FINAL REPORT

To:
Horticultural Development Council
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PC 237

The use of supplementary lighting in protected ornamental and edible crops: beyond the maximisation of biomass

HDC contract.

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Commercial – In Confidence

Project title: The use of supplementary lighting in protected ornamental and edible crops: beyond the maximisation of biomass

Project number: PC237

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Project Co-ordinators:

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The results and conclusions in this report are based on a series of crop scale observations, crop trials and more detailed field- and laboratory-based experiments. The conditions under which the studies were carried out and the results have been reported with detail and accuracy. However, because of the biological nature of the work it must be borne in mind that different circumstances and conditions could produce different results. Therefore, care must be taken with the interpretation of the results especially if they are used as the basis for commercial product recommendations.

Authentication

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

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Date……

Practical section for growers

1) **This project is a review of the current understanding of how lighting might be used to address specific quality issues in both ornamental and edible protected crops.**

2) **The project remit did not include either photoperiodic lighting or supplementary lighting aimed simply to increase crop biomass and yield by increasing total light interception. However, the review did consider the relative properties of high-pressure sodium (HPS) and metal halide (MH) lamps.**

3) **HPS lamps are extremely efficient in terms of light produced for a given input of electricity, and there is little doubt that they are the optimum lamp for supplementary lighting where plants are (i) grown long-term under supplementary lighting and (ii) the final mass of foliage or fruit are the key elements in determing the value of the crop. On the other hand, supplementation using HPS does has effects on plant habit, such as increased stem elongation, which may be undesirable in crops such as bedding or pot-grown herbs. The undesirable effects of HPS on plant habit is largely a function of the imbalance between red and blue/UV in the output of this type of lamp. There is considerable evidence that using MH lamps instead of HPS lamps produces a more compact plant habit that more closely meets the needs of commercial bedding production. In principle, replacing HPS with MH might deliver improved plant habit, but this needs to be assessed very carefully taking account of the economics of using the two different lamp types.**

4) **In principle, the undesirable effects effects of HPS on plant habit could be corrected by adding blue or UV light. Specific additions of blue light has been shown to improve plant habit under HPS lamps, and might use highly efficient blue light emitting diodes (LEDs). Equally, in many plants a lack of UV light causes increases in stem elongation and leaf area but surpresses branching. While specific UV supplements to improve plant morphology is technically feasible using readily available equipment, and is likely to be energy-efficient, using UV might also pose major health and safety issues that would require careful assessment in any commercial use. Practical systems for specific additions of blue or UV light in commercial crops have not been developed.**

5) **In herbs grown in the glasshouse under low-light conditions in winter, conventional supplementary light would be expected to increase the contents of many flavour or pharmolocological compounds. However, it is certainly not the case that all compounds in all species will respond in the same way. Also, since there may be trade-offs between growth and the production of flavour compounds, simple supplementary lighting may be a relatively inefficient route to specifically increasing the concentration of flavour compounds. On the other hand, supplementary lighting will deliver a balance of increased growth and modified tissue chemistry, both of which may be commercially desired.**

6) **Specifically manipulating the quality of light may be a more specific tool to manipulate the chemical composition of plant tissues. In particular specific supplementation using blue or UV light might be used to regulate growth (see 4) and stimulate the synthesis of a range of flavour compounds. There is limited experimental work confirming that such approaches can be effective, and need relatively low intensities of added light. However, responses are likely to be crop-specific, and there is insufficient evidence on which to base any suggestion for practical exploitation of this approach. The use of UV sources in a commercial setting will require especially careful assessment.**

7) **In crops grown with poor natural light, conventional supplementary lighting and/or specific supplements such as UV light are likely to result in increased leaf thickness, greater leaf strength and increases in the contents of anti-oxidant compounds Together, these changes would be expected to increase shelf-life in herbs grown under protection, although key questions such as the appropriate irradiance, duration or dose lighing, and when it needs to be applied for optimum effect of shelf life in specific crops, remain unknown.**

8) **In salad crops, especially lettuce, there is a specific problem of high nitrate concentrations when crops are grown under poor light in winter. There is no doubt that light is a key factor influencing foliar nitrate concentrations in lettuce, and in other salads such as spinach, and any measure taken to improve light levels within protected lettuce crops will have a proportional benefit in reducing nitrate concentrations in winter.**

9) **Conventional supplementary lighting for lettuce production in winter accelerates maturity and improve heading, but would also be expected to reduce nitrate concentrations in winter. However, some caution is necessary as supplementary lighting may also lead to increased tip burn in some varieties. There is evidence that supplementary lighting for as little as one night can substantially reduce nitrate concentrations in leaf tissues. Although the detailed requirements for such short-term lighting treatments remain poorly defined, it may be possible to use this approach for a short period before harvest specifically to "condition" the plant for low nitrate. This should incur lower running costs than standard supplementary lighting but requires either that the crop can be moved (possible in some hydroponic production systems), or the use of a mobile lighting system.**

10) **At present, glasshouses lighting relies on discharge lamps such as HPS and MH, and to a lesser extent on some types of fluorescent lamps. Lighting systems based on LEDs are advancing rapidly and are now used in a very wide range of applications. LEDs might have several benefits for use in horticulture. They have the potential to have very light outputs per input of electrical energy, exceeding the current best efficiencies seen in HPS lamps. LEDs already have service lifetimes substantially greater than conventional lamps, and this appears likely to increase further. Unlike discharge and fluorescent lamps, LEDs can be dimmed relatively easily, allowing supplementary lighting to be varied more in response to variation in sunlight, although how this would be translated in to energy efficiency and any specific effects on crop growth remain unclear.**

11) **LEDs are available that produce a wide range of wavebands (colours) that might be exploited in to horticulture, delivering a range of end-points as described under points 3-7 above. At present, LEDs in have not be exploited to any extent in horticulture, and practical approaches to their use in commercial holdings remain poorly defined.**

12) **New LED-based systems providing high light-outputs from compact system, but retaining the technical advantages noted under point 10, seem likely to challenge discharge lamps as the system of choice for horticultural lighting in the future. However, it may be ten-fifteen years before LED systems are competitive compared to conventional horticultural lighting systems.**

Science section

1. Introduction

1.1 Background to the project.

The use of supplementary lighting is a well-established tool in the production of a wide range of protected crops. The current "state of the art" uses modified high pressure sodium (HPS) lamps that deliver high outputs of photosynthetically active radiation (PAR: 400-700nm) at high electrical efficiencies. The aim of maximising light integral is to increase crop biomass and yield by increasing total light interception. However, supplementary lighting may also influence elements of crop quality, including plant habit, pigmentation and interactions with pests and pathogens, with consequences for the use of agrochemicals, whether growth regulators, insecticides or fungicides. The effects of light on crop quality may be due to the quantity of light provided to the crop, and/or its spectral balance, i.e. the quality of light. Research under HDC project CP19 is showing the potential of spectral modification to deliver improved quality in a range of crops, both ornamentals and edible crops (6-8). Useful end-points have included growth regulation in ornamental crops, improved leaf colour in leafy salads and increased oil yield in herb crops. The results of CP19 have also shown that shelf-life may be influenced by spectral modification, for example in salads and cut-flowers (8).

The data from CP19 have led growers and consultants to ask the question, can similar effects be delivered under glass? Whilst spectral filters can be deployed under glass (for example, to increase the ratio or red to far red light, and so deliver growth regulation (e.g. 27, 105, 125, 150, 167), this question from growers also focuses attention on methods of lighting crops. From the perspective of optimising the final product, the choice of HPS lamps may be open to question, especially given the range of lamp types and lighting technologies that are now available commercially. As originally conceived, this project aimed to review the state of knowledge in relation to:-

1) i) non-photosynthetic plant responses and ii) pathogen responses to the light environment, including both applied research and more fundamental work that could inform horticultural lighting strategies.

2) Review lighting technologies that might deliver supplementary lighting directed at specific commercial end-points, for example alternative discharge lamps, specific fluorescent sources for specific wavelengths, light emitted diodes etc.

As a result of feedback from the HDC Protected crops panel, the scope of the review of non-photosynthetic responses was expanded to include three distinct areas:

3) Non-photosynthetic responses to the light environment on plant morphology, and consequences for crop quality in bedding plants

4) The effects of the light environment on flavour compounds and shelf-life in herbs.

5) The effects of the light environment on nitrate concentration in lettuce.

These areas will be considered in turn (sections 2-4), but there are many links between them, and aspects of morphological responses to light (section 2) are also highly relevant to shelf life (section 3). I will start by considering how light varies in the environment, and how changes influence the biology of plants and their associated pests and pathogens.

1.2 Light as an environmental variable.

Light is an extremely dynamic component of the terrestrial environment. Changes are both quantitative, including variation in instantaneous irradiance, dose accumulated over time, and daylength, and qualitative, in terms of light spectral balance. Plants and their associated herbivores and pathogens may respond to each of these different components of variation.

1.2.i. Variation in the quantity of light.

The quantity of light falling on a surface at a given moment, usually referred to as "light intensity," is formally defined in terms of either energy per unit area (= irradiance) or quanta per unit area (= photon flux: see 26). Some elements of the variation in irradiance are predictable. For example variation with time of day, season and latitude are all functions of the elevation of the sun in the sky (the higher the solar elevation, the higher the irradiance). As a result, irradiance reaches a maximum near the equator, at mid-day, and, at mid-high latitudes, in mid-summer. Superimposed on these systematic geographical and seasonal variations in irradiance are variations due to factors like cloud cover, aspect on a sloping site, or shade from nearby structures or plant canopies. Some of these factors affect all wavelengths of light more or less equally, others are much more wavelength specific (see below). Many biological responses to light can be described as simple functions of irradiance, the rate of photosynthesis in plants is a typical example.

Although photosynthesis is a function of irradiance, growth is determined by the sum of photosynthetic carbon fixation over time which is, in turn, a function of the amount of light

received by the plant over that period. Thus, growth and yield, and many other long-term effects of light, are best described by the accumulated dose of photosynthetic radiation, for example by daily light integral (40, 92, 94). Light damage is also often a function of accumulated dose, as with many whole-plant responses to UV radiation (38, 65). Although rarely formalised as dose responses, plant chemistry is also influenced by light integrals, often with rather complex interactions with water and nutrient supply.

<table>
<tr><th>Colour / waveband</th><th>UV-B</th><th>UV-A</th><th>Blue</th><th>Green</th><th>Red</th><th>Far red</th></tr>
<tr><td>Wavelengths[a]</td><td>280-315nm</td><td>315-400nm</td><td>400-475nm</td><td>500-550nm</td><td>650-700nm</td><td>710-750nm</td></tr>
<tr><td>Humans</td><td>sunburn</td><td>suntan</td><td>Vision
rhythms</td><td>Vision</td><td>Vision</td><td>-</td></tr>
<tr><td>Bees</td><td>-</td><td>vision</td><td>vision</td><td>Vision</td><td>-</td><td>-</td></tr>
<tr><td>Some pests</td><td>???[b]</td><td>vision</td><td>vision</td><td>Vision</td><td>Vision</td><td>-</td></tr>
<tr><td rowspan="3">Plants</td><td rowspan="3">photomorph</td><td colspan="2">-</td><td>PS</td><td>PS</td><td rowspan="3">photomorph
rhythyms</td></tr>
<tr><td colspan="2">photomorph</td><td>???[c]</td><td>Photomorph</td></tr>
<tr><td colspan="2">Rhythyms</td><td></td><td>Rhythyms</td></tr>
<tr><td>Fungi</td><td>Damage
Photomorph</td><td colspan="2">photomorph</td><td>-</td><td>Photomorph</td><td>photomorph</td></tr>
</table>

Table 1. Responses of different organisms to different wavelengths of light. Key: **vision**- light perceived by the visual system and used to modify animal behaviour; **rhythms**- light used to regulate the innate day/night cycles of the organism in relation to daylength; **photomorph** = photomorphogenesis- light used to control the morphology of the organism; **PS**- photosynthesis.
Notes. a: the definitions of different wavebands can vary, those used here are indicative of commonly accepted usage. b: there are hints in the literature that some pests may respond directly to UV-B, but this remains unclear (117). c: there are occasional reports of specific plant responses to green (54) or yellow light (44) that are independent of well-defined responses to other wavelengths, but this is not confirmed.

