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Interaction Between Flowering Initiation and Photosynthesis

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1. Introduction

The vast majority of the biological processes are dependent on solar radiation. Photosynthesis is the main process which intermediate between light and plant development. Plants utilize solar radiation as a source of energy for photosynthesis, drives water and nutrient transport (Ballaré and Casal, 2000). Besides they use it as environmental cue to modulate a wide range of physiological responses from germination to fruiting (Suetsugu and Wada, 2003), modulates several metabolic pathways affecting cell metabolism, also is the basis to plant structure and molecule production, thus part of what is produced by photosynthesis is used in photomorphogenesis (Quail, 2007). That composes a complex development program called photomorphogenesis.

From many developmental processes that define plant form and function, flowering is of exceptional interest. A lot of horticulturally important plants are depended upon flowering. Much effort is being put into regulating the timing of flowering. Depending on particular species sensitivity to photoperiod, the transition of apex to the reproductive stage is affected by the duration of light (Leavy and Dean, 1998; Nocker, 2001). Many flowering-time studies are based on *Arabidopsis thaliana* model because classic events, the daylenght sensing mechanisms can be light mediated (Bernier et al., 1993). Over the years physiological studies have led to four separate but herewith interdependent models for the control of flowering: photoperiodic induction, non-photoperiodic (autonomous/vernalization), induction by gibberellins and by carbohydrates. The floral transition in biennial photoperiod-sensitive and cold-required plants is associated with an increased content of carbohydrates in apical meristems (Blazquez, Weigel 2000). According to Corbesier et al. (1998), the concentration of sucrose increases dramatically in phloem exudates upon photoinduction in both short and long day plants, even when the photoinductive treatment and accumulation of non-structural carbohydrates limits photosynthesis by feedback regulation (Araya et al., 2006; Araya et al., 2010; Paul and Driscoll, 1997; Paul and Foyer, 2001;). Moreover, sucrose may function as long-distance signalling molecule during floral induction (Bernier et al., 1993; Leavy and Dean, 1998). Meanwhile, accumulation of glucose has been shown to suppress expression of photosynthetic genes and induce leaf senescence, via the signalling hexokinase pathway (Dai et al., 1999). Araya et al. (2006) states, that repression of photosynthesis occurs mainly in leaves that accumulates starch. Though starch per se is not metabolically active,

hexokinase is a sensor for sugar repression of photosynthesis (Araya et al., 2010). According to Paul and Foyer (2001), starch synthesis is promoted when sucrose synthesis is restricted and in many plant species leaf starch serves as a transient sink to accommodate excess photosynthate that cannot be converted to sucrose and explored. Thus several mechanisms for the carbohydrate repression of photosynthesis have been discussed: accumulation of non-structural carbohydrates in leaves represses photosynthesis through sucrose synthesis and accumulation of sugar phosphates in the cytosol (Chen et al., 2005); through starch accumulation which causes the deformation of chloroplasts (Nakano et al., 2000); soluble sugars suppress the expression of photosynthetic genes (Paul and Foyer, 2001). Araya et al. (2006) describes carbohydrate repression of photosynthesis in relation to leaf developmental stages, as the metabolic roles of carbohydrates dramatically change depending on the leaf age. The photosynthetic system is constructed by importing carbohydrates to young sink leaves, while mature source leaves with high photosynthetic activities export photosynthates to sink organs. As *Apiaceae* plants form below-ground storage organs, the translocation of assimilates and the distinct distribution of biomass between leaves and storage organs is a sensitive indicator for changes in environment conditions. Thus the transport and distribution of non-structural carbohydrates between plant organs is important for triggering the complete sequence of photosynthesis action and floral evocation. The distinct distribution of biomass between the leaves and below-ground storage organ, forming a clear model of assimilate partitioning between source and sink, can be a sensitive indicator for changes in environmental conditions. Moreover, it can play a key role as 'cross-talk' of response pathway with other flowering induction pathways. Therefore it is important to understand the biological regularities of plant vegetative growth and generative development. The photo and thermo induction is needed for biennial plants for the formation of inflorescence stem and flowers. The biological background of juvenile period and insensibility to the influence of photo- and thermo induction in the physiology of plant ontogenesis is not explored in detail yet. However still, the participation of photosynthetic system and its primary metabolites in flower initiation processes is not clearly understood. It is sill unclear how photosynthetic pigments, non-structural carbohydrates and other materials distribute and interact during photo and thermo induction and during other flowering initiation processes. Thus, it is very important to understand the mechanisms of plant morphogenesis, to control the growth and development processes and theirs' ratio on the purpose to optimize the formation of productivity elements during different ontogenesis stages.

Despite on light duration (photoperiod), light quality (spectral composition) and quantity (flux density) also make influence on plant morphogenetic processes (Hohewoning et al., 2010; Matsuda et al., 2004). The genetic investigations showed that response to light is the outcome of various photoreceptors information acting through complex interacting signal network (Carvalho et al., 2011; Folta and and Childers, 2008; Leavy and Dean, 1998). Therefore this problem is being tried to solve by artificial lighting with solid-state light-emitting diodes (LEDs). As pant physiology and development is regulated not only via photosynthesis (chlorophylls, carotenoids) but also through specific photomorphogenetic photoreceptors (phytochromes, cryptochromes and phototropin) (Ballaré and Casal, 2000; Carvalho et al., 2011). Thus the results from LEDs lighting suggest that the precise selection of particular spectral components enables to modulate the photomorphogenetic responses of the plant (Folta and and Childers, 2008; Goins et al., 1997; Hohewoning et al., 2010; Matsuda

