Environmental and Experimental Botany 124 (2016) 100–109

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Evaluation of genotypic variation during leaf development in four *Cucumis* genotypes and their response to high light conditions

Xiaqing Yu[a,b], Rong Zhou[b], Xixi Wang[a,b], Katrine H. Kjær[c], Eva Rosenqvist[d], Carl-Otto Ottosen[c,*], Jinfeng Chen[a,b,*]

[a] State Key Lab for Crop Genetics and Germplasm Enhancement, Nanjing Agricultural University, China
[b] College of Horticulture Science, Nanjing Agricultural University, China
[c] Department of Food Science, Aarhus University, Denmark
[d] Department of Plant and Environmental Sciences, University of Copenhagen, Denmark

ARTICLE INFO

Article history:
Received 23 September 2015
Received in revised form 6 December 2015
Accepted 25 December 2015
Available online 30 December 2015

Keywords:
Chlorophyll content
Chlorophyll fluorescence
Cucumis
High light
Photosynthesis

ABSTRACT

Physiological responses to differences in light intensity were studied in four genotypes of *Cucumis* with differences in leaf greenness. The four genotypes were *C.* ×*hytivus* (synthesized allotetraploid, yellow-green); its parents, *C. hystrix* (wild *Cucumis* species, dark green) and *BeijingJietou* (cultivated cucumber, green); and *M1* (a chlorophyll deficient mutant of cultivated cucumber, yellow-green). The plants were subjected to a photosynthetic photon flux density (PPFD) of either 800 μmol m^{-2} s^{-1} or 200 μmol m^{-2} s^{-1} in climate chambers for 20 days. Plant growth, chlorophyll (Chl) content, gas exchange, Chl fluorescence parameters and carbohydrate partitioning in the four genotypes were studied. The four genotypes showed different amounts of Chl accumulation and the genotypic differences led to divergent photosynthetic capabilities, carbohydrate partitioning and photosynthetic responses to high light. The original natural habitat characteristics of the two species may also play an important role in the divergence. Moreover, the ability of the yellow-green *M1* to slowly increase the leaf Chl content during leaf development was aligned with a long leaf life span, maintaining high levels of photosynthesis, which was not the case in the yellow-green *C.* ×*hytivus*. In addition, F_v/F_m is such a sensitive parameter that it should not be evaluated alone for high light stress without the context of the prevailing growth light environment.

1. Introduction

Cucumis×*hytivus* J.F. Chen & J.H. Kirkbride (hereafter *C.* × *hytivus*) is an allotetraploid obtained between *C. hystrix* Chakr. (hereafter *C. hystrix*), a wild species closely related to cucumber, and *C. sativus* L., 'BeijingJietou' (hereafter *BeijingJietou*) through allopolyploidization (Chen and Kirkbride, 2000) with the aim to enlarge the narrow genetic base of the cucumber (Dijkhuizen et al., 1996). In addition to the morphological differences, *C.* ×*hytivus* exhibits chlorophyll (Chl)-deficiency resulting in a yellow–green leaf colour, in contrast to the green and dark green leaves of its parents (Fig. 1). Induced mutation is another method that can be used to broaden the genetic base (Ahloowalia and Maluszynski, 2001). A Chl-deficient mutant cucumber, named *M1*, was obtained from a commercial cucumber, *C.* L. 'Changchunmici', through ethyl methyl sulfone (EMS) induction (Fig. 1).

Chl-deficiency is a common consequence of induced mutation in many plant species (Falbel et al., 1996; Suzuki et al., 1997; Wu et al., 2007). In addition to causing the green colour, Chls are essential molecules that trap light energy in the antenna systems of the photosystems and drive photosynthetic electron transfer (Fromme et al., 2003). Given its important role in photosynthesis, Chl plays a critical role in the acclimation of plants to high light. In many plant species, Chl formation increases under high light intensity (Björkman, 1981; Mclaren and Smith, 1978), but in certain extreme cases, high light inhibits Chl biosynthesis in cucumber leaves due to photoinhibition (Aarti et al., 2007). Briefly, changes in Chl content are related to the photosynthetic performance of plants and their acclimation to changes in the light environment (Falbel et al., 1996). Indeed, sensitivity to photoinhibition varies both within and between plant species (Barber and Andersson, 1992). In addition to the lower Chl content in *C.* ×*hytivus*, low carotenoid contents were also observed (Yu et al., 2015).

* Corresponding author at: College of Horticulture Science, Nanjing Agricultural University, China. Fax: +86 2584396279.
E-mail addresses: coo@food.au.dk (C.-O. Ottosen), jfchen@njau.edu.cn (J. Chen).

http://dx.doi.org/10.1016/j.envexpbot.2015.12.009
0098-8472/

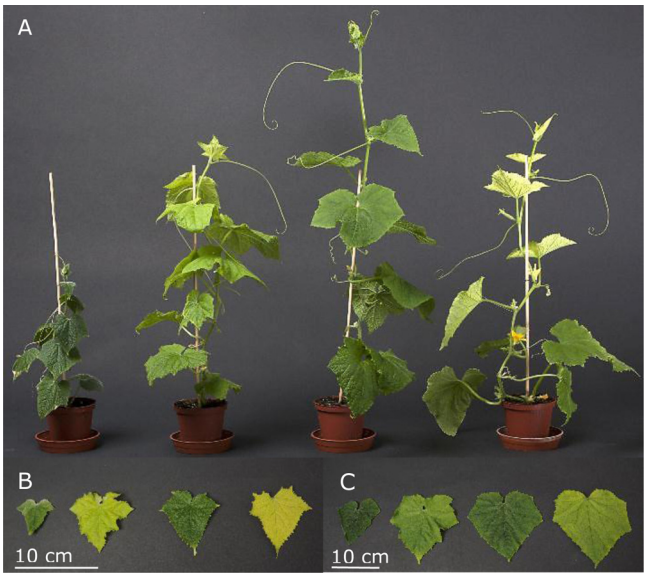

Fig. 1. Morphological difference of the four genotypes (from left to right): *C. hystrix*, *C.* ×*hytivus*, *BeijingJietou* and *M1* photographed 24 days after propagation, before the start of the light treatment; **A**, intact plants, **B**, the developing leaves and **C**, the first fully developed leaves.

Carotenoids are not only essential components of the photosynthetic antenna and reaction centre complexes but also protect the leaves against potentially harmful photo-oxidative processes when the light energy exceeds the photosynthetic capacity (Bartley and Scolnik, 1995). Carotenoids are synthesized in the xanthophyll cycle to reduce the transference of surplus energy to the photosynthetic apparatus (Demmig-Adams, 1990). In this process, excess energy is dissipated as heat (non-photochemical quenching) (Müller et al., 2001). Therefore, reduced carotenoid contents may have an effect on the photoprotection, which leads to increased sensitivity to high light.

Plants respond to the challenges posed by the variability of the natural environment in different ways. It is well known that plants acclimate to high light by changes in height, biomass, foliage number and arrangement (Bond et al., 1999; Huang et al., 2011) or by reducing the size of the light-harvesting complexes (LHCs) and producing thicker leaves (Müller-Moulé et al., 2004; Walters and Horton, 1994). Furthermore, plants from different habitats are able to acclimate to specific light environments (Demmig-Adams et al., 1997), but high-light species are more plastic than shade species (Strauss-Debenedetti and Bazzaz, 1991). In other words, the ability to acclimate to changes in light conditions differs among genotypes. In addition, heterosis or hybrid vigour is well known, as hybrid plants grow more vigorously and adaptively than their parents, an effect that also works in allopolyploids (Chen, 2013). This effect adds to the interest in investigating the response of four leaf-greenness *Cucumis* genotypes to high light conditions.

