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Integrated control in new light – final project report

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Part 1.1: Summary/Abstract

This 3-year project studied the potential to use light quality as a factor to improve the establishment of biocontrol agents (BCA) in greenhouse cropping systems. Under laboratory conditions, we identified organic carbon compounds that promote initial phases of BCA establishment (dispersal, settling) for 3 commercial BCAs (*Bacillus amyloliquefaciens*, BA; *Pseudomonas chlororaphis*, PC; *Streptomyces griseoviridis*, SG) and light quality combinations that promote BCA establishment in the presence of those C-sources. Light quality (460, 530, 660 nm, white light) strongly affected the fate of BCAs introduced to tomato. Interactivities are crop, BCA and light quality dependent. Given the severe light intensity decrease and spectral distribution distortion in the crop stand we at present recommend white light when introducing any of the three BCAs and blue (460 nm) and green (530 nm) for SG and PC in tomato. Successful BCA introduction demands optimized light distribution through the canopy.

Part 1.2: Main report (max. 10 pages)

Introduction

Microbial biocontrol agents (BCA) often show fabulous results under laboratory conditions, but are not always sufficiently consistent under commercial conditions. This is a considerable concern particularly under greenhouse conditions where very high values are at stake and consumer's tolerance for demolish is low. Grey mold and mildew are commonly causing disease on important greenhouse crops, both edible and ornamental ones. They can be controlled to a certain extent by greenhouse climate control. Options for chemical control are limited due to legal restrictions in crops with continuous harvest, such as tomato and cucumber, and due to rapid development of resistance in the pathogens. Improved efficiency of microbial biocontrol agents would therefore make a big difference for Swedish greenhouse horticulture.

This project dwelled into the possibilities to promote the efficacy of three commercial BCAs in greenhouse grown tomato through modification of the light and nutritional environment. To be a successful biocontrol agent, the BCA must be applied correctly, but they also must establish well in the plant canopy. For successful establishment, three steps are critical:

i. spreading on the target plant part
ii. settlement on the target plant part and
iii. expression of the antagonistic mode of action towards the target pathogen.

Our recent laboratory studies demonstrate that critical traits for the establishment of some biocontrol agents are dependent on light quality and nutritional factors (Alsanius et al., 2021, Gharaie et al., 2017, Karlsson et al., 2022). Light quality by itself affects some important leaf pathogens occurring in greenhouse crops, such mildew and grey mold, but also non-pathogenic and beneficial microorganisms that naturally live on leaves. Usually, greenhouse lighting is top placed, but an efficient establishment of BCAs in the entire canopy might require a shift to intercrop lighting strategies.

Background

Plants use wavelengths from approx. 400 to 700 nm in wavelength (visible light) as a source of energy for their primary (photosynthesis) and secondary (biomass formation, growth, development, secondary metabolite formation) metabolism. However, different wavelengths within the visible light spectrum have different effects on plant reactions and morphology. Also, light within the UV-spectrum (100-400 nm), far red light (700-800 nm) and infrared light (800-1000 nm) affect plants. Factors such as plant elongation, leaf size, leaf thickness, thickness of cuticle, and leaf pigmentation are directly affected by the spectral composition of the light that plants are exposed to, with blue, red, far red and UV-light generally recognized as the most important wavelengths in this respect, however in recent years, also the effects of green and yellow wavelengths has caught attention from academia. Within the present project, plant-light interactions have been reviewed in detail by Alsanius et al. (2019).
Using LEDs, the spectral composition can be matched to the photosynthetic demands of the plant (Morrow, 2008). Apart from the physiology of the crop, the spectral distribution of light also influences insects and the microbiota in the crop stand (Alsanius et al., 2017, Vänninen et al., 2010). The detrimental effect of UV-B on microorganisms associated with leaves is well-established (Kadivar and Stapelton, 2003, Newsham et al., 1997). The few studies that involve other wavelengths illustrate plant pathogen behavior, especially considering downy and powdery mildew (Reuveni and Raviv, 1997, Suthaparan et al., 2012, Suthaparan et al., 2014, Suthaparan et al., 2010a, Suthaparan et al., 2010b) or grey mold (*Botrytis cinerea*) (Nicot et al., 2001, Nicot et al., 1996, Elad, 1997). Also non-pathogenic microbes and microorganisms with the biocontrol capacity respond to light, even if they are non-phototrophic, use light as a signal to do lifestyle or metabolic changes. Such lifestyle changes may involve factors of importance for a successful introduction of biological control agents in the phyllosphere (Table 1).