et al., 2004). The light signal transduction pathways involve a complex system, which include photoreceptors absorbing particular wavelengths. Chlorophyll *b* absorb blue (absorption maximum at 430, 455 nm) and red (640nm) light, carotenoids absorb near 450 nm, and chlorophyll *a* absorb near 660 nm and triggers photosynthetic process (Bell et al., 2000; Carvalho et al., 2011), but these pigments reflect green light (Carvalho et al., 2011). The photomorphogenetic response depends on red (600 – 700 nm) and far-red (700 – 800 nm) absorbing phytochromes and blue/UV-A (320 – 400 nm) absorbing cryptochromes action (Bradburne et al., 1989; Bell et al., 2000; Carvalho et al., 2011). As it is known that blue light plays important roles in photomorphogenesis, chlorophyll biosynthesis, maturation of chloroplast, photosynthesis or stomatal opening (Hogewoning et al., 2010). Whereas red light is important for elongation processes, changes in plant anatomy, and development of photosynthetic apparatus of plants (Goins et al. 1997;). Thus blue and red LEDs have been used for studies in many areas of photobiological research such as photosynthesis, chlorophyll synthesis and morphogenesis with model plants such as *Arabidopsis*. However, very few studies have been carried out on the effects of LEDs on physiological responses or morphogenesis of *Apiaceae* plants. Besides, there is no much data about the effects of different solid-state light-emitting diodes spectral composition (blue, red, far-red, green, yellow, UV-A) on the growth and development of edible carrot, carbohydrate and chlorophyll contents and distribution between plant organs. Thus the manipulation of photosynthetically active and morphogenic light allows regulating allocation and use of photosynthate within the developing plant.

2. Materials and methods

2.1 Growth conditions and plant material

Edible carrot (*Daucus sativus* (Hoffm.) Röhl.) and common caraway (*Carum carvi* L.) were initially grown in vegetative tumbler, 54x34x15 cm in size, placed in a greenhouse until particular developmental level needed for special experiment (16-hour photoperiod and 21/16°C day/night temperature were maintained). Peat (pH $\approx$ 6) was used as a substrate.

2.2 Flowering initiation under controlled environment

Carrots with 5 and 9 leaves in rosette, common caraway with 9 leaves in rosette were grown in a phytotron chambers with different photo and thermo periods for 120 days: 0hr and +4˚C; 8hr and +4˚C; 16hr and +4˚C; 8hr and +21/17˚C; 16hr and +21/17˚C. Then evocation, flower initiation and differentiation processes were investigated under illumination with the photoperiod of 16-hr and +21/16±2°C day/night temperatures.

2.3 The control of morphogenesis and photophysiological processes by light-emitting diodes (LED)

To induce vernalization processes carrots with 9 leaves in rosette were moved from the greenhouse to the phytotron chambers under low temperature (+4°C) treatment for 120 days. Then evocation, flower initiation and differentiation processes were investigated under illumination with the photoperiod of 16 hour and +21/17±2°C day/night temperatures maintained for one month. The originally designed (Tamulaitis et al., 2005) light emitting diode based lighting units, consisting of commercially available wavelengths: blue (445 nm, LuxeonTM type LXHL-LR5C, *Lumileds Lighting*, USA), red (638 nm, delivered

by AlGaInP LEDs Luxeon™ type LXHL-MD1D, *Lumileds Lighting*, USA), red (669 nm, L670-66-60, *Epitex*, Japan), and far red (731 nm, L735-05-AU, *Epitex*, Japan) LEDs were used. Illumination with different spectra was generated by LED-based illuminator (Table 1). The lighting treatment started at vegetative stage. The analyses were performed before after four weeks LED treatment.

Light spectral components	**Photon flux densities, μmol $m^{-2}s^{-1}$**
445, 638, 669, 731 nm (Basal)	167,2
445, 638, 669 nm	167,9
445, 638, 731 nm	160,1
638, 669, 731 nm	169,5
455, 638 nm	160,4
638 nm	150,0

Table 1. The composition of light spectral components (LED)

2.4 Determination of photosynthetic pigments

About 0.2 g of fresh leaf tissue was ground with 0.5 g $CaCO_3$, washed with pure acetone, and filtered through cellulose filter. Sample was diluted till 50 ml with 100% of acetone. Chlorophyll *a*, *b* and carotenoids (carot.) were measured by spectrophotometric method of Wetshtein (Gavrilenko and Zigalova, 2003). The spectrum of photosynthetic pigments was measured at 440.5 nm, 662 nm and 644 nm respectively.

2.5 Determination of non–structural carbohydrates

Fructose (Fru) glucose (Glu) and sucrose (Suc) were measured by high performance liquid chromatography (HPLC) method. About 1 g of fresh plant tissue (leaves, zone of apical meristems or root-crop) was ground and diluted with +70° C 4 ml double distilled water. The extraction was carried out for 24 h. The samples were filtered using cellulose acetate (pore diameter 0.25 μm) syringe filters. The analyses were performed on Shimadzu HPLC (Japan) chromatograph with refractive index detector (RID 10A), oven temperature was maintained at +80° C. Separation of carbohydrates was performed on Shodex SC-1011 column (300 x 4.6 mm) (Japan), mobile phase – double distilled water. The sensitivity of the HPLC method was established using a method validation protocol (ICH, 2005).

2.6 Physiological indices

Flowering initiation stages were described according to Duchovskis (2000).

The net assimilation rate (NAR) of a plant was defined as its growth rate per unit leaf area (LA) for any given time period (day). It can be calculated as:

NAR (g cm^{-2} d^{-1})=(1/LA)(dW/dt), where LA is leaf area (cm^2) and dW/dt is the change in plant dry mass per unit time.

The leaf area was measured by "WinDias" leaf area meter (Delta-T Devices Lts, UK). Leaves and root-crops were dried in a drying oven at 105° C for 24 h for the determination of dry mass.

2.7 Statistical analysis

The analysis were performed in seven (biometrical measurements) or five (analytical measurements) replications and data analysis was processed using one-way analysis of

variance *Anova*, the Duncan 's LSD test to trial mean at the confidence level $p = 0.05$. The standard deviation of mean to express values of NAR was used.

3. Results and discussion

3.1 Flowering and physiological signals

As flowering is the first step of sexual reproduction, thus the timing of the transition from vegetative growth to generative development is very important in agriculture, horticulture or plant breeding (Bernier et al., 1993; Nocker, 2001). During juvenile period plants are insensitive to any flowering inductive factor and are not able to form reproductive organs. The minimal developmental level to accept photo and thermo inductive factors for flowering induction for various plants differs (Duchovskis et al., 2003). Much of plant development occurs at the shoot apical meristem (SAM). The acquisition of reproductive competence is marked by changes in the morphology and physiology of vegetative structures, where SAM is the primordia for growth of vegetative organs (leaves) or is responsible for transition to reproductive development (Leavy and Dean, 1998).

