Management of the greenhouse microclimate in relation to disease control: a review

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Abstract – The microclimate of the greenhouse when considered as a relatively homogeneous entity is well understood, and there are models of crop growth, and environmental parameters that enable expert decision-support systems to be derived, and automatic environment controls affecting productivity to be designed. However, the microbial microclimate of pathogens in the boundary layer on the phylloplane is poorly understood, and disease escape measures are not yet incorporated into automatic environment control systems. Because biocontrol microorganisms necessarily inhabit the same ecological niche as microbial pathogens, describing environments on the phylloplane that encourage biological control without also enhancing pathogenesis presents very difficult engineering challenges. This review examines the dilemmas in designing environments that maximise productivity, encourage disease escape, and permit biological control.

expert system / greenhouse microclimate / biological control / disease forecasting / epidemic modelling / disease escape

Résumé – Mise au point : la conduite du microclimat en serre en relation avec le contrôle des maladies. Le microclimat des serres, lorsqu'il est considéré comme une entité homogène, est bien connu. Il existe ainsi des modèles simulant la croissance des plantes et les paramètres environnementaux qui permettent d'élaborer des systèmes experts d'aide à la décision et des dispositifs automatiques de contrôle de l'environnement pour améliorer la production. Cependant, le microclimat qui affecte la flore pathogène dans la couche limite du phylloplan, est mal connu, et, à l'heure actuelle, on ne sait pas comment incorporer les mesures d'échappement aux maladies dans les systèmes de contrôle automatique de l'environnement. Comme les micro-organismes utilisés pour la lutte biologique occupent nécessairement la même niche écologique que les organismes pathogènes, la description des environnements sur le phylloplan qui favorisent la lutte biologique sans accroître le développement des organismes pathogènes, présente de grandes difficultés technologiques. Cette mise au point examine le dilemme auquel il faut faire face pour la mise au point d'environnements qui permettent d'obtenir de bonnes récoltes, favorisent l'échappement aux maladies et, en même temps, permettent la lutte biologique.

systèmes experts / microclimat en serre / lutte biologique / prévision de maladies / modélisation épidémiologique / échappement aux maladies

1. INTRODUCTION

In the latter part of the twentieth century, concerns about food safety, environmental pollution, worker safety, and the rapid development of resistance to chemicals stimulated extensive research in the development of systems for Integrated Pest and disease Management (IPM) and alternatives to chemical pest and disease control in greenhouse crops [1]. While biological control agents for most arthropod pests of greenhouse crops have been

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developed and successfully applied in greenhouse crops around the world [141], the development and commercial application of biological control agents for diseases has, in general, lagged behind that for arthropod pests [42]. The slower development and commercial acceptance of biological controls for diseases has been attributed [43] to the complexity of the systems involved, uncertain economic returns for companies that develop them, difficulties in matching the microclimate requirements of biological control agents to the microclimates in greenhouses and to established climate management practices designed solely for productivity.

For the most part, blueprint schedules for greenhouse crop production have evolved empirically [31, 102, 105]. With the advent of expert systems in advanced greenhouse technology [127], it has become necessary to quantify the several factors contributing to productivity, as well as those that reduce it, and to translate their effects into real-time input for integrated expert systems. However, the expert content and jargon of such decision support systems have to be fully intelligible to the grower [146], who must therefore have significant input into their design [26]. Indeed, Day [31] has argued that simple approaches to modelling and forecasting greenhouse environments have achieved, and can be expected to achieve, practicable control of crop growth. Empiricism with local calibration is an essential feature in the implementation of optimised models.

Much of the work designed to enhance productivity has been done with scant attention to its implications in making crops more or less susceptible to diseases and arthropod infestations [12, 63, 80]. Since diseases and arthropod damage can account for around 30% of crop losses [63], the direct effects of environmental factors on pathogens and arthropods, and on commensal and introduced biological control microorganisms, as well as the stresses that predispose crops to infection [109, 125], cannot be ignored. Moreover, because of the many environmental, toxicological, and resistance problems resulting from pesticides, alternative methods of control are research priorities [141]. In general, the environmental factors promoting biological control by bacteria and fungi, namely low water vapour pressure deficits (VPD), free water on leaf and fruit surfaces, and moderate temperatures, are very similar to those promoting infection by pathogens. If at all possible, then, those environmental factors must be managed with great precision. Failing this, however, it is very desirable to augment this approach with other disease escape measures, such as genetic resistance to the primary pathogens in the host plant (always the primary control measure), eliminating the inoculum by, for example, pasteurising media, disinfesting water and hydroponic solutions, the use of dis-

ease-free planting material, modifying plant habit and spacing to reduce the duration of surface wetness that invites infection, and maintaining good greenhouse and personal hygiene to minimise pathogen dispersal [12, 79].

In unheated, plastic-covered greenhouses common in the Mediterranean basin, the microclimate is more influenced by the outside weather than is that of the heated greenhouses, sometimes with supplementary lighting, in higher latitudes [128]. Insolation, too, is affected by latitude. Even the pattern of the epidemic is different. Whereas in the Mediterranean, grey mould in tomatoes mostly takes the form of leaf and fruit spotting [128], it appears rather as basal stem lesions in Canada and northern Europe. It is therefore impossible at present to construct a generalised model for a particular pathogen in a particular crop, and this is another reason why growers' empirical input is so important.

However, given that there are certain basic premises for epidemics everywhere, it is incumbent on the modeller to be able to predict the onset of dangerous conditions, such as the deposition of dew [71], and then to arrange immediate switching of reversing conditions, in this example, to increase air temperature and hence increase VPD, increase through-the-crop ventilation, and expel moist air to the outside. This is less easily done in unheated, plastic-covered greenhouses without automatic control, where the grower's reaction to rain is to close the openings, thereby lowering VPD, and risking the deposition of dew [128].