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Table 1. Processes, mechanisms and lifestyles for successful integration of microbial biocontrol agents in the phyllosphere

Process	Mechanism	Lifestyle
Biosurfactant formation	Decreasing surface tension → Enhanced microbial motility on the leaf surface	Planktonic
Biofilm formation	Establishment in single species or multiple species aggregates in patches at nutrient rich sites → protection towards environmental stress and predation	Sessile

Plants and crop stands are holobionts, consisting of a host (= the target crop) and all of its symbiontic (*indigenous*) microorganisms (Theis et al., 2016). The plant as a holobiont is divided into various compartments (*spheres*). The phyllosphere (canopy, leaves) is one of these. Within these spheres, the indigenous microbiota colonizes strategic sites enabling them to settle and to sustain their metabolism. Appendix 1 (Alsanius et al., manuscript) shows a map of interactivities between the indigenous microbiota and the plant canopy and on leaves. Both BCA and plant pathogens may be viewed as invaders (*alien organisms*, see appendix 1). In contrast to aerial plant pathogens, BCA are not well adapted to the environment they will are introduced to (greenhouse, canopy) and meant to act within. They carry the heritage of fermenter-assisted proliferation, where nutrients and environmental conditions are optimized to harvest maximum cell yield, and of storage, which is characterized by low metabolic activity. It is self-evident, that their ability to compete with well-established and well-adapted organisms for the same resources and sites is limited.

Needs addressed

Within the framework of this project we translate our findings on light induced establishment of biocontrol agents into optimized biocontrol activity in greenhouse settings. We explored the possibilities

- to tailor improved establishment and activity of biocontrol strains and simultaneously mitigate the proliferation of leaf pathogens in greenhouse crops through light quality regimes for three commercial BCAs, with documented control of two decisive foliar diseases, namely grey mold and powdery mildew: *Bacillus amyloliquefaciens* (BA), *Pseudomonas chlororaphis* (PC) and *Streptomyces griseoviridis* (SG).
- to determine the length of exposure and course of events for different light qualities for improved BCA establishment and efficiency,
- to identify the optimal position for the light ramps in the crop stand based on metabolic information of the three BCAs.

Materials and methods

In this project we concentrated on the active agent of three commercially available biocontrol products, namely *Bacillus amyloliquefaciens* (RhizoVital® 42fl), *Pseudomonas chlororaphis* (Cedemon) and *Streptomyces griseoviridis* (Mycostop). Pure culture strains of all three were propagated under laboratory conditions, transferred into cryo-cultures and stored at -80°C. The strains were marked using spontaneous antibiotic resistance (BA: streptomycin; PC and SG: ampicillin) to enable the organisms' reisolation in plant/greenhouse experiments. Target crops are displayed in Table 2. LED lamps (Heliospectra AB, Gothenburg, Sweden) were employed at an intensity of 50 µmol m^{-2} s^{-1} in laboratory and greenhouse experiments as displayed in Table 3.

Table 2. Target crops involved into the different parts of the project

Part	Target crop	Justification of choice
2	Poinsettia (*Euphorbia pulcerima*)	Crop architecture allowing distinct analysis of light distribution within the crop stand
3A	Begonia (*Begonia × hiemalis*) cv. 'Rebecca' and 'Blitz'	Cuticle properties (waxy) Low presence of trichoma

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	Tomato *(Solanum lycopersicum* L.) cv. 'Picolino F_1'	Highly susceptible to grey mold (*Botrytis cinerea*)
3B	Tomato *(Solanum lycopersicum* L.) cv. 'Cappricia^{RZ} F_1'	Replacing Picolino which was permanently withdrawn from the market Highly susceptible to grey mold (*Botrytis cinerea*)

Table 3. Light treatment in laboratory and greenhouse experiments

Project part	Site	Dark	Monochromatic (wavelength, nm)						Polychromatic
			400	420	460	520/530	600	660	white
1	Laboratory	●	●	●	●	●	●	●	
2	Greenhouse				●	●		●	●
3	Greenhouse				●	●		●	●

Part 1: Selected BCAs response to light and nutrients

Phenotypic microarrays were performed at a density of six replicates per strain and treatment on two sole carbon source panels (PM01, PM02; Biolog Inc., Hayward, CA, USA) according to the manufacturer's standard protocols. In total 190 different carbon sources were exposed to six light regimes during a period of 96 h. The approach followed the protocol previously described in Gharaei et al. (2017) and Alsanius et al. (2021) with light treatment conditions as in Table 3. Temperature was kept at 22 °C. Dark incubated panels were read every 15 min by a computer integrated camera system. Light exposed panels were monitored manually according to a previously established growth curve. Post-incubation assays on biosurfactant and biofilm formation were conducted according to Alsanius et al. (2021).

Part 2: Distribution of light in the crop stand

A grid (1 m^2) was developed for monitoring the light distribution within the crop stand. Poinsettia of comparable size and height as well as developmental stage were purchased at a local greenhouse market garden and placed in the greenhouse as displayed in *Figure 1* and exposed to different light regimes (Table 3) with top fixed LED ramps. All natural light was excluded. Plant architecture (height, breadth, core surface, number of leaves, internode length, leaf angle), crop parameters (leaf area, canopy fresh and dry weight) and photosynthetic parameters were registered. Distribution of light intensity and spectrum was measured at different canopy layers (Skye SKP 215, Skye instuments, Llandrindod Wells, UK) (*Figure 1*) s and compared to BCAs response to selected carbon sources identified in part 1.

