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[The results and conclusions in this report are based on an investigation conducted over a one-year period. The conditions under which the experiments were carried out and the results have been reported in detail and with 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 interpretation of the results, especially if they are used as the basis for commercial product recommendations.]

AUTHENTICATION

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

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GROWER SUMMARY

Headline

- Spectral manipulation achieved with LEDs can control plant morphology and flowering time, improve crop quality, and increase strike rates of vegetative cuttings.
- Many of these benefits can be achieved in glasshouses under low light conditions.
- Careful design of a light spectrum could replace the use of PGRs while increasing crop yields.
- Insect light responses and performance are also strongly affected by light quality.
- An improved understanding of insect light responses will aid the development of better sticky traps for improved pest monitoring and aid design of light treatments that minimise pest performance while also helping select and optimise the best biocontrol agents for LED systems.

Background

In protected horticulture there is an ongoing process of technical advancement and optimisation of production systems. These processes drive improvements in both quality and consistency while reducing environmental footprints. In the current market, many crops are in demand year-round and extending seasons or achieving year round production holds significant business potential. While year-round production is desirable, a major limiting factor for profitable winter production is the energy required to both heat and light glasshouses. The high energy efficiency of LED lighting systems was one factor that attracted attention and the most energy efficient LED currently on sale provides an energy saving of 36% (latest Philips interlights have a lamp efficacy of 3 µmol J^{-1}) compared to 600W HPS lighting systems (lamp efficacy 1.92; Lighting: In Practice). A 36% saving in electricity costs has the potential to greatly improve the economics of winter production especially if yields can be improved, as is often reported for tomato crops in the press (Practical hydroponics & greenhouses article, Philips news room). LED efficiency continues to improve, promising further efficiency improvements in the coming years. While the energy efficiency of LEDs is of significant benefit for horticulture, the spectral flexibility (colour options) of LEDs also hold equal if not greater potential gains for many aspects of horticulture.

During the winter months, crop yield and quality diminish due to the low natural light levels that limit photosynthesis. Plants become etiolated under these conditions and mitigating the effects of low light can be required, such as by the use of plant growth regulators to prevent stretching in ornamental plant production. Increasing the light intensity with artificial lighting systems boosts winter growth rates, but plants may still stretch and be of poor quality if the light spectrum is incorrect. This is because plants possess an array of light-sensitive compounds called photoreceptors that regulate plant responses by sensing different parts of the spectrum. There are several types of photoreceptor, each of which is sensitive to specific regions of the spectrum (Figure GS1, see Lighting: The principles for more detail of plant light responses). Plants respond to the amounts of blue, red, far-red, and UVB light encountered in their environments. For high quality plant production, plants must receive sufficient light for photosynthesis but must also receive light of the correct spectral balance to achieve the appropriate morphology.

Light quality has the potential to influence many aspects of plant growth, but the effects of light quality on pests and beneficial invertebrates are also highly relevant. Invertebrate vision systems are highly diverse. Some insects have monochromatic vision, whereas bees and wasps can perceive UV, blue, and green light, and some flies have the ability to see five colours of light. Altering the light environment is expected to disrupt invertebrate behaviour as their colour perception and ability to sense light intensity will be altered. In addition to the direct effects of light quality on invertebrates, indirect effects are also expected as a result of changes in the chemistry and/or morphology of the host plants. Light quality is expected to alter the flavour and scent of plants, which could alter pest host selection and feeding behaviour, as well as the ability of the plant to respond chemically to pest attack.

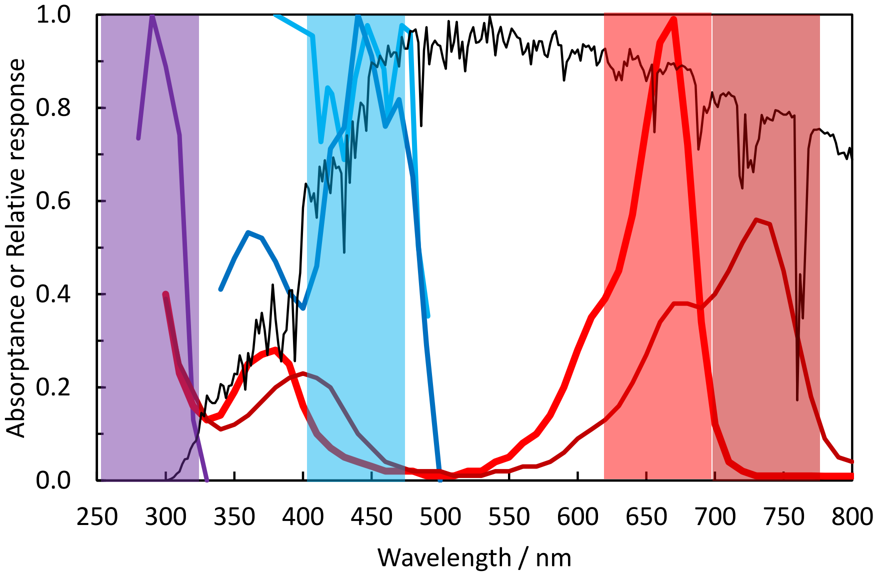


Figure GS1. Plant light responses. Action spectra for UVR8 (purple line, Gardner *et al.,* 2009), cryptochrome (pale blue line, Briggs and Christie 2002), phototropin (dark blue line, Briggs and Christie 2002), and the absorption spectra of phytochrome B in its dark inactive state (dark red line) and its light activated state (red line). The black line shows the solar spectrum (expressed as relative photon irradiance) and the coloured bands indicate the regions of the spectrum with relevance to spectral manipulation for crops.

In this report, we examine the potential for manipulating plant light responses by altering the light spectrum with LED lighting systems. The results are separated by sector (PO, PE, and HNS), with an additional entomology section sector examining invertebrate responses.

Summary

Protected edibles

The influence of different combinations of red, blue and far-red light, as well as intensity of light, on morphology and growth rate were examined in lettuce, tomato, cucumber, sweet pepper, basil, sage, parsley and coriander. All species were sensitive to changes in light quality and the responses were similar between species. Increasing the blue light percentage resulted in plants becoming more compact with shorter internodes and leaves (Figure GS2). Light treatments with higher blue percentages also resulted in the strongest pigmentation. Light treatments with 60% blue: 40% red light resulted in the most compact plants. Plants grown under 100% red light had long but curled leaves, whereas plants grown under 100% blue light had long but flattened leaves (Figure GS3). Plant biomass was found to correlate with total plant leaf area and so changes in light quality influenced growth rate via manipulation of leaf size, not via spectral effects on photosynthetic rate. Plant biomass was greatest in plants grown under treatments with between 6% and 20% blue light (Figure GS4). Under 100% red light, plant mass decreased due to a combination of factors including low light capture (leaves were curled) and reduced stomatal opening (leading to lower photosynthetic carbon gain). Biomass decreased as the blue light proportion increased, largely due to the reduction in leaf area.

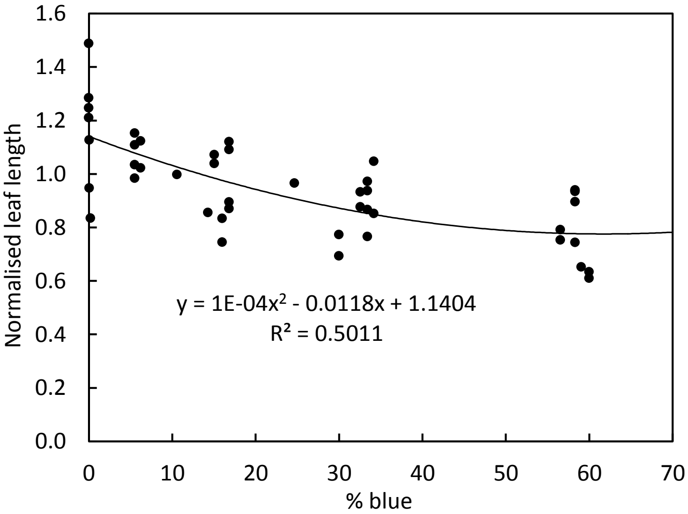


Figure GS2. The influence of blue light percentage of red: blue mixtures on leaf length. Leaf lengths were normalised so the relative changes in leaf length of different species could be compared. Graph includes data from tomato, cucumber, parsley, coriander, cucumber, lettuce and sweet pepper.

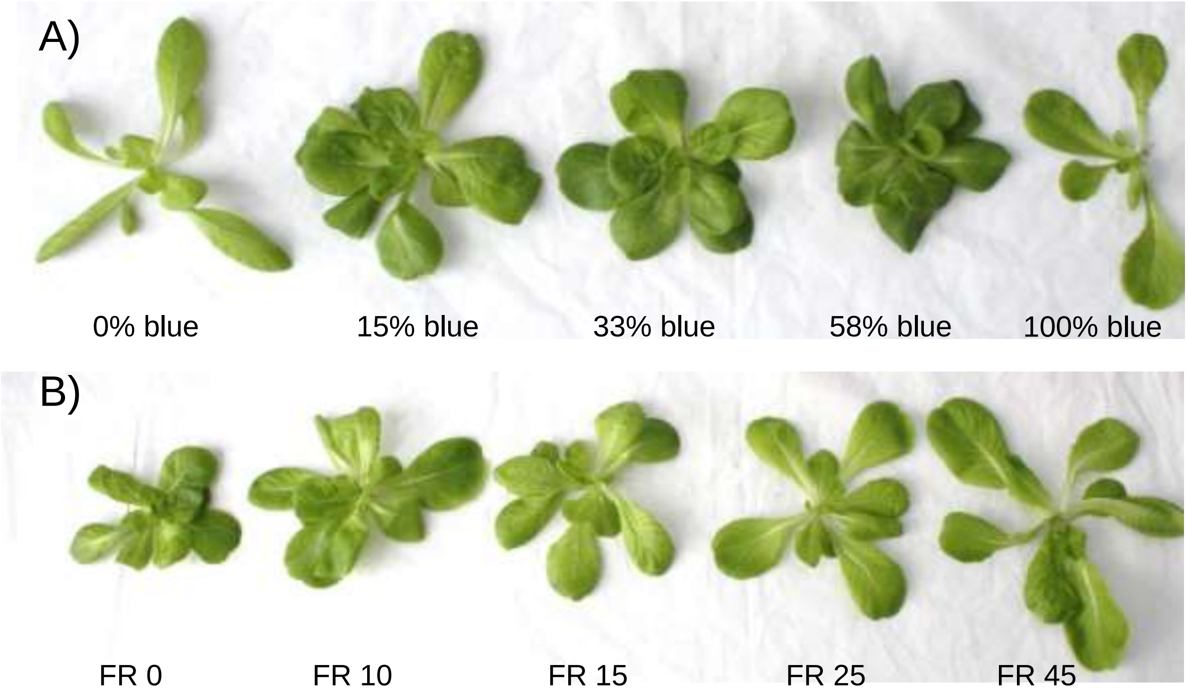


Figure GS3. The influence of light quality on the morphology of young lettuce plants. **A)** Plants grown under different red: blue ratios. **B)** Plants grown under different amounts of far-red (FR) light (values provided in units of µmol m^{-2} s^{-1}).

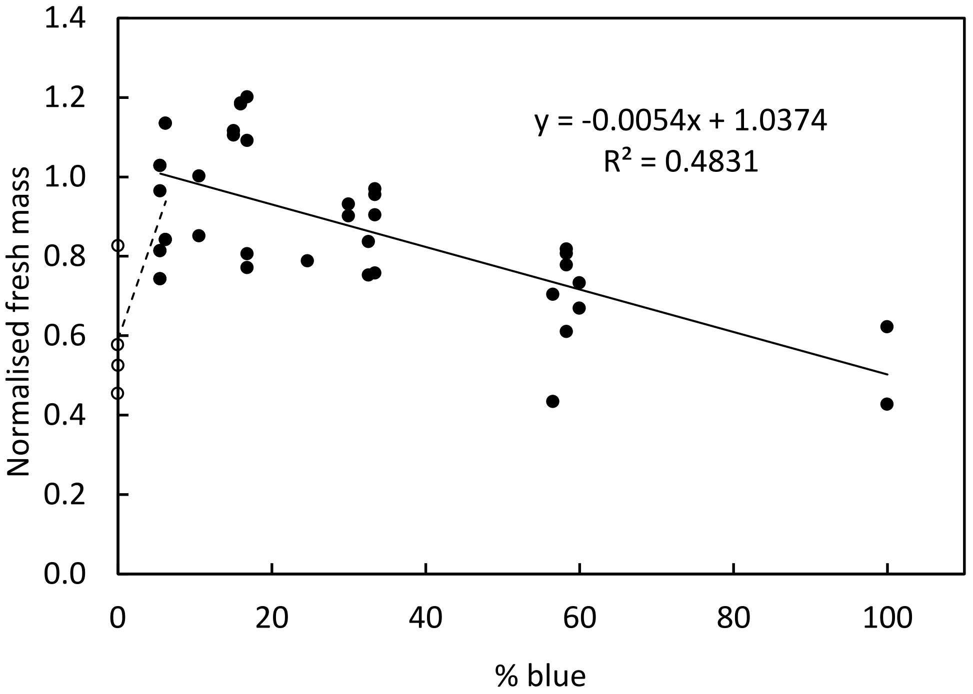


Figure GS4. The relationship between blue light percentage (red: blue mixture) and normalised plant fresh mass. Data are normalized so relative changes in biomass can be compared between species that differ greatly in size. Graph includes data from tomato, cucumber, parsley, coriander, cucumber, lettuce and sweet pepper.

Inclusion of far-red light in the spectrum resulted in increases in internode, petiole and leaf length, and a reduction of leaf pigmentation (Figure GS3). Fresh mass was found to increase as far-red intensity increased (Figure GS5). Some of the increase in fresh mass was caused by an increase in plant water content, presumably caused by an increase in cell size. In general, the far-red responses were stronger than blue responses. This means that blue light treatments may be insufficient to completely correct issues with plant morphology if far-red light is the cause. However, trials performed in a glasshouse demonstrated that the benefits of LED lights (manipulation of morphology) can be achieved in the glasshouse during the winter months when problems with plant quality are most likely to be encountered.

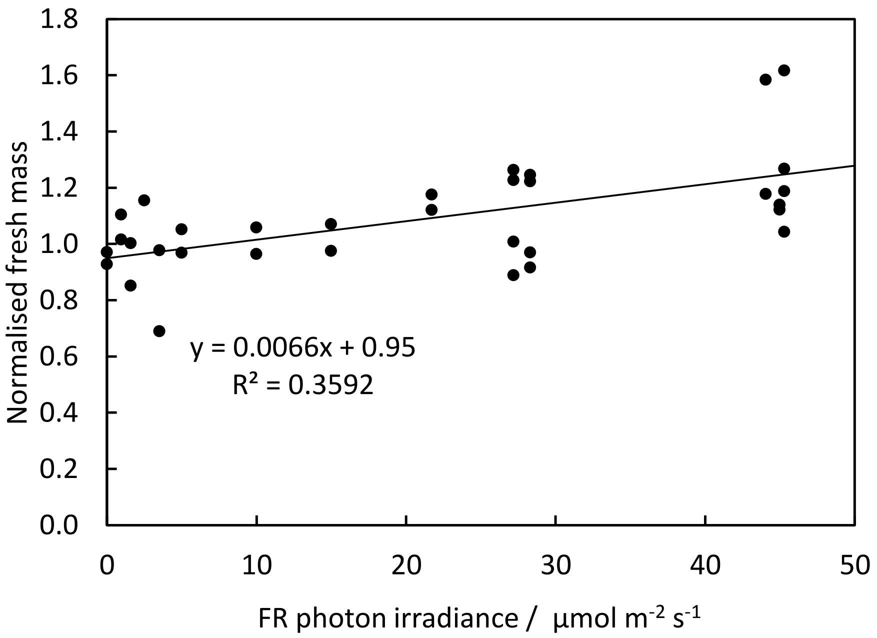


Figure GS5. The relationship between far-red photon irradiance (added to a red: blue mixture containing 15% blue) and normalised plant fresh mass. Data are normalized so relative changes in biomass can be compared between species that differ in size. Graph includes data from tomato, cucumber, parsley, coriander, cucumber, lettuce and sweet pepper.

Increasing the total amount of LED light (increasing the daily light integral) increased the growth rate (measured as fresh or dry mass) and robustness of leaves and stems. However, higher light intensities increased running costs but did not necessarily result in better plant quality. This was because higher light intensities also resulted in plants becoming more compact (often ‘too compact’). In the case of sweet pepper this resulted in the plants becoming shorter as the intensity increased, even though the plant mass increased (Figure GS6). Combining spectral manipulation and intensity could potentially be used to maximise growth rates while maintaining plant morphology.

Figure GS6. The influence of light intensity on sweet pepper plants.

Our improved understanding of plant light responses has aided the development of a model that can predict the size of lettuce leaves under any combination of light quality and intensity. This model will be useful in testing our understanding of crop light responses and, once applied to different crops and morphologies, the model will provide a useful new tool to help growers select the appropriate LED lights for specific crop applications.

While the different species responded in a fairly consistent manner to changes in light quality, the light treatments that produced the best quality plants differed between species. For example, cucumber required far-red light to form natural looking plants, while other crops benefited from treatments without far-red. Overall, the results demonstrate that plant morphology can be manipulated by changing the light quality. Light spectra can be adjusted to meet the needs of growers and light treatments can be selected to maximise yield or deliver plants that meet specific morphological requirements.

Protected ornamentals

The effects of different combinations of red, blue and far-red light, as well as the overall amount of light, on morphology and flowering time were investigated in pansy, petunia, pelargonium (Figure GS7), begonia and chrysanthemum. Morphological responses of ornamental plants were similar to those of the edible crops examined. Light treatments containing 60% blue light produced the most compact plants, the greatest biomass was achieved under 11% blue light, far-red light increased plant stretching, and higher light intensities increased growth rate and plant compactness.

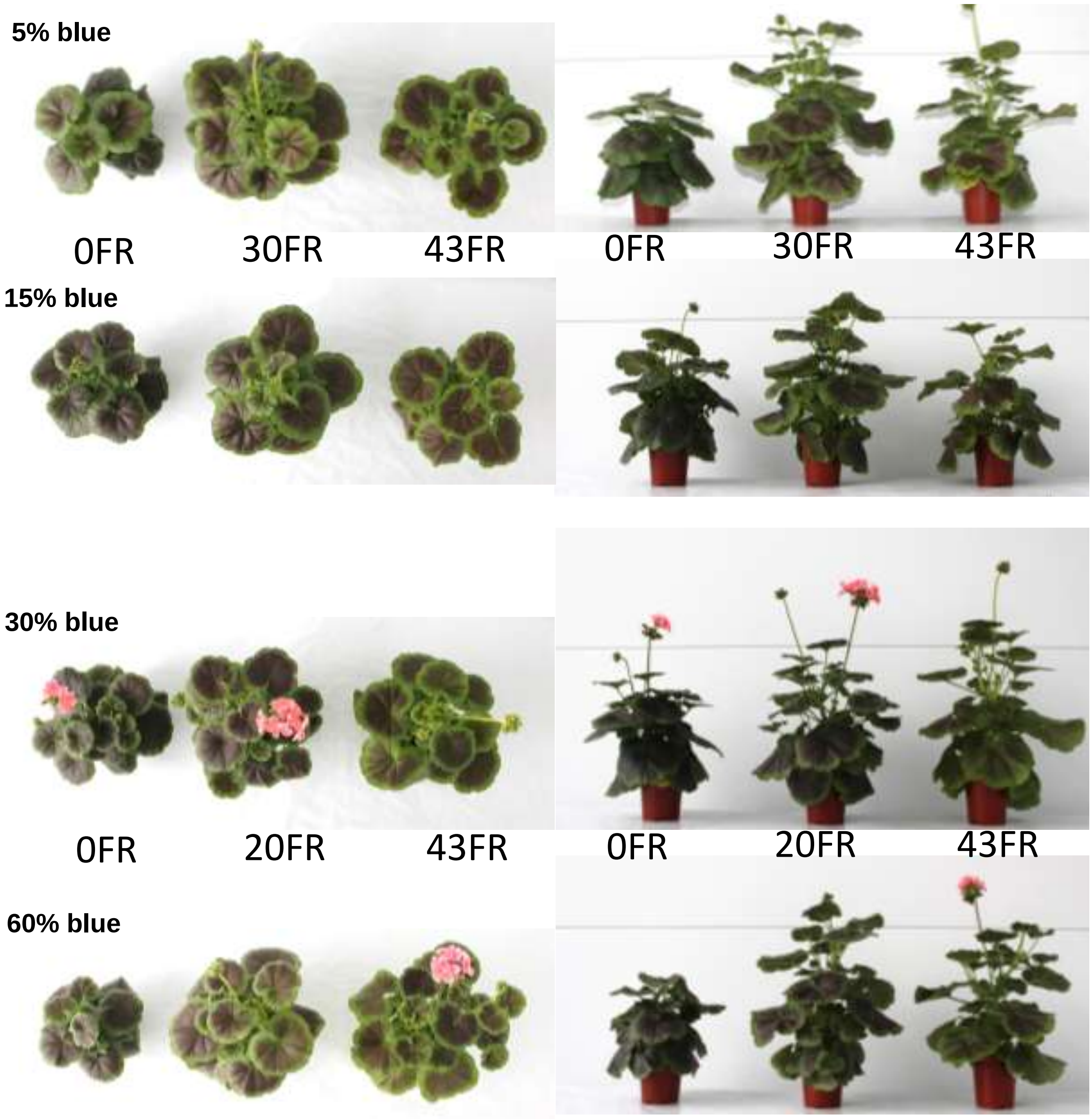


Figure GS7. Photographs of pelargonium plants grown under twelve combinations of red, blue and far-red light. Plants were imaged from above and from the side.

Flowering times were also strongly influenced by light quality and quantity. Red light was found to delay flowering while blue and far-red light promoted flowering. Flowering speed was also affected by speed of growth. This meant that for petunia, while flowering was promoted by blue light, the 30% blue treatment flowered before the 60% blue light treatment because the overall growth rate was slower in the 60% blue treatment. Inclusion of far-red in the light treatments promoted flowering in long-day flowering plants (Figure GS8). Under the highest far-red treatments, flowering occurred up to 2 weeks sooner than the no far-red treatment. While far-red promoted flowering, its negative impact on crop morphology meant that the plants, with the exception of begonia, were unmarketable. Further investigation of transient far-red treatments that initiate flowering but do not alter morphology are desirable.

Figure GS8. The influence of far-red light on petunia morphology and flowering after 52 days growth.

Increasing the light intensity provided mixed results for the ornamental plants. For petunia and chrysanthemum the brightest light intensity (360µmol m^{-2} s^{-1}) resulted in excellent quality plants, and the petunias from this treatment began flowering 35 days after sowing (Figure GS9). However, pansy and pelargonium morphology became too compact at the highest light intensity and pansy flowering speed was maximised at 200 µmol m^{-2} s^{-1}. For pansy, 200 µmol m^{-2} s^{-1} resulted in the most energy-efficient treatment and arguably produced the best quality plants. For petunia, while the 200 µmol m^{-2} s^{-1} treatment was the most energy-efficient, there were clear improvements in plant quality and time to flowering at higher intensities that may provide improved sales.

Figure GS9. Petunia plants grown under different light intensities. Photographs taken 35 days after sowing and nine days after transplantation to six-packs. Numbers indicate the total PAR photon irradiance measured in µmol m^{-2} s^{-1}.

Chrysanthemum was the only short-day flowering plant examined in this trial. Light quality had no influence on flowering time and plants produced flower buds 2 weeks after the day length was shortened to 8 hours. Once under short days, the negative influence of far-red on morphology was enhanced and flower stems rapidly elongated, with plants becoming unmarketable. The highest light intensity treatment kept plants compact without the need for PGRs and resulted in plants with the greatest number of flowers.

These results demonstrate the potential to manipulate crop morphology and flowering by manipulating the spectral composition of light. Trials performed in a glasshouse setting demonstrate that the control of plant morphology can also be achieved in the presence of background sunlight, at least during the winter months when natural light levels are low and day lengths are short. These results demonstrate the potential for LED lighting systems to reduce the requirements for PGRs.

Hardy nursery stock propagation

We investigated the influence of different combinations of red, blue and far-red light on the survival and rooting of cuttings of photinia, eleagnus, rhododendron, lavender, thyme, santolina, iberis and clematis. We also used tomato to examine the effects of light quality on hormonal status of cuttings and how this influences root development.

Light quality was found to strongly influence cutting survival. Blue light was found to decrease survival (Figure GS10), probably due to increased dehydration caused by blue-light-induced stomatal opening. Across all species 100% red light resulted in the best survival rates, though some species, such as iberis, were unaffected by up to 30% blue light. In light treatments with more than 30% blue light, eleagnus cuttings were found to shed all their leaves. This was probably due to a drought-induced increase in ABA synthesis. Far-red light was also found to reduce cutting survival in these species. Identifying the reasons for this response was beyond the scope of this project and further experimentation is required to understand this phenomenon.

In addition to affecting survival, the rooting of cuttings was also influenced by light quality (GS11). Rooting was highly variable between species but overall 100% red light treatments provided the best conditions for rooting. While cuttings rooted fastest under these conditions, any shoot growth that occurred was etiolated, reducing plant quality. If cuttings are to be rooted under red light they should be moved to treatments containing some blue light as soon as rooting occurs. Timing and careful consideration of quantities of blue light may be crucial here, however, as increasing blue light percentage was found to inhibit root formation. Far-red light was also found to reduce rooting in the species examined in these

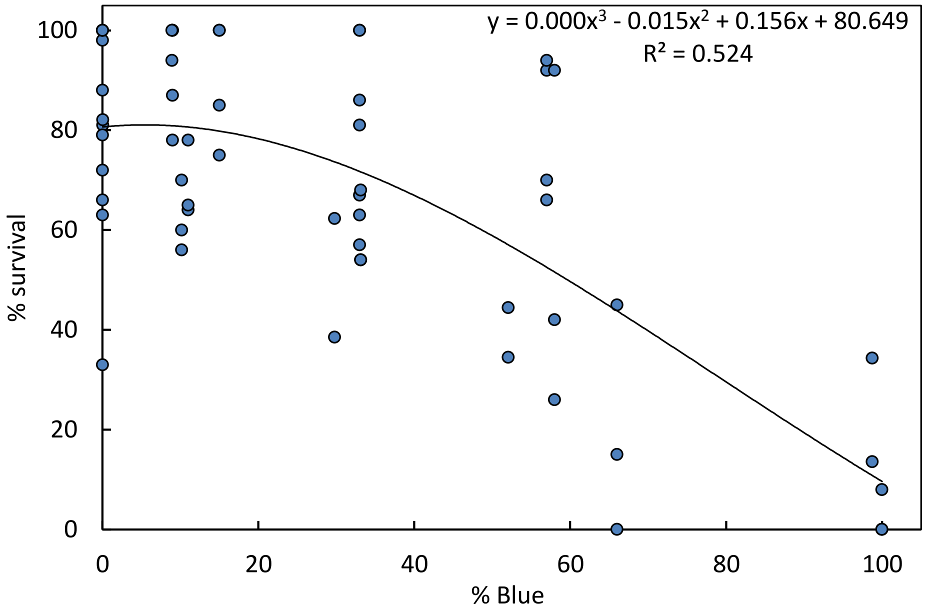


Figure GS10. The relationship between post-excision blue light percentage (% blue) and the percentage of cuttings surviving. The data are combined from experiments performed on eight species (photinia, rhododendron, eleagnus, santolina, iberis, clematis, lavender, and thyme).

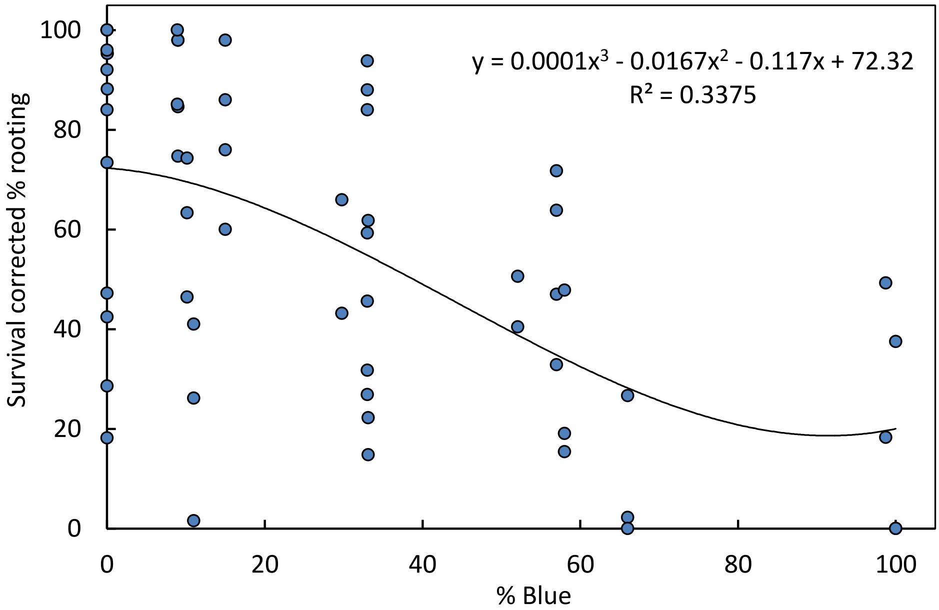


Figure GS11. The relationship between post-excision blue light percentage (% blue) and the survival-corrected percentage of cuttings that rooted. The data are combined from the experiments performed on eight species (photinia, rhododendron, eleagnus, santolina, iberis, clematis, lavender, and thyme).

trials. This was in contrast to the results for chrysanthemum (reported in the PO section), where far-red was found to increase speed of rooting.

Lighting stock plants was found to influence the survival and rooting of cuttings. Supplemental light treatment (50 µmol m^{-2} s^{-1} provided for 12 hours per day) of stock plants increased the survival and speed of rooting of santolina and iberis cuttings. The supplemental lighting is thought to increase the carbohydrate reserves in the cuttings, which aids rooting and survival. Night-break LED lighting provided to santolina stock plants, with the aim of preventing winter dormancy, resulted in etiolation of the stock plants, which produced weaker cuttings. In this case the carbohydrate reserves of cuttings are thought to have been reduced by the night-break lighting treatments.

We used tomato as a model system for examining the influence of light quality on the hormone status of cuttings and how this influenced rooting. We examined the concentration of 11 plant hormones (Table GS1) and found that their concentrations changed over the first 48 after cutting collection. Large transient changes in hormone concentration were observed, especially over the first 24 hours. After 48 hours the concentration of auxin (IAA) in the bottom 4 cm of the stem of cuttings was found to decrease as the blue light percentage increased (Figure GS12). This demonstrates that light quality alters the endogenous concentration of hormones in cuttings and re-emphasizes the importance of auxin in the process of rooting cuttings.

Table GS1. List of the plant hormones measured by CEBAS-CSIC, Murcia, Spain.

Type of hormone	**Acronym**	***Full chemical name***
Ethylene biosynthesis	ACC	*1-Aminocyclopropane-1-carboxylic acid*
Cytokinins	tZ	*trans-Zeatin*
	ZR	*Zeatin riboside*
	iP	*Isopentenyladenine*
Gibberellins	GA1	*Gibberellin A1*
	GA3	*Gibberellin A3 or Gibberellic acid*
	GA4	*Gibberellin A4*
Auxin	IAA	*Indole-3-acetic acid*
Other	ABA	*Abscisic acid*
	JA	*Jasmonic acid*
	SA	*Salicylic acid*

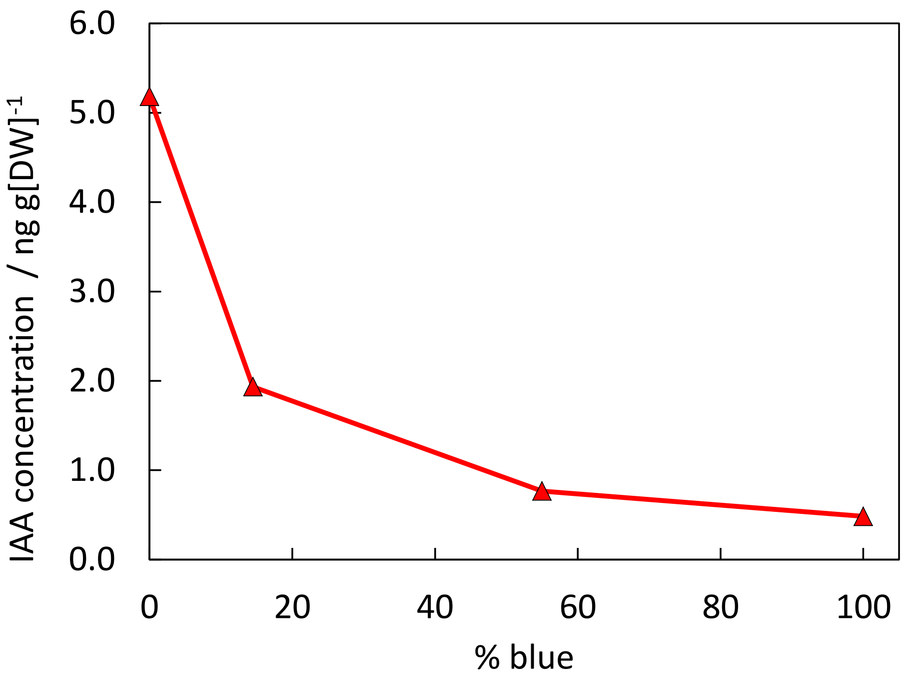


Figure GS12. The average concentration of auxin (IAA) in the bottom 4 cm of stems of tomato cuttings 48 hours after collection and exposure to the different red: blue light treatments.

Entomology

Under red: blue light treatments, yellow sticky traps no longer appear yellow. This reduces their attractiveness to pest species making it difficult to detect pest populations using conventional yellow sticky traps prior to damage being seen in the crop. Blue sticky traps were also found to be less attractive to pests in the LED unit at STC, even though they did appear blue. This is thought to be due to the presence of numerous blue LEDs in the unit that were more attractive to insects than the blue traps. Our research indicates that under red: blue LED treatments fluorescent materials that emit yellow or green light in the presence of blue light are far more attractive than standard yellow sticky traps, enabling earlier detection of pest species. Such improved sticky traps are also expected to be beneficial in glasshouse settings.

Pest performance was found to vary with changing light treatment, though with pest responses varying according to pest / host combination. Peach-potato aphids (*Myzus persicae*) were found to have high mortalities and low fecundity when cultured on lettuce plants grown under 66% blue: 33% red light. This was thought to be caused by the aphids finding it difficult to feed on the compact plants. The same aphid species performed least well on verbena plants cultured under 33% blue: 67% red light. In contrast, cotton aphid (*Aphis gossypii*) performed least well on verbena plants grown under 100% red light. Two-spotted spider mite (*Tetranychus urticae*) performed best on cucumber plants grown under 100% red light and worst on plants grown under 33% blue light. Further work is required to understand the factors driving differences in pest performance under different light treatments, and explain why these vary according to pest/host combinations. Characterising whether effects on pests are direct (i.e. light influencing the pest) or indirect (e.g. light influences the plant, which effects the pest) will also be of use to understand and optimise lighting regimes as a pest control tool. Though no consistent patterns in pest responses were found between species/hosts, these results are encouraging nonetheless as they support that pest populations can be manipulated using light in LED production systems. Furthermore, as pest performance was generally poor under combined red: blue treatments, it is perhaps safe to surmise that production systems using these wavelengths should not be highly susceptible to pest outbreaks, at least for those pests tested. .

