Quantity and quality of light affect growth and reproduction of the invasive annual plant *Impatiens glandulifera*

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Preface

I do feel privileged having studied ecology at UMB, mainly due to its unique combination of disciplines, peaceful surroundings and inspiring course teachers. Also, the open and non-formal attitude displayed by many high profile researchers not only benefits the curious student, but also gives you the chance to meet some really nice people. In my view, short distances across campus facilitate the interplay between curiosity and knowledge, being a fundamental asset of academic culture. My curiosity revolves to a large extent around the relationships in forest ecosystems, which may be a partial explanation for why I looked to the canopies as I extensively mapped the species described in this master thesis. Indeed, most questions on the character of this capricious newcomer came to me from observations in different environments.

Fulfilling this thesis represents much to me, and I send my sincerest thanks to my supervisors for their unique guidance. Mikael: thank you for sharing your knowledge, time, providing me with seedlings for the field experiment and for being available at all times. Having you as a teacher and main supervisor has strengthened my curiosity and motivation. Knut Asbjørn: thank you for all your aid in realising the field experiment, analyses, managing complicated machines and for improving my understanding of plants. Without your help, I seriously doubt the plants used in the study would have made it as far as they did. Olav: Thank you for sharing your experience during my time as a master student, for your continuous aid in shaping this thesis, and, not the least, for giving me entry to the mapping project in Lier, which made the work for this thesis possible. A big thank you to my friends and family for all the things we share in our lives. I send a special thank you to Markus for being such a good friend to me since I came to Ås, and for reminding me, from time to time, that it can't rain all the time. Finally, I send my most warm thanks to my parents Gabriella and Tore for their love, support, stimulation of my critical thinking and for opening my eyes to biology.

Ås, April 20th 2012

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Abstract

Biological invasions occur worldwide and are among the primary causes of biodiversity loss. Some ecosystems are more prone to biological invasions due to interactions between traits of the invasive species and their new environment. For plants, light quantity and quality affect community invasibility, and previous studies show that the performance of the invasive summer-annual *Impatiens glandulifera* (Royle) is negatively affected by shade due to reduced light quantity, but effects of light quality have not been addressed yet. Here I have examined how below-canopy light regimes affect the performance of *I. glandulifera*. My study is based on a factorial field experiment in which 135 plants were grown under three different light treatments to separate effects of light quantity and quality. Analyses consisted in sequential harvesting and gas exchange measurements using live plants. I show that the combined effects of reduced light quantity and altered light quality below perennial canopies reduce growth and reproduction of *I. glandulifera*. Light quantity and light quality also affect different aspects of plant physiology and morphology. As these results demonstrate that *I. glandulifera* is negatively affected by below-canopy light conditions, such environments are less invasible for this species.

Contents

Introduction

Some non-native species are considered invasive when occurrences in recently colonised areas greatly exceed those found within their native ranges. Biological invasions may severely alter the abundances of native species and ecosystems processes (Mack et al. 2000), and may have profound social and economic impacts (Pimentel et al. 2005). Governments and environmental agencies implement measures aiming at preventing biological invasions and ameliorating undesired consequences. However, such measures differ in their approach to the phenomenon of biological invasions, focusing on different components of interactions between invasive species and their new invaded environments.

There is a common notion of non-native plant species invasions being less frequent where there is an established plant cover (Crawley 1986; Rejmánek 1989; Rejmánek et al. 2005; Parendes & Jones 2000). In plant communities dominated by perennial competitor species (*sensu* Grime 1977), resources become highly limiting to the performance of an invader plant species. As the tree canopy closes with succession, the reduced light quantity in the forest floor may prove highly challenging to growth and reproduction of plants growing in the field layer. In addition, sub-canopy radiation yields a different spectral composition than above-canopy radiation due to selective light filtering by chlorophyll. On the one hand, wavelengths readily absorbed by chlorophyll are reduced, while on the other hand, the proportion of green light increases due to the lower absorbance of green light by chlorophyll (McCree 1972). In addition, different wavelengths stimulate photomorphogenic responses, allowing plants to acclimate to the environment.

The red-far red ratio (R:FR) is lower in below-canopy radiation, and is an environmental signal which stimulates morphological and physiological responses. Altered performance and morphology due to light quality has been demonstrated for several plant species (Morgan & Smith 1979; Leicht & Silander 2006; Ballaré et al. 1990; Weinig 2002). Plants respond to below-canopy light regimes by the use of phytochromes (Smith 2000), whose two different states absorb red and far red light, respectively. These and other photoreceptors allow plants to acclimate to different light regimes. Interestingly, light quantity and quality may affect different components of such responses (Li et al. 2001).

Clearly, light is a resource which can both vary in quantity and quality. Even though light, as other resources, is normally less abundant in late-successional plant communities, availability may vary both on a spacial and temporal scale due to environmental heterogeneity (Davis et al. 2000). It is widely recognised that plant communities are dynamic, and disturbance may strongly affect structure and species composition (Pickett & White 1985). The dominance of plants with a strong competitive ability, particularly woody perennials, is disrupted by stochastic events such as flooding, fire, logging, landslides and avalanches. Fast-growing species with a high allocation of resources to reproduction obtain higher abundance in communities subjected to frequent disturbance (Grime1977). Thus, disturbance may yield increased invasibility by increasing resource levels and removing strong competitor species (Davis et al. 2000; Tilman 2004).

Impatiens glandulifera (Royle) is a summer-annual which has achieved a widespread distribution across Europe, where it is considered highly invasive. *I. glandulifera* is native to Himalaya, and the first documented introduction to Europe occurred in the UK 1839. Further spread of the species was accelerated in the middle of the 20th century with the aid of altered land use practices (Pyšek & Prach 1995). In Norway, the distribution of *I. glandulifera* has reached all counties except Finnmark, and the species is classified as a high-risk species in the 2007 Norwegian Black List.

I. glandulifera occurs typically alongside streams as well as other environments subjected to flooding (Pyšek & Prach 1993), and is able to rapidly colonise disturbed sites (Andrews et al. 2009). The invasiveness of the species its typical formation of dense stands have triggered several studies, yielding an increasing amount of knowledge regarding responses to different resource levels. Subsequent to successful establishment, the species may rapidly obtain dominance in herbaceous stands through high seed production followed by synchronous germination, which in turn yields a rapid monopolisation of light when seedlings emerge in spring (Beerling & Perrins 1993).

Experiments and field observations have examined the performance of *I. glandulifera* under woodland canopy cover. Establishment of I*. glandulifera* appears to be negatively affected by increased height of the tree stand (Bastl et al. 1997). The species is negatively affected by shading lowering irradiance under 30% of full daylight (Beerling & Perrins 1993), but is anyhow considered

to be shade tolerant (Beerling & Perrins 1993, Andrews et al. 2009) and able to reproduce under low irradiance by the aid of acclimation mechanisms (Andrews et al. 2009).

Between 2009 and 2011, I documented extensive observations of *I.glandulifera* along the river Lierelva in Buskerud, Norway. Here, the species has invaded large areas along the river, and it appears that *I. glandulifera* was first introduced close to a small tributary stream in the upper reaches of the river before gradually achieving an extensive distribution along the main channel. Even though the step-wise colonisation of the area remains unclear to date, it is obvious that the area around Lierelva has been favourable to the colonisation of *I. glandulifera*. The species is notorious for its adaptations to humid environments, in particular around streams which aid the dispersal of seeds (Pyšek & Prach 1994).

On a finer spatial scale, the distribution of *I. glandulifera* exhibited some patterns in relation to the surrounding environment. Dense stands were common in open areas, particularly along agricultural fields and in early-succession riparian vegetation (Fig.1). Observations were less frequent and less dense under closed perennial canopies. Interestingly, *I. glandulifera* had a somewhat different morphology when growing in these shady environments as compared to in more open conditions.

Figure 1. Dense stand of *I. glandulifera* between agricultural field and woodland in Lier, Norway.

As light quality may have strong effects on the performance of invasive plants (Leicht & Silander 2006), I suggest that the qualitative aspect of light as a resource deserves consideration when assessing the performance of *I. glandulifera* within woodland. In this study I have therefore examined the performance of *I. glandulifera* in response to lower irradiance and altered distribution of wavelengths characteristic to the field layer of deciduous woodland. By separating these two components using two different shading treatments, I asked the following questions: does the quality of incoming light influence growth, reproduction, morphology, allocation patterns and leaf chlorophyll content of *I. glandulifera*? What could such responses reveal considering acclimation of *I. glandulifera* to woodland conditions? And, finally: Are woodland environments less prone to invasions by *I. glandulifera* than more open environments?

