root zone CO_2 supplementation of aeroponically grown lettuce, with root zone temperatures of 20 - 38°C, increased the Rubisco concentration and protected plants against photoinhibition, potentially due to increased NO_3^- uptake (He *et al.*, 2013). This increased the dry weight of lettuce shoots and roots by 1.8 and 2.5-fold, respectively, but decreased the shoot:root ratio at $CO_2 \geq 10{,}000$ ppm (He *et al.*, 2010). Therefore, adjusting the root zone temperature and CO_2 concentration can improve growth, mineral uptake and nutritional content.

Root exudation and microbial interactions during aeroponic cultivation

Plants release an estimated 20% of assimilated carbon as root exudates, which includes high and low molecular weight compounds that can inhibit or benefit growth (Kuzyakov & Domanski, 2000; Badri & Vivanco, 2009; Baetz & Martinoia, 2014; Delory *et al.*, 2016; Mommer *et al.*, 2016; Huang *et al.*, 2019). It is important to understand the effects of root exudation during aeroponic cultivation because the nutrient solution is recycled for some time within closed systems (Fig. 3a). For example, plant autotoxicity can arise from exuded organic acids within recycled nutrient solutions (Yu & Matsui, 1993; Yu & Matsui, 1994; Asao *et al.*, 2003; Hosseinzadeh *et al.*, 2017). However, little is known about the types, concentrations and variation in recycled root exudates for distinct crop species grown using aeroponic systems, and its consequences for plant performance. Because the physical and chemical properties of nutrient solutions alter when atomized into aerosols (Hinds, 1999), root exudates might alter chemically or precipitate, changing the effects of exudates on plant and/or microbial growth. Plants also release volatile organic compounds (VOCs) into the root zone (Dudareva *et al.*, 2006; Widhalm *et al.*, 2015; Delory *et al.*, 2016; Pickett & Khan, 2016; Vivaldo *et al.*, 2017) that might partition into the aerosol phase (Odum *et al.*, 1996; Sander, 2015) and, therefore, incorporate autotoxic compounds into aerosol droplets (Fig. 3a). Incorporation of VOCs into aerosol droplets will change the aerosol vapour pressure, potentially altering the concentrations of nutrients delivered to the roots. Since root exudate compounds such as the polysaccharide xyloglucan increase substrate cohesion (Galloway *et al.*, 2018), exudate compound(s) might alter thin-film retention and nutrient uptake by changing cohesion and adhesion characteristics at the interface between thin-films and root surfaces (Fig. 2b, Fig. 3a).

Root exudates are important for microbial growth and shaping rhizosphere microbial communities (De-la-Peña *et al.*, 2008; Chaparro *et al.*, 2014; Hugoni *et al.*, 2018; Sasse *et al.*, 2018). There are relatively few studies of root microbiome development during aeroponic cultivation (Fig 3a). One recent study identified that the root-associated microbial community of aeroponically grown-lettuce was dominated by proteobacteria and distinct from microbial communities present on the germination trays or nutrient solution (Edmonds *et al.*, 2020). Given that some bacterial species are unculturable after aerosol dispersion (Reponen *et al.*, 1997; Dabisch *et al.*, 2012; Zhen *et al.*, 2013) and each atomization method affects bacterial membrane integrity and cell survival differently (Fernandez *et al.*, 2019), more extensive characterization of microbial communities at the root-aerosol interface and within the nutrient solution will be informative. This might identify beneficial or inhibitory effects of these microbial communities upon the aeroponic productivity, for a variety of crops throughout their development. This could inform the development of probiotic microbial treatments to support biofertilization and biocontrol, including protection of the crop and aeroponic system from invasion by human and plant pathogens. One method to introduce such probiotics could be to inoculate the seeds at the point when they are moistened to break dormancy and induce germination.