The effectiveness of biocontrol agents under the different light spectra was also investigated. Casual observations have indicated that biocontrol agents that fly (for example parasitic wasps) perform less well than those that crawl (for example predatory mites) when released in the LED4CROPS facility. Our experimental results indicate that the parasitic wasp *Aphidius matricariae* was able to parasitize the aphid *Myzus persicae* when placed in the vicinity of infested plants illuminated with different red: blue light mixtures. Flight activity trials indicate that two wasps species, *A. matricariae* and *A. colemani,* fly when exposed to all the different light treatments, even 100% red light, only minimal flight activity was recorded when wasps were given no light at all. This supports that premise these wasps can use their green photoreceptors (which are expected to detect red LED light), as well as their blue photoreceptors, to initiate flight under red: blue LED production systems. Extended flight trials, designed to see if these wasp species can travel towards aphid host plants in a larger flight arena, showed flight towards host plants was greatest under light treatments with low blue percentages. This result perhaps hints again at the importance of the wasps green photoceptors in promoting visual plant recognition under red light, , though the influence of different light treatments on the ability of the plant to produce wasp-attracting chemicals (e.g. volatile chemicals produced in response to pest attack) could also explain this result. This is a particularly interesting topic for future work, as it may be possible to select light regimes that promote pest-infested plant signalling to biological control organisms, optimising biological control efficiency by allowing infested plants to ‘stand out from the crowd’ more clearly. In any case, these data indicate that parasitic wasps can potentially be used as biocontrol agents in red: blue LED-lit systems. However, further work will be required to identify what release rates and release strategies would be required for effective aphid control when wasps are not restrained within flight cages. The predatory activity of *Phytoseiulus* on two-spotted spider mite was found to be unaffected by different red: blue LED light treatments. This backs up our casual observations that predatory mites provide good control of pests in LED-lit systems.

Financial Benefits

Reduced running costs

Advances in LED technology continue to improve energy efficiency, with the newest systems achieving efficacies of 3.0 µmol J^{-1} (Philips, Interlights), a 36% energy saving when compared to 600W HPS lamps, which have an efficacy of 1.92 µmol J^{-1}. LED systems with the highest efficacy tend to produce predominantly red light with as low as 6% blue light. To achieve the light regulation of growth described in this report, higher percentages of blue light may be required and this will lower the lamp efficacy ratings.

Glasshouses lit with LED lighting systems are expected to require an increased heating requirement of approximately 10% in comparison with HPS lit systems. These increased heating requirements should be considered when making the transition to LEDs, but it should also be noted that the costs associated with running heating systems are considerably lower than those associated with lighting systems and, overall, LED systems will result in a reduced energy bill. Furthermore, because LEDs cause less heating, light and temperature management can be uncoupled allowing greater control over crop performance and reduced loss of CO_2 (vents open less regularly). Lights can also potentially be used during warmer weather when light levels are low but when HPS lamps would overheat plants. This increased climate control may enable improved crop quality and yields. Improved yields for reduced energy inputs provides opportunity for sustainable intensification of UK horticulture.

While reduced energy bills provides a compelling reason to invest in LED lighting systems, the ability to manipulate light spectra (change the colour of the light) provides a wider range of opportunities to optimise commercial crop production that may have a greater impact on business competitiveness than energy saving alone.

Protected Edible crops

There is a growing demand for season extension and/or year round production of UK-grown fresh produce. Maintaining plant yields through the winter requires supplemental lighting. HPS lighting has been the standard system of choice for many years but maintaining plant quality with HPS lamps can be challenging due to the low amount of blue light they produce (6%). Under supplemental HPS lamps plants grow taller, leading to quality issues, and generating red pigmentation in lettuce crops is difficult. With spectral manipulation, plant quality can be kept within specification without the need to resort to other climate control measures, such as drops in temperature that potentially increase the risks of plant disease due to the concurrent increases in humidity. Removing the need to steer crops using temperature will potentially increase growth rates as optimal temperatures for growth can be maintained. With a more consistent light environment, plant growth will be more consistent which potentially reduces labour costs as less intervention will be required to control crop quality.

The measurements examining growth rates under the different intensities of light can be used to determine crop light requirements. When combined with measurements of sunlight this information could be used to refine lamp switching controls. Lights could then be turned on when low natural light levels are expected to reduce plant growth and/or quality and turned off when natural light levels are not limiting to growth rates and quality. This information has implications for current HPS installations but as more sophisticated LED lighting systems with integrated dimming become affordable we will have a better understanding of how to exploit them to best effect.

Protected Ornamental crops

Many ornamental crops are grown during the winter months when low light conditions result in poor morphology. Multiple applications of plant growth regulator may then be required to maintain plant quality. The morphology of ornamental crops explored in this trial responded similarly to the PE crops. Increasing blue light (up to 60%) increased plant compactness but reduced growth rate, and far-red caused plant stretching. The results from these trials indicate that spectral manipulation has the potential to replace the use of PGRs, especially for crops than only require PGRs during periods of low light. This provides businesses with alternative approaches to crop management and ‘protects’ future crop production against the possible loss of PGRs.

In addition to morphological control, spectral manipulation can also alter flowering time and provide growers with more control of when crops hit full bloom. As the changeable weather during the spring season greatly affects bedding plant sales, delaying (exclude far-red from the growth environment or provide more red light) or hastening (addition of far-red light) flowering by adjusting light quality could help reduce crop waste and improve profitability. Even ensuring plants are in flower for specific target dates can be challenging with variable weather conditions. Flexible LED lighting strategies will help steer plants into flower at the appropriate date to ensure sales target are met.

Hardy Nursery Stock

Improving the strike rates of cuttings has the potential to greatly improve the efficiency and profitability of a propagation business due to the labour intensive nature of this work.

Achieving an optimal lighting environment provides one route by which strike rates can be improved. The relative improvements that can be achieved with LED lighting will partly depend on the ability of each species to root and the factors that currently limit rooting. In these trials, altering the light spectrum had profound effects on strike rates. Strike rates of santolina cuttings ranged from 100% under red light to as low as 8% under 60% blue + 40% red light.

Assuming a challenging species currently achieves a strike rate of 50%, generating 1000 plants to meet market demands will require collection, processing, and sticking of 2000 cuttings. Assuming optimisation of lighting improves strike rates to 80%, the total number of cuttings required to meet market demands would be reduced to 1250 cuttings. This would result in a 38% reduction in space, labour, and resource use, or an equivalent increase in sales. Even lighting easy-to-root species could be beneficial if rooting speeds are increased, as this can enable improved turnover and space-use efficiency. Furthermore, optimising the lighting for cuttings could reduce the need for treating cuttings with rooting powder, which would further reduce production and labour costs.

From the perspective of installation and running costs, lighting cuttings is more compelling than lighting stock plants because more cuttings than stock plants can be illuminated with a single lamp. Assuming the lighting requirements of cuttings are 50 µmol m^{-2} s^{-1} and the selected lamps have an efficacy of 2.7 µmol J^{-1}, lighting a 10 m^2 growing area only requires 195 W of electricity (approx. 1 Philips top light). Assuming the lights operate for 16 hours each day, energy consumption would be 3.1 kWh per $10m^2$ per day. If rooting takes 30 days and electricity costs range between £42 and £56 per MWh (energy pricing based on data taken from FEC Energy Weekly update email), then lighting a $10m^2$ growing area will cost between £3.9 and £5.2 per month in electricity. At a plant spacing of 4cm, 6250 cuttings can fit in 10 m^2 area bringing the electricity cost to between 0.06 and 0.08p per cutting. Assuming each cutting sells for 50p an improved strike rate of 10% would increase sales volume by 625 plants with a total value of £313 from the $10m^2$ area per month, more than enough to cover the installation and running cost of an LED system. It is also expected that the quality of the cuttings would be improved. This could result in further increases in sales due to improved customer satisfaction or the ability to produce a more diverse portfolio of products.

Action Points

To make use of most of the data generated in this report, growers would need to invest in LED lighting systems. The results outline the benefits provided by different regions of the light spectrum and how light intensity influences plant quality. These results will provide a baseline from which growers can begin to develop their own light treatments while performing small scale trials. It is recommended that small onsite trials are carried out before large scale investments are made. This is for two reasons: 1) to ensure the light treatments are appropriate for the specific varieties being grown, and 2) to help growers develop the appropriate crop management strategies (it is expected that LED lighting systems will require altered crop water and heating requirements). This research program has generated a considerable amount of information about plant light responses that will aid design of light treatments aimed at achieving specific plant responses.

The cutting rooting experiments indicate that light spectra have a large influence on strike rates. LED lighting systems can be used to greatly improve rooting efficiency of cuttings directly, or indirectly if mother stock plants are lit. Propagation requires relatively low intensities of light so installation and running costs would be proportionally lower than for crop growth. If the installation of lights is deemed too expensive, similar results may be achievable by using spectral filters that remove the majority of blue light.

For growers interested in using LED lighting we have outlined several steps that should be taken to ensure a successful installation. It is advisable to seek out independent expert advice to help you through this process.

1. Identify the desired outcome of a lighting system. The aim of an installation may be to improve crop quality, increase yield, or reduce energy consumption, and each desired outcome may require a different lighting system. Equally it may be possible to select a lighting design that achieves a good compromise between quality and yield.

2. Determine the lighting regimes required to achieve these goals and consider whether LEDs are required or if spectral filters can be used. For guidance on lighting measurements and converting between different measurement units see the AHDB Horticulture technical guide Lighting: The principles. If available, historical records of crop yield and the light environment at your site can be used to identify periods of the year where insufficient natural light is available. This can be used to infer crop light requirements. Crop lighting requirements should be determined in units of µmol m^{-2} s^{-1} or mol m^{-2} d^{-1} and lighting suppliers should be able to advise how many of their lights will be required to achieve these goals.

3. Conduct small-scale trials to examine crop performance and learn how management strategies will need to be revised. If possible, the LED trials should be performed in a region/zone of your crop production facility where irrigation and temperature can be controlled independently to the rest of the production area. This is not always

possible but crop water and temperature requirements may differ, especially in comparison with HPS lighting.

4. It is important to have accurate measurements of the light environment within a crop production area when performing lighting trials. LED lighting systems should not be measured using Lux meters. The best type of sensor for measuring LED lighting for crop production would be a PAR meter which measures the light that can be used by plants for photosynthesis and makes measurements in units of μmol m^{-2} s^{-1}. Good quality sensors should be used, and it should be noted that some models of PAR sensor are not designed for red:blue light environments and should be avoided.
5. Use the trial results to determine the economics of an LED lit production system for your site / crop, and use this information to inform decisions on further investment in LED lighting.

SCIENCE SECTION

Section 1. Introduction & Methods

1.1. Background information

Sunlight provides the energy that supports the vast majority of Earth's ecosystems. Plants convert this solar light energy to carbohydrates and ATP (chemical energy) via the process of photosynthesis. This carbohydrate is used to build vegetative biomass, leaves and stems, which in turn undergo more photosynthesis, powering the production of flowers, seeds and fruit. While sunlight provides the energy for growth, it also contains a considerable amount of information that indicates the season (changes in day length and intensity), the location in the environment relative to other plants (changes in red far-red ratio indicates location within plant canopies), and elevation (more UVB light is present at high altitude). Changes in light quality have a direct influence on photosynthetic rates (McCree 1971, Hogewoning *et al*., 2014), but also have profound influences on plant morphology and development that enable plants to acclimate to their environment (Davis & Burns 2017). Plant phenotype is extremely plastic in response to changes in light quality, enabling a species to maximise its chances of survival in the range of conditions encountered in its ecological niche. In shaded environments a plant may grow tall to reach brighter light conditions (etiolated growth), while in harsh full-sun conditions it may remain compact, which decreases water use, and produce high concentrations of pigments that provides protection against sun damage. The ability to detect day length also helps plants maximise reproductive success by ensuring flowers are produced during a season when pollinators are present and that environmental conditions are optimal for seed/fruit production. Many of these responses (for example changes in leaf size and pigmentation) can also impact plant growth rates by altering light interception and photosynthetic carbon assimilation (Wiengand & Richardson 1983). While this plasticity ensures plant life cycles can be completed in a variable environment, it can provide significant challenges in horticultural production systems where highly uniform crops are desirable. A good understanding of plant light responses can be used to ensure crops are grown under light conditions that produce crops with the desired characteristics.

Plants have evolved a range of photoreceptor (light-sensitive compounds that induce light responses) sensory systems that enable them to respond to changes in the natural light environments by directing changes in phenotype to match the conditions encountered. Plants possess several families of photoreceptor, each of which are sensitive to different regions of the light spectrum (Figure 1.1). UVB light is detected by a photoreceptor called

UVR8 (Brown et al 2009). UVB light is highly damaging to plants and so these photoreceptors are very responsive to low intensities of UVB. UVB / UVR8 induces plants to increase their pigmentation (Chalker-Scott 1999), reduce stem extension (Brown *et al*., 2009), and increase the robustness of plant tissues (Wargent *et al*., 2009). Blue light is sensed by several families of photoreceptor. The cryptochromes and phototropins (Briggs & Christie 2002) regulate a wide range of blue responses (including plant height, pigmentation, leaf morphology, phototropism, stomatal opening, and circadian rhythms) that are relevant to producing high-quality plants. The red and far-red responses are regulated by a family of photoreceptors called the phytochromes (Demotes-Mainard *et al*., 2015). These are perhaps the most extensively researched photoreceptors, and regulate many plant light responses (including plant height, pigmentation, leaf shape, circadian rhythms, induction of flowering, and day-length sensitivity). Many plant responses, for example plant height, are regulated by multiple photoreceptors. Full control of these responses in growing systems is likely to require the development of light treatments that provide the correct balance of each colour. As multiple responses are under the control of light, light treatments designed to influence one aspect of plant quality may have negative impacts on other aspects. For example, light treatments designed to enhance leaf pigmentation may result in slow growth and delayed flowering.

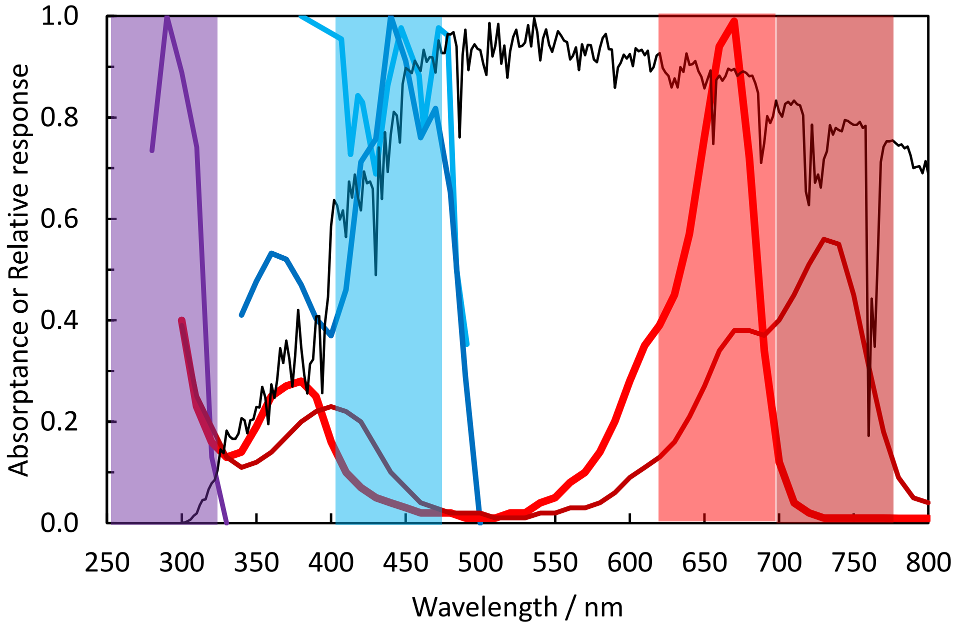


Figure 1.1. Plant light responses. Action spectra are shown for UVR8 (purple line, Gardner *et al.,* 2009), cryptochrome (pale blue line, Briggs and Christie 2002), phototropin (dark blue line, Briggs and Christie 2002), and the absorption spectra of phytochrome B in its dark inactive (dark red line) and light-activated (red line) states. The black line shows the solar spectrum (expressed as relative photon irradiance) and the coloured bands indicate the regions of the spectrum with relevance to spectral manipulation for crops.

A considerable body of scientific knowledge on plant light responses has been generated over the last century and our understanding of the molecular basis of these responses has advanced considerably in the last 40 years. However, it is only now possible to make practical use of much of this information in horticulture due to the introduction of light emitting diode (LED) lighting systems. While some of the benefits of spectral manipulation can also be achieved through spectral filters (see AHDB project Paul *et al.* 2006 - CP 019) LEDs provide the potential to control plant growth independently of the seasons. LED lighting systems provide several advantages over other lighting technologies used in horticulture (high pressure sodium [HPS], fluorescence lamps, and incandescent bulbs, see Davis 2015 AHDB Technical Guide Lighting: The principles for more information) in that they are robust and contain no glass or heavy metals, they have low operating temperatures so they can be placed close to plants, and they can be more energy efficient (see Pearson *et al*, 2015- CP139 and AHDB Technical Guide Lighting: In Practice). But perhaps most importantly the emission spectra of LEDs can be altered to generate a range of light conditions designed to manipulate plant light responses and control plant development, for example by improving crop quality, removing the need for plant growth regulators (PGRs), or increasing the efficiency of propagation.

Many plant growth regulators influence growth by interrupting the natural hormone signalling. Light also influences the synthesis and transport of hormones and so carefully designed light treatments have the potential to replace the need for PGRs. There is a complex network of interactions between light and hormone signalling systems and there are several key signalling components that work to integrate these two signalling systems (Lau & Deng 2010). These signal integrators are also involved in integrating light and hormone signalling with temperature sensing (Franklin 2009). As our understanding of crop light responses develops it will be possible to design light and temperature treatments that work together to control crop growth, morphology, and development.

Efficient propagation requires an environment conducive to the development of adventitious roots. Adventitious rooting is also under the regulation of hormones. Significant changes in hormone concentrations occur rapidly following excision of cuttings and these changes play important regulatory roles in both the initiation and ongoing development of roots (see Druege *et al.,* 2016 for a detailed review on adventitious root development). Carbohydrate concentration in cuttings also plays an important role in adventitious rooting. To grow roots, cuttings must convert starch into sugars that can fuel root growth. This mobilisation of sugars is dependent on the reserves contained within the cuttings (which are dependent on the light and temperature environment prior to collection) and is induced/regulated by hormone concentrations. The influence of light quality on hormone production and transport in cuttings is expected to have a significant impact on adventitious rooting.

While it is important to create a light environment that is suitable for the production of high quality plants, it is also important to understand how pest and beneficial invertebrates will respond to the changes in light quality. Without this knowledge, it becomes difficult to ensure that pest populations are efficiently monitored and ensure that biological control methods are successful. Light quality can have direct and indirect influences on both pest and beneficial invertebrate effectiveness. Direct effects are caused by invertebrate vision systems, which vary greatly between phylogenetic groups. Behavioural vision responses can even differ between sexes. Vision systems are diverse in their spectral sensitivity (Briscoe & Chittka 2001): fly species possess five visual pigments; hymenoptera, including bees and wasps, are tri-chromic (UVA, blue, and green receptors), and many species have monochromic vision systems. Invertebrates are also diverse in their behaviours and both positive (Macdowall 1972) and negative (Varjú 1976) phototactic responses have been observed. Understanding these responses could potentially aid development of light treatments that disrupt pest responses but also aid development of traps and integrated pest management strategies.

Here we report the results of a three-year project examining light responses of several plant species relevant to the protected edible (PE), protected ornamental (PO), and the hardy nursery stock (HNS) sectors as well as the responses of pest and beneficial invertebrate species (See table 1).

Table 1.1. List of species examined for each horticulture sector. Numbers in brackets indicate the year of the study during which each species was examined.

PE Species		**PO Species**		**HNS Species**		**Invertebrates**	
Basil	(1.3)	Begonia	(1)	Clematis	(2)	***Pests***	
Coriander	(3)	Chrysanthemum	(3)	Eleagnus	(1)	Aphids	(2)
Cucumber	(1,3)	Pansy	(1,2,3)	Iberis	(2)	Spider mite	(2)
Lettuce	(1,2,3)	Pelargonium	(1,2)	Lavender	(3)		
Parsley	(3)	Petunia	(1,2,3)	Photinia	(1)	***Beneficial***	
Sage	(1)			Rhododendron	(1)	Predatory mites	(3)
Tomato	(3)			Santolina	(2)	Parasitic wasps	(3)
Pepper	(3)			Thyme	(3)		

Report structure

The experiments performed in this project were arranged in work packages examining different aspects of light quality: light intensity; red: blue ratio; red: far-red ratio and blue: red: far-red ratios. However, with the aim of making the data in this report more accessible to the reader, the report has been separated into six main sections: 1) Introduction and General methods that apply to all experiments, 2) Spectral effects on plant growth: Protected Ornamental, 3) Spectral effects on plant growth: Protected Edibles, 4) Glasshouse trials, 5) Improving propagation through spectral manipulation (HNS crops), and 6) Invertebrate light responses (cross-panel relevance). Methods used for specific trials are provided within the relevant sections. Results within the plant growth trials sections are arranged by species. At the end of each major section all the results are examined collectively to highlight general rules regarding plant light or insect responses that can be used as guides for future implementation of spectral manipulation.

1.2. General methods

Climate in the crop production facilities.

The temperature in the LED4CROPS facility was maintained at 21°C throughout the experiments. Humidity and CO_2 levels were monitored but not controlled. Crops were irrigated according to crop needs. Regular irrigation was provided by the automated ebb-and-flood irrigation system. The irrigation solution was maintained at an EC of 2 mS/cm and a pH of 5.5-6.5 (see Table 1.2 for details of the nutrient solution). When required additional water was applied to plants by hand.

In addition to growth in the LED4CROPS facility, crops were also grown in a closed container. A range of different lighting systems were tested within this facility. The temperature in this facility was also maintained as close to 21°C as possible during the trials. Plants were hand-irrigated as required using a dilute fertilizer solution (Table 1.2)

Table 1.2. Details of irrigation feed mixture. All values are given in mg/l.

	LED4CROPS		LED container
	Desired concentration	Mean measured concentration	Measured concentration
Nitrate N	122	194	5.2*
Sulphur	59	295	174.5
Boron	0.29	0.36	0.20
Copper	0.12	0.20	0.54
Manganese	0.34	0.51	0.33
Zinc	0.34	0.60	0.98
Iron	1.17	1.70	0.65
Chloride	96	47.8	105.5
Phosphorus	28	51.2	29.2
Potassium	265	242	114
Magnesium	42	47	19.91
Calcium	148	209	78.2
Sodium	21	50	22.1
Molybdenum	0.06	NA	NA

* Total nitrogen concentration was ~100 mg l^{-1} and provided as a different form of nitrogen.

Light treatments

Across all experiments, photoperiod was maintained at 16 hours unless otherwise stated. Images of the different LED facilities are provided in Figure 1.2. Figure 1.3 shows the spectra of the Philips LED lights used in the main LED4CROPs facility. Figure 1.4 shows the spectra of white LED systems (Valoya, Solid LIte, Heliospectra) used in the container facility.

Measurements of the light spectrum and intensity were performed during each experiment using a portable Jaz Spectroradiometer (Ocean Optics). The measured light data associated with each experiment are provided in the tables in Appendixes. Within each section the light treatments used are defined in the text and the relevant tables in the appendix are identified.

The blue, green, red, far-red, and photosynthetically active radiation (PAR) light intensities were calculated from the measured light spectra by integrating the measured values between 400-500 nm, 500-600 nm, 600-700 nm, 700-800 nm, and 400-700 nm respectively. All values are reported in units of micromoles of photons per meter squared per second (µmol m^{-2} s^{-1}). Daily light integrals were calculated in units of moles of photons per meter squared (mol m^{-2}) for PAR wavelengths.

Several estimates of light quality are used throughout this report, namely blue percentage (% blue), red:far-red ratio, and phytochrome photostationary state (PSS). The %B was determined as the percentage of PAR light that is blue light, and was calculated as the blue intensity divided by PAR intensity. Red-far-red ratios were determined as the red intensity divided by the far-red light intensity. Estimates of PSS were calculated using the methods of Sager et al. (1988).

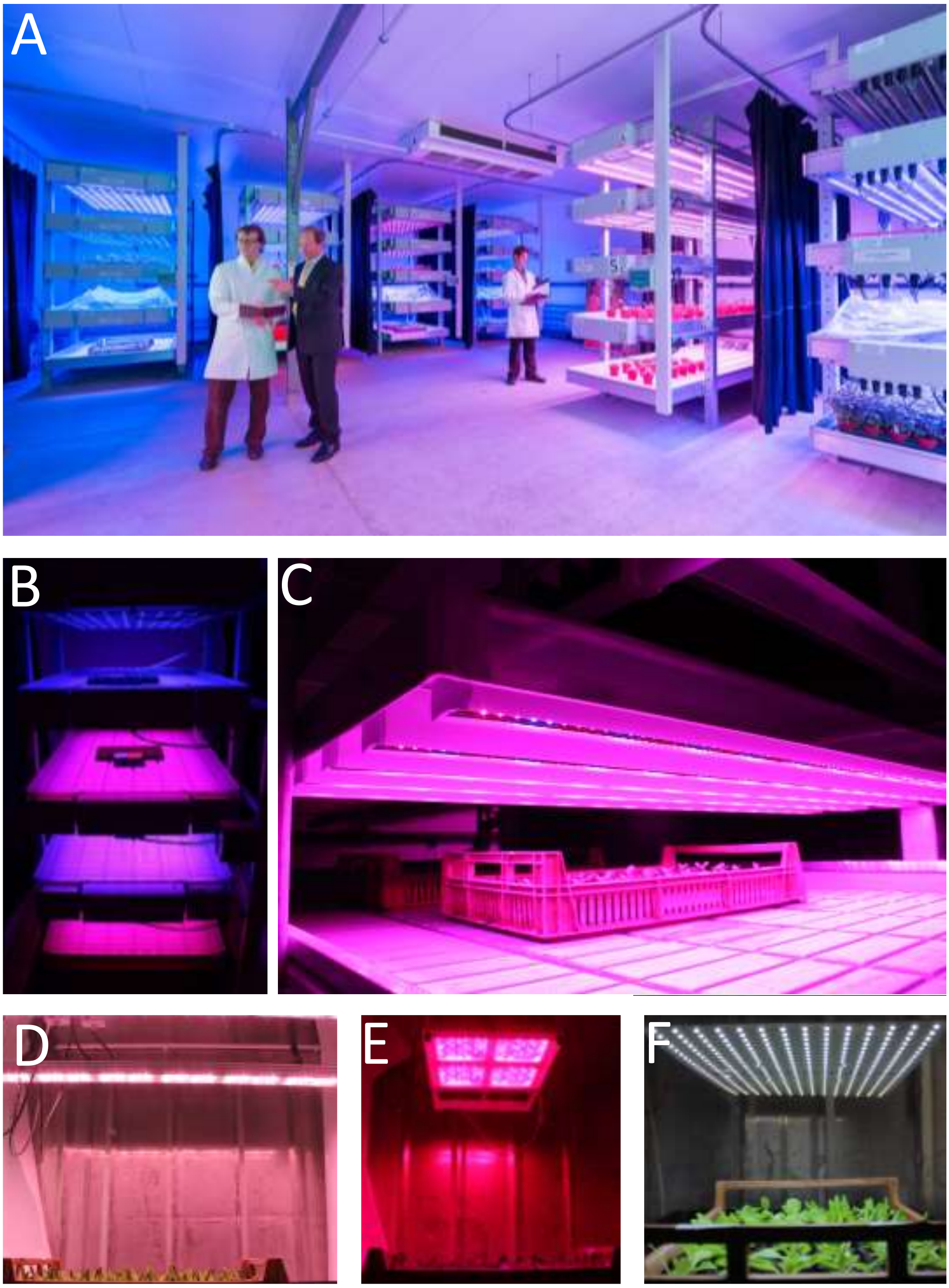


Figure 1.2. Images of LED facilities used in the experiments. **A-C)** Images from the LED4CROPS facility, **A)** general view of the LED4CROPs facility, **B)** a research rack with each shelf having different red:blue treatments, **C)** the mobile light rack used in WP 1.2. **D-F)** Images from the LED container facility, **D)** a Valoya AP673 LED, **E)** a Heliospectra lamp with a red-blue light treatment, **F)** a Solidlite LED lamp.

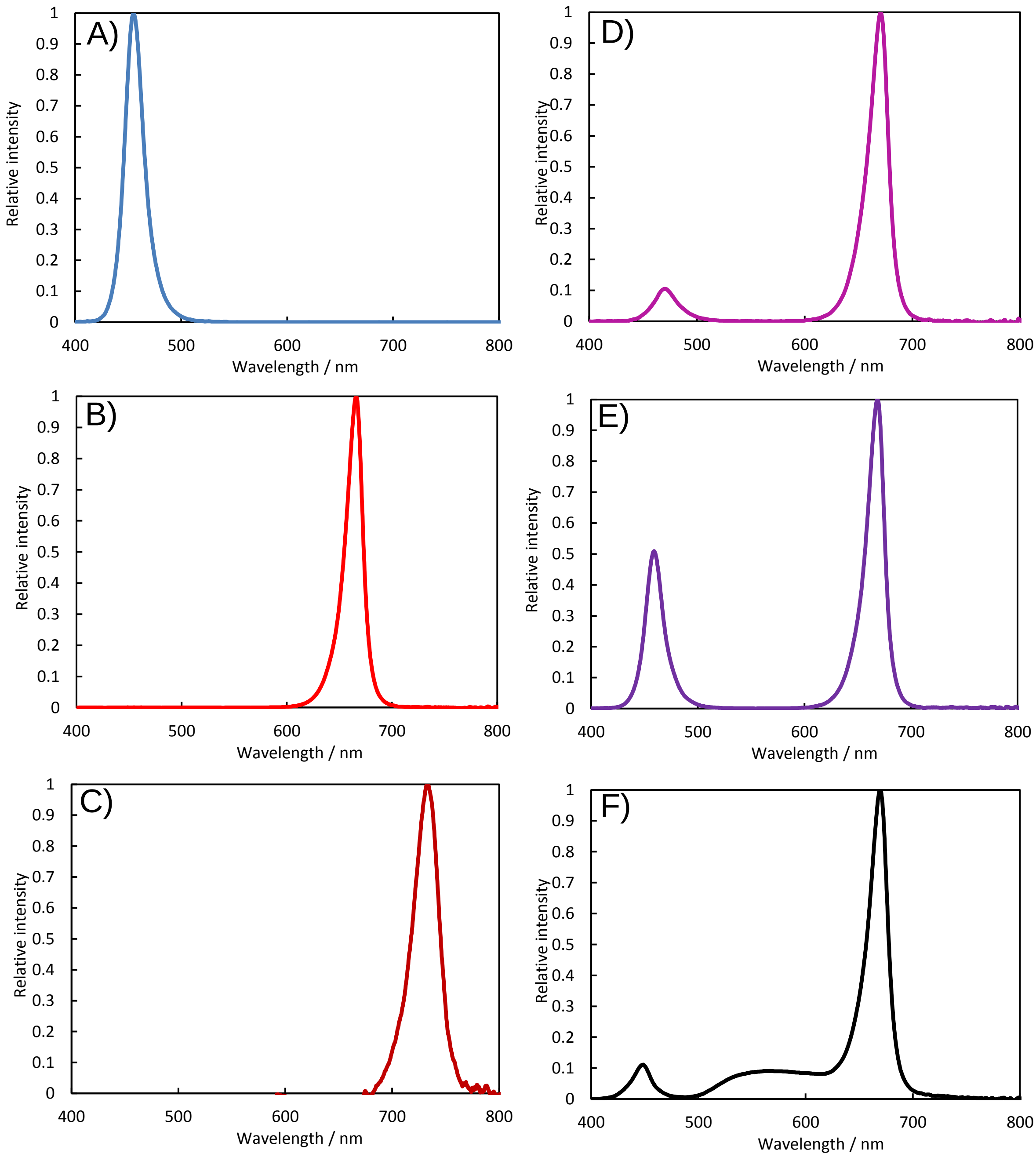


Figure 1.3. The spectra of the LED lights used in the LED4CROPS facility experiments. **A)** Blue Philips Research module. **B)** Red Philips Research module. **C)** Far-red Philips Research module. **D)** Red:blue Philips production model. **E)** Hi-Blue Philips production module. **F)** Red:white Philips production module.

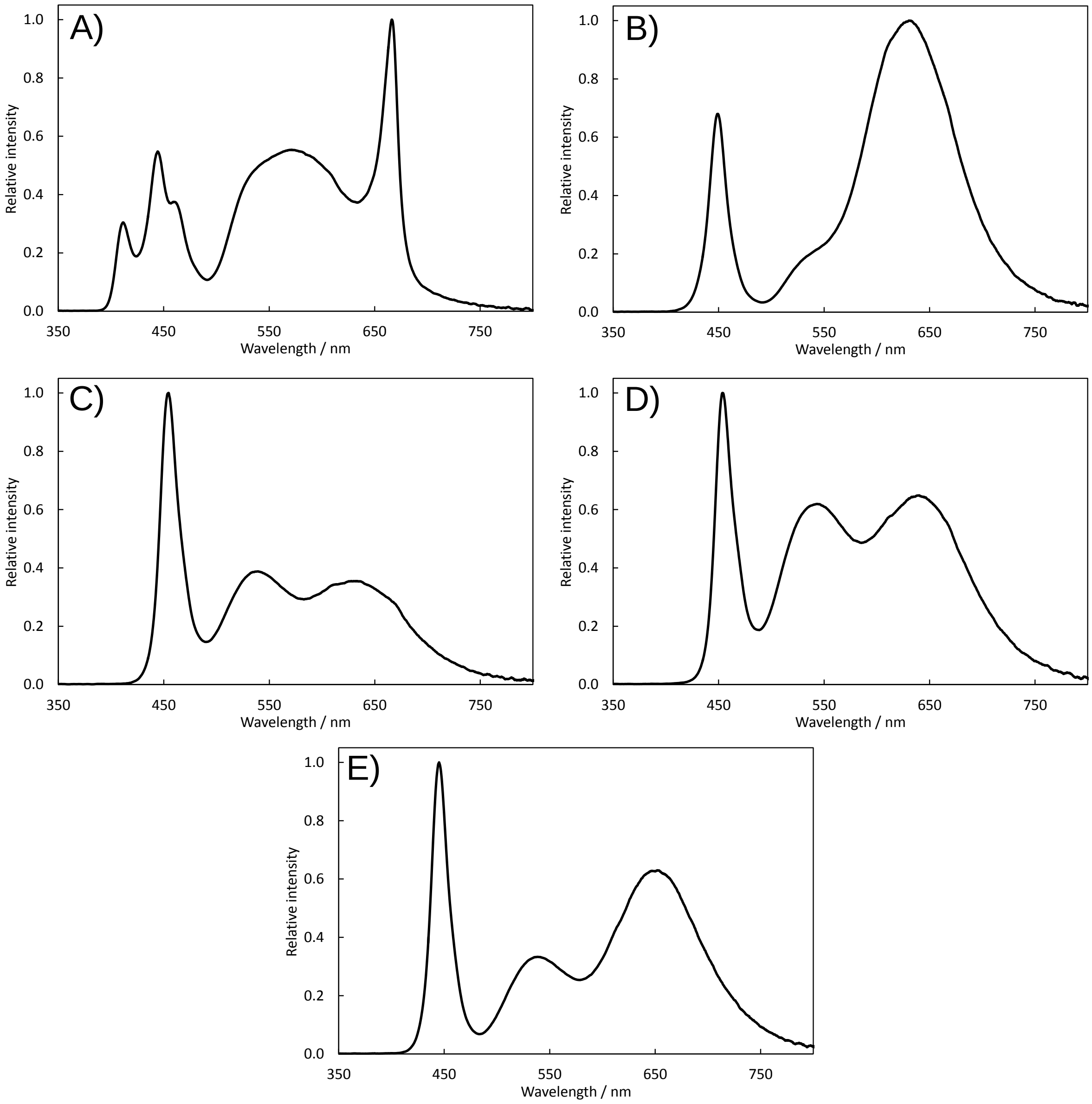


Figure 1.4. The spectra of the LED lights used in the container facility. **A)** Valoya NS2. **B)** Valoya AP67. **C)** Solid lite CWW. **D)** Solid lite DPM. **E)** Solid lite DPA.