I addressed these questions by growing *I. glandulifera* under different light regimes in a factorial field experiment. The respective effects of low irradiance and sub-canopy light quality were separated by having two shade treatments with comparable irradiance levels but different R:FR ratios, while in a third treatment plants were grown in open and full light conditions. Finally, light conditions in the field experiments were compared to light conditions in a riparian area along Lierelva.

Materials and methods

Plant material, transplantation and acclimation

My study in based on 4 events of sequential harvesting and gas exchange measurements on live plants, and I have measured the following plant traits: dry weights of aboveground parts, individual number of flowers and seed pods, shoot height, leaf area ratio (LAR; area of leaves:total plant weight), leaf weight ratio (LWR; weight of leaves:total plant weight), specific leaf area (SLA; area of leaves:weight of leaves), leaf chlorophyll *a* and *b* quantity, and CO_2-uptake at different irradiance levels.

Seedlings were transplanted on May 20th 2011 (hereby referred to as day 0). Seedlings which had developed a single node of true leaves were carefully extracted from a garden edge. Of these seedlings, 145 were randomly assigned to two different kinds of pots for transplant using peat-based potting compost (84% peat, 10% fine sand, 6% clay). Among these, 55 were transplanted to 3.5 litre

plastic pots (Group 1) and 90 where transplanted to 5 litre plastic pots (Group 2). Transplants were randomly placed in clusters under a heavily shaded plot for acclimation.

Study design

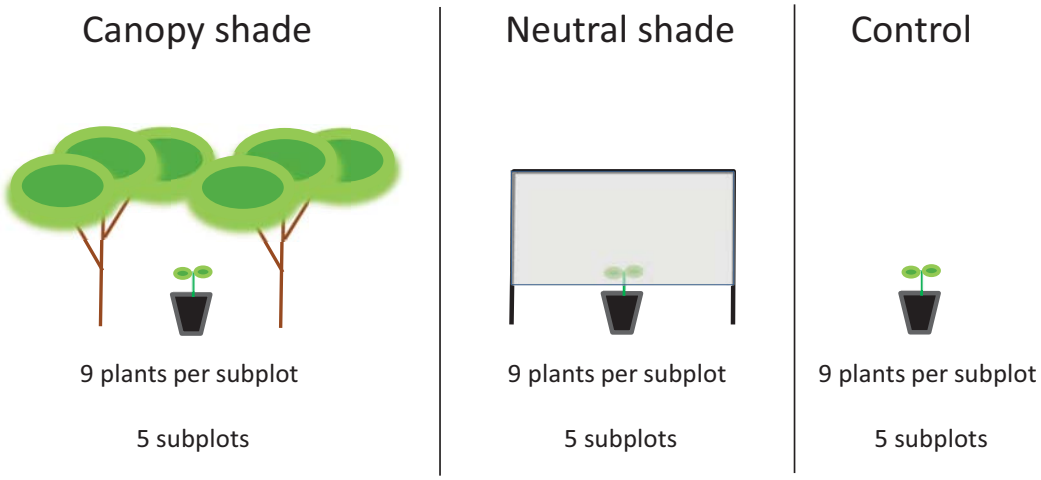

Figure 2. Design scheme for distribution of transplants among treatment replicates.

On day 10, all transplants from Group 2 where labelled and randomly distributed among 15 plots subdivided into 3 treatments, namely Canopy Shade, Neutral Shade and Control. From Group 1, 10 transplants were randomly extracted for start harvest analysis, while remaining transplants were randomly distributed among the replicates of the 3 different treatments. The transplants within replicates of all treatments were arranged in 3x3 clusters. The placement of the pots was changed every 5 days by rotation to even out differences in light received by each plant. After harvest 1, remaining plants of each replicate were arranged forming a pentagon containing a sixth plant in the middle. After harvest 2, remaining plants were arranged forming a triangle.

The experiment was set up in a research field with open lawns and clusters of hedges and trees at the Norwegian University of Life Sciences (559570 E , 6616096 N, 102m a.s.l.). Transplants assigned to Canopy Shade treatment were randomly distributed among 5 replicates placed in the undergrowth of a mixed stand of *Sorbus aucuparia*, *Aesculus hippocastanum* and *Acer platanoides* (Fig. 2).

Transplants assigned to Neutral Shade treatment were randomly distributed among 5 shading cages (Fig. 2). Each structure consisted of $4m^2$ of aluminium shading net allowing 25% transmission supported by 1x1m horizontal framed raised maximum 130 cm above ground level by 4 10x10cm beams. Shading nets were draped over the support structures in a manner which evenly reduced incoming light. East, South and West-facing sides were covered so that no unfiltered direct sunlight could reach spaces above the plastic pots. Each structure was placed at sufficient distance to neighbouring structures to avoid shading effects between replicates.

Transplants assigned to Control treatment were randomly distributed among 5 subplots next to the Neutral Shade structures (Fig. 2). The remaining plants after the start harvesting were randomly assigned to harvests 1, 2 or 3, which occurred at days 36, 53 and 60, respectively. All replicates were frequently watered throughout the experiment to keep the soil moist. All pots were watered with a nutrient solution containing 36,0 mol m^{-3} N, 3,5 mol m^{-3} P, 10,7 mol m^{-3} K until drip-through.

At each harvest, three plants were taken from each replicate and moved to a nearby laboratory for photographing and analyses. Leaves were cut at the point where the petiole was as wide as the lamina and counted. Leaves less than 1cm maximum width were omitted. Total leaf area per plant was measured using a LI-300 Area Meter (LI-COR Biosciences, Lincoln, Nebraska, USA) .The main stem was stripped of branches before being severed from the roots. Height of the primary shoot was measured before parting and drying. Plant parts were dried at $70^{O}C$ for 48 hours in a drying chamber and weighted.

Chlorophyll analysis

During harvests 1, 2 and 3, a circular tissue sample of 0.82 cm^2 was cut from the topmost developed leaf of each individual with a cork borer, at the central part of the lamina next to the middle nerve. Each leaf disk sample was put into a vial containing N,N-dimethylformamide (DMF) for chlorophyll extraction. For leaf disks cut from the the first harvest, 5 ml DMF were utilised, while 3 ml where used for the second and third harvests.

Solutions were inserted into a Plastibrand 12,5x12,5x45mm disposable cuvette (Brand GMBH & CO, Germany). Absorbance was measured using a Shimadzu UV-1800 UV-VIS spectrophotometer

(Shimadzu, Japan). Analyses of samples were performed using the program UVProbe ver. 2.34 (Shimadzu, Japan) at wavelengths 647 and 664, corresponding the absorption maxima of chlorophyll *b* and *a*, respectively. To ensure that samples did not contain undesired suspended objects, absorbance was also measured at 750 nm. Chlorophyll concentrations were calculated according to Moran (1982).

Gas exchange measurements

On day 48, gas exchange measurements were performed on one random plant from each replicate of all treatments in a nearby laboratory using a CIRAS-1 Portable Photosynthesis System (PP-systems, UK) with a mounted PLC 5B automatic cuvette. The regulated light source was an attached halogen lamp. The topmost fully developed leaf was clamped by a cuvette with light control at the middle length of the lamina at the side of the middle nerve. Settings used were CO_2 concentration of 380 ppm, relative humidity 50%. Measurements were performed under the following irradiance levels (photon flux density, PFD): 0, 50, 100, 250, 500 and 1000 μmol m^{-2} s^{-1}. To obtain 0 PFD, the halogen lamp was switched off. Values of CO_2 uptake were recorded once measurements were deemed stable, usually between 90 to 150 seconds after insertion into the cuvette.

Irradiance and R:FR measurements

Subplots for Canopy Shade treatment were selected based on irradiance measured 1 m above ground using a LI-250 Light Meter (LI-COR Biosciences, Lincoln, Nebraska, USA). Irradiance measurements were performed in clouded weather between 15:30 and 16:00 on May 27th. Subplots receiving 25-30% of irradiance received in the open were deemed suitable. On day DAG, wholesky pictures were taken using a digital camera with an attached Fisheye lens at each Canopy Shade Subplot and in close proximity to Control subplots (Fig. 3). Wholesky pictures were analysed in Gap Light Analyzer image software (GLA, ver. 2.0). Values of transmitted light for Canopy Shade subplots were corrected using the values found for the Control location.