Prediction systems, imperfect as they may be, can be incorporated into comprehensive and interactive electronic decision support systems. Clarke et al. [5, 26] and Jewett et al. [85] described such a holistic, hierarchical expert system for greenhouse crops. A change in the hierarchy at one of its six levels affects the other five, so that, for example, a temperature change cascades to affect plant infection, pesticide efficacy, biological control activity, pests and disease vectors, and ultimately productivity, and the grower's profit. The grower's response to these events is largely empirical but the integration of management protocol into automatic environment control systems can be achieved [84]. There is also the opportunity to predict the effects of disease on yield from models of crop growth and epidemic development [119].

This paper discusses greenhouse climate manipulation for disease control in the phyllosphere and identifies the gaps in the knowledge that are hindering further development and application of biological disease control in the greenhouse industry.

2. THE CROP MICROCLIMATE

The greenhouse microclimate as a whole is distinct from, but not independent of, the outdoor climate. Bailey [1985] termed this the greenhouse macroclimate. It is far from uniform, but is often monitored and controlled as though it were, ignoring the boundary layer microclimates at plant surfaces. Parameters such as air temperature, humidity, CO_2 concentration, light levels, air movement, pH, and osmoticum, can be manipulated to some extent to regulate crops on a time schedule, and to obtain economic production. The possible degree of climate control depends on the greenhouse structure, the climate outside, the available climate-control equipment, and the skill and knowledge of the greenhouse operator [31].

The development and widespread adoption of computerised, climate-control systems for greenhouses in the last 20 years have greatly enhanced the ability of growers to manipulate the microclimate inside greenhouses. Computer software for climate control in commercial greenhouses [146] has evolved in a heuristic way to a level where a grower, with observations of the crop status, and with experience and skill, can adjust settings and trajectories for climate variables to control crop growth and development, but less confidently, to avoid conditions that would stress the crop and predispose it to disease or arthropod pests.

2.1. Greenhouse structures and climate control equipment

Greenhouses vary in structural complexity from simple plastic-film covered tunnels, heated or unheated, with or without assisted ventilation, to tall, multi-span, gutter-connected units covering several hectares. The trend towards taller and larger greenhouse units favours the uniformity of lighting, since shadows cast by higher structural members move around more. It enhances natural ventilation by increasing the "chimney effect" [132] and it creates a larger buffer space above the crop for better mixing of ventilation air. Thus, having this buffer space allows for more precise control of humidity within the crop at low VPDs. The optimum height of greenhouses seems not to have been determined, but the gutter heights for new construction increase each year. Computational fluid dynamics techniques have already been applied to assess air movement patterns with different greenhouse vent designs [96, 104], and further application is needed to optimise the design of greenhouses and their venting and air circulation systems which are so critical for effective gas exchange at the phylloplane.

Although the term glasshouse is commonly used in Europe for greenhouses, on a world-wide basis most new greenhouses are not covered with glass, but with plastic film, usually polyethylene [135]. Whereas much progress has been made in horticultural film technology [108] "designer films" with spectral transmission properties tailored to specific crops have yet to be realized in practice. There is currently a debate over UV blockers; some manufacturers have removed them from their films to allow transmission of the UV light perceived by pollinating bees [91, 92], while it is known that exclusion of near UV light is effective in reducing the sporulation of *Botrytis cinerea* [150]. Greater wavelength selectivity and better understanding of the effects of specific wavelength bands are needed before designer films with disease control benefits can be realised.

Depletion of the earth's ultraviolet (UV) radiation absorbing ozone layer is changing the radiation environment, especially at high elevations. With the increase in UV radiation at some locations and at some periods of the year, it is becoming more important to reduce the radiation and heat stresses [109] that predispose greenhouse crops to disease and pollination problems and that deactivate biological controls. Automatic shading systems [86], shade curtains [151] and shade paints [59] can be employed in addition to wavelength selective greenhouse covers to reduce radiation stresses. Fogging with droplets of <10 μm that evaporate before reaching the plant [65], evaporative cooling and surface spray cooling systems can also be employed to reduce heat stresses and to combat high VPDs that often impede biological controls (Sect. 3). These systems, however, require high purity water which is often in short supply in those regions where they are most needed and thus systems for water purification and conservation are important for biological control.

Radiation to and from leaves and fruit, and convective heat transfers, can lead to tissue temperatures significantly different from ambient air temperatures [29, 126, 129], and cooler leaves often are sites for dew deposition [72]. Dew and other forms of surface wetness invite bacterial and fungal pathogens (Sect. 3.1.1).

In humid regions or during some periods of the year, dehumidification is necessary to avoid condensation on leaves or on greenhouse surfaces from which it may drip and splash disease propagules to neighbouring plants. Simultaneous heating and ventilation is the most practical and effective method of expelling humidity from greenhouses [132] but it is energy intensive. Heat exchangers that can preheat incoming ventilation air with latent and sensible heat recovered from exhausted greenhouse air [16, 120] would be effective at reducing the cost of dehumidification if they could be

economically incorporated into greenhouse designs. A simple design change from a semi-circular to a gothic arch shape for film covered greenhouses has been effective at enhancing condensation runoff from the underside of greenhouse films to drip-collecting gutters. Improvements in the effectiveness and longevity of additives and spray-on coatings for antifogging films would further enhance this important mode of dehumidification in both heated and unheated greenhouses.