Energy consumption and energy use efficiency

Energy consumption was calculated only for LED energy consumption and not for the heating and cooling requirements in the LED4CROPS facilities. Daily energy consumption per unit area (E_D in units of kWh m^{-2}) was determined as:

$$E_D = (W_T \times h) / A \qquad (1)$$

Where W_T is the total wattage of LEDs per plot, *h* is operational hours per day (16h in most cases) and A is the area of plot.

Crop energy consumption (E_C with units of kWh m^{-2} crop $^{-1}$) was determined as:

$$E_C = E_D \times d \qquad (2)$$

Where *d* is the number of days required to produce the crop.

For crops where plant spacing was changed during production, as was the case for bedding plants following transplantation of plug plants, energy consumption was determined per plant (E_P with units of kWh $plant^{-1}$) as:

$$E_P = [E_{D1} \times A_{P1} \times d_1] + [E_{D2} \times A_{P2} \times d_2] \qquad (3)$$

Where A_{Px} is the area taken by each plant and the subscript number represents the different periods of production and d_x is the duration of each production period in days.

Crop energy use efficiency (*U*) was either determined as energy use efficiency per area (U_A) or as energy use efficiency per plant (U_P).

$$U_A = E_C / Y_M \qquad (4)$$

$$U_P = E_P / Y_P \qquad (5)$$

Where Y_M is the crop yield per m^{-2} and Y_p is the crop yield per plant. Unless otherwise stated yields were determined as total fresh mass of the shoot.

Leaf morphology

Total leaf area of individual plants was determined by detaching leaves and placing them on a Li-Cor Li-3100 area meter. Leaf shape assessments were made by measuring the length and width of leaf blades. Petiole lengths were also measured for leaves with a defined boundary between the leaf blade and the petiole. In leaves like those found on lettuce and petunia, where there is no distinct petiole (the leaf lamina extends all the way back to the stem), only leaf length was determined. For compound leaves like those of coriander and parsley, the length of the petiole, petiolule, rachis, and the leaflet length and width were all measured separately.

Leaves are rarely perfectly flat and usually exhibit some form of curvature. Leaves can be curled in two directions, displaying lateral (Figure 1.5A) and longitudinal curvature (Figure 1.5B). In lateral curvature, the sides of the leaf curl downward. In longitudinal curvature, the tip of the leaf curls downward. Leaves often curl in both directions, creating a convex surface when viewed from above. Unless otherwise stated, the measurements of leaf curvature made in these experiments assess lateral curvature. The extent of leaf curvature was assessed by determining the projected leaf width and the width of the leaf after uncurling (flattened leaves). Curvature, referred to as leaf curling index (CI), was quantified as the ratio between the two measurements (CI = projected width / flattened width). Flat leaves have a CI close to 1 while heavily curved leaves have values < 0.5.

The angle at which leaves are held relative to the floor is important for the appearance of a crop and also has implications for how effectively plants can capture light. Both petiole and leaf angle are influenced by light quality. Leaf and petiole angles were determined using a protractor held against the stem of the plant. The vertical (usually in line with the stem) is assigned an angle of 0° (see Figure 1.6C). A leaf held parallel to the floor would have an angle close to 90° while a leaf hanging downwards will have an angle greater than 90°. For leaves exhibiting longitudinal curvature, determining leaf angle can be challenging. In these cases, petiole angle is often a more robust measurement.

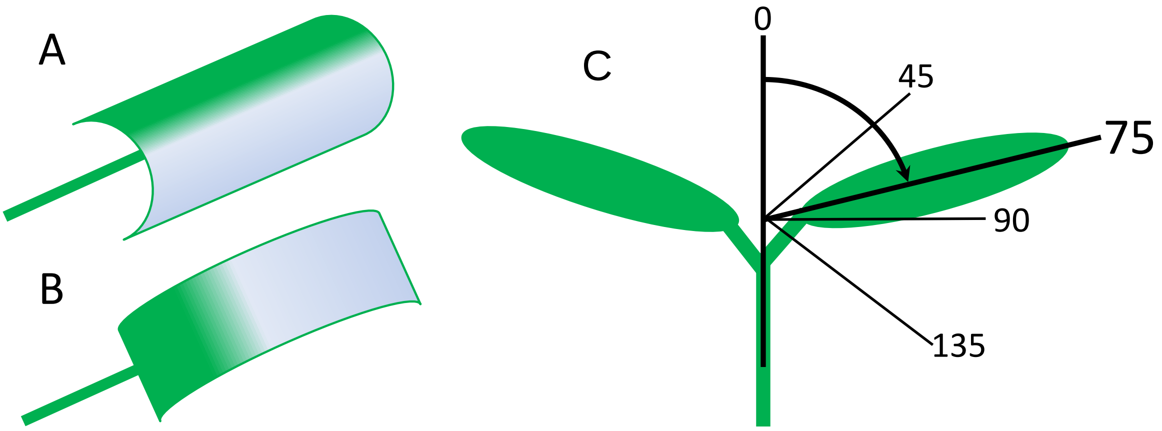


Figure 1.5. Diagrammatic representation of the two directions of leaf curling. **A)** Lateral curvature. **B)** Longitudinal curvature. **C)** Diagram showing how leaf lamina angle was measured.

Chlorophyll content meter (CCM)

Estimates of chlorophyll content were made using an AtLeaf chlorophyll content meter (CCM200, AtLeaf). At least five leaves, all from separate plants, were measured per species for each light treatment. Measurements were made on the youngest fully expanded leaf of each plant.

Visual assessment of pigmentation.

Visual assessments were made for red lettuce leaves to assess which light treatments induced the greatest anthocyanin concentrations. For the visual assessments, plants were scored on an arbitrary scale of 1 to 5, where 1 = very little pigmentation and 5 = very strong pigmentation.

Comparison of data between species

The large diversity in morphology and physiology between species makes direct comparisons between trials difficult. Data were normalised to make it possible to compare the light responses of tall and short species. Here, each parameter of a species was normalised to the mean value for that species. This is illustrated using internode lengths for tomato grown under ten different light treatments as an example. First, the mean internode length for tomato is calculated across the ten light treatments, then each of the ten internode measurements is divided by the mean internode length. Using this approach the normalised internodes of all species have a mean value of one. This allows proportional changes in morphology in response to light quality to be compared between species where internodes may differ by 10 or more fold.

Section 2. Spectral effects on plant growth: Protected Edibles

2.0. INTRODUCTION

Many high value horticultural food crops are produced under protection to improve quality and consistency as well as extending the growing season. Currently much of this production relies on sunlight and, therefore, there are seasonal restrictions on quality and growth rate. To enable year round production in the UK, as is increasingly required by retailers, a growing number of organisations are providing artificial lighting to enable yearround

production. In most cases growers are using high-pressure sodium (HPS) lighting due to a combination of factors, including preowned HPS installations, the lower installation costs of HPS compared to LED systems, and lack of confidence/experience of using LEDs. However, interest in LEDs remains high due to their lower running costs and potential spectral benefits and a growing number of organisations are beginning to make substantial investments in LED lighting systems. In this section we examine the responses of a range of commercially important edible crops to light quality. These experiments explore the potential for improving plant quality using spectral manipulation thus enabling growers to avoid problems in crop quality associated with poor winter light levels.

Crops examined include

- Lettuce
- Tomato
- Sweet pepper
- Cucumber
- Basil
- Sage
- Coriander

Parsley2.1. LETTUCE

2.1.1. Methods specific to lettuce experiments

Two varieties of Lettuce seed were provided by Enza Zaden: Alega (a winter variety) and Amica (a summer variety). Seed were sown on 5 cm peat blocks and covered with vermiculite. Peat blocks were irrigated three times per day with the automated ebb-and-flood irrigation system to maintain peat block moisture content. Plants were grown for 3 weeks before assessment. Ten plants of each variety from each light treatment were assessed for plant fresh mass, plant dry mass, leaf number, leaf length, leaf width, and leaf shape.

Light treatments

The lettuce plants were grown under a wide range of light treatments examining different aspects of light quality. Within the LED4CROPS facility the influence of: red: blue ratio (Appendix: Light treatments, Table 1); red: far-red ratio (Appendix: Light treatments, Table 2); photon irradiance (Appendix: Light treatments, Table 3); and combined red: blue: far-red (Light treatments Appendix, Table 4) treatments were examined. We also examined the influence of different white LED light spectra on lettuce crops in an additional growing room/container facility (Appendix: Light treatments, Table 5). For all experiments the day length was set at 16 hours.

Modelling lettuce leaf size

Based on our knowledge of plant light responses we generated five hypotheses aimed at describing the influence of light on lettuce leaf length:

1) There is a theoretical 'dark-leaf-size' (L_D), which is the length a leaf would grow in darkness if there was no resource limitation to growth.
2) Increasing blue light intensity provides a restriction (R_B) to leaf growth.
3) Increasing red light intensity provides a restriction (R_R) to leaf growth.
4) Increasing green light intensity reduces the restriction (R_G) to leaf growth.
5) Increasing far-red light intensity reduces the restriction (R_F) to leaf growth.

The light responses increase in magnitude with increasing light but saturate at a given irradiance. The responses therefore require asymptotic terms and this can be approximated using negative exponential equations (2 & 3 below). During the model parameterisation the functions for R_{fr} and R_g were found to be linear over the light intensities examined and so the models were simplified to the linear functions.

Thus leaf length (*L*) was modelled using the algorithm:

$$L = L_D - (R_B - R_G + R_R - R_{FR}) \qquad (1)$$

where

$$R_B = a * 1 - e^{(-\alpha\frac{b}{a})} \qquad (2)$$

$$R_R = b * 1 - e^{(-\beta\frac{r}{b})} \qquad (3)$$

$$R_{FR} = c * FR \qquad (4)$$

$$R_G = d * G \qquad (5)$$

where R_B, R_R, R_{FR}, and R_G are the changes in leaf length in response to blue, red, far-red, and green light respectively. B, R, FR, and G are the photon irradiances of blue red, far-red, and green light, respectively. a, b, c, d, α, and β are the coefficients that describe the magnitude and shape to the light responses.

Model parameterisation

Model parameterisation was performed using a non-linear least squares procedure in R (R core team, 2015) using the '`nls`' function and '`nlstools package`' (Version 1.0-2; Baty & Delignette-Muller, 2015). Approximate starting values for each model parameter were provided based on a rough manual parametrisation performed using Microsoft Excel. Normality of residuals was checked using standard regression and Q-Q diagnostic plots in R. Bootstrap and t-based confidence intervals were calculated for each model parameter in each model. The fits of the final fitting models were compared using the Akaike information criteria (AIC) procedure.

Model validation

The fitted model was initially compared by linear regression against the parameterisation dataset that included data from red: blue ratio treatments, intensity treatments and far red supplementation experiments. This approach only tests if the model is able to explain the variation in the data used to fit the model. To validate the model, linear regressions against a 'blind' dataset (i.e., data not used to parameterise the model) is required. Our validation data set contained light treatments with different red: blue: far-red combinations and PAR intensity plus far-red treatments.

2.1.2. Results

The influence of red: blue light treatments on lettuce

The two lettuce varieties responded similarly with respect to biomass change when grown in under the different red: blue light treatments, though the response magnitudes differed (Figure 2.1). The greatest biomass of both varieties was achieved under 11% blue and biomass decreased rapidly as the blue percentage both increased and deceased from this value. The Alega plants achieved a greater biomass than the Amica plants under all treatments. Leaf number was also greatest under the 11% blue light treatment and lowered rapidly under 100% red light. In contrast to the biomass data, leaf number decreased more

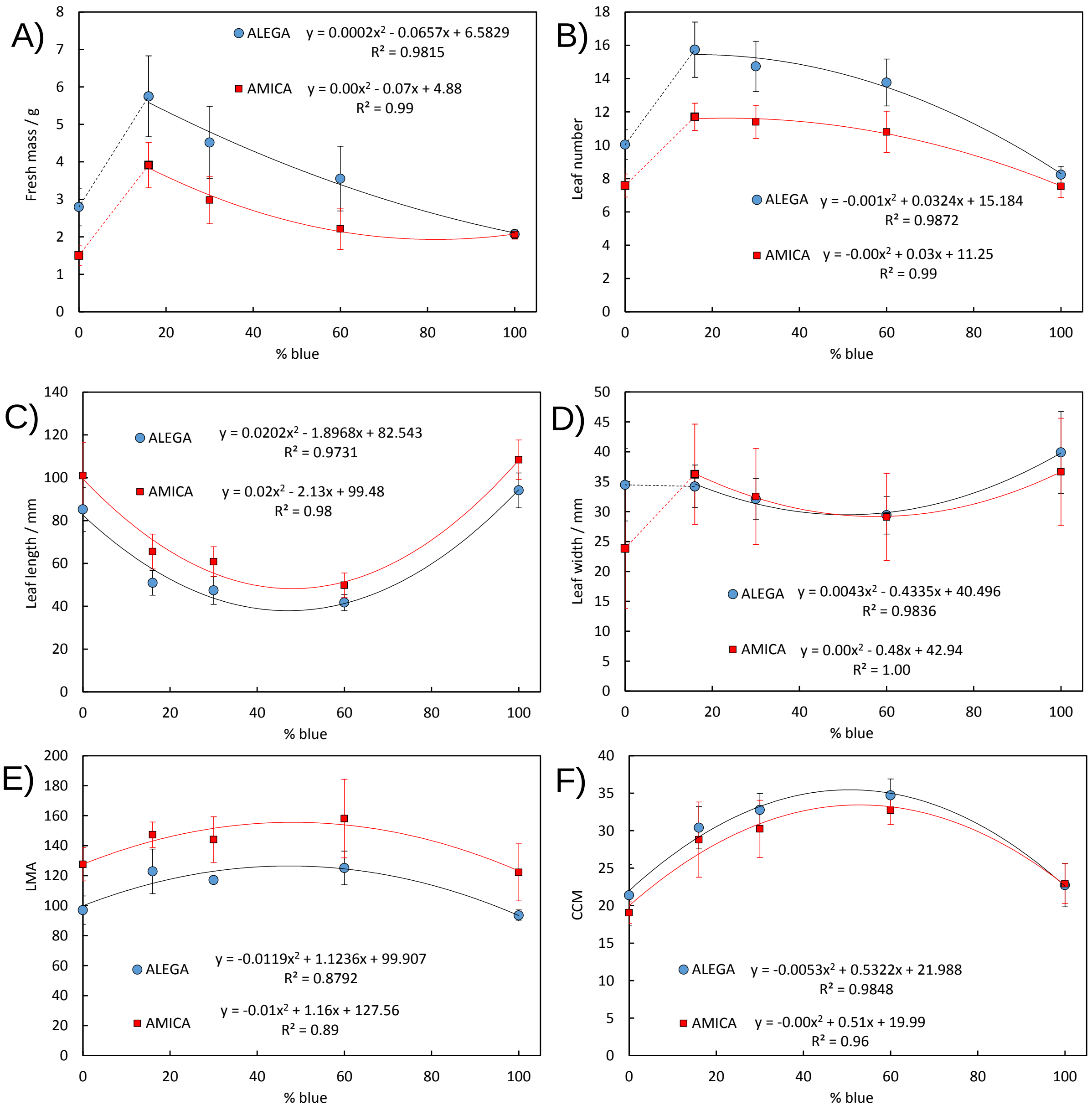


Figure 2.1. The influence of blue percentage of a red: blue light mixture with an intensity of 200 µmol m^{-2} s^{-1} on the growth and morphology of two Lettuce varieties (Amica and Alega). Error bars indicate standard deviation.

slowly as the blue percentage increased, indicating that the changes in mass were associated with changes in resource partitioning rather than just differences in growth rate. The morphology of the two lettuce varieties differed, with the leaves from the Amica plants having a more curled phenotype than those of the Alega plants (Figure 2.2). The light treatments strongly influenced the appearance of both varieties. Under 100% red light, both varieties had severely curled, long etiolated leaves (Figure 2.1C). Plants were also etiolated under the 100% blue light treatments, but leaves were less heavily curled. When grown under light mixtures containing both red and blue light, the plants had a more natural appearance with shorter leaves, though Amica leaves were still curled under these conditions. Leaf mass area (LMA) was greatest under 60% blue light, indicating that the shorter narrower leaves were thicker. Chlorophyll content was also highest in the 60% blue light treatment and lowest under the 100% red light treatment.

Red: far-red treatments

The addition of far-red light to the spectrum resulted in etiolation of the two lettuce varieties (Figure 2.3) and resulted in poor-quality plants with paler green leaves. Fresh mass of the Alega plants increased slightly as far-red increased but the Amica mass was unaffected by far-red light (Figure 2.4A). While the fresh mass of the Alega plants increased, the number of leaves was found to decrease (Figure 2.4.B). Amica leaf number was not influenced by far-red. For both varieties, leaf length increased linearly with increasing far-red, while leaf width was unaffected (Figure 2.4C and 2.4B). Leaf curling was observed to increase, especially for the Alega variety, as far-red light increased. This may have reduced the light capture potential of the larger leaves, which may explain why biomass was less influenced by far-red than expected.

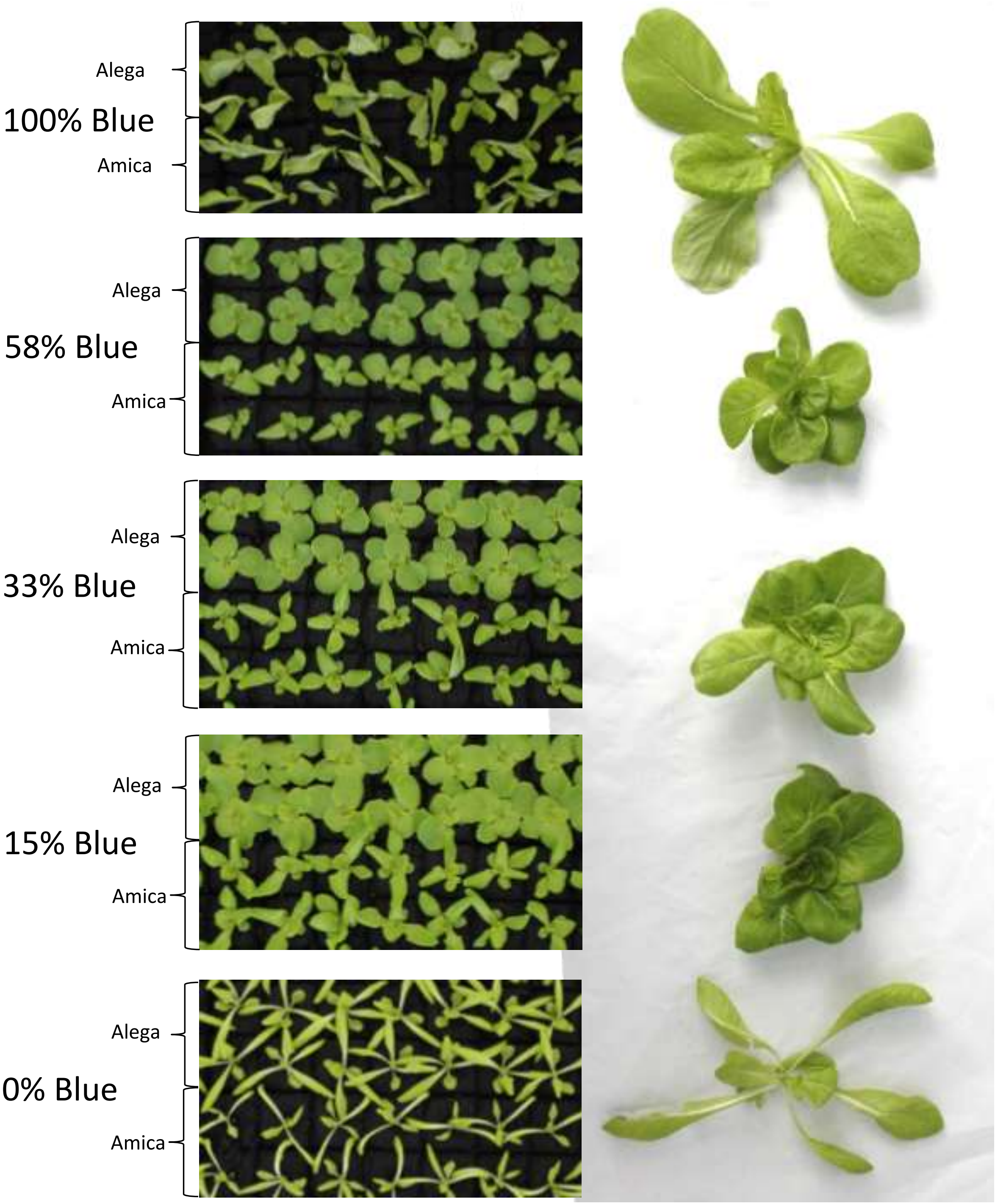


Figure 2.2. Images of two lettuce varieties, Alega and Amica, grown under lights with different red: blue ratios for 19 days. The close-up plant images on the right show representative Alega plants from each light treatment.

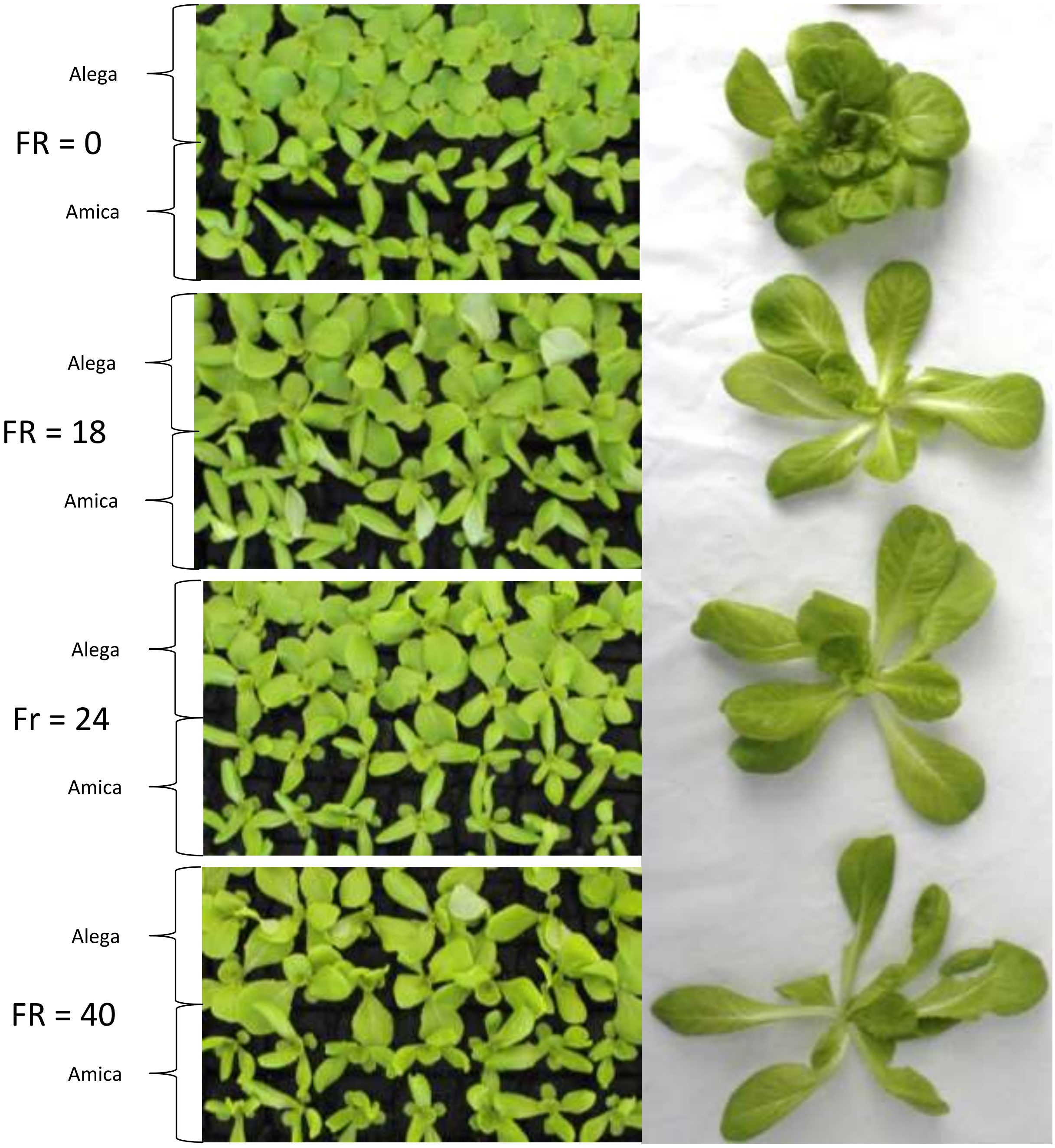


Figure 2.3. Images of two lettuce varieties, Alega and Amica, grown under lights with different amounts of far-red light. The close-up plant images on the right show representative Alega plants from each light treatment.

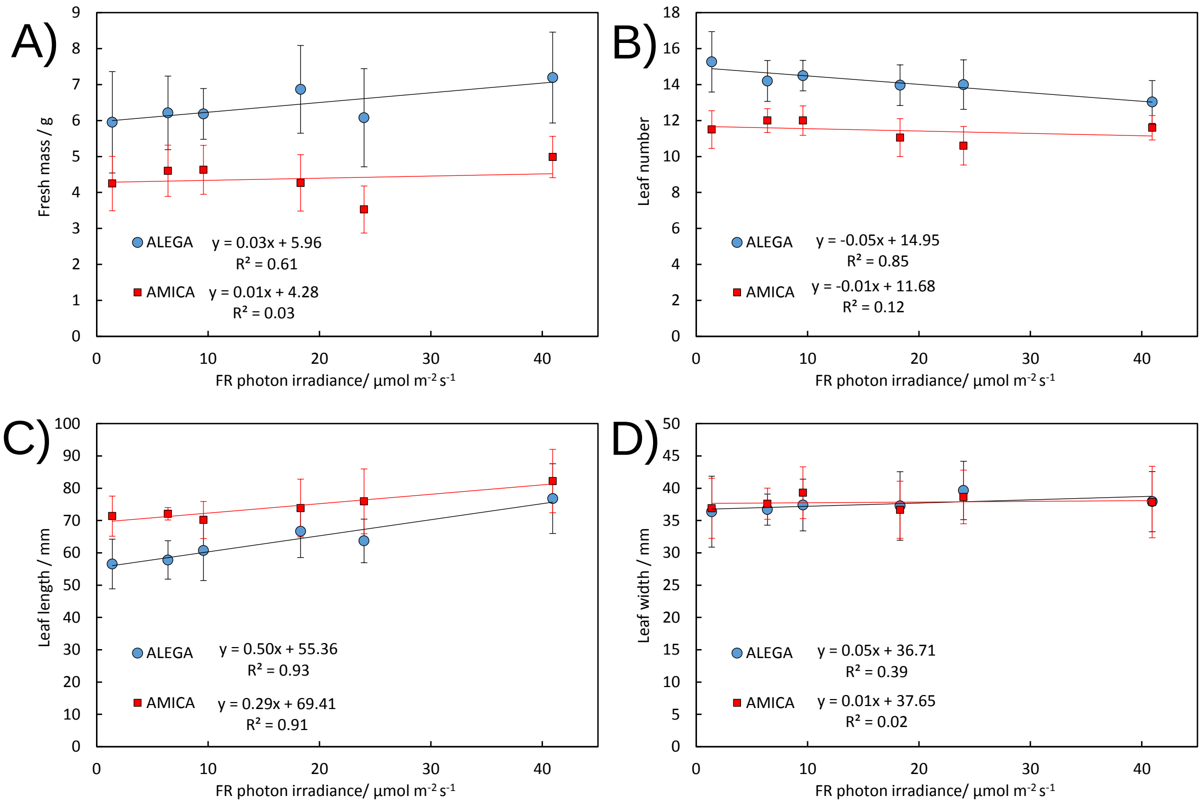


Figure 2.4. The influence of far-red light on growth and morphology of two lettuce varieties, Amica and Alega. **A)** Shoot fresh mass collected after 21 days growth, **B)** mean number of leaves per plant, **C)** length of the fourth leaf, **D)** width of the fourth leaf. Error bars indicate standard deviations calculated using the measured values from all three replicates.

Combined red: blue: far-red treatments

To examine how blue, red, and far-red responses interact we grew the two lettuce varieties under eight light treatments where two red: blue ratios, (30 and 60% blue light) were combined with different amounts of additional far-red light (0, 11, ~20, and ~35 µmol m^{-2} s^{-1}). During the experiment there was a fault in the 60% blue no far-red light treatment that resulted in the plants receiving a low dose of blue light through the night-period. This resulted in data that were not useable. However, because a similar treatment was included in work package 2.1b the missing data could be replaced. While the light treatments were the same, the plants were grown on different dates so where these data points are presented they are identified by open symbols (Figures 2.5 and 2.6).

For Alega plants (Figure 2.5) far-red light was observed to increase shoot biomass for both the 60 and 30% blue treatments. For the 60% blue treatments, mass increased linearly with far-red intensity but for the 30% blue treatment the greatest mass was observed with the 20 µmol m^{-2} s^{-1} far-red treatment (Figure 2.5A). Leaf number was observed to decrease as

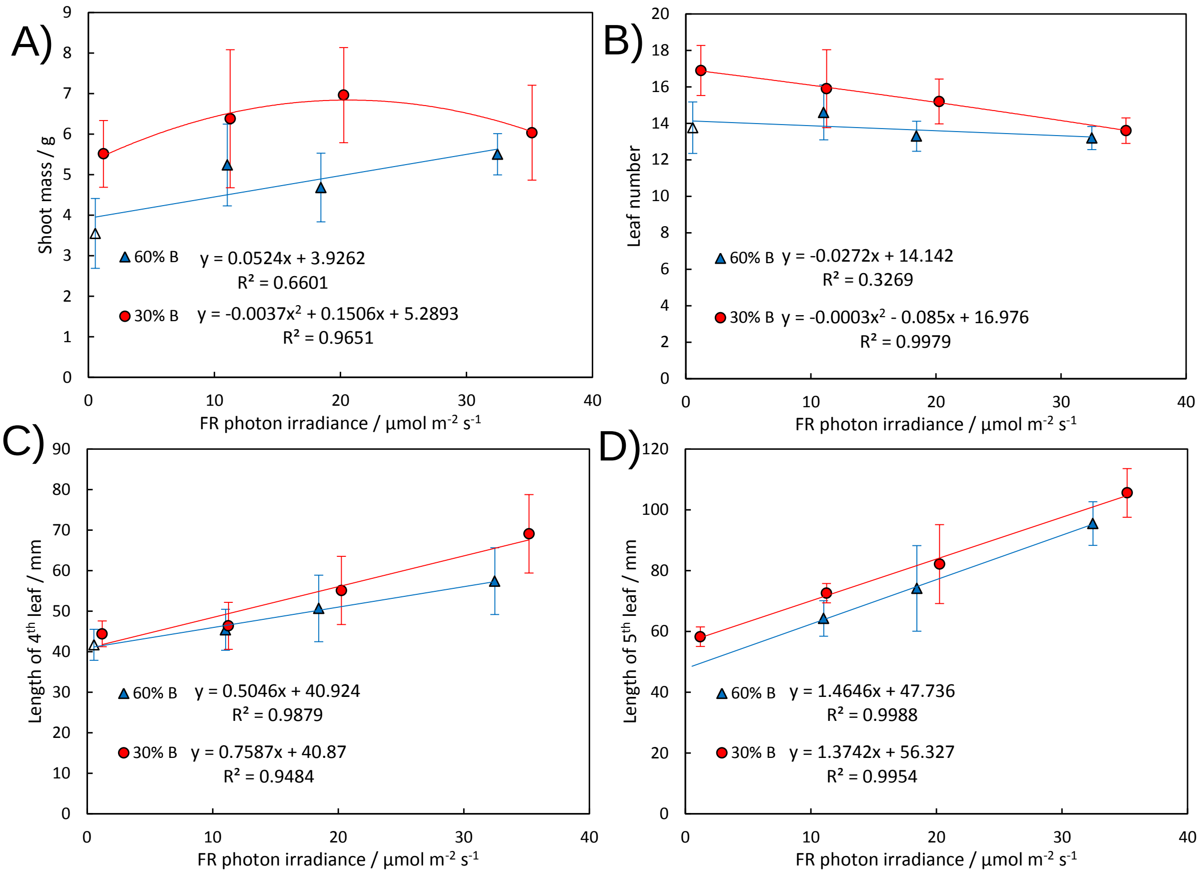


Figure 2.5. Influence of far-red on the **A)** fresh mass, **B)** leaf number, and the length of the **C)** 4th and **D)** 5th leaf of three-week-old Alega lettuce plants grown under 30% blue and 60% blue light treatments. The open symbols indicate data taken from WP2.1b to replace values from the 60% blue with no far-red light treatment.

far-red intensity increased for both the 30 and 60% blue light treatments though leaf number was higher in the 30% blue light treatment and decreased more rapidly with far-red than in the 60% blue treatments (Figure 2.5B). Leaf length of the 4th and 5th leaves (Figure 2.5 C&D) increased linearly with increasing far-red intensity. Leaf width was observed to increase as far-red intensity increased for both 60% and 30% blue light treatments.

For the Amica plants grown under 30% blue light, fresh mass was observed to increase as far-red intensity increased (Figure 2.6A), with the greatest increases occurring between 0 and 11 µmol m^{-2} s^{-1} of far-red. For the plants grown under 60% blue light, far-red resulted in a linear increase in fresh mass. Amica leaf number was not influenced by far-red intensity (Figure 2.6B), but far-red resulted in a linear increase in leaf length with both 30% and 60% blue treatments (Figure 2.6 C&D) and, in contrast to Alega, this response was greatest for the 60% blue treatments. Far-red had little influence on the width of Amica leaves.