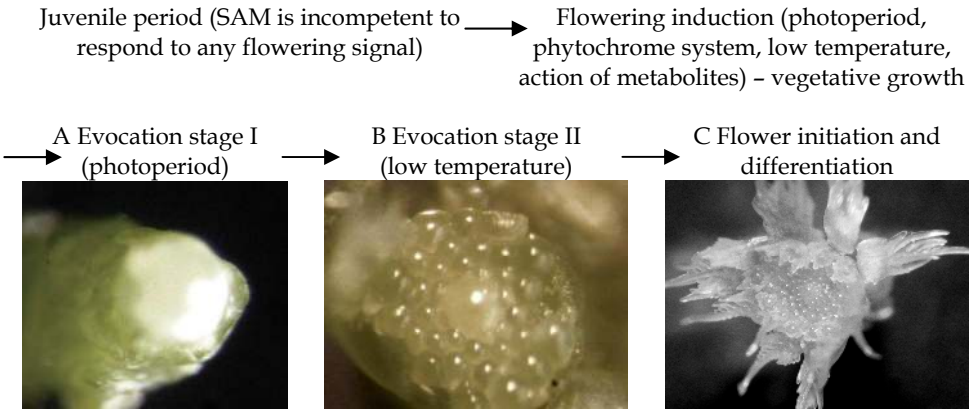

Fig. 1. Model of flowering initiation.

The flowering initiation of biennial plants is a multicomponent and multistep mechanism. It has several stages: flowering induction, evocation, flower initiation and differentiation, gamete initiation and destruction of flowering stimulus (Duchovskis, 2004). Furthermore, it is essential to know the limiting factors of flowering initiation and further development. Endogenous and exogenous factors affecting this process are the complex ones and they depend on solid action of photosynthesis and metabolism systems (Gibson, 2004). Plant flowering initiation processes are related to the duration of juvenile period. During this period plants are insensitive to any inductive factor and are not able to form reproductive organs (Bernier et al., 1993; Duchovskis et al., 2003; Leavy and Dean, 1998). The model of flowering initiation is presented in Fig. 1. According to this model, flowering can occur when certain limiting factors are present at the apex at the right time and in the appropriate concentrations. The multifactoral control model of flowering shows, that a number of promoters and inhibitors, including assimilates, are involved in controlling the developmental transition (Bernier et al., 1993; Gibson, 2004; Németh, 1998).

According to Németh (1998), for the majority of the most important vegetables of the *Apiacea* family temperature between 5–10°C proved to be the most effective for flowering, however both lower (5°C) and higher (15°C) temperatures might have an inductional effect. Duchovskis (2000) stated that the formation of inflorescence axis (5 formed leaves in rosette for carrots) means that photo induction ended and after that the processes of second evocation stage began. The thermo induction conditioned the formation of inflorescence axis elements (evocation stage II) when carrots had 8–9 leaves in rosette (Duchovskis et al., 2003). However, in opposite to high temperature, low positive temperature caused faster development rate of carrots independently from duration of photoperiod (Table 2). As for caraway, it seems that juvenile period is longer than in carrots. Németh (1998) noticed that optimal induction regime for caraway might lie between 5°C and 8°C, which is effective when lasting more than two weeks. In case of caraway, scientific data are very few. Putievsky (1983) examined the effect of day length and temperatures on the flowering of three *Apiacea* species: caraway, dill and coriander. The tree spices exhibited different reactions to the treatments. Caraway developed flowers under all experimental circumstances (18/12°C or 24/12°C day and night temperatures, with 10 h or 16 h photoperiods). Pursuant to other authors, a longer vegetative growth of caraway at low (4°C) temperature and short day (SD) (8 h) occurred, whereas earlier flowering was preceded by long day (LD) (16 h) and low temperature, and the duration of photoperiod did not affect flowering rate under treatment with high temperature (see Table 2). Thus, both a shorter period as well as high temperatures results in partial flowering of treated species. It might mean either that caraway does not need any short day induction for flower initiation at all, or that any photoperiodic response is effective only with interaction of low temperatures (Németh, 1998).

Confirming the conception of flowering induction and evocation of wintering plants, we assume that the mechanisms of photo and thermo induction in edible carrot and common caraway are independent and autonomous. That's why the minimal developmental level to accept these flowering inductive factors differs.

Species	Number of developed leaves	Treatment				
		+4°C-0h	+4°C-8h	+4°C-16h	+21/17°C - 8h	+21/17°C - 16h
Carrot	5	-	4	4	2	2
	9	-	5	5	3	3
Caraway	9	-	2	4	3	3

Table 2. The transition level from vegetative to generative stage in edible carrot and common caraway. Note. 1 point – the lowest development rate, 5 points – the most intensive.

According to our data there were no drastic changes in accumulation of photosynthetic pigments during transition from vegetative growth to generative development (Table 3). During flower initiation and differentiation the significant decrease of chlorophyll *a* and carotenoids was observed under low temperature and short photoperiod treatment, whereas normal temperature and SD photoperiod conditioned the significant increase of these

pigments for carrots with 5 leaves in rosette. In opposite to younger plants, the accumulation of photosynthetic pigments was significantly effected by low temperature already in first evocation stage. Moreover during flower initiation and differentiation maturated plants accumulated significantly less photosynthetic pigments under LD photoperiod.