Like the range of complexity that is found in greenhouse structures, climate-control equipment also varies in complexity. Relatively simple systems have any combination of manually operated ventilators, air-moving fans, forced air heaters, CO_2 burners, foggers, shade or thermal curtains and piped steam or hot-water heat systems. In more complex systems each piece of equipment is controlled by separate thermostats or timers. However, in the most advanced and integrated systems, equipment is computer driven to achieve setpoint trajectories [84]. Integration of plant response measurements with automatic climate control could in the future give the precision in crop management sought by growers to meet marketing constraints, such as flowers for Christmas and Easter or continuity of production for vegetable markets. Climate controls also have the potential to avoid conditions favourable to disease, but are rarely so used.

Notwithstanding the capabilities of modern computers, there are several reasons why precision in climate control is not realised in practice [31, 146], not least being the grower's acceptance (or suspicion) and mastery of the software. As experience in constructing a comprehensive expert system for just one crop has shown [127], the adjustment of one parameter has a cascade effect on all other parameters. Reconciling expert opinions from different disciplines is extremely difficult, if not impossible; to expect a single grower to achieve a workable balance is hardly feasible. And software is usually programmed by technicians with little or no experience of horticulture. To master the software currently available, a grower has to learn how to programme upwards of 150 parameters per zone [140]. He must observe greenhouse and crop performance on a daily basis, and then continually re-adjust the parameters as the outdoor climate fluctuates and crop status changes. Given the tasks that a grower must complete each day, optimizing the adjustment of computer parameters is an overwhelming task that often goes undone.

In practice, greenhouses are partitioned into often too few control zones each with centrally or even peripherally located temperature and humidity sensors. The assumption is invalid that each zone behaves as a perfectly stirred reactor [137] and that a single set of sensors can measure the true spatial average climate in a zone.

There can be steep vertical and horizontal climate gradients. There are also marked gradients in photosynthetically active radiation (PAR) depending on the orientation of the greenhouse and plant arrangements within, shading from the structural members [60] and from adjacent crops [62, 136]. Despite stirring by variously sited fans and ducts, there are also gradients in temperature ([4, 87, 144], Fig. 1); and in humidity ([87], Fig. 2). Carbon dioxide, with its sink at the stomata, may even be detrimentally depleted in a canopy in a tightly closed greenhouse [113] with its soil source covered by plastic, and the air not stirred enough. Furthermore, significant errors in climate measurement can be made if sensors are not properly shielded from direct sun to avoid solar heating, or aspirated to minimise boundary layer effects, or checked and calibrated regularly to ensure accuracy. Improved designs of structures, such as the high gutter houses with their better climate buffering capacity, and improved climate control equipment, such as properly balanced hot-water heat systems, can improve the spatial uniformity of climate in the cropping zone. Such improvements reduce the likelihood of hot, cold, shaded, stagnant, or dripped-on spots that would predispose a crop to disease.
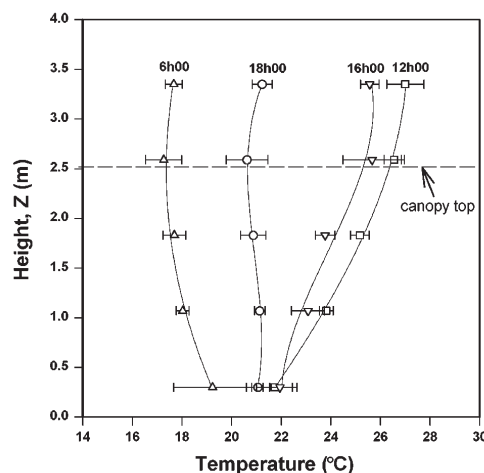
Figure 1. Vertical temperature profiles of the macroclimate in a low eave (2.3 m) glasshouse with a fully developed cucumber canopy, on March 9, 1996 at Harrow, Ontario, Canada. Data points at each sampling height are the mean of readings from six temperature sensors spaced 76 cm apart across the glasshouse. The sensors were fitted with concentric-tube radiation shields. Each sensor was aspirated by drawing air horizontally through the centre tube of the radiation shield at a velocity > 2 m/s.

Midnight Relative Humidity (%)

Noon Relative Humidity (%)
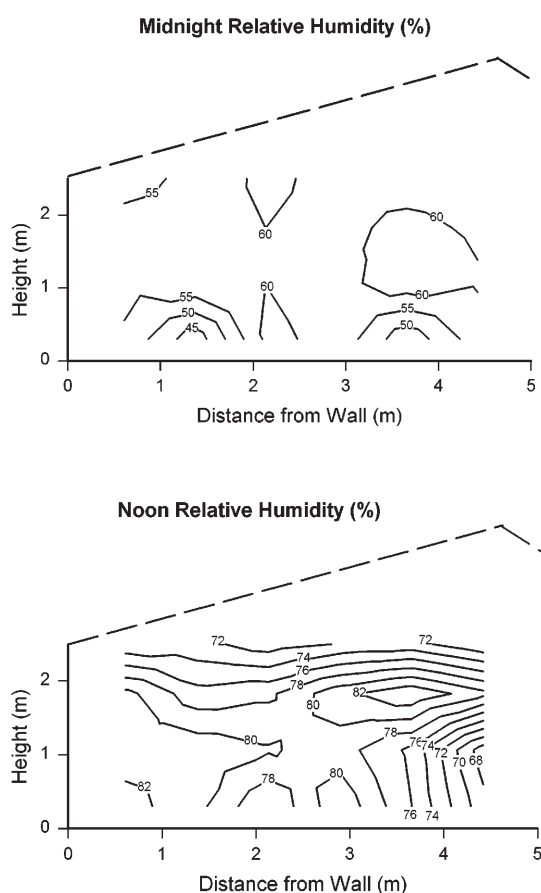
Figure 2. Vertical relative humidity profiles of the macroclimate in a low eave (2.3 m) glasshouse with a fully developed cucumber canopy, on March 9, 1996 at Harrow, Ontario, Canada. These profiles were derived from the readings of a 4 × 6 grid of relative humidity sensors (Model 1H-3602-C, Hycal Co., El Monte, CA, USA) spaced 76 cm apart. The relative humidity sensors were shielded and aspirated by the same methods as described in the caption for Figure 1.