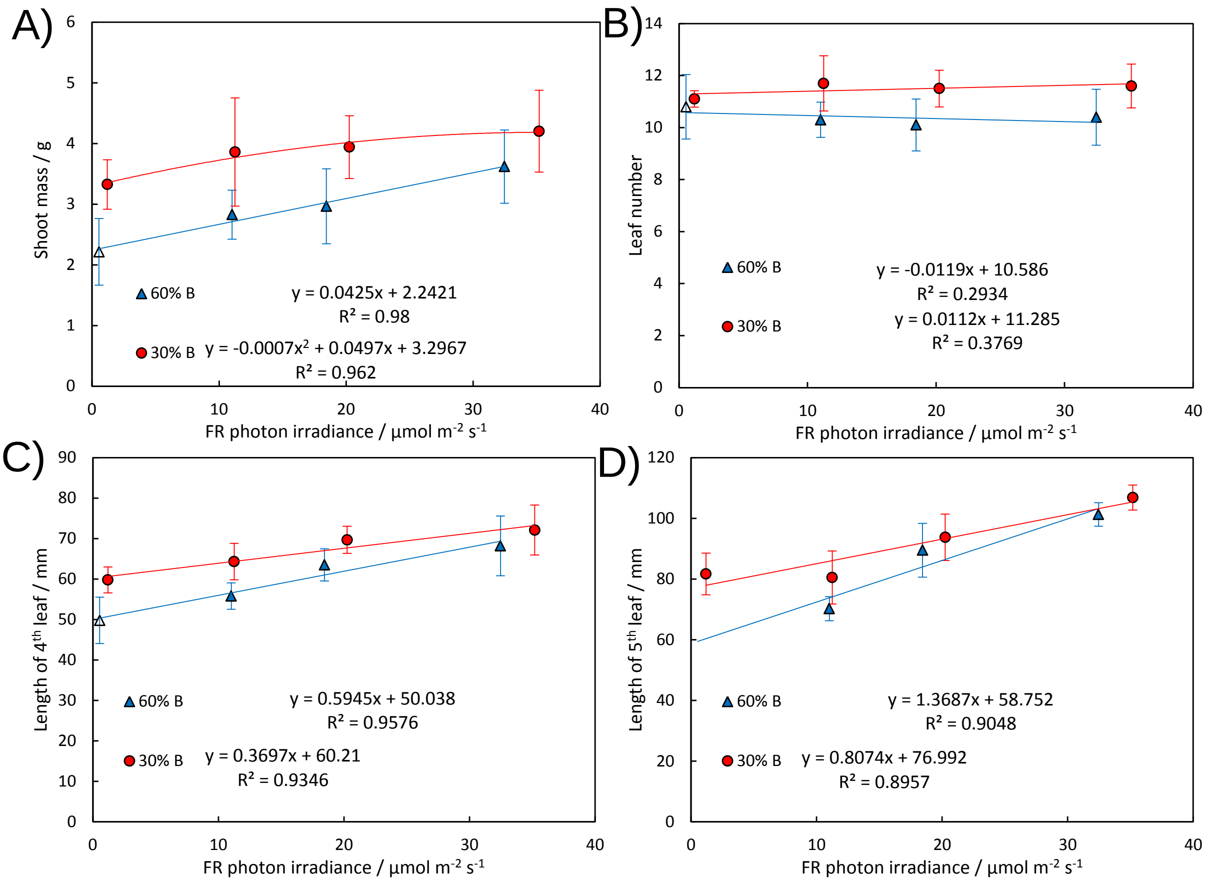


Figure 2.6. Influence of far-red on the **A)** fresh mass, **B)** leaf number and the length of the **C)** 4th and **D)** 5th leaf of three-week-old Amica lettuce plants grown under 30% blue and 60% blue light treatments. The open symbols indicate data taken from WP2.1b to replace values from the 60% blue with no far-red light treatment.

Light intensity / daily light integral

Both Alega and Amica lettuce varieties germinated within 3 days of sowing and produced plants that were disease-free but that varied considerably in size and quality between the light treatments (Figure 2.7). Plant fresh weight (Figure 2.8) and dry weight (data not shown) increased as daily light integral (DLI) increased. The plants grown under the strobe light gained considerably less biomass than the plants grown under the constant light treatment with the same DLI, and the plants under the mobile light rack barely grew at all. Morphology differed between the two varieties, with the Amica variety having a more curled leaf. To assess the effect of light treatment on leaf morphology, the length and width of the second true leaf were measured (Note: the plants grown under the mobile light treatment grew so slowly that they did not possess a second true leaf and so are excluded from this analysis). Leaves of Amica were longer than those of Alega but were similar in width (Figure 2.8C). The leaf length of both varieties was observed to decrease as the light intensity increased, though this relationship was more pronounced for Alega than for Amica. Leaf width was found to increase slightly as light intensity increased, and this relationship was more pronounced in Amica than in Alega. The curling index (CI, calculated as projected leaf width / flattened leaf width) demonstrated that Amica leaves were more curled than the Alega leaves in all light treatments. Both varieties were found to have a more pronounced curvature at intermediate light intensities. In the two light treatments that received the same DLI (strobe and low light-5.7 mol m^{-2}), the plants of both varieties grew more slowly under the strobe treatment but had longer leaves that were slightly wider and less curled (Figure 2.7).

The energy use efficiency (EUE = plant fresh weight per square meter / LED electricity consumption per square meter; Figure 2.9B) of the different light treatments was calculated to determine the optimal light conditions for crop production. For the Alega variety the energy use efficiency was greatest under a DLI of 16 mol m^{-2} d^{-1} but for Amica it was greatest under the 22 mol m^{-2} d^{-1} treatment. For both varieties, a large drop in EUE was observed for the plants grown in the strobe light treatment compared to the constant light treatments with the same DLI. The EUE of Alega was greater than that of Amica in all treatments. One possible explanation for this is the difference in leaf area available to capture the light between the varieties, which was caused by the different leaf curvatures. To test this, the EUE data were plotted versus the DLI multiplied by the CI (Figure 2.9B). The data from the two varieties were found to be more similar when the DLI data was corrected for leaf curvature, suggesting that the differences in EUE between Amica and Alega were partially caused by differences in light interception between the varieties.

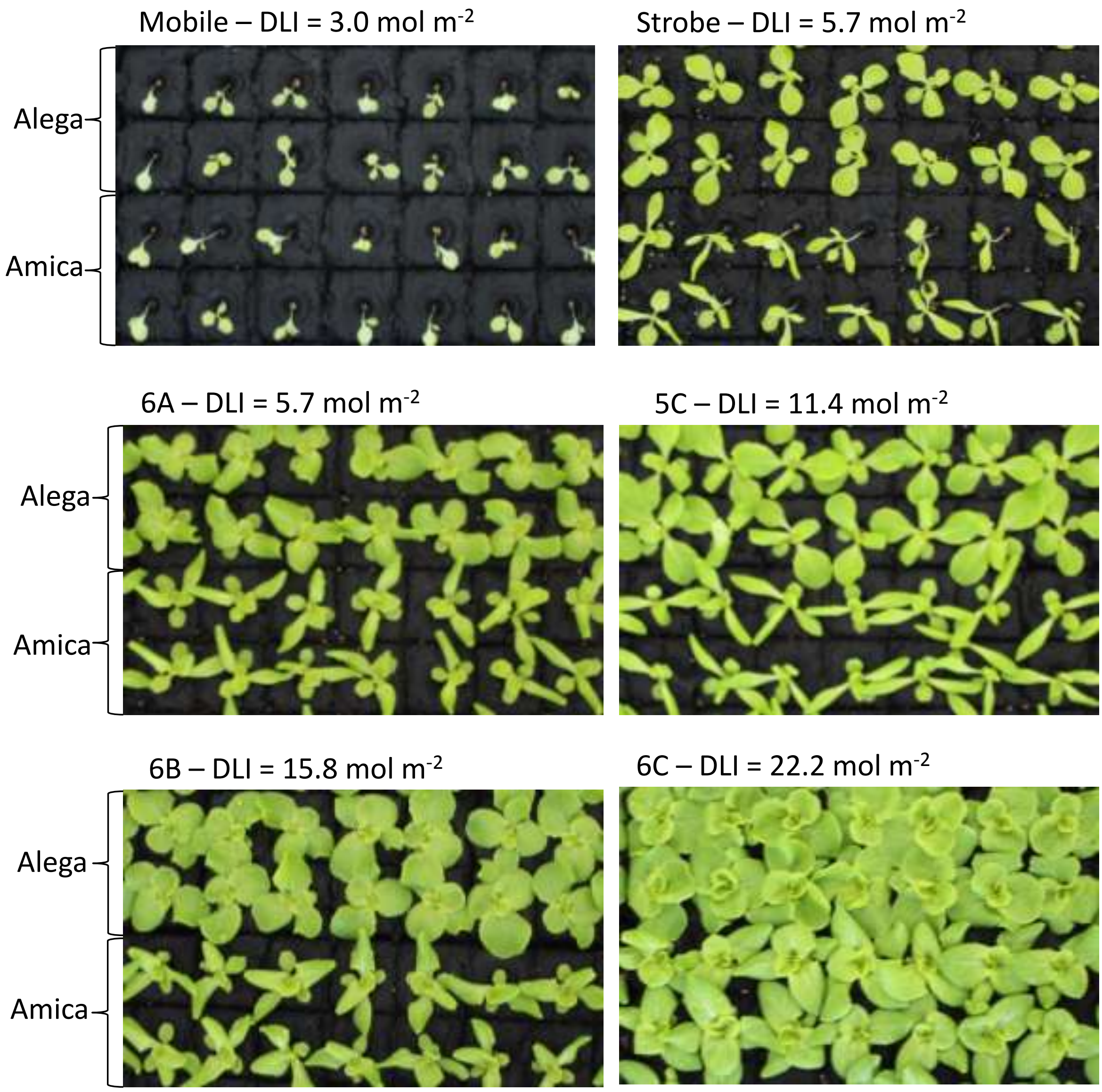


Figure 2.7. Images of two lettuce varieties, Alega (top two rows of plants in each picture) and Amica (bottom two rows of plants in each picture), grown under 6 different light treatments designed to assess the effects of energy-saving lighting strategies and different daily light integrals on plant growth and morphology 19 days after sowing.

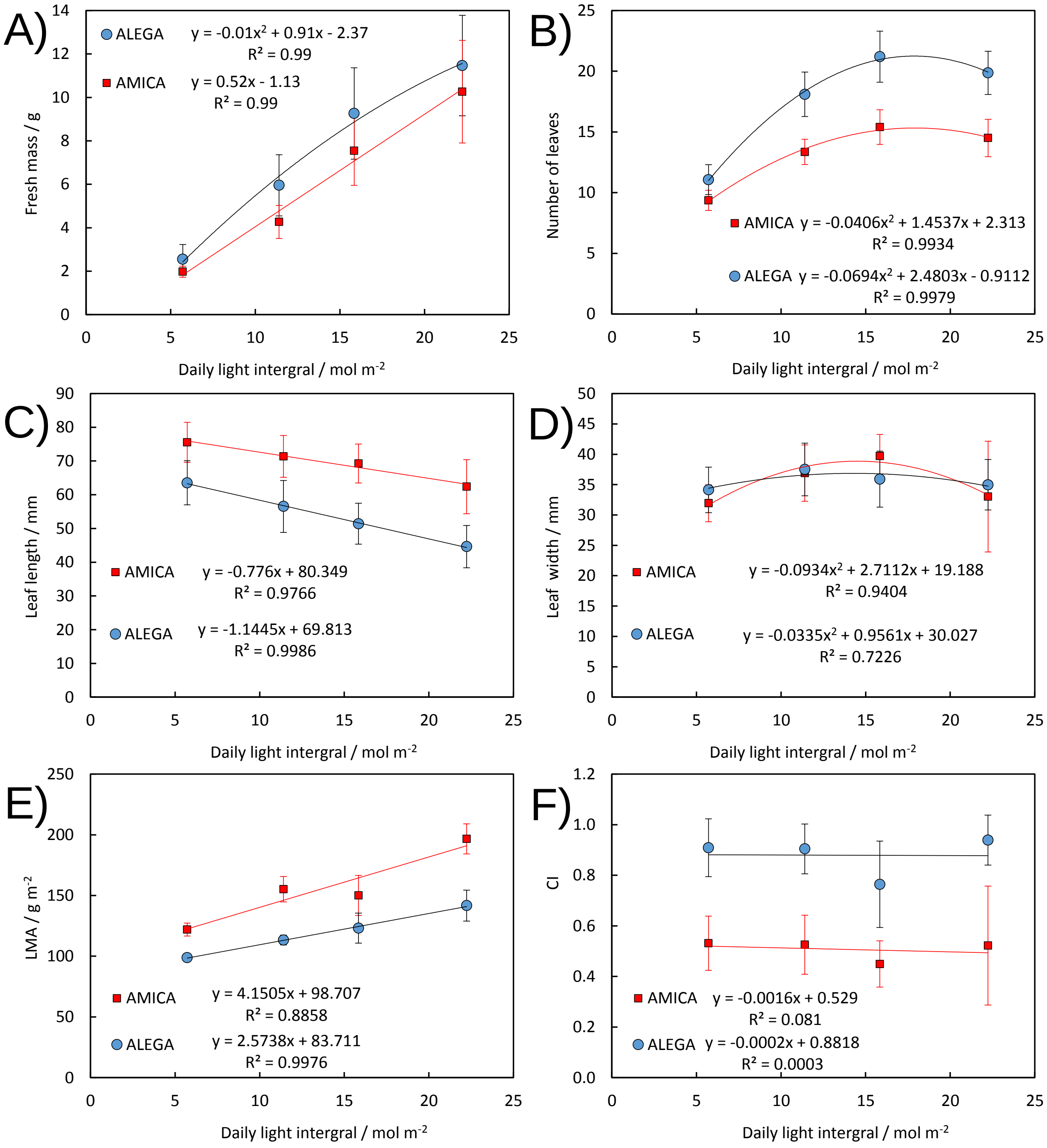


Figure 2.8. The influence of daily light integral (DLI) on the **A)** fresh mass, **B)** number of leaves per plant, **C)** length of the fifth leaf, **D)** width of the fifth leaf, **E)** the leaf mass per area (LMA), and **F)** the leaf curling index of the two lettuce varieties. Error bars indicate the standard deviations calculated from all the measurements of the three replicate trials.

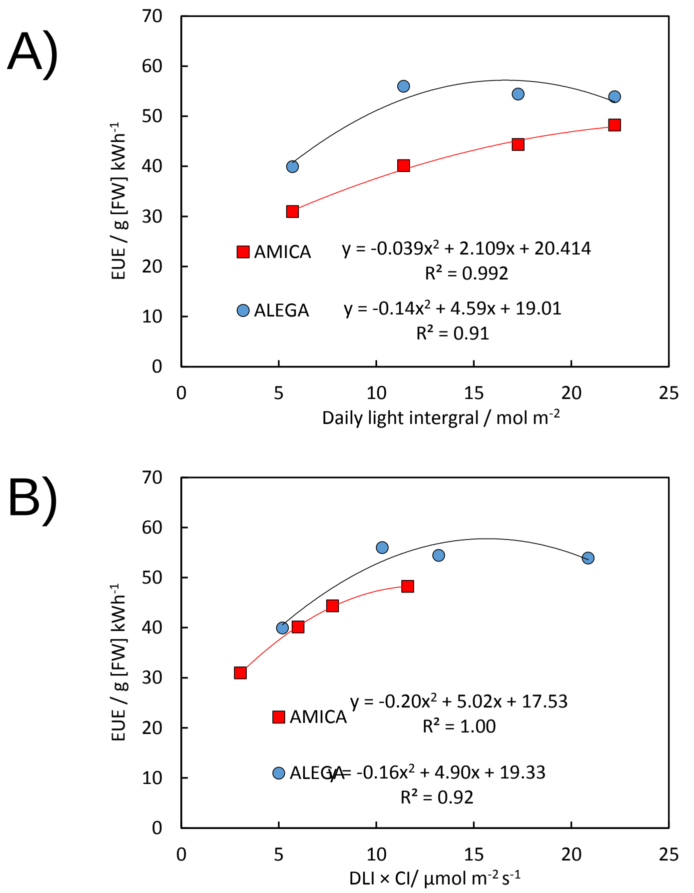


Figure 2.9. A) The influence of daily light integral (DLI) on electrical energy use efficiency (EUE). **B)** Shows the same data as in A), but with the DLI values scaled to account for differences in leaf curling (CI).

Different shades of white light

Lettuce plants were grown for 21 days under five different white LEDs, each with a slightly different light spectrum. The different treatments were provided by two Valoya lights (NS2 and AP673) and three Solidlite units (DPM, DPA & CWW). Under all light treatments, plants were healthy and showed no signs of pests or disease (Figure 2.10). The leaves of the Amica variety were more curled than those of the Alega variety. Plant growth, assessed as fresh mass at final harvest, was found to be influenced by the proportion of the incident light that could be used for photosynthesis (the lamp photosynthetic efficiency, Figure 2.11). Biomass was greatest under the Valoya AP673 lamp, where the calculated lamp photosynthetic efficiency was 89.9%. Growth was lowest under the CWW Solidlite lamp, where the lamp photosynthetic efficiency was 83.9%.

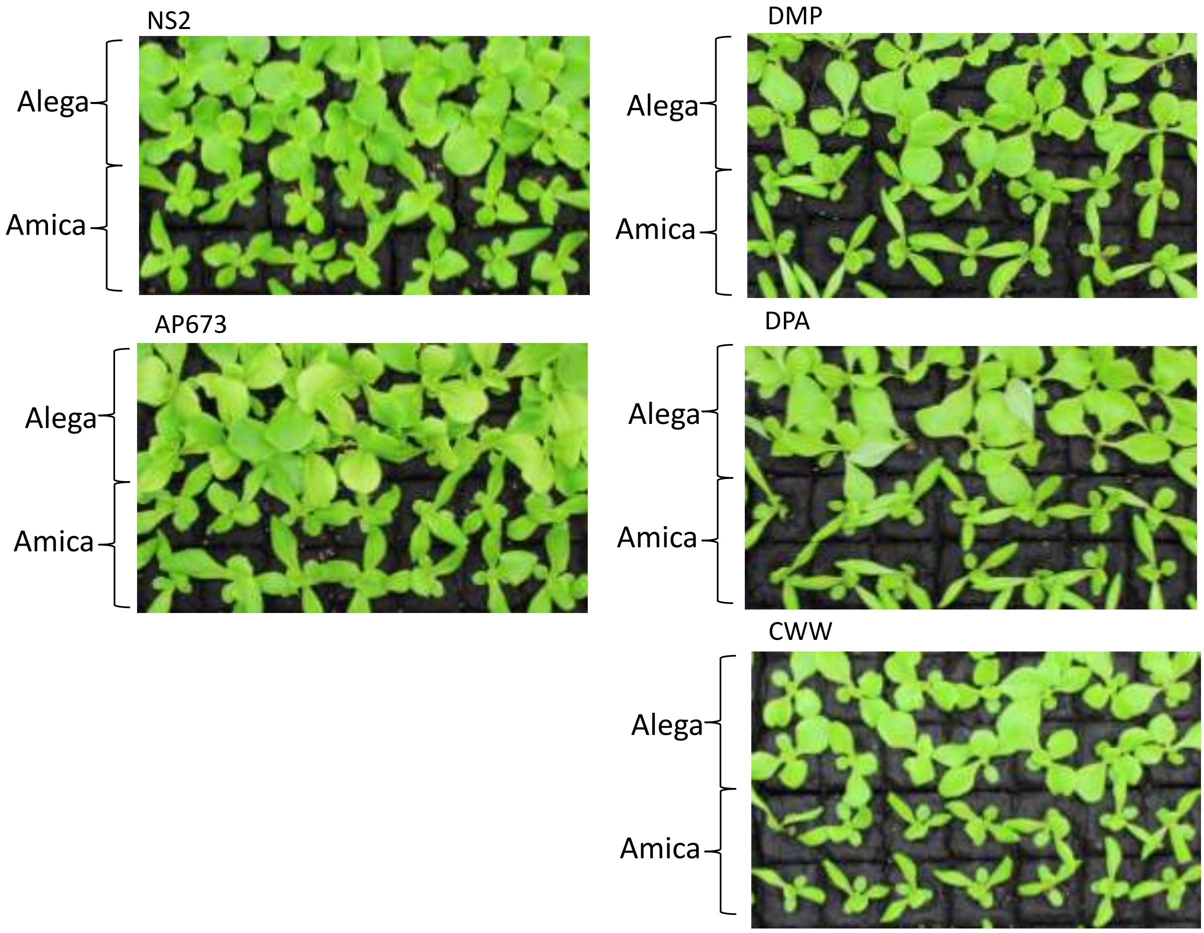


Figure 2.10. Photographs of two lettuce varieties (Alega and Amica) taken after 19 days growth under five different white light LED spectra. NS2 and AP673 were Valoya LED lamps and DMP, DPA, and CWW were Solidlite lamps.

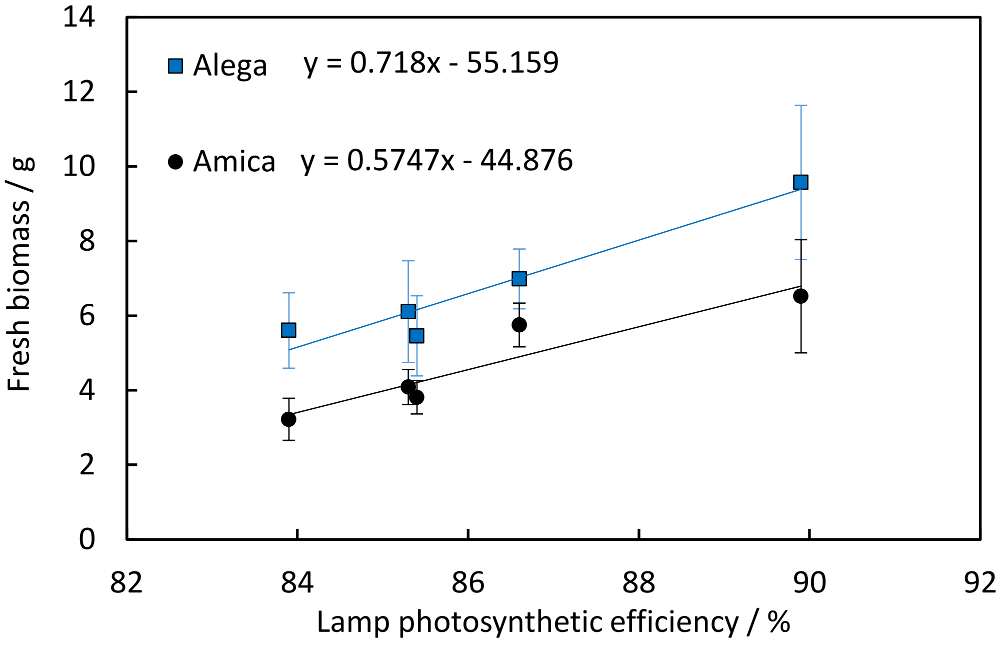


Figure 2.11. The influence of the lamp photosynthetic efficiency (calculated using the lamp emission spectrum, the photosynthetic action spectra provided by McCree 1971, and the mean leaf light absorptance spectrum of 25 plant species provided by Davis *et al*. 2011) on the fresh biomass accumulation of the two lettuce varieties. Error bars indicate standard deviations.

Modelling leaf size

The model was fitted to the measured leaf length data for Alega (Figure 2.12 A) and Amica (Figure 2.13) separately. Both models provided a good description of the measured data with R2 values >0.8, though the Alega model was a better fit. The model parameters are provided in Table 2.1 for Alega and Table 2.2 for Amica. For both lettuce varieties, all seven parameters were found to be highly significant in the model. While this demonstrates that the model can describe the variation in the measured data, the real test of a model is how well it can describe a blind data set, i.e., a data set that was not used during the fitting procedure. To validate the model, we used the model to predict leaf size for several light treatments that were different to those used for the model parameterisation. When these predictions were compared to the measurements of leaf length for Alega (Figure 2.12B) and Amica (figure 2.13B) the model was found to perform well. For the Alega plants, 15 light treatments were available to test the model and its performance was very good: the slope of regression line was ~1 and the R2 was 0.9. For the Amica variety only 9 data points were available to test the model and the model performance was less good, with regression slope of 0.92 and R2 of 0.46.

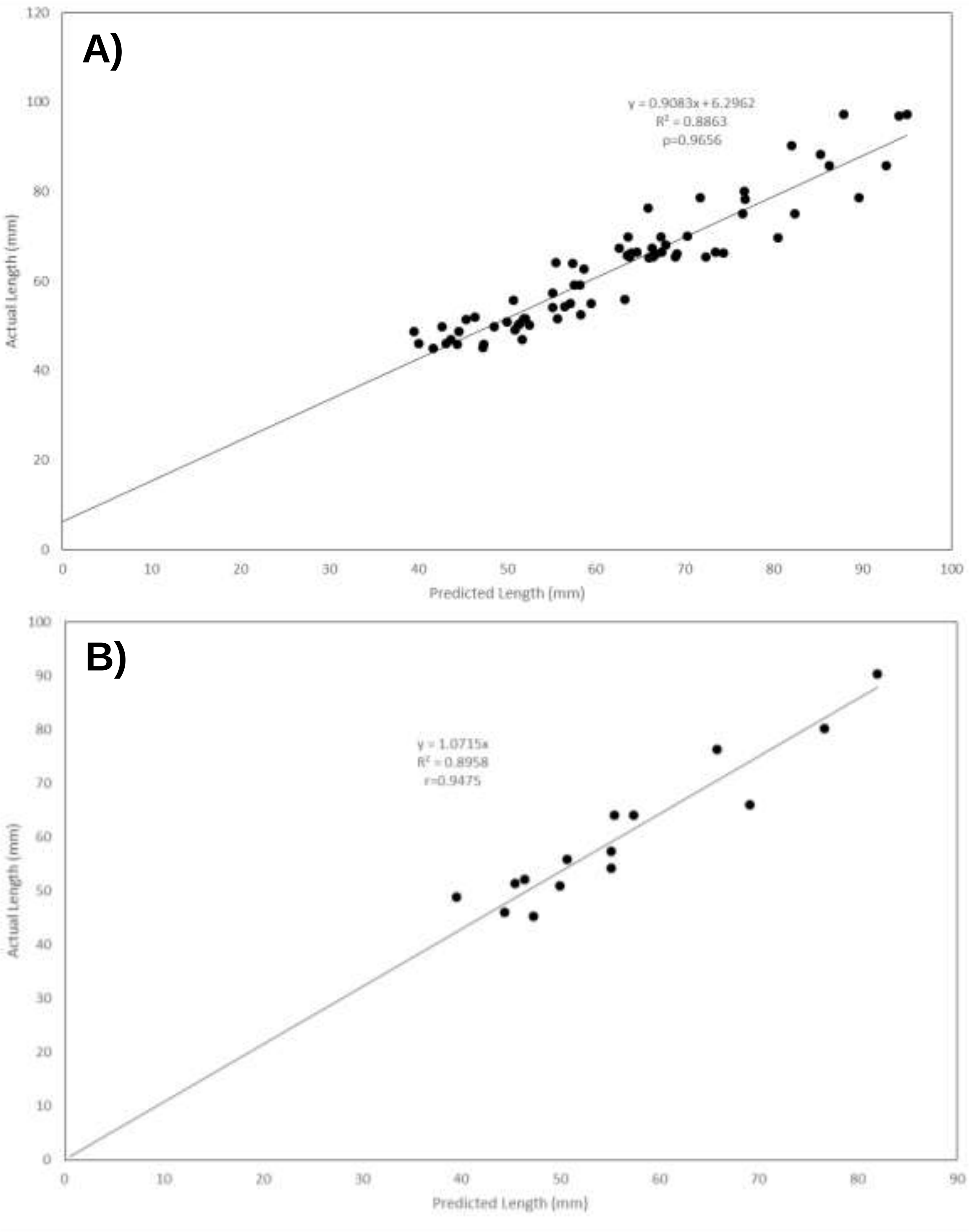


Figure 2.12. Plots of modelled versus measured Alega leaf lengths for **A)** the parameterisation data set and **B)** the validation data set.

Table 2.1 Mean estimates of model coefficients for leaf length in *Lactuca sativa* cv. Alega, including standard error (SE) and t-based probability. Bootstrap parameter estimates at the 2.5% and 97.5% intervals are included. Significance codes: 0 '***', 0.001 '**', 0.01, '*' 0.05, '.' 0.1.

	t-based				Bootstrap		
Coefficient	**Value**	**SE**	**P-value**	**Significance**	**Median**	**2.5%**	**97.5%**
L_D	140.23	2.39	58.65	***	140.38	135.71	145.82
a	43.40	1.54	28.11	***	43.61	40.55	46.96
α	3.35	0.26	12.65	***	3.38	2.84	3.87
b	51.97	2.05	25.39	***	51.95	47.58	56.84
β	60.74	16.85	3.61	***	61.75	31.29	94.83
c	0.60	0.04	16.47	***	0.60	0.53	0.68
d	0.19	0.01	12.59	***	0.19	0.16	0.22

Table 2.2. Mean estimates for model coefficients for leaf length in *Lactuca sativa* cv. Amica, including standard error (SE) and t-based probability. Bootstrap parameter estimates at the 2.5% and 97.5% intervals are included. Significance codes: 0 '***', 0.001 '**', 0.01, '*' 0.05, '.' 0.1.

	t-based				Bootstrap		
Coefficient	**Value**	**SE**	**P-value**	**Significance**	**Median**	**2.5%**	**97.5%**
L_D	147.73	2.56	57.64	***	147.67	143.64	152.72
a	36.20	1.71	21.16	***	36.35	33.23	39.65
α	1.37	0.14	9.92	***	1.37	1.09	1.70
b	57.58	2.39	24.06	***	57.59	53.42	62.26
β	89.28	19.14	4.67	***	88.88	53.34	128.13
c	0.29	0.04	7.46	***	0.28	0.21	0.36
d	0.14	0.02	9.17	***	0.14	0.11	0.17

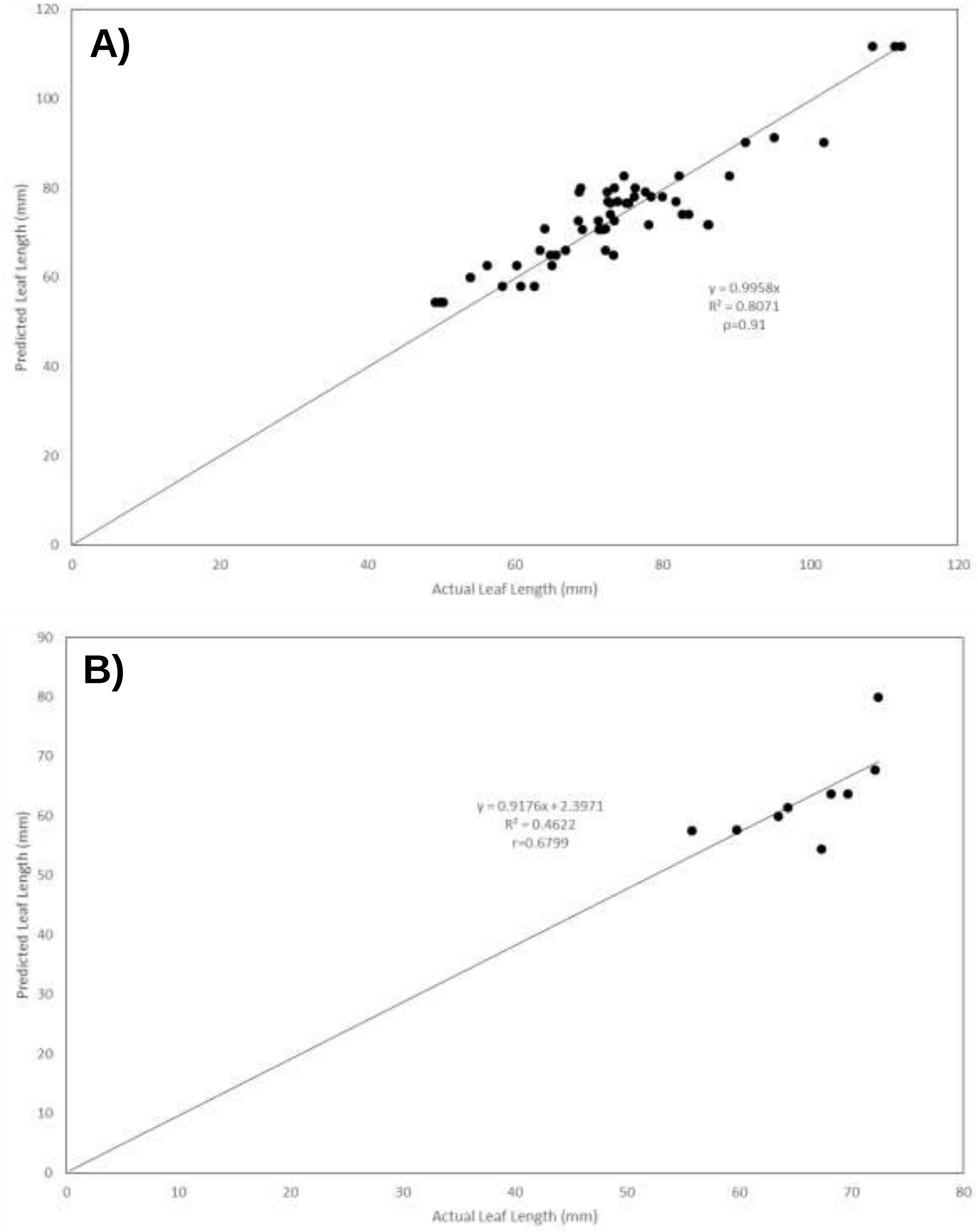


Figure 2.13. Plots of modelled versus measured Amica leaf length for **A)** the parameterisation data set and **B)** the validation data set.

2.1.3. Key Findings: Lettuce

- The greatest biomass was achieved under red: blue mixtures containing 11% blue light. Red: blue treatments with 60% blue light resulted in the most compact plants.
- Increasing the daily light integral increased biomass accumulation while decreasing leaf size.
- Plants grown under a constant intensity (during the light period) gained a higher biomass than plants grown under a strobing light even though the daily light integral was the same.
- Far-red had little influence on biomass, but a negative influence on morphology.
- The influence of light quality on leaf length can accurately be modelled. This model has the potential to enable the development of light treatments designed to produce specific plant qualities.

2.2. TOMATO

2.2.1. Methods

Seed of tomato c.v. Roterno were sown on pre-wet rockwool plugs, covered with vermiculite, and placed under a red: blue light treatment containing 11% blue light in the LED4CROPS facility on the 22nd March 2017. Once germinated the plugs were moved to 3 inch rockwool blocks and placed under one of the sixteen light treatments. Plants were irrigated once per day using the automated irrigation system.

Light treatments

Fifteen treatments were examined. Twelve treatments comprising of four red: blue ratios (6% blue, 15% blue, 30% blue, and 60% blue), each with three different far-red intensities (0, 20, and 40 or 50 µmol m^{-2} s^{-1}). The PAR photon irradiance of these treatments was set as close to 200 µmol m^{-2} s^{-1} as possible (Appendix: Light treatments, Table 6). For these treatments light was provided by Philips GreenPower research modules. Three treatments with differing PAR intensities (105, 194, and 378 µmol m^{-2} s^{-1}) were also included (Appendix: Light treatments, Table 3). For these treatments light was provided by Philips GreenPower production modules (11% blue light).

2.2.2. Results

Across all the light treatments, shoot dry mass correlated linearly with leaf area (Figure 2.14). This suggests that light quality influences growth rate by causing differences in leaf area that influence light capture and that the influence of light quality on photosynthetic performance is of limited importance.

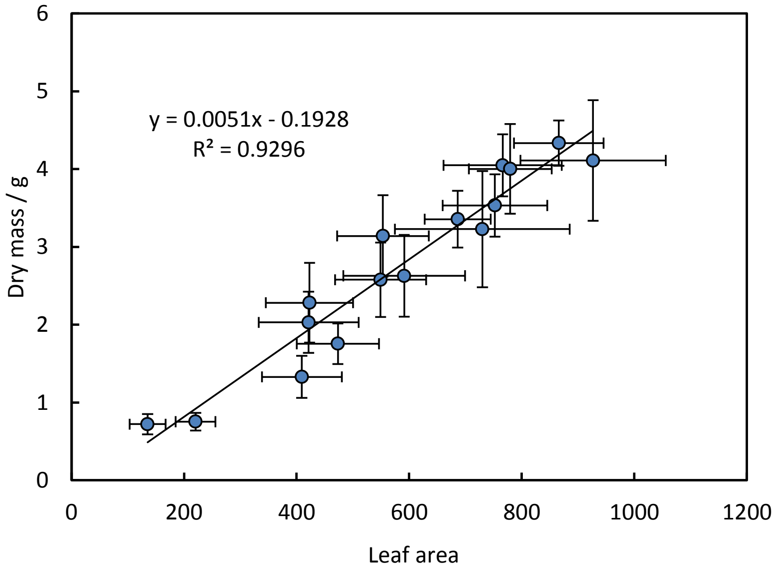


Figure 2.14. Correlation between tomato plant shoot dry mass and leaf area.