Increased light intensity can increase carbon gain, leading to higher yields. However, excessive light can lead to damage to the photochemical process and to photoinhibition (Demmig et al., 1987; Srivastava and Strasser, 1996). Thus, to what extent will higher light levels lead to photoinhibition? Within a range of light levels, an increase in the light absorption by chlorophyll will lead to an increase in photosynthetic CO_2 fixation. Above a certain light level, however, the plant will be incapable of utilizing all of the energy absorbed for photosynthesis, and then photoinhibition occurs (Demmig-Adams and Adams, 1992). It has been revealed that photosystem II (PSII) is vulnerable to strong light stress, and damage to PSII is often the first manifestation of stress in a leaf (Havaux and Tardy, 1997; Mathur et al., 2011). The functional consequences of photoinhibition include reduction of the maximum quantum efficiency of photosystem II (F_v/F_m), making this parameter a reliable and reproducible measure of photoinhibition (Krause et al., 1995).

Chl fluorescence measurements provide a rapid, non-invasive method for the early detection of damage to the photosynthetic apparatus (Maxwell and Johnson, 2000; Murchie and Lawson, 2013; Zhou et al., 2015) and have been used to detect high light stress in the tomato (Han et al., 2010; Janssen et al., 1992), lettuce (Fu et al., 2012) and 14 wild and cultivated species (Ögren and Rosenqvist, 1992). Moreover, gas exchange measurements and carbohydrate analysis should be coupled with Chl fluorescence measurements to obtain a broad picture of plant responses to environmental changes, such as high light. In addition to the pigmentation difference in young leaves, it is unclear what happens to the leaf during leaf development. Non-invasive physiological approaches enable us to investigate the physiological state of leaves during different leaf developmental stages.

This study aims to investigate the morphological alternations and dynamic physiological effects of high light on four Cucumis genotypes that differ in leaf greenness (*C. hystrix*, *C.*×hytivus, BeijingJietou and M1) by following their developing leaves. The deficiency of carotenoid in C. ×hytivus (unpublished data) may lead to more severe photoinhibition under high light, which can be detected by Chl fluorescence parameters. We hypothesize that an elevated light level can differentiate the varied photosynthetic response of the four genotypes, in which the variation of Chl plays an important role.

2. Materials and methods

2.1. Plant material and growth conditions

Four genotypes of *Cucumis* were used: the wild species Cucumis hystrix Chakr. (2n = 24, genome HH), the synthesized species C. ×hytivus (2n = 38, genome HHCC), the cultivated cucumber C. sativus 'BeijingJietou' (BeijingJietou, 2n = 14, genome CC) and the chlorosis mutant of commercial cucumber 'Changchunmici' (M1, 2n = 14, genome C_MC_M). The seeds were sown Sep 30, 2013, and the seedlings were grown in a greenhouse with set points of 25/20 °C day/night, ambient CO_2, 60–70% relative humidity (RH) and a 20 h photoperiod with a combination of natural and supplemental light (SON-T 400W, Philips, Eindhoven, The Netherlands, red/far-red ratio: 1.2, according to Shibuya et al., 2012). Due to the different growth rates of the four genotypes, the plants were cultivated in the greenhouse for 30 days to produce cuttings of equal size. Plastic pots (11-cm diameter, 0.5 L) filled with a peat-based potting mix (Pindstrup 2, Pindstrup Mosebrug A/S, Ryomgaard, Denmark) were used to plant the cuttings. The plants were irrigated every morning by flooding the greenhouse Table for 15 min with a nutrient solution (pH 6.0, EC 2.34 dS m^{-1}) consisting of N (185 mg L^{-1}), P (27 mg L^{-1}), K (171 mg L^{-1}), Mg (20 mg L^{-1}) and micro nutrients.

2.2. Light treatments

Prior to the light treatments, the plants were transferred into two walk-in growth chambers (MB teknik, Brøndby, Denmark) with broad-spectrum LED lights (FL300, Fionia Lighting, Søndersø, Denmark) from Nov 18 to Nov 24 at a density of 25 pots m^{-2}. Each chamber accommodated two tables, established as plots, and every plot had four randomly distributed pots of each genotype. The chamber set points were controlled to 25/20 °C day/night, 60% RH, 400 ppm CO_2 concentration, and 14 h/10 h light/dark with 200 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) (daily light integral, DLI: 10.08 mol m^{-2} day^{-1}) measured at the tops of the plants using a LI-250A quantum sensor (LI-COR, Lincoln,

NE, USA). The air temperature and RH were continuously measured by a Humitter 50U/50Y(X) (Vaisala, Helsinki, Finland) placed at the tops of the plants and recorded by a logger (Datataker, Thermo-Fisher Scientific Australia Pty Ltd., Scoresby, Australia). Plants were irrigated twice per day (>20% drainage day^{-1}). The electrical conductivity and pH of the drain water were monitored daily and adjusted to 1.8 dS m^{-1} and pH 5.8, respectively. On Nov 25, half of the plants of each genotype were transferred into another growth chamber with the same settings except for an increased light level of 800 μmol m^{-2} s^{-1} PPFD (DLI: 40.3 mol m^{-2} day^{-1}), which is above the light saturation point of C. hystrix and C. ×hytivus and close to the light saturation point of BeijingJietou (Yu et al., 2015). At the onset of the light treatments, the plants were approximately eight leaves old.

The plants were grown at different light levels in the chambers for a period of 20 days. Non-invasive measurements were taken at four-day intervals on the developing leaf (young leaf marked with a label at the beginning of the experiment, which became senescent at the end of the experiment). During the experiment, the border plants (adjacent to the chamber walls) were not sampled.

2.3. Plant growth

All of the morphological data were collected with four repetitions. For each genotype and treatment, the leaf area (LA) of the developing leaves of four randomly picked plants was non-destructively measured at an interval of four days. The shape of developing leaf was manually copied on a piece of paper, and the paper cut was subsequently measured using a LI-3100C area meter (LI-COR, Lincoln, NE, USA). At the end of the experiment, the number of leaves on the main stem was recorded by counting from the youngest leaf from the top to the last true leaf above the cotyledonary node. Total leaf number (TLN) was counted for all of the unfolded leaves above the cotyledonary node from the whole plant, and total leaf area (TLA) was measured using a LI-3100C area meter (LI-COR, Lincoln, NE, USA). The leaves, stems and fruits were dried separately at 80 °C for 24 h to measure the dry weight (DW). Specific Leaf Area (SLA) was calculated as SLA = TLA/leaf DW.

2.4. Chlorophyll content

The total leaf Chl content was non-invasively monitored using a Dualex 4 (FORCE-A, Orsay, France), delivering readings in units of μg cm^{-2} (Cerovic et al., 2012). For each genotype, three random plants of each treatment were measured. For each measurement, readings were taken from three sections on both sides of each leaf, and the mean value of each leaf was obtained immediately.

2.5. Gas exchange measurements

An infrared gas exchange (IRGA) system (CIRAS-2; PP-systems, Amesbury, MA, USA) was used for gas exchange measurements with a leaf cuvette of 2.5 cm^2 (leaf area) and a mounted LED light unit. The settings were 400 ppm CO_2, 25 °C temperature, and 65–70% RH, resulting in a vapour pressure deficit (VPD) of approximately 1.0 kPa with a 200 cm^3 min^{-1} cuvette flow. Measurements were taken on the developing leaf at 200 and 800 μmol m^{-2} s^{-1} PPFD in the morning (9:00–12:00). All parameters were recorded when the net photosynthetic rate (P_n) and stomatal conductance (g_s) reached steady-state, at least 5 min after acclimation.

2.6. Chlorophyll fluorescence

The maximum quantum efficiency of photosystem II (F_v/F_m) was measured in the afternoon (3 h before darkness) using a Handy-PEA, Plant Efficiency Analyser (Hansatech Instruments, Kings Lynn, UK) after dark-adapting the leaf for 30 min using a leaf clip (Hansatech, Instruments, Kings Lynn, UK). The maximum light intensity was 3000 μmol m^{-2} s^{-1}, which was sufficient to generate maximal fluorescence (F_m). Measurements were performed on the developing leaf and the first fully developed leaf. Three random spots in each leaf were measured with three replications each, resulting in nine values for each treatment and genotype.