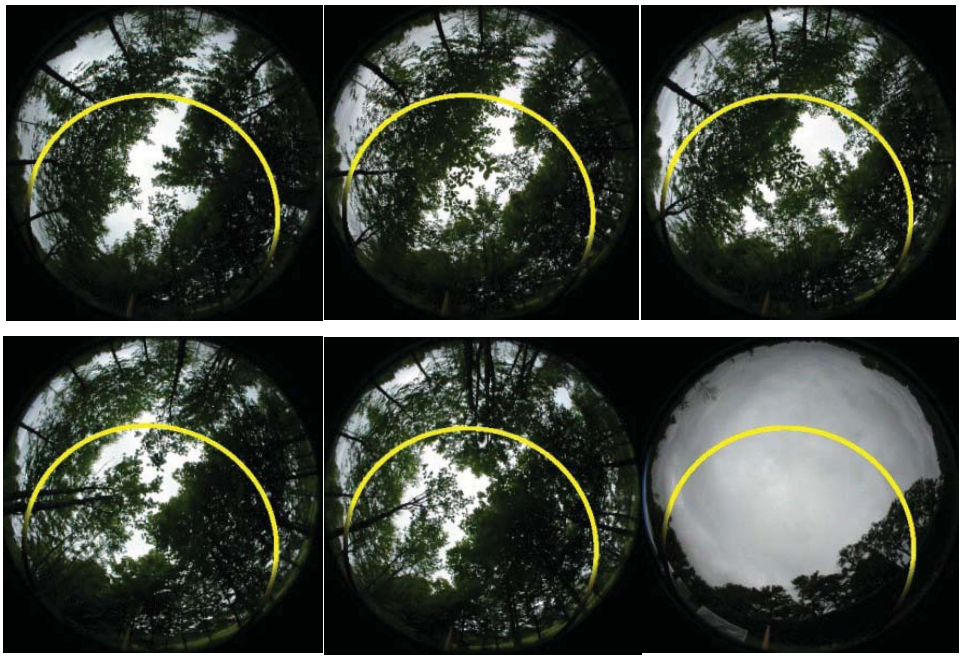

Figure 3. Whole-sky images from Canopy Shade subplots and Control area including plotted sunpaths for the period of the field experiment. Top row left to right: Canopy Shade a, b, c. Bottom row left to right: Canopy Shade d, e, Control.

Irradiance was recorded every five minutes for each treatment using a S-LIA-M003 quantum sensor (Onset Computer Corporation, Bourne, MA, USA) connected to a Hobo H21-002 Micro Station Data Logger (Onset Computer Corporation, Bourne, MA, USA). The quantum sensors were placed 20 cm above ground next to the replicates of each treatment, except for the net shade treatment where the sensors were installed in the southernmost shading cage 50 cm above ground level in a position where shading by the plants was minimal. For daily average PFD, bottom values were excluded. During the evening of day 57, R:FR ratios were recorded for each shade subplot and next to Control subplots using a SKR 110 660/730nm sensor (Skye Instruments Ltd., Llandrindod Wells, Powys, UK) held 10 cm above the top of the highest plant in the subplot.

Light measurements in riparian area

In order to compare light quantity in the field experiment to light quantity in a natural area where *I. glandulifera* was present, a transect was established from the riverbank of Lierelva, through the riparian strip to a nearby field edge in Lier, Norway (571059E, 6627439N, 12m a.s.l.) on September 20th.

Wholesky pictures were taken at four points along the transect using a digital camera with an attached Fisheye lens (Fig. 4). Images were processed as described for images taken in the experimental area.

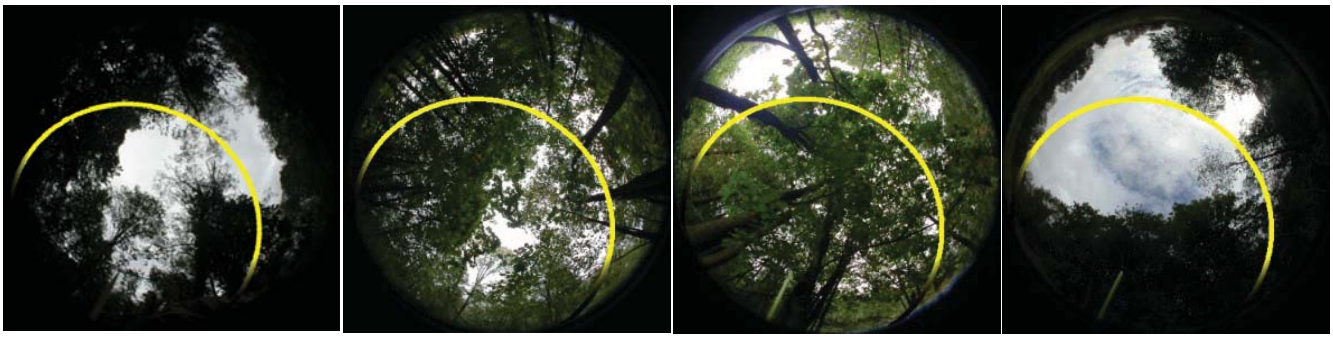

Figure 4. Wholesky pictures from a riparian strip in Lier including plotted sunpaths for the period of the field experiment. Left to right: 1-4.

Data analysis

Two-way analyses of variance (ANOVA) were performed on data from measurements and calculations spanning over two or more harvest events. Light treatment and harvest event were fixed factors for all responses except for CO_2 uptake, where light treatment and PFD were fixed factors. Tukey's range tests were performed to examine which treatments yielded significantly different responses at confidence level 0.99. All statistical analyses were executed using Minitab 16 for Windows.

Results

Shading had a significant effect on different morphological and physiological properties (Tab. 1). Differences in some of these properties, namely height, leaf size, leaf thickness and number of flowers and fruits were also clearly visible (Fig. 5).

Aboveground DW was significantly lower for individuals grown under canopy shade, while differences between Net Shade and Control treatments were non-significant (Fig. 6). When comparing number of flowers and fruits between different treatments, the only significant difference was found between Canopy Shade and Control (Fig. 6).

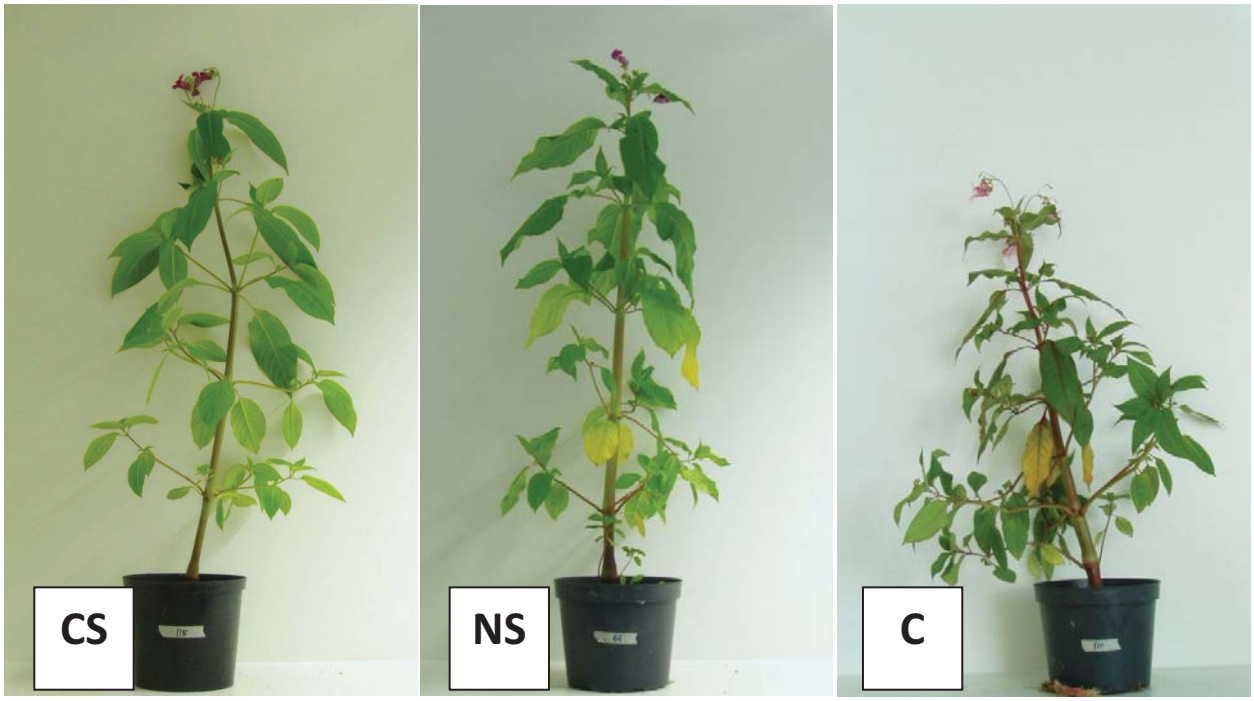

Figure 5. Photographs taken on day 60 showing one individual from each treatment.
CS: Canopy shade. NS: Neutral shade. C: Control.