Combined red, blue and far-red treatments

The tomato plants were grown under twelve light treatments that differed in red: blue ratio (but constant PAR photon irradiance) and far-red intensity. Plants were observed to respond strongly to the different light qualities (Figure 2.15). The most prominent response of these tomato plants to light quality was the stem elongation occurring in the presence of far-red light, but plants were also responsive to changes in the red blue ratio. Internode length was found to decrease non-linearly as blue percentage increased from 5% to 60% (Figure 2.16A), but to increase linearly as far-red intensity increased (Figure 2.16B). A multiple regression analysis indicated that blue percentage and far-red intensity could account for 90% of the variability in the measured internode lengths and both parameters gave highly significant contributions to the model (intercept P-value = <0.0001, $X_{[\%blue]}$ P-

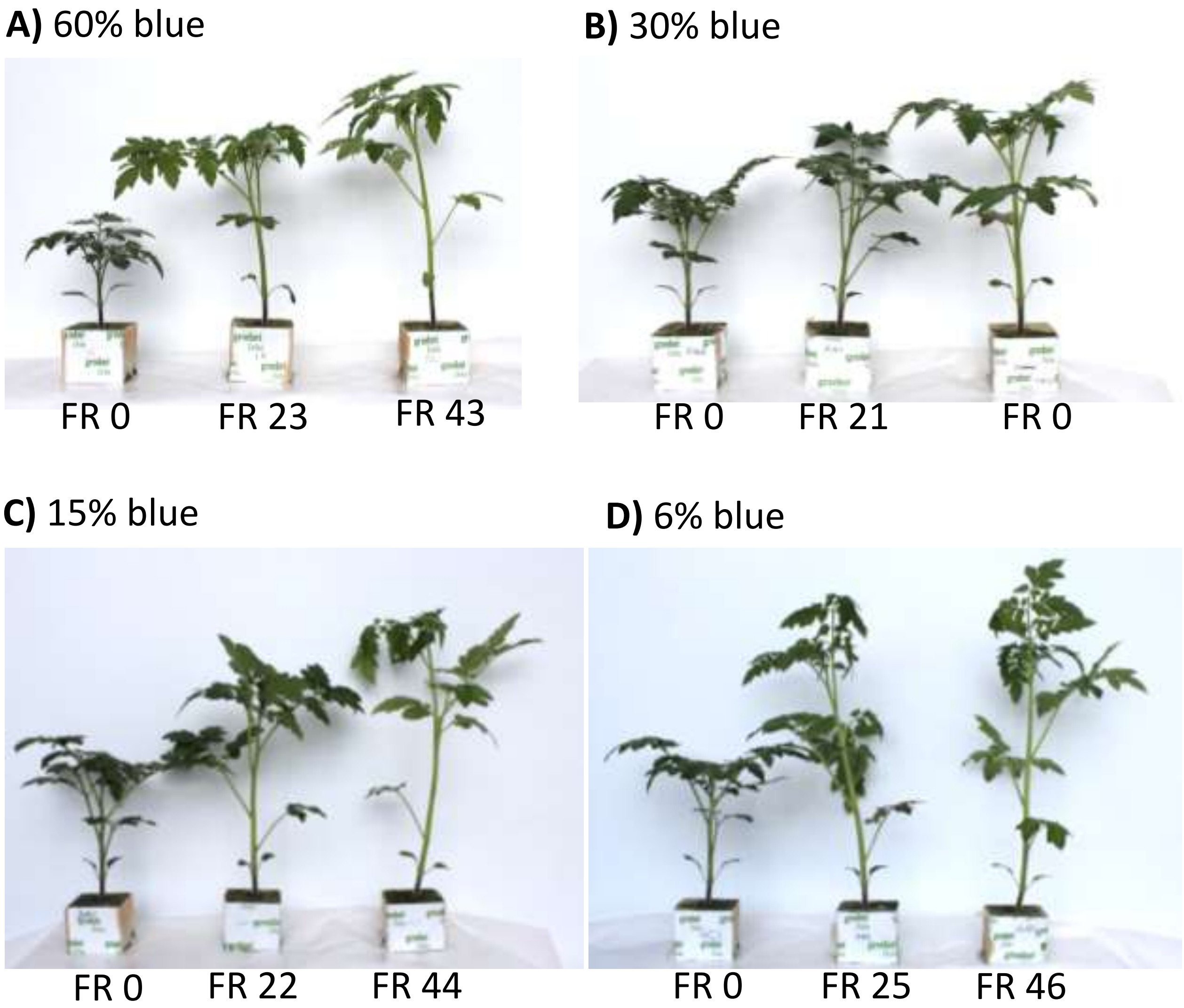


Figure 2.15. Images of tomato plants grown under light treatments differing in blue percentage and far-red photon irradiance.

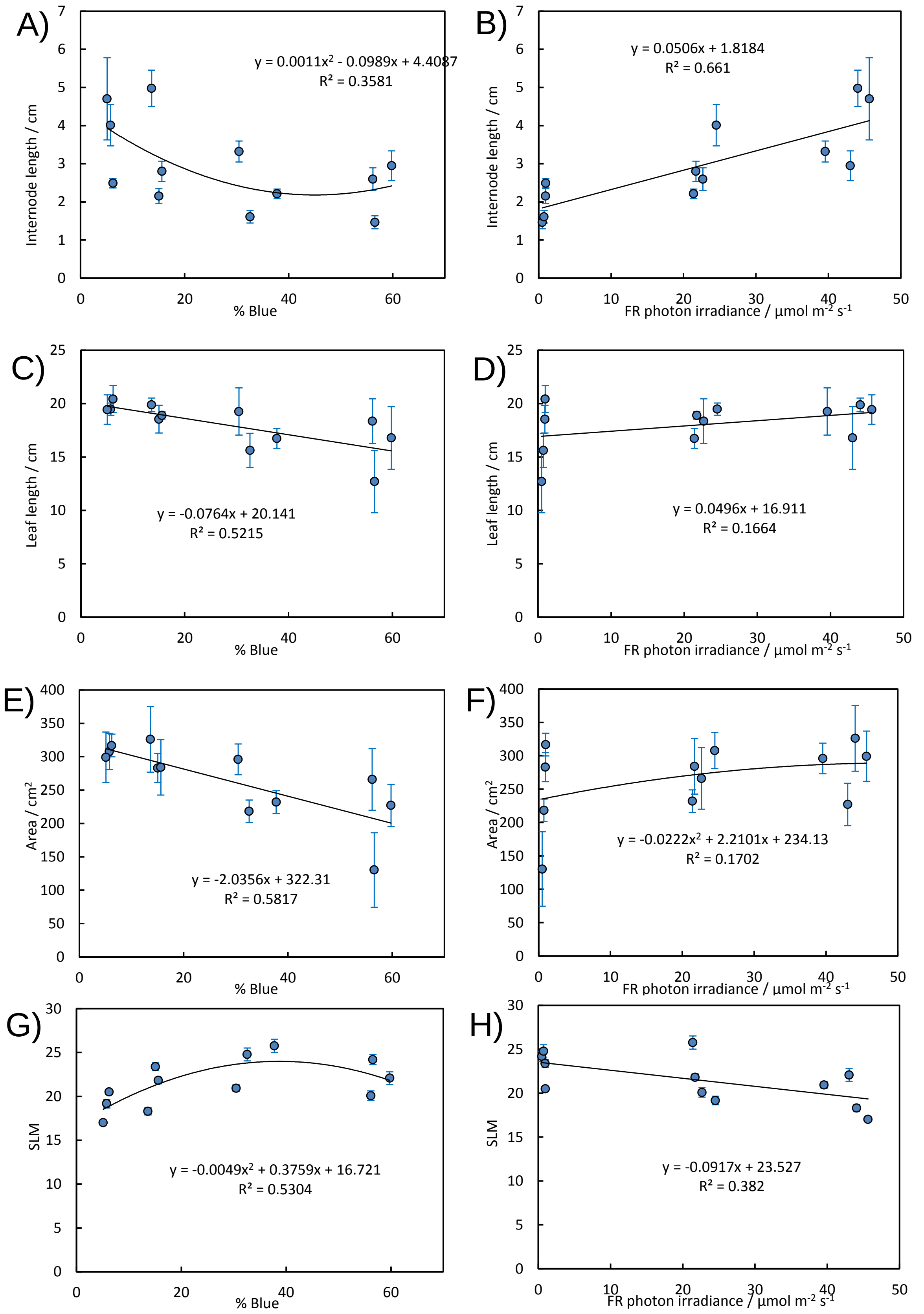


Figure 2.16. The influence of blue light percentage (left side **A,C, E & G**) and far-red photon irradiance (right side **B, D, F & H**) on the internode length (**A & B**), leaf length (**C & D**), total leaf area (**E & F**), and specific leaf mass (**G & H**) of tomato plants.

value =0.001, X $_{[\text{far-red}]}$ P-value = <0.0001). Leaf length (Figure 2.16 C&D) and leaf area (Figure 2.16 E&F) were found to decrease linearly as the blue percentage increased, with leaf length decreasing by 25% from 20 cm at 5% blue to ~15cm at 60% blue, and leaf area decreasing from 300 cm^2 to 200 cm^2 over the same blue percentage range. Far-red was observed to have little influence on leaf length and leaf area. Only under the high blue light (30 and 60% blue) treatments was far-red found to influence leaf length and only then at far-red intensities between 0 and 20 µmol m^{-2} s^{-1}. Leaf thickness, estimated as specific leaf mass (SLM, Figure 2.15 G&H), was found to increase as blue light percentage increased to 30%. As the blue percentage increased to 60%, SLM remained similar or decreased slightly. As far-red light increased, SLM was found to decrease linearly. Net assimilation (dry mass / leaf area), was found to be unaffected by blue light percentage. A weak influence of far-red on net assimilation was observed but this response was not significant.

The influence of PAR photo irradiance on tomato

Tomato plants were grown under light treatments ranging in PAR photon irradiance between 100 and 400 µmol m^{-2} s^{-1}. The plants from the highest light intensities were very robust plants with stiff stems. Under the lowest light treatments, the plants were relatively spindly with a narrow/weak stem. Interestingly, as light intensity increased, plant height was observed to decrease linearly (Figure 2.17A) even though these plants had more leaves. Internodes were found to decrease in length with a non-linear function (Figure 2.17B). However, leaf area (and leaf number) increased with light intensity (Figure 2.17E) as did shoot fresh mass (Figure 2.17D). The net assimilation was observed to increase as the light intensity increased (Figure 2.17E) but light use efficiency was found to decrease as the light intensity increased (Figure 2.17F).

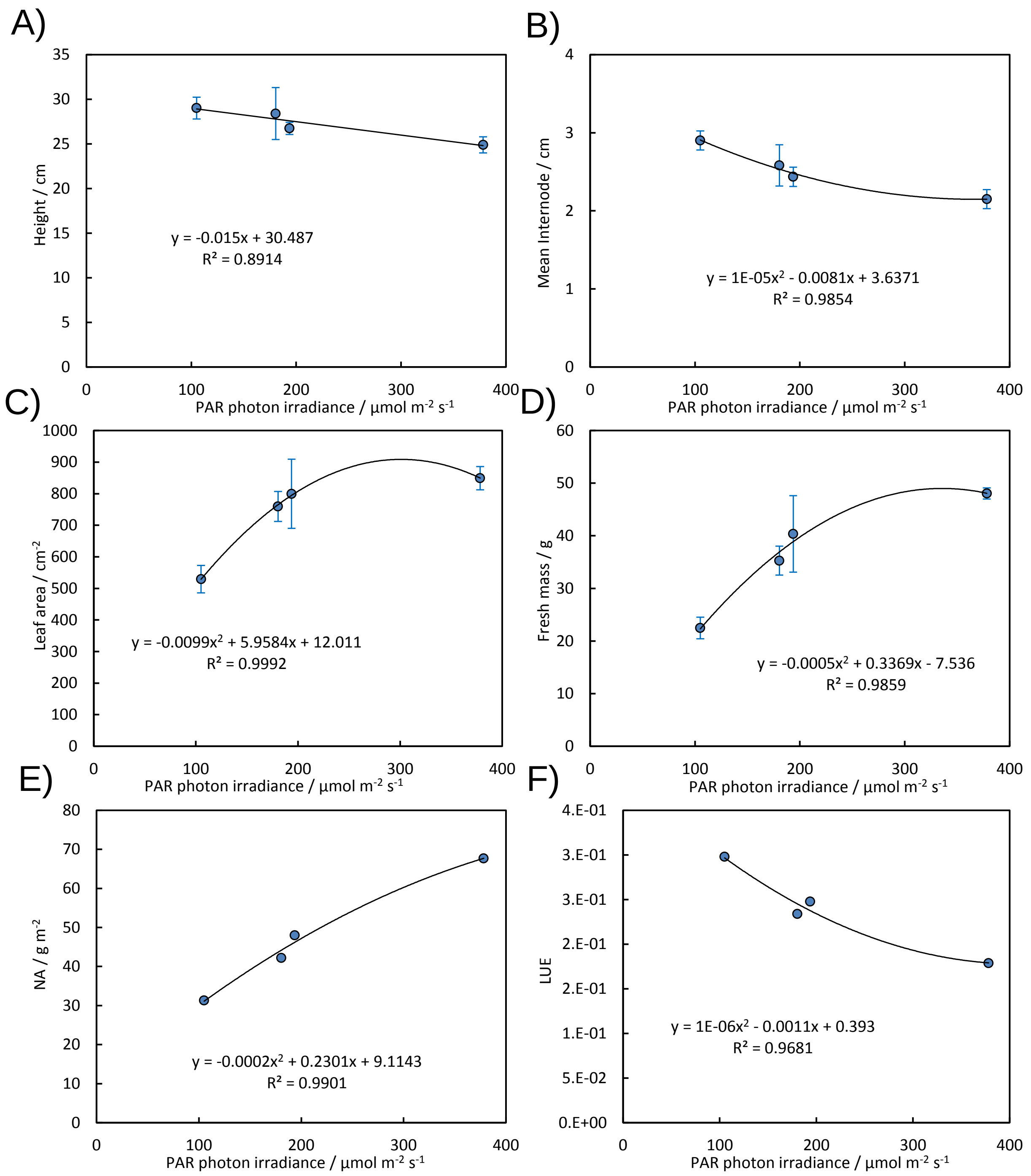


Figure 2.17. The influence of PAR photon irradiance on the morphology and growth of tomato plants. **A)** Plant height, **B)** internode length, **C)** total plant leaf area, **D)** shoot fresh mass, **E)** net assimilation (NA) calculated as dry mass divided by leaf area, and **F)** light use efficiency (LUE) calculated as NA divided by photon irradiance.

2.2.3. Key findings - Tomato

- Spectral manipulation can be used to control the morphology of tomato plants under LED light environments grown without sunlight.

- Tomato internodes are highly sensitive to far-red photon irradiance and stretch proportionally with far-red photon irradiance. Inclusion of far-red was not considered necessary for production of high-quality tomato plants.

- Light treatments with 60% blue light produced the most compact plants; however, these plants also had the lowest leaf area and biomass.

- Plant dry mass accumulation was greatest in the light treatments with 16% blue light.

- Leaf area controls biomass accumulation in tomato.

- Increasing photon irradiance resulted in tomato plants developing a more compact morphology with a more robust stem.

2.3. PEPPER

2.3.1. Methods

Seed of sweet pepper c.v. 'Stanley' (provided by Elsoms Seeds Ltd) were sown on wet rock wool plugs, covered with vermiculite, and placed under a red: blue light treatment containing 11% blue light. Once germinated the plugs were moved to 3 inch rockwool blocks and placed under one of the experimental light treatments.

Light treatments

Fifteen treatments were examined. Twelve treatments comprising of four red: blue ratios (6% blue, 15% blue, 30% blue and 60% blue) each with three different far-red intensities (0, 20, and 40 or 50 µmol m^{-2} s^{-1}). The PAR photon irradiance of these treatments was set as close to 200 µmol m^{-2} s^{-1} as possible (Appendix: Light treatments, Table 6). For these treatments light was provided by Philips GreenPower research modules. Three treatments with differing PAR intensities (105, 194 and 378 µmol m^{-2} s^{-1}) were also included (Appendix: Light treatments, Table 3). For these treatments light was provided by Philips GreenPower production modules (11% blue light).

2.3.2. Results

Combined red, blue, and far-red treatments

The morphology of the pepper plants was strongly influenced by both the blue percentage and the far-red intensity of the light spectrum (Figure 2.18) with the far-red induced stretching of plants being the most prominent response. Leaf number was similar in all the treatments and most plants had visible flower buds at the end of the trial period. Increasing the far-red light intensity resulted in a linear increase in plant height and internode length, while increasing the blue light percentage resulted in a decrease in internode lengths (Figure 2.19 A&B). The effect of far-red light was dominant to the effect of blue light in this species. Leaf petioles responded similarly to the internodes with more far-red increasing lengths and more blue light reducing lengths (Figure 2.19 C&D). Leaf length was observed to decrease as the blue percentage increased and to increase as the far-red intensity increased (Figure 2.17 E&F). For this parameter the effects of blue light were slightly greater than the far-red response. In contrast to the other responses, total leaf area was predominately controlled by the blue percentage.

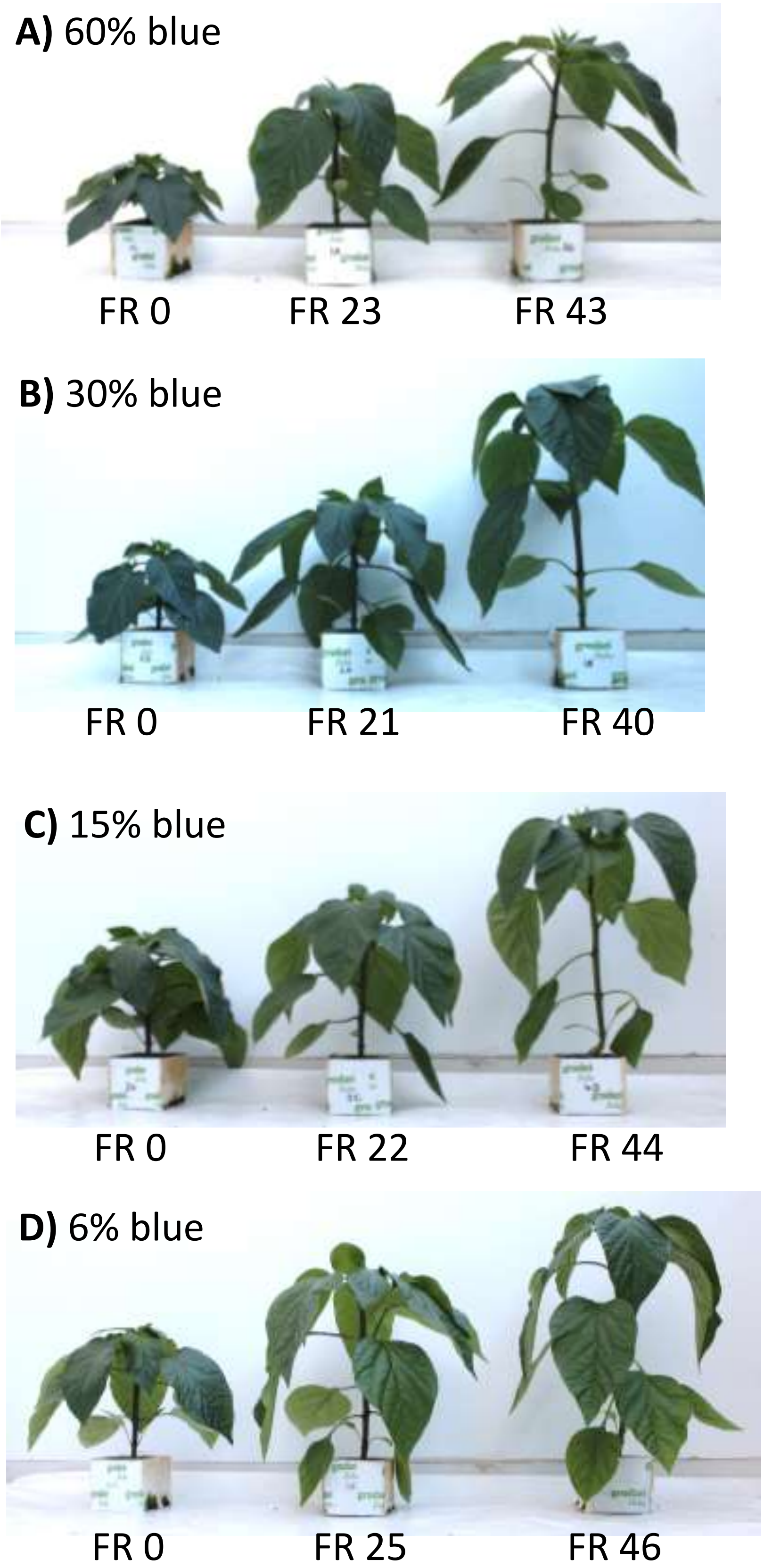


Figure 2.18. Sweet pepper plants grown under twelve light treatments that differed in the blue percentage and the photon irradiance of the far-red light.

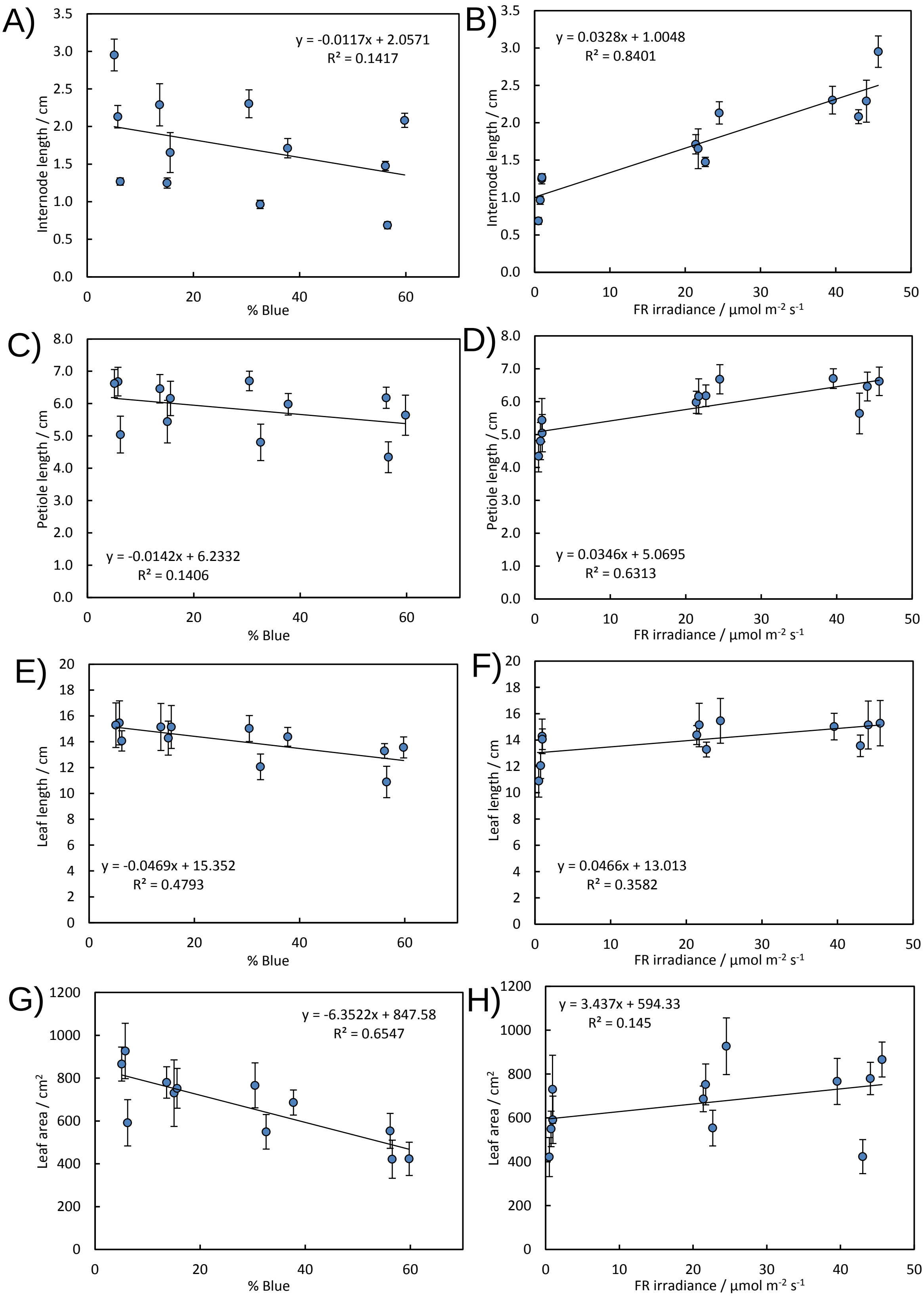


Figure 2.19. The influence of blue percentage (left hand graphs) and far-red photon irradiance (right hand graphs) on **A&B)** internode lengths, **C&D)** petiole lengths, **E&F)** leaf length, and **G&H)** leaf area of sweet pepper plants.

A weak positive correlation between net assimilation with both blue percentage and far-red photon irradiance was observed (Figure 2.20 A&B). However, across all the light treatments examined, leaf area was the main factor controlling dry mass accumulation (Figure 2.20 C).

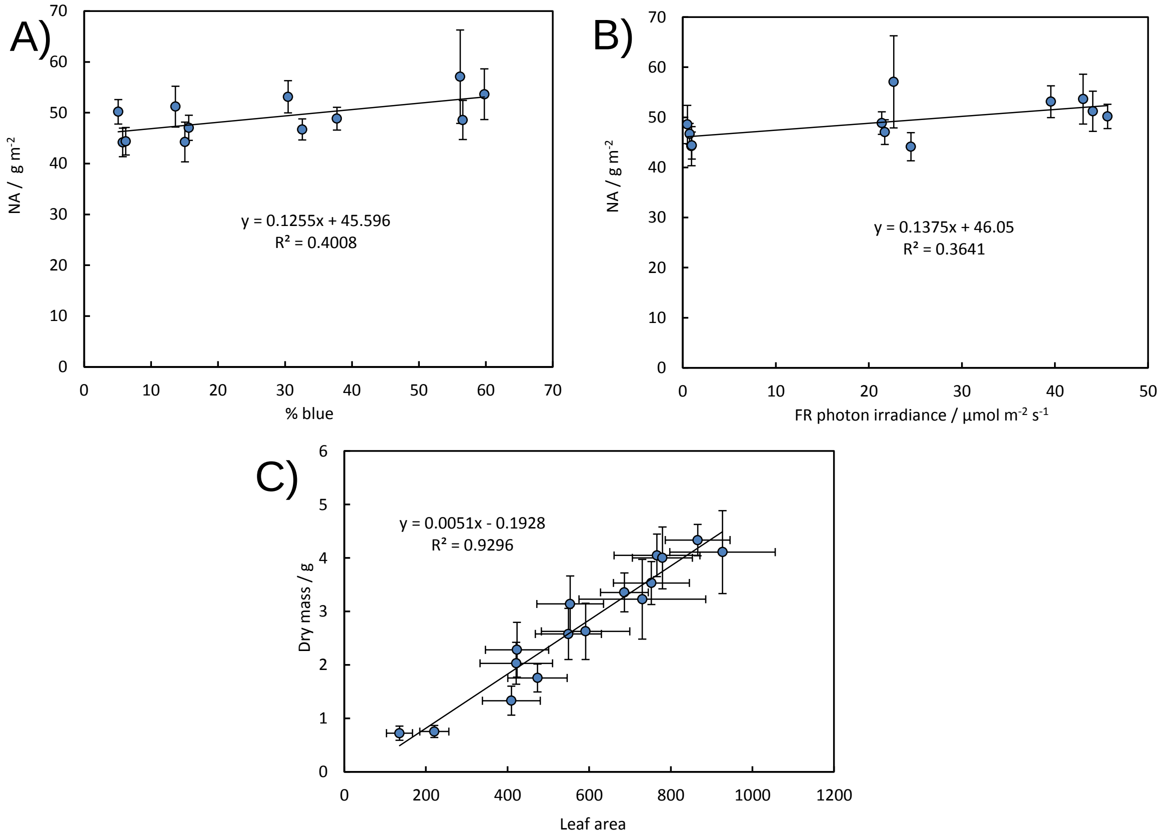


Figure 2.20. The relationship between net assimilation (NA) with **A)** blue light percentage and **B)** far-red photon irradiance. **C)** The correlation between leaf area and dry mass of sweet pepper plants.

The influence of PAR photon irradiance on sweet pepper

As the photon irradiance was increased, plant height was observed to decrease, with a reduction in internode length being the major cause of this reduction in height (Figure 2.21 A). Petiole and leaf blade length also decreased resulting in an increase in plant compactness as intensity increased (Figure 2.21 B&C). Leaf area remained similar between the treatments as irradiance increased. Net assimilation increased as the light intensity increased (Figure 2.21E) while light use efficiency (Figure 2.21F) decreased slightly as photon irradiance increased.

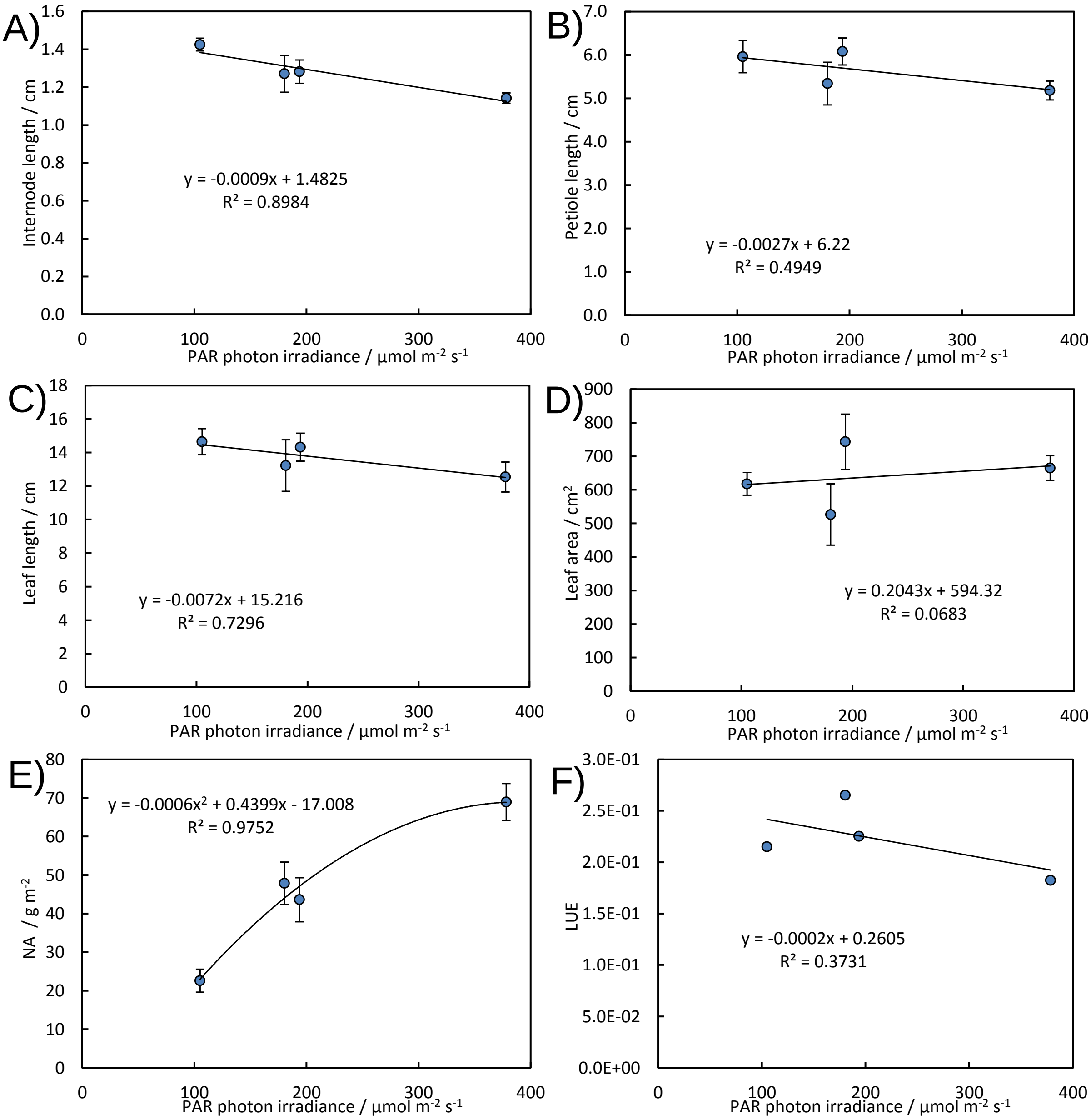


Figure 2.21. The influence of PAR photon irradiance percentage on **A)** internode lengths, **B)** petiole lengths, **C)** leaf blade lengths, **D)** total leaf area, **E)** net assimilation (NA), and **F)** light use efficiency (LUE) of sweet pepper plants.

2.3.3. Key findings – sweet pepper

- Spectral manipulation can be used to control the morphology of sweet pepper plants under LED light environments with no sunlight.
- Sweet pepper internodes are highly sensitive to far-red photon irradiance and they stretch proportionally with far-red photon irradiance. Inclusion of far-red was considered necessary for production of high quality sweet pepper plants.
- Light treatments with 60% blue light produced the most compact plants; however, these plants also had the lowest leaf area and biomass.
- Plant dry mass accumulation was greatest in the light treatments with 16% blue light.
- Leaf area controls biomass accumulation in sweet pepper.
- Increasing the photon irradiance resulted in sweet pepper plants developing a more compact morphology with a more robust stem.

2.4. CUCUMBER

During the year one trials cucumber plants were observed to exhibit pronounced responses to changes in red: blue ratio (Figure 2.22; for details of light treatments see Appendix: Light treatments, Table 1) and far-red photon irradiance (Figure 2.23; for details of light treatments see Appendix: Light treatments, Table 2). The most compact plants were observed under light treatments with 66% blue light and no far-red light. In the absence of far-red, cucumber plants were regarded as too compact for commercial situations. Far-red light caused plant internodes and, therefore, plant height to increase linearly with increasing far-red intensity providing a morphology that was more appropriate for commercial applications. During the third year of the trials, we further investigated the effects of light quality on cucumber morphology and physiology.

Figure 2.22. Photographs of representative cucumber plants grown under four different red: blue light treatments. The same plants are shown from the side and from above.