Development	Treatment	Eddible carrot						Common caraway		
		5 leaves			9 leaves			9 leaves		
		Chl *a*	**Chl** *b*	**Carot.**	**Chl** *a*	**Chl** *b*	**Carot.**	**Chl** *a*	**Chl** *b*	**Carot.**
Evocation stage I	4ºC-8h	1.97ab	0.51ab	0.83ab	2.55b	0.56a	0.78b	1.62c	0.52c	0.55abc
	4ºC-16h	1.92ab	0.51ab	0.90b	2.09a	0.65b	0.65a	1.42b	0.49abc	0.59c
	21ºC-8h	2.08b	0.52ab	0.84ab	1.76a	0.53a	0.56a	1.22a	0.40a	0.48a
	21ºC-16h	1.92ab	0.55b	0.73ab	1.98a	0.56a	0.61a	1.45b	0.50bc	0.53abc
Evocation stage II	4ºC-8h	1.74ab	0.55ab	0.66ab	1.74ab	0.53a	0.65ab	1.40abc	0.38d	0.61b
	4ºC-16h	1.97ab	0.63ab	0.72b	2.15b	0.67c	0.73ab	1.62c	0.45c	0.75c
	21ºC-8h	2.03ab	0.63ab	0.61b	2.09ab	0.56abc	0.73b	1.22a	0.26a	0.46a
	21ºC-16h	2.19b	0.68b	0.68ab	2.08ab	0.61abc	0.64ab	1.47bc	0.44c	0.64b
Flower init. and diff.	4ºC-8h	1.70a	0.58ab	0.57a	2.09bc	0.69bc	0.67c	1.13b	0.25b	0.39bc
	4ºC-16h	1.89abc	0.59ab	0.76bcd	2.16c	0.71c	0.68c	0.89a	0.18a	0.32a
	21ºC-8h	2.47c	0.61ab	0.81d	2.00bc	0.69bc	0.60d	1.28c	0.31c	0.41c
	21ºC-16h	1.87abc	0.78b	0.61ab	1.19a	0.37a	0.41a	1.06b	0.23b	0.40bc

Table 3. The distribution of photosynthetic pigment content during different flowering initiation stages in leaves of edible carrot and common caraway. The values with the same letters are not significantly different with P≤0.05

In relation to leaf developmental stages the repression of photosynthesis by non-structural carbohydrate accumulation was examined by Araya et al. (2006) in *Phaseolus vulgaris* L. They noticed that carbohydrate accumulation on photosynthesis repression is significant in the source leaves, but not in the young sink leaves. According to our data, in carrot with 5 leaves in rosette significantly the highest content of glucose was observed under low temperature and SD treatment on first evocation stage (Table 4). However the correlation between chlorophyll content and glucose was week. The accumulation of glucose in carrot leaves mostly was effected by low temperature and LD photoperiod. Meanwhile in caraway leaves significantly bigger contents of glucose were determined under LD and normal temperature during evocation. Paul and Stitt (1993) stated that at low temperature hexose

does not induce sugar repression. It is likely that more than one trigger is involved in modulating the carbohydrate signal perception or transduction. Observing the transition from vegetative growth to generative development, linear correlation was noticed under LD treatment in carrot with 5 leaves in rosette. But for carrots with 9 leaves in rosette such linear correlation was affected by low temperature and SD photoperiod. This may occur due to higher contents of glucose in older plants leaves. Krapp and Stitt (1995) noticed that cold exposure prevents carbohydrate export from leaves.

Development	Treatment	Eddible carrot						Common caraway		
		5 leaves			9 leaves			9 leaves		
		Chl *a*+*b*	Glu	COREL	Chl *a*+*b*	Glu	COREL	Chl *a*+*b*	Glu	COREL
Evocation stage I	4ºC-8h	2.48ab	3.18c	-0.3	2.67ab	5.75c	-0.6	2.14b	1.11c	-0.8
	4ºC-16h	2.43ab	0.37ab	-0.4	2.74b	5.01c	-0.9	1.85a	0.40a	1.0
	21ºC-8h	2.60b	0.72b	1.0	2.28ab	3.15a	-1.0	1.62a	0.87b	-1.0
	21ºC-16h	2.47ab	0.02a	1.0	2.60ab	3.31a	-0.9	1.75a	1.58d	-0.5
Evocation stage II	4ºC-8h	2.62abc	2.17c	0.2	2.46ab	1.00b	1.0	1.78a	0.82c	0.7
	4ºC-16h	2.60abc	4.59d	1.0	2.82b	2.00c	0.4	2.07c	0.21a	0.9
	21ºC-8h	2.43a	0.13a	0.8	2.69ab	0.49a	-0.6	1.58a	0.65b	-0.2
	21ºC-16h	2.87c	1.39b	-0.1	2.69ab	1.06b	-0.3	1.81abc	1.10d	0.5
Flower nit and diff.	4ºC-8h	2.28a	1.95a	-0.3	2.68bc	2.56b	-1.0	1.28abc	1.22d	0.9
	4ºC-16h	2.51a	1.67a	1.0	2.87c	3.12c	0.2	1.13a	0.25a	0.8
	21ºC-8h	3.26b	1.74a	-0.7	2.69bc	2.17b	-0.2	1.59c	0.80c	-1.0
	21ºC-16h	2.45a	3.19b	0.9	1.49a	0.40a	-0.5	1.32abc	0.45b	-0.7

Table 4. The correlation between chlorophyll a and b sum and glucose during different flowering initiation stages in edible carrot and common caraway leaves. The values with the same letters are not significantly different with P≤0.05

Moreover, both chlorophyll and glucose contents were significantly higher in carrot with 9 leaves in rosette, but the correlation was week under low temperature and SD photoperiod in flower initiation and differentiation stage. This is in agreement that mature source leaves export primary metabolites to sink organs, while carbohydrates in young sink leaves are used for photosynthetic system construction. In case of caraway, low correlation in second evocation stage was observed under normal temperature and SD due to significantly low contents of chlorophylls and decrease of glucose concentration. In other developmental stages strong or linear correlation in caraway was observed. Araya et al. (2010) observed negative relationship between leaf carbohydrate content and photosynthetic rate. They showed that leaf photosynthesis is influenced by changing carbohydrate level rather than through modifying sensitivity of the leaf to the carbohydrate level.

Photosynthesis and synthesis of primary metabolites occurs in leaves. Plants of *Apiacea* family are interesting because they form crop-root. It is important to handle mechanisms which regulate photosynthates export from source leaves in response to the demand in the growing sink organs of plant. One of widely cited possibilities is that sugar repression is associated with Rubisco and its distribution to other parts of the plant (Lu et al., 2002; Paul and Stitt, 1993; Paul and Foyer, 2001). The changes in carbohydrate accumulation are frequently in response to changes in the balance between supply and demand for fixed carbon perceived from dark reactions (Farrar et al., 2000). Moreover sink regulation of photosynthesis is highly dependent on the physiology of the rest of the plant, which regulates photosynthesis through signal transduction pathways (Paul and Foyer, 2001).

According to our data (Table 5), under low temperature significantly higher concentrations of hexoses were determined in apical meristems of carrots with 5 and 9 leaves in rosette during transition from vegetative growth to generative development.