Shoot height was significantly lower for control plants, while differences between shade treatments were non-significant (Fig. 6). The only significant differences in LWR between treatments were found for control plants, for which LWR was higher (Fig. 6). For LWR, there was a significant interaction between harvest event and light treatment (Tab. 1).

Plants grown under canopy shade had wider and thinner leaves than plants growing both under net shade and control, reflected in significant differences in SLA and LAR between all treatments (Fig. 7). For SLA and LAR, there was also a significant interaction between harvest event and light treatment (Tab. 1).

Canopy shade treatment yielded leaves with significantly lower chlorophyll content to leaf area than control and neutral treatment (Fig. 7). Differences between neutral shade and control were non-significant (Fig. 7). When comparing chlorophyll *a*:*b* ratios, values were significantly higher for control, while differences between shade treatments were non-significant (Fig. 7). There was a

significant interaction between harvest event and light treatment for chlorophyll content and chlorophyll *a*:*b* ratio.

Photosynthetic CO_2 uptake differed significantly between all treatments (Fig. 8). Differences were most pronounced at 500 and 1000 µmol m^{-2} s^{-1}. There was a significant interaction between PFD and light treatment (Tab. 1).

Calculated and recorded PFD was slightly lower for Canopy Shade than Net shade (Tab. 2, Tab. 4), in particular on sunny days (Tab. 4).

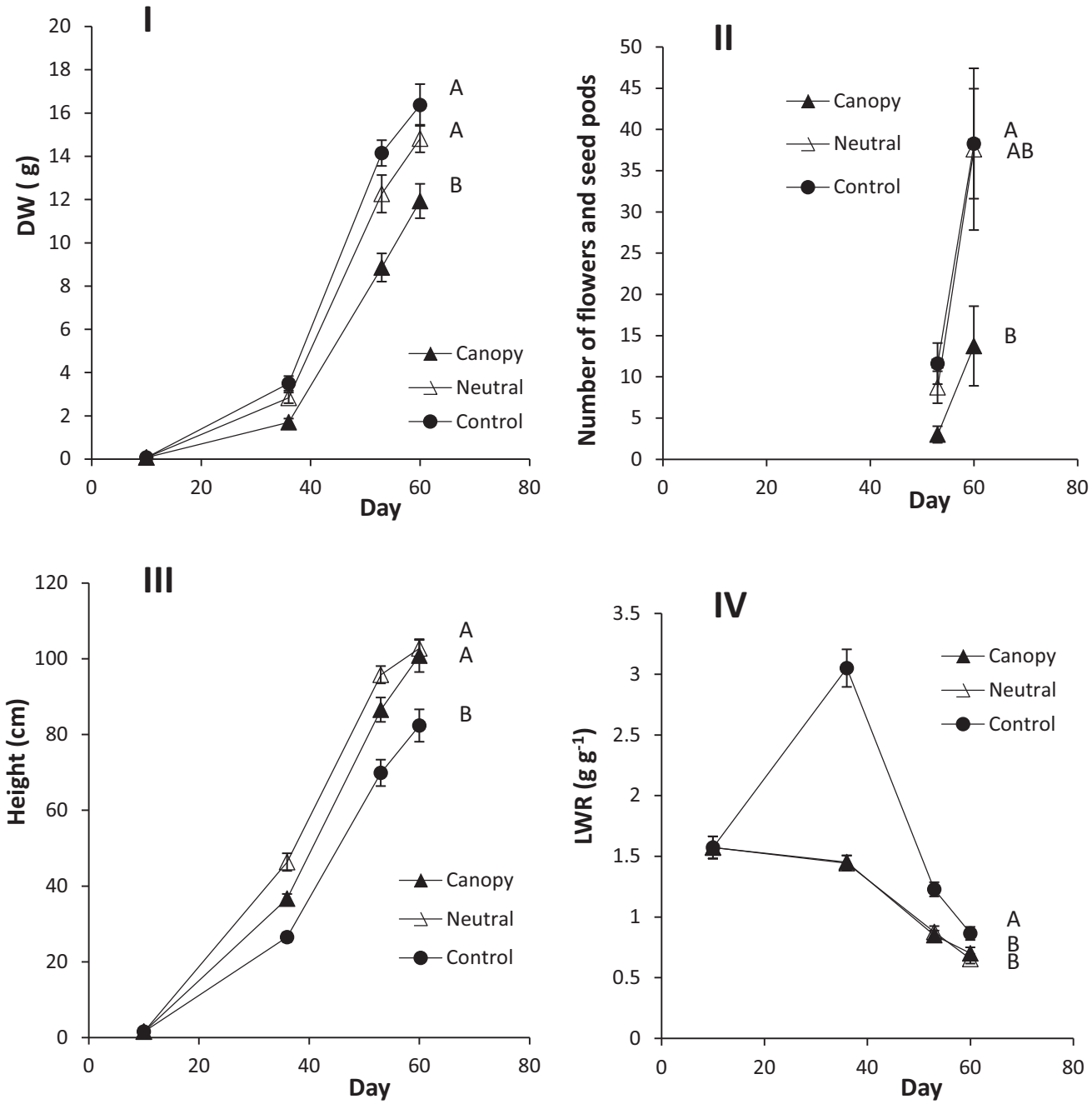

Figure 6. Effect of shading on the performance of *Impatiens glandulifera.* Letters group different treatments using Tukey's range test. Error bars show ±1SE. I: Aboveground dry weight. II: Reproduction. III: Shoot height. IV: Leaf Weight Ratio.