2.7. Carbohydrate content

Leaf samples for carbohydrate analysis were taken from the first fully developed leaf, immediately frozen in liquid nitrogen and stored at −80 °C. Carbohydrate content was analysed according to the method of Shanmugam et al. (2013). Before extraction, the samples were freeze-dried using a lyophilizer (Martin Christ GmbH, Gamma 1–20, Schwabach, Germany) for three days, then ground in a mixer mill (MM200, Retsch Inc., Haan, Germany) with a steel ball. The soluble sugars (including glucose, fructose and sucrose) were extracted with 80% ethanol and 20% HEPES. The pooled supernatants containing the soluble sugars were analysed by ion chromatography using a pulsed amperometric detector (PAD) with a gold electrode (Dionex, ICS 3000, Sunnywale, Canada), using 200 mM NaOH as the eluent. Then, ddH2O was added to the tubes with the leaf pellets and autoclaved for 90 min. To degrade the starch into glucose units, the samples were mixed together with enzyme buffer solution. The samples were centrifuged and filtered, and the glucose units representing the starch fraction were measured by ion chromatography using PAD.

Table 1
Plant growth characteristics among the four genotypes under low and high light. Values are mean ± SE ($n = 4$). Different letters within the same column indicate significant differences at 0.05 ($P < 0.05$). Level of significance: NS, non-significant; *, $P < 0.05$; **, $P < 0.01$.

Genotype	Treatment	TLN, $plant^{-1}$	Leaf DW, g	Stem DW, g	Fruit DW, g	TLA, cm^2	SLA, cm^2 g^{-1}
C. hystrix	low light	35 ± 4^{b}	2.65 ± 0.47^{e}	0.78 ± 0.16^{d}	–	638 ± 100.2^{f}	243 ± 8.6^{ab}
	high light	58 ± 3^{a}	6.56 ± 1.29^{cd}	1.81 ± 0.47^{cd}	–	1079 ± 203.5^{ef}	165 ± 1.7^{c}
C. ×hytivus	low light	29 ± 1^{bc}	6.21 ± 0.68^{cd}	1.94 ± 0.28^{cd}	0.27 ± 0.097^{c}	1713 ± 173.4^{cd}	277 ± 7.8^{a}
	high light	57 ± 3^{a}	16.17 ± 0.22^{b}	5.08 ± 0.10^{b}	0.63 ± 0.113^{c}	3154 ± 46.8^{b}	195 ± 0.3^{bc}
BeijingJietou	low light	18 ± 1^{d}	6.41 ± 0.14^{cd}	2.97 ± 0.25^{c}	0.54 ± 0.037^{c}	1882 ± 157.5^{c}	293 ± 20.8^{a}
	high light	34 ± 2^{b}	19.74 ± 0.64^{a}	10.91 ± 0.98^{a}	1.97 ± 0.302^{b}	3995 ± 121.9^{a}	202 ± 0.9^{bc}
M1	low light	17 ± 1^{d}	4.62 ± 0.98^{de}	1.56 ± 0.33^{cd}	1.29 ± 0.666^{bc}	1283 ± 124.9^{de}	295 ± 43.1^{a}
	high light	27 ± 1^{c}	7.72 ± 0.59^{c}	2.61 ± 0.23^{c}	4.97 ± 2.422^{a}	1239 ± 126.9^{de}	160 ± 4.7^{c}
Genotype effect		**	**	**	*	**	NS
Light effect		**	**	**	**	**	**
Genotype × light effect		**	**	**	NS	**	NS

2.8. Statistical analysis

Two-way analysis of variance (ANOVA) was performed to reveal the differences between the genotypes and light treatments within one day of treatment using the R software (i3862.15.0, www.r-project.org/). Mean separations were performed using the Duncan Multiple Range Test of $P < 0.05$. SPSS 16.0 (SPSS Inc., Chicago, IL, USA) was used for the Pearson correlation analysis.

3. Results

3.1. Morphology

The morphology of the four genotypes is clearly different (Fig. 1), as shown by the genotypic dependency of plant growth parameters in Table 1 and Fig. 2. Further, the leaf expansion and Chl accumulation are different among the four genotypes. The differences in physiology are reflected in the different gas exchange and Chl fluorescence parameters.

The high light treatment (20 days at 800 μmol m^{-2} s^{-1} PPFD for 20 h) did not result in photo-bleaching or other macroscopic damage to any of the genotypes. On the contrary, all four genotypes exhibited significantly increased total leaf number (TLN) and DW (Table 1). However, the increase in light had no effect on the leaf number of the main stem in M1, whereas BeijingJietou had significantly more leaves by day 5 (Fig. 2C and D). High light also increased the number of leaves on the main stem in C. ×hytivus and C. hystrix after day 15 and day 20, respectively (Fig. 2A and B). BeijingJietou showed the highest increase in DW under high light: leaf DW increased by 208%, stem DW by 267%, and fruit DW by 265%. LA also increased by 112%. C. hystrix had higher leaf DW (148%) in high light than in low light. C. ×hytivus also showed higher leaf DW (160%), stem DW (162%) and TLA (84%) under high light. In M1, the leaf DW was increased by 67%, and the fruit DW was 3.9 times higher

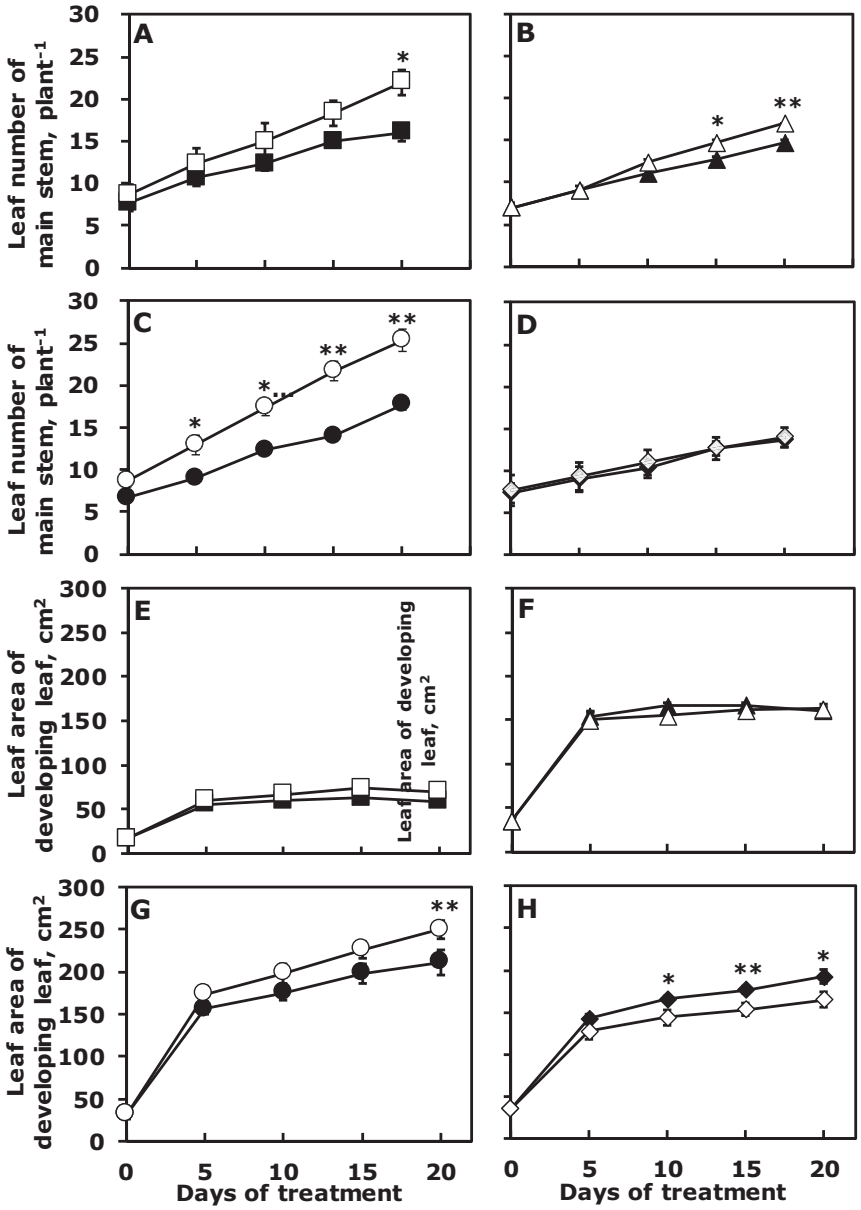

Fig. 2. The development of number of leaves of the main stem (**A–D**) and leaf area of the developing leaf (**E–H**) of *C. hystrix* (squares), *C. ×hytivus* (triangles), *BeijingJietou* (circles) and *M1* (diamonds) in the low light (black shapes) and the high light (white shapes) treatment. The data are mean values ± SE ($n = 4$), and $^{*}(P < 0.05)$ and $^{**}(P < 0.01)$ indicate significant difference between the treatments.