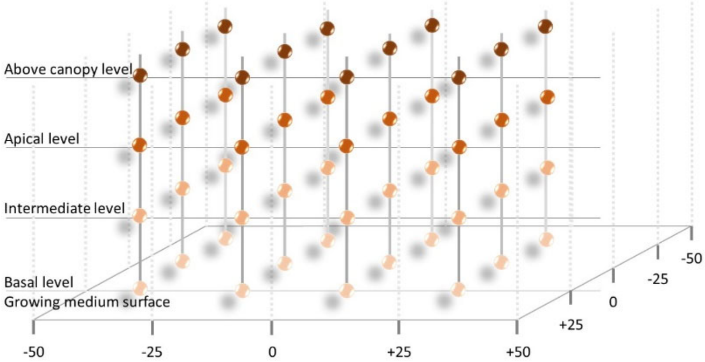

Figure 1. Grid för measurement of light distribution in the crop stand of Poinsettia. Points for measurements are restricted to plants within the crop stand (unbroken lines); blind plants (dotted lines) are excluded. Color intensity of dots increases with plant height from basal level to above canopy level. (illustration: B. Alsanius)

Part 3: Presence of selected BCA in Begonia and tomato under different light regimes

Target crops are displayed in *Table 2* and either grown from seeds (tomato) or as rooted cuttings (Begonia) in peat based growing medium in a semi-commercial-sized chamber with blind screens at 21 °C ± 2. As a general treatment during the growing period, tomatoes were irradiated with High Pressure Sodium lamps for a 14-h photoperiod. For BCA provocations, light treatments displayed in Table 3 were employed during 48 h. Single strain solutions were prepared from pure cultures of the three BCAs and applied as described by Hellström et al. (submitted). Six samples were harvested after 2, 4, 6 and 24 h post inoculation (hpi) and the BCAs reisolated as viable counts. Light distribution parameters as well as crop architecture, biomass as well as photosynthetic characteristics were measured.

Results

Part 1

Light exposure together with specific carbon source increased the respiration in all three BCA, but light quality-nutrient respiration interactions varied between the organisms. Respiration of single carbon sources was stimulated in the short-waved light spectrum for BA and PC whilst respiration of carbon sources by SG was favored under red light exposure. Biosurfactant was formed only in the presence of capric acid in all three BCA. The combination light quality and sole carbon source increased biofilm formation in all three BCA. In general, biofilm formation increased under exposure to darkness for BA, whereas it significantly increased under short waved light for PC and SG Figure 2. We identified 12 (BA), 3 (PC) and 4 (SG) compounds of particular interest for biofilm formation under various monochromatic conditions.

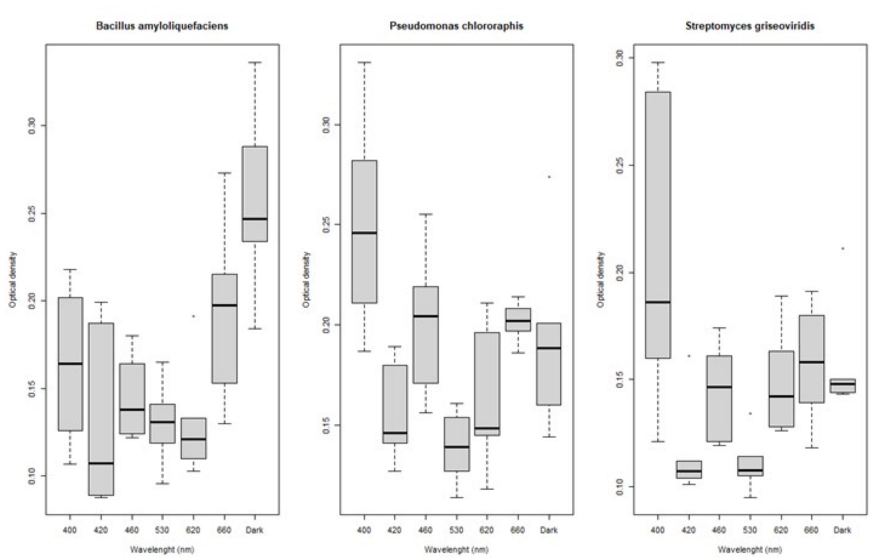

Figure 2. Boxplot of biofilm formation by B. amyloliquefaciens, P. chlororaphis *and* S. griseoviridis *after 96 h of exposure to different light quality. (Illustration: M. Karlsson)*

