The project studied the effect of light intensity and spectral composition on the growth, development and metabolism of several crops. Our phytotron growth systems equipped with modulated LED lighting technology provided a unique opportunity for these studies. Our research focused on cultivating several crop species, including leafy (spinach), and fruit-producing (tomato) vegetables. Tomato was studied at different developmental stages (young and mature plants). Finally, investigations were completed additionally with studies of chilli and herbs. Our special aim was to understand how light can determine plant product characteristics: such as appearance and quality and how the light can be used for targeted manipulation of plant metabolism by changing the light intensity and spectral composition

Thus, we aimed to answer several questions:

1. What is the effect of light intensity and spectral composition on the growth and development of spinach and tomato plants?
2. Whether the optimal spectral composition depends on the light intensity?
3. Whether the best light combination depends on species or genotype?
4. How do the different light components affect the primary and secondary metabolism?
5. Which photoreceptors participate in the different morphological processes and different primary and secondary metabolisms?
6. What is the most important light factor in these processes: The absolute amount or the proportion of different light components?
7. Whether the plant metabolism and yield quality can be modified by changes in the light environment during development to produce functionalized foods?
8. How much time is necessary for inducing modifications?

Results:

1: To determine the best light combinations (in terms of light intensity and spectral distribution) for growing spinach and tomato seedlings indoor, these seedlings were grown under different light regimens, namely at low (250 µmol/ m^2 s), medium (450 µmol/ m^2 s) and high (650 µmol/ m^2 s) light intensities under different spectral combinations (5-30% blue light proportions) and at fixed green regions (10%) provided by blue, red and white LED.
In the case of **spinach** plants, the spectral composition caused slight (but significant) variations in the plant height and leaf number and high variations in plant weight and leaf area at all (250, 450 and 650 µmol m-2 s-1) light intensities. **The highest plant height was given when the plants were grown at R/G/B= 85/5/10 and the lowest was when the highest proportion of blue was applied**. This indicates an **inhibitory effect of blue light on stem elongation**. These tendencies were observed at all light intensities; however, the **blue light-induced inhibition of elongation was slightly reduced when the light intensity was high**. Evidently, the increase in light intensity provided elevated biomass production due to the increase of the photosynthetic activity of plants. The slope (differences between the weights of plants vs proportion of blue light) was slightly higher at medium light intensity as compared to others indicating that the manifestation of the effect of **spectral composition on biomass production depends on the light intensity** too. The leaf number was hardly affected both by the spectral composition and light intensity, but **the leaf area and the leaf density changed** significantly, especially **with the spectral composition**. The **leaf area increased with increasing the proportion of red light**, **while leaf density (specific leaf area, cm^2/ g FW) increased with increasing the proportion of blue light.** These results indicated that the different spectral regions affect differently to the different morphological parameters. Studying several physiological parameters, it was found that the **photosynthetic activity of spinach leaves affected strongly both the light intensity and spectral**

composition. With increasing light intensity, the CO_2 assimilation rate increased and the effective quantum yield of PS II decreased intensively (as usual), while **with an increase in the proportion of blue light, the stomatal was more open, but the Pn was lower than those at higher red light proportion**. **This contrary behaviour of Pn and gs regulation suggested different regulatory mechanisms**. The CO_2 metabolism differed under red and blue light: At low Ci levels different Rubisco activity, while at high Ci levels, the utilisation of triose phosphate metabolites can contribute to the changes of CO2 assimilation in red light, while under blue light, both the stomatal movements and RuBP regeneration processes can contribute to the spectrum-dependent changes of photosynthesis. Our results supported the hypothesis that the red- and blue-light-induced stomatal opening differs both in sensitivity and mechanisms: the red-light syndrome is mainly related to the accumulation of sugar metabolites including sucrose in mesophyll cells while the blue-light-induced stomatal opening is mediated rapidly by photoreceptor phototropin in guard cells, where the malate accumulation was observed through the activation of mitochondrial respiration.

Studies of the effect of light intensity and spectral combinations in **tomato** plants revealed many specific correlations. An **increase in light intensity resulted in a suppression of stem elongation** (the plant height decreased) and **an increase in stem diameters, leaf area and biomass production**. However, the increase in biomass production was more intense than the leaf expansion resulting in a light-intensity-dependent decrease of the specific leaf area. The spectral dependence showed interesting correlations. Namely, we found that **many morphological and physiological parameters, such as plant height, specific leaf area, photosynthetic activity and stomatal conductance changed linearly with the increase in the proportion of blue light.** While the plant height, specific leaf area and photosynthetic activity (Pn) of plants decreased linearly with the increase in the proportion of blue light, the stomatal conductance showed an inverse relationship. We also observed that the blue light stimulated the stomatal opening in the case of tomato too (similarly as found for spinach). **Other parameters, including stem diameter, leaf area, biomass production and the number of flowering plants grew up only to a critical blue% value, but above this threshold, the blue light had adverse effects. These tendencies were similar at all light intensities.**

In **adult tomato plants**, the effect of light intensity and spectral composition also **modified the growth, flowering and yield production**. The plant height was the highest at low light intensity and under a high proportion of red light, which can be well explained by the shade avoidance syndrome. The largest plant green mass was also measured at low light intensity and with a lot of red light indicating that **the low light intensity and too much of red light induced the production of leafy biomass instead of inducing flowering and fruit production.** Therefore, these light combinations are useless for fruit-ripening plants. **At elevated light intensity, the elevated photosynthetic activity did not improve the plant biomass significantly, indeed the fruit production was stimulated**. These results indicated that the increase in light intensity in an adequate phase of plants can improve the yield production. In addition, **the number of flowers and thus the number of fruits was the highest at high proportion of blue light**. However, **at low light with a high proportion of blue light, only small fruits were developed**, as shown by the low fruit weight per pc. With **a high red ratio, fewer but larger** (in diameter and weight) tomato fruits were formed, even at a low (250 µmol m-2 s-1) light intensity.

Overall, **these investigations highlighted the importance of an adequate light environment in indoor cultivation systems related to both light fluence and spectral composition and in growth and development**. Furthermore, **we presented evidently that the light intensity and spectral composition regulate the growth and development in interaction**.