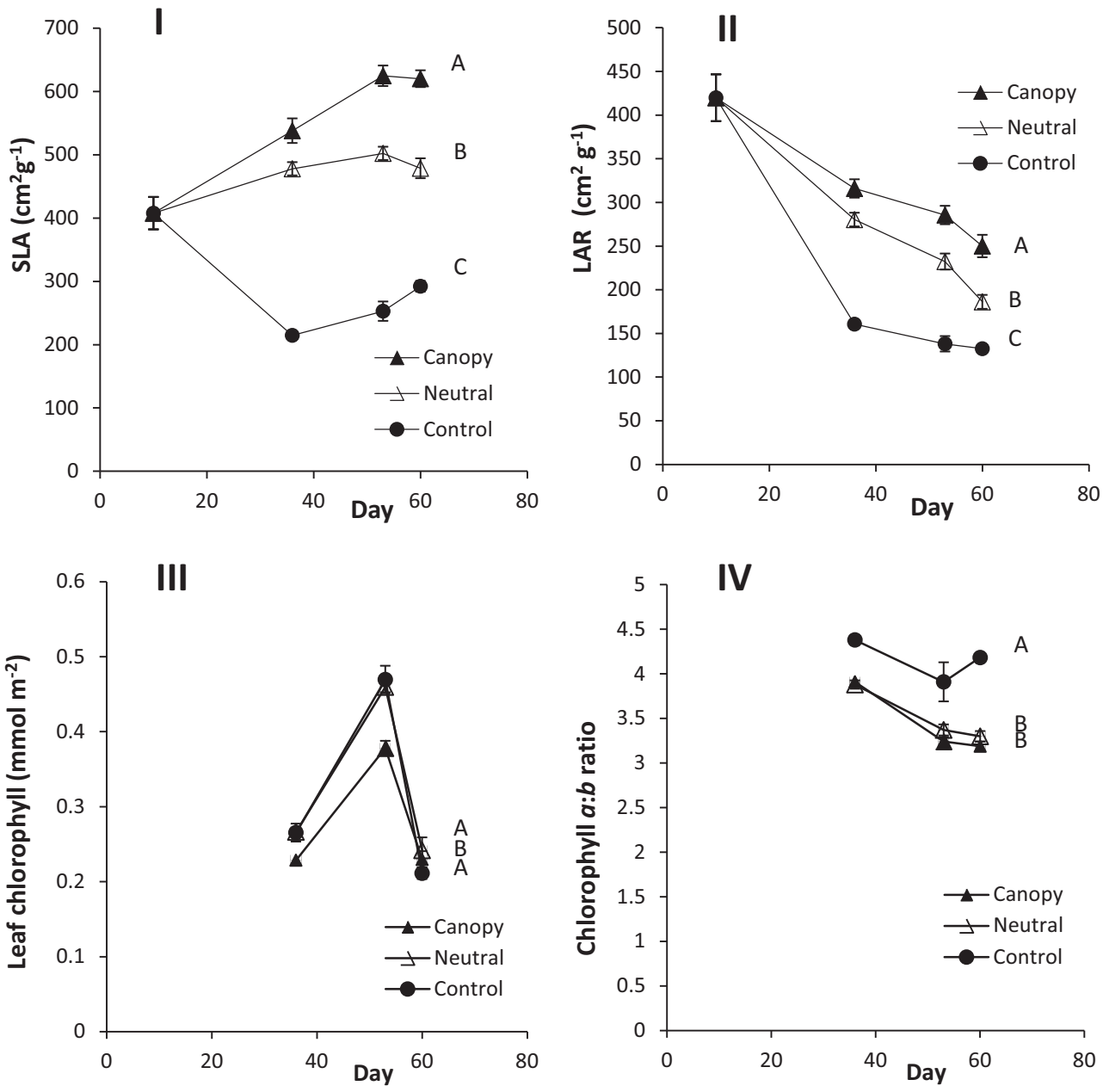

Figure 7. Effect of shading on leaves of *Impatiens glandulifera*. Letters group different treatments using Tukey's range test. Error bars show ±1SE. I: Specific Leaf Area II: Leaf Area Ratio. III: .Leaf chlorophyll content. IV: Chlorophyll *a*:*b* ratio.

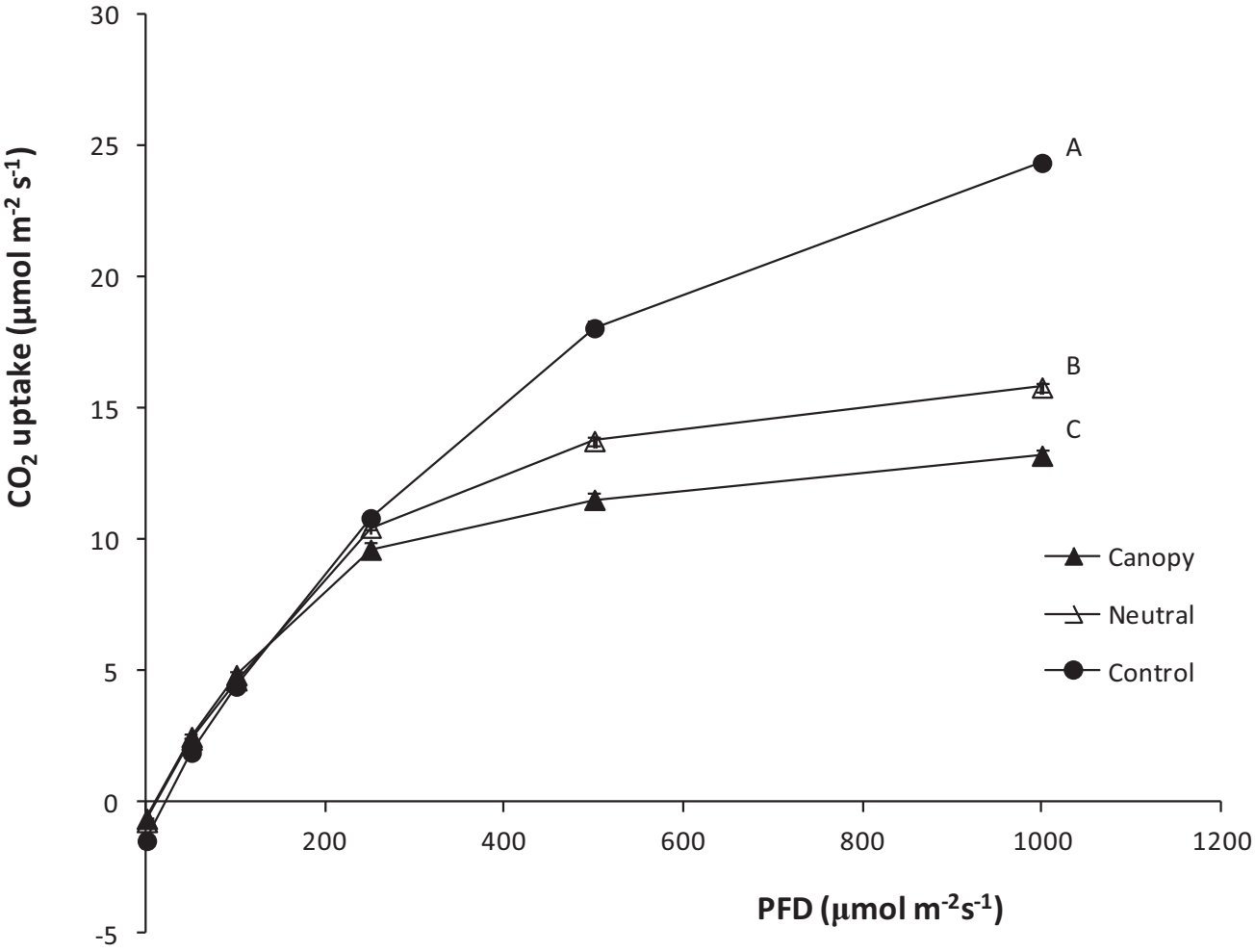

Figure 8. Photosynthetic rates in leaves of *I. glandulifera* subjected to different light regimes. Letters group different treatments using Tukey's range test.. Error bars show ±1SE.

Table 1. Two-way ANOVA of aboveground DW (g), number of flowers and fruits, shoot height (cm), leaf weight ratio (g g^{-1}), specific lead area (cm^2 g^{-1}), leaf area ratio (cm^2 g^{-1}), leaf chlorophyll content (mmol m^{-2}), chlorophyll *a*:*b* ratio and CO_2-uptake (µmol m^{-2} s^{-1}) for *Impatiens glandulifera*. Significant differences at confidence level 0.95 are shown in bold, while significant differences at confidence level 0.99 are marked with *.

	Aboveground DW			**Flowers and fruits**			**Shoot height**			**Leaf weight ratio**		
	DF	*F*	*P*	*DF*	*F*	*P*	*DF*	*F*	*P*	*DF*	*F*	*P*
Light treatment	2	27,97	**<0,001***	1	5,73	**0,005***	2	44,67	**<0,001***	2	61,63	**<0,001***
Harvest event	2	281,24	**<0,001***	2	25,33	**<0,001***	2	342,88	**<0,001***	2	231,77	**<0,001***
Interaction	4	2,11	0,083	2	1,69	0,190	4	0,98	0,420	4	5,46	**<0,001***

	Specific leaf area			**Leaf area ratio**			**Leaf chlorophyll content**			**Chlorophyll *a*:*b* ratio**		
	DF	*F*	*P*	*DF*	*F*	*P*	*DF*	*F*	*P*	*DF*	*F*	*P*
Light treatment	2	501,64	**<0,001***	2	195,77	**<0,001***	2	11,63	**<0,001***	2	57,29	**<0,001***
Harvest event	2	14,31	**<0,001***	2	38,35	**<0,001***	2	271,34	**<0,001***	2	34,5	**<0,001***
Interaction	4	3,81	**0,006***	4	3,7	**0,007***	4	5,49	**<0,001***	4	2,54	**0,043**

	CO_2 uptake		
	DF	*F*	*P*
Light treatment	2	87,14	**<0,001***
PFD	5	927,99	**<0,001***
Interaction	10	36,59	**<0,001***

Table 2. Total transmitted irradiance using Fisheye images for experimental area and natural riparian area. Corrected values for experimental subplots were obtained using control value.