Part 2

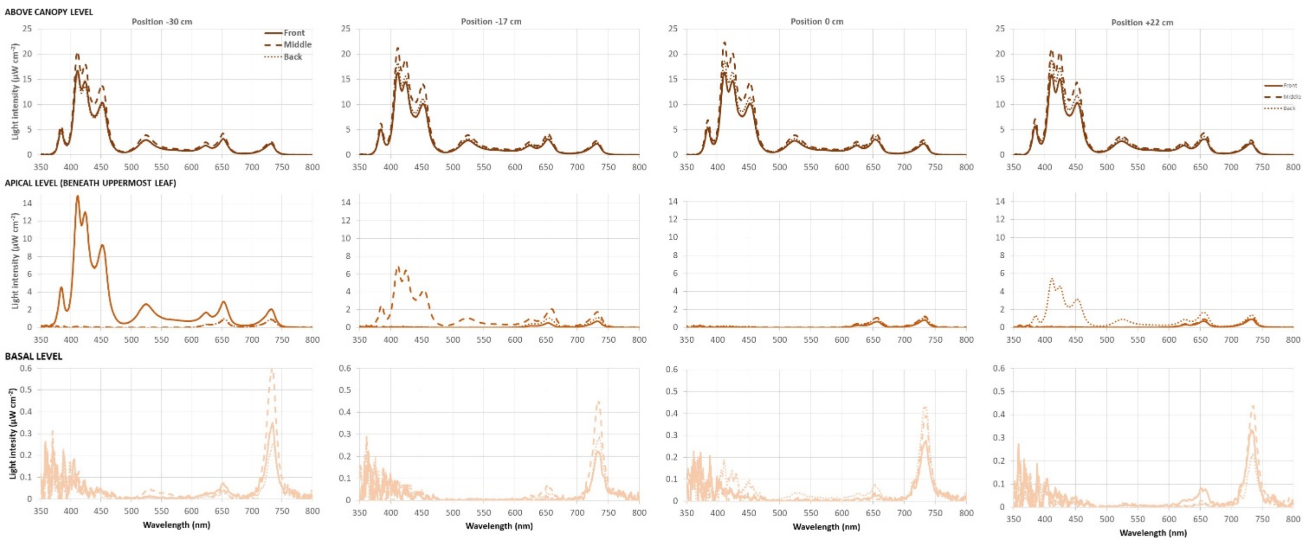

Figure 3. Spectral distribution of visible light (nm) and light intensity (µW cm^{-2}) above and within the canopy of Poinsettia under white LED within a 1 m^2 crop stand (position x: -30 cm, -17 cm, 0 cm, +20 cm; position y:-35 cm (front, unbroken line), 0 cm (middle, broken line), +25 cm (back, dotted line)): above the canopy, beneath the uppermost leaf (apical level), in the middle and at the basal level. For spatial reasons, the illustration from the center level are omitted. NB! deviations in y-axes scales. (Illustration: B. Alsanius).

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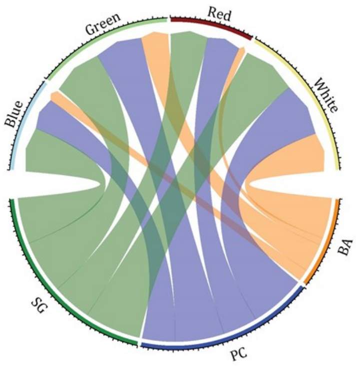
As expected the light intensity drops dramatically already beneath the uppermost leaf and substantial changes in spectral distribution were absorbed as demonstrated in Figure 3. Towards the basal level, far-red light increased. Comparable observations were done under monochromatic LED exposure.

Part 3



Log CFU reisolated from the two crops varied significantly (tomato > Begonia). Significant differences in reisolated BCA were detected between the three BCAs, light sources and light exposure length as well as for all two- and three-factor interactions. Polychromatic light exposure supported all three BCAs. In contrast to SG and PC, reisolation of BA was poor from tomato exposed to any monochromatic treatment (Figure 4).

Figure 4. Average log CFU g^{-1} of the three biocontrol agents (BCA; S. griseoviridis*, SG;* P. chlororaphis*, PC;* B. amyloliquifaciens*, BA) re-isolated from tomato leaves after 48 h of exposure to poly- (monochromatic (LED; blue: 420 nm, green: 520 nm, red: 660 nm) and white LED) light. Breadth of the arrows in the cord diagram depict occurrence of the individual BCA in response to the light treatments.(Illustration: M. Hellström).*

To account for the dramatic changes in light spectral distribution and light intensities within the canopy, tomato plants were partitioned and samples were taken from the apical and middle tiers. All three BCAs established well under polychromatic light. Reisolation of BA exposed to 460 and 660 nm was low irrespective of leaf position. Reisolation of PC and SG was higher from apical than middle tier leaves. Polychromatic white and monochromatic light at 530 nm sustained numbers of reisolated PC and SG best during all 48 h, however, but exposure to 460 nm for 48 h increased numbers of reisolated PC.