2: **The best light combination for the cultivation of spinach plants was around 5-10/ 10/85-80 % blue/green/red light proportion depending on the light intensity**. At low light (250 µmol/ m^2 s)

10/10/80, while at moderate or elevated light intensities, 5/10/85 % blue/green/red light proportion provided the best spectral combination for the cultivation of spinach plants indoor. We also found that although the increase in light intensity increased the biomass, the increase in light intensity resulted in a less increase in biomass (no more than 30-40 %) than the double or triplicate energy cost required for producing elevated light intensities. Thus, we concluded that the cultivation of spinach plants is sufficient even under relatively low light intensity (250 µmol/ m^2 s). (However, our preliminary results at 100 µmol/ m^2 s showed that the too-low light intensity causes many adverse effects on the growth (elongated plants with low biomass).

In the case of **tomato plants, the optimal spectral conditions were found under 15 : 10: 75 % of blue: green: red regions at moderate and high light intensities (450 and 650 µmol/ m^2 s), while at low light (250 µmol/ m^2 s) intensity elevated (20%) proportion of blue light are preferred**. According to the results, in general, moderate light intensity with a 15B:10G:75R spectral combination seems suitable for the cultivation of tomato seedlings due to energetic reasons, however, it should also be mentioned that **elevated light intensity induced the flowering in tomato plants**. The shortening in the development period has also huge agronomic importance.

In adult plants, for stimulation the flowering **elevated light intensity (above 500 µmol/ m^2 s) with a higher proportion of blue light (20%) is desirable**, however, at the **ripening phase, the change of light environments toward a higher proportion of red light (above 80%) is also suggested** according to the desired properties of fruits (see below 4. point).

According to these investigations, it can be concluded that **the optimal spectral combination depends on the applied light intensity. At moderate or high light intensities lower proportion (5-15% , depending on species) is enough**, however, **if this light intensity is not available, a higher proportion of blue light is recommended to use to alleviate the adverse effect of low light intensity**. **The investigations confirmed that light intensity and spectral composition regulate the growth in interaction**.

3:

Comparing the two spinach **cultivars** (cv. Matador and cv. Popey), we found **significant differences between the genotypes in all parameters**, especially in plant height, weight, leaf area, specific leaf area and SPAD values. In general, the spinach Popey is lighter, but greener than Matador, especially at 250 and 450 light intensities, however, **they showed similar tendencies in all parameters measured as described above** (1. and 2. points).

In the case of tomato, 4 tomato cultivars were investigated for morphological parameters, but only 2 (cv. Mano and cv. Vilma) were investigated in detail. Although **significant differences were also found between the genotypes** (e.g. the tomato cv. Mano is higher with bigger and less green leaves as compared to cv. Vilma, which is a small, compact and dark green plant), **both genotypes showed similar tendencies both for the light intensity and spectral composition.** The seeds of the other 2 tomato genotypes (cv. Mobil and Roma) did not seem homogenous in the habits, therefore we eliminated them from further investigations.

However, it can be said that similar tendencies (with different absolute values) were observed for the given parameters mentioned above within the genotypes both in the case of spinach and tomato plants. However, **comparing the tomato and spinach plants, we found a shift in the optimal spectral composition and fluence.** We found that **lower light intensity and a higher proportion of red light**

(85%) is optimal for the cultivation of leafy spinach plants as compared to fruit-producing tomato seedlings.

4.

The effect of light intensity and spectral composition was also studied on the changes of primary and secondary metabolism. Some **common features** have been observed both **for spinach and tomato plants**, namely: **the red light stimulated the accumulation of carbohydrates**, while the **blue light induced the protein (and amino acid) biosynthesis** both in spinach and tomato plants. In addition, the light intensity also forced the synthesis of both carbohydrates and proteins due to the increase of absorbed and utilized light energy. Furthermore, our investigations revealed that the **carbohydrate accumulation depended linearly** with the proportion of blue light (namely carbohydrate content decreased with the increase of the proportion of blue light), while **the protein accumulation showed** non-linear correlations rather it followed the **threshold hypothesis** in the case of tomato seedling.

In the case of **spinach** plants, the **mineral composition and ascorbate** content was also measured. We found that both light intensity and spectral composition affected the mineral content in spinach leaves: The **free nitrate content decreased with the increase of light intensity** (mainly **due to its incorporation into organic amino acids and proteins**). It was also supported by the elevated activity of nitrate reductase and the expression of genes responsible for nitrate reduction (nitrate reductase) and transport (nitrate transporter 1.3; 1.4; 1.5). In addition, the **nitrate content** was also lower under **high proportion of blue light due to the elevated expression of nitrate reductase**, glutamine synthase and several nitrate transporter genes (1,4, 5). The amount of **potassium and iron decreased with the increase of light intensity**, however at the lowest light intensity,100 µmol/ m^2 s) the K and Fe uptake was reduced. The changes in the **proportion of blue light slightly (not significantly) modified the K uptake**, however, **the increase in the proportion of blue light reduced the light intensity differences in Fe content. Ca content increased with the increase of light intensity, while Mg showed slight light-induced modifications**.

Elevated **ascorbate content** was reached with the **increase of light intensity as well as with the increase of the proportion of blue** light in spinach leaves. **Surprisingly**, **the blue-light-induced accumulation of ascorbate was not correlated with the expression of ascorbate biosynthetic pathways**, namely the gene of L-galactono-1,4-lacto dehydrogenase (GLDH) belonging to the main ascorbate synthesis pathway, with the L-gulonolactone oxidase *(*GULO6) gene, which controls the ascorbate synthesis through the glucose pathway and with myo-inositol oxygenase (MIOX1) as the ascorbate can also be synthesised through myo-inositol**. Rather** ascorbate content **showed correlation with** the transcript level of dehydroascorbate reductase 2 (DHAR2) which participates in the **regeneration of ascorbate**.