Root morphology and anatomy in aeroponic cultivation

Root morphology and architecture affects aerosol capture and thin-film formation. For example, aeroponically grown roots can have increased root hair abundance compared with hydroponically grown roots (Kratsch *et al.*, 2006), which will in turn influence aerosol capture (Fig. 3b). Given that root hair development is both dynamic and influenced by environmental heterogeneity and the nutrient or water status of plants (Gilroy & Jones, 2000; Vissenberg *et al.*, 2020), it will be valuable to assess how root hairs develop on aeroponically-grown plant species at a variety of developmental stages. More research is required to establish which microscale and/or macroscale root traits are important for aerosol capture at various developmental stages, considering differences between crops. This knowledge might influence the aerosol properties (e.g. droplet size) and nutrient dosing regimen that are administered at each developmental stage to optimize aerosol capture and nutrient- and water-uptake.

Because the anatomy of root cell layers influences nutrient and water uptake (Enstone *et al.*, 2002), it is important to understand how root anatomy might be influenced by aeroponic cultivation. For example, the exodermal hydrophobic barriers differ between the maize root hypodermis following aeroponic and hydroponic culture (Fig. 3b) (Zimmermann & Steudle, 1998; Freundl *et al.*, 2000; Meyer *et al.*, 2009; Redjala *et al.*, 2011). Hydroponically grown maize roots lacked exodermal hydrophobic barriers, whilst hydrophobic barriers were present in the exodermis, 30 - 70 mm from the root tips, following aeroponic cultivation (Fig. 3b) (Zimmermann & Steudle, 1998). Greater depth of knowledge of root anatomical specializations during aeroponic culture would be informative across a wider range of crops, at various developmental stages. We speculate that species with thicker hydrophobic barriers might require longer aerosol atomisation periods, using droplets containing greater nutrient concentrations.

Diel cycles and photoperiod in aeroponic cultivation

The light conditions in indoor farms can be tuned to crop requirements. For example, the photoperiod influences the growth and development of many plant species (Turner *et al.*, 2005; Song *et al.*, 2015). Since the light spectrum influences the morphology and metabolite content, altering the spectrum can adjust the shape, flavour, fragrance or nutrient content of vertically farmed crops (Darko *et al.*, 2014; Dou *et al.*, 2017; Fraser *et al.*, 2017; Holopainen *et al.*, 2018).

The specificity in the timing and intensity of aeroponic nutrient dosing provides opportunities to align daily aeroponic and lighting regimes for optimal growth (Fig. 3a). Daily fluctuations in fertilization could be applied, such as day- and night-specific nutrient mixes. This strategy has been proposed to manipulate the nutrient composition of salad crops (Albornoz *et al.*, 2014), capitalizing on diurnal stomatal opening and transpiration stream activity. By providing greater nitrogen concentrations to the roots during the dark period and lower concentrations during the light period, nitrogen over-accumulation within leaves can be prevented (Albornoz *et al.*, 2014). Diel fluctuations in nutrient concentrations also appear to increase the yield of some tomato varieties (Santamaria *et al.*, 2004).

The relationship between the light/dark cycle and the endogenous circadian rhythm influences plant growth and development. Laboratory experiments with *Arabidopsis thaliana* identified that mismatch between the endogenous circadian period and period of the day/night cycle reduces growth and causes mismanagement of transitory starch reserves (Dodd *et al.*, 2005; Graf *et al.*, 2010). This relationship between circadian rhythms and light conditions is important for vertical farms. For example, lettuce growth rates can be estimated from circadian rhythm parameters of the seedlings, and this information used to transfer the best-performing seedlings from the nursery to the farm (Moriyuki & Fukuda, 2016). This can maximise the number of individual plants meeting certain growth criteria (Moriyuki & Fukuda, 2016). Similarly, the timing of artificial light and dark cycles during tomato cultivation influences tomato growth and survival (Highkin & Hanson, 1954). This might explain why humans selected for a longer circadian period and later circadian phase during tomato domestication to higher latitudes with longer photoperiods (Müller *et al.*, 2016; Müller *et al.*, 2018). Therefore, knowledge of circadian biology can be exploited to optimize daily lighting regimes in vertical farms to maximise productivity. In future, it might be possible to exploit integrated plant growth models that incorporate knowledge of circadian rhythms (Chew *et al.*, 2014) to optimize photo- and thermoperiodic conditions for specific vertically farmed crop varieties.

Conclusions and recommendations for future work

We conclude by suggesting strategic areas of future research to underpin increased productivity and sustainability of aeroponic vertical farms.