Discussion

The interest into light-phyllosphere interactions has increased during recent years, esp. with respect to non-phototrophic leaf colonizers. To the best of our knowledge, this is the first project engaging into the fate of BCAs and light impacts on establishment of BCAs. Our data supports our hypothesis that light affects the establishment of BCA in the phyllosphere. However, data retrieved under laboratory conditions (part 1) could fully be supported by the findings in planta. There are multiple explanations for this:

(i) Part 3 data have not been normalized with respect to spectral distribution nor light intensity.

(ii) Wavelength, temperature and nutritional conditions but not humidity were in focus in the laboratory experiments. This needs to be followed up as there is increasing evidence that non-phototrophic bacteria also show circadian clock dependence (Kahl et al., 2022).

Limitations

The onset of the SARS-Cov2 pandemic in December 2019 significantly affected the progress in the project, leaving several factors outside our control. We coped with the lock-down of SLU facilities and restricted presence on campus for employees and with repeated illness and quarantine amongst project staff in relation to conduction of the project. However, we did not control the broken supply chains for certain material, esp. culture-independent (DNA-, RNA-based) analysis; nor were we able to foresee the market withdrawal of the grey mold susceptible tomato cultivar after one year of experiments and difficulties to purchase an alternative cultivar. This requested the repeat of the initial greenhouse experiments, leading to time constraints. Due to quarantine restriction, a validation step under commercial greenhouse conditions as well as the intended workshops together with growers could not be conducted. A "post-mortem" workshop for the branch is planned for April 2023.

Conclusions

Spectral composition and light intensity is an important feature for establishment of BCA in the phyllosphere. Crop-BCA interactions are crop specific. BCAs' response to spectral distribution and exposure

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dose is organism specific. There is a need to optimize the plant environment for the introduced organisms (see appendix 1).

Relevance and recommendations

Spectral composition and light intensity is a tool to improve the establishment of BCA in the phyllosphere. Currently, polychromatic white light and light intensity of at least 50 µmol m^{-2} s^{-1} appear to be the most promising when using top lighting. But updates on this information will be released with respect to light quality-biofilm formation. Future studies need

(i) To disentangle the interactivities between light; foliar pathogens and BCAs efficacy.
(ii) To introduce humidity and circadian clock variables.
(iii) To monitor the expression of biocontrol activity from the introduced BCAs' perspective on a physiological level (RNA) and from the perspective of disease reduction under small scale conditions, as well as validated under commercial conditions.

Result dissemination

Scientific publications, *Published*	Alsanius, B.W., Karlsson, M.E., Rosberg, A.K., Dorais, M., Naznin, T., Khalil, S., and Bergstrand, K.-J. (2019). Light and microbial lifestyle: The impact of light quality on plant-microbe interactions in horticultural production systems - a review. Horticulturae *5*, 41. doi: 10.3390/horticulturae5020041.
	Alsanius, B.W., Vaas, L.A.I., Gharaie, S., Karlsson, M.E., Rosberg, A.K., Wohanka, W., Khalil, S., and Windstam, S. (2021). Dining in blue light impairs the appetite of some leaf epiphytes. Frontiers in Microbiology *12*, 725021. doi: 10.3389/fmicb.2021.725021.
	Alsanius, B.W., Bergstrand, K.-J., and Karlsson, M.E. (2020). Integrated greenhouse production in new light: improved LED-assisted biocontrol of aerial diseases. Acta Horticulturae *1296*, 293-296. doi: 10.17660/ActaHortic.2020.1296.38.
Scientific publications, *Submitted*	Karlsson, M.E., Hellström, M., Bergstrand, K.-J., Alsanius, B.W. The power of light, impact on the performance of biocontrol agents. Submitted
	Hellström, M., Karlsson, M.E., Kleman, I., Bergstrand, K.-J., Alsanius, B.W. Artificial light quality changes colonization ability of biocontrol agents under greenhouse conditions. Submitted.
	Alsanius, B.W., Hellström, M., Karlsson, M.E., Bergstrand, K.-J., Rosberg, A.K. Integrated production in new light: light quality in greenhouse horticulture and its impact on the phyllosphere microbiome. Submitted.
Scientific publications, *Manuscript*	Alsanius, B.W., Bergstrand, K.-J., Hellström, M., Vetukuri, R.R., Becher, P., Karlsson, M.E. The power of light – phyllosphere dilemmas.
	Hellström, M., Karlsson, M.E., Darlison, J., Bergstrand, K.-J., Alsanius, B.W. Bacterial DeLight: deciphering how light affects introduced bacterial biocontrol agents in the phyllosphere.
	Alsanius, B.W., Hellström, M., Karlsson, M.E., Bergstrand, K.-J. The meaning of light: potential interactivities between phenotypic plasticity of biological control agents, light distribution within the crop stand and plant architecture.
	Hellström, M., Karlsson, M.E., Vetukuri, R.R., Becher, P., Bergstrand, K.-J., Alsanius, B.W. Interactivities between light quality, biological control agents and control of grey mold (*Botrytis cinerea*) in tomato.
Conference publications/ presentations	Alsanius, B.W. Integrated greenhouse production in new light: improved LED-assisted biocontrol of aerial diseases. Poster presented at *ISHS GreenSys2019 - International Symposium on Advanced Technologies and Management for Innovative Greenhouses, June 16-20, 2019, Angers, France*