		% transmitted	% corrected
Control		88,1	-
Subplot	A	19,6	22,3
	B	21,3	24,1
	C	19,7	22,4
	D	23,0	26,1
	E	16,8	19,1
	Average	20,1	22,8
Transect location			
	1	42,7	-
	2	17,5	-
	3	16,4	-
	4	71,3	-

Table 3. R:FR values measured on day 57.

	Subplot	R:FR
Canopy shade	**A**	0,57
	B	0,49
	C	0,51
	D	0,51
	E	0,5
Net shade	**A**	0,78
	B	0,78
	C	0,79
	D	0,77
	E	0,8
Control	**-**	0,98

Table 4. Recorded irradiance at treatment locations for the logging period. PFD values are given in µmol m^{-2} s^{-1}

	Canopy Shade		Net Shade		Control
Day	PFD	% shading	PFD	% shading	PFD
20	112	23,4	137	28,6	480
21	28	26,8	29	28,0	105
22	28	27,0	29	28,4	102
23	45	25,7	49	27,7	177
24	188	22,2	232	27,4	846
25	175	21,1	230	27,7	832
26	134	22,3	165	27,5	600
27	103	17,7	165	28,3	583
28	87	19,5	132	29,6	446
29	30	27,2	30	27,7	110
30	117	22,9	128	25,1	512
31	66	22,8	70	24,1	289
Average	92,8	23,21	116	27,51	424

Discussion

Morphological responses

In terms of aboveground DW and reproduction, the overall performance of *I. glandulifera* was reduced under woodland canopy cover. This was not the case for plants grown under the neutral shading structures, which suggests that light quality had a substantial effect. Average R:FR ratios were 50% higher in neutral shade than canopy shade at the end of the field experiment (Tab. 3).Thus, light regimes typical for a woodland field layer affect the performance of *I. glandulifera* through lowered irradiance and altered light quality. When considering that average daily irradiance was slightly lower for Canopy Shade than Neutral Shade (Tab. 2; Tab. 4), it is worth mentioning that differences in irradiance among some Canopy Shade subplots were as high or even higher (Tab. 2).

Some shade responses in *I. glandulifera* are in line with earlier notions on the species being shade tolerant (Andrew et al. 2009; Beerling Perrins 1993). However, the species also exhibited shade responses common to shade avoiders, most strikingly increased stem elongation, lowered LWR and

lowered chlorophyll content for both shade treatments. The lowered main shoot height under both types of shade corresponds to findings from studies of several herbaceous species. Morgan & Smith (1979) compared a number of species considered shade avoiders with shade tolerant species. Lowering the R:FR ratio yielded increased stem elongation, being more pronounced in the former than the latter. The relative *Impatiens parviflora* also displays "shade avoider"-responses to lowered R:FR ratio, including increased stem elongation (Whitelam & Johnson 1982).

Andrews et al. (2005) found a negative relationship between shoot height and irradiance for *I. glandulifera*. Results from my study are in line with these findings, as shoot height was lowest for control where irradiance was highest. Phytochrome is involved in stem extension through perception of lowered R:FR ratio and lowered irradiance. At day 58, the higher part of a plant grown in canopy shade broke due to strong winds. Indeed, plants grown in canopy shade may have been less robust, as this treatment yielded significantly less aboveground DW than neutral shade to sustain increased shoot height.

Comparisons of LWR between treatments suggest that irradiance and not light quality affects DW partitioning in *I. glandulifera*. The species appears to allocate more resources to photosynthetic capacity when growing in the open. In *I. parviflora*, irradiance has no effect on LWR, while R:FR ratio and blue light does (Hughes 1965). It is not uncommon that altering the spectral distribution may yield different responses between closely related species (Fitter & Ashmore 1974; Leicht & Silander 2006). Even when different plant species may possess the same array of photoreceptors, it is common that signal pathways differ between species (Dale 1988; Smith 2000).

Both shade treatments yielded higher SLA than control, which was highest for Canopy Shade treatment. For *I. parviflora*, a similar effect has been demonstrated (Evans & Hughes 1961). Irradiance and light quality influence leaf morphology through cell division, cell expansion or both (Dale 1988). In *Rumex obtusifolius,* leaf thickness is lowered both by lowering the R:FR ratio and lowering irradiance (Dale 1988). Shade-tolerant species commonly possess smaller palisade cells and fewer palisade layers than when growing in high irradiance. For shade-tolerant species growing under closed canopies, such responses optimise resource use for interception of available light.

Different parts of the light spectrum are involved in photomorphogenic responses in leaves, as plants possess different photoreceptors for different wavelengths. Red and blue light increase cell wall extensibility (Lambers et al. 2008), which may explain why SLA was higher for Canopy Shade than neutral. Barkan et al. (2006) demonstrated that low levels of supplemental UV-B light stimulate leaf expansion through cell enlargement in *Phaseolus vulgaris*, while high levels yielded smaller leaves.

LAR was significantly higher for the shade treatments than control. Differences in LAR between shade treatments is attributed to higher values of SLA in Canopy Shade plants, as LWR were similar at all harvests (Fig. 7). In *I. parviflora*, LAR increases at low irradiance, attributed to increased SLA. In the same species, blue light stimulates lateral leaf expansion through cell enlargement while maintaining the same number of cells (Hughes 1965).

Chlorophyll content

Leaf chlorophyll content was significantly lower for Canopy Shade, while between neutral shade and control differences were nonsignificant (Fig. 7). For several plant species, lowering the R:FR ratio reduces leaf chlorophyll concentration (Morgan & Smith 1979). Thus, it may be possible that low R:FR ratio yields lower chlorophyll concentration in *I. glandulifera* without altering the chlorophyll *a*:*b* ratio. The significantly higher chlorophyll *a*:*b* ratio in plants growing in the open demonstrates that *I. glandulifera* shifts the balance of photosystems as a response to increased irradiance, which is a common acclimation mechanism for plants growing in open conditions.

Photosynthetic rate

Photosynthetic CO_2 uptake increased for all treatments with increased irradiance, but less so for plants grown in shade (Fig. 8). Such differences may be attributed to acclimation to different light regimes. Differences in photosynthetic activity at high irradiance reflect differences in SLA and total leaf chlorophyll content. Control plants had thicker leaves with higher chlorophyll content, and could therefore increase CO_2 uptake with increased irradiance. Thus, it is not surprising that there was a significant interaction between light treatment and PFD (Tab. 1).

Differences in photosynthetic rates reflect differences in aboveground DW. As plants grown in canopy shade had lower CO_2 uptake, it is not surprising that aboveground DW was significantly

lower than the other treatments. Such a relationship has also been shown for the highly invasive plant *Eupatorium adenophorum* (Zheng et al. 2009). For *I. glandulifera* , a strong positive correlation between biomass and irradiance has been demonstrated (Andrews et al. 2005). In this study, high LWR, chlorophyll content and photosynthetic activity in plants grown in the open could be responsible for higher aboveground DW.

Reproduction

Reproductive performance was strongly reduced for plants grown in canopy shade, where average numbers of flowers and fruits were about a third of those counted on plants growing in the open. Interestingly, differences between plants receiving neutral shade and control treatments were nonsignificant, which suggest that the former were able to maintain a high reproductive output despite lower irradiance. The causative agents for differences in reproduction between plants grown under canopy shade and in open conditions remain unknown, but may be due to physiological differences, different light quality, or a combination of these.

It should not be excluded that the Canopy Shade treatment merely delayed growth and developmental stages in *I. glandulifera*. If the field experiment would have been sustained until plants died, results would include a more thorough assessment of reproduction. Still, the low photosynthetic rates and aboveground DW of plants grown in canopy shade indicate that plants receiving this treatment would have had less photosynthate to invest in reproduction throughout the season. Also, control treatment yielded plants which invested significantly more DW in leaves, which would further accentuate the aforementioned tendency. The length of the field experiment covered a substantial part of the growing season of *I. glandulifera*, and thus the displayed differences in reproduction give a strong indication of season-wide performance.