1. Understand why aeroponic cultivation can be more productive than hydroponic or soil cultivation, to inform crop breeding and farm engineering. Potential testable hypotheses concern altered photosynthetic performance, oxygen availability, stomatal physiology and water relations, nutrient supply, carbohydrate partitioning, and resource competition within the root- and aerial-phases of plants in growing trays. This also involves the identification of why certain genotypes are better suited to aeroponic cultivation, because this might allow the breeding of varieties with enhanced performance during aeroponic cultivation or extension of the range of crops that can be cultivated with aeroponics.

2. Understand root developmental architecture under standardized aeroponic conditions for a key range of crops at a variety of developmental stages, and how this differs from hydroponic- and soil-based cultivation. Growing conditions reflect the local environment, technologies and crop varieties, so comparing model crops under standardised conditions might provide insights to inform cultivation conditions.

3. Understand the relationship between aeroponic droplet size, nutrient content, droplet deposition and plant performance. This is important to identify aerosol generation technology or regimes that are appropriate and most profitable for each crop at a variety of developmental stages. It will also inform optimization of crop quality and nutrition within aeroponic systems.

4. Understand the relationship between aeroponic fertilization and daily (24 h) cycles upon crop performance. The relationship between daily cycles of environmental conditions (e.g. lighting, airflow, temperature, humidity), aerosol supply and composition, and crop metabolism presents opportunities to adjust crop performance, appearance, nutrient composition and flavour.

5. Establish experimental and analytical frameworks for comparison of vertical farming technologies for a range of crops. Frameworks should collate productivity metrics and resource consumption to allow assessment of the environmental and economic sustainability of each technology. This could underpin more rapid technological development and collaboration towards improved food security.

6. Understand the nature and recycling of root exudates within the nutrient solutions of closed aeroponic systems. This includes identification of recirculated compound types, their crop species-dependency, chemical and physical changes in exudates caused by aerosol generation, and crop performance impacts. This is important for greenhouse and vertical farm engineering, and pairing crops with optimum cultivation technologies.

7. Understand how different aeroponic atomization methods affect microbial community structure at the root-aerosol interface, and the consequences for crop productivity, crop protection, food safety and farm engineering.

Author contributions

The article was conceived by BME, JRF and AND. CAG designed and produced the figures. BME, LRM, CAG, BR, JRF and AND wrote the article.

Acknowledgements

AND is grateful to The Royal Society for awarding an Industry Fellowship (SIF\R2\182028). This work was funded the UK Biotechnology and Biological Sciences Research Council (SWBIO DTP awards BB/J014400/1 and BB/M009122/1, and Institute Strategic Programme GEN BB/P013511/1) and Innovate UK (Industrial Strategy Challenge Fund).

Figure legends

Figure 1: Hydroponic irrigation methods include drip irrigation, deep water culture, nutrient film technique and flood and drain. In drip irrigation systems, a nutrient solution is fed into a variable growing medium that supports the root system. Deep water culture submerges roots in nutrient solution, with plants supported by a membrane preventing aerial tissue immersion. Nutrient film method exposes the bottom of the root bed to a flowing nutrient solution whilst the top of the root bed remains exposed to air. Flood and drain systems immerse the root system with a nutrient solution for a period of time. Subsequently, this is drained and collected into a reservoir to aerate the root bed. Aeroponics atomizes the nutrient solution, which deposit onto the root surface. Aero-hydro systems atomize nutrient solution whilst exposing the lower root bed to recirculated nutrient solution. Air pumps are common during deep water culture and can be added to other systems to increase root zone oxygen.

Figure 2. Models for irrigation cycle and nutrient exchange during aeroponic horticulture. (a) Proposed aeroponic thin-film replenishment cycle. During the deposition phase, aerosol droplets deposit onto the root surface. Smaller aerosol droplets might access spaces between root hairs. Droplets might also collide, gain volume and exit the aerosol, landing on roots or collecting into the nutrient solution at the bottom of the bed. Retention refers to the accumulation of thin-films over areas of the root surface that persist for a period of time. These are likely to be heterogeneous, leading to heterogeneous gas exchange and nutrient uptake. During the decay phase, thin-films will be removed by evaporation and gravity in a manner dependent upon root architecture, surface tension and relative humidity. Thin-films are replenished by generation of further aerosol. (b) Model for nutrient uptake and gas exchange within an aeroponic system. As aerosol droplets become deposited, the quantity of gas exchange between the root and the environment will decrease and nutrient availability increase.