In the case of young **tomato seedlings**, we found that **the increase of light intensity stimulated the accumulation of both primary and secondary metabolites**, including the amount of soluble carbohydrates, proteins, anthocyanin and flavonoid contents. However, we also found that these metabolites showed changes with the changes in the proportion of blue light. Namely, **carbohydrate content decreased linearly, while the anthocyanin and flavonoid content increased linearly with the increase of the proportion of blue light**. **The elevated flavonoid and anthocyanin content was also correlated to the expression of genes of phenylalanine ammonia-lyase (PAL) and Chalcone synthase (CHS), which are part of the phenylpropanoid and flavonoid biosynthetic pathways**. The protein content did not show a linear tendency, rather it followed the threshold hypothesis. Chlorophyll content and carotenoid content changed rather by the light intensity and they were slightly affected by the spectral composition.

In adult tomato plants, besides monitoring the growth and flowering, **the yield quality and quantity** were also determined through monitoring of the amount and size of fruits (see above), their colour (lycopene content), sweetness (sugar content) and organic acids content, which determines primarily the taste of tomato fruits and acidity of the fruits. We found that both the effect of light intensity and spectral composition affected the quality of fruit: **The highest amount of soluble sugar was measured in the fruits of plants grown under a red-dominant spectrum, but the sugar content also increased with increasing light intensity.** In contrast**, the acid content (mainly the amount of malic acid and citric acid) of fruit increased with the increase of blue light proportion**. According to these, sweet tomatoes were obtained under a red-dominant light, while the fruit was mainly acidic under a blue-dominant light. In addition, tomato contains lots of antioxidants including **lycopene** (which gives tomato colour) and **ascorbic acids**. **Lycopene content did not change significantly with the changes in spectral composition, while the ascorbic acid level increased significantly under blue light.** Similarly, **flavonoid content** (flavonoids are also strong antioxidants) **also increased with the rise of blue light.** Thus, **the total antioxidant status of tomatoes was the highest under blue light combined with elevated light intensity.**

These investigations demonstrated that **light regulation of synthesis of primary and secondary metabolites strongly depends not only on the light intensity but also on the spectral combinations and even in some cases on their interactions** (i.e. the spectral compositions dependence is also regulated by the light intensity). These studies are important in the understanding of light (spectral and intensity) dependent regulation of primary and secondary metabolisms.

5.

One of the most important aims was to determine **the participation of photoreceptors in the regulation of growth, development and metabolism**. Therefore, both in the case of spinach and tomato, the expression of several genes responsible for growth, flowering and metabolism were studied together with the expression of photoreceptors Phytochrome A, B, cryptochromes and Phototropins.

In the case of **spinach plants**, elevated **expression of *PHYA* was detected under FR application**, while **the lowest expression was detected under high light intensity**. ***PHYB* is activated by red light**, but there **was no significant difference under other light spectral compositions**. **Blue light** caused the most prominent effect on the expression of photoreceptors ***CRY1*, *PHOT1* and *2*,** resulting in elevated expression of these genes as compared to those of control, red and far-red light.

In addition, **the high-light-induced** reduction in nitrate content was correlated with **the** elevated **expression of nitrate reductase (*NR*) and nitrate transport (*NRT1.4* and *NRT1.5*) genes**, which showed **a significant correlation with the expression of blue-light mediated *CRYPTOCHROME 1* (*CRY1*) and *PHOTOTROPIN* 2 (*PHOT2*) photoreceptors**. **Fe content showed a moderate correlation with the expression of PhyB**.

The expression of several **genes** responsible for **ascorbic acid biosynthesis** and metabolism was also studied. The L-galactono-1,4-lacto dehydrogenase (GLDH) synthesises ascorbate through the main ascorbic acid production pathway in plants. The expression of the *GLDH* gene showed light dependence, as the highest expression was found under FR and the lowest under high light completed with blue light. A similar trend was found in the case of the *GULO6* gene, which controls the ascorbate synthesis through the glucose pathway. However, ascorbate can be synthesised through myo-inositol too, where the myo-inositol oxygenase (*MIOX1*) plays a role in the synthesis. **The expression of this gene was induced by red light, but other light was mainly unaffected.** The dehydroascorbate reductase (**DHAR)** participates in the regeneration of ascorbate. Its gene is **highly expressed under**

blue light as well as under FR light, while in other cases there were no significant differences between the light treatments. In contrast, the blue-light-induced accumulation of ascorbate was not correlated with the transcript level of genes responsible for de novo synthesis of ascorbate, (*GLDH*, *MIOX1*, *GULO6*), but rather with the transcript level of dehydroascorbate reductase 2 (*DHAR2*). **Its correlation with *PHOT1* and *2* indicates that the ascorbate regeneration is more important than the de novo synthesis in the blue-light-induced ascorbate accumulation.**

In **tomato** plants, the expression of photoreceptor genes, including of phytochromes (PHYA, PHYB1 and PHYB2), cryptochromes (CRY1 and CRY2) and phototropins (PHOT1 and PHOT2) together with the expression of PAL, CHS1 and CHS2 responsible for the anthocyanin and flavonoid biosynthesis were investigated under different spectral composition (at 5, 15 and 30% blue light) and light intensities (250, 450 and 650 μmol m-2 s-1). In addition, as some plants have already been transferred from the vegetative phase to flowering under several light spectral combinations and intensities during the 28 days experimental period, the flowering-induced genes such as SINGLE FLOWER TRUSSS (SFT) florigen and its regulator genes CONSTANS (CO1) and CONSTANS-LIKE (COL) were also studied.

Among the photoreceptor genes, **the expression of PHYB2 decreased and CRY2 increased with the increase of blue light proportion gene at all light intensities** in both cultivars, while clear tendencies were not found in the expression of PhyA and PhyB1 genes as well as in the expression of Cry1.

The **stem elongation (plant height) and specific leaf area were strongly affected by red light mediated by the expression of PHYA and suppression of CRY2 genes**. **The accumulation of carbohydrates and chlorophyll is controlled by PHYB1 and PHYB2, while CRY2, PAL, CHS1 and CHS2 are strongly correlated with the accumulation of anthocyanins and carotenoids**.