under high light (Table 1). Significantly lower SLA was observed in all four genotypes under high light (Table 1). As shown in Fig. 2, the developing leaves of the four genotypes consistently expanded rapidly during the first five days. C. hystrix had significantly smaller leaves than the others. The developing leaf of C. hystrix and C. ×hytivus was fully expanded on day 5, but decreasing leaf area was observed on day 20. The leaf area of the developing leaves in M1 and BeijingJietou continued to increase for the following 15 days but more slowly than the first five days. The LA of developing leaves in C. hystrix and C. ×hytivus was not affected by the high light treatment, but a significant increase in the LA of developing leaves was observed on day 20 in BeijingJietou and from day 10 to 20 in M1 (Fig. 2G and H).

3.2. Pigmentation

The four genotypes exhibited differences in Chl accumulation during leaf development under both low and high light (Fig. 1 and 3). On day 0, the developing leaf (i.e., the first unfolded young leaf) had the highest Chl content in C. hystrix, followed by BeijingJietou, whereas it was lowest in C. ×hytivus and M1, reflecting the variation in leaf colour (Fig. 1B and 3). On day 5, the Chl content of the developing leaf in BeijingJietou reached its maximum, 27.4 $\mu g\,cm^{-2}$, whereas C. hystrix had the highest Chl content of its developing leaf on day 10. Developing leaves of C. ×hytivus and M1 showed delayed Chl accumulation, achieving the maximum Chl content on day 15 (Fig. 3C and D). However, the percentage of Chl increase and maximum Chl content in C. ×hytivus were 209% and 30.0 $\mu g\,cm^{-2}$, which were significantly lower than the values in M1 of 259% and 43.8 $\mu g\,cm^{-2}$ (Fig. 3). After reaching the maximum value, the Chl content of the four genotypes decreased due to leaf senescence, being most pronounced in BeijingJietou (Fig. 3C). The Chl accumulation of C. hystrix and M1 was not affected by the high light treatment (Fig. 3A and D), whereas significantly higher Chl content (increased by 58% on day 5) was observed under high light in BeijingJietou during the first 10 days (Fig. 3C). In contrast, the Chl content of C. ×hytivus under high light was significantly lower than under low light from day 15 (Fig. 3B).

3.3. Photosynthesis

On day 0, no significant genotypic difference in P_n was observed among the four genotypes (Fig. 4). However, a significant genotypic difference in P_n was observed under both low and high measuring light from day 5 to 20. A decrease in P_n due to Chl degradation and senescence of the leaves was observed in all four genotypes but was most pronounced in BeijingJietou (Fig. 4C). High light affected the developing leaf of the four genotypes at different times during the experiment, corresponding to the day of the maximum Chl content. A significant high light effect on P_n was observed on day 5 under low measuring light and on days 5 and 10 under high measuring light. Moreover, significant interactions between genotypes and PPFD treatments were observed on day 20 under low measuring light and on days 5, 10 and 20 under high measuring light. In C. hystrix, P_n increased by up to 41% under high measuring light on days 5 and 10 of the high light treatment (Fig. 4A). BeijingJietou grown at high light exhibited significantly higher P_n (up to 57%) under both low and high measuring light levels on day 5 (Fig. 4C). In M1, significantly higher P_n was measured at both light intensities at the end of the light treatments (Fig. 4D). High PPFD led to a significant increase in P_n in C. ×hytivus on day 10, while decreased P_n was observed in C. ×hytivus under both high and low measuring light intensities at the end of the treatment (Fig. 4B). Significant linear correlation between Chl content and P_n under both low and high measuring light was observed in C. hystrix and BeijingJietou (Fig. 5A and C). No correlation was observed in C. ×hytivus, while there is a significant linear correlation between Chl content and P_n under 200 $\mu mol\,m^{-2}\,s^{-1}$ PPFD in M1 (Fig. 5B and D).

3.4. Chlorophyll fluorescence

The four genotypes exhibited varied F_v/F_m patterns (Fig. 6). The F_v/F_m of the developing leaf in C. hystrix decreased gradually with leaf age (Fig. 6A) while F_v/F_m remained unchanged in the developing leaf in BeijingJietou (Fig. 6C). As the leaf Chl content increased in C. ×hytivus and M1, their F_v/F_m ratios both increased marginally (Fig. 6B and D). In C. hystrix, a significant decrease in F_v/F_m was observed on day 15 of the high light treatment (Fig. 6A).

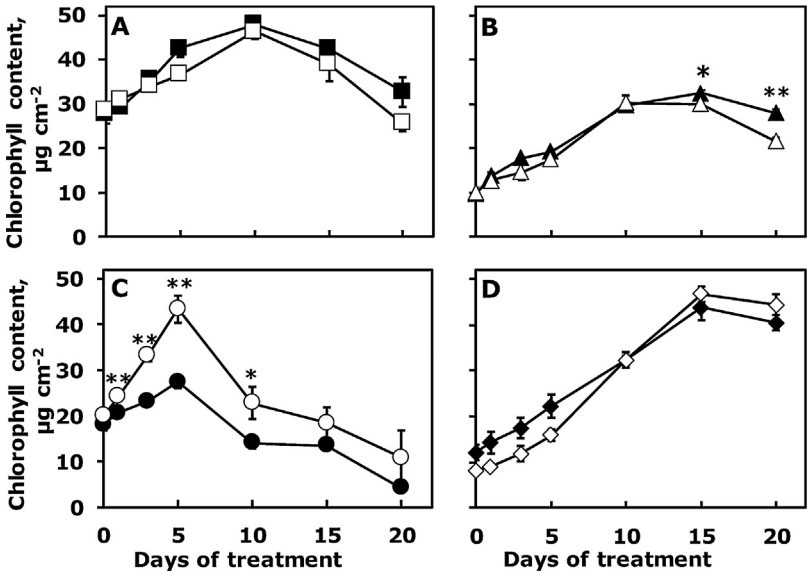

Fig. 3. The development of leaf chlorophyll content (monitored by Dualex 4) of the developing leaf of *C. hystrix* (**A**, squares), *C. ×hytivus* (**B**, triangles), *BeijingJietou* (**C**, circles) and *M1* (**D**, diamonds) in the low light (black shapes) and the high light (white shapes) treatment. The data are mean values ± SE ($n = 3$), and $^{*}(P < 0.05)$ and $^{**}(P < 0.01)$ indicate significant difference between the treatments.