Figure 3. Interactions between aeroponically grown plants and their environment. (a) Interactions between the aerial and root phases and their environment. Light/dark conditions and diel nutrient supply cycles might be optimized to enhance plant productivity. The root zone CO_2 and O_2 concentrations affect plant productivity and have potential for manipulation to enhance productivity. Volatile organic compounds (VOCs) released into the root zone might alter the aerosol properties and nutrient availability. Interactions between root exudate compounds and nutrient solution ions will affect thin-film development and retention. Root exudates will shape the aeroponic microbial community and microbial exudates might, in turn, affect crop productivity and protection. (b) Root architecture and anatomy can differ between hydroponic and aeroponic cultivation, with aeroponically-cultivated roots having increased root hair abundance and hydrophobic barriers in the exodermis (shown in red) compared with hydroponic cultivation.

Table 1. A variety of factors will influence root thin-film thickness and retention during aeroponic cultivation. The aerosol phase describes factors that influence airborne aerosol properties, and the thin-film phase refers to factors that influence the deposition, retention and decay of root-surface aqueous films. In addition to aerosol physics and chemistry, thin-film thickness and retention will depend upon crop type.

	Property	**Characteristics**	**Outcomes**	**References**
Aerosol Phase	Aerosol particle size distribution	Most atomisation techniques will not generate a monodisperse ensemble of aerosol. Aerosol droplet size may change after generation.	Increases in size distribution introduce variation in deposition efficiency across the root system. Larger droplets are more likely to deposit on roots close to the point of aerosol generation.	(Shum *et al.*, 1993) (Nuyttens *et al.*, 2007)
	Aerosol particle velocity	After generation, aerosol droplet velocity is generally likely to decrease.	Aerosol particle velocity will impact the aerosol distribution throughout the root system, impacting uniformity of aerosol capture efficiency.	(Shum *et al.*, 1993)
	Hygroscopicity	The chemical composition of an aerosol will determine its reaction to changes in the relative humidity of the surrounding gas phase. Water will evaporate out of, or condense into, the droplet in response to imbalances	Changes in droplet size distribution. Changes to nutrient solution electrical conductivity and pH.	(Mitchem *et al.*, 2006) (Odum *et al.*, 1996) (Topping *et al.*, 2005)

		between the water activity of the droplet and root chamber environmental conditions.		
	Electrostatic Effects	Some atomization processes can induce electrostatic charges in aerosol.	Given that both the root and aerosol phase can have charge effects, aerosol droplets might be repelled or attracted to the root system.	(Xi *et al.*, 2014)
Thin-film Phase	Evaporation rate	Rate of water evaporation from the thin-film to the gas phase.	We predict that evaporation of water from the thin-film will alter pH and electrical conductivity of thin-film nutrient solution.	(Sultan *et al.*, 2005)
	Gravity	We speculate that at a certain volume, the thin-film will accumulate sufficient mass that gravity will cause it to drip from the root.	We speculate that gravity effects will produce crop-specific and developmental stage variation in the refresh rate of the nutrient solution on the plant root.	This is a testable hypothesis
	Root system architecture	Spatial configuration of all roots (primary, lateral, accessory roots) in three dimensions, which changes during plant development.	Root system density and configuration is predicted to affect aerosol droplet capture efficiency, thin-film thickness, and thin-film residency- and replenishment rate	(Wyslouzil *et al.*, 1997) (Osmont *et al.*, 2007)
	Root hair density and length	Root hairs are tubular epidermal protrusions from the root surface. Root hair properties such as	Increased root hair density and length is predicted to capture droplets more effectively than glabrous roots or	(Wyslouzil *et al.*, 1997) (Grierson *et al.*, 2014)

	density and length affect the root surface area available for absorption of water and nutrients.	roots with shorter/ fewer hairs, which will affect thin-film formation and residence time.	
Root surface properties and root exudation	Topological features of root surface, and variety of compounds that roots exude by passive and active processes.	We predict that root surface characteristics and the root exudate mixture will affect the formation and residency of thin-films by altering adherence/coherence of aqueous droplets on the root surface.	(Badri & Vivanco, 2009) (Galloway *et al.*, 2018)