1.2.ii Variation in the quality of light

Light quality is the balance between different wavelengths. Different organisms perceive different wavelengths in different ways (Table 1). In human terms this is the balance between different colours. Every shade and hue that we perceive is a function of the balance between

red, green and blue, the three primary colours that are detected by specific pigments in the eye. Other animals, including pest insects, may perceive different "primary colours" (Table 1). Plants and fungi have no eyes but do possess pigments that are specific photoreceptors for different wavelengths, so they can detect changes in the balance of different wavelengths (colour in human terms).

1.2.iii Biological responses to the light environment

Organisms perceive changes in the quantity and quality of light and use them as "cues" to regulate their metabolism, physiology, development and behaviour. For plants, photosynthetic responses to light are clearly central to growth, and are well defined in terms of both light quantity and quality. The direct effects of light on photosynthetic carbon fixation through to biomass production are not within the scope of this project, although the effects of daily light integral on flavour compounds and other secondary metabolites (see section 3) are probably mediated largely through effects on integrated carbon fixation (see below). However, the spectral response of photosynthesis and its contrast with that of human vision is pertinent to how light is measured in horticulture, and this has consequences for assessing the efficiency of different types of lamp. These subjects are considered in Box 1. Non-photosynthetic responses to light can be considered in terms of specific responses to specific wavelengths. These are summarised in Table 2 and their potential horticultural exploitation is considered in detail in sections 2-4.

Commercially, it may be necessary to consider the effects of lighting on crop interactions with pests and pathogens. In general, plants grown under low PAR or UV-B are expected to be less resistant to pest or disease attack but such effects of light on the crop may interact with effects on pests or pathogens (146), which may be important for the overall management of the crop. For example, insects use light across a wide range of wavelengths (at least 320-800nm) for finding mates, foraging for food and orientation. Not surprisingly, the overall light environment can have wide-ranging effects of insects, for example adults of some insect herbivores prefer high-light locations for egg laying (4), and in some ecological studies such effects outweigh changes in host quality of shade-grown plants (160). There are specific UV effects on some insects, for example where insects can perceive longer wavelength UV, conditions deficient in these wavelengths can disrupt foraging and dispersal. This has been shown to be significant in both experimental studies (118) and in the use of UV-opaque plastics for the control of horticultural pests such as thrips and whiteflies (reviewed by 143). Equally, there is a risk that

Box 1. Light, vision, plants and measurements.

Photosynthesis is driven by much the same portion of the light spectrum as is detected by the human eye. In human terms this part of the light spectrum is perceived as the colours of the rainbow, violet through to red. In physical terms different colours equate to different wavelengths of light, with violet being the shortest wavelengths at around 400 nanometres (nm) through to the longest wavelength red at around 700nm. The light spectrum from 400-700nm is called "visible light" for human responses, and in terms of plant responses, is called "photosynthetically active radiation" or in simpler terms "plant active radiation" (PAR).

Visible light extends from 400 to 700nm but the human eye has a peak sensitivity in the green-yellow at around 550nm (Figure 1a). Sensors designed to measure the intensity or brightness of light as we perceive it mimic this peak in the green-yellow, the contributions from blue and red light are deliberately minimised. Light intensity measured in this way to match human vision is expressed in units of lux. Plant active radiation also extends from 400-700nm, but plant responses have no peak at 550nm. In fact the most useful wavelengths for driving photosynthesis are the blue and the red, with the *minimum* being in the green (Figure 1b). So lux meters respond most to the light that plants use least efficiently.

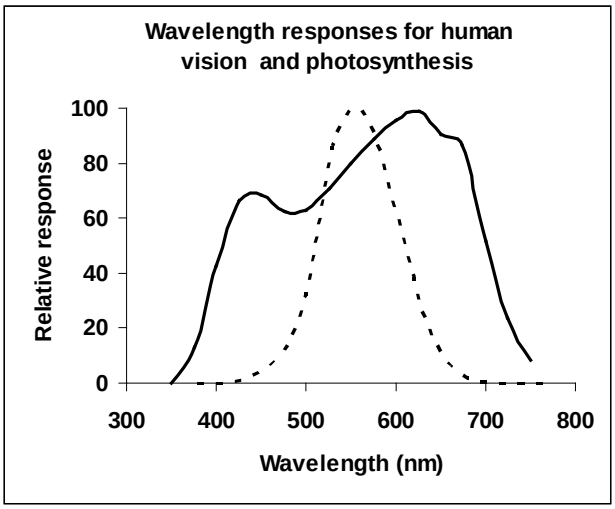


Figure 1. The wavelength responses of human vision (dotted line) and photosynthesis (solid line).

In both cases data are expressed relative to the maximum response (=100%), which falls at c. 550nm (yellow-green) for human vision, around 625nm (red) for photosynthesis. Note that the photosynthesis curve has the secondary peak at around 450nm (blue) and is generally "broader" with greater than 50% efficiency across almost the full range 400-700nm. By contrast, efficiency in human vision exceeds 50% only between c 510-610nm.

The human vision data are taken from the standard CIE photopic curve. The photosynthetic data are based on responses for a range of crops (McCree, 1972).

The discrepancy between lux and PAR matters little so long as all measurements are made under the same light source. Problems arise when a lux meter is used to measure light from different sources, for example natural sunlight and light from a high-pressure sodium (HPS) lamp. 1000 lux in sunlight provides 19 units PAR, but 1000 lux from a HPS lamp provides only 12 units PAR. At the other extreme, some fluorescent tubes designed for plant growth can deliver 30 units PAR per 1000lux. In essence, providing 1000 lux from a HPS lamp does not replace 1000lux of sunlight, but more like 630lux. Put another way, using lux can result in errors in measuring the light that really matters to plants of as much as 40%.

Accurate measurement of light useful to plants should be as PAR, which is used throughout this report. Measuring PAR is no more difficult than measuring lux, a range of simple sensors are widely available. One issue that is sometimes discussed as a problem with PAR is that it is typically expressed in units of micromole quanta per square metre per second ($\mu mol\ m^{-2}\ s^{-1}$) which is a less easy term than "lux". In practice, PAR can also be expressed as watts per square metre ($W\ m^{-2}$), which may be a more convenient term for general use.

One area where the alternative methods of measuring light is important is in assessing the efficiency of lamps. HPS lamps can produce up to 140 lux per watt electrical power, while metal halides typically produce around 90 lumens per watt. This almost 50% greater efficiency of HPS lamps based on lux values is slightly misleading when outputs are assessed in terms of PAR. As a result of the contrasting spectra of the two lamp types MH lamps produce more plant effective radiation per lux than HPS (around 12 μmole/1000lux for HPS and 14 μmole/1000lux for MH). Overall, this result in plant weighted efficiencies around 30% higher in HPS than MH, still a substantial difference but not so marked as suggested by lux values. Running costs for lighting is clearly fundamental issue for growers, especially with continuing increases in energy prices, but it may be that these costs need to be integrated with those of other inputs, such as plant growth regulators.

UV-deficient conditions can interfere with the normal behaviour of pollinators (47, 121, 122). In the field, UV might also influence herbivore populations through the suppression of entomopathogens, whether nematodes (55), fungi (20, 21), bacteria (124) or viruses (158) and in this sense, the UV-deficient environment of protected cropping systems may be beneficial for biocontrol. The influence of shade on plant-pathogen interactions has been much less studied than comparable effects on plant-pest interactions. Many pathogenic fungi may respond directly to spectral balance, as a cue to regulate sporulation, but exposed fungal tissues can be vulnerable to UV-B radiation, and solar UV-B is a major constraint on the spore survival of many pathogens (135). Such responses show rather complex interactions, for example when plastic films are used to modify spectral balance as a component of disease control in horticulture 144, 145). These broader "agroecological" elements of plant-pest-pathogen interactions should not be overlooked in considering over novel approaches to lighting, even if they are probably unlikely to be major factors influencing commercial decisions.

2. The effects of light on morphology and growth regulation in bedding plants.

2.1 Commercial background to the problem

Bedding plants are often produced under conditions of (i) relatively low light during the autumn-spring period and (ii) relatively high-density populations that results in changes in light spectrum that may induce the so-called "shade avoidance" response (see above). While low light can suppress growth in terms of biomass accumulation (especially below-ground), the shade response typically results in stem elongation, reduced leaf expansion and thickness, and suppressed branching (169, 173). Together, these responses lead to a suite of crop characteristics, stem elongation ("stretching"), reduced branching, reduced leaf thickness etc., that are undesirable not only in bedding but also in other ornamentals, vegetable propagation crops etc. The standard horticultural approach to overcoming these quality issues in ornamentals is currently to use chemical growth regulants to treat the symptoms, rather than the cause of the undesirable morphology. The range of commercially available growth retardants act through a number of specific modes of action, but all act to suppress at some stage the series of steps that allow plants to respond morphologically to a changed light environment. Typically this involves inhibiting the synthesis of the gibberellin family of plant hormones which promote stem elongation (141). There is no doubt that chemical growth regulants are highly effective, but their use is coming under increasing scrutiny for a number of reasons (Neil Bragg, Stuart Coutts, Harry Kitchener, pers comms.):-

Table 2. An overview of plant photomorphogenic responses to different wavelengths of light.

Waveband	Plant response
UV-B 280-315nm	Responses are relatively well-defined although no specific photoreceptor has been defined. Increasing UV-B within the environmental range typically results in:- • reduced stem elongation, • reduced leaf expansion, • increased leaf thickness, • increased branching, • increased pigmentation (especially anthocyanins and flavonoids), • modified tissue chemistry In addition there are a number of responses that show greater species to species variation, including reduced biomass production, increased resistance to pests and pathogens (but some examples of reduced resistance with some treatments)[1].
UV-A 315-400nm and	Known to be detected by at least three photoreceptors (shared with blue) with involvement in stomatal movements, phototropism and photomorphogensis. Whole plant responses to specific manipulations of UV-A are poorly-defined, but the effects of increasing UV-A within the environmental range appear to relate to the photoreceptor cryptochrome, and typically results in:- • Reduced stem elongation • Reduced leaf expansion • Increased branching • Increased pigmentation (especially anthocyanins and flavonoids)
Blue 400-475nm	Known to be detected by at least three photoreceptors (shared with UV-A) with involvement in stomatal movements, phototropism and photomorphogensis The effects of specific manipulations increases in blue at the whole plant scale are typically- • Reduced stem elongation • Reduced leaf expansion • Increased branching • Increased pigmentation (especially anthocyanins and flavonoids)
Red and far red[2] 650-700nm 710-750nm	The effects of the ratio of red to far-red light (R:FR) detected by the phytochrome family of photoreceptors are well defined in terms of both fundamental photoecology and crop responses. Decreasing R:FR results in what is known as the "shade avoidance response" in many, but not all, species. The shade avoidance response is typified by:- • Increased stem elongation • Reduced leaf expansion • Suppressed branching • Reduced foliar pigmentation (greening) Recent evidence is beginning to show the links between shade avoidance and plant defence against pest and pathogen attack. Low R:FR seems to suppress defence mechanisms independently of any effect of low irradiance or dose, and this can result in changes in the physical and chemical properties of tissues.