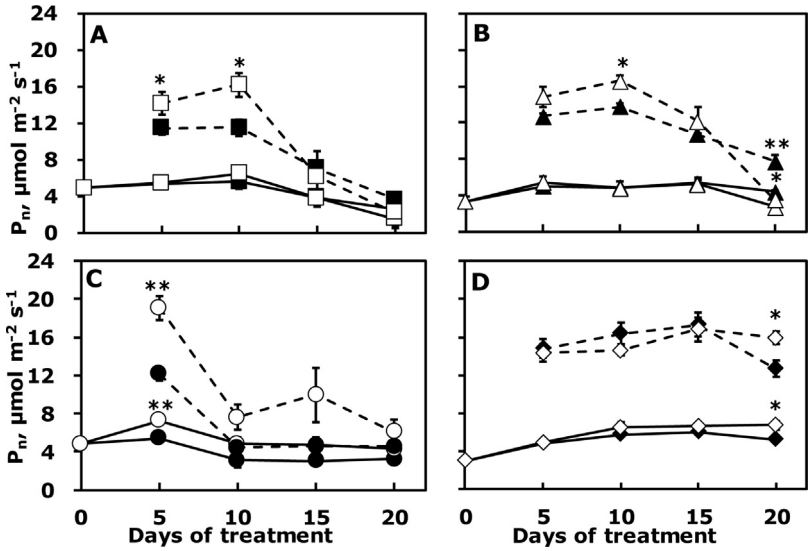

Fig. 4. The development of the rate of net photosynthetic (P_n) of the developing leaf of *C. hystrix* (**A**, squares), *C.* ×*hytivus* (**B**, triangles), *BeijingJietou* (**C**, circles) and *M1* (**D**, diamonds) measured under 200 μmol m^{-2} s^{-1} (solid lines) and 800 μmol m^{-2} s^{-1} (dash lines) in the low light (black shapes) and high light (white shapes) treatment. The data are mean values ± SE ($n = 3$), and $^{*}(P < 0.05)$ and $^{**}(P < 0.01)$ indicate significant difference between the treatments.

The developing leaf of C. ×hytivus had lower F_v/F_m values in high light compared to low light (Fig. 6B). For BeijingJietou, lower values of F_v/F_m were also observed in high light (Fig. 6C). High light resulted in a significant drop in F_v/F_m in M1, particularly in the young leaf, from 0.77 to 0.66 (Fig. 6D). No correlation was observed between Chl content and F_v/F_m.

3.5. Carbohydrates

After 20 days of high light treatment, neither genotype nor treatment effect was observed on the glucose content (Table 2). However, there was a significant genotype dependency of the fructose content, with significantly higher fructose content in C. hystrix (Table 2). For the sucrose content, total soluble sugar content and starch content, no genotype effect was found; however, there were significant light effects (Table 2). High light led to the accumulation of sucrose in BeijingJietou, which contributed to the higher total soluble sugar content. Both BeijingJietou and M1 showed starch accumulation after 20 days of high light treatment. No significant high light treatment effect was found on the carbohydrate content in C. hystrix and C. ×hytivus.

4. Discussion

4.1. High light acclimatization

We explored the response of four genotypes of cucumber (Cucumis) with varied Chl content towards elevated light intensity for a period of 20 days. The four genotypes displayed divergent photosynthetic acclimation to the high light. However, none of them were severely photoinhibited. A long-term increase in light often results in an increased capacity for photosynthesis in terms of leaf area, dry weight and Chl (Murchie and Horton, 1997). All four genotypes showed increased growth and biomass accumulation under high light.

Plants respond to changes in environmental conditions in many ways, ranging from long-term processes such as altered leaf anatomy to the short-term adjustment of protein stoichiometry within the photosynthetic apparatus (Demmig-Adams and Adams, 1992). Photosynthetic acclimation is defined as adjustment in the composition of the photosynthetic apparatus within individual cells, and lies between long-term and short-term changes (Walters, 2005). However, the capacity to alter the photosynthetic components according to the light environment is dependent on species, as the light requirements for a given species depend on habitat and growth strategy (Murchie and Horton, 1997). As we hypothesized, the response to high light was linked to the leaf greenness of the different related genotypes. In addition to the clear difference in Chl accumulation of the four genotypes per se, high light also affected Chl depending on genotype. The Chl content of the developing leaf in BeijingJietou increased immediately under high light, corresponding to the results in the sun leaves of wheat (Lichtenthaler et al., 1981). High light did not significant changes in Chl content in C. hystrix and M1, but decreased the Chl content in the later experimental period in C. ×hytivus. The higher Chl content in BeijingJietou under high light aligns to the enhanced photosynthesis, which ultimately resulted in more leaves and increased biomass. However, it is not clear that whether higher Chl concentration promotes photosynthesis or enhanced photosynthesis induces an increase in Chl content because it needs more. Anderson et al. (1988) demonstrated that it is the ratio of Chl *a*/*b* showed a strong correlation to the growth irradiance, rather than Chl concentration per leaf area. In our case, the effect of changing light intensity on Chl concentration varied among species within Cucumis.

The long-term developmental process in response to changes in light conditions takes effect over a period of weeks. After 20 days, all four genotypes had consistently lower SLA in high light, which can be a result of thicker leaves in terms of longer palisade cells, additional cell layers and larger cells, as Lichtenthaler et al. (1981) observed in beech, and/or accumulated starch. Moreover, M1 also differs morphogenetically from the other genotypes in response to high light. Under high light, M1 increased TLN by more leaves on branches but showed an unchanged number of leaves on the main stem, whereas the other genotypes showed increases in leaf number on both the main stem and the branches. In Sinapsis alba high light resulted in the accumulation of soluble sugars and starch (Wild and Zerbe, 1977). In our study, BeijingJietou accumulated sucrose and starch, whereas M1 only accumulated starch in the leaves. No high light effect on the carbohydrates was observed in C. hystrix and C. ×hytivus. The significantly higher sucrose content of