The algorithms for control of temperature, artificial shading, humidity, and CO_2 interact in ways that depend on whether the whole system is cooling or heating. Conflicts arise, for example, when opening ventilators to release surplus hot air, which will adversely affect humidity and CO_2 concentration. The use of fogging to cool the atmosphere has the risk, in overrun, of depositing water on leaves and fruit. Such conflicts have, for the most part, been unresolved by computerised control [31, 146]. Ultimately the grower must make the reconciliation between maximizing timely production and controlling pests and diseases.

2.2. Modelling the greenhouse microclimate

Greenhouse microclimate at the level of the phylloplane where disease and growth processes occur, is difficult if not impossible to measure. Instruments, however small and aspirated or not, alter the microclimate by shading, by heat conduction, or by impeding gas exchange [148, 149]. Thus, to control greenhouse microclimate optimally, models to predict the microclimate [144] at the phylloplane must be based on measurements made some distance away. Microclimate variables have been modelled (Tab. I) using mechanistic, black box, neural networks, fuzzy logic, artificial intelligence, expert systems, computational fluid dynamics, etc., with varying degrees of success.

Mechanistic models are useful because they help to explain and simulate the physics of the microclimate and they can lead to improved equipment and control algorithm design, but they are often too complex to be used for control. Simple, yet robust dynamic mathematical models developed by system identification techniques are better suited to greenhouse control applications [31, 143]. Processes with fast responses to microclimate, such as photosynthesis and transpiration, lend

Table I. Some greenhouse crop-climate models.

Components	Processes	References
Entire greenhouse	Energy balances	14, 92, 134
CO_2	Source and sink interchanges	97, 134
Evapotranspiration	Gas and energy flows	52, 130, 152, 153, 154, 155, 156, 164
Humidity	Water vapour dynamics	6, 20, 131, 168
Surface wetness	Dew formation and guttation	24, 39, 57, 71, 148
Radiation	Radiant energy flows and photosynthesis	58, 135, 156
Temperature	Heat flow patterns	143
Ventilation	Gas flow dynamics	95, 103, 152

themselves to automatic model-based control, whereas processes with long-term responses such as crop growth and development are better left to the control of the grower with support from decision-support systems [146].

Despite much theoretical modelling, very little progress has been made in practice to implement models and optimal control schemes. For growers to accept them, model-based controls must be demonstrated to have a direct benefit in terms of a production management problem, such as biological control of disease. For the control companies [139], models must be designed to be universally applicable to different crops. They must be easier to use and independent of hardware before they will be implemented in commercial systems. This will require the development of universal protocols for information exchange between greenhouse computer systems [84], and object oriented software for greenhouse control that is transportable between systems [53–56]. Decision-support systems [26] advise the grower how to apply models using information and knowledge from many different sources.

2.3. Modelling crop response

Like microclimate variables themselves, the response of crops to microclimate is difficult if not impossible to measure continuously and instantaneously. The delays in responses are too long, and there are no models of long term responses of crops to trajectories of microclimate variables which might help in designing optimal control strategies. It is for this reason the "speaking plant" approach, where plant responses are measured and continuously fed back to control systems [66], has not been successful in practice [31].

The methodology for deriving optimal control is still debated and sound validation of models is often lacking. Optimal control approaches using crop models are discussed by van Straten et al. [146]. Van Pee and Berckmans [143] reviewed a number of crop response models, few of which have been validated. In a study of economic benefits, Van Henten et al. [140] estimated there was a 15% increase in profits when a lettuce crop was optimally controlled with a growth model rather than by empirical methods. TOMGRO, a greenhouse tomato growth and development model, has undergone extensive development and validation [32, 33, 73, 88] but it is too complex to be applied in commercial greenhouses. An example of a successful application of a simple optimal-control system in commercial greenhouses is the "Greenhouse CARE System" [48, 49], a decision-support system for scheduling flowering and controlling

height of Easter lily (*Lilium longiflorum* Thunb.) based on night and day temperature settings. It identifies production goals for flowering date and plant height; identifies intermediate milestones using phenological data readily collected by the grower; monitors them, and compares them with performance control charts; quantifies the need for management changes with feasible options; and recommends control actions to the grower. Another system, SERRISTE, that determines set points for computer control of the macroclimate, was developed by Martin-Clouaire et al. [101] but it does not seem to have been implemented commercially. SERRISTE is the only model to have considered disease escape, although only from macroclimate data.

Whereas there are numerous disease forecasting models based on weather data for field crops and orchards (Sect. 3.6), there are few disease forecasting models that can predict the onset of dangerous conditions in greenhouse crops. Nor can they be used as the basis of a rapid enough computer control reaction to reverse those conditions. This is surprising given that data to implement such models are routinely collected by the greenhouse computer systems and unlike the field situation, there is opportunity to manipulate climate in greenhouses. Modelling of crop response to microclimate once an outbreak has occurred might appear to be unnecessary when the objective is to avoid disease altogether. However, while they could prove invaluable in managing secondary phases of an epidemic and enhancing biological or chemical control, few such models are reported [119].