[1] The effects of UV-B on crop pests and diseases complicated because UV-B can have direct effects on many pests and pathogens: see main text.

[2] Note that phytochromes are also central to plants ability to measure the duration of night, and hence to to the control of flowering and development in many species. The manipulation of this response by light is the basis of commercial "night-break" lighting, but this topic is beyond the scope of this review.

1) Consumer demand for plants not treated with agrochemicals
2) Cost of treatment
3) The possible over-effectiveness of compounds, leading to poor growth and development of plants in the final garden environment.
4) Health and safety of users, and environmental concerns.

Thus, there is a need for alternative, non-chemical approaches to growth regulation. Given that the fundamental plant response that is being managed is to the light environment, there is obviously an *a priori* case for considering light as a tool for growth regulation. The use of supplementary lighting is a well-established tool in the production of a wide range of protected crops, but is largely designed for cost effective provision of photosynthetically active radiation to increase DLI. However, given the known effects of a range of wavelengths of light on plant morphology (see Tables 1 and 2) it would be expected that the spectrum of light might be important for crop. Here I consider (i) the basic features of the light environment within protected cropping and (ii) the current understanding of how different types of lighting influence can influence plant growth and morphology.

2.2 Scientific background to the problem

As noted above plants do not respond to light purely through photosynthetic carbon fixation. The light environment is used by plants to regulate growth, development and tissue chemistry, and these responses are controlled via a series of photoreceptors that respond to specific wavelengths of light, not total light integral. Key wavelengths in non-photosynthetic responses are red/far-red (phytochromes), blue/UV-A (cryptochromes, phototropins) and UV-B (currently ill-defined UV-B photoreceptors). Although there are "textbook" studies of the specific effects of different wavelengths of light, in many cases plant responses to the light environment are the result of rather complex interactions between irradiance and the balance between these different wavelengths. Thus, not only R:FR but the balance between red and blue light, between UV and PAR, or between UV-B and PAR may all interact to produce an overall response to light quality. In terms of the responses of protected crops, two fundamental elements of light under glass and with supplementary lighting need to be considered.

(a) Compared with field sunlight, the glasshouse environment is deficient in UV-A and completely lacks UV-B.

(b) HPS lamps are strongly biased towards the red, and produce little or no blue or UV light. Even HPS lamps that are modified to increase the output of these shorter wavelengths (e.g.

"SON-AGRO") are still very unbalanced compared with sunlight. This is unlikely to influence photosynthetic responses, but the lack of shorter wavelengths clearly has the potential to affect plant morphology.

2.2.a Crop responses to the deficiency in UV wavelengths under glass.

Plants show well-defined responses to both UV-A and UV-B radiation (see Table 1 and 2). Plant responses to UV-B radiation (290-320nm) have been intensively studied, although largely in the context of stratospheric ozone depletion (reviewed by 136, 137, 157). However, a large number of experiments where solar UV-B has been experimentally reduced of removed show a range of significant responses across many species and locations. Responses to UV-B attenuation include increased growth stem elongation, leaf area but reduced branching and leaf thickness (136, 137, 157). The pigmentation of leaves and flowers may also be affected (98, 130 and see 6-8). Although comparing different UV environments produced by different photoselective plastics, recent results from HDC project CP19 (6-8 and see137) confirm that allowing crop seedlings to be exposed to solar UV produces more compact plants, with shorter stems, smaller leaves and thicker leaves. There is evidence that plants propagated under full solar UV perform better when transplanted to the field than those produced under glass, and effect that has been observed in lettuce, cabbage, cauliflower and bedding such as *Argyranthemum* (8). CP19 results also confirm that the effects of UV are not confined to UV-B, reductions in UV-A can also be significant (137). Although less-well understood than UV-B responses, there is increasing awareness that UV-A can induce a wide range of responses, including many previously considered to be primarily due to UV-B (5, 51, 85, 86, 98, 99).

Since much of the large body of fundamental research in to plant UV responses uses UV-B lamps, it seems likely that specific supplementation of UV in UV-deficient environments such as glasshouses could provide agronomically useful responses such as control of growth, improved leaf colour, altered pigment content (reviewed by 136, 137). There are limited studies of the use of UV-B specifically to regulate the growth of young seedlings of bedding and vegetable crops (11, 17, 61). In some cases this achieved effective growth regulation which persisted when seedlings were transferred to low light or darkness for several days, mimicking the conditions during transport (11). Thus, even within this specific applied context, the results of using UV lamps appear to be similar to the beneficial effects of UV-transparent cladding plastics observed in CP19. However, in other cases, effective growth regulation by UV

supplementation against low background PAR was delicately balanced with gross damage (17, 61), highlighting the great care needed in deploying UV supplements in crops.

2.2.b Crop responses to supplementary lighting using different light sources.

The contrasting effects HPS and MH lamps on plant growth and morphology has been known for more than two decades (171), and has been formally investigated for a number of crops. Such investigations require careful design and interpretation to separate the possible confounding effects of irradiance/dose and spectral quality. For example, in a recent comparison of tomatoes growing in controlled environment conditions, with all PAR supplied by either HPS or MH lamps, plants growing under HPS lamp types were taller and flowered and fruited earlier, but chlorophyll content was generally greater in leaves under MH lamps (184). These data were obtained using equal densities of 1000W lamps, and given the lower efficiency of MH lamps PAR irradiances were approximately 30% lower under than under HPS lamps (184). In some respects this type of comparison based on equal lamp densities may be entirely appropriate for horticultural purposes, in the sense that it considers the simple replacement of HPS with MH on a “lamp for lamp” basis. However, by changing irradiance this design is poor for understanding the inherent properties of the light produced by different lamps. Thus, the studies comparing HPS and MH considered below have been careful to provide the same irradiance from all treatments.

In potato, stem and internode lengths of young plants were significantly greater under HPS compared to MH, and dry weight was not affected, although there was variation between cultivars in the response (181). In a growth chamber study cucumber grown at 600 $\mu mol\ m^{-2}\ s^{-1}$ PAR from MH or HPS lamps showed no difference in growth rate but leaf area per plant dry weight was reduced and leaf area per unit leaf dry weight increased with MH lamps (100). In a similar growth-room study lettuce cv 'Waldmann's Green produced greater leaf area and biomass under HPS than MH (179). However, compared with MH, HPS caused undesirable stem elongation in lettuce, spinach and mustard (171). The usual assumption is that the difference between HPS and MH lamps is the low blue content of HPS lamps. When lettuce was grown under HPS and MH lamps with additional lighting to provide the same blue content, growth and morphology was relatively similar, although there were some residual differences that were attributed to a specific effect of yellow light (580-600nm: 44). That study forms part of a series of elegant studies by Bruce Bugbee and co-workers, which have done much to clarify the basis of the contrasting effects of HPS and MH. Soybeans grown in controlled

environments were 30% shorter and had 14% less dry weight under MH than HPS at the same irradiance, but seed yield was not significant affected (42). This result was corroborated by Wheeler et al (178), who also noted that blue-rich fluorescent lamps produced plants with short stems compared with HPS. They went on to show that stem length in soybean became progressively shorter with increasing supplemental blue light added to HPS until a total of approximately 30 μmol m^{-2} s^{-1} of blue (from HPS and BL supplement) was present in the spectrum. Beyond this, extra blue light had no effect. They noted that using high-pressure sodium or other blue-deficient sources for lighting at low to moderate photosynthetic photon flux levels (<500 μmol m^{-2} s^{-1}) may cause abnormal stem elongation, but this can be prevented by adding a small amount of supplemental blue light (178). Similarly, small additions of blue light against a high background irradiance of red light can reduce stem elongation in lettuce seedlings (76). Using background lighting more pertinent to normal horticultural practice, increasing blue light from 0% to 6% increased leaf area in lettuce due to an increase in cell expansion and, to a lesser extent, cell division (45). In the same study an increase in the blue light fraction from 0% to 26% decreased internode length in soybean by specifically by inhibiting cell division but increasing blue light from 6% to 26% reduced soybean leaf area by decreasing cell expansion (45). Manipulating the blue balance of both HPS and MH lamps by adding blue showed confirmed that both lettuce and soybean are blue-sensitive, but that wheat is not (43). In *Phaseolus* bean, decreasing the proportion of blue while holding PAR irradiance constant resulted in increased stem extension at the expense of leaf growth (109).

The benefits of balancing the spectrum provided by HPS lamps by specifically adding blue light was also discussed at the recent 5th Symposium of Artificial Lighting in Horticulture , for example adding blue to HPS using light emitting diodes (LEDs) improved biomass and fruit yield in tomato and fruit yield in tomato and cucumber (41). However, in general, the effects of different lamps for supplementary lighting of long-term glasshouse crops are less clear. For roses grown for cutflowers, plants of the cultivar 'Samantha' grown with supplementary lighting (70 to 75 μmol m^{-2} s^{-1}) from either HPS or MH lamps produced 10% more flowers under MH with no marked effect of quality or shelf life (146). By contrast in the rose cultivars 'After Glow', 'Obsession' and 'Royalty' 100 μmol m^{-2} s^{-1} PAR supplements from HPS produced 5-25% more flowers than the same supplement from MH lamps (120). There are also reports that the shelf-life of roses produced under HPS is longer than that of flowers produced with MH 58).

2.3 Conclusions

(a) There is evidence from a wide range of plants that HPS is the optimal lamp for increasing biomass production and producing plant "bulk". There is little doubt that HPS lamps are the optimum lamp for supplementary lighting where plants are (i) grown long-term under supplementary lighting and (ii) the final mass of foliage or fruit are the key elements in determing the value of the crop.

(b) Supplementation using HPS does has undesirable effects on plant morphology, perhaps most especially in young plants. Increased stem elongation under HPS is reported in many species, while effects on leaf area are more variable. In general, where the commercial quality is a function of compact growth, the photomorphogenic effects of HPS are likely to counteract any benefit arising from increased biomass.

(c) The undesirable morphological response to HPS is largely a function of the imbalance between red and blue/UV in the output of this type of lamp. The lack of UV may compound the deficiency in this waveband that is unavoidable using standard horticultural glass.

(d) MH lamps produce both blue light and UV-A and so their spectral balance is closer to that of sunlight than HPS lamps. There is considerable evidence that using MH lamps instead of HPS lamps produces a more compact plant morphology that more closely meets the needs of commercial bedding production. In principle, replacing HPS with MH might deliver improved plant morphology, but this needs to be assessed against (i) the inherent difference in efficiency and (ii) the relative costs of the two lamp types (see section 5).

(e) The undesirable effects of HPS on morphology of a number of species has been corrected by the specific addition of blue light, for example using blue LEDs. This approach has the merit of exploiting the inherent efficiency and lower cost of HPS, while correcting spectral balance by adding another highly efficient lamp. Given the current state of LED technology, this approach is probably technically possible now, but how it might be implemented in a practical system for commercial use remains unclear.