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	Hellström, M. LED light affects biocontrol activity of selected BCA strains. Poster presented at *"Phyllosphere 2022", July 17-21, 2022, Davis, CA., USA*
	Hellström, M. Artificial light quality changes colonization ability of biocontrol agents under greenhouse conditions. Oral presented at *"International Horticultural Congress (IHC), S06 INNOVATIVE TECHNOLOGIES AND PRODUCTION STRATEGIES FOR SUSTAINABLE CONTROLLED ENVIRONMENT HORTICULTURE", August 14-20, 2022, Angers, France*; Symposia - IHC 2022
	Alsanius, B.W. Integrated production in new light: light quality in greenhouse horticulture and its impact on the phyllosphere microbiome. Oral to be presented at *ISHS GreenSys 2023, October 22-27, 2023, Cancun, Mexico*
Other publications, *media etc.*	Hellström, M., Karlsson, M.E., Bergstrand, K.-J., Alsanius, BW. Bekämpning i nytt ljus. Viola 2021
	IX International Symposium on Light in Horticulture, Alnarp, 2021; Convenors: S. Khalil, K.-J. Bergstrand, M. Karlsson, A.K. Rosberg*; June 8-12, 2021, Alnarp, Sweden;* partly funded by Partnerskap Alnarp publically opening for free-of-charge participation of 10 Swedish stakeholders (growers etc) International Symposium on Light in Horticulture 2020 | June 8-12 2020 | Malmö, Sweden (ishslight2021.se)
	Alsanius, BW., Hellström, M., Bergstrand, K.-J., Karlsson, M.E. Ljus hjälper biologiska bekämpningsmedel att etableras i växthuskulturer. Faktablad (LTV), in press
	Alsanius, BW., Hellström, M., Bergstrand, K.-J., Karlsson, M.E. Blue-print för förbättrad etablering av *Pseudomonas chlororaphis* och *Streptomyces griseoviridis* i bladskärmen av växthustomater. Faktablad (LTV), manuscript.
Oral communi-cation, *to sector, students etc.*	Alsanius, B.W. Optimized integrated control in greenhouse systems sees the light. Oral presentation; LRF/SLF workshop April 2019, Alnarp
	Alsanius, B.W. Optimized integrated control in greenhouse systems sees the light. Oral presentation within *MSc course "Microbial Horticulture", VT 2019*
	Karlsson, M.E. Light-microbe-plant interactions. Oral presentation within *MSc course "Microbial Horticulture", VT 2020, 2021 and 2022*
	Hellström, M. Integrated control in new light: Does light affect the presence of biocontrol agents in the phyllosphere of greenhouse grown tomatoes? Publically announced oral presentation within the *seminar series at the Dept of Biosystems and Technology, Dec 6, 2022*
	IX International Symposium on Light in Horticulture, Alnarp, 2021; Convenors: S. Khalil, K.-J. Bergstrand, M. Karlsson, A.K. Rosberg*;* June 8-12, 2021, Alnarp, Sweden; partly funded by Partnerskap Alnarp publically opening for free-of-charge participation of 10 Swedish stakeholders (growers etc). International Symposium on Light in Horticulture 2020 | June 8-12 2020 | Malmö, Sweden (ishslight2021.se)
Student thesis	Will be finalized in 2024 (M. Hellström, PhD student)
Other	Patents not yet applicable, but considered for the future

References

ALSANIUS, B. W., BERGSTRAND, K.-J., HARTMANN, R., GHARAIE, S., WOHANKA, W., DORAIS, M. & ROSBERG, A. K. 2017. Ornamental flowers in new light: artificial lighting shpares the microbial phyllosphere community structure of greenhouse grown sunflowers (*Helianthus annuus* L.). *Scientia Horticulturae,* 216**,** 234-247. doi: 10.1016/j.scienta.2017.01.022.

ALSANIUS, B. W., BERGSTRAND, K.-J., HELLSTRÖM, M., VETUKURI, R. R., BECHER, P. & KARLSSON, M. E. The power of light – phyllosphere dilemmas. *manuscript*.

ALSANIUS, B. W., KARLSSON, M. E., ROSBERG, A. K., DORAIS, M., NAZNIN, T. M., KHALIL, S. & BERGSTRAND, K. J. 2019. Light and microbial lifestyle: The impact of light quality on plant-microbe interactions in horticultural production systems - a review. *Horticulturae,* 5**,** 41. doi: 10.3390/horticulturae5020041.