In all diseases of plants initial host-pathogen interactions occur at the surface of the plant, and it is important to recognise that models of the greenhouse macroclimate (sensu [5]) do not necessarily describe conditions at the phylloplane. For example, the computer's recognition of potential or actual dew deposition on leaves can only be made with at least simultaneous monitoring of temperatures of air and both sides of leaves, as well as of VPD and other parameters such as wind velocity and radiation. We believe this field to be a major research priority; connections between greenhouse macroclimate and microclimate of the phylloplane have yet to be made, and computer programmes are not yet ready to recognize, and to institute reversal of disease-threatening conditions at the plant surface.

There follows a discussion of the microclimates in which pathogens and their commensal microorganisms live, and which have to be described more accurately if diseases are to be controlled by changing the environment, as well as by enhancing the environment for hyperparasites, antagonists and competitors.

3. THE MICROBIAL MICROCLIMATE

Within the greenhouse, microclimate is a term that has to be qualified by magnitude. Thus, horticultural literature speaks of the greenhouse macroclimate [5] or the microclimate as an entity distinguished from the climate outside. However, within the greenhouse, within-canopy, and headspace microclimates are distinct. So are microclimates of potted plants on the ground or on a bench, ventilated or not. The microclimates in tall row crops are again distinct, and depend on whether they grow in a soil groundbed or in a hydroponic system with plastic completely covering the ground, with or without forced air ventilation, and with various heating and cooling systems [12].

With respect both to infection and biological control, the microclimate in the boundary layer [17] of the phyllosphere is of profound importance, but again, the term is relative.

For epiphytic bacteria, both parasitic and saprophytic, the boundary layer is 2–3 µm thick, in which there is presumed to be little or no air movement. There are gradients of oxygen and water vapour from the stomata outwards, and CO_2 inwards, at least during active photosynthesis. Bacteria in lenticels, stomata, and intercellular spaces are either in a water film, or in a very low VPD.

For fungal spores, the boundary layer is 10–30 µm, with correspondingly very steep gradients, while for sporulating fungi with long conidiophores and spore chains, the boundary layer is 300–400 µm, with lessening gradients. Dispersable terminal spores on long chains as in the Erysiphales and *Alternaria* spp., for example, are presumed to be in a moving air layer, even though they can still be below leaf hairs [64, 162]. Conidiophores of some Peronosporales, like *Bremia lactucae* Regel, and the Hyphomycete *Botrytis cinerea* Pers.:Fr. are hygroscopic, and respond to changes in VPD to achieve spore release and dispersal [75, 77].

Technical difficulties in measuring climate parameters in the ill-defined boundary layer [17, 148, 149] preclude other than inference as to its nature as a habitat. Even the thickness of the layer can be only loosely defined by the size of the organism it contains. However, for physiologists and pathologists, it is best regarded as an indeterminate layer on the phylloplane, with, probably, very steep gradients in temperature, VPD, and gas concentrations. For engineers, there are the velocity boundary layer, the thermal boundary layer, and the concentration boundary layer [74].

3.1. Water

3.1.1 Surface wetness

It is axiomatic that all fungal spores and bacteria require a wet host surface to achieve infection. In the phyllosphere, infection of the undamaged cuticle of leaf, stem, or fruit from fungal spores occurs after the spore germinates in a drop of water. Typical of the many fungi that penetrate the cuticle is the ubiquitous grey mould pathogen *Botrytis cinerea*. Its conidium has a mucilaginous sheath that changes the hydrophobicity of the airborne conidium to hydrophilicity after immersion in water, and helps it to adhere to the substrate. Infection is limited by the duration of the water drop [13, 77, 147, 166, 167], but it also depends on several other factors, such as temperature, the presence of exosmosed nutrients on the cuticle, inoculum age and concentration, age of the underlying host tissue, and the commensal microorganisms. Typically, infection is achieved within 5–8 h, during which the conidium must remain wet. Conidia of the cucumber pathogen *Didymella bryoniae* (Auersw.) Rehm achieve infection within 1–2 h [3, 145]. The tomato pathogen *Colletotrichum coccodes* (Wallr.) S.J. Hughes was found not to infect leaves at < 15 °C, while leaf discs from plants at 20 or 25 °C had increasing lesion numbers when leaf wetness exceeded 12 and 98 h, respectively [18]. There was also a positional effect; leaf susceptibility increased with age, with leaf discs having 23.8, 29.0, and 34.0 lesions respectively, taken from the top, middle and bottom of plants subject to 24 h leaf wetness at 25 °C. Whereas powdery mildew fungi were long thought to infect dry cuticles [159], more recent research indicates that a minimum wet period is necessary for infection [21, 22, 34, 80, 114, 115]. Like conidia of *B. cinerea*, conidia of the powdery mildew *Blumeria graminis* (DC.) Speer f. sp. *hordei* Em. Marchal change from hydrophobicity to hydrophilicity after alighting, and perhaps also obtain water exuding through an enzymically-changed host cuticle [19]. It is also possible that hydrophilic fungal spores, like dust particles, act as nuclei for the formation of dew droplets [72].

Paradoxically, overhead water sprays, and water sprays applied at considerable pressure, about 470 kPa, control some powdery mildews, at least briefly [82, 110, 158]. The mechanism for this is poorly understood, but it has been attributed to damage to the thallus, washing off of the conidia, and the dispersal of antagonist microorganisms [81].

Facultative fungal parasites, like *B. cinerea*, and bacteria, like the soft-rotting *Erwinia* spp., can build up considerable inoculum potential as saprophytes in moribund tissue, and from those bases infect contiguous healthy tissues. Thus, *B. cinerea* can readily infect tomato fruit

from infected fallen petals stuck to the fruit by a water film. Similarly, *D. bryoniae* invades cucumber fruit from persistent, wet, infected flowers [145]. Soft rot bacteria spread rapidly through harvested produce stored wet. Disease prevention in all these situations depends on keeping the plant dry at all times.