(f) There is clear evidence that the lack of UV under glass increases stem elongation and leaf area, and surpresses branching in many species. The lack of UV-B and the reduction in UV-A may both contribute to this response. The use of specific UV supplements to improve plant morphology is (i) technically feasible using readily available equipment, (ii) likely to be energy-efficient, and (iii) may deliver benefits in terms of the ability of plants to perform

well after transplanting to the field. However, the use of UV raises major health and safety issues that would require careful assessment in any commercial use (see section 5).

(g) The effects of HPS lamps on plant morphology highlights the risks associated with using any light source with a very unbalanced spectrum. Light quality with the PAR range may be relatively unimportant for driving photosynthesis but does have major effects on photomorphogenesis. LEDs are increasingly available, have high efficiency and costs are falling (see section 5) but most produce a narrow spectrum of light. This narrow spectrum may be useful to complement other lamps (see (e) above), and white LEDs may come to replace conventional lamps in the forseeable future (see section 5), but any use of coloured LEDs for glasshouse lighting requires careful assessment.

(h) The bulk of the research reviewed in this section has been with species other than commercial bedding plants. Fundamental plant photobiology suggests both (a) that most responses to light quality will occur to a greater or lesser extent in most species and (b) that inter- and intra-specific variation in the magnitude of response will occur. Any commercial assessment of lighting for growth regulation in bedding should be founded on more targetted, applied research.

3. The effects of light on quality components in herb crops: flavour and shelf life.

3.1 Commercial background to the problem

Supplementary lighting is used routinely in the production of pot-grown herbs. Current practice uses supplementary lighting to increase daily light integral under low light conditions, and is aimed at a number of commercial end-points (Claire Donkin, pers comm.):

(i) increased yield/biomass,

(ii) improved foliage colour (low light conditions lead to pale green leaves which are commercially undesirable),

(iii) Avoidance of specific physiological disorders that are thought to be light-related (e.g. in basil, coriander and chives),

Other commercially desirable end-points that might be delivered via lighting strategies are improved flavour, increased shelf-life, and improved plant morphology (aiming to produce a compact plant in the pot). Since light effects on morphology have been dealt with in section 2, I concentrate here on flavour and shelf life.

3.2 Scientific background to the problem.

The scope of this review was limited to two main areas, flavour and shelf-life. In both cases, published information specifically dealing with herb crops is limited, but information available on the responses of other species can provide some relevant information, within the usual limits of extrapolation between species and environments. Thus, it is pertinent to review the fundamental literature on the effects of light on the basic properties of a crop that contribute to flavour and shelf life.

Flavour

Flavour compounds are derived from plant secondary metabolism, but the key pathways and compounds clearly differ between crops. In the majority of herbs, flavour compounds are produced by three distinct metabolic pathways. These are the phenylpropanoid (PPP) pathway, mevalonate (MVA) pathway and methylerythritol 4-phosphate (MEP). Members of the onion family (Alliaceae) have sulphur-containg compounds as their main flavour components, and these are synthesised via the cysteine sulphoxide pathway (CSO). The details of these different pathways are not important to this review, but how they respond to the light environment is,

since different herb crops have different flavour compounds produced by different pathways, each of which may show different responses to light quantity and quality. For example:-

- The typical flavour and aroma of basil is produced by a mixture of phenylpropenes, monoterpenes and sesquiterpenes. Some basil cultivar are rich in terpenoids (e.g. linalool, ocimene, geranial or neral), in others phenylpropenes (e.g. eugenol) predominate. Phenylpropenes are synthesised via PPP, monoterpenoids and sesquiterpernoids via MVA and MEP i.e. all three pathways are involved in determining flavour in this crop.

- In peppermint the key components menthol and menthone are both monoterpenes (MVA/MEP).

- In the Umbelliferae, the primary components of both coriander (linalol, alpha pinene) and dill (carvone, limonene) are monoterpenes (MVA and MEP), while in parsley the main components are limonene (another monoterpene) and myristicin (a phenylpropanoid, PPP).

There is little published literature on how specific flavour compounds respond to specific elements of the light environment. Thus, while it may be possible to make some generalisation about the responses of flavour compounds to light, based on the substantial fundemental literature on how secondary metabolism is influenced by the light environment, it is unlikely that all crops will respond in the same way. Indeed different cultivars within crops my show subtle differences depending on their precise composition. Much the same arguments apply for herbs grown for the production of pharmacological compounds, since these are also mostly plants secondary metabolites synthesised via the same pathways as discussed above.

Shelf life

Understanding of the fundamental mechanisms affecting shelf life of produce other than fruit is relatively limited. However, as well as post-harvest decay due to microbial infection[3], (a) the antioxidant metabolism of leaves, and (b) cell and leaf biomechanical properties appear to play significant roles in the shelf life of “leafy produce” such salads, fresh herbs, fresh vegetables and cut flowers. There may be links between these two mechanisms through changes in leaf

[3] Post-harvest light treatments, mostly involving the use of UV-C irradiation, have been proposed as an anti-microbial treatment for fresh vegetables (e.g. 2, 3, 63), and may extend shelf-life in some cases. Although beyond the scope of this review, such treatments do highlight the potential antimicrobial effects of light. Whether such irradiations have any physiological effect on the harvested crop is not clear.

thickness. Antioxidant metabolism can be partly related to many of the chemical changes noted above. Other key plant anti-oxidants such as carotenoids (including pro-vitamin A), ascorbate (vitamin C), tocopherol (vitamin E) and glutathione are influenced by light because they are key components of plants innate defence systems against oxidative damage resulting from high light conditions.

3.2.i Light and plant secondary metabolism

1) Light quantity (Daily light integral)

There is a general principal in plant ecophysiology that the synthesis of secondary metabolites competetes with growth for key precursors, whether photosynthate or nutrients. When growth is limited by photosynthate, plants generally invest few resources in secondary metabolism. Conversely, when growth is limited by nutrients or water, the plant is likely to have "spare" photosynthate that can not be used for growth, but can be diverted in to secondary metabolism. Thus, the effect of light on flavour compounds will interact to some extent with water and fertiliser applications. Assuming that normal horticultural practices make water and nutrients non-limiting to growth, synthesis of flavour compounds, whatever their synthetic pathway, would be expected to limited by photosynthate. Under high light conditions photosynthate supply may be limited by CO_2 concentration in the atmosphere, but otherwise light will be the key limiting factor. Thus, these basic principles of plant ecology predict that under low light conditions, supplementary lighting would allow plants to divert more photosynthate to secondary metabolism, increasing light will lead to increased concentrations of flavour compounds. Whether these predictions hold true depends (a) on whether the basic theory is correct and (b) whether the theory holds for specific crops and compounds.

There is a large body of basic literature that tests the basic theory on the effect of the light environment on plant secondary metabolism. An analysis of almost 150 published experimental studies in woody species (95) confirmed that the concentrations of most secondary metabolites increased with increasing light. Indeed, shading appeared to have a far stronger influence on such compounds than nutrient supply (95). When these responses were divided into three subgroups, phenylpropanoids (PPP), hydrolysable tannins (PPP) and terpenoids (MVA/MEP), all three were reduced by shading, with phenylpropanoids showing the greatest response (95). More recent research confirms that shading reduces concentrations of secondary metabolites in herbaceous as well as woody species (22, 36, 70, 71, 83, 149, 168). For monoterpenoids and sesquiterpenoids there are many ecophysiological studies confirming that production increases with light. Data for a range of species suggests that the response to instantaneous light

environment is probably saturated at irradiances around 500 μmole PAR m^{-2} s^{-1} (9,000-1,0000 lux: Kuhn et el, 2004; Owen et al., 2002). Of course, it is certainly not the case that low light reduces the concentration of all secondary metabolites in all plants (49). Specificity is best characterised for phenolic compounds in woody species, synthesised via PPP metabolism. For example, in poplar low light reduced proanthocyanidins (condensed tannins) but had less effect on phenolic glycosides (70). In birch total phenolics and soluble proanthocyanidins were reduced by shading, but gallotannins (hydrolysable tannins), cell-wall-bound proanthocyanidins and flavonoids (including kaempferols and quercetins) were not affected (71).

The results of these basic ecophysiological studies are borne out by experimental studies of the effects of light on specific compounds, including a relatively limited literature of light and flavour components in herb crops. In mint, increasing DLI from 10 to 15 mole PAR m^{-2} increased the concentration (% w/w by FW) of menthol by 60% and menthone by 20% (50). Over this relatively limited range concentrations of both compounds were simple linear functions of DLI (50). Here increased DLI was through increasing daylength, irradiance was held constant at 200 μmole PAR m^{-2} s^{-1}, but since there seems to be no direct effect of photoperiod on oil synthesis, it is likely that this response in genuinely a function of light received by the crop. In the medicinal herb *Hypericum perforatum* (St Johns Wort) the concentration of the active ingredient (hypericins) also increased linearly with increasing DLI (22).

2) Light quality (spectral balance)

In birch (*Betula pendula*) increasing R:FR shifted the balance of phenolics from chlorogenic acids to flavonoids, but had no effect on proanthocyanidins (169). This effect was distinct from those of increasing UV-B, which increased concentrations of many flavonoids (kaempferols and quercetins) and chlorogenic acids (169). Increased R:FR increased total phenolics in seedlings of *Impatiens capensis* (176), although both these authors and Tegelberg el al. (169) linked changes in phenolics with the reduced growth observed at higher R:FR. This may reflect competition between secondary metabolism and the shade avoidance response, which has recently been discussed (31). This may have wider consequences than flavour compounds, since there are also indications that R:FR can directly influence host disease resistance. Red light suppressed powdery mildew of cucumber, and the effect appeared to be reversed by far-red (156). Exposure to red light before inoculation also induces resistance to *Botrytis cinerea* in some plants (81, 90, 142).

The effects of UV-B on plant phenolics are now very well established, at least for compounds synthesised via the PPP, where various steps in the pathway are under the control of blue, UV-A and UV-B. In general, increased exposure to UV-B results in increased concentrations of total phenolics (15), although there are exceptions (104, 106, 147). Specific phenolic compounds may show contrasting responses to UV-B, with flavonoids showing particularly consistent increases (102, 103, 147, 169, 174, 175), with well established dose responses in some cases (38). It is of note that such dose responses generally show major responses across a range measured in kJ m^{-2} d^{-1}, compared with MJ m^{-2} d^{-1} for DLI of photosynthetic radiation i.e. UV-B effects occur with much lower inputs of light energy. In some cases, the effects of UV-B interact with those of R:FR (159). UV-A may also induce flavonoids in some species (69).