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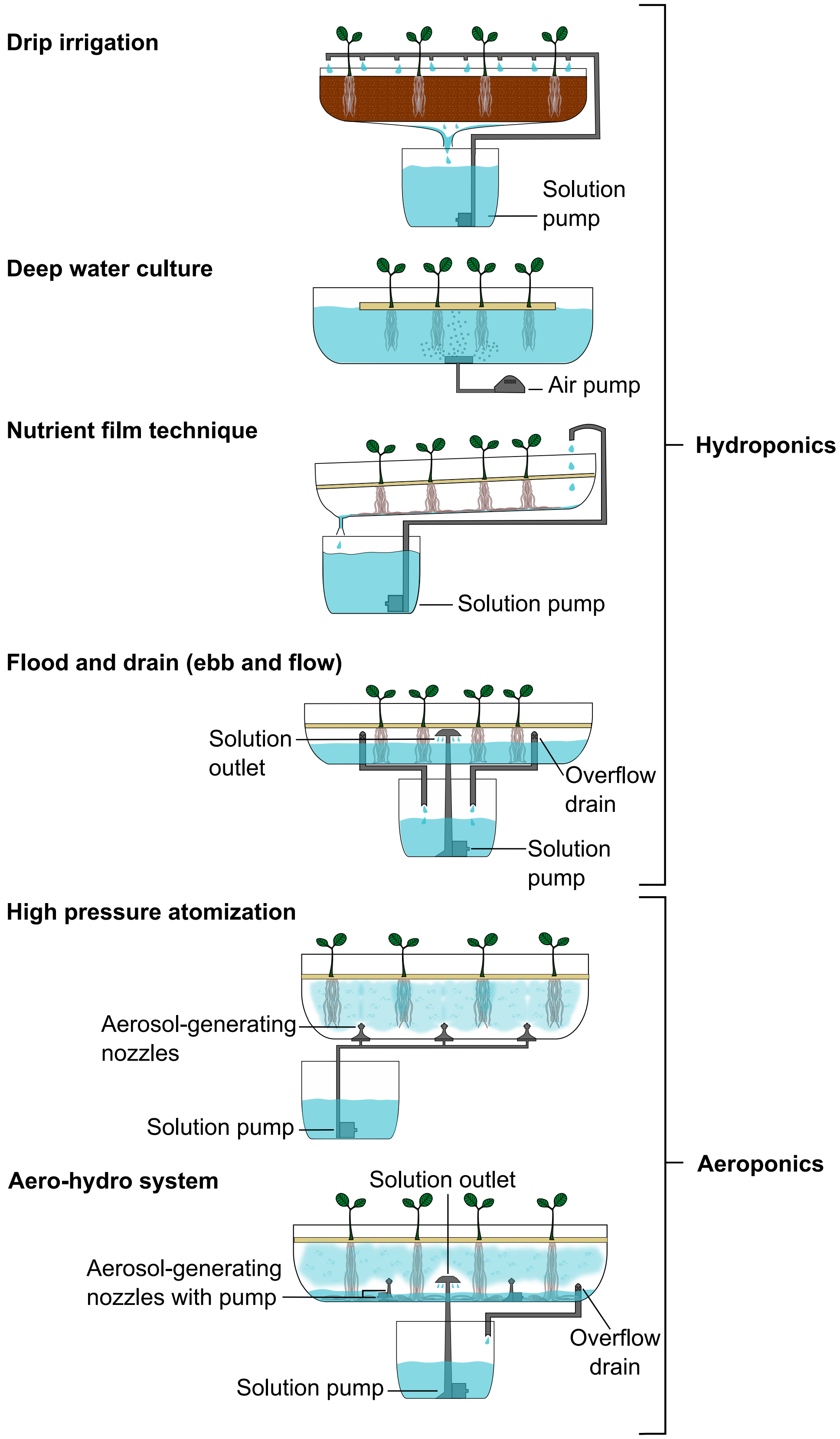