From my field work in Lier, I noted that in the late summer, *I. glandulifera* commonly developed seed pods continuously, yielding seed pods of different levels of maturation. The length of the field experiment was not sufficient to yield continuous maturation of seeds. In *I. parviflora,* once seeds are set, available resources are directed towards their maturation, even on the expense of plant weight (Hughes 1965). If *I. glandulifera* displays the same ability, plants with a higher photosynthetic rate and higher DW would have sufficient resources to sustain the production and maturation of a high number of seeds. Interestingly, there was a significant interaction between light

treatment and harvest event for LWR and chlorophyll content (Tab. 1), suggesting that these values where lower at the end of the experiment due to increased allocation to reproduction (Fig. 6; Fig. 7).

Why is Impatiens glandulifera invasive?

The emerging field of invasion biology includes different approaches to understanding biological invasions, and has also introduced an array of new terms to ecology. Still, such terms are not necessarily mutually exclusive, but describe different aspects of the invasion process. Understanding why *I.* glandulifera is highly invasive requires considerations of these aspects. Together, invasibility, propagule pressure and species traits determine the outcome of non-native species introductions in a given environment (Davis et al. 2000, Davis et al. 2005; Thompson et al. 2001). Propagule pressure accounts for dispersal (Lockwood et al. 2005), while invasibility is the defined as the susceptibility of a community to biological invasions (Lonsdale 1999, Davis et al. 2005).

As such aspects represent different points of view of the invasion process, researchers do emphasise these aspects differently. Traits of invasive species are commonly addressed as they may have a potential for improving management. Screening non-native species for particular traits has been advocated as a means to prevent biological invasions (Kolar & Lodge 2001). Accordingly, a non-native species may be revealed as invasive by recognising traits shared by several other invasive species. This approach has proven somewhat difficult, as studies give mixed results (Thompson et al. 1995; Meiners 2007). Combined approaches to understanding biological invasions focus on interactions between species traits and the environments in which they become established (Tucker & Richardson 1995). Also, experimental studies show that invasive plant species display traits whose benefits vary with resource availability and time (Thompson et al. 2001).

Invasibility is a community-wide property, but does also include other aspects of the invasion process. Different theories explain variations in invasibility by focusing on one or more of the following factors, or a combination of these: diversity of resident species and functional groups; resource availability; physical stress; and biotic interactions (see Fridley et al. 2007 for a review). A general theory of invasibility proposes that temporal and spatial variations in the availability of limiting resources are the main drivers of invasibility (Davis et al. 2000). Accordingly, any factor that would increase the availability of resources, and thus invasibility, would do so in two ways: i.e.

either by decreasing the resource use of the present plant community or by increasing the resource supply faster than the present plant community may sequester it (Davis et al. 2000). The theory has been corroborated in experimental and observational studies for different taxa, including higher plants (Thompson et al. 2001; Davis & Pelsor 2001).

Results from my study suggest that light limits the performance of *I. glandulifera* in woodlands with established canopies, which could be deemed less invasible to *I. glandulifera*. Then, if resource availability influences invasibility, how is *I. glandulifera* favoured in resource rich environments? Ruderal traits (*sensu* Grime et al. 1977) such as short life cycles, rapid growth and major allocation to reproduction, are favourable in environments where strong competitors are few or absent, and resources are abundant (Rejmánek & Richardson 1996, Mehrhoff 1998). Such traits, along with phenotypic plasticity and wide tolerances for environmental conditions, are typical for invasive species (Rejmánek et al. 2005). The invasiveness displayed by *I. glandulifera* in some environments should then be interpreted as a combination of traits and environmental conditions, as *I.* glandulifera is better able in taking advantage of high resource availability than native species. Indeed, previous studies show that with abundant resources, *I. glandulifera* displays the same characteristics as crop and weedy plants (Andrews et al. 2009).

In favourable conditions, a single *I. glandulifera* plant is able to produce an abundant number of short-lived seeds (Grime et al. 1988). As the species only reproduces through cross-pollination (Beerling & Perrins 1993), the viability of a population is strictly dependent on successful maturation of seeds and their germination the following season. Then, any factor limiting seed production would be expected to decrease dispersal and invasion of *I. glandulifera* in a given territory. With abundant light and nutrients, *I. glandulifera* has higher reproduction, rendering such environments more invasible to *I. glandulifera*. The species possesses traits which may increase performance in shade with nutrient addition (Andrews et al 2009). In my study, *I. glandulifera* was supplied with additional nutrients throughout the period of the field experiment. Thus, results should be interpreted as a display of the performance of *I glandulifera* in a light regime typical of woodland floors, but with high nutrient availability.

The common assumption of forests being less invasible has been criticised, as few studies consider invasive shade tolerant species (Martin et al 2009). Such controversies may be avoided if

community invasibility is assessed using a single-species approach. Species possess unique set of traits which reflect adaptations to particular environments. Thus, a community which may appear less invasible for one species might be highly invasible for another. Results from this study suggest that plant communities possessing an established canopy are less invasible for *I. glandulifera*. Below-canopy light conditions do not necessarily negate the establishment and dispersal of *I. glandulifera*, but may slow the invasion process by decreasing recruitment to the species' seed bank. Indeed, interspecific plant competition has proven to be the fastest way to control the invasive weed *Jacobea vulgaris* (Dauer et al. 2012).

Through the second half of the 20th century, *I. glandulifera* had strongly increased its distribution in Europe (Pyšek & Prach 1995), and the expansion could be correlated with anthropogenic destruction of riparian plant communities (Beerlig & Perrins 1993). A partial explanation for such phenomena may be increased resource availability. Commonly, removal of established perennials by disturbance increases resource availability, even on a small spatial scale (Thompson et al. 2001). Indeed, during my field observations in Lier, *I. glandulifera* appeared in dense stands were vegetation was cleared. It is not unlikely that removal of the perennial vegetation enhanced environmental conditions for *I. glandulifera*, as it is known that the species is favoured by some degree of disturbance in some habitats (Perrins et al. 1993; Grime et al. 1988). Within the riparian strip along Lierelva where light quantity was measured (Tab. 2), very few plants were observed, while there was a dense stand at the edge of the strip where light was more abundant.

Disturbance and eutrophication may act synergistically to increase invasibility (Burke & Grime 1996). In a study in southern Bohemia, Czech Republic, early-successional stages were more prone to invasions by *I. glandulifera* than older successional stages, in particular where nutrients were added (Bastl et al. 1997). The species is also particularly associated with bare earth (Grime et al. 1988), but the reason for this remains unclear. Competitive exclusion of other herbaceous plants might involve shading, and the species does also display signs of allelopathy when grown with other herbaceous species (Vrchotova et al. 2011; Scharfy et al. 2010). Interestingly, *I. glandulifera* has only a weak negative impact on seedling growth of some tree species (Ammer et al. 2011), suggesting that *I. glandulifera* does not inhibit succession of some plant communities.

Conclusion

Findings from this study demonstrate that light quality affects growth and reproduction of *I. glandulifera*. Substantial differences in physiology, morphology and overall performance between shade treatments suggest that light quality effects should be considered when assessing the invasibility of a plant community for *I. glandulifera*. Both light quality and quantity are vital to a plant's performance, as species have evolved to respond differently to environmental stimuli to optimise resource use. Clearly, the phenotypic plasticity possessed by *I. glandulifera* enables higher reproduction where light is abundant.

Even though *I. glandulifera* is generally considered as shade-tolerant, it displays traits typical for shade avoiders, which are of importance when assessing performance in different light conditions. The observed elevated performance in open habitats is in line with previous studies on invasive r-strategists. *I. glandulifera* has higher DW, photosynthetic rate and reproduction where light is more abundant. Decreased light availability may provide a partial explanation for why the species is less abundant under established perennial canopies. Destruction of established perennial vegetation will thus enhance the invasion of *I. glandulifera.*

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Appendix I.