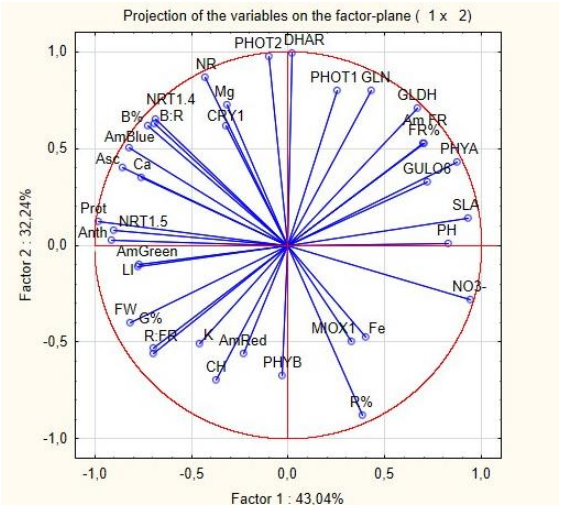
The expression of the **tomato florigen gene SFT** and **its regulator genes CO1 and COL showed** higher **expression at 15% blue light than at 5 and 30% blue light** at all light intensities in both tomato cultivars. The elevated expression of these genes corresponded with the high number of flowered plants grown under these spectral combinations.

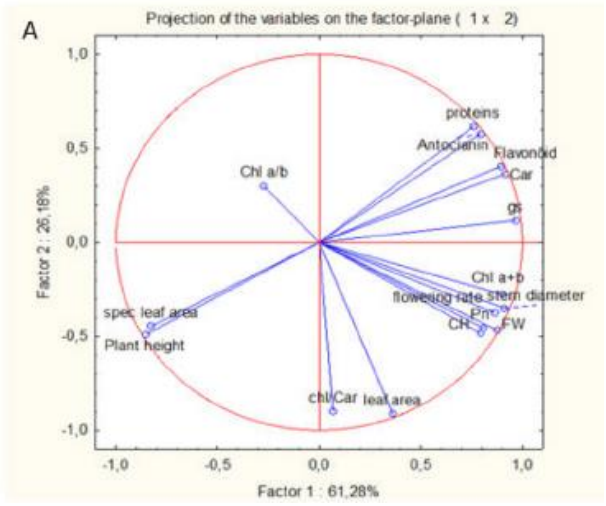
Among the genes responsible for secondary metabolism, the Phenylalanine ammonia-lyase (PAL) and Chalcone synthase (CHS) are enzyme initiators in the phenylpropanoid and flavonoid biosynthetic pathways including anthocyanin biosynthesis. The expression of the genes PAL, CHS1 and CHS2 showed clear light-dependent characteristics, namely the transcript level of PAL and CHS1 genes increased with the rise of the proportion of blue light at all light intensities in both cultivars. In the case of CHS2, higher expression of CHS2 was found at 15% of blue light as compared to 5 and 30% of blue. This trend was observed in both cultivars at all light intensities, except at high light in cv. Mano where the higher the blue light proportion, the greater the transcript level of CHS2.

Correlation analysis between the expression of the above-mentioned genes revealed a strong connection between the PHB1 & PHB2, CRY2 & PAL and PAL & CHS1. Medium correlation was found between CRY1 & PHYB2, PHYA & CHS2, Cry2 & CHS1 and CHS2, PAL & CHS2, CO1 & COL and CHS1 &CHS2. Further analyses were performed to reveal the connection between gene expression and changes in metabolic levels. The results showed **a strong correlation between the contents of anthocyanin and flavonoids & CRY2, PAL, CHS1; and between the carotenoid content & CRY2 and PAL. Medium correlation was revealed between the number of flowering plants & CO1, CHS2; the carbohydrate content (CH) & PHYB1 and PHYB2; anthocyanin and flavonoid contents & CHS2 and between carotenoids & CHS1 and CHS2. Interestingly, the chlorophyll content was associated with the expression of several genes, such as PHYA, PHYB1, PHYB2, CRY2, PAL, CHS1, CHS2. A negative correlation was found between the chl a/b ratio & PHYA and between the protein content & PHYA.**

These studies revealed correlation networks among the photoreceptors and genes responsible for growth and metabolism.

Spinach Tomato





6.

The next question was: “What is the most important light factor in growth and metabolism “ It was investigated **whether the absolute amount or the proportion of different light** components **are important** in the regulation.

In spinach plants the correlation analyses revealed that the light intensity (e.g. **the absolute amount of light**) **was the main factor for biomass production, carbohydrate, protein, anthocyanin and flavonoid accumulation, and also for the decrease in free nitrate content**. Related to spectral composition, **the broad white light spectrum was the main factor for biomass production and anthocyanin accumulation**, while **the absolute amount of red light was the most important factor for carbohydrate accumulation**. The **absolute amount of blue light caused the main effect on Ca** content. **The nitrate content was affected inversely both by the absolute and relative (%) amount of blue light as well as by the B:R proportion.** All of these light factors were important for ascorbate accumulation but in contrast to nitrate, **the amount of ascorbate showed a positive correlation with the absolute, relative (%) amount of blue light and with the B:R proportion**. In those experiments, were FR application occurred, **the plant height and specific leaf area were affected by the absolute, relative amount of far-red light and by R:FR ratio**, while these light factors determined also the amount of **K in an inverse direction**. In addition, the PCA analysis revealed correlations among the amount and proportion of blue light as well as B:R ratio & photoreceptor Cryptochrome1, among the amount and proportion of far-red light and Phytochrome A, while the red light correlated with the expression of Phytochrome B gene.

In tomato seedlings, **plant height correlated negatively with the absolute amount of blue and green light** (there was no far-red application in these experiments), **fresh weight, flowering time and carbohydrate content with the absolute amount of green and red light**. **Leaf area showed a correlation with the absolute amount of green and red light as well as with R%** (and negatively with

B%). **The amount of proteins, anthocyanins and flavonoids showed correlations with the absolute amount of green light and blue%** (and thus inversely with red%).

This type of correlation analysis revealed **the importance of different light factors in the different morphological traits and in metabolic profile**, meanwhile many common features have been found in light regulation of the growth, development and metabolism in spinach and tomato seedlings.