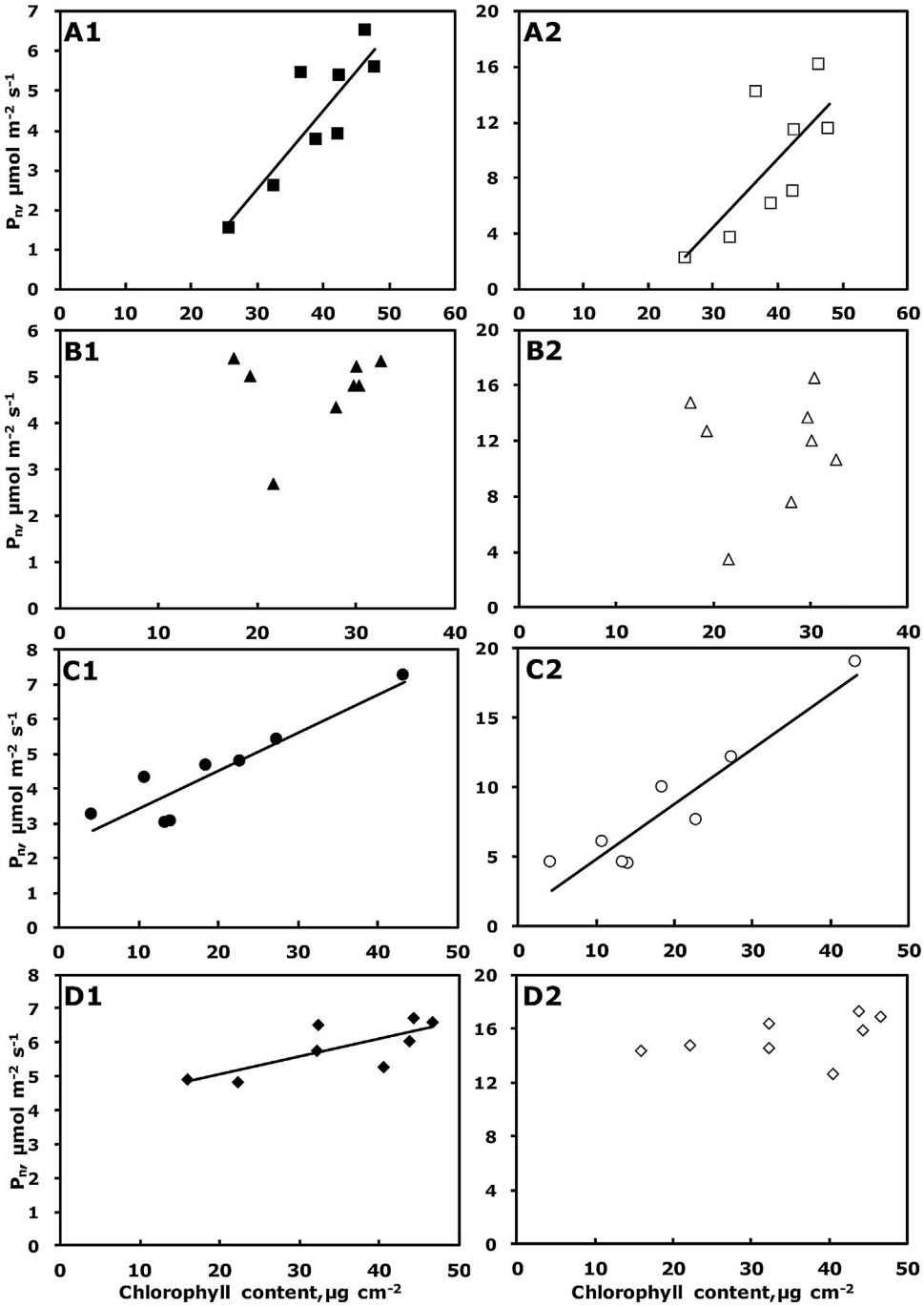

Fig. 5. Correlations between Chl content and P_n, measured under 200 μmol m^{-2} s^{-1} (black, left) and 800 μmol m^{-2} s^{-1} (white, right), of *C. hystrix* (**A**, squares), *C.* ×*hytivus* (**B**, triangles), *BeijingJietou* (**C**, circles) and *M1* (**D**, diamonds).

BeijingJietou leaves under high light might explain the overall increased dry weight in the leaf, stem and fruit.

Plants that occupy sunny habitats (sun plants) are generally capable of higher photosynthetic rates at high light levels than plants restricted to shaded locations (shade plants) (Björkman, 1981). In some shade-adapted species, even moderate increases in growth light intensity can lead to reversible photoinhibition rather than acclimation (Jurik et al., 1979). We assume that BeijingJietou is relatively better at acclimating to sunny conditions, showing a higher P_n increase under high light than the other genotypes. This ability to acclimate consequently leads to higher improvement of dry matter accumulation, which is the target for breeders in selecting suitable genotypes for high yield production as a commercialized cucumber cultivar. C. hystrix was considered as a shade-adapted plant (Yu et al., 2015). However, our results showed that C. hystrix is a facultative shade plant, as suggested by the significant increased P_n and biomass and 68–69% lower SLA (same to BeijingJietou) under high light, which is also fit for a climber plant.

4.1.1. The role of Chl in the photosynthetic acclimatization

In fully developed healthy leaves of pea, the Chl concentration per area was unaffected by the growth light level, even though the rate of oxygen evolution was gradually acclimating to the increased light level (Anderson et al., 1988). Even though the photosynthetic apparatus acclimated by changing stoichiometry between Chl

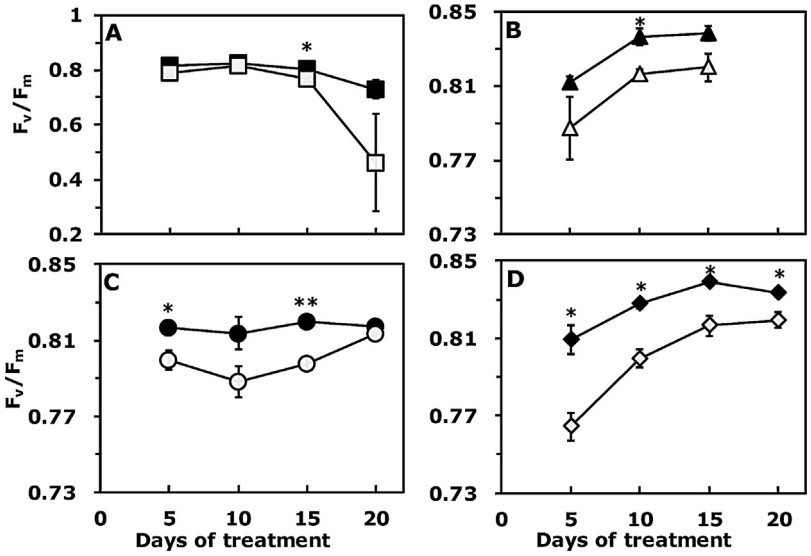

Fig. 6. The development of F_v/F_m of the developing leaves of *C. hystrix* (**A**, squares), *C.* ×*hytivus* (**B**, triangles), *BeijingJietou* (**C**, circles) and *M1* (**D**, diamonds) measured by Handy PEA in the low light (black shapes) and the high light (white shapes) treatment. The data are mean values ± SE ($n = 3$), and $^{*}(P < 0.05)$ and $^{**}(P < 0.01)$ indicate significant difference between the treatments.

allocated to different components there was no correlation between Chl concentration per leaf area and photosynthesis (Anderson et al., 1988), which has also been shown in other studies (Hesketh, 1963; Šesták, 1966). In our experiment, we observed a linear correlation between Chl content per leaf area and P_n in the parent species, C. hystrix and BeijingJietou. However, in our experiment we followed the developing leaf so the increase in Chl content was accompanied by an increase in P_n as the leaf approached maturation. In the end of the experiment the drop in Chl content was most pronounced in BeijingJietou accompanied with low P_n and this species showed clearest visual signs of yellowing leaves in the end of the experiment. However, even though the high light caused moderately lower F_v/F_m in BeijingJietou, two out of four measuring days PSII was still not severely degraded during the experiment. As for the synthesized allotetraploid, C. ×hytivus, unlike it parents, no correlation was observed. It can be related to the effect of "genomic shock" (McClintock, 1984; Zhuang et al., 2009) resulting in disruption in a number of regulatory and developmental processes, including Chl deficiency.

4.2. Delayed Chl accumulation

Although C. ×hytivus and M1 exhibited similar phenotypic changes in leaf colour corresponding with later Chl accumulation, they behaved differently in response to high light. This difference may be related to the different origins of the induction of Chl deficiency. Chl deficiency in mutants always results in decreased P_n and thereby reduced carbon-related biomass production, which is the reason for abortion or slow growth in most cases (Chen et al., 2009; Wu et al., 2007). However, the result of blocked Chl biosynthesis can be substantially overcome over time (Falbel et al., 1996; Wu et al., 2007; Dong et al., 2013), which is also consisitent with the results for M1. Moreover, M1 maintained high P_n throughout the experimental period, giving M1 a longer leaf life span to accumulate more photosynthetic products. In addition to the higher fruit DW under high light, M1 showed potential for yield improvement in cucumber.

The Chl deficiency in C. ×hytivus did not obviously affect its growth. C. ×hytivus exhibited yellow-green young leaves with lower Chl content, which could be the result of "genomic shock" (McClintock, 1984; Zhuang et al., 2009). In this study, the Chl

Table 2
Carbohydrate content among the four genotypes under low and high light. Values are mean ± SE ($n = 4$). Different letters within the same column indicate a significant difference at 0.05 ($P < 0.05$). Level of significance: NS, non-significant; *, $P < 0.05$; **, $P < 0.01$.