Contaminated water is also a source of bacteria, such as the soft-rotting *Erwinia carotovora* (Jones) Bergey et al. [111], and the tomato bacterial canker pathogen *Clavibacter michiganensis* subsp. *michiganensis* (Smith) Davis et al. Both of these diseases are often found predominantly in crop rows below greenhouse gutters, suggesting leakage and splashing of rain or condensate running from the roof, and carrying dust from neighbouring fields [36, 103].

3.1.2. Transpiration

Vascular pathogens, such as *Fusarium oxysporum* f. sp. *lycopersici* (Sacc.) W.C. Snyder and H.N. Hans., *F. oxysporum* f. sp. *dianthi* (Prill. and Delacr.) W.C. Snyder and H.N. Hans., *Verticillium albo-atrum* Reinke and Berthier, and *V. dahliae* Kleb. enter the root system from conidia or from microconidia (*Fusarium oxysporum* ff. spp.) through broken rootlets or at the point of emergence of lateral roots from main roots. Their passive passage up the xylem elements depends on an active transpiration stream [10], and propagules can be found in the xylem near the top of the shoot.

At very low VPD, transpiration is greatly reduced or stopped, but root pressure can continue to pump water up the shoot [15, 28], resulting in exudation of water from stomata, hydathodes, and the cut ends of petioles left at deleafing and disbudding, and in the waterlogging of leaf tissues. Persistent surface water interferes with wax deposition, depriving the plant of one defence [8], while waterlogged tissues invite the invasion of tissues by bacteria when transpiration resumes, and exuded water is sucked back into the plant [79, 97]. Wilson [152] described the ingress of conidia of *B. cinerea* into xylem vessels of deleafed tomato plants by the reversal of the transpiration stream, to establish a latent infection [80], the symptoms of which do not appear until 10–12 weeks later.

The cessation of transpiration and guttation interfere with the transport of calcium to distal parts of leaves and shoots, resulting in local deficiency [61, 76], and repeated diurnal exudation and evaporation of guttated water leaves toxic deposits of salts at hydathodes and leaf margins. Tissues so damaged are the more susceptible to facultative parasites [160, 161]. Root pressure can, to some extent be controlled, and guttation avoided by manipulating the osmotic potential of the rhizosphere, pore space

and oxygen supply, temperature, light, and atmospheric VPD [106].

3.1.3. Vapour pressure deficit

Good evidence to support the hypothesis that VPD is always low in the phyllosphere boundary layer is scant because of the technical difficulties in measuring it there [148, 149]. Investigating infection by powdery mildew fungi, where the role of water has been the most obscure, Delp [35], Frampton and Longrée [50], Longrée [99], Ramsey et al. [116], Schnathorst [124], and Yarwood and Hazen [163], among others have suggested that there is a steep water vapour gradient from the saturated intercellular spaces, through the stomata, to a millimetre or two beyond the leaf surface, and beyond that to the microclimate of the crop canopy.

A model of a 3 mm boundary layer has been derived by Ferro and Southwick [47] from Fick's law of diffusion [74]. In still air, the water vapour transfer rate E_w away from substomatal vesicles (assumed to be saturated) is

$$E_w = -D_w \frac{d\rho}{dz}$$

where D_w is the molecular diffusion coefficient of water vapour in air, ρ is the water molecule concentration in the unstirred air layer, and z is the distance away from the leaf. From this is derived

$$E_w = \frac{\rho(z_1) - \rho(z_2)}{\int_{z_1}^{z_2} \frac{1}{D_w} dz}.$$

Normally, $\rho(z_1)$ is taken as the concentration at the evaporating surface; hence $z_1 = 0$. The equation indicates a linear water molecule concentration gradient from the substomatal vesicle. However, Schnathorst [124] derived a non-linear gradient. Gradients can, of course, be altered by relative leaf and air temperatures, and by wind.

In the 10–30 μm boundary layer, VPDs are presumed to be very low. Even moderate temperature falls will allow dew to form, and probably far more frequently than has been supposed, and certainly when leaf temperatures are appreciably lower than air temperature, as they often are at night. Also guttation occurs at low VPDs in restricted ventilation. In either case, infection from resident pathogens can be expected. Temperature sensors have to be very accurate, and in the right position to detect the dewpoint on leaves [123]. They also have to

be correctly oriented, and close to the phylloplane [94], or they have to be remote reading, like infrared sensors.

In addition to the factors that govern infection on the phylloplane, the microclimate within the 300–400 μm boundary layer determines fungal sporulation and spore liberation. Pycnidial fungi, like *Didymella bryoniae* sporulate better than the Hyphomycetes in very low VPDs, and exude tendrils of hydrophilic spores that are dispersed by workers' fingers or water splash. While Hyphomycetes, like *Botrytis cinerea*, can sporulate in moderately low VPDs, many have a hygroscopic spore release mechanism, depending on rapidly rising or falling VPD, which explains their diurnal spore release patterns in the field [75]. It also helps to explain spore releases during worker activity in greenhouses; sudden changes in the humidity of the 300–400 μm boundary layer must occur when the canopy is disturbed [68]. There are probably also torsional forces in leaf flutter and turbulence that release spores [30], as from the long chains of powdery mildew spores [7].

3.2. Temperature

Optimum temperatures for disease expression have been cited for many diseases in many crops [23, 79], and their planned avoidance might effect disease escape [79]. However, most of those temperatures have been derived from measurements at unspecified sites in a greenhouse or experimental growth chamber, not from the phylloplane boundary layer. Moreover, those temperatures reflect a mean of all those that contribute to the several processes of pathogenesis and defence reactions. As pointed out in Section 2.2, temperatures in boundary layers can differ markedly from ambient temperatures measured elsewhere in the greenhouse. The distinction is also important because of the effects of temperature fluctuations on VPD and dewpoint in the boundary layer.