Spinach:

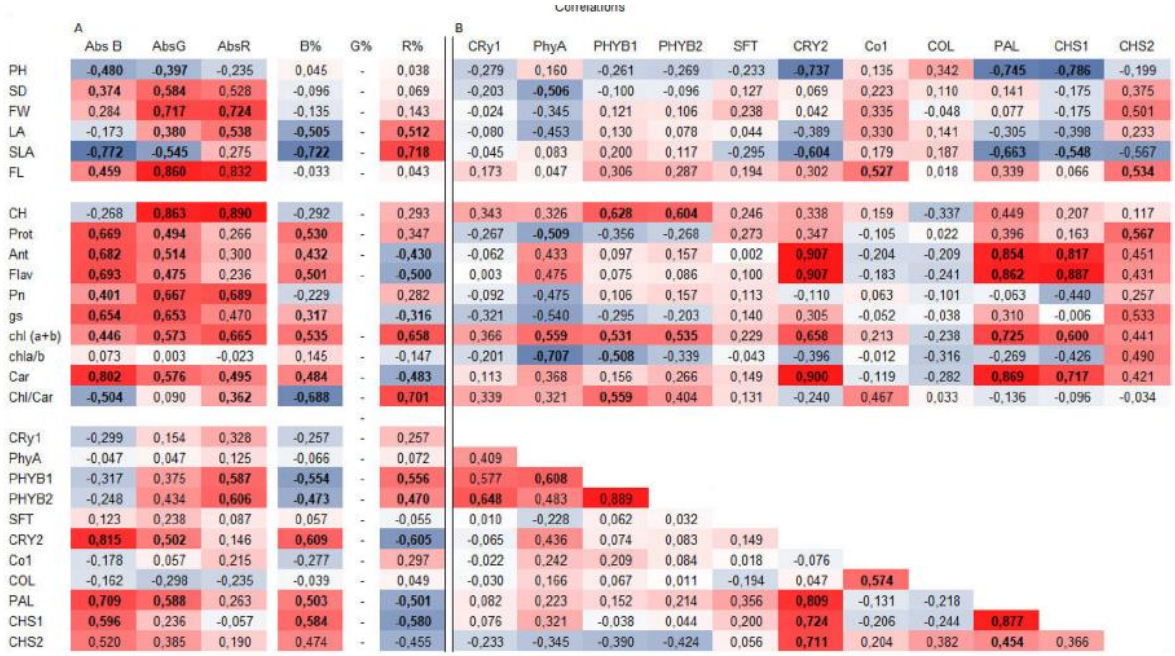
A

	LI	B	G	R	FR	B%	G%	R%	FR%	B:R	R:FR	PHYA	PHYB	PHOT1	PHOT2	CRY1
PH	-0.299	-0.653	-0.290	0.224	**0.833**	-0.726	**-0.831**	0.319	**0.833**	-0.700	**-0.802**	0.786	-0.120	-0.141	-0.178	-0.339
FW	**0.897**	0.522	**0.893**	0.652	-0.579	0.290	0.583	-0.046	-0.585	0.236	0.609	**-0.814**	0.147	-0.746	-0.371	-0.136
SLA	-0.555	-0.714	-0.528	-0.065	**0.812**	-0.705	**-0.811**	0.308	**0.816**	-0.655	**-0.806**	**0.885**	-0.067	-0.107	-0.015	-0.326
K	0.014	0.061	-0.001	-0.064	**-0.844**	0.160	**0.842**	0.253	**-0.844**	0.098	**0.847**	-0.687	0.168	-0.273	-0.336	0.018
Ca	0.797	**0.828**	0.800	0.269	-0.187	0.697	0.187	-0.605	-0.190	0.694	0.187	-0.487	-0.133	0.085	0.415	0.532
Mg	0.168	0.761	0.179	-0.448	0.213	0.754	-0.215	**-0.859**	0.213	**0.807**	-0.276	0.125	-0.238	-0.339	0.756	0.174
Fe	-0.541	-0.613	-0.545	-0.141	-0.045	-0.513	0.045	0.733	-0.039	-0.552	0.057	0.187	-0.045	0.155	-0.482	-0.499
NO3-	-0.649	**-0.910**	-0.648	-0.002	0.522	**-0.883**	-0.521	0.627	0.527	**-0.842**	-0.516	0.706	0.275	-0.002	-0.386	-0.500
CH	0.733	-0.349	0.724	**0.929**	-0.402	-0.329	0.408	0.761	-0.406	-0.621	0.459	-0.593	0.533	**-0.836**	-0.757	-0.321
Prot	**0.830**	**0.847**	**0.822**	0.275	-0.578	0.742	0.580	-0.458	-0.584	0.703	0.585	**-0.801**	-0.095	0.179	-0.189	0.432
Anth	**0.918**	0.793	**0.916**	0.442	-0.486	0.598	0.489	-0.357	-0.492	0.582	0.489	-0.749	0.139	0.346	0.050	0.196
Asc	0.652	**0.925**	0.654	-0.029	-0.360	**0.877**	0.360	-0.707	-0.363	**0.884**	0.329	-0.554	-0.052	0.065	0.472	0.370
NR	0.290	0.744	0.299	-0.265	0.156	0.798	-0.157	**-0.861**	0.152	**0.809**	-0.166	-0.046	-0.581	0.623	**0.862**	**0.829**
NRT1.4	0.312	**0.807**	0.313	-0.325	-0.300	**0.910**	0.298	-0.764	-0.303	**0.893**	0.281	-0.412	-0.404	0.504	0.720	**0.821**
NRT1.5	**0.891**	**0.859**	**0.892**	0.355	-0.409	0.766	0.412	-0.460	-0.415	0.645	0.405	-0.672	0.027	-0.367	0.111	0.097
GLN	-0.288	-0.004	-0.277	-0.335	0.736	0.080	-0.738	-0.442	0.738	0.138	-0.752	0.677	-0.352	0.772	0.685	0.470
MIOX1	-0.259	-0.527	-0.270	0.126	-0.178	-0.556	0.179	0.643	-0.172	-0.495	0.153	0.030	**0.917**	-0.147	-0.500	-0.414
GLDH	-0.496	-0.224	-0.483	-0.397	**0.897**	-0.108	**-0.898**	-0.332	**0.898**	-0.069	**-0.900**	**0.880**	-0.553	0.700	0.589	0.294
DHAR	-0.142	0.447	-0.129	-0.552	0.504	0.581	-0.507	**-0.830**	0.504	0.613	-0.531	0.415	-0.644	**0.847**	**0.936**	0.691
GULO6	-0.762	-0.625	-0.763	-0.403	0.125	0.440	-0.129	0.372	0.129	-0.460	-0.122	0.788	-0.201	0.626	0.233	0.186
PHYA	-0.667	-0.444	-0.654	-0.417	**0.917**	-0.355	**-0.919**	-0.095	**0.920**	-0.305	**-0.933**		-0.356	0.125	0.319	-0.173
PHYB	0.049	-0.319	0.034	0.680	-0.507	-0.405	0.509	0.788	-0.503	-0.369	0.490	-0.356		-0.399	-0.641	-0.414
PHOT1	-0.544	0.610	-0.539	-0.578	0.135	0.555	-0.348	-0.525	0.347	0.394	-0.381	0.453	-0.399		**0.825**	0.686
PHOT2	-0.149	0.675	-0.137	-0.678	0.370	**0.803**	-0.374	**-0.891**	0.370	0.758	-0.411	0.319	-0.641	**0.825**		0.635
CRY1	0.090	0.377	0.090	-0.222	-0.080	0.527	0.078	-0.489	-0.081	0.509	0.089	-0.173	-0.414	0.686	0.635	