Meanwhile in caraway apical meristem zone low temperature conditioned significantly higher accumulation of fructose and under normal temperature exposure significantly higher contents of glucose were determined during transition from first to second evocation stage. This means that glucose can act as morphogenetic factor and regulate the mechanisms of plant development and flowering (Borisjuk et al., 2003; Gibson, 2005). This is in correlation with our data, because the best development of carrot was observed under low temperature, and high development rate of caraway was observed under normal temperature (Table 2). The best development rate of caraway was observed under low temperature and LD (Table 2), this can be explained by significantly high content of sucrose in apical meristem zone (Table 5) during evocation. Moreover there were no significant differences in sucrose content in caraway leaves and the concentrations were very low. Besides, high contents of sucrose were detected in root-crop of caraway. It is known that many plant developmental, physiological and metabolic processes are regulated by soluble sugars such as glucose and sucrose and by other signaling molecules (Gibson, 2004). A lot of scientists investigated the sucrose distribution in apex and in other plant tissues (Bodson and Outlaw, 1985; Lejeune et al., 1993; King and Ben-Tal, 2001). It is presumed that the supply of sucrose to apical meristemic tissues is important for flower induction. Still it may not be the specific flowering induction stimulus and independent from the response to the photoperiod duration. In agreement with other authors (Borisjuk et al., 2002), the highest sucrose concentrations were determined in cells which can actively divide (Tabe 5). Carrots with 9 leaves in a rosette can accept the stimulus of photo induction. Unlike caraway, during the evocation, high temperature disturbs sugar metabolism in carrot apical meristems. Such sugar metabolism and transport to apical meristems can determine the differences in plant development processes (Table 2). Also it may depend on the special plant requirement to photo and thermo induction for the acceptation of flowering stimulus. After transition to generative development during flower initiation and differentiation intensive accumulation of sucrose in apical meristems and transport from leaves to root-crop was observed (Table 5). It is known that sucrose may be converted to glucose and fructose by acid invertase (Mansoor et al., 2002) or it can be reduced from starch by sucrose synthase (Sturm et al., 1999). There is contrary data about feedback inhibition of photosynthesis.

Development	Treatment	Eddible carrot, 5 leaves								
		Root-crop			Apical meristem zone			Leaves		
		Fru	Glu	Suc	Fru	Glu	Suc	Fru	Glu	Suc
Evocation stage I	4ºC-8h	7.40c	7.32b		6.31b	4.60a	0.33a	2.99c	3.18c	
	4ºC-16h	1.62ab			12.90d	13.11d	0.53b	2.22c	0.37ab	
	21ºC-8h	0.41a			4.56a	5.96b	1.93d	0.05a	0.72b	
	21ºC-16h	2.62b	1.57a		10.07c	7.00c	0.95c	0.04a	0.02a	
Evocation stage II	4ºC-8h	8.41c	5.23c		6.34a	3.63a	0.47a	4.26ab	2.17c	1.05a
	4ºC-16h	3.82a	3.12a		12.91c	10.34c	0.75a	5.12b	4.59d	1.03a
	21ºC-8h	3.88a	3.99b	3.38b	8.43ab	6.25b	1.68c	2.37ab	0.13a	1.52b
	21ºC-16h	7.75c	6.28d	2.12a	10.11b	5.52b	1.34c	3.64ab	1.39b	3.04c
Flower init. and diff.	4ºC-8h	4.91c	6.16d	8.41a	4.04c	4.43d	8.86b	1.60a	1.95a	0.16a
	4ºC-16h	4.34d	4.47c	10.28a	2.91b	2.32b	10.59c	1.28a	1.67a	0.09a
	21ºC-8h	0.60a	1.16a	25.37b	2.14a	0.24a	7.46a	2.71b	1.74a	1.06b
	21ºC-16h	4.86c	3.99b	32.03c	4.66d	3.88c	16.36d	3.82c	3.19b	
Eddible carrot, 9 leaves										
Evocation stage I	4ºC-8h	7.11c	8.81b	6.95a	7.10c	8.80b	6.92a		5.75c	
	4ºC-16h	12.25d	7.85a	14.60b	12.22d	7.82a	14.53b		5.01c	
	21ºC-8h	1.63a		16.49c	2.40a		16.43c		3.15a	0.77b
	21ºC-16h	4.61b		18.50d	4.60b		18.43d		3.31a	0.08a
Evocation stage II	4ºC-8h	4.19d		24.01d	6.48d	2.23c	11.12b	3.83d	1.00b	
	4ºC-16h	3.49b		18.47c	4.07c		7.79a	2.76c	2.00c	
	21ºC-	2.25a	2.07b	6.80a	1.83a	0.21a		2.34b	0.49a	

Development	Treatment	Eddible carrot, 5 leaves								
		Root-crop			Apical meristem zone			Leaves		
		Fru	Glu	Suc	Fru	Glu	Suc	Fru	Glu	Suc
	8h									
	21°C-16h	3.69bcd	1.39a	9.20b	3.57b	0.88b		1.11a	1.06b	
Flower nit. and diff.	4°C-8h	4.60c	3.42c	18.27a	5.82c	2.47c	5.10bcd	3.15d	2.56b	
	4°C-16h	4.32b	4.67d	17.41a	5.84c	5.32d	4.64b	2.95c	3.12c	
	21°C-8h	0.79a	1.71b	23.68b	3.59d	1.42b	1.95a	1.96b	2.17b	
	21°C-16h	1.03a	0.25a	26.33c	2.15a	0.42a	5.56d	1.35a	0.40a	
Common caraway, 9 leaves										
Evocation stage I	4°C-8h	0.67c	0.50b	3.58a	0.65c	0.63b	4.49a	2.63b	1.11c	0.34ab
	4°C-16h	1.16d	0.27a	5.43c	1.12d	0.33a	4.71b	2.19a	0.40a	0.60ab
	21°C-8h	0.40b	2.11d	7.85d	0.37b	2.63d	10.01d	3.28c	0.87b	0.87b
	21°C-16h	0.22a	1.02c	5.10b	0.23a	1.23c	6.51c	2.29a	1.58d	0.21ab
Evocation stage II	4°C-8h	0.40c	0.30b	2.03a	2.60d	0.50b	1.21a	2.20a	0.82c	0.34ab
	4°C-16h	0.70d	0.20a	2.97b	1.73c	0.20a	5.43c	2.00a	0.21a	0.60ab
	21°C-8h	0.23b	1.50d	6.00c	1.34b	1.12c	3.89b	2.97b	0.65b	0.87b
	21°C-16h	0.10a	0.60c	3.03b	0.71a	1.50d	6.82d	1.90a	1.10d	0.21ab
Flower init. and diff.	4°C-8h	0.26b	1.01c	5.43b	1.47c	0.24c		1.80d	1.22d	
	4°C-16h	0.31c	1.20d	7.40c	1.08b	0.97d	1.30b	1.05c	0.25a	0.38b
	21°C-8h	0.04a	0.50a	5.40b	0.77a	0.03a	0.08a	0.83a	0.80c	
	21°C-16h	0.04a	0.80b	2.43a	1.16b	0.10b	0.04a	0.93b	0.45b	0.37a