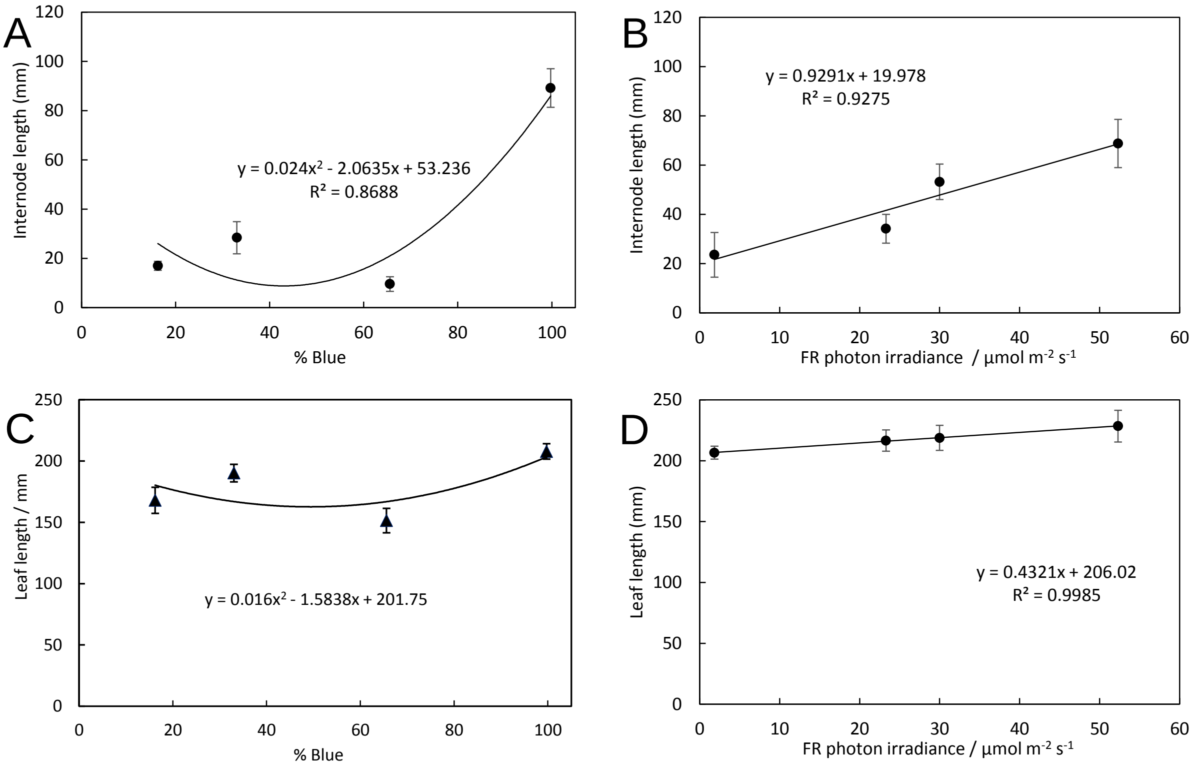


Figure 2.23. The influence of blue light percentage (**A&C**) and far-red photon irradiance (**B&D**) on internode length **A&B)**, and leaf length **C&D)** of cucumber plants. Error bars indicate the standard deviation.

2.2.1. Methods

For the year three trials, cucumber seed were sown on pre-wet rock wool blocks, covered in vermiculite, and placed under the different light treatments. Seed were sown on the 26th September 2016 and the plants were harvested on the 10th October 2016 when plants were 14 days old.

Light treatments

The plants were grown under 20 different light treatments. Four light treatments examined the influence of different red: blue ratios (100% red, 14% blue, 60% blue, and 100% blue) under a low light intensity of 100 µmol m^{-2} s^{-1} (Appendix: Light treatments, Table 7). Twelve light treatments examined the combined influence of red, blue, and far-red light when the PAR photon irradiance was approximately 200 µmol m^{-2} s^{-1} (Appendix: Light treatments, Table 6). For each of the four red: blue ratios (60%, 30%, 16% and 5% blue) three difference far-red photon irradiances were examined (0, 20, and 40 µmol m^{-2} s^{-1}). Four treatments were used to examine the influence of PAR photon irradiance (100, 191, 235, and 320 µmol m^{-2} s^{-1}) when the red: blue ratio was 11% blue (Appendix: Light treatments, Table 3).

2.4.2. Results

Red: blue ratio under low light intensities

For the cucumber plants grown under low light intensities (100 µmol m^{-2} s^{-1}), red: blue ratio had a large influence on morphology (Figure 2.24). As observed during the year one trial the most compact plants were observed under the 60% blue light treatments and the 100% blue light treatment exhibited considerable stem stretching. The greatest leaf size and area was observed under the 16% blue light treatment. Under the 100% red light treatment (0% blue) total leaf area was observed to decrease in comparison to the 16% blue treatment.

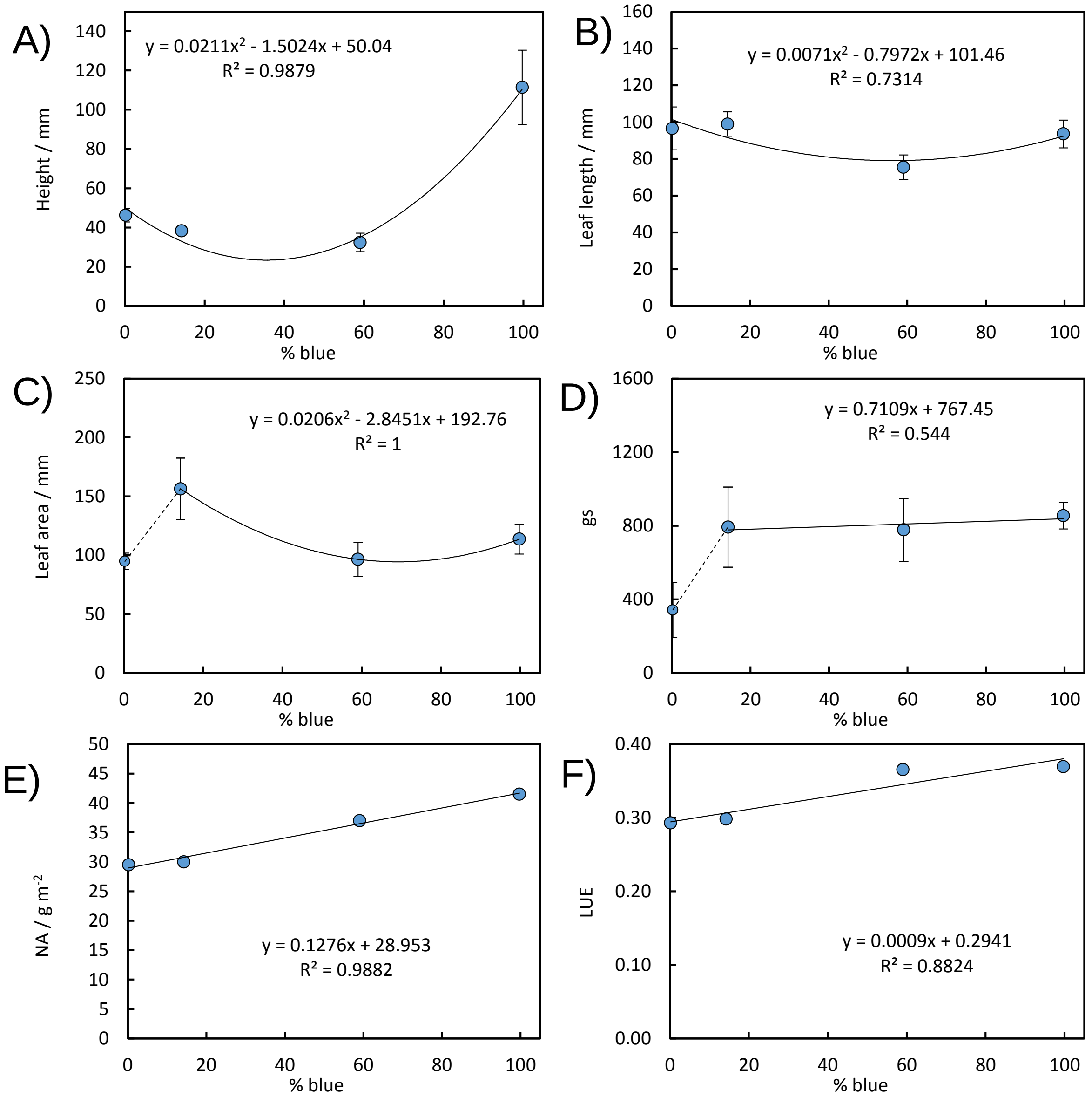
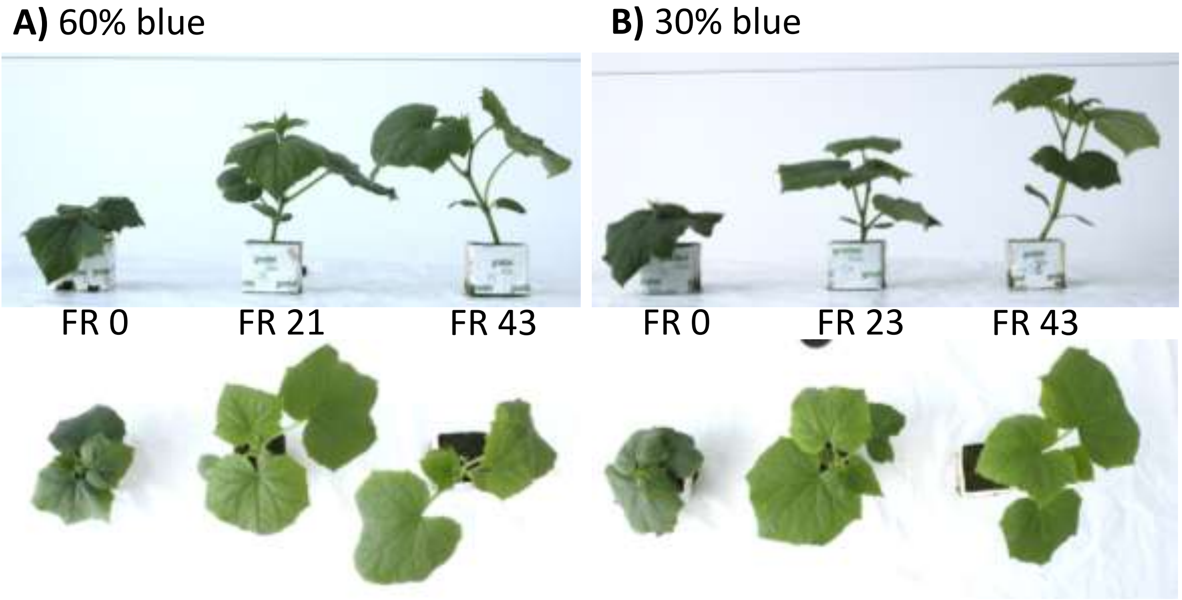


Figure 2.24. The influence of light quality on cucumber plants grown under a photon irradiance of ~100 µmol m^{-2} s^{-1}. **A)** Plant height, **B)** length of leaf lamina, **C)** total leaf area, **D)** stomatal conductance (g_S), **E)** net assimilation (NA) calculated as shoot dry mass divided by leaf area, and **F)** light use efficiency (LUE) calculated as NA divided by photon irradiance.

Stomatal conductance was observed to be lowest under the 100% red light treatment. For the three light treatments containing blue light the conductance values were similar and did not increase with blue proportion as expected.. The net assimilation and light use efficiency were observed to increase as the blue percentage increased.

Combined red, blue, and far-red treatments

Across all the treatments where the photon irradiance was 200 µmol m^{-2} s^{-1} the far-red light had the most pronounced influence on morphology (Figure 2.25). The high far-red (42 µmol m^{-2} s^{-1}) treatment plants were nearly touching the lights after 14 days, which resulted in the need to harvest the trial earlier than planned. The far-red light caused the leaves to increase in area and have a paler green appearance.



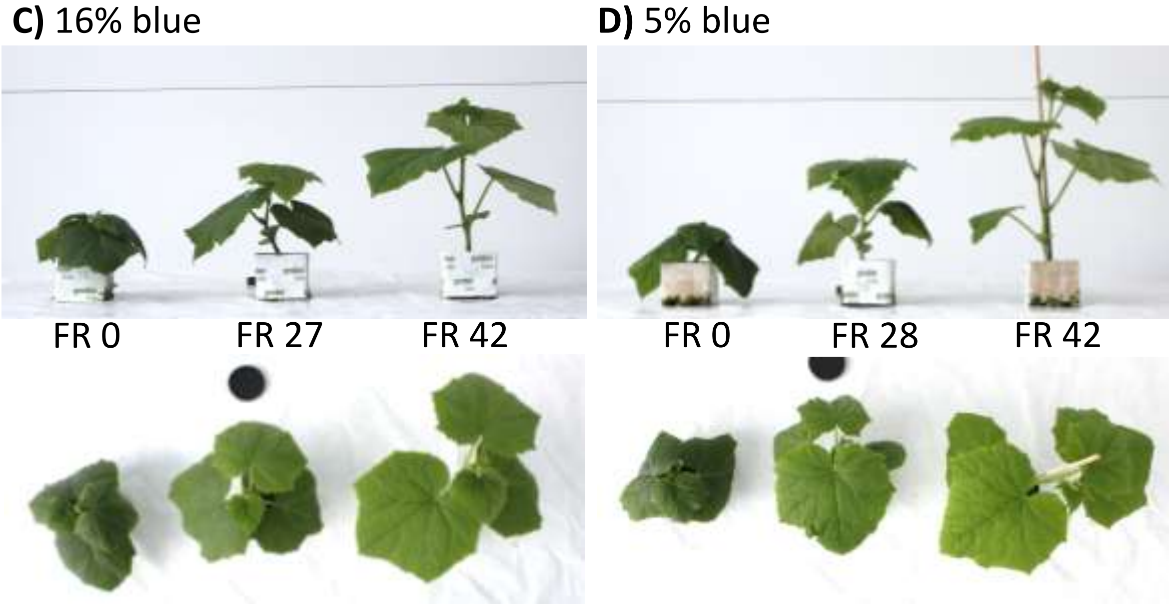


Figure 2.25. Images of cucumber plants grown under the twelve light treatments where the photon irradiance was 200 µmol m^{-2} s^{-1}. Plants are shown from the side and above.

If we first examine the morphological and physiological responses of the plants from light treatments with no far-red light we can compare how the plant responses to red: blue ratio at 200 µmol m^{-2} s^{-1} (Figure 2.25) differ from those observed under the lower photon irradiances (Figure 2.22). As in the low intensity treatments, the most compact plants were observed under the 60% blue treatments. However, in contrast to the low intensity treatments where plant height was observed to decrease between 0 and 15% blue, plant height increased between 5 and 16% blue light. Leaf size and area responded similarly under the two light intensities, and both phenotypes were observed to decrease as blue

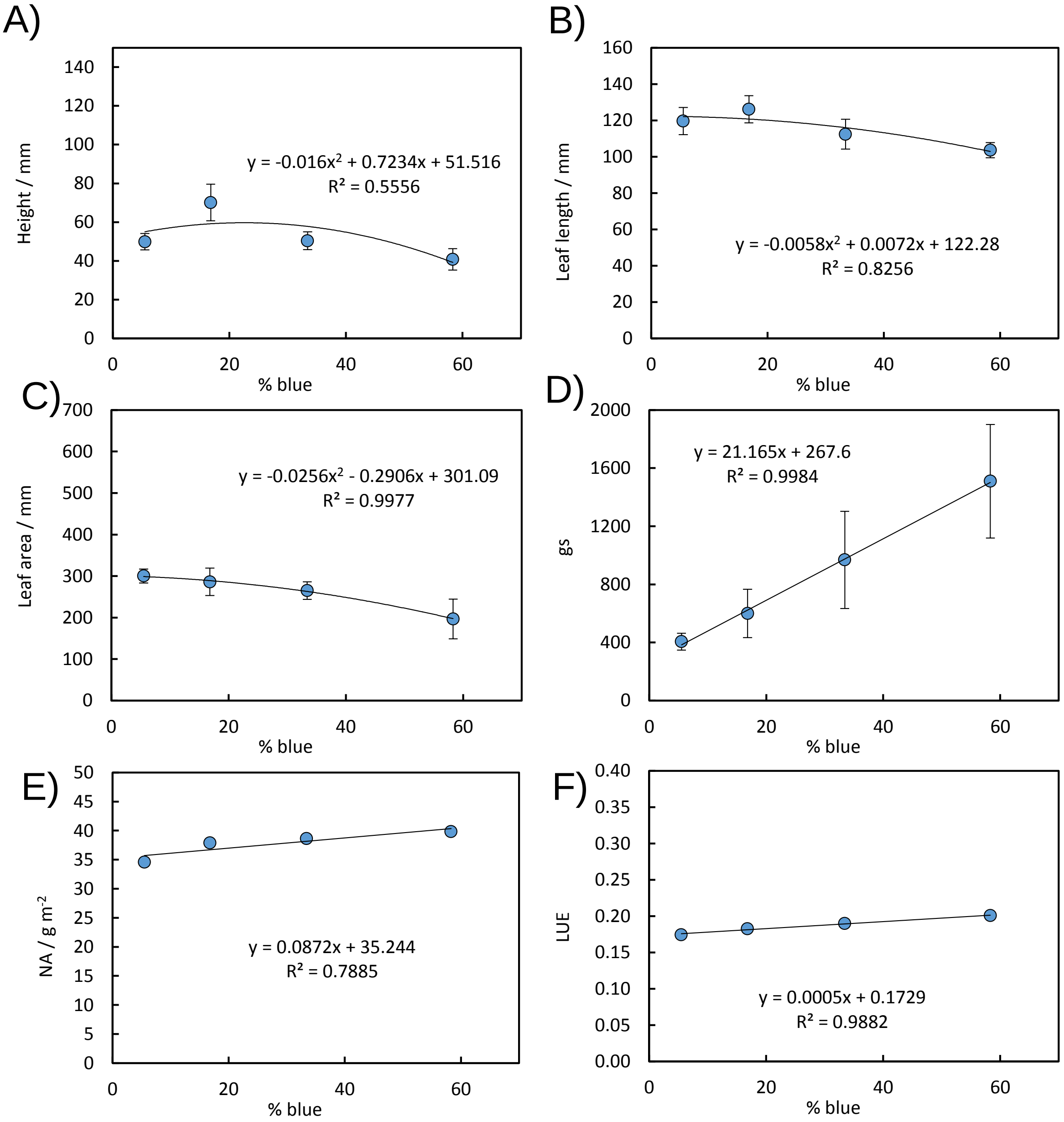


Figure 2.26. The influence of red: blue ratio on cucumber plants grown under a photon irradiance of ~200 µmol m^{-2} s^{-1}. **A)** Plant height, **B)** length of the leaf blade, **C)** total leaf area, **D)** stomatal conductance (g_S), **E)** net assimilation (NA) calculated as shoot dry mass divided by leaf area, and **F)** light use efficiency (LUE) calculated as NA divided by photon irradiance.

percentage increased. In contrast to the response at 100 µmol m^{-2} s^{-1}, stomatal conductance was observed to increase as the blue light percentage increased at 200 µmol m^{-2} s^{-1}. As was the case at 100 µmol m^{-2} s^{-1} both NA and LUE were observed to increase with blue light percentage, though this response was less pronounced.

When we examine the effects of far-red light on morphological and physiological responses of cucumber (Figure 2.27) large responses can be seen. Internode, plant height, leaf size, and total leaf area all increased as the far-red intensity increased. In contrast, stomatal conductance was observed to decrease as far-red increased. Net assimilation and light use efficiency were both observed to be unaffected by the far-red intensity.

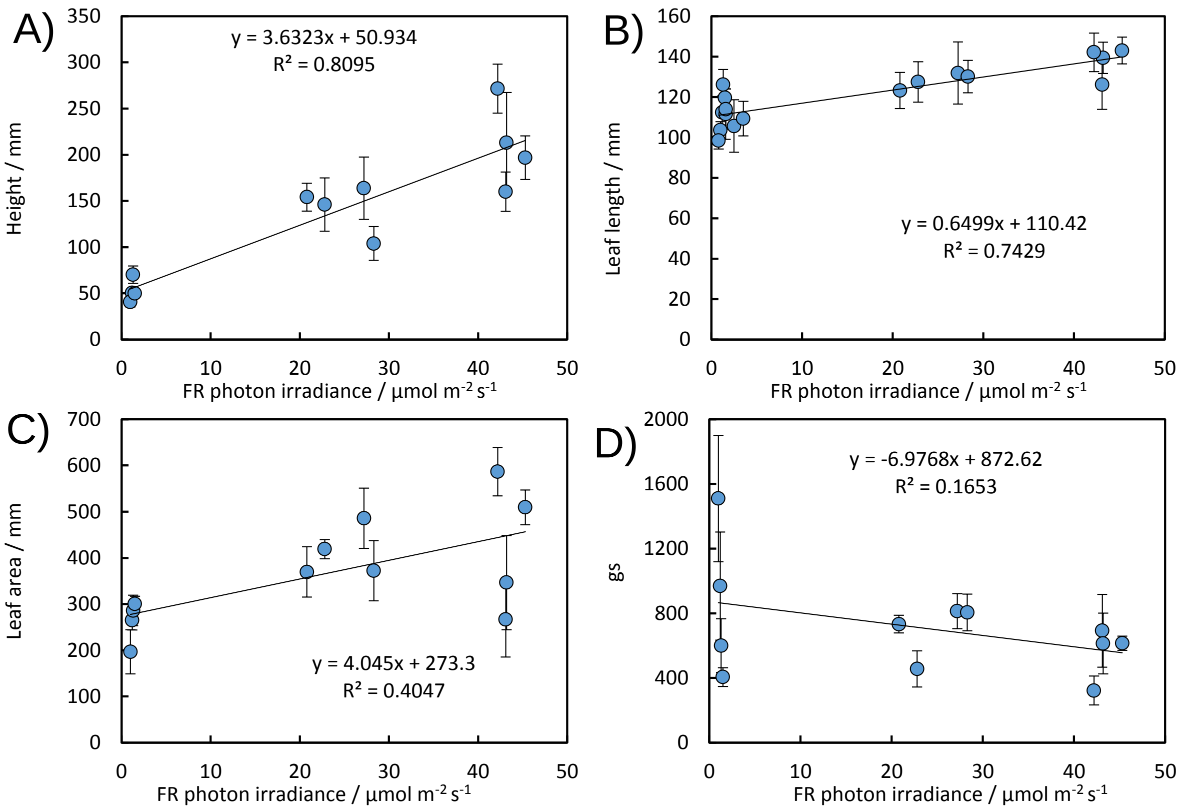


Figure 2.27. The influence of light quality on cucumber plants grown under a PAR photon irradiance of ~200 µmol m^{-2} s^{-1} supplemented with different photon irradiances of far-red light. **A)** Plant height, **B)** length of the leaf lamina, **C)** total leaf area, and **D)** stomatal conductance (g_S).

The influence of PAR photon irradiance on cucumber

As PAR photon irradiance increased plant height and biomass were observed to increase (Figure 2.28). While higher intensities resulted in taller plants, internode lengths were observed to decrease slightly resulting in plants becoming more compact. Leaf size was not influenced by light intensity; however, due to an increase in the number of leaves per plant, total leaf area was affected. Interestingly, stomatal conductance was observed to decrease as intensity increased. As expected, net assimilation increased with increasing light intensity and light use efficiency decreased. Across all twenty light treatments, leaf area was found to have a linear correlation with shoot dry mass (Figure 2.29). This indicated that the changes in light quality predominantly influenced the growth rate of cucumbers by influencing plant morphology and not via effects on photosynthetic rate or stomatal conductance.

2.4.3. Key Findings - Cucumber

- Cucumbers grown in the absence of far-red light remain too compact for conventional commercial purposes. The 60% blue light regime resulted in the most compact plants.

- Stem length and leaf size increased linearly with increasing far-red intensities. Optimal crop morphology can be achieved by altering the far-red intensity.

- Cucumber plants were more sensitive to changes in light quality expected to be controlled by phytochromes than by other types of photoreceptor.

- Leaf area is the primary factor controlling for biomass accumulation in cucumber plants.

- In the absence of blue light (100% red treatments) stomatal conductance drops significantly. This combined with a smaller leaf area and poor morphology for light capture resulted in reduced growth rates and plant quality.

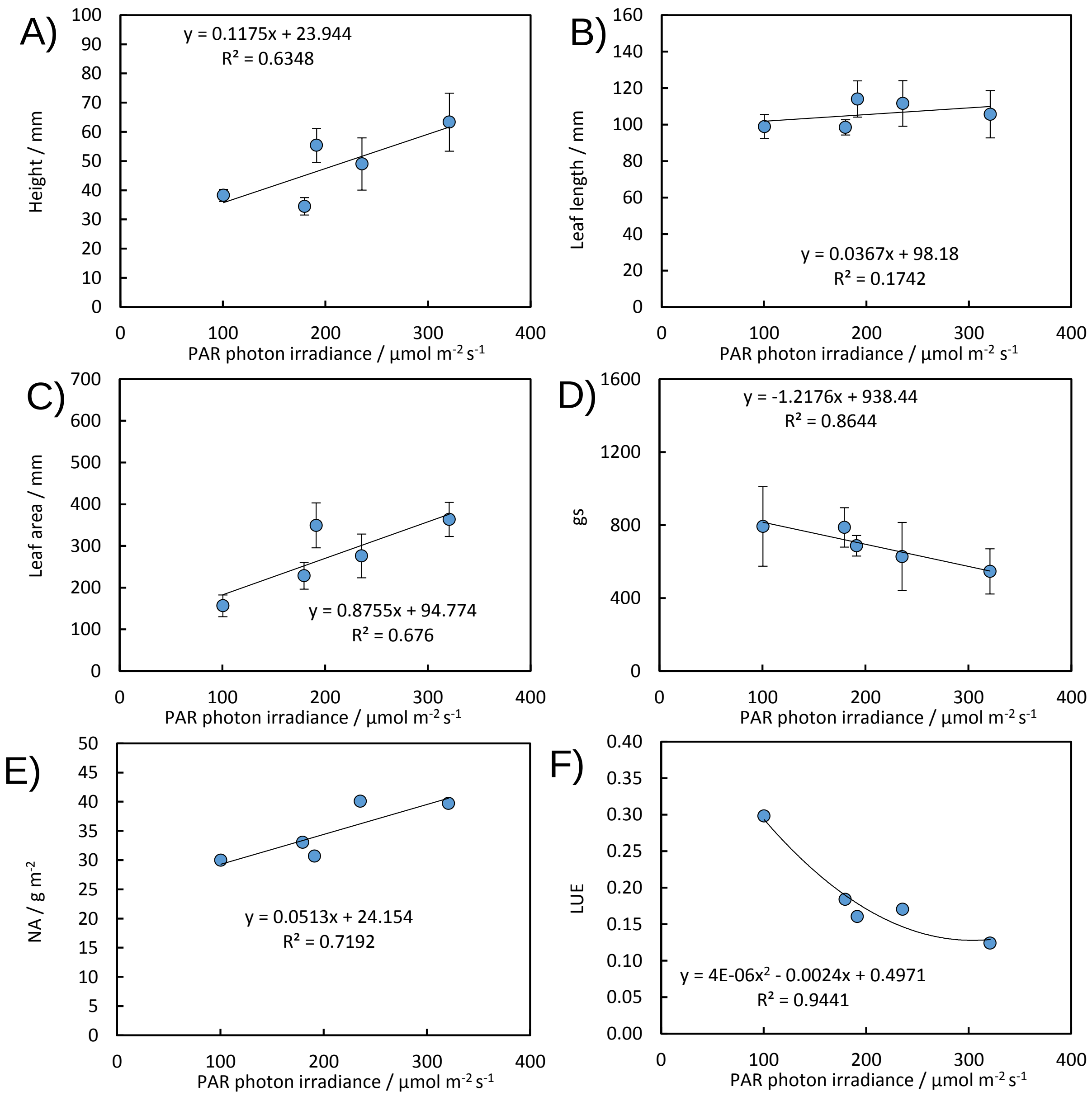


Figure 2.28. The influence of PAR photon irradiance on cucumber plants grown under a red: blue light mixture with 11% blue. **A)** Plant height, **B)** length of blade of the X leaf, **C)** total leaf area, **D)** stomatal conductance (g_s), **E)** net assimilation (NA) calculated as shoot dry mass divided by leaf area, and **F)** light use efficiency (LUE) calculated as NA divided by photon irradiance.

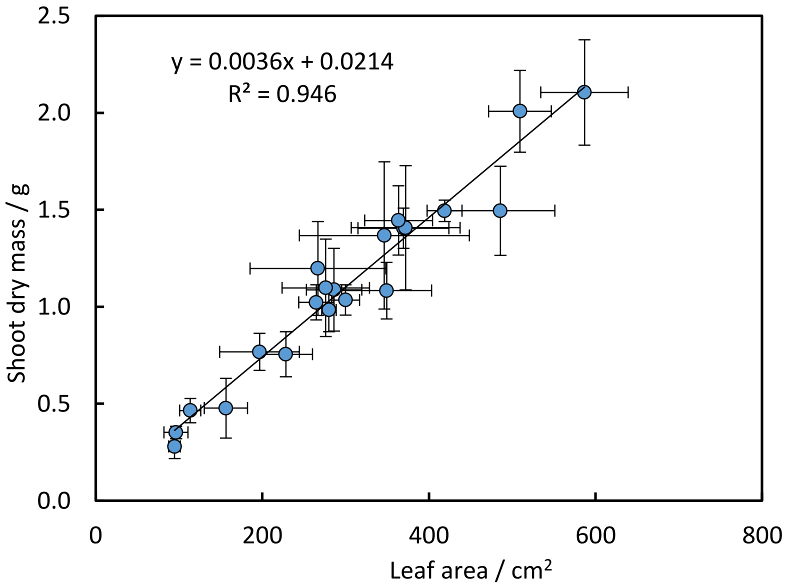


Figure 2.29. The correlation between leaf area and shoot dry mass for cucumber plants grown under 20 different light treatments.

2.5. BASIL

During the year one trials we examined the effect of different red: blue ratios (15%, 33%, 66%, and 100% blue – Appendix: Light treatments, Table 1) and different red far-red ratios on basil growth and morphology (0, 15, 30 and 48 µmol m^{-2} s^{-1} – Appendix: Light treatments, Table 2). Increasing the blue light percentage was found to reduce internode lengths and plant height and also to alter the position of the leaves (Figure 2.30). Leaves were held parallel to the floor in high blue light environments while leaves hung downwards (epinastic phenotype) under low blue environments.

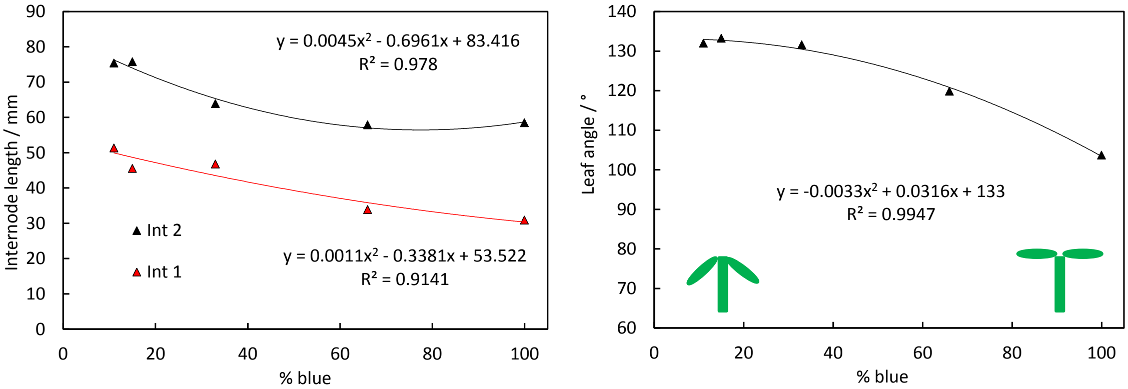


Figure 2.30. Influence of blue light percentage (% blue) on **A)** the length of the 1st two internodes, and B) leaf angle of basil plants grown under the different red: blue light treatments. The diagrams in figure **B)** demonstrate the appearance of the plants at the two treatment extremes.

The photosynthetic performance of basil grown under different red blue treatments was also measured (Figure 2.31). The greatest photosynthetic rates were observed in plants grown under 100% blue light, despite these plants growing more slowly than those in the other light treatments. The lowest photosynthetic rates were observed in the red: white light treatment. When the maximum gross photosynthetic rates were plotted versus the blue percentage contained within the light, photosynthetic potential (P_{max}) was found to increase with increasing blue light percentage. Respiration rates were found to decrease (become less negative) as blue percentage increased. The far-red treatments were found to have little influence on basil growth and morphology during this first trial. This may have been partially because the plants were arranged (two plants per six pack) to minimise shading in the canopy. Commercially protected basil is grown with multiple plants per pot and may respond more strongly to far-red light. During the third year of this trial we have explored the light responses of basil to light treatments with combined red, blue, and far-red treatments and different light intensities with approximately 20 plants sown per pot.

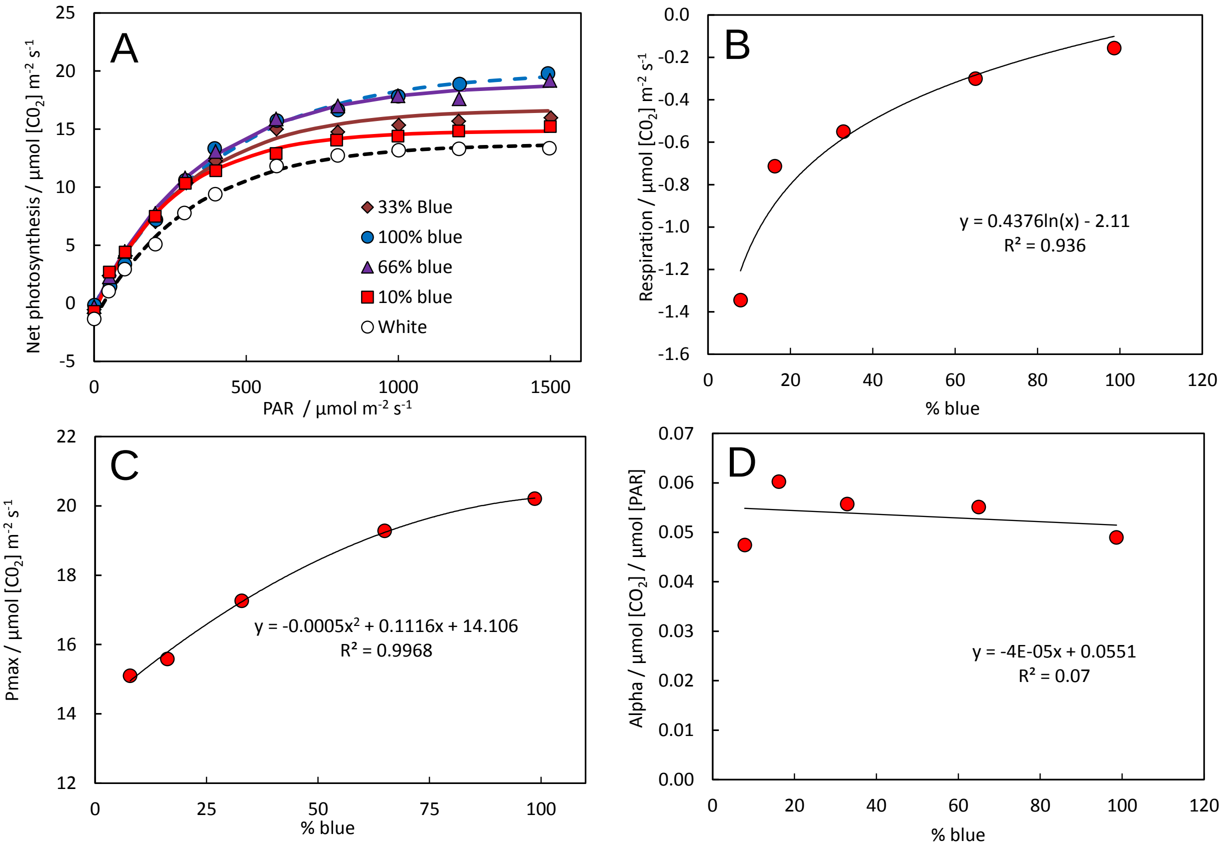


Figure 2.31. **A)** Net photosynthetic light response curves of basil plants grown under five different light treatments. The influence of blue percentage (% blue) on **B)** the measured respiration rate in darkness, **C)** maximum gross photosynthetic rate (P_{max}), and **D)** the slope of the net photosynthesis curve in light-limiting conditions (Alpha).