Specific understanding of how light quality infleunce flavour components in herb crops remains limited to a few species. It is notable that these specific experimental studies do not always confirm the predictions that would be derived from the background literature on light and secondary metabolism. Thus, hypothetically, UV-B might be expected to increase phenylpropanoids more than terpenoiuds due to differential effects on the synthetic pathways. However, in experiments with basil, the chemical changes induced by supplemental UV-B in the glasshouse were complex (87). In young plants UV-B increased the phenylpropanoid methyl eugenol but decreased linalool, a terpenoid. The increase in phenylpropanoids as such eugenol persisted throughout development, but as plants aged terpenoids were also enhanced. There was some evidence that UV-B had the greatest effect on phenylpropanoids, but all compounds showed three-four fold increases in content[4] (87). These results may reflect the wider changes of UV-B in this crop, for example this waveband seems to be required for the normal development of oil glands (80), and induces other structural changes such as decreased specific leaf area (87). Similarly, a crop such as peppermint in which terpenoids are the major component might be expected to show little response to increased UV-B. Experimentally UV-B increased some compounds (menthone, menthofuran and menthyl acetate) but decreased menthol (87) highlighting specific effects within the biosynthetic pathway (112). UV-A responses depended on when plants were treated. UV-supplementation during the day increased the contents of both menthofuran and menthol, but if supplementation was at night UV-A decreased essential oil and menthol content (111). In recent work within CP19 using spectral-selective claddings, the plastic that transmitted the full solar spectrum did significantly increase oil per unit dry weight in black peppermint compared with more UV-opaque materials, but

altering the light quality reaching the crop had little effect on oil concentration and chemical profile in thyme, rosemary or sage (6-8). Different genotypes of spearmint with contrasting chemical compositions showed contrasting responses to UV-B. In this case the chemical balance between different compounds (all terpenoids) was unaltered but a genotype rich in carvone and dihydrocarvone showed large increases in these compounds in response to UV-B, but much smaller increases occurred in a genotype rich in piperitone oxide and piperitenone oxide (89).

3.2.ii Shelf life

As noted above, leaving aside microbial decay, shelf-life in leafy products appears to be a function of (a) antioxidant metabolism and (b) cell wall properties and tissue biomechanical properties. Most research in to the physiology and metabolic basis of shelf life in fresh vegetables relate to the effects of treatments such as controlled atmosphere packaging, chilling, or specific post-harvest treatments, such as short-term heating, irradiation or application of specific chemicals (e.g. 48, 96, 106, 115, 123, 139). The effects of the growing environment and the innate properties of the crop at harvest seem to be much less well investigated. However, in spinach, between-cultivar variation in shelf-life were related to the development of oxidative stress. Long-lasting leaves developed less oxidative damage during storage, and this was associated with greater activity of ascorbate peroxidase and higher concentrations of ascorbate (75). The rate of senescence of watercress, parsley, and sage was correlated with total antioxidant capacity of harvested material, with different components of anti-oxidant defence being more or less important in the different species (138). The concentration of specific catabolic enzymes may always have important consequences for shelf-life, especially visual changes such as loss of colour due to chlorophyllase or some peroxidasess, or tissue browing due to polyphenol oxidases (10, 68, 74, 79, 101, 113).

In baby leaves of rocket, lollo rosso lettuce and red chard shelf-life was increased by 1 to 2 days when the crop was harvested at the end of the day compared with leaves harvested at the start of the day. This was associated with differences in photosynthetic capacity, leaf water relations, and leaf biomechanical properties, with both plasticity and elasticity being greater late in the day (33). However, commercial shelf life is also a function of the ability of crops to withstand processing. Under these conditions, crop processability appears to be related to lower % plasticity and smaller epidermal cells, whether these changes were induced by variation in the environment, or treatments such as salt stress or mechanical stress (32, 125).

[4] Recent papers submitted to the project crop panel suggest that this observation has been confirmed by work at the University of Nottingham (30)

3.2.ii a The effects of light on plant antioxidants

The antioxidant metabolism of plants has been intensively investigated since it plays a key role in protecting plants from a range of environmental stresses, not least high light. A wide range of compounds and enzyme systems contribute to antioxidant metabolism, with different systems and interactions acting in different species. Here I focus on a broad overview of key responses to light of the major compounds and systems, and how they relate to shelf-life.

Give that excess light can induce oxidative damage in leaves, it is not surprising that the concentration or activity of many elements of anti-oxidatant metabolism are induced by light. Most published research in this area relates to "high light", that is photosynthetic radiation at irradiances sufficiently high to risk damage to photosynthetic systems, or UV-B. The effects of other elements of light quality are relatively poorly known. Many phenylpropanoids such as anthocyanins and flavonoids are induced by high light and/or specifically by UV-B. They are considered to play a key role as "sun-screens" protecting exposed tissues from excess light, but they are also effective antioxidants (e.g. 9, 66). The effects of light on these compounds is discussed above (section 3.2.i). Carotenoids fulfill a range of roles in anti-oxidant metabolism but the xanthophyll cycle is one key element of photoprotection in many species (39). The the pool of xanthophyll cycle pigments and the antioxidant capacity of the cycle are decreased in leaves grown under low light conditions (57, 77, 107). There is evidence that UV-B may specifically induce xanthophyll cycle photoprotection (57, 64, 107). α- tocopherol is also accumulated in response to high light (57, 67, 77, 107) but UV-B appears to cause increases in some species and decreases in others (82, 97, 155). Ascorbate (vitamin C) and associated enzymes that contribute to anti-oxidant systems are also light-induced, with some direct experimental data from protected crops (1, 25, 57, 107). UV-B induces ascorbate-based antioxidant metabolism (35, 93, 116, 153) but the effect of UV-A appears to be variable (69). Similarly, another element of anti-oxidant chemistry, glutathione and its associated enzymes are higher in leaves grown under high light (1, 25, 57, 107), and also in leaves exposed to UV-B (14, 19, 35, 93) but not UV-A (69). Superoxide dismutase, another anti-oxidant enzyme is increase in leaves under high light conditions (1, 25, 107), but responses to UV-B appear to vary between species and cultivars (14, 35, 183). Specific changes such as browing in cut tissues are due to the action of the enzyme polyphenol oxidase (PPO) on a range of phenolic compounds (10). While UV-B may increase the concentration of the substrates of this reaction (see section 3.2.i) there is some evidence that it reduces the activity of PPO (12). There appears to be no data on how UV-B might influence chlorophyll degradation, except at very high doses (e.g. 88, 110).

3.2.ii b. The effects of light on leaf morphology and biomechanical properties

Reduced leaf thickness is a typical response of plant growing at low irradiance (78, 129, 131-133, 170, 180), although the magnitude of changes varies between species and genotypes. These changes in leaf thickness contribute to increases in photosynthetic efficiency at lower irradiance and photoprotection at high irradiance, where they interact with anti-oxidant metabolism (127, 128, 133). In addition, in the grass (*Festuca arundinacea*) high R:FR ratios increased leaf thickness, under low light conditions (180). Exposure to UV-B also increases leaf thickness consistently across many species (reviewed by 157).

Ecological studies show that leaves grown under high light have greater mechanical toughness in a wide range of species (16, 46, 71, 108, 114, 148, 152), although this is not always the case (149). Similarly, formal measurement of leaf elasticity shows that this is increased in leaves produced under high light, partly a function of bulk leaf morphology, partly to changes in specific tissues such as the main vein (126, 151). There seems to be little understanding of the effects of light spectrum on leaf mechanical properties. However, I am aware of PhD research in the Netherlands that shows decreased leaf elasticity in response to UV-B(19). The current HDC-funded PhD studentship at Lancaster (PC) is also beginning to suggest that such changes can occur rapidly on exposure to UV-B (unpublished).

3.3 Conclusions.

To summarise in very broad terms:

(a) Increasing light quantity (DLI) is likely to result in a general increase in the concentration of plant secondary metabolites and this would be expected to include most flavour or pharmolocological compounds. However, given the specificity of light responses, it is certainly not the case that all compounds in all species will respond in the same way.

(b) Simple increases in DLI will influence growth as well as secondary metabolism, and in the low light environment of glasshouses in winter, additional photosynthate may be more likely to be allocated to growth than secondary compounds. Thus, simply increasing DLI may be a relatively inefficient route to specifically increasing the concentration of flavour compounds. On the other hand, increasing DLI will deliver a balance of increased growth and modified tissue chemistry, both of which may be commercially desired.

(c) Light spectral manipulation may provide a more specific tool to manipulate the chemical composition of plant tissues. Plants grown in dense stands will receive a relatively low

R:FR ratio, and specific supplementation in the red might deliver benefits by regulating growth and increasing concentrations of flavour compounds and other commercial compounds (see section 2). However, standard HPS lamps are quite effective red sources, in my judgement specific supplementation using red light would not be expected to provide much additional benefit.

(d) Specific supplementation using blue, UV-A or UV-B would also be expected to regulate growth and stimulate the synthesis of a range of secondary metabolites. This might be achieved using (i) a broad-band lamp rich in these shorter wavelengths, such as MH, or (ii) the use of specific lamps delivering specific wavelengths. The limited experimental work in this area confirms that the latter approach can be effective, especially since effects are induced at much low irradiances or doses than those caused by PAR (see above). However, there is insufficient evidence on which to base any suggestion for practical exploitation of this approach, in terms of the optimum irradiance, duration, dose, timing or spectral disribution of light treatments. In particular, the use of UV sources in a commercial setting will require careful assessment (see section 5).

(e) Increasing light quantity (DLI) is likely to result in (i) increased leaf thickness and greater leaf strength and (ii) increase the anti-oxidant capacity of leaves. Together, it would be expected that increased DLI would increase shelf-life, although key questions such as the appropriate irradiance, duration or dose lighing, and when it needs to be applied for optimum effect of shelf life, remain unknown.

(f) Specific supplementation using UV-B would be expected increase leaf thickness and anti-oxidant capacity, resulting in increased shelf life. However, so far as I am aware there is no published research on the effects of UV on shelf life, so As noted above, the use of UV sources in a commercial setting will require careful assessment.

4. The effects of light on nitrate concentration in lettuce and other salads.

4.1 Commercial background to the problem

High nitrate concentration is a major challenge for the protected lettuce industry. EU regulations no. 194/97 and 563/ 2002 specify the maximum limits for nitrate concentration in lettuce. The regulatory limits are-

4500 μg/g fresh weight for winter crops (harvested Nov-April)

3500 μg/g fresh weight for summer crops (harvested May-October)

At present the UK has a derogation that exempts production for the domestic market from these limits providing. (i) an industry code of good practice is adopted, (ii) a continuous monitoring programme established and (iii) research undertaken to achieve the legislative targets

This derogation was due for renewal in January 2005, but negotiations continue. Should the derogation be removed, samples exceeding the regulatory limits would be unmarketable. The Food Standard Agency (FSA) monitoring programme for nitrate in UK-grown lettuce and spinach found that in surveys of nitrate levels in between 3 and 5 % of UK glasshouse lettuce samples exceeded the regulatory limit (2000, 2001 & 2002, Food survey information sheet 63/04). Clearly, failure to meet nitrate targets would be a major threat to growers. These failures occur despite the adoption of Good Agricultural Practice and particularly the system of nitrogen fertiliser management developed under HortLINK project P202. Thus, new solutions to the problem of high nitrate are an urgent requirement for UK growers.

Commercial experience points to a key role of light in determining nitrate concentrations. Firstly, high nitrate is a particular problem in winter crops grown in northern European, i.e. when light level are low. Higher light during summer, or in southern Europe, avoids excessive nitrate concentration (Graham Ward, pers comm., and also see 182). The use of supplementary lighting to stimulate growth in winter crops, which is widespread in Holland and the Scandinavian countries but not in the UK, also reduces nitrate concentration. There is also a common observation that nitrate concentrations are high in material harvested in the morning, but much lower in material harvested later in the day (Graham Ward, pers comm.).