Table 5. The distribution of non-structural carbohydrates between edible carrot and common caraway organs. The values with the same letters are not significantly different with P≤0.05

It has been found that inhibition of photosynthesis occurs in both starch-storing and low accumulating species (Goldschmidt and Huber, 1992). Recent evidence suggests that night-time hexose content derived from starch may provide long term signals for gene expression responsible for feedback regulation. A lag in starch degradation lasts till there is a drop in leaf sucrose, thus the information on the carbohydrate status of the chloroplast may contribute information on the assimilate status of the leaf (Paul and Foyer, 2001).
The effects on Rubisco expression depends not only on distribution between plant organs (Lu et al., 2002), but also on leaf age (Aryae et al., 2006). Since carbohydrate accumulation in the leaves leads to nitrogen release from Rubisco, then sugar signaling is dependent on both nitrogen and carbon status of the plant (Paul and Foyer, 2001). Moreover glucose and sucrose is supposed to be signaling molecules for flowering initiation (Gibson, 2005; King and Ben-Tal, 2001) and their metabolism and supply to apical meristemic tissues determine the plant development. Thus sugars must be considered in the wider context of other important factors, not only as a part of signals that coordinate source-sink interaction.

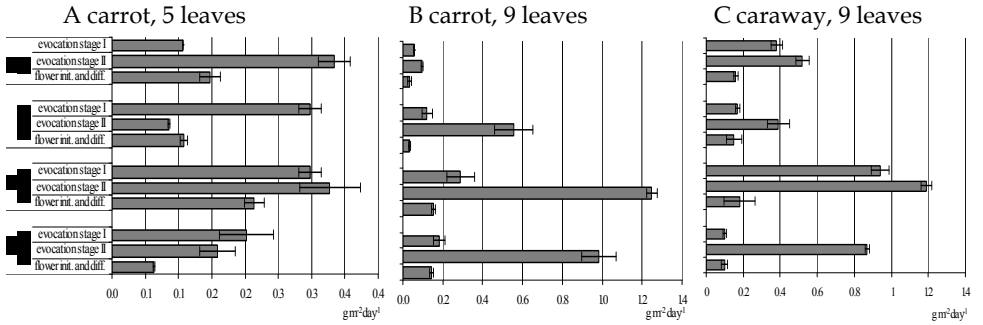

Fig. 2. The distribution of net assimilation rate during different flowering initiation stages in edible carrot and common caraway.

Net assimilation rate (NAR) is related to whole-plant net photosynthetic rate on an area basis and is primary determinant of relative growth rate, which can change daily and over the growing season (Shipley, 2006). Moreover NAR depends on biomass accumulation in a given area and on CO_2 assimilation during day, thus leaf area plays an important role in photosynthesis (Cho et al., 2007; Evans and Pooter, 2001). Therefore normalized photorespiration processes would improve net assimilation rate. Apart of light, temperature is one of indirect factors effecting photosynthesis as critically high temperature accelerates the los of water and stomata closing (Öpik, Rolfe, 2005). According to our data the common trend of NAR increase during second evocation stage was determined (Fig. 2). Such data confirms that plants can accept photo- and thermo- inductive stimulus, and the duration of juvenile period can be associated with maturity of photosynthetic pigments system. Besides normal temperature conditioned higher values of NAR in carrot and caraway with 9 leaves in rosette. The decrease of NAR in all cases was observed in flower initiation and differentiation stage (Fig. 2). This can be related with carbohydrate transport from leaves to root-crop and apical meristem (Table 5). Common trends allow presuming that photosynthetic apparatus of plant not only supply metabolites for morphogenetic processes but also proximately participates in these processes.

3.2 Photophysiological processes: Manipulation by light-emitting diodes

In agreement with other authors (Yanagi et al., 2006), our results show that the elimination of both red (669 nm) and far-red (731 nm) light, which is utilized in the reversible transformation of phytochrome, suppresses floral initiation (Table 6). Although plants were treated by low positive temperatures required for floral induction, after treatment with above-mentioned illumination (455, 638 nm or sole 638 nm) carrots remained in the vegetative stage (Table 6). Also, for these treatments the sugar concentration was low and distribution of hexoses and sucrose was the same in roots and in leaves (Table 8). The elimination of only far-red (445, 638 and 669 nm), red (455, 638 and 731 nm) or blue (638, 669 and 731 nm) light did not have such a dramatic effect on the suppression of plants flowering (Table 6). These results imply that at least far-red is required to invoke floral initiation, probably mediated by phytochrome response. This is in agreement with Ballaré and Casal (2000), where they states that both phytochromes and cryptochrome are involved in photoperiod sensing and accelerate flowering. The effect of the absence of blue light might be lower than that of the absence of far-red light (Table 2). Similarly to our results a study of the light wavelength range for floral induction is required, because floral initiation by red and far-red lighting seems to be mild in strawberry plants (Yanagi et al., 2006). In higher plants there are general pathways in the transduction of photoperiodic/photomorphogenetic signals. Effects of different environmental stimuli (e.g., flowering occurs in response to long photoperiod as well as to low red to far-red ratio) often result in the same developmental or morphogenetic pattern depending on the plant life strategy. According to our results, when red to far-red ratio was equal to zero (445, 638 and 669 nm) even 38% of plants formed the elements of inflorescence axis (flower initiation and differentiation started). In treatments where red to far-red ratio was equal to 50% (445, 638, 669 and 731 nm; 445, 438 and 731 nm; 638, 669 and 731 nm), the development of carrots was lower (Table 6). In other words, photoperiodic and photomorphogenetic light signals trigger similar stress-avoidance response. In long-day plants with competitor strategy the same conditions influence rapid flowering and bolting response (Tarakanov, 2006).