It is therefore incumbent on the grower to measure temperature as close to the boundary layer as possible. Fortunately this can be done by remote infra-red sensors but there still remain logistical problems in how many measurements should be integrated, and where in the canopy they should be taken, in the shade or not. The grower at least can arrange empirically good air circulation to lessen temperature gradients.

3.3. Radiation

Plants are predisposed to various diseases by inappropriate day lengths or inadequate PAR. For example, Douglas fir seedlings (*Pseudotsuga menziesii* (Mirb.) Franco) were very susceptible to grey mould (*B. cinerea)* in a fibreglass house in which surface wetness and optimum temperatures for infection occurred for periods 14.5 times longer than in a neighbouring plastic house [112]. The seedlings in the fibreglass house were also etiolated and more succulent, with undue amounts of highly susceptible senescent tissues.

As well as the effects of poor light on the host, many fungi, including *B. cinerea*, have a requirement for near UV light (320–380 nm) to induce sporulation. This effect can be temporarily reversed by blue light (400–450 nm) [46, 95]. Screening out near UV light offers a means of reducing sporulation in greenhouse crops, and there are reports of lower incidences of grey mould under plastics with higher blue: near UV transmission ratios [69, 117, 118, 122, 138, 150]. Similarly, the incidence of tomato early blight caused by *Alternaria solani* Sorauer [138] and of white mould (*Sclerotinia sclerotiorum* (Lib.) De Bary [70]) were reduced by near UV blocking covers.

3.4. CO_2 and other gases

There is no evidence that the concentrations of CO_2 and O_2 encountered in greenhouses affect pathogenicity or the activity of biological control organisms in the phyllosphere. The concentrations of CO_2 required to impair the growth of *B. cinerea* in culture are 2–3 orders of magnitude greater than those encountered in the greenhouse [134].

Ethylene, however, predisposes carnations [130] and roses [41] to grey mould. More ethylene is evolved from the diseased carnations [130]. Ethylene might also trigger the transition of latent infections to aggression [80]. Adequate ventilation and the roguing of diseased flowers should eliminate those problems.

3.5. Epidemic modelling and forecasting

While there have been many models proposed to describe epidemics in the field [67, 71], few, if any, have addressed epidemiology wholly and exclusively within the greenhouse as an isolated entity.

Precise management of the greenhouse climate for successful application of disease avoidance measures in greenhouses will require advanced climate control and decision-support systems that use climate history and models of the processes that occur. Knowledge bases and expert systems [26, 127] will assist the grower in optimizing the control of the many factors contributing to disease development and productivity. Many of the

models and the software platforms required for this advanced hierarchical system of control already exist [9, 146]. However, they remain to be integrated into commercial systems that can provide advice or control actions in near realtime [31, 139]. Despite the advanced modelling of the greenhouse macroclimate, it seems anomalous that most disease forecasting systems for greenhouse crops are so far based on the weather outside.

Thus, there are various models describing epidemics in relation to weather, for example, epidemics of gray mold caused by *Botrytis cinerea* in cucumber [44, 45, 128, 164], in tomatoes [40, 128], in roses [90, 100], gerbera [89], and conifer seedlings [112, 166, 167]. Arny and Rowe [3] and van Steekelenberg [145] characterized the epidemiology of *Didymella bryoniae* in cucumbers; and Cobb et al. [27] and Powell and De Long [114] that of the powdery mildew *Sphaerotheca pannosa* (Wallr.:Fr.) Lév. var. *rosae* Woronichin in roses. Most of these models are based on the duration of surface wetness and ambient air temperature. Generally forecasting epidemics has not so far been done quickly enough to take prophylactic action, either by modifying the environment, or by applying pesticides. By the time those data have been collected and analysed, infection has probably already started, within an hour or two of the arrival of the inoculum [12]. Yunis et al. [164] derived a model for grey mould in unheated cucumber crops in plastic greenhouses in a semi-arid area of Israel, using only qualitative outside weather data. Outbreaks of grey mould occurred following weeks when the average period of leaf wetness, as determined by electronic sensing, exceeded 7 h/d, and night temperatures lay between 9 and 21 °C for more than 9 h/d. Shtienberg and Elad [128], using similar outside weather data, developed BOTMAN (*Botrytis* Manager) for cucumber and tomato crops, also in unheated Israeli greenhouses. BOTMAN depends on the accuracy of weather forecasts for 4-day periods. Disease severity values are assigned to each of the following weather parameters: rain quantity (mm/d); number of rainy days (> 0.9 mm); maximum temperature in the ranges < 9 °C, 10–21 °C, 22–26 °C, > 26 °C; minimum temperature in the ranges < 5 °C, 6–9 °C, 10–21 °C, > 21 °C; number of days with 5/8 cloud cover for > 6 h/d; and the number of days with hot, dry weather (< 25% relative humidity [RH] for more than 4 h). Disease severity values are summed for a risk index. The BOTMAN example is only indirectly related to greenhouse microclimate.

In a cut-flower crop like roses, only 1–3 lesions, each from a single conidium of *B. cinerea*, are sufficient to make a flower unmarketable [89], and so managing the microclimate to reduce the inoculum is correspondingly an important goal, even when the infections are latent [80, 89, 100, 121]. Although petal flecking in roses was more prevalent in late summer and autumn [89], the numbers of airborne conidia could not be correlated with any environmental factor. Petal flecking, however was positively correlated with mean relative humidity up to 7 d before harvest (but not with VPD) and with numbers of trapped airborne conidia, and negatively correlated with global radiation outside the greenhouse.