B

	PH	FW	SLA	K	Ca	Mg	Fe	NO3-	CH	Prot	Anth	Asc	NR	NRT1.4	NRT1.5	GLN	MIOX1	GLDH	DHAR	GULO6
PH		-0.474	**0.936**	-0.720	-0.424	-0.268	0.181	**0.813**	0.155	-0.743	-0.577	-0.688	-0.297	-0.707	-0.567	0.466	0.169	0.658	0.014	0.228
FW	-0.474		-0.711	0.386	0.548	-0.009	-0.183	-0.651	0.752	0.787	**0.834**	0.540	-0.001	0.194	**0.840**	-0.674	-0.234	-0.783	-0.446	-0.475
SLA	**0.936**	-0.711		-0.709	-0.545	-0.172	0.188	**0.879**	-0.242	**-0.862**	-0.721	-0.679	-0.263	-0.654	-0.717	0.599	0.359	0.721	0.149	0.307
K	-0.720	0.386	-0.709		-0.204	-0.401	0.494	-0.390	0.207	0.323	0.105	0.039	-0.273	0.197	0.094	**-0.810**	-0.098	-0.738	-0.498	0.373
Ca	-0.424	0.548	-0.545	-0.204		0.576	**-0.885**	-0.776	0.268	**0.833**	**0.865**	**0.887**	0.764	0.725	**0.845**	0.211	-0.328	-0.142	0.422	**-0.908**
Mg	-0.268	-0.009	-0.172	-0.401	0.576		-0.681	-0.443	-0.395	0.346	0.415	0.746	0.637	0.533	0.512	0.426	-0.205	0.215	0.660	-0.535
Fe	0.181	-0.183	0.188	0.494	**-0.885**	-0.681		0.453	-0.132	-0.559	-0.672	-0.747	-0.711	-0.564	-0.601	-0.517	-0.007	-0.127	-0.543	**0.895**
NO3-	**0.813**	-0.651	**0.879**	-0.390	-0.776	-0.443	0.453		-0.180	**-0.851**	**-0.806**	**-0.868**	-0.765	**-0.859**	**-0.820**	0.240	0.572	0.433	-0.259	0.503
CH	0.155	0.752	-0.242	0.207	0.268	-0.395	-0.132	-0.180		0.360	0.545	0.086	-0.364	-0.304	0.459	-0.520	0.275	-0.634	-0.692	-0.439
Prot	-0.743	0.787	**-0.862**	0.323	**0.833**	0.346	-0.559	**-0.851**	0.360		**0.929**	**0.870**	0.557	0.747	**0.905**	-0.284	-0.408	-0.539	0.105	-0.648
Anth	-0.577	**0.834**	-0.721	0.105	**0.865**	0.415	-0.672	**-0.806**	0.545	**0.929**		**0.868**	0.420	0.534	**0.948**	-0.255	-0.177	-0.560	-0.053	**-0.842**
Asc	-0.688	0.540	-0.711	0.039	**0.887**	0.746	-0.747	**-0.868**	0.086	**0.870**	**0.868**		0.669	0.773	**0.894**	0.001	-0.273	-0.321	0.362	-0.777
NR	-0.297	-0.001	-0.321	-0.273	0.764	0.637	-0.711	-0.765	-0.364	0.557	0.420	0.669		**0.878**	0.415	0.577	-0.581	0.374	**0.876**	-0.533
NRT1.4	-0.707	0.194	-0.692	0.197	0.725	0.533	-0.564	**-0.859**	-0.304	0.747	0.534	0.773	**0.878**		0.519	0.194	-0.539	-0.027	0.641	-0.435
NRT1.5	-0.567	**0.840**	-0.717	0.094	**0.845**	0.512	-0.601	**-0.820**	0.459	**0.905**	**0.948**	**0.894**	0.415	0.519		-0.282	-0.282	-0.535	0.020	-0.774
GLN	0.466	-0.674	0.599	**-0.810**	0.211	0.426	-0.517	0.240	-0.520	-0.284	-0.255	0.001	0.577	0.194	-0.282		-0.038	**0.900**	**0.831**	-0.235
MIOX1	0.169	-0.234	0.359	-0.098	-0.328	-0.205	-0.007	0.572	0.275	-0.408	-0.177	-0.273	-0.581	-0.539	-0.282	-0.038		-0.191	-0.456	-0.061
GLDH	0.658	-0.783	0.721	-0.738	-0.142	0.215	-0.127	0.433	-0.634	-0.539	-0.560	-0.321	0.374	-0.027	-0.535	**0.900**	-0.191		0.728	0.153
DHAR	0.014	-0.446	0.149	-0.498	0.422	0.660	-0.543	-0.259	-0.692	0.105	-0.053	0.362	**0.876**	0.641	0.020	**0.831**	-0.456	0.728		-0.253
GULO6	0.228	-0.475	0.307	0.373	**-0.908**	-0.535	**0.895**	0.503	-0.439	-0.648	**-0.842**	-0.777	-0.533	-0.435	-0.774	-0.235	-0.061	0.153	-0.253	