2.5.1. Methods

For the year three trials approximately 20 seeds of basil c.v. ‘Mariam’ were sown on Levington M2 substrate in 10 cm pots on the 19th October 2016. Pots were covered with clear plastic until the seeds germinated. On 18th November 2016 (21 days after sowing), plants were assessed for height, internode length, leaf size and area, as well as fresh biomass.

Light treatments

Twelve treatments comprising of four red: blue ratios (6% blue, 15% blue, 30% blue, and 60% blue) each with three different far-red intensities (0, 20, 40 or 50 µmol m^{-2} s^{-1}). The PAR photon irradiance of these treatments was set as close to 200 µmol m^{-2} s^{-1} as possible (See Appendix: Light treatments Table 6). For these treatments light was provided by Philips GreenPower research modules.

2.5.2. Results

Combined red: blue and far-red treatments

The plants germinated and grew rapidly, and had no pests or diseases during this trial (Figure 2.32). The basil plants were grown under twelve light treatments with different combinations of red, blue, and far-red light. Internode lengths decreased linearly as the blue light percentage increased (Figure 2.33A) while far-red caused a linear increase in internode length (Figure 2.33B). Leaf area was found to be independent of blue percentage (Figure 2.33C) and far-red photon irradiance (Figure 2.33D). Fresh mass was also found to be unaffected by light quality (Figure 2.33 E&F).

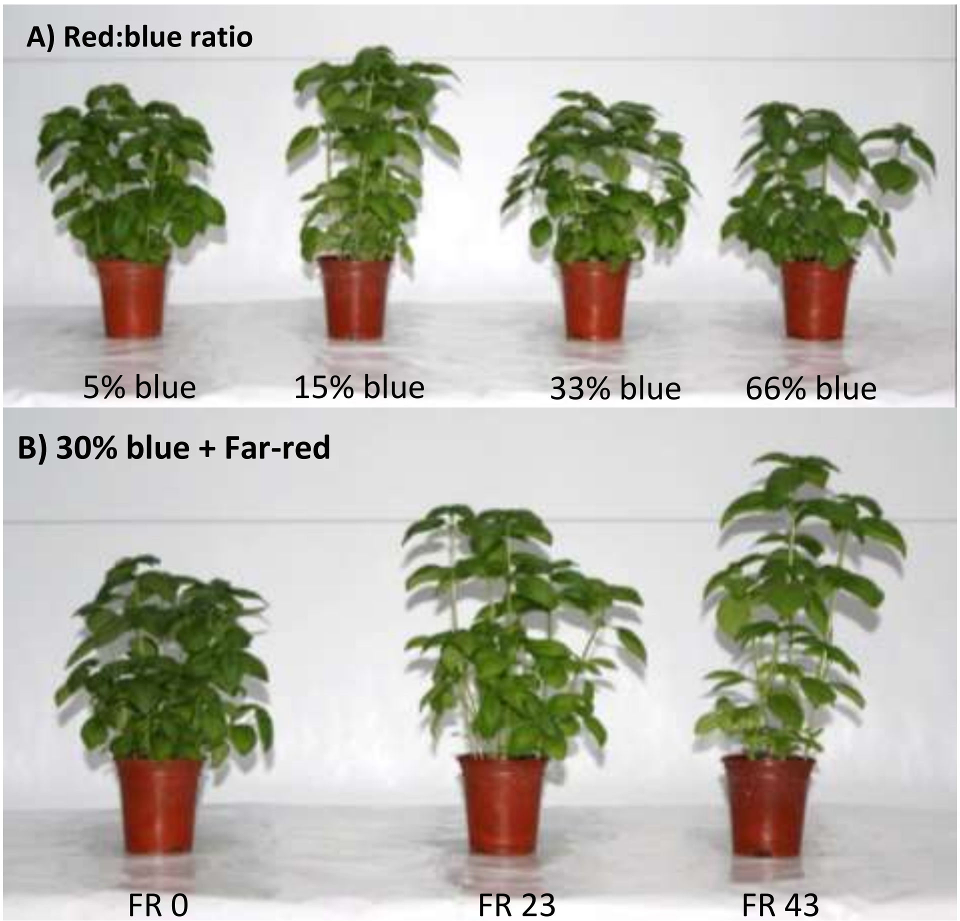


Figure 2.32. Images of basil plants grown under a range of light treatments. **A)** The influence of different red: blue ratios on basil plants. **B)** The influence of adding far-red light to a red: blue mixture containing 30% blue light.

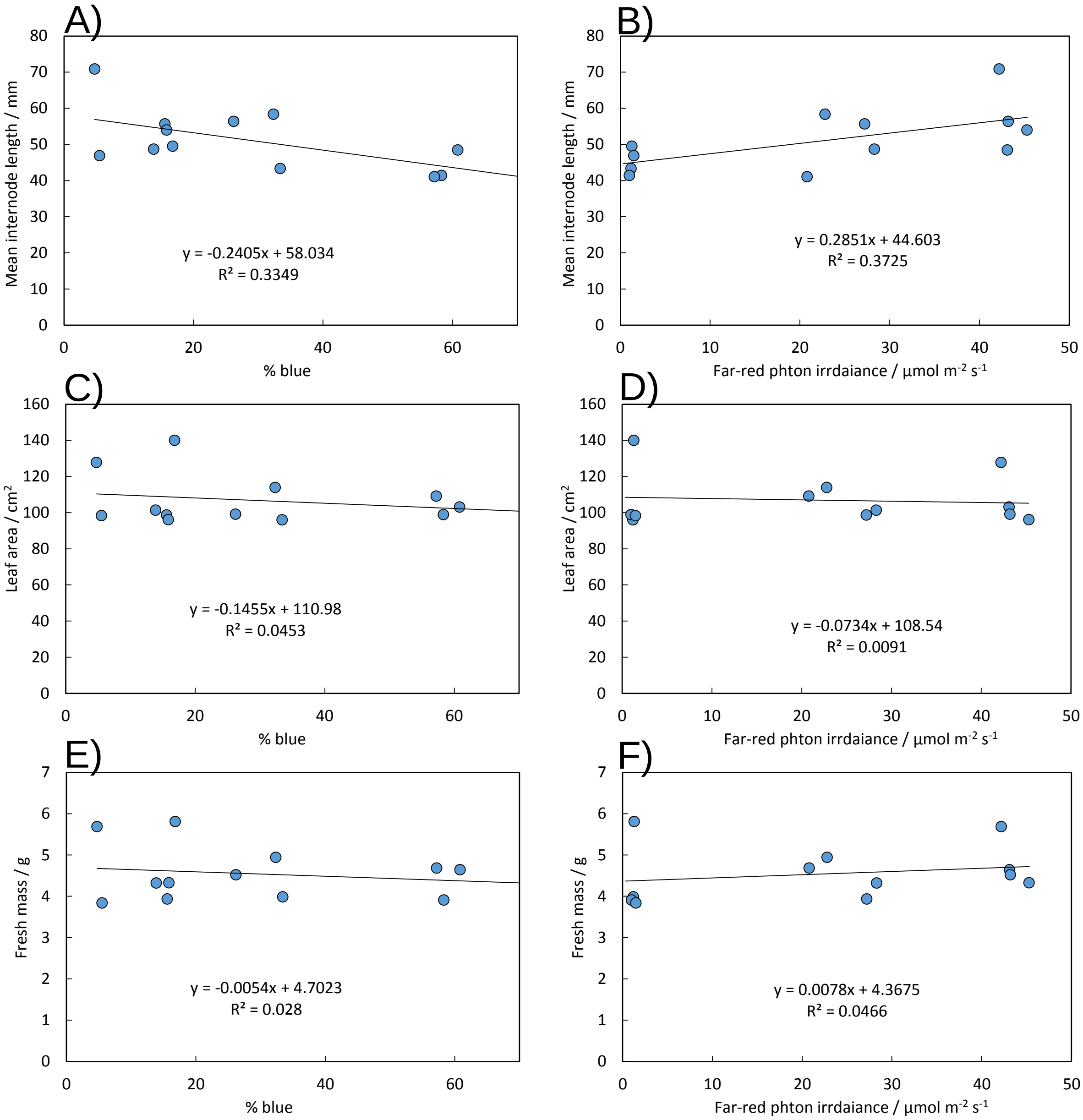


Figure 2.33. Effects of light quality in the morphology and biomass of basil plants grown under twelve red: blue: far-red light mixtures. Left side graphs **(A, C & E)** show the influence of blue percentage (% blue) while the right side graphs **(B, D & F)** show the influence of far-red photon irradiance. **A&B)** Mean internode lengths. **C&D)** Total leaf area. **E&F)** Fresh mass.

The influence of photon irradiance on basil performance

Basil plants were grown under different photon irradiances (Figure 2.34) to examine how morphology and growth rate were affected. As light intensity increased, plants became taller (Figure 2.35A) but more compact with shorter internodes (Figure 2.35B). Both leaf area (Figure 2.35C) and fresh mass (Figure 2.35D) increased as light intensity increased. The plants grown under the highest light intensity were much bushier, tougher plants than those from the lower light intensities and the main stems were thick and stiff to the touch. Increasing the light intensity in this variety was not expected to shorten production times as crop height was only slightly increased.

Figure 2.34. Photographs of basil plants grown under different photon irradiance when the red: blue mix contains 11% blue light.

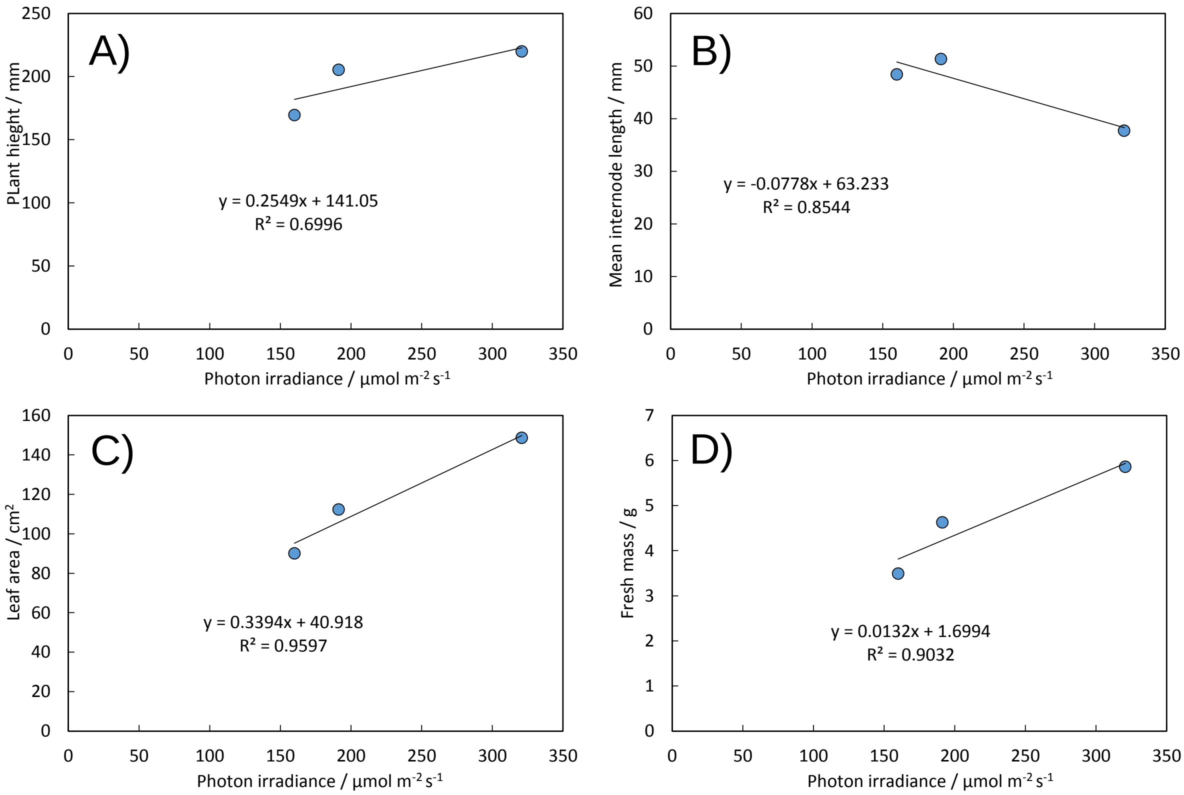


Figure 2.35. The influence of photon irradiance on **A)** plant height, **B)** mean internode length, **C)** leaf area, and **D)** fresh mass of basil plants. Light spectrum was a red: blue mixture containing 11% blue light.

2.5.3. Key findings – Basil

- Basil morphology and internode length, can be manipulated by light quality. Far-red light increases internode lengths while increasing blue light reduces internode length.

- Increasing the total light intensity increased plant mass and increased plant compactness. However, if plants are marketed at a certain height, increasing the light intensity may not increase production times.

- Maximum potential photosynthetic rates were regulated by the blue light percentage not total light intensity.

- Uncontrolled sensory tests indicate that altering the light spectrum changes the aroma and flavour of the basil plants. No scientific measurements have been made to confirm this.

2.6. SAGE

The experiments examining sage responses to light quality were performed in year one. The main findings of this work are summarised here. For more details see the year 1 report.

2.6.1. Methods

Seeds of sage were sown on Levington M2 substrate in 1 inch cells on the 13th May 2014. Trays were covered with clear plastic until the seeds germinated. Plugs were potted up into six-packs at the appropriate stage. To prevent any influence of shading, only 2 plants (diagonal opposites) were potted into each six pack. Plants were assessed for plant height, internode length, leaf size, and leaf shape, as well as fresh biomass of leaves and stems.

Light treatments

Sage plants were grown under nine light treatments. Four examined the influence of red: blue ratio (15% 33% 66%, and 100% blue – Appendix: Light treatments Table 1). For the 100% blue treatment, the total PAR was lower (145 µmol m^{-2} s^{-1}) than for the other treatments (200 µmol m^{-2} s^{-1}) due the limitations of the LED installation. Four examined the influence of far-red light photon irradiances (0, 15, 30, and 48 µmol m^{-2} s^{-1} - Appendix: Light treatments Table 2) For the far-red treatments the background light was a red: blue light mixture containing 11% blue light. One treatment was a white light treatment containing 8% blue, 20% green, and 72% red light.

2.6.2. Results

The sage grew slowly but produced healthy plant material. The size and morphology of the plants was influenced by the light treatments. The sage plants grown under 11% blue light had the greatest fresh mass and were the tallest plants. Mass and height was observed to decrease as the blue light percentage increased (Figure 2.36). The number of side branches produced by the sage plants also decreased as the blue percentage of light increased. Light quality was observed to influence plant partitioning and the leaf: stem mass ratio was found to increase with blue percentage. The sage leaves were flat (no leaf curling was observed) and held at a similar angle in all light treatments. Leaf size was found to decrease as blue percentage increased.

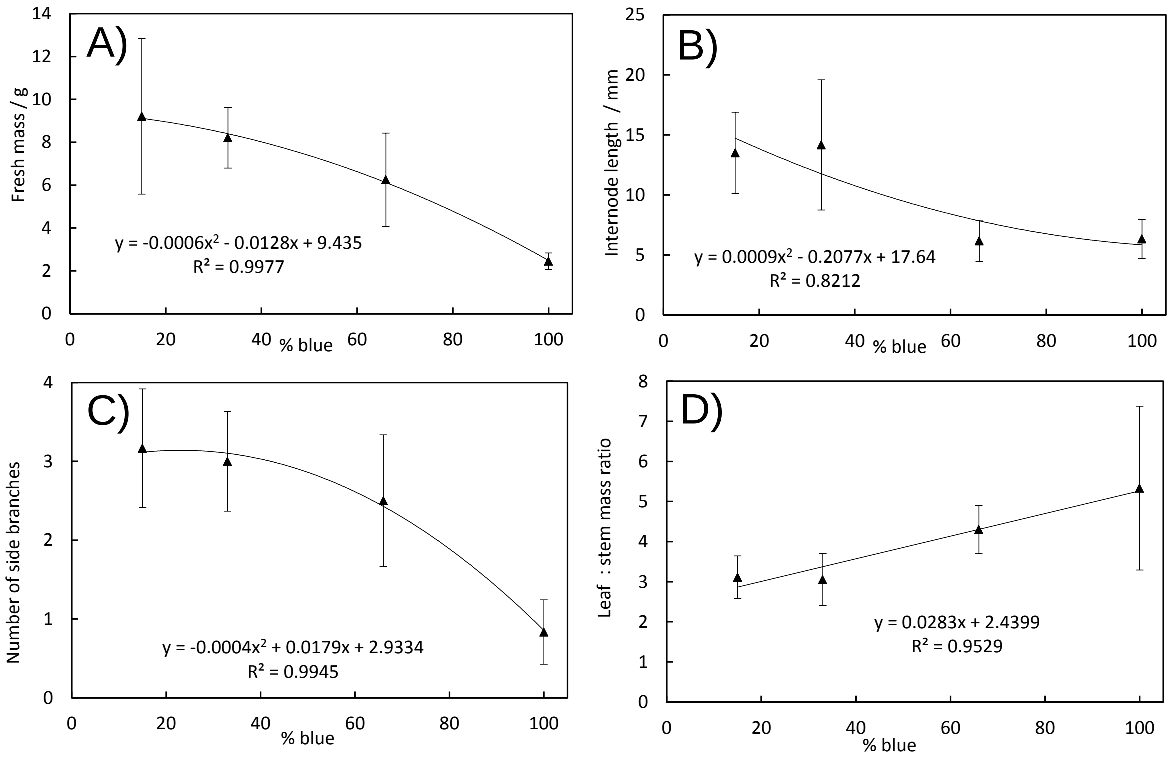


Figure 2.36. Sage fresh mass and morphological parameters at the final harvest on 14th July 2014. The influence of blue percentage on **A)** plant mass, **B)** internode length, **C)** number of side branches formed on the plants, and **D)** leaf to stem mass ratio. All error bars indicate standard deviations.

To examine the physiological state of the sage plants, photosynthetic rate was measured in plants grown under five light treatments: four red: blue light treatments (15, 33, 66, and 100% blue) and one control red: white treatment (8% blue). The photosynthetic light response curves and other calculated photosynthetic parameters are shown in Figure 2.37. The maximum photosynthetic rate (P_{max}) was found to correlate with the intensity of the growth light environment. The slope of the light-limited region of the photosynthetic responses curve (alpha) was found to decrease as blue percentage increased. As with the basil plants, sage respiration rates were found to decrease (become less negative) with increasing blue percentage. The P_{max} and alpha parameters of the leaves grown under the red: white light (data points for 8% blue light) were lower than may have been expected based on the correlation observed with blue percentage for the four other values. This may indicate that the low blue percentage in this light treatment is insufficient to fully activate the photosynthetic machinery in this species.

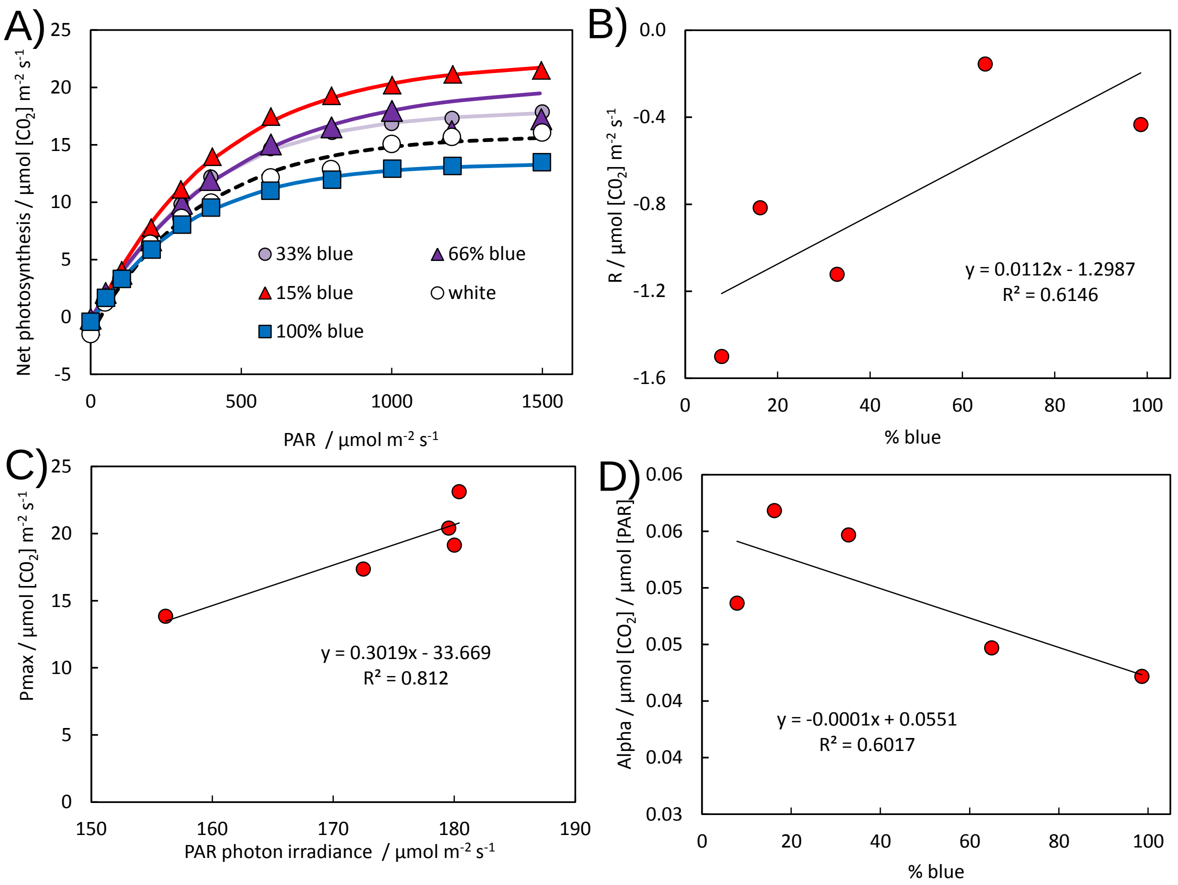


Figure 2.37. A) Net photosynthetic light response curves of sage plants grown under five different light treatments. **B)** The influence of blue percentage (% blue) on the measured respiration rate in darkness. **C)** The influence of PAR photon irradiance in the growth environment on maximum gross photosynthetic rate (P_{max}). **D)** The influence of blue percentage (% blue) on the slope of the light-limited photosynthesis (Alpha).

The effects of far-red light on sage

The sage plants were found to have a weak response to the addition of far-red light. The plants grown under no far-red were the shortest plants throughout the experiment. While the presence of far-red light resulted in an increase in plant height, the growth stimulus was not observed to be dose dependent: *i.e.*, increasing the far-red intensity from 15 to 48 µmol m^{-2} s^{-1} resulted in no additional growth, indicating that the far-red effect was saturated below 15 µmol m^{-2} s^{-1} in these experimental conditions. This limited response to far-red light may be a result of the experimental design. As the plants were arranged to reduce shading between plants the effects of far-red may have been attenuated.

2.6.3. Key Findings - Sage

- Sage morphology can be manipulated by light quality, though there is an interaction with growth rate. More compact plants had slower growth rates.

- Sage biomass and number of side shoots decreased as blue percentage increased, probably due to a lower overall biomass accumulation.

- Maximum potential photosynthetic rates were regulated by the total light intensity not blue light percentage.

2.7. CORIANDER

2.7.1. Methods

Several coriander seed were sown on moist peat based substrate (M2, Levington) in six packs and covered with plastic to keep the seed moist during germination. Six packs were placed under the different light treatments in the LED4CROPS facility on the 19th October 2016. Plants were irrigated using the automated irrigation system. Plants were photographed and harvested on the 6th December (48 days after sowing).

Light treatments.

Fifteen treatments were examined. Twelve treatments comprising of four red: blue ratios (6% blue, 15% blue, 30% blue, and 60% blue), each with three different far-red intensities (0, 20, and 40 or 50 µmol m^{-2} s^{-1}) were used. The PAR photon irradiance of these treatments was set as close to 200 µmol m^{-2} s^{-1} as possible (see Appendix: Light treatments, Table 6 for full details). For these treatments, light was provided by Philips GreenPower research modules. Three treatments with differing PAR intensities (105, 194, and 378 µmol m^{-2} s^{-1} - Appendix: Light treatments, Table 3) were also included. For these treatments light was provided by Philips GreenPower production modules (11% blue light).

2.7.2. Results

Combined red, blue, and far-red treatments

The coriander plants remained healthy and disease free during the trial. As with other species the most obvious response was the stretching that occurred in the presence of far-red light (Figure 2.38). Total plant height was found to decrease slightly as the blue light percentage increased (Figure 2.38A) but large increases in height were observed as the far-red intensity increased (Figure 2.38B). The compound leaves of coriander consist of several parts: petioles, petiolules, rachis, and leaflets. We measured the responses of each of these leaf sections to the different light qualities. The length and width of the leaflets (Figure 2.38C) was found to change in response to blue percentage with the smallest leaflet being observed under light treatments with greater than 30% blue light and the largest leaflets occurring under the 5% blue light treatment. Far-red intensity did not influence leaf blade size but did influence the leaf stems (petiole, petiolule, rachis - Figure 2.38D). The lengths of the three leaf stem sections were found to increase linearly with increasing far-red photon irradiance. The greatest far-red-induced extension was observed in the petiole as this was the longest leaf section; however, proportional increases were similar for the three leaf sections.

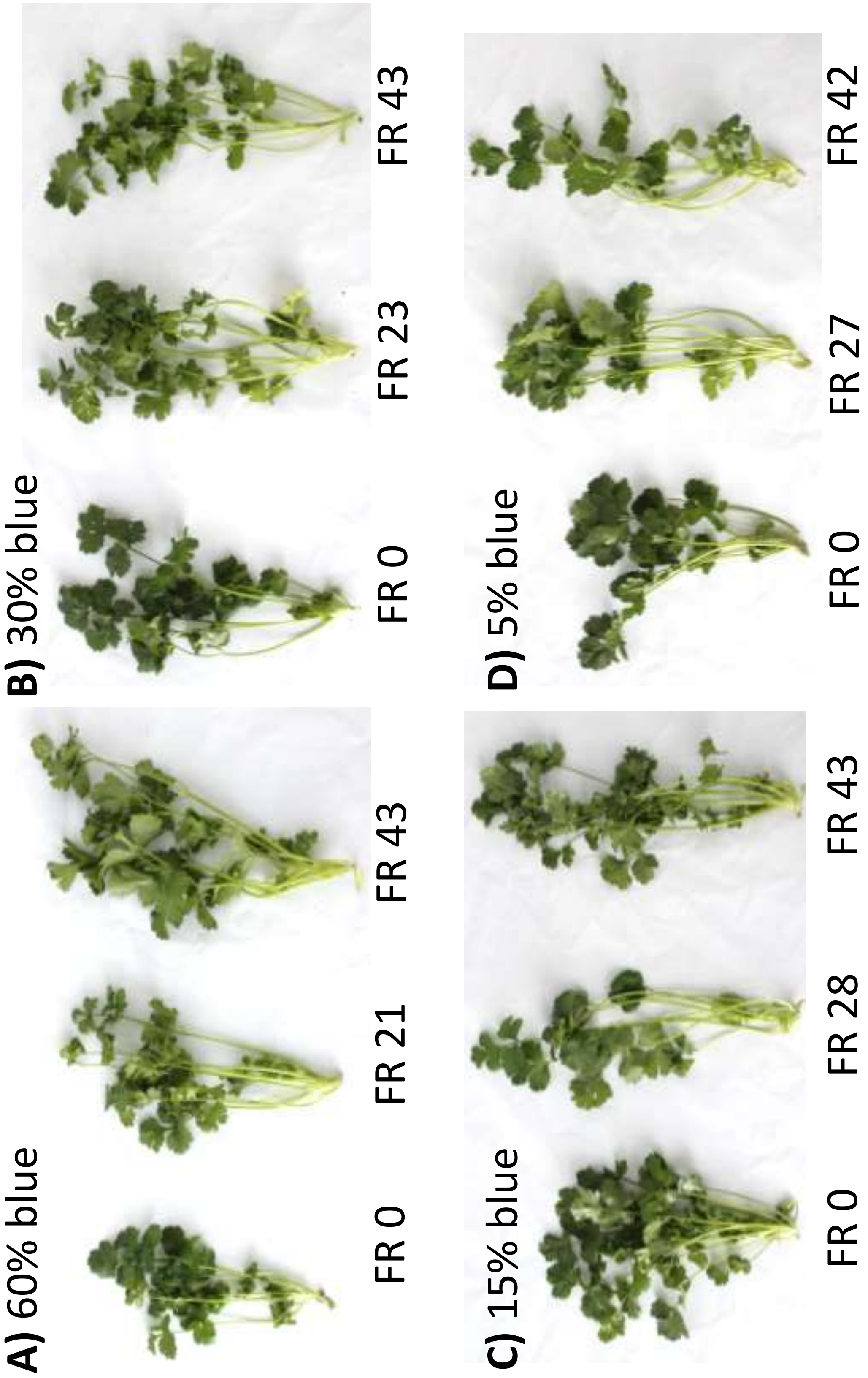


Figure 2.38. Images of coriander plants grown under twelve light treatments which differed in blue percentage (values provided at top left of each image) and far-red photon irradiance (values provided below each plant).

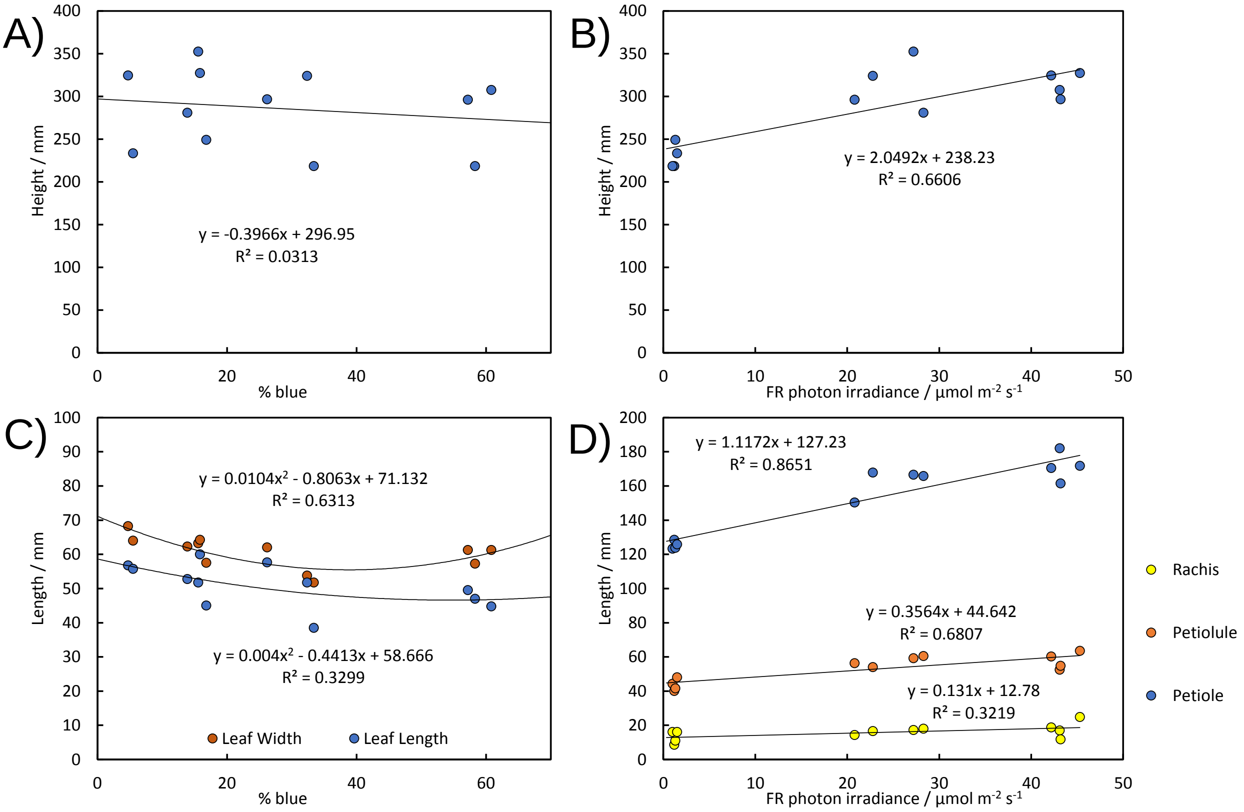


Figure 2.39. The influence of light quality on coriander morphology. The influence of **A)** blue percentage and **B)** far-red photon irradiance on plant height. **C)** The influence of blue light percentage on the length and width of leaflets. **D)** The influence of far-red photo irradiance on the lengths of different sections of the compound leaves.

The influence of photon irradiance on coriander morphology

Coriander plants were grown under three different photon irradiances. Plant quality was observed to increase as the intensity increased with plants producing progressively more leaves with more robust stems and leaves (Figure 2.40). Fresh mass and leaf number were

Figure 2.40. Images of coriander plants grown under three different PAR photon irradiance (values provided below each plant) for 48 days. Note only one plant from each pot is shown.

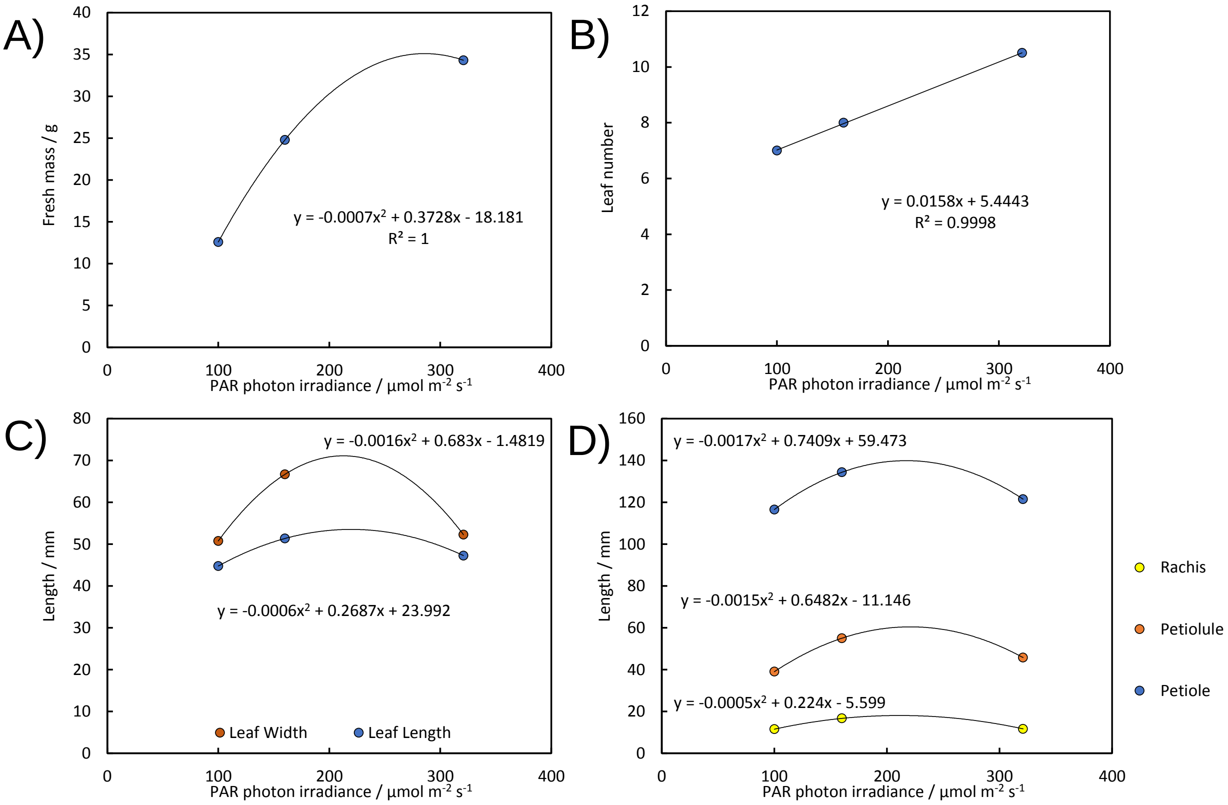


Figure 2.41. The relationships between coriander **A)** fresh mass, **B)** leaf number, **C)** leaflet width and length, and **D)** lengths of different sections of compound leaves with photon irradiance when the light spectrum contains 11% blue light.

both observed to increase with photon irradiance (Figure 2.41 A&B). All the measured leaf size parameters (Figure 2.42 C&D) were observed to increase between 100 and 191 µmol m^{-2} s^{-1} but to decrease as the irradiance further increased to 320 µmol m^{-2} s^{-1}.