4.2 Scientific background to the problem.

The concentration of nitrate in leaves is a function of (i) nitrogen uptake and transport from the roots and (ii) nitrogen metabolism within the leaves themselves. Nitrate accumulates to high concentrations when uptake exceeds metabolism. Light affects this balance in a number of

ways, either through direct effects (e.g. through photosynthesis or the activation of key enzymes) or indirect effects (e.g. by interacting with the control of innate cycles in metabolism).

A key element in the control of nitrate metabolism is the enzyme nitrate reductase (NR). NR is part of the chain of enzymes that converts nitrate in to organic forms of nitrogen, such as amino acids. Thus, increased NR activity results in lower concentrations of nitrate. Two aspects of NR are pertinent to the growers' observation of variation in nitrate concentration at harvest.

(i) NR activity shows an innate rhythm even when plants are kept under constant light or darkness. Plants moved from normal growing conditions in to constant light have maximum NR activity during what would have been day, with activity much lower during what had been the night period (172).

(ii) Superimposed on this innate rhythm NR activity is stimulated by increasing photosynthetic radiation (e.g. 34, 91, 134, 161). This may involve a number of mechanisms, but the supply of energy from photosynthesis is itself important: low light provides too little photosynthetic energy to drive nitrate reduction.

An innate rhythm also exists in nitrate uptake (177), with uptake higher during "night" than "day", even when plants are grown under constant darkness.

In most species these different aspects taken together result in a peak in NR activity near the middle of the photoperiod but a maximum in nitrate uptake at night. These patterns, in turn, result in nitrate accumulating over-night and then falling progressively to a minimum in late afternoon, consistent with commercial observations of variation in nitrate in glasshouse-grown lettuce. One additional factor acting in the field but not under glass may be the suppression of NR activity by UV-B radiation (13), although this has not been confirmed under realistic conditions.

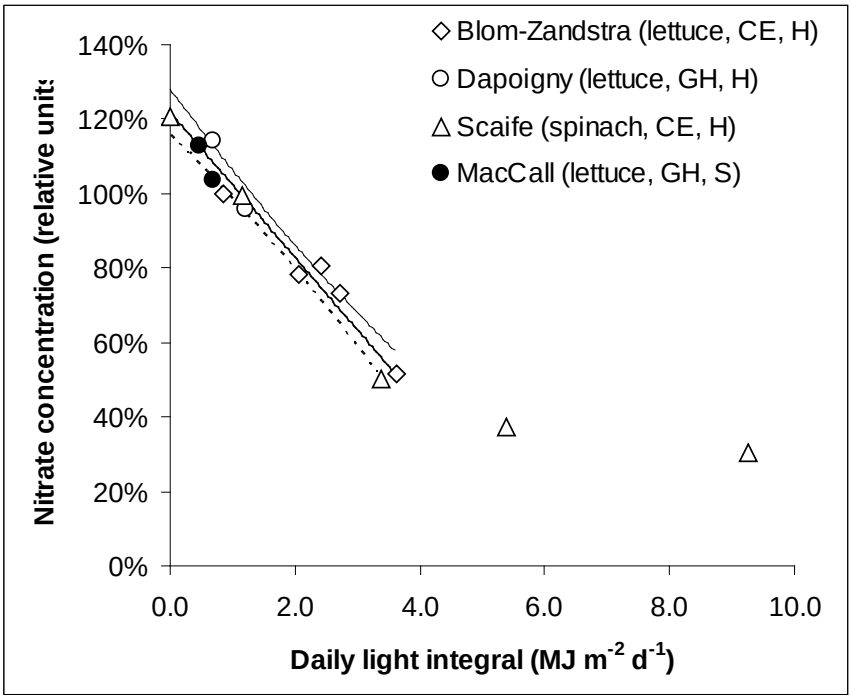
4.2 Nitrate and lighting

There are a substantial number of research papers showing that NR activity increases with increasing light and a number of papers also confirm that this results in a decrease in nitrate concentration with increasing light. These are summarised in Table 3, which does not seek to report all such studies but simply to highlight key findings and patterns. It is clear that foliar nitrate decreases with increasing light, whether light treatments are imposed by shading of ambient sunlight, supplementary lighting in glasshouses or lighting treatments within growth rooms. Given the different approaches used it is notable that data from a range of studies for both lettuce and spinach can be integrated in to a single light dose response (Figure 2).

Table 3 Overview of research in to the effects of lighting on nitrate concentrations in lettuce and other salad crops. Note that this table is not an exhaustive list of all relevant papers, it focuses on those where some clear quantitative relationship between defined light treatments and nitrate concentration can be derived. For other reports of the effect of light on nitrate in salad species see 28, 29, 56, 59, 60, 140.

Authors	Growth conditions	Light treatments	Crop	Result
Blom-Zandstra & Lampe (18)	CE room (?) Hydroponics	0.9-3.6 MJ m^{-2} d^{-1} PAR.	Lettuce	Nitrate in cell sap decreased linearly with increasing light. 2.0 MJ m^{-2} d^{-1} PAR reduced nitrate concentration by about 20%, 3.6 MJ m^{-2} d^{-1} PAR reduced nitrate by almost half.
Dapoigny *et al.*(37)	Glasshouse in July-August and Nov-Dec. Hydroponics	Ambient and 40% shade (approx 9 & 5 MJ m^{-2} d^{-1} PAR in summer, 1.2 and 0.7 in winter)	Lettuce	Nitrate per unit FW increased c.20% by shading in summer, c. 30% in winter. Nitrate per unit DW was highly positively correlated with water content: the lower nitrate concentration at higher light was consistent with the lower water content.
De Pinheiro-Hemriques & Marcelis (72)	Glasshouse in February Hydroponics	Ambient and 40% shade	Lettuce	Nitrate per unit FW increased 10% by shading. A smaller increase on DW concentration exaggerated by lower %DW content at lower light.
Steingrover et al., 1993 (164)	Glasshouse in December Hydroponics	27 µmol m^{-2} s^{-1} PAR from 17.00 to 08.00 for 1-8 d pre-harvest.	Lettuce	Low intensity night lighting decreased nitrate per unit DW by up to 10% but on a FW basis had variable effects, including increases with short duration lighting. This was due to increased DW/FW with night lighting.
Steingrover et al., 1986 (162)	CE room Hydroponics	1.3 MJ m^{-2} d^{-1} PAR with or without additional 0. 3 MJ m^{-2} d^{-1} PAR provided at night.	Spinach	Low intensity lighting at night providing a 0.3 MJ supplement reduced nitrate concentration during darkness or at start of day by 25%. Appeared to be due to reduced uptake as well as increased metabolism.
Scaife & Scholomer (154)	CE chambers Hydroponics	1-26 MJ m^{-2} d^{-1} PAR @14h/d plus 44 MJ m^{-2} d^{-1} PAR @ 24h/d	Spinach	Nitrate concentration decreased progressively with increasing light, 3.4 MJ m^{-2} d^{-1} PAR reduced nitrate by about 50%. Response appears to become saturated at higher light integrals, increasing from 5 to 9 MJ m^{-2} d^{-1} PAR had no additional effect.

Figure 2



A synthesis of quantitative responses of nitrate concentrations in lettuce and other salad crops to supplementary lighting. Data from each paper have been calculated so that all are expressed as a daily light integral, and changes in nitrate expressed as a relative change. While there are limits on this synthesis, it does illustrate a consistent, more or less linear decrease in nitrate with increase light supplements at relatively low daily light integrals.

Whilst this synthesis can not be used for precise prediction, it does reveal the broad pattern of response. Nitrate per unit FW is a negative linear function of daily light integral (DLI) up to around 4 MJ m^{-2} d^{-1} PAR. Most studies with lighting have referred to light intensity (irradiance) rather than DLI, and it is possible that these two elements of the light environment may have some independent effects (see below). However, DLI is consistent with the progressive decline in nitrate concentration over the course of the day observed by growers, and provides a basis on which to assess the pattern of variation in nitrate, and responses to possible commercial lighting treatments.

Increases in light integral above the threshold of around 4 MJ m^{-2} d^{-1} PAR has little further effect on nitrate concentration. Within the range 0-4 MJ m^{-2} d^{-1} PAR an increase in PAR of 1 MJ m^{-2} d^{-1} PAR would be expected to reduce nitrate concentration by around 15-20%. To put that figure in context, the maximum nitrate concentrations reported in the 2003 FSA survey of winter-grown protected lettuce was around 5200 compared with the statutory limit of 4500 µg/g fresh weight, so a reduction of around 14% would bring even this extreme sample below the required limit.

4.3 Conclusions.

a. There is no doubt that light is a key factor influencing foliar nitrate concentrations in lettuce, and in other salads such as spinach. The light dose response curve derived from the literature is consistent with the well-established observation that low light during winter leads to nitrate accumulation. The light response curve highlights that any measure taken to improve light levels within protected lettuce crops will have a proportional benefit in reducing nitrate concentrations in winter.

b. "Conventional" supplementary lighting for lettuce production in winter can accelerate maturity and improve heading and would also be expected to reduce nitrate concentrations in winter. MacCall & Willumsen (119) showed that supplementary lighting of 36 μmole m^{-2} s^{-1} (approx) from HPS lamps reduced nitrate from 4580 to 4216 μg/g fresh weight. Typical regimes of 100-120 Wm^{-2} for up to 16h day appear to be successful in avoiding problems with excess nitrate concentration as well as improving growth and yield (59). However, some caution is necessary as supplementary lighting may also lead to increased tip burn in some lettuce cultivars (59). Supplementary lighting (50 μmole m^{-2} s^{-1} for 12 or 16h from HPS lamps) also improved growth and reduces nitrate concentration in spinach and lambs lettuce (28). Of course, the capital and running costs of supplementary lighting systems are a substantial issue commercially.

c. Supplementary lighting specifically for reducing nitrate is supported by the research literature. Steingrover *et al.*, (163) showed that the supplementary lighting providing 0.3 MJ m^{-2} s^{-1} for one night reduced nitrate in spinach by 25%. In lettuce Fukada *et al.*, (56) showed that there was a near-linear relationship between supplementary lighting providing 0.25-1.3 MJ m^{-2} s^{-1} and reductions in nitrate two days after treatment. Again, a low supplement (0.25 MJ m^{-2} s^{-1}) was sufficient to reduce nitrate by 25% compared with un-lit conditions (56). However, there are also reports that short-term lighting may reduce nitrate in lettuce on a dry weight basis, but is less consistent on a fresh weight basis, and may interact with nitrate concentration in the growing medium (164). Although the details of such short-term lighting treatments remain poorly known, the approach would be to provide light for only a limited period prior to harvest to "condition" the plant for low nitrate (i.e. lighting would not be aimed to stimulate growth or yield). Key unknowns are the light intensity required and the duration. The few papers in this area suggest (i) that lighting for as little as 24h pre-harvest (including over-

night lighting) can significantly reduce nitrate concentration in the final crop, (ii) that light intensities within the normal range of supplementary lighting, or perhaps a little lower are sufficient to induce the effect[5] but (iii) there may some risks associated with very low intensity supplementary light which have increased nitrate in at least one study (164). Whether or not "conditioning" lighting poses a threat of increased tip-burn (59) is also unknown.

d. Commercially conditioning lighting would incur lower running costs than standard supplementary lighting since the duration would be limited to a few days at the end if the crop cycle. Capital costs might also be reduced assuming that lighting was confined just to areas about to be harvested. However, this would require either that the crop can be moved, or the use of a mobile lighting system to allow lamps to be positioned over specific areas. If mobile lights were to be used then the requirement might be rather different from the mobile lighting systems are used commercially for some crops in some countries to provide cyclical supplementary lighting. The requirement may be closer to mobile lighting systems used for sports turf. Capital costs per unit area of the type of mobile lighting system required is unclear. Perhaps a more readily-deployed approach in some cases would be to integrate conditioning lighting in to hydroponics systems for lettuce cultivation in which the crop is moved through the production area are it matures. In this system, lighting could be confined to the area holding plants just for a defined period prior to harvest.