Treatment	Flowering initiation stages (%)			
	Vegetative	Evocation I	Evocation II	Flower initiation and differentiation
445, 638, 669, 731 nm		65	35	
445, 638, 669 nm		27	35	38
445, 638, 731 nm		40	60	
638, 669, 731 nm	22	11	67	
445, 638 nm	100			
638 nm	100			

Table 6. The development rate of edible carrot after one month LED treatment.

Photosynthetic system plays an important role in plant development. Moreover photosynthesis is the main process that interact between light and plant development (Carvalho et al., 2011) In photoperiodic plants, there is strong experimental evidence that leaves produce promoters and inhibitors of flowering when exposed to favorable and unfavorable conditions, respectively (Bernier and Prilleux, 2005). These signals are transported from the leaves to the apical meristem with metabolites of photosynthesis

process. Plants are adapted to utilize a wide-spectrum of light to control photomorphogenetic responses (Björn, 1994). Various parts of light spectrum serve as signals providing organism with important information from their environment. Besides through photosynthesis light modulates several metabolic pathways which invoke photomorphogenetic response (Quail, 2007). Appropriate combinations of red and blue light have great potential for use as a light source to drive photosynthesis due to the ability to tailor irradiance output near the peak absorption regions of chlorophyll. There are close relations between plant photosynthesis and photoperiodic response based on source-sink relations (Tarakanov, 2006). Chlorophyll *b* and inactive phytochrome form (P_r) have absorption spectrum at 660 nm, the elimination of this red light (445, 638 and 731 nm) resulted in significantly low rate of photosynthetic pigments synthesis (Table 7) and due to transport from leaves conditioned significantly the highest sucrose content in carrot root-crop (Table 8). In the contrary, the elimination of far-red light (445, 638 and 669 nm) stimulated synthesis of chlorophylls and carotenoids (Table 7). The absorption spectrum of carotenoid and chlorophyll *a* is at blue light region. The elimination of this blue light did not influence the content of chlorophyll *a* but dramatically influenced sucrose transport from leaves and apical meristemic tissues: a high level was found in carrot root (Table 8).

Treatment	Chl *a*	Chl *b*	Carot.	Chl *a*+*b*	Glu	COREL
Before LED	1.48 ±0.13	0.50 ±0.03	0.58 ±0.05	1.98 ±0.17	7.73 ±0.06	-0.9
445, 638, 669, 731 nm	1.34ab	0.57bc	0.36a	1.54a	1.44b	-1.0
445, 638, 669 nm	1.67d	0.59bc	0.53d	2.27c	2.63c	0.1
445, 638, 731 nm	1.16a	0.42a	0.35a	1.42a	7.07e	-0.4
638, 669, 731 nm	1.49bcd	0.62c	0.46bcd	2.21bc	4.24d	-1.0
445, 638 nm	1.34ab	0.47a	0.42ab	1.85abc	0.58a	-0.8
638 nm	1.39abcd	0.56bc	0.38a	1.95abc	0.71a	0.8

Table 7. The content of photosynthetic pigments and correlation between chlorophyll *a* and *b* sum and glucose in edible carrot leaves before and after LED treatment. The values with the same letters are not significantly different with $P \leq 0.05$

According to King (2006), the transported sucrose is effective as a florigen even if its main action is the energy supply. Moreover, conversion of sucrose to glucose can control flowering. According to Bernier and Perilleux (2005), mutants that block photosynthetic carbon metabolism usually exhibit late flowering as could be expected for a plant that shows flowering due to a photosynthetic response. The stability of photosynthetic pigment contents in growth runs without blue (638, 669 and 731 nm) and only with 638 nm lighting (carotenoid absorption maximum) shows very strong participation of photosynthetic system antennal complex (Table 7). Thus antennas permit organisms to increase greatly the absorption cross section for light without having to build an entire reaction center and associated electron transfer system for each pigment, which would be very costly in terms of cellular resources. In photomorphogenesis the attention falls on red/far-red light absorbing phytochromes (Carvalho et al., 2011; Yanagi et al., 2006). These photomorphogenetic receptors operate through interactions with one another and with signaling systems, thus forming complex response networks (Spalding and Folta, 2005). Thus the elimination of far-red light (455, 638 and 669 nm) showed week correlation between chlorophyll content and

glucose, and the elimination of red light (455, 638 and 731 nm) conditioned negative medial correlation (Table 7). Meanwhile the elimination of both active components, responsible for phytochrome reversion, showed strong correlation (455, 638 nm; sole 638 nm). Negative linear correlation was observed when both 669 and 731 nm components were combined in illumination treatment (Table 7).

Root-crop			Apical meristem zone			Leaves		
Fru	**Glu**	**Suc**	**Fru**	**Glu**	**Suc**	**Fru**	**Glu**	**Suc**
Before LED								
3.29 ±0.09	3.78 ±0.07	43.69 ±1.68	5.57 ±0.94	-	0.37 ±0.17	5.76 ±0.25	0.73 ±0.06	1.52 ±0.21
445, 638, 669, 731 nm (Basal)								
2.07b	20.86e	0.10a	3.20d	0.17a	2.25d	7.10e	1.44b	0.13a
445, 638, 669 nm								
2.34b	10.95d	0.86b	2.34c	10.95d	0.86b	9.85f	2.63c	0.07a
445, 638, 731 nm								
5.49d	6.63c	13.09d	1.98b	1.17b	0.37a	3.40c	7.07e	1.05c
638, 669, 731 nm								
3.08c	1.54b	25.78e	1.98b	1.67c	0.47a	4.44d	4.24d	0.90b
445, 638 nm								
1.21a	0.77a	1.93c	1.31a	0.87b	2.12d	1.02a	0.58a	5.37e
638 nm								
1.41a	0.75a	1.56c	1.21a	0.83b	1.60c	1.23b	0.71a	1.85d

Table 8. The distribution of non-structural carbohydrates among carrot organs before and after LED treatment. The values with the same letters are not significantly different with $P \leq 0.05$