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ALSANIUS , B. W., VAAS, L. A. I., GHARAIE, S., KARLSSON, M. E., ROSBERG, A. K., WOHANKA, W., KHALIL, S. & WINDSTAM, S. 2021. Dining in Blue Light Impairs the Appetite of Some Leaf Epiphytes. *Frontiers in Microbiology,* 12**,** 725021. doi: 10.3389/fmicb.2021.725021.
ELAD, Y. 1997. Effect of filtration of solar light on the production of conidia by field isolates of *Botrytis cinerea* and on several diseases of greenhouse-grown vegetables. *Crop Protection,* 16**,** 635-642. doi: 10.1016/S0261-2194(97)00046-X.
GHARAIE, S., VAAS, L. A. I., ROSBERG, A. K., WINDSTAM, S. T., KARLSSON, M. E., BERGSTRAND, K.-J., KHALIL, S., WOHANKA, W. & ALSANIUS, B. W. 2017. Light spectrum modifies the utilization pattern of energy sources in Pseudomonas sp. DR 5-09 *PLOS ONE,* 12**,** e0189862. doi: 10.1371/journal.pone.0189862.
HELLSTRÖM, M., KARLSSON, M. E., KLEMAN, I., BERGSTRAND, K.-J. & ALSANIUS, B. W. Submitted. Artificial light quality changes colonization ability of biocontrol agents under greenhouse conditions.
KADIVAR, H. & STAPELTON, A. E. 2003. Ultraviolet radiation alters maize phyllosphere bacterial diversity. *Microbial Ecology,* 45**,** 353-361. doi: 10.1007/s00248-002-1065-5.
KAHL, L. J., ECKARTT, K. N., MORALES, D. K., PRICE-WHELAN, A. & DIETRICH, L. E. P. 2022. Light/Dark and Temperature Cycling Modulate Metabolic Electron Flow in Pseudomonas aeruginosa Biofilms. *mBio,* 13**,** e0140722. doi: 10.1128/mbio.01407-22.
KARLSSON, M. E., HELLSTRÖM, M., BERGSTRAND, K. J. & ALSANIUS, B. W. 2022. The power of light, impact on the performance of biocontrol agents. *submitted*.
MORROW, R. C. 2008. LED lighting in horticulture. *HortScience* 43**,** 1947-1950.
NEWSHAM, K. K., LOW, M. N. R., MCLEOD, M. R., GREENSLADE, P. D. & EMMETT, B. A. 1997. Ultraviolet-B radiation influences the abundance and distribution of phylloplane fungi on pedunculate oak (*Quercus robur*). *New Phytologist,* 136**,** 287-297. doi: 10.1046/j.1469-8137.1997.00740.x.
NICOT, P. C., MERMIER, M. & VAISSIERE, B. E. 1996. Differential spore production by Botrytis cinerea on agar medium and plant tissue under nearultraviolet light-absorbing polyethylene film. *Plant Disease,* 80**,** 555-558.
NICOT, P. C., MORISON, N. & MERMIER, M. 2001. Optical filters against grey mould of greenhouse crops. *In:* VINCENT, C., PANNETON, B. & FLEURAT-LESSARD, F. (eds.) *Physical Control Methods in Plant Protection.* Berlin, Heidelberg: Springer.
REUVENI, R. & RAVIV, M. 1997. Control of downy mildew in greenhouse-grown cucumbers using blue photoselective polyethylene sheets. *Plant Disease,* 81**,** 999-1004.
SUTHAPARAN, A., STENSVAND, A., SOLHAUG, K. S., TORRE, S., MORTENSEN, L. M., GADOURY, D. M., SEEM, R. C. & GISLERÖD, H. R. 2012. Suppression of powdery mildew (*Podosphaera pannosa*) in greenhouse roses by brief exposure to supplemental UVB radiation. *Plant Disease,* 96**,** 1653-1660.
SUTHAPARAN, A., STENSVAND, A., SOLHAUG, K. S., TORRE, S., TELFER, K. H., RUUD, A. K., MORTENSEN, L. M., M., G. D., SEEM, R. C. & GISLERØD, H. R. 2014. Suppression of cucumber powdery mildew by supplemental UV-B radiation in greenhouses can be augmented or reduced by background radiation quality. *Plant Disease,* 98**,** 1349-1357. doi: 10.1094/PDIS-03-13-0222-RE
SUTHAPARAN, A., STENSVAND, A., TORRE, S., HERRERO, M. L., PETTERSEN, R. I., GADOURY, D. M. & GISLERÖD, H. R. 2010a. Continuous lighting reduces conidial production and germinability in the rose powdery mildew pathosystem. *Plant Disease,* 94**,** 339-344. doi: 10.1094/PDIS-94-3-0339.
SUTHAPARAN, A., TORRE, S., STENSVAND, A., HERRERO, M. L., PETTERSEN, R. I., GADOURY, D. M. & GISLERØD, H. R. 2010b. Specific light-emitting diodes can suppress sporulation of *Podosphaera pannosa* on greenhouse roses. *Plant Disease,* 94**,** 1105-1110. doi: 10.1094/PDIS-94-9-1105.
THEIS, K. R., DHEILLY, N. M., KLASSEN, J. L., BRUCKER, R. M., BAINES, J. F., BOSCH, T. C. G., CRYAN, J. F., GILBERT, S. F., GOODNIGHT, C. J., LLOYD, E. A., SAPP, J., VANDENKOORNHUYSE, P., ZILBER-ROSENBERG, I., ROSENBERG, E. & BORDENSTEIN, S. R. 2016. Getting the hologenome concept right: an eco-evolutionary framework for hosts and their microbiomes. *mSystems,* 1**,** e00028-16. doi: 10.1128/mSystems.00028-16.
VÄNNINEN, I., PINTO, D. M., NISSINEN, A. I., JOHANSEN, N. S. & SHIPP, L. 2010. In the light of new greenhouse technologies: 1. Plant-mediated effects of artificial lighting on arthropods and tritrophic interactions. *Annals of Applied Biology,* 157**,** 393-414. doi: 10.1111/j.1744-7348.2010.00438.x.