Genotype	Treatment	Glucose, mg g^{-1}	Fructose, mg g^{-1}	Sucrose, mg g^{-1}	Total soluble sugar, mg g^{-1}	Starch, mg g^{-1}
C. hystrix	Low light	0.41 ± 0.05^{a}	4.11 ± 0.26^{a}	9.80 ± 2.36^{ab}	14.32 ± 2.56^{ab}	21.59 ± 4.12^{bc}
	High light	0.48 ± 0.14^{a}	4.43 ± 0.36^{a}	11.32 ± 3.57^{ab}	16.23 ± 3.56^{a}	24.63 ± 2.43^{bc}
C. ×*hytivus*	Low light	0.36 ± 0.03^{a}	2.45 ± 0.47^{bc}	5.61 ± 0.61^{bc}	8.42 ± 0.90^{bc}	13.76 ± 2.57^{c}
	High light	0.52 ± 0.13^{a}	2.71 ± 0.48^{bc}	11.10 ± 2.11^{ab}	14.33 ± 1.81^{ab}	19.82 ± 0.71^{bc}
Beijinglietou	Low light	1.13 ± 0.66^{a}	1.67 ± 0.36^{c}	3.49 ± 0.39^{c}	6.29 ± 0.49^{c}	18.77 ± 2.10^{bc}
	High light	0.95 ± 0.53^{a}	1.76 ± 0.23^{c}	12.91 ± 0.91^{a}	15.62 ± 1.45^{a}	38.00 ± 7.41^{a}
M1	Low light	0.43 ± 0.09^{a}	2.19 ± 0.12^{bc}	9.29 ± 1.12^{ab}	11.91 ± 1.13^{abc}	15.13 ± 0.52^{c}
	High light	0.47 ± 0.04^{a}	3.16 ± 0.79^{ab}	9.46 ± 1.32^{ab}	13.09 ± 2.01^{ab}	28.89 ± 5.88^{ab}
Genotype effect		NS	**	NS	NS	NS
Light effect		NS	NS	**	**	**
Genotype × light effect		NS	NS	NS	NS	N

content of developing leaves in C. ×hytivus significantly decreased during the later period of high light. The loss of green colour caused by Chl breakdown is the most obvious sign of leaf senescence (Schelbert et al., 2009), and the P_n of C. ×hytivus decreased in concert with the decrease of Chl content. Therefore, it is suggested that high light accelerated leaf senescence in C. ×hytivus. Chl content can be decreased by high light as a consequence of excess light energy that exceeds the plant's needs (Aarti et al., 2007). High light led to decreased Chl content in C. ×hytivus but not in other genotypes. It could therefore be modelled using the 'supply and demand' dynamic of Chl accumulation and photo-bleaching (Falbel et al., 1996). From another perspective, this result indicates that the lower Chl content in C. ×hytivus may be sufficient to meet its photosynthetic requirement. The difference in photosynthetic performance between C. ×hytivus and M1 under high light might suggest that the Chl deficiency is due to allopolyploidization and/or mutation.

4.3. F_v/F_m—the indication of high light stress

A lower F_v/F_m is frequently observed when plants are subjected to abiotic stresses including high light stress (Fu et al., 2012; Han et al., 2010; Janssen et al., 1992; Krause et al., 1995; Zhou et al., 2015). The light stress is known as photoinhibition where the decreased functionality of PSII is shown as a reduction in F_v/F_m (Barber and Anderson, 1992; Long and Humphries, 1994; Krause et al., 1995). Therefore, it is possible to detect plant damage under stress much earlier than by observing the changes in morphology. The significant decrease in F_v/F_m found in the four genotypes under high light half of the measurement days at first glance seems to conflicts with the increase of P_n and biomass. However, the primary effect of decreasing F_v/F_m on photosynthesis is a decrease in the apparent maximum quantum yield at low light where the decrease in F_v/F_m is on the same magnitude that the decrease in apparent quantum yield (Ögren and Sjöström, 1990). Therefore, at moderate photoinhibition the most pronounced effect on the photosynthetic light response curve is seen at low and intermediate light and less so at high light. Therefore, a moderate increase in light level can lead to moderate decrease of F_v/F_m that is not reflected in photosynthesis at higher light levels. Furthermore, even slightly photoinhibited plants that are exposed to higher light level will harvest and successfully process more light, than plants that are not photoinhibited and exposed to lower light levels.

5. Conclusions

In summary, we tested the response of four genotypes with different foliar greenness to differences in light intensity, and none of the four genotypes were photoinhibited at the high light intensity. However, the four genotypes exhibited genotypic differences not only in Chl content but also in photosynthetic capacity, growth habit and response to high light. Further, with similar delayed Chl accumulation, M1 exhibited the ability to prolong its leaf life span, maintaining high levels of photosynthesis, whereas this ability was not observed in C. ×hytivus. In addition, to evaluate the effect of light stress detected by F_v/F_m it has to be put into the context of the prevailing growth light environment and not evaluated alone.

Contributions

Xiaqing Yu performed the experiments and the supervisors (Jinfeng Chen, Carl-Otto Ottosen and Eva Rosenqvist) assisted with planning, instruction and finalizing the paper as part of the PhD project of Xiaqing Yu. Rong Zhou assisted in performing the experiment and in the data analysis. Xixi Wang assisted in the planning and data analysis. Katrine H. Kjær helped with the data analysis and manuscript writing.

Acknowledgments

This research was partially supported by the key program from the NSFC (31430075); the "973" Project (2012CB113900); the "863" project (2012AA100102); and the National Supporting Programs (2013BAD01B04-10). We thank Ruth Nielsen, Kaj Ole Dideriksen and Helle Kjærsgaard Sørensen for their help in conducting the measurements. The first author's visiting project was supported by grants from the Danish Government Scholarship and the China Scholarship Council.

References

Aarti, D., Tanaka, R., Ito, H., Tanaka, A., 2007. High light inhibits chlorophyll biosynthesis at the level of 5-Aminolevulinate synthesis during de-etiolation in cucumber (*Cucumis sativus*) cotyledons. Photochem. Photobiol 83, 171–176.
Ahloowalia, B.S., Maluszynski, M., 2001. Induced mutations—a new paradigm in plant breeding. Euphytica 118, 167–173.
Anderson, J.M., Chow, W.S., Goodchild, D.J., 1988. Thylakoid membrane organisation in sun/shade acclimation. Aust. J. Plant Physiol. 15, 11–26.
Barber, J., Andersson, B., 1992. Too much of a good thing: light can be bad for photosynthesis. Trends Biochem. Sci. 17, 61–66.
Bartley, G.E., Scolnik, P.A., 1995. Plant carotenoids: pigments for photoprotection, visual attraction, and human health. Plant Cell 7, 1027–1038.
Björkman, O. 1981. Responses to different quantum flux densities. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (eds.) Encyclopaedia of plant physiology. n. s. vol. XIIA, Physiological plant ecology. Springer Verlag Berlin . pp 57–107.
Bond, B.J., Farnsworth, B.T., Coulombe, R.A., Winner, W.E., 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. Oecologia 120, 183–192.
Cerovic, Z.G., Masdoumier, G., Ghozlen, N.B., Latouche, G., 2012. A new optical leaf-clip meter for simultaneous non-destructive assessment of leaf chlorophyll and epidermal flavonoids. Physiol. Plant. 146, 251–260.
Chen, J.F., Kirkbride, J.H., 2000. A new synthetic species of Cucumis (*Cucurbitaceae*) from interspecific hybridization and chromosome doubling. Brittonia 52, 315–319.
Chen, T., Zhang, Y., Zhao, L., Zhu, Z., Lin, J., Zhang, S., Wang, C., 2009. Fine mapping and candidate gene analysis of a green-revertible albino gene *gra(t)* in rice. J. Genet. Genomics 36, 117–123.
Chen, Z.J., 2013. Genomic and epigenetic insights into the molecular bases of heterosis. Nat. Rev. Genet. 14, 471–482.
Demmig, B., Winter, K., Krüger, A., Czygan, F.C., 1987. Photoinhibition and zeaxanthin formation in intact leaves a possible role of the xanthophyll cycle in the dissipation of excess light energy. Plant Physiol. 84, 218–224.
Demmig-Adams, B., 1990. Carotenoids and photoprotection in plants: a role for the carotenoid zeaxanthin. Biochim. Biophys. Acta 1020, 1–24.
Demmig-Adams, B., Adams, W.W., 1992. Photoprotection and other responses of plants to high light stress. Annu. Rev. Plant Physiol. Mol. Biol. 43, 599–626.
Demmig-Adams, B., Adams, W.W., Grace, S.C., 1997. Physiology of light tolerance in plants. Hort. Rev. 18, 215–246.
Dijkhuizen, A., Kennard, W.C., Havey, M.J., Staub, J.E., 1996. RFLP variation and genetic relationships in cultivated cucumber. Euphytica 90, 79–87.
Dong, H., Fei, G.L., Wu, C.Y., Wu, F.Q., Sun, Y.Y., Chen, M.J., Ren, Y.L., Zhou, K.N., Cheng, Z.J., Wang, J.L., Jiang, L., Zhang, X., Guo, X.P., Lei, C.L., Su, N., Wang, H., Wan, J.M., 2013. A rice *virescent-yellow leaf* mutant reveals new insights into the role and assembly of plastid caseinolytic protease in higher plants. Plant Physiol. 162, 1867–1880.
Falbel, T.G., Meehl, J.B., Staehelin, L.A., 1996. Severity of mutant phenotype in a series of chlorophyll-deficient wheat mutants depends on light intensity and the severity of the block in chlorophyll synthesis. Plant Physiol. 112, 821–832.
Fromme, P., Melkozernov, A., Jordan, P., Krauss, N., 2003. Structure and function of photosystem I: interaction with its soluble electron carriers and external antenna systems. FEBS Lett. 555, 40–44.
Fu, W., Li, P., Wu, Y., 2012. Effects of different light intensities on chlorophyll fluorescence characteristics and yield in lettuce. Sci. Hortic. 135, 45–51.
Han, H., Gao, S., Li, B., Dong, X.C., Feng, H.L., Meng, Q.W., 2010. Overexpression of violaxanthin de-epoxidase gene alleviates photoinhibition of PSII and PSI in tomato during high light and chilling stress. J. Plant Physiol. 167, 176–183.
Havaux, M., Tardy, F., 1997. Thermostability and photostability of photosystem II in leaves of the *Chlorina-f2* barley mutant deficient in light-harvesting chlorophyll *a*/*b* protein complexes. Plant Physiol. 113, 913–923.
Hesketh, J.D., 1963. Limitations to photosynthesis responsible for differences among species. Crop Sci. 3, 493–496.