2.7.3. Key Findings - Coriander

- Coriander morphology can be manipulated by altering spectral composition but also by adjusting photon irradiance.

- Different parts of the compound leaves responded to different aspects of light quality. Blue percentage influenced leaflet length and width, while far-red photon irradiance influenced the length of petioles, petiolules, and rachis.

- Overall far-red light was found to have a negative influence on plant quality.

- The greatest light intensities produced plants with the best quality and the greatest mass.

2.8. PARSLEY

2.8.1. Methods

Several flat-leaved parsley seed were sown on moist peat based substrate (M2, Levington) in six packs and covered with plastic to keep the seed moist during germination. Six packs were placed under the different light treatments in the LED4CROPS facility on the 19th October 2016. Plants were irrigated using the automated irrigation system. Plants were photographed and harvested on the 6th December (48 days after sowing).

Light treatments.

Fifteen treatments were examined. Twelve treatments comprising of four red: blue ratios (6% blue, 15% blue, 30% blue, and 60% blue) each with three different far-red intensities (0, 20, and 40 or 50 µmol m^{-2} s^{-1}) were used. The PAR photon irradiance of these treatments was set as close to 200 µmol m^{-2} s^{-1} as possible (see Appendix: Light treatments, Table 6 for full details). For these treatments light was provided by Philips GreenPower research modules. Three treatments with differing PAR intensities (105, 194 and 378 µmol m^{-2} s^{-1} – Appendix: Light treatments, Table 3) were also included. For these treatments light was provided by Philips GreenPower production modules (11% blue light).

2.8.2. Results

Combined red, blue, and far-red treatments

The parsley plants were grown under twelve light treatments each with the same total photon irradiance (~200 µmol m^{-2} s^{-1}) but with four different combinations of red and blue light and three different far-red photon irradiances. The plants were healthy and pest and disease free during this trial (Figure 2.42). The plant appearance differed between the treatments with far-red light causing stretching of the compound leaves. Plant height was observed to decrease linearly as blue percentage increased from 5% to 60% and to increase linearly as far-red intensity increased (Figure 2.43 A&B). Leaflet length was found to decrease slightly as blue percentage increased but leaflet width was unaffected (Figure 2.43C). Increasing the far-red light intensity was found to cause a large increase in the length of the petiole and a slight increase in petiolule length, but had no influence on rachis length. Net assimilation, calculated as plant dry mass divided by leaf area, was observed to decrease linearly with increasing blue percentage (Figure 2.43E) and to increase linearly with increasing far-red intensity (Figure 2.43F).

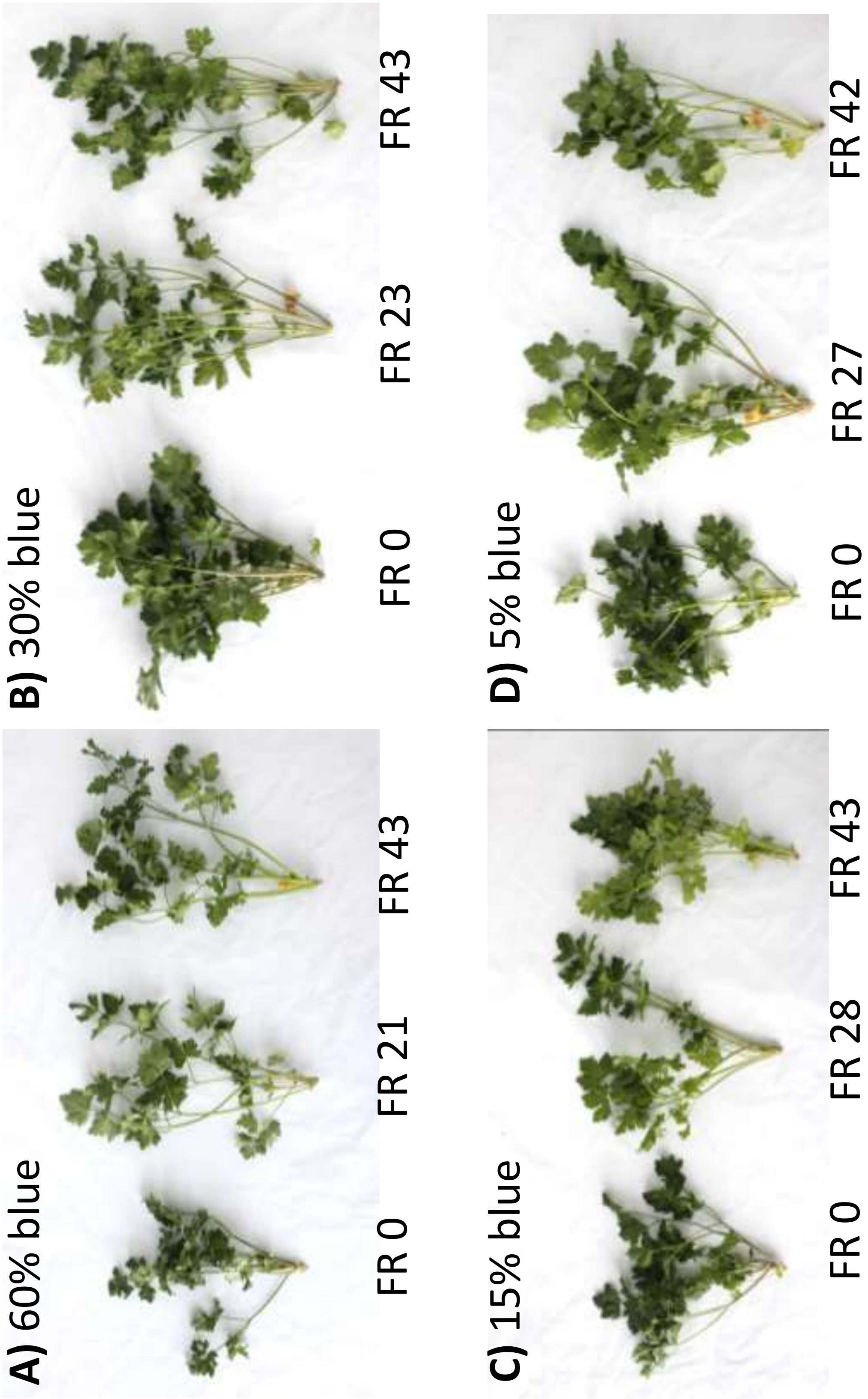


Figure 2.42. Images of parsley plants grown under the twelve light treatments which differed in blue percentage (values provided at top left of each image) and far-red photon irradiance (values provided below each plant, units = µmol m^{-2} s^{-1}).

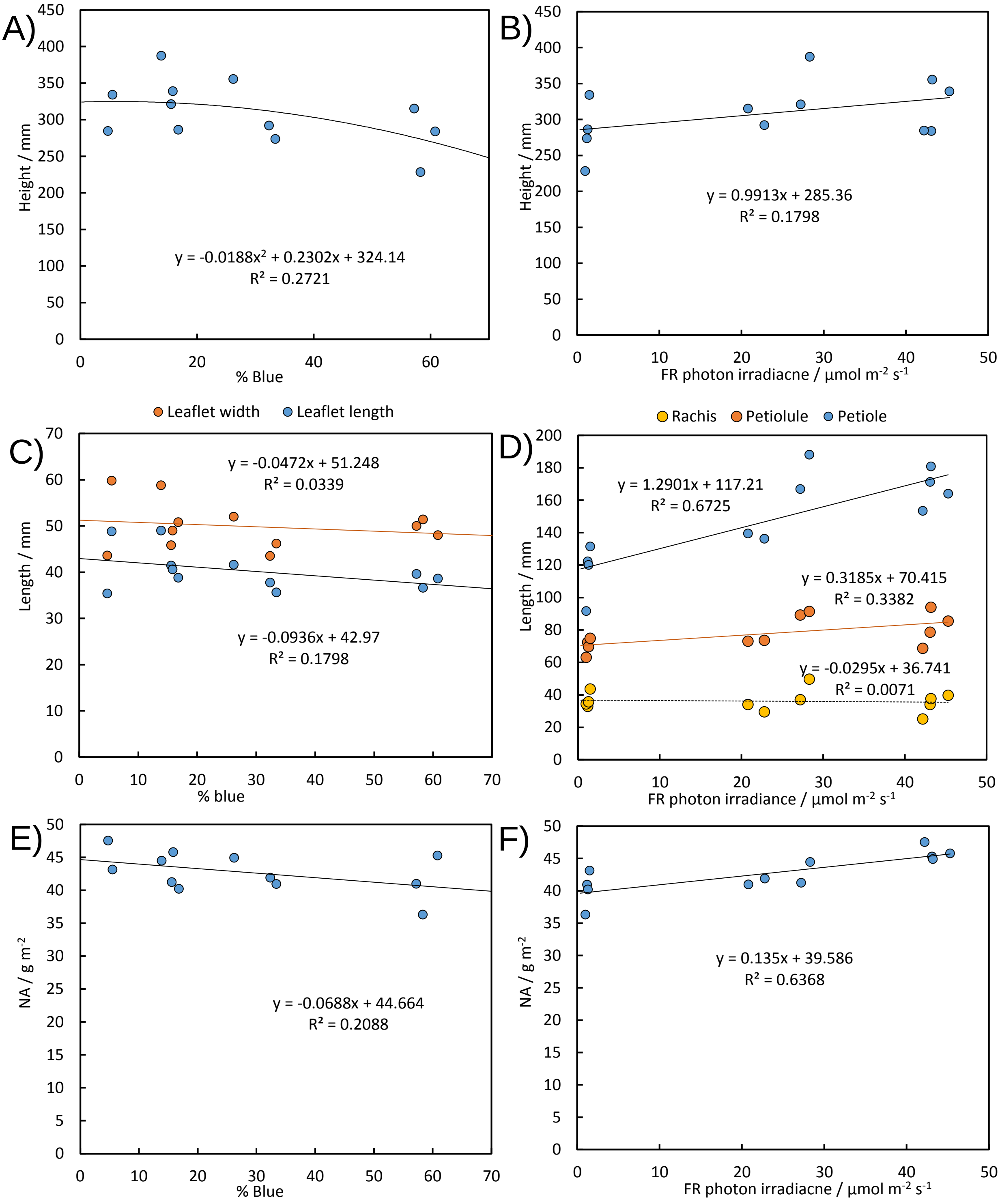


Figure 2.43. The influence of blue percentage (Left side) and far-red photon irradiance (right side) on **A&B)** plant height, **C)** length and width of the leaf blade, **D)** the length of three different section of the compound leaves (petiole, petiolule and rachis), and **E&F)** net assimilation (NA) of parsley plants.

The influence of photon irradiance on parsley morphology

Parsley plants were grown under three different photon irradiances to assess plant responses to light intensity. The plants differed considerably in appearance (Figure 2.44) with plants in the lowest light having a spindly appearance and those from the greatest intensity light having a leafy robust appearance.

Figure 2.44. Images of parsley plants grown under three different PAR photon irradiances, values provided below each plant in units of µmol m^{-2} s^{-1}.

While the appearance of the plants differed, height was similar across the three light intensities (Figure 2.45A). The lengths of the three sections of the stem (petiole, petiolue, and rachis) were found to only change a small amount as the light intensity changed (Figure 2.45B). Net assimilation increased linearly as the light intensity increased. Light use efficiency decreased as the light intensity increased.

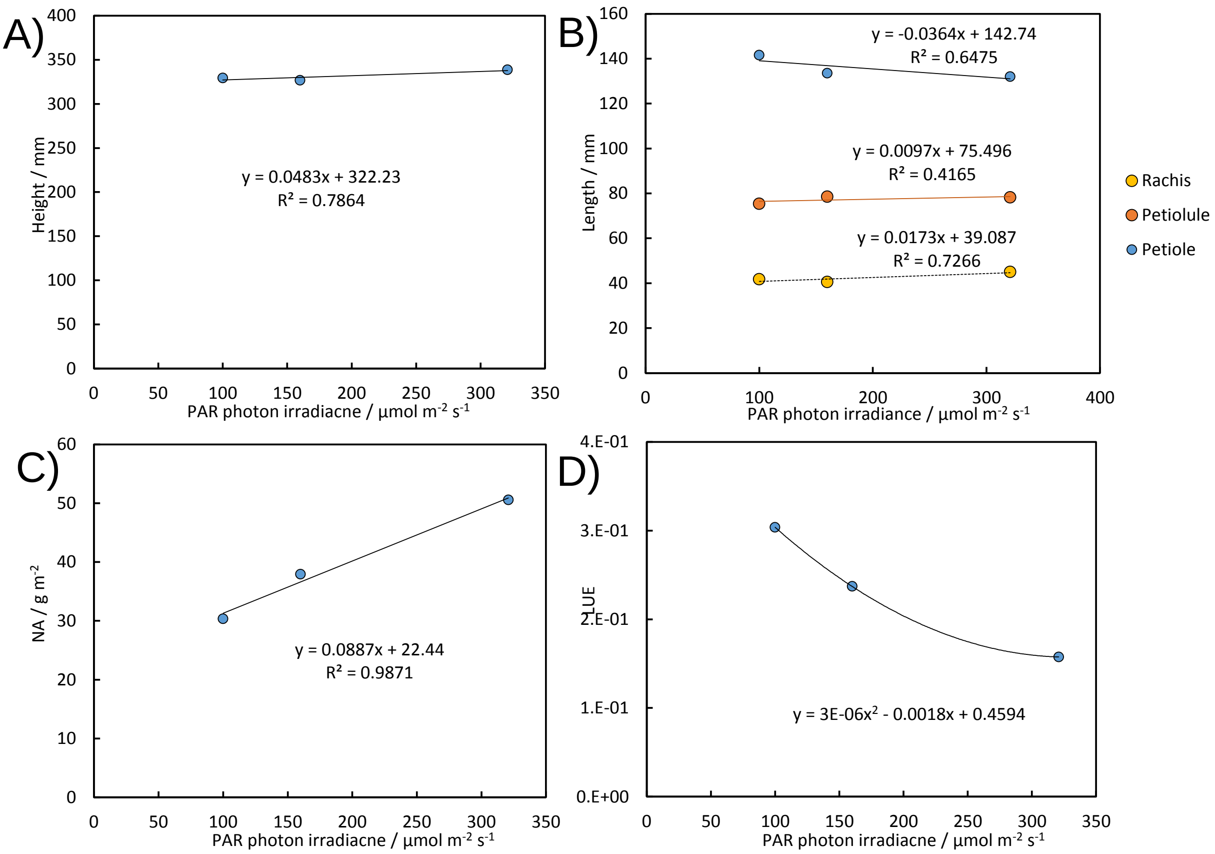


Figure 2.45. The influence of photon irradiance (of red: blue light spectrum with 11% blue light) on the **A)** plant height, **B)** length of three sections of the compound leaf (petiole, petiolule and rachis), **C)** the net assimilation, and **D)** the light use efficiency (LUE) of parsley.

2.8.3. Key findings - Parsley

- Parsley leaves are less sensitive to changes in light quality than some of the other species examined but spectral manipulation still holds the potential for controlling plant morphology.

- Increasing the light intensity speeds up parsley growth rates and improves plant quality but, unlike in other species, does not reduce plant height.

- Far-red light causes stretching of the petiole but not the rachis of the compound leaf.

- Growth rate is predominately controlled by leaf area.

2.9. DISCUSSION OF PROTECTED EDIBLES WORK

Effects of light quality on morphology and biomass

These trials have shown that LED lighting systems can be used to produce a wide range of edible crops to a high standard and that the colour of the light spectrum can be used to manipulate the morphology of those plants. Our understanding of crop responses to different LED light spectra has greatly advanced and this information will aid the implementation of LED lighting systems in commercial settings as well as the development of future crop lighting systems. Furthermore, this information can be used to help growers understand the crop responses in existing installations with the aim of optimising crop production.

Due to the morphological and evolutionary diversity between the species examined the size of the measured phenotypes (internode lengths and leaf sizes) varied considerably. However, when the light responses of the different plants were normalised to remove the large differences in magnitude (Figure 2.46), the responses of the different species to light quality were found to be highly similar in both shape and relative magnitude of response. Increasing the proportion of blue light in the spectrum caused plants to become more compact (smaller leaves and shorter internodes) with the most compact plants occurring under light treatments with about 60% blue light. These changes in compactness were non-linear in shape. These results are consistent with other work examining plant light responses (Davis & Burns 2016). Plants grown under 100% blue light were less compact: this was believed to be due to changes in the phytochrome (red: far-red) signalling pathway. The calculated phytochrome photostationary state (PSS) for a 100% blue light treatment is 0.52: to achieve a similar PSS value for a red: blue treatment containing 30% blue light would require a far-red photon irradiance of 35 µmol m^{-2} s^{-1}. The addition of far-red light to the light spectrum caused plants to become less compact (longer leaves and internodes) and these responses were found to vary linearly with increasing far-red photon irradiance. The far-red responses observed in these trials are consistent with similar studies examining crop responses to light quality (Runkle and Heins 2001). Our experiments examining combined red, blue, and far-red light were also able to access the relative impact of the different photoreceptor pathways (blue responses versus red: far-red responses) on plant qualities. In most of the crops examined, the far-red effects were dominant to those of the blue light responses. This means that increasing the blue light proportion may be insufficient to reduce the effects of far-red light. However, careful selection of light treatments containing red, blue, and far-red light can be used to generate crops with specific qualities as each light combination produced plants with unique qualities. The model developed to explain the lettuce leaf size will also aid our development of optimised light treatments. Further development of this model and its application to other species and morphologies will have many potential applications. This improved understanding of the relative impacts of different regions of the spectrum will be useful in understanding how LED light spectra influence plant responses in glasshouses where sunlight is expect to have a dominant influence.

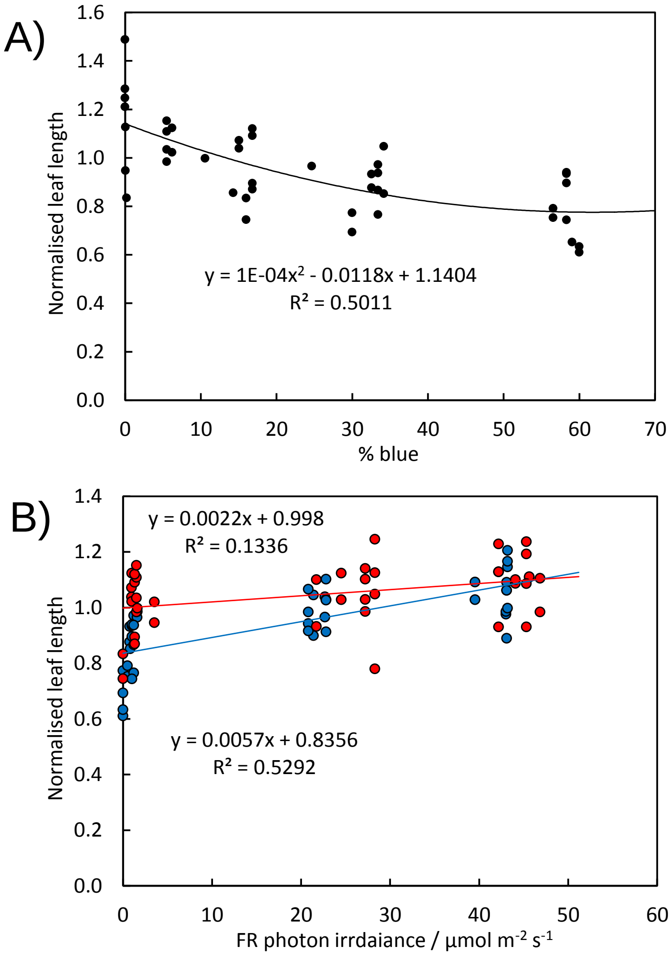


Figure 2.46. The influence of **A)** blue percentage and **B)** far-red photon irradiance (red points and line indicate data from light treatments with 0-20% blue light and blue points and line indicate data from light treatments with 20-90% blue light) on the normalised leaf length of tomato, cucumber, parsley, coriander, cucumber, lettuce, and pepper. Data were normalised by dividing the measured value by the mean measured value of the data for each species.

While morphology of crops is important, many edible crops are sold based on mass. Achieving marketable mass rapidly, using the minimum inputs, is important for achieving economic viability. In these trials the greatest fresh biomass yields were achieved in light treatments containing between 5 and 20% blue light (Figure 2.47). LED systems with low blue percentages also have the highest lamp efficacy so the greatest yield can be achieved for the lowest energy consumption. Plant yields decreased under 100% red light, probably due to multiple reasons including reduced stomatal opening and reduced access to CO2; reduced effective leaf area due to leaf curling (blue light is involved in leaf flattening, de Carbonnel *et al*., 2010), leaf angle (resulting in poor light capture), and potentially reduced photosynthetic performance (Trouwborst *et al*., 2010). As the blue light percentage increased from 5-20% the yields were observed to decrease and plants grown under 100% blue had similar mass to those from the 100% red light treatments. Addition of far-red light was found to result in an increase in fresh mass. It would be appealing to describe the differences in yield achieved under the different light treatments purely in terms of the different photosynthetic rates expected under the different light qualities based on the findings of McCree (1971) and Emerson (1957); indeed, many LED manufacturers discuss their lamp spectra in these terms. With this approach, the decrease in yields encountered

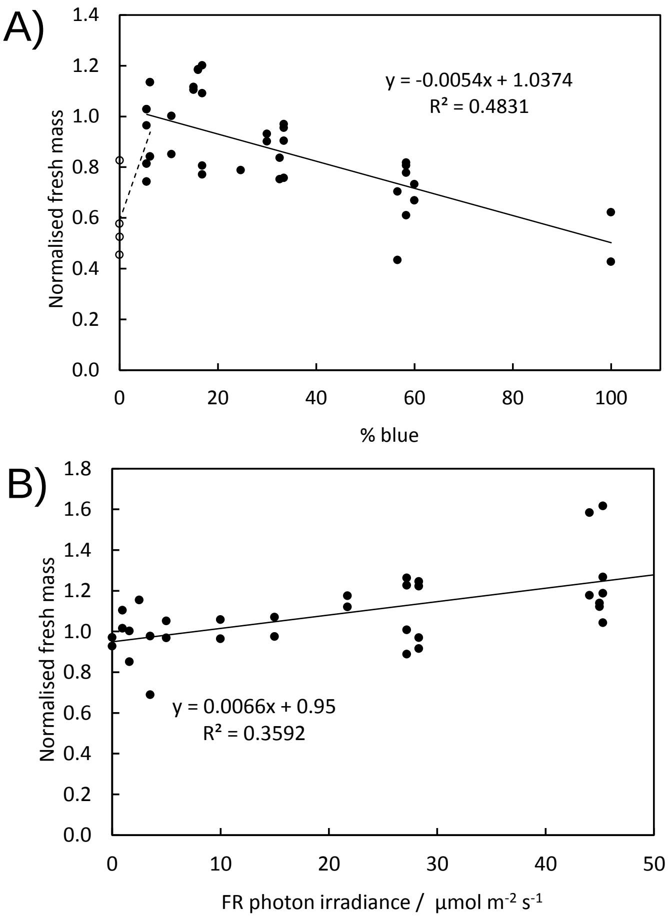


Figure 2.47. The influence of **A)** blue percentage (data for treatments with no far-red are shown) and **B)** far-red photon irradiance (only data with blue percentages between 10 and 16% are shown) on the normalised fresh mass of tomato, cucumber, parsley, coriander, cucumber, lettuce, and pepper. Data were normalised by dividing the measured value by the mean value of the data presented.

as the blue percentage was increased could be described based on the lower quantum yield of photosynthesis for blue compared to red light. The increased yields associated with adding far-red could be described based on an increase in photosynthetic rate associated with the Emerson enhancement effect (i.e. photosynthetic rates are greatest when both photosystems are equally activated). However, our data do not support this description of the data. Instead the main factor driving differences in biomass was the leaf area of the crops, which was influenced by light quality (Figure 2.48). The correlation between leaf area and growth rates has previously been demonstrated in several species (Porter & Remekes1990,Bullock Nielson & Nyquist 1988, Kalssen et al 2003, Goins et al 2001).

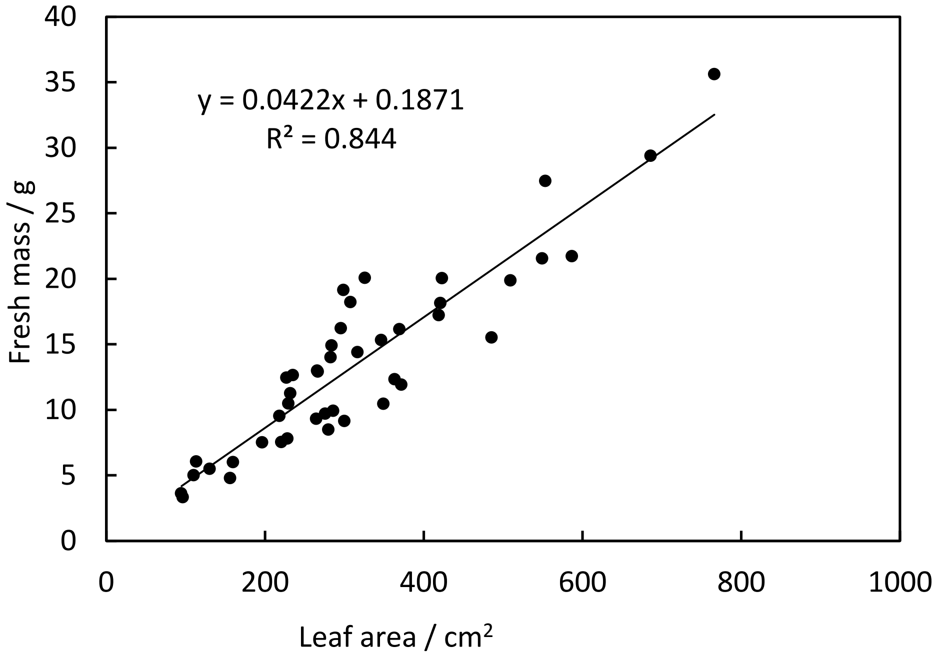


Figure 2.48. The relationship between fresh mass and leaf area. The data set includes values for tomato, cucumber, basil and sweet pepper.

With the effects of leaf area removed from the data via the calculation of net assimilation rate (NA) or light use efficiency (LUE = dry mass ÷ leaf area ÷ PAR photon irradiance), it is possible to examine the data for secondary effects of light quality in plant performance. For parsley, NA and LUE values were found to decrease as the blue percentage increased and to increase as far-red photon irradiance increased. This suggests that the light quality was affecting the photosynthetic performance of this species as described by McCree (1971) and Emerson (1957) but we have no photosynthetic measurements to confirm this. For all other species examined, far-red was observed to have little effect on NA and LUE values. This means that the increases in fresh biomass associated with the far-red treatments in these species results from a greater water content and not an increase in photosynthetic carbon gain. For tomato, LUE was affected by neither blue percentage nor far-red photon irradiance. For cucumber and pepper, LUE was observed to increase with blue percentage (which was the opposite of the expectation based on McCree 1971) but was unresponsive to far-red light. These findings are consistent with those of Snowden, Cope & Bugbee (2016), where increasing blue light percentages resulted in increases in NA for pepper and cucumber but not tomato. Their conclusion, based on seven species, was that as blue percentage increased the lower leaf expansion and growth rate resulted in reduced self-shading within the canopy. With reduced self-shading a greater proportion of the leaf area is exposed to the maximum light intensity, which results in greater photosynthesis and therefore net assimilation rate. While self-shading is no doubt having some influence on the results, and differences in canopy structure between species could cause different responses to light quality, this explanation is inadequate to describe all our experimental data. If differences in self-shading resulting from different canopy structure were the major cause of the changes in NA and LUE then we would expect to see an influence of far-red light. In our experiments, increasing far-red intensity resulted in greater leaf area and canopy volume, which would be expected to result in an increase in self-shading and therefore decreases in NA and LUE as far-red intensity was increased. Unless the increased shading caused by having larger leaves is equally counteracted by a reduction in shading caused by increased internode and petiole lengths, then some factor/s other than self-shading must also be affecting plant growth. A number of alternative explanations are available that are associated with long-term acclimation to the different light environments. Neither this study nor that of Snowden, Cope & Bugbee (2016) examined the amount of biomass invested in roots. Differences in shoot and root partitioning between species in response to light quality could result in some of the observed differences. Also in this study, we observed a higher maximum potential photosynthetic rate in basil leaves that had been grown under light treatments containing higher proportions of blue light. In contrast, sage plants grown under the same conditions showed no increase in photosynthetic potential in response to blue percentage. These results suggest that A) long term acclimation to a light environments can influence photosynthetic performance and B) that photosynthetic responses differ between species. It is possible that these photosynthetic responses are contributing to the differences in plant performance but it is equally probable that multiple factors are interacting and differentially affect the performance of each species. More research will be required if we are to fully understand these responses.

Light Spectral and leaf pigmentation

In addition to the effects on plant morphology and growth rate, light quality also impacts pigments and other secondary metabolites. Red, far-red and blue light have been implicated in the regulation of chlorophyll synthesis (Tripathy and Brown 1995*;* Miyashita et al. 1997;Tanaka et al. 1998; Huq et al. 2004; Kim et al. 2004a;Moon et al. 2006; Li et al. 2010). Our results also find blue and red/red-far light to have important roles in regulating chlorophyll contents. Plants grown under 60% blue light were visibly darker green than those grown under lower percentages and 100% blue light. Far-red light was also observed to reduce the greenness of leaves. Chlorophyll content meter (CCM) readings varied greatly between species but once the data were normalised to the mean value for each species the effects of light quality were highly consistent between species (Figure 2.49). Variations in chlorophyll contents are expected to influence photosynthetic rate and plant growth, so may have contributed to some of the effects on LUE discussed above. While

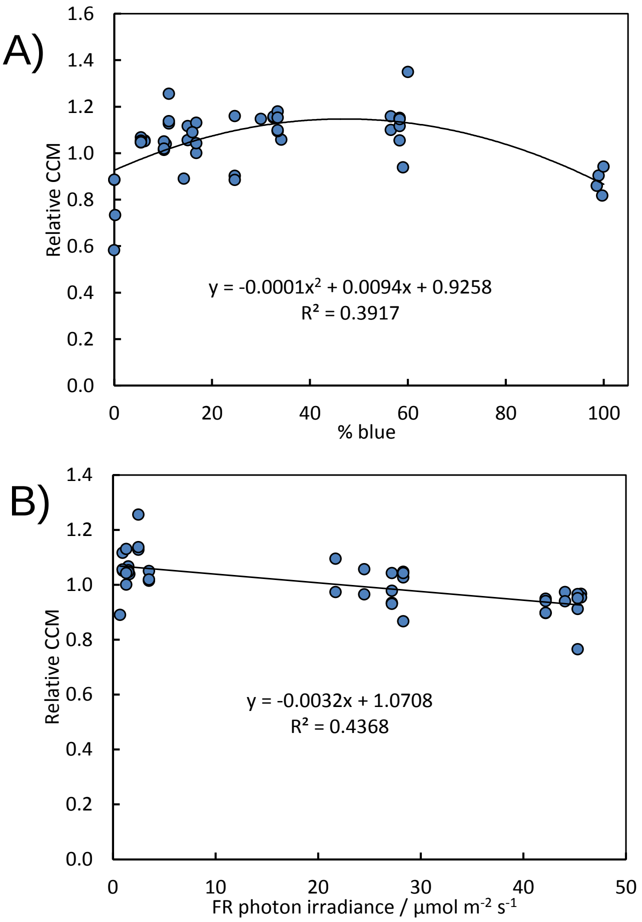


Figure 2.49. The relationships between normalised chlorophyll content (measured using a hand held AtLeaf chlorophyll content meter) with **A)** blue light percentage and **B)** far-red photon irradiance. Data from tomato, cucumber, sweet pepper, coriander, parsley, basil, and lettuce are presented.

other pigments such as carotenoids were not examined in this work, their concentrations are expected to correlate with chlorophyll concentration. Other secondary metabolites such as those associated with aroma and flavour in herbs are reported to differ based on light environment (Amaki et al. 2011). We did not measure the concentrations of these compounds, but we observed qualitative changes in the aroma and flavour of basil plants grown under different light treatments using simple sensory assessments. In particular, far-red light was observed to reduce the strength of the basil aroma. Further experiments will be required to ascertain quantitative changes in aromatic compounds and how these compounds effect flavour and aroma.

Quantity of light

Increasing the light intensity increases biomass and plant quality but the extra light required comes at a cost. The increased costs are associated with a requirement for more lamps to be installed and a greater running cost. If the light intensity is doubled, the installation and running cost are also expected to double, assuming the same types of lamps are used. However, biomass and growth rate are not observed to increase at the same rate. This is because plant light use efficiency decreases as the light intensity is increased. As the crop yields do not increase proportionally with costs some other aspect must increase sales values to gain a return from the higher investment. Higher light intensities can result in shorter crop production cycles resulting in higher output per area. Adjusting the light intensity may allow a smaller facility to achieve sufficient yields. However, it is perhaps the increase in plant quality that can achieved by increasing the light intensity that provides the greatest potential for better sales. At intensities of near 200 µmol m^{-2} s^{-1} (DLI of 11.5 mol day^{-1}) good quality plants are produced but they have characteristics similar to autumn and spring grown crops. At intensities of 380 µmol m^{-2} s^{-1} (DLI of 21.9 mol day^{-1}) the plants have similar or even better quality to those grown in summer conditions. The optimal light intensity for any specific crop, from an economic perspective, will be influenced by the qualities desired from a specific crop and the energy inputs required to achieve the perfect plants. Many factors beyond the scope of this report are also expected to influence economics. However, these data will provide a good starting point for assessing potential crop yield/quality and it is expected that different crops and markets will benefit from different light environments. It should also be kept in mind that LED efficacies are increasing rapidly and this will change the economics of ROI periods.

It is perhaps no surprise that increasing the light intensity resulted in greater biomass with a more robust structure for all the species examined. Where the results become interesting is when we consider how the increasing light intensities affect plant morphologies. Much of the data in this work is reporting plant responses in terms of blue percentage and morphologies such as internode lengths can be accurately predicted based on this information, but only when the light intensity is similar between the different treatments. When the light intensity was increased but blue percentage kept at constant, internode lengths and leaf sizes were observed to decrease. This is because as the intensity increased the total amount of blue and red light increased and this causes the progressive transition of photoreceptors from a relaxed, shade condition to an active sun condition. This results in an increasing restriction of organ expansion and resources are invested in thicker more robust tissues rather than simply increasing in size. The model we developed to predict plant light responses uses absolute light intensities rather than relative proportions of each colour of light. This matches our understanding of the biology of photoreceptors and allows the model to accurately predict leaf sizes under different light intensities and spectra. With further development this model could be applicable to any crop and could eventually predict the optimal light environment for crops.