During the reproductive phase of development a lot of new structures are formed, the photosynthetic apparatus is complete. Photosynthetic pigments can participate like structural material for carbohydrates biosynthesis. Moreover photomorphogenetic responses may involve changes in the partitioning of photoassimilates (Ballaré and Casal, 2000). Both, light quantity and quality are known to affect the contents and the ratio of individual proteins and pigment-protein complexes of the photosynthetic apparatus. It is well known that blue light promotes stomatal opening and influences the biochemical properties of photosynthesis. Table 8 shows that though the variation between hexoses and sucrose in different lighting treatments was different, but we found that when the total amount of monocarbohydrates is high, the levels of sucrose are low. Contrarily where the concentrations of monocarbohydrates were low, the amounts of sucrose were high. The significant decrease of sucrose content in leaves was observed under basal LED treatment and without far-red component. Significantly the lowest contents of hexoses and the highest contents of sucrose in leaves were detected under blue and red lighting (455 and 638 nm). Ballaré and Casal (2000) stated that increased export of photosynthates from leaves is due to low red and far-red ratio.

Menard et al. (2005) showed that plants grown under blue fluorescent lamps had higher chlorophyll *a*-to-*b* ratios, smaller amounts of light-harvesting chlorophyll *a*/*b*-binding protein of photosynthetic system II per unit chlorophyll content, and higher ribulose-1.5-

bisphosphate carboxygenase/oxygenase activities per unit leaf area compared to plants grown under red fluorescent lamps. Our data shows that elimination of blue light (638, 669 and 731 nm) influenced the highest net assimilation rate (Fig. 3). 2-3 times bigger values of NAR was observed in lighting treatments without red (669 nm) or without far-red (731 nm) components. Since NAR is closely related to biomass accumulation, CO_2 assimilation during day, thus the production of assimilates is one of the most important components (Cho et al., 2007; Evans and Pooter, 2001; Shipley, 2006). This correlates with our data, as the highest contents of total carbohydrates (44.1 mg g^{-1}, 40.25 mg g^{-1} and 40.85 mg g^{-1} in fresh weight respectively) was exactly under discussed lighting conditions (Table 8). Thus this indicates that net assimilation rate is correlated with changes in photoassimilates content but this increase was not involved by changes in photosynthetic pigment contents (Table 7).

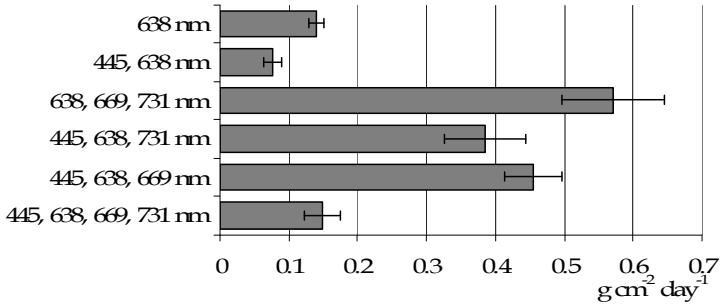

Fig. 3. The distribution of net assimilation rate in edible carrot after LED treatment.

4. Conclusion

To summarize, the following conclusions can be drawn.

The photosynthesis system and carbohydrate metabolism not only supplies morphogenetic processes with metabolites, but also tendentiously varies during ontogenesis, especially during transition from vegetative growth to generative development. Normal development of carrots and caraway was observed only when particular ratio of fructose, glucose and sucrose in different flowering initiation stages constituted. The active supply of glucose and sucrose to apical meristems is important not only for flower induction but as signalling molecule it also participates in source-sink interaction. Notwithstanding, it is not the specific induction stimulus for flowering and is independent from response to photoperiodic duration. Besides temperature make stronger effect on carrot flowering initiation, morphogenetic effects, and on non-structural carbohydrate metabolism neither photoperiod regimes during different ontogenesis stages. Long day and vernalization determines almost full flowering, high temperatures independently from photoperiod results in partial flowering and short day and vernalization is the limiting factor of caraway flowering.

Plant photosynthetic and photomorphogenetic processes, biosynthesis of primary and secondary metabolites and expression of genes can be controlled by light spectral composition. The elimination of both red (669 nm) and far-red (731 nm) or only blue (445 nm) light appeared to suppress floral initiation, under such conditions vegetative growth of carrots was observed. In contrary, the elimination of solely far-red light resulted in faster

differentiation of influorescence axis. The elimination of solely red (669 nm) or blue (445 nm) light resulted in a low synthesis rate of photosynthetic pigments and conditioned carbohydrate transport from carrot leaves. Meanwhile, the elimination of solely far-red light resulted in the opposite effect. Dominating 638-nm light was found to considerably contribute to the excitation of the carotenoid antennal complex of the photosynthetic system. The ratio of blue and red light is less important for photosynthesis system than the ratio of different red lights. Blue (445 nm), red (638 and 669 nm) and far-red (730 nm) light and their ratio are very important for photomorphogenetic processes during different plant developmental stages.

Common trends allow presuming that light signals perceived by specific photoreceptor system control the morphology and development of plants and photosynthetic apparatus of plant not only supply metabolites for morphogenetic processes but also proximately participates in these processes. Studies with individual plants in pot of experiments are important steps, but the results of these studies, due to great species and varieties diversity, can not be directly scaled up to predict the impacts of photomorphogenetic manipulations at the biennual plant level.

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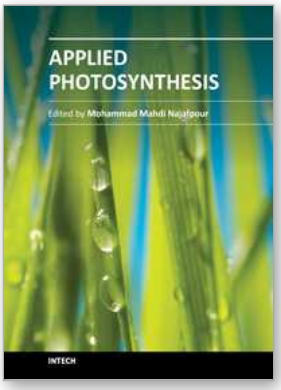

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Photosynthesis is one of the most important reactions on Earth, and it is a scientific field that is intrinsically interdisciplinary, with many research groups examining it. This book is aimed at providing applied aspects of photosynthesis. Different research groups have collected their valuable results from the study of this interesting process. In this book, there are two sections: Fundamental and Applied aspects. All sections have been written by experts in their fields. The book chapters present different and new subjects, from photosynthetic inhibitors, to interaction between flowering initiation and photosynthesis.

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