Huang, D., Wu, L., Chen, J.R., Dong, L., 2011. Morphological plasticity, photosynthesis and chlorophyll fluorescence of *Athyrium pachyphlebium* at different shade levels. Photosynthetica 49, 611–618.
Janssen, L.H., Wams, H.E., Van Hasselt, P.R., 1992. Temperature dependence of chlorophyll fluorescence induction and photosynthesis in tomato as affected by temperature and light conditions during growth. J. Plant Physiol. 139, 549–554.
Jurik, T.W., Chabot, J.F., Chabot, B.F., 1979. Ontogeny of photosynthetic performance in *Fragaria virginiana* under changing light regimes. Plant Physiol. 63, 542–547.
Krause, G.H., Virgo, A., Winter, K., 1995. High susceptibility to photoinhibition of young leaves of tropical forest trees. Planta 197, 583–591.
Lichtenthaler, H., Buschmann, C., Döll, M., Fietz, H.J., Bach, T., Kozel, U., Meier, D., Rahmsdorf, U., 1981. Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. Photosynth. Res. 2, 115–141.
Long, S.P., Humphries, S., 1994. Photoinhibition of photosynthesis in nature. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45, 633–662.
Mathur, S., Jajoo, A., Mehta, P., Bharti, S., 2011. Analysis of elevated temperature-induced inhibition of photosystem II using chlorophyll a fluorescence induction kinetics in wheat leaves (*Triticum aestivum*). Plant Biol. 13, 1–6.
Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence-a practical guide. J. Exp. Bot. 51, 659–668.
McClintock, B., 1984. The significance of responses of the genome to challenge. Science 226, 792–801.
Mclaren, J.S., Smith, H., 1978. Phytochrome control of the growth and development of *Rumex obtusifolius* under simulated canopy light environments. Plant Cell Environ. 1, 61–67.
Murchie, E.H., Horton, P., 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: chlorophyll content, photosynthetic capacity and habitat preference. Plant Cell Environ. 20, 438–448.
Murchie, E.H., Lawson, T., 2013. Chlorophyll fluorescence analysis: a guide to good practice and understanding some new applications. J. Exp. Bot. 64, 3983–3998.
Müller, P., Li, X.P., Niyogi, K.K., 2001. Non-photochemical quenching. A response to excess light energy. Plant Physiol. 125, 1558–1566.
Müller-Moulé, P., Golan, T., Niyogi, K.K., 2004. Ascorbate-deficient mutants of *Arabidopsis* grow in high light despite chronic photooxidative stress. Plant Physiol. 134, 1163–1172.
Ögren, E., Rosenqvist, E., 1992. On the significance of photoinhibition of photosynthesis in the field and its generality among species. Photosynth. Res. 33, 63–71.
Schelbert, S., Aubry, S., Burla, B., Agne, B., Kessler, F., Krupinska, K., Hortensteiner, S., 2009. Pheophytin Pheophorbide Hydrolase (Pheophytinase) is involved in chlorophyll breakdown during leaf senescence in *Arabidopsis*. Plant Cell 21, 767–785.
Šesták, Z., 1966. Limitations for finding a linear relationship between chlorophyll content and photosynthetic activity. Biol. Plant 8, 336–346.
Shanmugam, S., Kjaer, K.H., Ottosen, C.O., Rosenqvist, E., Kumari Sharma, D., Wollenweber, B., 2013. The alleviating effect of elevated CO_2 on heat stress susceptibility of two wheat (*Triticum aestivum* L.) cultivars. J. Agron. Crop Sci. 199, 340–350.
Shibuya, T., Endo, R., Hayashi, N., Kitaya, Y., 2012. High-light-like photosynthetic responses of *Cucumis sativus* leaves acclimated to fluorescent illumination with a high red:far-red ratio: interaction between light quality and quantity. Photosynthetica 50, 623–629. doi:http://dx.doi.org/10.1007/s11099-012-0071-1.
Srivastava, A., Strasser, R.J., 1996. Stress and stress management of land plants during a regular day. J. Plant Physiol. 148, 445–455.
Strauss-Debenedetti, S., Bazzaz, F.A., 1991. Plasticity and acclimation to light in tropical moraceae of different successional positions. Oecologia 87, 377–387.
Suzuki, J.Y., Bollivar, D.W., Bauer, C.E., 1997. Genetic analysis of chlorophyll biosynthesis. Annu. Rev. Genet. 1, 61–89.
Walters, R.G., 2005. Towards an understanding of photosynthetic acclimation. J. Exp. Bot. 56, 435–447.
Walters, R.G., Horton, P., 1994. Acclimation of *Arabidopsis thaliana* to the light environment: changes in composition of the photosynthetic apparatus. Planta 195, 248–256.
Wild, A., Zerbe, R., 1977. Effect of different light intensities on nitrate reductase-activity, concentration of soluble-proteins and soluble reducing sugars of *sinapis alba* during growth from germination to flowering of plants. Biochem. Physiol. Pflanzen 171, 201–209.
Wu, Z., Zhang, X., He, B., Diao, L., Sheng, S., Wang, J., Guo, X., Su, N., Wang, L., Jiang, L., 2007. A chlorophyll-deficient rice mutant with impaired chlorophyllide esterification in chlorophyll biosynthesis. Plant Physiol. 145, 29–40.
Yu, X., Hyldgaard, B., Rosenqvist, E., Ottosen, C.O., Chen, J., 2015. Interspecific hybridization in *Cucumis* leads to the divergence of phenotypes in response to low light and extended photoperiods. Front. Plant Sci. 6 (802) doi:http://dx.doi.org/10.3389/fpls.2015.00802.
Zhou, R., Yu, X., Kjær, K.H., Rosenqvist, E., Ottosen, C.O., Wu, Z., 2015. Screening and validation of tomato genotypes under heat stress using F_v/F_m to reveal the physiological mechanism of heat tolerance. Environ. Exp. Bot 118, 1–11.
Zhuang, Y., Chen, J.F., Jahn, M., 2009. Expression and sequence variation of the cucumber *Por* gene in the synthesized allotetraploid *Cucumis* × *hytivus*. Mol. Biol. Rep. 36, 1725–1731.

简介：本文通过对具有不同叶色的4中基因型进行不同光照强度处里，发现叶色型差异不仅表现在Chl含量，而且在光合作用能力，生长习性和对高光的反应。