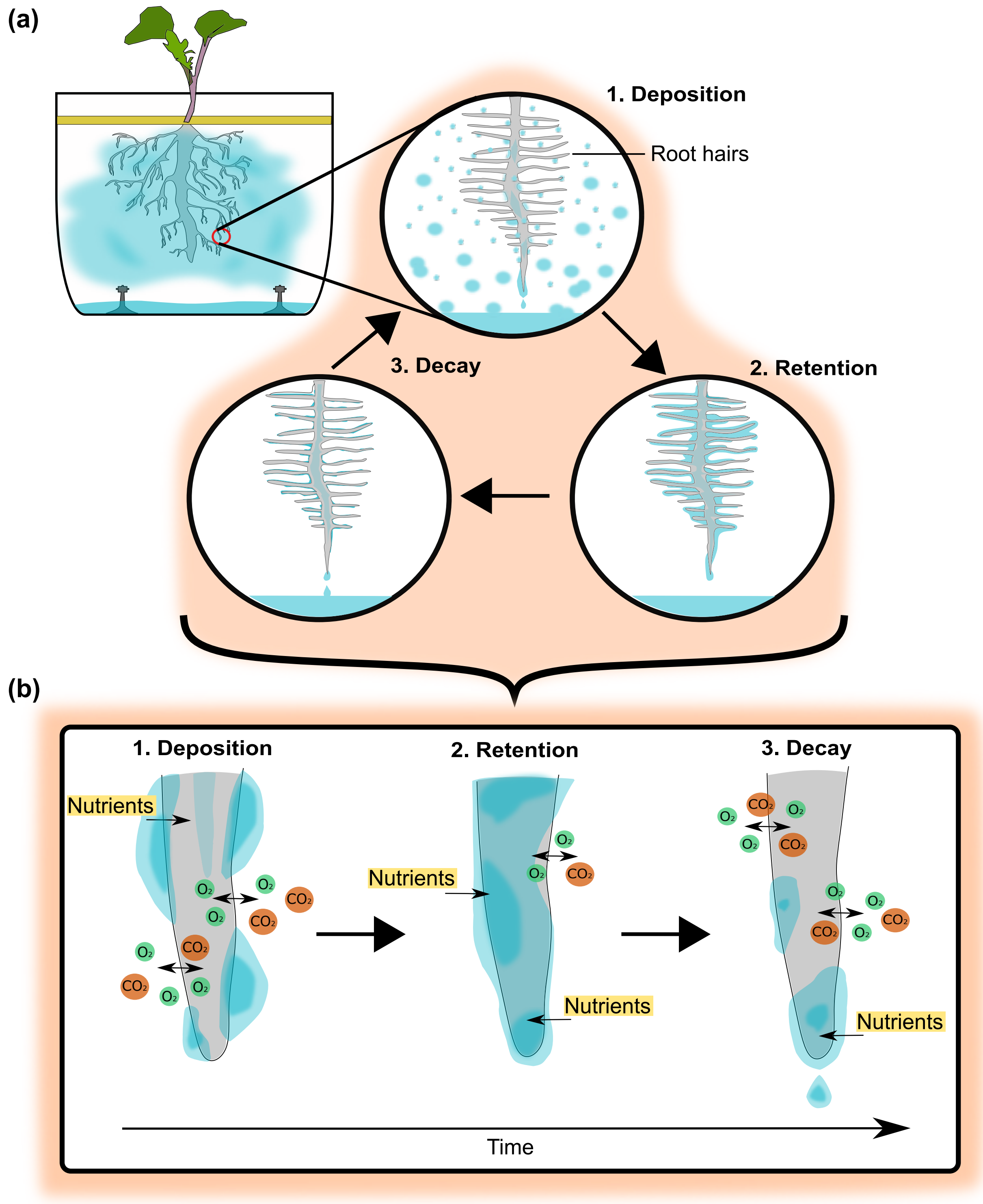
Eldridge et al. Fig. 1



Eldridge et al. Fig. 2



Eldridge et al. Fig. 3