[5] Based on very limited published data (56, 163), short-term conditioning lighting may be more effective than conventional supplementary lighting, perhaps reducing nitrate concentration by up to 35% per 1 MJ m^{-2} d^{-1} added light (cf 15-20%: see Figure 3), but this requires confirmation.

5. Lighting technologies.

5.1 High pressure sodium versus metal halide lamps

One fundamental question for this project is whether there might be commercial advantages of using MH lamps in place of HPS lamps where "quality" rather than "bulk" is the prime commercial need. In essence, the simple answer to this question is yes. Based on the fundamental understanding of the effects of light spectrum, and a fair body of more applied research, there is a solid case to be made that MH lamps would deliver improved quality, whether in terms of non-chemical growth regulation (see section 2) or increased secondary metabolism and/or shelf life in herbs (see Section 3). However, that simple answer is probably not correct commercially given the additional costs of using MH lamps in terms of increased cost per bulb, reduced bulb life and somewhat lower PAR output per input of electrical energy (although this final difference is less marked in terms of PAR than lux: see Box 1). It would be relatively simple to assess the relative costs of a simple "lamp for lamp" replacement of HPS by MH lamps but, on the basis of this review, I believe that this might be of little value commercially. The review highlights additional issues that should be considered in making this comparison. For crop responses such as growth regulation, the lower PAR provided by MH may be misleading since there are at least some indications in the literature that a desirable morphology might be achieved by lower PAR under MH than HPS. A "lamp for lamp" replacement of HPS by MH with no attempt to provide the same total DLI from supplementary lighting might provide a better morphology. It might even be the case that desirable end-points could be achieved using MH lamps for shorter periods each day. Clearly, this conclusion is highly specific to specific crops, and certainly does not apply generally where supplementary lighting aims simply to increase DLI. It is speculative even for crops where growth regulation or other quality elements are a priority but if (a) commercial pressures focus on quality including, for example, the reduction of elimination of chemical growth regulants and (b) if any lighting is considered to be commercially feasible on grounds of cost, then the use of MH rather than HPS should be considered. Solutions for specific crops can probably only be devised on the basis of specific investigation, whether on-holding trials or targeted research.

5.2 Light emitting diodes (LEDs) for supplementary lighting.

Over the last four-five decades, LED technology has made exponential advances, and this type of light source is now used in a very wide range of applications. There is a huge

technical literature on the design and use of LEDs but this overview is focussed on their key properties as they relate to their possible application in horticulture (also see 165). .

(a) Efficiency The luminance efficiency (light output per input of electrical energy) of typical LEDs now approaches 50 lumens per watt for red, yellow and green LEDs, and while efficiency remains lower for white and blue LEDs (around 25 lumens per watt for most commercially available white LEDs), these are improving rapidly. This compares with efficiencies exceeding 60 lumens per watt for fluorescent and discharge lamps, but it is anticipated that LED efficiencies will exceed those of other lamp types within the foreseeable future, perhaps attaining 200 lumens per watt.

(b) Lifetime. Current white LEDs have cited lifetimes of around 50,000h, and this might be improved to 100,000h. This compares with typical lifetimes of >20,000h for HPS and 10,000-15,000h for MH lamps. A lifetime of 100,000h is equivalent to the lamp being used 18h per day continuously for 15 years.

(c) Flexibility. Unlike discharge and fluorescent lamps, LEDs can be dimmed relatively easily. This offers new possibilities in horticultural lighting since, in principal, supplementary lighting could be modulated continuously in relation of incident sunlight. Although conventional lighting is typically controlled so that lamps are only switched on when the solar input falls below a certain threshold, this “on-off” cycle is limited by the negative aspects of very frequent lamp switching. LEDs have the potential to allow much more subtle control of supplements in relation to sunlight, although how this would be translated in to energy efficiency and any specific effects on crop growth remain unclear.

(d) Spectrum. Commercially available LEDs cover a wide range of wavebands of relevance to horticulture, from the UV-A through to the red (Table 4). These distinct colours are a function of the relatively narrow waveband of light produced by most LEDs, which contrasts with the rather broad spectra of “conventional” horticultural lamps. The wavelengths produced are an inherent properties of the semi-conductor materials used to produce the LED. As a result spectral properties are constant over the life of the lamp, in contrast with the change in spectrum seen over ageing in many conventional lamps.

The narrow band-width produced by LEDs may be a positive or negative feature, depending on the horticultural application. The narrow spectrum produced by any single LED is undesirable for photosynthetic lighting since it results in photomorphogenic

responses that typically constrain growth (see section 2). As a result, formal studies of the use of LEDs as a sole light source for plant growth typically use mixtures of different colours to achieve a more balanced spectrum (84, 165, 166). Where photomorphogenic responses are the desired outcome, then the narrow bandwidth of LEDs may be desirable. With the correct choice of LED it may be possible to provide light which is "tuned" to a particular photoreceptor (e.g. 660nm for phytochrome, 470, 430 or 395nm for cryptochrome). The possible applications of such narrow-band LEDs are discussed below (section 5.3) and see also Section 2.

Color	Wavelength
Ultra red	660
Super red	633
Super orange	612
Orange	605
Yellow	585
Pure Green	555
Super Blue	470
Blue violet	430
UV-A	395

Table 4. Summary of commercially available LEDs grouped by colour and peak wavelength.

White LEDs which are categorised in the same way as fluorescent tubes, in to "warm white", "cool white" etc. and have broad spectral outputs encompassing the whole of the PAR waveband. Spectra are relatively smooth, without the very narrow peaks typical of some fluorescent and discharge lamps, and the overall balance between different wavebands (colours) depends on whether they are "warm" or "cool". The spectral distribution of white LEDs should be entirely adequate for supplementary lighting when this technology becomes applicable in horticulture.

(e) Conventional "discrete" LEDs, are small units with relatively limited light output per unit are probably impractical in commercial glasshouse use. LEDs can be brought together in to arrays, but this raises problems of dissipating the substantial heat generated, which limits efficiency, performance, and reliability. Units with sufficient numbers of discrete LEDs for photosynthetic lighting may be impractical, but linear arrays are a possible source of specific wavelengths, e.g. using red or blue LEDs for photomorphogenic manipulation (see section 5.3). A more promising technology may be Large High Brightness Arrays, where multiple LEDs are manufactured together in a single unit. Such systems avoid many of the problems of bringing together large

numbers of discrete LEDs and appear to be the route forward for uses that require high light outputs from a compact source. For example, such units are being used in small-scale lighting in plant research, and discussed for use in research controlled environment facilities.

Despite the many positive characteristics of LEDs outlined above, most research into their use for plant lighting relates to very specific uses, including plant production in entirely enclosed environments, for example for space exploration. Research in to the horticulture use of LEDs is limited, but extends back more than a decade (e.g. 23, 24, 76). Early research highlighted the need to provide a balanced spectrum, then combining red LEDs with blue fluorescent tubes (23, 24, 62, 76, 156), but showed that with an appropriate spectrum, such systems could produce plants of comparable quality to standard lighting systems. More recent work uses combination of red and blue LEDs (84, 166), or a mixture of several colours (165) to achieve a balanced spectrum. Again, good growth and plant morphology have been obtained using LEDs as the sole source of light in many, but not all studies, and this approach may be close to commercial feasibility for propagation rooms, *in vitro* propagation etc. (84, 165, 166). LEDs also have current potential for providing specific wavelengths of light (see Section 5.3).

Looking to the future, increases the luminance efficiency of LEDs and reductions in their unit cost continue, and their use in a range of lighting contexts is driving rapid progress. Within the foreseeable future, large high brightness arrays producing white light could provide very high electrical efficiencies, combined with exceptionally long- lifetime. Packaged into appropriately designed luminaries, this type of LED are likely to be a competitive alternative to conventional horticultural lighting technologies for supplementary lighting in glasshouses. Discussions at the 5th Symposium of Artificial Lighting in Horticulture suggested that this point might be reached within the next ten-fifteen years.

5.3. Specific sources for specific wavelengths

As noted in sections 2-4 there may be commercial needs that could be meet by specific supplementation using short wavelengths (blue, UV-A, UV-B) wavelengths

5.3 (i). Red light

Given their cost and high electrical efficiency, red LEDs with peak outputs at around 660nm may be considered to be the optimal choice of lamps where narrow-band supplementation with red light is required. This might deliver growth regulation by increasing R:FR ratio

(but see Section 2), indeed linear arrays of red LEDs are becoming the system of choice for manipulating R:FR in growth room facilities. In controlled environments, adding red light from LEDs against a low background irradiance increased biomass and flower number in salvia and marigold (73) but it is hard to attribute this response specifically to R:FR rather than increased PAR. Initial DEFRA-funded studies in to the use of red LEDs in bedding crops in the UK produced rather inconclusive results (J.J.J. Wiltshire, ADAS. pers comm.). In practice, HPS lamps deliver quite high irradiances around 660nm and given their widespread use, low cost and high efficiency, they may be the most practical approach to delivering red light. Another approach to increasing R:FR is the use of photoselective plastics within glasshouses. This approach has proved successful in many crops (e.g. 27, 105, 125, 150, 167), but care may be required in the UK since typical R:FR shift films reduce PAR by up to 25%.

5.3.(ii) Blue light

Blue light might be provided either using blue fluorescent tubes or blue LEDs. Research facilities are progressively moving from the former to the latter, using linear arrays of blue LEDs for specific illumination in the blue. However, such blue LED arrays remain too expensive at present for use over a large area. Discrete LEDs are affordable and efficient, and might be considered in specific situations to "balance" the spectrum of HPS lamps (see section 2). This might require relatively small numbers of units, but how this might be delivered in a commercial context is not clear. Blue fluorescents are certainly more easily implemented in the shorter term and might also be used in combination with HPS to provide a more balanced spectrum. However, fluorescent tubes bring inevitable problems with shading, and the combined shading from both tubes and HPS fittings might be a major limit on using them together. Given that blue and UV light induce many similar plant responses but responses to UV occur at much lower doses, the use of UV sources might be preferable in terms of the number of lamps required to achieve a given effect, with the benefit of less shading and reduced capital and running costs.

5.3 (ii) Ultraviolet radiation

Although LEDs emitting long-wavelength UV-A are becoming available, the only current technology suitable for implementation in commercial production would be fluorescent lamps designed specifically to have peak outputs in the desired UV range. There are a wide range of commercially available fluorescent tubes that have peak outputs in the UV rather

than PAR. Apart from their specific spectral output, they are usually equivalent to standard fluorescent tubes in terms of the control gear and fittings that they require, and are available in a range of lengths and power outputs.

1) Spectral output. Any assessment of lamps for specific UV lighting needs to consider two factors, the effectiveness of different wavelengths in inducing the desired response (known as the action spectrum) and the output spectrum of the lamp.