Tomato



Correlations

	A						B										
	Abs B	AbsG	AbsR	B%	G%	R%	CRy1	PhyA	PHYB1	PHYB2	SFT	CRY2	Co1	COL	PAL	CHS1	CHS2
PH	-0,480	-0,397	-0,235	0,045	-	0,038	-0,279	0,160	-0,261	-0,269	-0,233	-0,737	0,135	0,342	-0,745	-0,786	-0,199
SD	0,374	0,584	0,528	-0,096	-	0,069	-0,203	-0,506	-0,100	-0,096	0,127	0,069	0,223	0,110	0,141	-0,175	0,375
FW	0,284	0,717	0,724	-0,135	-	0,143	-0,024	-0,345	0,121	0,106	0,238	0,042	0,335	-0,048	0,077	-0,175	0,501
LA	-0,173	0,380	0,538	-0,505	-	0,512	-0,080	-0,453	0,130	0,078	0,044	-0,389	0,330	0,141	-0,305	-0,398	0,233
SLA	-0,772	-0,545	0,275	-0,722	-	0,718	-0,045	0,083	0,200	0,117	-0,295	-0,604	0,179	0,187	-0,663	-0,548	-0,567
FL	0,459	0,860	0,832	-0,033	-	0,043	0,173	0,047	0,306	0,287	0,194	0,302	0,527	0,018	0,339	0,066	0,534
CH	-0,268	0,863	0,890	-0,292	-	0,293	0,343	0,326	0,628	0,604	0,246	0,338	0,159	-0,337	0,449	0,207	0,117
Prot	0,669	0,494	0,266	0,530	-	0,347	-0,267	-0,509	-0,356	-0,268	0,273	0,347	-0,105	0,022	0,396	0,163	0,567
Ant	0,682	0,514	0,300	0,432	-	-0,430	-0,062	0,433	0,097	0,157	0,002	0,907	-0,204	-0,209	0,854	0,817	0,451
Flav	0,693	0,475	0,236	0,501	-	-0,500	0,003	0,475	0,075	0,086	0,100	0,907	-0,183	-0,241	0,862	0,887	0,431
Pn	0,401	0,667	0,689	-0,229		0,282	-0,092	-0,475	0,106	0,157	0,113	-0,110	0,063	-0,101	-0,063	-0,440	0,257
gs	0,654	0,653	0,470	0,317		-0,316	-0,321	-0,540	-0,295	-0,203	0,140	0,305	-0,052	-0,038	0,310	-0,006	0,533
chl (a+b)	0,446	0,573	0,665	0,535	-	0,658	0,366	0,559	0,531	0,535	0,229	0,658	0,213	-0,238	0,725	0,600	0,441
chla/b	0,073	0,003	-0,023	0,145	-	-0,147	-0,201	-0,707	-0,508	-0,339	-0,043	-0,396	-0,012	-0,316	-0,269	-0,426	0,490
Car	0,802	0,576	0,495	0,484	-	-0,483	0,113	0,368	0,156	0,266	0,149	0,900	-0,119	-0,282	0,869	0,717	0,421
Chl/Car	-0,504	0,090	0,362	-0,688	-	0,701	0,339	0,321	0,559	0,404	0,131	-0,240	0,467	0,033	-0,136	-0,096	-0,034
					-												
CRy1	-0,299	0,154	0,328	-0,257	-	0,257											
PhyA	-0,047	0,047	0,125	-0,066	-	0,072	0,409										
PHYB1	-0,317	0,375	0,587	-0,554	-	0,556	0,577	0,608									
PHYB2	-0,248	0,434	0,606	-0,473	-	0,470	0,648	0,483	0,889								
SFT	0,123	0,238	0,087	0,057	-	-0,055	0,010	-0,228	0,062	0,032							
CRY2	0,815	0,502	0,146	0,609	-	-0,605	-0,065	0,436	0,074	0,083	0,149						
Co1	-0,178	0,057	0,215	-0,277	-	0,297	-0,022	0,242	0,209	0,084	0,018	-0,076					
COL	-0,162	-0,298	-0,235	-0,039	-	0,049	-0,030	0,166	0,067	0,011	-0,194	0,047	0,574				
PAL	0,709	0,588	0,263	0,503	-	-0,501	0,082	0,223	0,152	0,214	0,356	0,809	-0,131	-0,218			
CHS1	0,596	0,236	-0,057	0,584	-	-0,580	0,076	0,321	-0,038	0,044	0,200	0,724	-0,206	-0,244	0,877		
CHS2	0,520	0,385	0,190	0,474	-	-0,455	-0,233	-0,345	-0,390	-0,424	0,056	0,711	0,204	0,382	0,454	0,366	

7. We also tested whether the changes in light environment **during the development** can modify the growth and especially metabolism. **It can be an important question for producing functionalized foods.** For testing this, **spinach plants were cultivated under optimal light environment**, but **before harvest the spectral compositions were changed for a week**, and we tested their effect on the yield quality. Although the changes in light intensity and spectral composition did not modify the growth parameters (because the plants were mainly developed), they strongly affected the leaf composition. Similarly, as we observed before, the increase in light intensity induced the accumulation of primary metabolites (carbohydrates and proteins) and **decreased the free nitrate content** in leaves. Together with a **high proportion of blue light** they also **stimulated the accumulation of ascorbate (vitamin C) and increased the TAC activity in leaves**. The present investigations demonstrated that the yield quality of spinach leaves can be improved significantly by the increase of light intensity and the proportion of blue light for a week before harvest. **This process enriched the spinach leaves with health-promoting compounds without a significant increase in energy consumption**. According to this technique app. 40% of the total energy (kWh) can be saved as compared to those where the given light spectra and light intensity would have been applied for the total cultivation period. In addition, it should keep in mind, that those spectral combinations with provided good results (elevated light intensity and high blue light proportion would not be good for growth during a long cultivation period.