4. BIOLOGICAL CONTROL

Biological control, the use of resident or introduced hyperparasitic or antagonistic microorganisms to suppress microbial plant pathogens, is ipso facto very dependent on appropriate microclimates [42]. For the most part, these microclimates remain undefined. By comparison with the microclimates that enable the biological control of arthropods by other arthropods [142], they appear to be rather narrow in range, which might explain the relative lack of success of biological disease control. Notwithstanding, against the continuing problems with chemical control noted earlier, biological control of diseases in greenhouse crops has potential value, not least because it is generally supposed that appropriate microclimates can be achieved there. However, this is more easily said than done.

Biological control: synecology

In order to exert biological control over pathogens, combatant microorganisms must exist in the same ecological niche on the phylloplane, and be ecologically competent there for a minimum time [2, 42]. Even microorganisms inducing resistance in the host by prior inoculation, for the most part, have very similar ecological requirements as the later putative parasites [107]. Other mechanisms of biological control, namely, antibiosis sensu lato and siderophore production, competitive saprophytic ability, cross protection and passive exclusion, hyperparasitism, and hypovirulence, depend on the close proximity of pathogen and biological control microorganism [2, 42, 79]. It is axiomatic that microbial interactions occur either in a water matrix or at least in very low VPDs [42].

There are essentially two main approaches to biological control: enhancing and maintaining populations of resident biological control agents by modifying the chemical and physical environment; or applying large populations of them from commercial preparations [51]. The former approach requires considerable synecological knowledge of host, parasite, and biological control

organisms. However, the autecology of biological control organisms in the absence of their microbial hosts is generally very poorly known. This knowledge is needed to answer growers' questions about survival between applications, or whether the organism will move with its pathogen host, as the crop grows; or whether it will survive in the greenhouse between crops. For example, the life of *Ampelomyces quisqualis* Ces. away from its host powdery mildews is virtually unknown, so ways of enhancing its populations prior to the appearance of powdery mildew in a crop, or ensuring that it travels with airborne powdery mildew within the crop, are a matter of guess [81, 83].

The second approach largely uses commercial products rather like chemical sprays, with scant regard for maintenance of the population once applied. As Jarvis [79] has pointed out, hyperparasites and antagonists do not act unimpeded on a pathogen. There must be chains of other microorganisms affecting their activity, all of which are affected adversely or benignly by each other, and by the physical and chemical environment. Thus, no microorganisms that adversely affect *A. quisqualis* are known, although its tolerance and susceptibility to some fungicides are known [133]. It is also unknown, for example, whether near UV-blocking film affects its sporulation.

Because biological control microorganisms occupy the same ecological niche on the host, and because their microclimate requirements for optimum activity are similar to those of the pathogens, manipulating their environment to enhance populations is fraught with risks of encouraging pathogens. For example, interspersing applications of conidial suspensions of *A. quisqualis* with water sprays [83] in order to improve its dispersal is likely to invite water-dependent pathogens like *B. cinerea* and *D. bryoniae*.

Sporothrix flocculosa Traquair, Shaw and Jarvis, the yeast-like fungus in the product Sporodex™, requires close contact with its host powdery mildew fungi, since it kills by destroying the integrity of the plasmalemma without penetrating. Against *Podosphaera fusca* (Fr.) U. Braun and N. Shishkoff on cucumber, *S. flocculosa* is most active at temperatures of 26–28 °C and VPDs lower than 0.6 kPa [82]. Although its conidia are applied in aqueous suspension, and are water-splash dispersed, they can also be airborne [78]. As with *A. quisqualis*, one of the practical problems is to maintain effective populations on powdery mildew colonies developing on the top leaves of 2-m tall cucumber plants in an environment that may be drier than lower in the canopy. At present repeated applications are necessary for situations like this [11], but it may well be that better understanding of hyperparasite autecology would solve this

problem. To some extent the biological control agents can be protected from higher VPD by adding a miscible oil to the spore suspension [38].

Virtually all trials with biological control fungi and bacteria in the greenhouse have assumed that low VPDs and moderate temperatures are required for sustained action but there are very few studies to give precision to instructions on the label for use in applying and maintaining populations. There are even fewer studies on enhancing natural populations already present. In either case it has to be recognized that generalised assumptions from fungal and bacterial biology are inadequate; each species has to be characterized precisely in its synecology on the phylloplane [37, 42, 79].

5. CONCLUSION

Managing greenhouse macroclimate (sensu [5]) for disease control requires a conceptual step beyond greenhouse macroclimate as an entity distinct from that outside. We must recognize that microclimate at the level of the phylloplane is distinct from the macroclimate of the greenhouse. It is the microclimate at the phylloplane that directly impacts plant growth, as well as disease and biological control organisms there. It is that microclimate that needs to be controlled. This climate is separated from the macroclimate of the greenhouse, which is far from uniform, by thermal, concentration, and velocity boundary layers that give rise to steep gradients in temperature, VPD and CO_2. Measurement of microclimate variables at the level of the phylloplane for control purposes is difficult thus it is best to predict them using models based on measurements made at some distance from the phylloplane. Current research is focussing on the development of models of microclimate together with models of crop growth and development that can be used for optimal control of the greenhouse microclimate.

Within fairly broad limits, the microclimate in the phyllosphere has relatively little effect on the efficacy of chemical pesticides, but biological control agents, both arthropod and microbial, are profoundly affected by adverse physical and chemical environments, and by commensal microorganisms too. Until now, biological control organisms have been used mostly with the same mentality and application techniques as chemical pesticides, and their patchy success has shown this is not good enough. Like pathogens, biological control microorganisms have a rather narrow environment for optimum activity, so this must be accurately catalogued and maintained in their immediate habitat on the plant surface.

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