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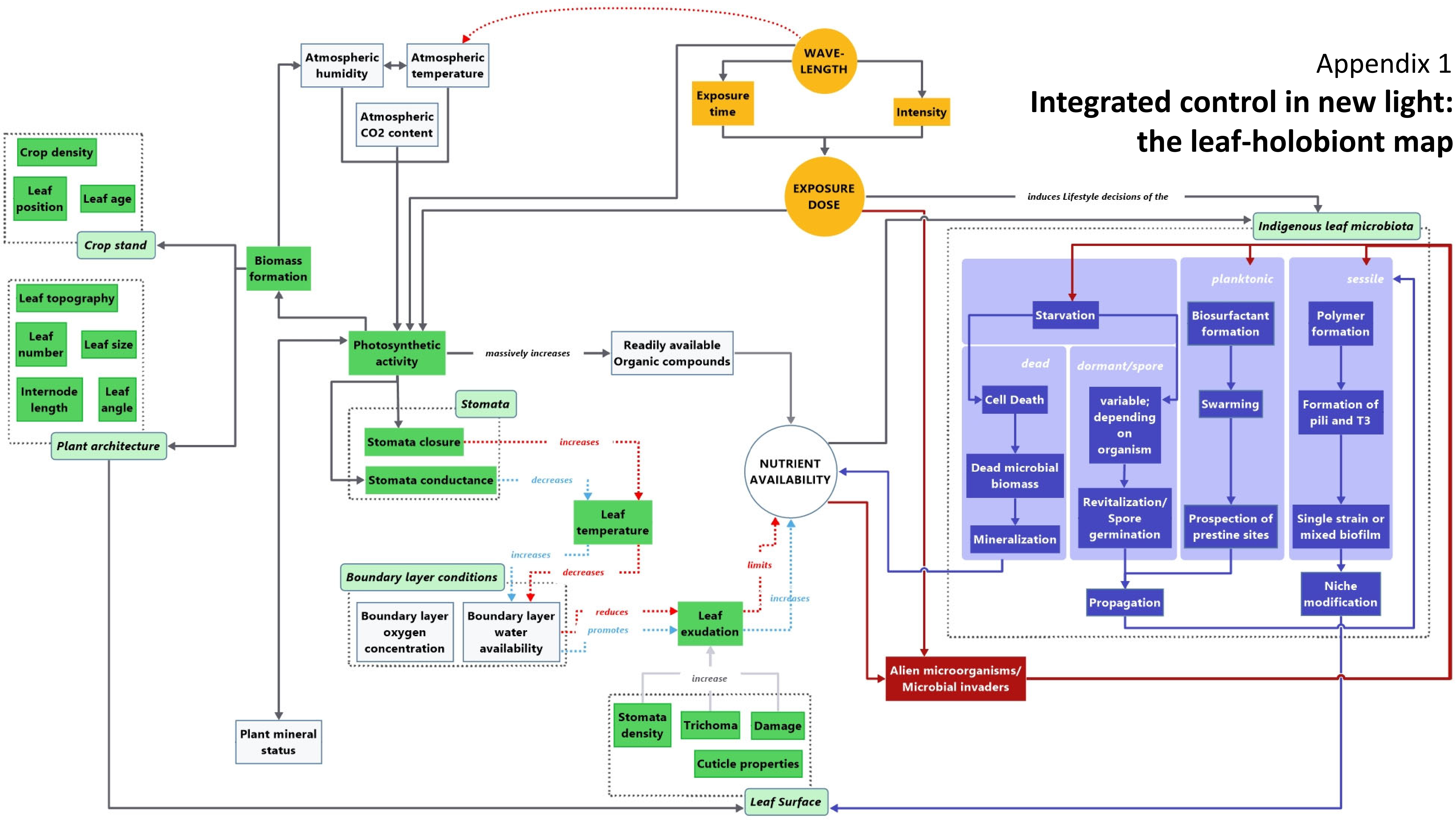
Appendix 1

Integrated control in new light: the leaf-holobiont map



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