This experiment demonstrated that **a week period is enough for reprogramming of metabolism**.

8

In the next step, we tested **how much time is enough for reprogramming of metabolism**. Since photosynthetic processes are really sensitive to changes in light intensity and spectral compositions, the short-term changes in the light intensity and spectral composition were studied on the function of photosynthesis and in the change of metabolic processes in spinach leaves. We demonstrated that **within a short (15 min) time, red light provided more CO_2 assimilates per electron produced in spinach leaves**, while the **stomatal opening was stimulated more intensively by blue light** than by red

or white lights. However, these processes strongly depended on light intensity too. With the increase in light intensity, the red- and blue-light-induced spectrum-dependent changes were more pronounced. **Interestingly, white light containing wide spectral regions showed a similar light response to blue light in electron transport processes, and to red light in the behaviour of stomatal opening, while in CO_2 assimilation characteristics, the white light resembled blue light at low light intensities and red light at high light.** Furthermore, changes in spectral composition **modified** the primer **metabolic processes** as well. Red light induced the sugar accumulation, while more organic acids belonging to respiration streamline were produced under blue and white lights. These changes occurred even **within a short (30 min) period**.

These results support the previous results indicating that the changes in light intensity and spectral composition affect the photosynthetic processes in interaction. **The new finding: the light-induced changes occurred even within a short (30 min) time frame draw the attention to the importance of the changes in the light environment during experiments, measurements and under sample collections**.

Further investigations:

Besides achieving the aims of the project, **additional experiments** were also performed with the use of **chilli and a herb** called **Catharanthus**.

Chilli is widely used as a food additive and a flavouring and colouring agent and also has great importance in health preservation and therapy due to the abundant presence of **many bioactive compounds, such as polyphenols, flavonoids, carotenoids, and capsaicinoids**. Most of these secondary metabolites are strong antioxidants. In these experiments, the effect of light intensity and spectral composition was studied on the growth, flowering, and yield of chilli together with the accumulation of secondary metabolites in the fruit. Two light intensities (300 and 500 µmol m^{-2} s^{-1}) were applied in different spectral compositions. High light intensity increased the harvest index (fruit yield vs. biomass production) and reduced the flowering time of the plants. In these traits the absolute amount of different spectral regions paid an important role, the proportion of green light and the R/B ratio also had an influence. Among the light-induced changes, the increase of light fluence and the proportion of blue light stimulated flowering and yield in chilli, whereas low amounts of blue light enhanced green mass accumulation. Secondary metabolite production in the fruit was also affected by spectral composition and light fluence. The **phenolic content and the radical scavenging activity were stimulated by blue light** where its absolute amount was the main factor, **whereas capsaicin accumulation was suppressed by blue light**. **The red colour of the fruit (provided by carotenoids) was inversely correlated with the absolute amount of blue, green, and far-red light**. The results suggest that **a single spectral combination is not sufficient to ensure the optimal growth of chilli along the whole life cycle, only an adjustable light environment can ensure such conditions in indoor cultivation systems**. The accumulation of secondary metabolites could be modified by the adjustment of light intensity and spectral composition; however, **different types of metabolites required different light environments**.

Common periwinkle (**Catharanthus** roseus L.) is also an important medicinal plant used by the pharmaceutical industry. Our work aimed to determine the effect of light intensity on the primary and secondary metabolic processes, using various photosynthesis and targeted and untargeted analytical techniques. Growth light had only limited effects on the photosynthetic electron transport processes, although membrane stability seemed slightly higher in plants growing under higher light conditions. **The reduced growth light caused a reduction in certain primary metabolites, including amino acids and sugars, and it also reduced the contents of most of the phenolic compounds, such as coumaric**

acids, quercetin, kaempferol, rutin and their derivatives. In addition, **under blue light application, we also observed an intense alkaloid accumulation including vinblastine and vincristine which are important for medical industry alkaloids together with their precursors**, as compared to other light environments. These results also support that plant metabolism can significantly be modified by the changes in light environment, which is an easy mode to manipulate the metabolism and reach desired effects.

All of these results are published in 6 scientific papers, one is under evaluation and some others are still waiting for publication.

Brief summary

The investigations revealed many relationships between the changes in the light environment (including the changes of both the light intensity and spectral composition) and the growth and development, flowering and primary and secondary metabolisms. It was **revealed that many morphological traits such as plant height, specific leaf area, physiological parameters including photosynthetic activity of plants and stomatal conductance and the accumulation of several primary and secondary metabolites (for instance carbohydrate, chlorophyll, carotenoid, anthocyanin and flavonoid contents) showed a linear correlation with the changes of the proportion of blue light. Others, including stem diameter, biomass, leaf area and protein content grew up only to a point. Above this threshold, the blue light had adverse effects.** While **red light stimulates biomass production and accumulation of carbohydrates. blue light forced the accumulation of proteins, their precursors, amino acids, secondary metabolites including anthocyanins and flavonoids** in many species. However, the **light regulation of different metabolic pathways can be different, as presented in the case of chilli peppe**r. It was also determined which photoreceptors participated in the different morphological and primary and secondary metabolic processes. Furthermore, we also determined what was the most important light factor (namely the absolute amount or the proportion of different light components) in these processes.

The optimal light intensity and spectral combinations depend on the genotypes and developmental stages of plants, but hardly on the cultivars, however, the optimal spectral combination depends on **the light intensity** too. **If the light intensity is too low, an elevated proportion of blue light is suggested to use.** These results showed that **light intensity and spectral composition regulate the growth and metabolism of tomato plants in interaction**. We also demonstrated that the changes in **light environments can modify the metabolism very quickly (photosynthesis within 15 min, primary metabolism within 30 min, and secondary metabolism within a day) which can be manifested in a significant modification in the yield quality within a week.**

All of our results supported our theory that for ensuring the optimal light conditions indoor or to manipulate the metabolism in order to achieve the desired effect, **a programable light environment is recommended to be used adequately for species and developmental stages**.

During this period (2019-2024) 6 papers have been published, however, one paper is under review and another is under preparation.