   UV action spectra are the subject of much investigation, and there is no definitive action spectrum that can be applied to all crop responses (51-53, 137). However, as a general rule, most plant responses increase with decreasing wavelength, and this increase is typically logarithmic rather than linear[6]. Thus, the same response can be invoked by far less energy or photons when short-wavelength UV is used. This offers a tempting approach to using UV commercially, since it offers scope of producing responses using a low density of lamps per unit area, minimising capital and running costs. However, in my view, this approach needs a degree of caution, as discussed below.

   Lamps are available with peak outputs ranging from the mid-UV-B up to longer UV-A, and with more or less broad output spectra. The correct choice of lamp will be a vital step in any move to develop commercial UV lighting.

   (a) Specific UV-B tubes have formed the backbone of fundamental research in to plant UV responses. These tubes have peak outputs around 310-315nm and tails to approx. 270nm and 340nm. They are powerful in invoking plant responses but the short wavelength element of their output (270-290nm) is outside the range to which plants are exposed in nature, and is well known to cause plant damage (e.g. bronzing, reddening leaf curling, chlorosis and even tissue death with intense exposure). There is no fixed irradiance or dose at which damage occurs, and plants are especially vulnerable when growing at low PAR. In research use, this type of tube is wrapped with a special polymer filter to remove these damaging wavelengths, but this filter need to be replaced every few days. This is time consuming and I believe that filtering in this way is impractical in commercial use. Without filtering the "margin of safety" between the desired response and crop damage might be too small and too

[6] Note that this has major implications for measuring UV. Using a broad-band sensor that does not take account of the action spectrum leads to entirely spurious comparisons between lamps and sunlight, and hence to entirely inappropriate treatments. Any research in to the use of UV in horticulture must quantify treatments correctly.

variable for reliable commercial use, although this can only be confirmed experimentally.

An additional practical concern is that unfiltered UV-B tubes can pose a significant health and safety risk (see Appendix 1). While this is not insurmountable through good working practices (see below), it would require very careful risk assessments. Thus, although UV-B tubes could offer a highly efficient route to UV supplementation, and have been used in the few studies considering the practical use of UV (11, 87, 112), my view is that their use in commercial settings requires very careful assessment, and should only be considered if alternative lamps can not be used.

(b) Specific UV-A tubes. A range of UV-A tubes are available commercially with peaks between 330 and 370nm depending on the specific lamp. In comparison with UV-B tubes (see above) UV-A tubes are far less likely to cause plant damage or pose a health and safety risk, and would not need filtering. However, given current understanding of plant action spectra, such lamps (especially those with peaks in the longer UV-A) will produce far less effect per unit light energy, requiring more lamps per unit area in a commercial setting. That said, recent assessments of plant action spectra (51-53, 137), and results from CP19 (6-8, 137) suggest that longer wavelength UV-A may have greater effects than believed previously, and this approach should not be excluded in any experimental assessment of the use of UV supplementation.

(c) "Sunlamps". The lamps produced for the commercial sun-tanning industry are typically broad-band UV sources with an output largely in the UV-A but including some long-wavelength UV-B. They are a far closer match to the UV spectrum of sunlight than specific UV-A or UV-B tubes. Hypothetically, a lamp that "replaces" the UV component of sunlight that is filtered-out by glass might be very good for supplemental UV-lighting but, so far are I am aware, such lamps have not be used in plant research, and their precise effects are unknown.

2) Health and safety. Any UV source poses a potential health and safety risk, but the threat increases with decreasing wavelength (see Appendix 1). Based on research experience and good practices, the best approach to minimising any risk to workers from UV exposure would be to design operations to avoid working with the UV lamps switched-on

except when this is unavoidable. However, there is some evidence in the literature that UV supplements given outside the normal working day may not produce the desired response (111). Minimising health and safety issues will require a balanced assessment of lamps type as well as the duration and timing of treatment required to produce the desired response.

3) Fittings. The waterproof fittings used for fluorescent in wet or moist environment s have covers which, although transparent to PAR, will absorb large proportions of UV. Thus, in research use lamps are usually mounted "bare" using waterproof end-caps, with the control-gear mounted remotely. In commercial use this would have the advantage of reducing crop shading due to the fittings, but may require custom-built systems rather than any "off-the-shelf" solution.

6. Overall conclusions

As originally proposed, this review had a tight focus on the use of lighting to deliver growth regulation in ornamental plants. As it finally developed, its scope was far wider, including a range of quality issues in both ornamental and edible crops. One issue that unites all these crops is that at a time of spiralling energy costs, any use of lighting in protected crops is inevitably under intense scrutiny. This clearly applies to all of the possible approaches discussed here. However, what the literature reviewed here demonstrates is that the commercial case for lighting frequently extends beyond simply increasing crop growth or biomass. Economic assessments of lighting should be made on the basis of the total commercial value of the crop produced. What is clear from this review is that appropriate lighting can deliver specific, commercially-desirable end-points in a range of crops, encompassing aspects such as nitrate for salad crops, morphology in ornamentals, and morphology and oil content in herb crops. The extent to which these "quality" aspects influence the economics of lighting will depend on the assessment of individual growers in the context of their key markets, and, clearly, there is unlikely to be a single answer to meets the needs of all growers, even within a single sector. Of course, any complete assessment of the economics of lighting requires an understanding of how much of what type of lighting is required when, to deliver what irradiance, DLI or spectral quality. The contrasting economics of conventional supplemental lighting as opposed to "conditioning lighting" for reducing nitrate in lettuce is a good example from this review. Again, this review has highlighted the abundance of literature that demonstrates that "all light is not equal", certainly not in terms of many crop quality aspects. The universal use of high-pressure sodium

lamps is logical for maximising biomass, and given the high efficiency of HPS lamps the case for any alternative needs especially careful assessment in the current environment of high energy costs. This is, perhaps, a key area where current research is inadequate to provide growers with a solid basis on which to assess choice of lamp for commercial use, certainly for the range of specific end-points considered here. Most publications in to the effect of spectral quality have a clear bias towards fundamental rather than applied research, and have not adequately addressed key commercial questions, such as how many lamps will be required per unit crop area, and how long would lamps need to be run and so on. If the benefits that might be delivered through the use of lamps with specific spectral properties, whether MQ, fluorescent tubes or LEDs, are considered commercially attractive, then there is a significant need for research that bridges the gap between the existing fundamental research and its exploitation in UK horticulture. Much the same applies in considering the use of "novel" lighting technologies such as white LEDs for supplemental lighting. LED technology is advancing rapidly, and in the fullness of time may offer economic advantages even over HPS. There seems little doubt that white LEDs will be increasingly adopted in other industries, and that unit costs will fall, but their effective application in horticulture will require considered research in to how their characteristics can best be exploited. The current economic conditions of high energy costs and, in many cases, low margins for many crops are not ideal for the adoption of lighting in many commercial situations. Set against this are other changes, for example the withdrawal of many agrochemicals. The fundamental photobiology underpinning the responses discussed here will not change, and the innovative use of lighting for specific end-points should not be overlooked as the balance of commercial pressures change in the future.

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APPENDIX 1. SAFETY CONSIDERATIONS THE USE OF UV LAMPS

The health risks associated with exposure to ultra-violet radiation involve two primary targets, the eyes and skin, and may be divided into acute and chronic effects

EYES The best-known acute effect of UV-B is photokeratoconjunctivitis better known as "snow-blindness" or "arc-eye". Photokeratoconjunctivitis can be considered as having two elements, photokeratatis, damage to the cornea, and photoconjunctivitis, damage to the conjunctiva. The cornea is more sensitive than the conjunctiva but both organs show broadly similar spectral responses. Injury results from exposure to UV-B and UV-C with a greatest damage resulting from wavelengths around 270nm. UV-A radiation causes photokeratoconjunctivitis only at very high fluxes (the threshold for injury at 270nm is 30 J m-2, at wavelengths greater than 320nm the threshold is 10,000 J m-2). The most typical symptom of photokeratoconjunctivitis is an acute irritation, similar to the sensation of having sand in the eyes. Symptoms usually do not develop until 6-12 hours after exposure and rarely persist for more than 48h. Photokeratoconjunctivitis is not considered to be directly related to long-term eye-injury.

Chronic UV-exposures may result in cataracts, a change in the lens of the eye resulting in progressive loss of vision. The induction of cataracts by intense short-term exposures occurred in the range 295-320nm but the threshold fluxes for this type of injury were substantially higher than those for photokeratoconjunctivitis. Acute exposure to UV-B from lamps might result in photokeratoconjunctivitis, and this itself is likely to minimise the risk of long-term or permanent eye damage.

SKIN Erythema, sun-burn, results from acute exposures to UV-B and UV-C radiation. Erythema is distinct from the pigment accumulation apparent as a "sun-tan" and UV-A radiation induces erythema only at extremely high fluxes (greater than 10,000 W/m2). Erythema is a complex condition and threshold fluxes and action spectra may vary according to what area of the skin is studied and what assessment criteria are used. Erythemal action spectra have been intensively studied and for severe sun-burn the most damaging wavelengths are in the range 290-300nm. However, if assessments are based on less severe erythema this peak is far less pronounced, wavelengths less than 300nm being of roughly equal effectiveness. The most generally accepted overall action spectrum gives equal weight be wavelengths between 200 and 300nm: at longer wavelengths effectiveness declines exponentially with increasing wavelength.

The most serious hazard associated with chronic exposure to UV radiation is the development of skin cancers. The more common types of skin cancer, non-melanoma skin cancers (NMSCs) are

generally non-lethal and readily treated. There are two main types of NMSC: basal cell carcinoma (BCC) and squamous cell carcinoma (SCC). SCC is the more dangerous but BCC the more common. It is generally accepted that chronic exposure to UV-B is a major factor in determining the incidence of NMSCs. The action spectrum for SSC in mice shows a rapid increase in effectiveness at wavelengths below c. 340nm and has its maximum at around 300nm.

Malignant melanoma (MM) is less common than NMSCs but is far more serious unless detected and treated at an early stage. There is good epidemiological and experimental data indicated that the occurrence of MM (in at least some of its forms) is correlated with exposure to UV radiation. The precise relationship between MM and UV-B remains unresolved but certain links are well described, for example severe and intermittent erythema is associated with increased MM in later life. Such quantitative data as is available suggests that the increased risk of skin cancer resulting from increased exposure to UV-B is smaller for MM than SCC.

Exposure limits for broad-band UV-B radiation have been recommended by the Non-Ionising Radiation Committee of the International Radiation Protection Association (IPRA). The IRPA specifies a general limit for exposure to wavelengths greater than 315nm: this states that the intensity from 315-400nm hitting unprotected skin not to exceed 1.0 mW/cm2 for periods longer than 1000 seconds or flux not to exceed 1.0 J/cm2 for shorter exposure time. In practice, the spectral output of commercial UV-B lamps is such that it is the wavelengths shorter than 315nm which are the greater problem. For these shorter wavelengths, the limits are wavelength dependent and for wavelengths produced by commercial UV lamps the limits are as follows:

Wavelength	Limit (maximum exposure (mJ/cm2) per 8h day)
290	4.7
300	10.4
305	50.0
310	200.0
315	1000.0

In practice, in research facilities the practical problems in actually determining exposure against these limits has led to the common working practice being to design operations to avoid working with the UV lamps switched-on except when this is unavoidable (for example when measuring lamp output or UV distribution). When work has to be done under functioning lamps then workers must wear full protective clothing to cover all exposed skin and eyes. This is probably a practical approach, the harder issue may be whether the required crop response can be produced in ways that remove the need for UV lamps to be switched on during normal crop management operations.