Leaf area (LA) (cm^2), leaf dry weight (LDW) (g), leaf number (LN), main shoot length (SL) (cm), main shoot dry weight (SDW) (g), number of undeveloped (U) and fully developed (D) flowers (FL) and number of seed pods (Pod) of *I. glandulifera.*

Sample ID	Treatment	Harvest	LA	LDW	LN	SL	SDW	FLW		Pod
								U	D	
28	-	0	9,83	0,032	6	7,4	0,025	-	-	-
6	-	0	11,29	0,028	7	10,3	0,024	-	-	-
29	-	0	8,92	0,029	7	6,5	0,015	-	-	-
17	-	0	27,16	0,077	7	10,9	0,050	-	-	-
16	-	0	13,35	0,028	6	7,5	0,017	-	-	-
145	-	0	31,85	0,077	7	10,8	0,039	-	-	-
58	-	0	24,82	0,063	8	12,8	0,045	-	-	-
79	-	0	12,66	0,031	7	8,7	0,023	-	-	-
55	-	0	18,00	0,064	6	7,6	0,042	-	-	-
122	-	0	10,89	0,021	2	6,9	0,011	-	-	-
1	CS	1	769,90	1,480	38	42,9	1,065	-	-	-
48	CS	1	989,40	1,930	55	43,2	1,171	-	-	-
50	CS	1	483,20	0,855	27	40,2	0,677	-	-	-
4	CS	1	433,30	0,776	29	34,9	0,560	-	-	-
8	CS	1	741,40	1,262	44	40,1	0,838	-	-	-
45	CS	1	331,30	0,550	28	30,3	0,489	-	-	-
20	CS	1	275,50	0,432	13	31,8	0,327	-	-	-
40	CS	1	370,80	0,595	26	40,4	0,548	-	-	-
27	CS	1	569,60	0,988	35	41,6	0,720	-	-	-
21	CS	1	452,20	0,941	22	34	0,637	-	-	-
3	CS	1	404,50	1,037	27	32,9	0,760	-	-	-
33	CS	1	622,80	1,007	33	35,9	0,574	-	-	-
25	CS	1	276,40	0,634	16	28,9	0,376	-	-	-
13	CS	1	592,40	1,141	34	33,4	0,646	-	-	-
30	CS	1	696,40	1,579	38	39,7	0,965	-	-	-
11	NS	1	697,60	1,618	26	44,6	1,120	-	-	-
10	NS	1	730,40	1,568	32	48,7	1,223	-	-	-
49	NS	1	775,30	1,572	42	52,1	1,239	-	-	-
41	NS	1	733,40	1,473	38	43,9	0,887	-	-	-
31	NS	1	980,90	2,244	49	43,2	1,262	-	-	-
19	NS	1	666,70	1,302	28	39,4	0,891	-	-	-
22	NS	1	847,60	1,751	35	41	0,984	-	-	-

Sample ID	Treatment	Harvest	LA	LDW	LN	SL	SDW	FLW		Pod
								U	D	
34	NS	1	781,80	1,782	30	52,4	1,426	-	-	-
46	NS	1	788,00	1,633	43	39,7	0,938	-	-	-
14	NS	1	1043,80	2,210	47	66,3	1,936	-	-	-
7	NS	1	1022,40	2,180	47	54,6	1,751	-	-	-
18	NS	1	549,00	0,957	31	44,8	0,610	-	-	-
44	NS	1	1055,70	2,563	52	50,9	1,687	-	-	-
47	NS	1	168,50	0,322	9	25,8	0,322	-	-	-
5	NS	1	850,50	1,795	43	47,5	1,187	-	-	-
15	C	1	870,40	4,953	63	25,7	1,601	-	-	-
38	C	1	412,10	2,007	39	22,3	0,543	-	-	-
2	C	1	540,30	2,544	45	28,4	0,815	-	-	-
32	C	1	360,30	1,830	31	21,8	0,509	-	-	-
36	C	1	462,60	2,160	35	26,2	0,770	-	-	-
23	C	1	762,50	3,444	61	27,3	1,053	-	-	-
39	C	1	686,10	2,824	50	26,7	0,948	-	-	-
24	C	1	681,90	2,950	57	23,1	0,756	-	-	-
43	C	1	453,00	1,788	47	24,1	0,570	-	-	-
12	C	1	200,00	0,953	20	18,9	0,490	-	-	-
37	C	1	656,50	3,268	55	40,4	1,585	-	-	-
9	C	1	740,10	3,527	57	29,9	1,438	-	-	-
26	C	1	442,40	1,902	33	24,5	0,482	-	-	-
35	C	1	532,60	2,432	49	29,3	0,886	-	-	-
42	C	1	500,50	2,592	40	28,9	0,865	-	-	-
56	CS	2	3364,90	5,316	107	86,9	5,060	2	0	0
53	CS	2	2020,60	3,197	61	69,1	3,316	0	0	0
63	CS	2	3119,00	4,808	84	100,1	5,717	4	1	1
105	CS	2	2108,90	3,557	73	88,6	4,528	2	0	0
112	CS	2	2389,10	3,685	77	91,4	4,667	2	1	1
98	CS	2	1945,70	2,930	43	93,1	4,969	0	0	0
61	CS	2	1812,60	2,516	56	82,6	3,085	1	0	0
96	CS	2	2215,00	3,142	69	77,3	3,310	3	2	0
59	CS	2	2075,40	3,173	44	89,0	4,241	0	0	0
71	CS	2	1916,00	3,135	55	79,4	4,008	0	0	0
119	CS	2	2568,90	5,709	61	82,7	7,320	0	0	0
95	CS	2	2937,50	4,742	86	89,2	5,116	8	3	3
131	CS	2	2166,10	3,490	54	67,5	3,230	0	0	0
74	CS	2	3225,30	5,325	84	82,4	5,245	4	2	1
99	CS	2	3160,00	5,592	74	119,0	8,710	4	0	0
124	NS	2	2794,10	5,759	70	108,4	10,081	2	0	0

Sample ID	Treatment	Harvest	LA	LDW	LN	SL	SDW	FLW		Pod
								U	D	
60	NS	2	3613,50	7,257	111	101,8	7,583	16	2	0
75	NS	2	3050,70	6,510	96	107,1	9,979	5	1	0
104	NS	2	2313,20	5,170	112	82,2	4,569	6	2	3
72	NS	2	2680,70	5,276	104	92,3	5,740	4	3	1
86	NS	2	3411,10	7,463	86	99,2	9,087	5	3	0
84	NS	2	3769,00	7,407	107	96,4	7,781	5	3	1
97	NS	2	3486,10	7,112	111	98,8	6,533	13	5	6
62	NS	2	2309,00	4,660	73	86,6	4,535	3	0	0
87	NS	2	2969,60	5,590	90	89,8	5,641	8	3	3
137	NS	2	3726,40	7,401	104	102,3	7,632	14	3	4
134	NS	2	1411,60	3,160	53	106,0	6,218	2	0	0
68	NS	2	2883,30	5,070	83	96,9	5,924	0	1	1
51	NS	2	2539,60	4,699	63	88,4	4,795	0	0	0
64	NS	2	1293,20	2,220	48	80,6	3,070	3	0	0
106	C	2	2100,60	6,339	99	65,8	5,102	16	3	3
109	C	2	2268,80	8,934	118	47,4	5,724	8	0	0
129	C	2	1923,90	6,854	107	55,7	5,317	13	1	0
93	C	2	2116,40	8,070	99	61,2	5,404	16	3	5
138	C	2	2394,80	9,510	95	80,6	7,652	5	0	0
136	C	2	1908,20	6,720	102	57,4	5,424	6	1	0
135	C	2	2198,10	8,458	129	74,0	6,600	3	1	0
91	C	2	1946,30	7,527	94	92,3	8,560	4	0	1
140	C	2	929,30	7,496	100	83,6	7,987	6	0	0
111	C	2	759,00	6,955	98	55,2	4,580	16	3	3
89	C	2	1967,60	6,900	95	65,1	5,052	13	7	7
65	C	2	1979,30	6,938	85	72,1	7,128	0	2	0
70	C	2	2512,10	8,785	94	91,1	10,098	0	0	0
57	C	2	1904,00	6,921	103	68,1	5,023	16	4	5
120	C	2	2110,20	8,618	98	78,5	7,538	3	0	0
132	CS	3	2548,90	4,345	53	110,6	9,244	0	0	0
117	CS	3	3163,20	5,095	93	77,5	6,339	17	10	9
139	CS	3	-	-	-	109,2	10,238	7	2	0
128	CS	3	2506,70	3,870	66	101,4	5,803	0	0	0
107	CS	3	3509,70	5,875	85	136,6	13,536	0	0	0
67	CS	3	2938,30	3,945	63	115,4	7,187	3	0	0
144	CS	3	2278,00	3,313	71	70,6	3,156	3	2	1
83	CS	3	3722,50	5,786	83	102,6	7,644	4	1	0
121	CS	3	2644,70	4,840	56	116,4	9,598	0	0	0
130	CS	3	3455,60	5,550	97	91,7	6,762	28	11	19

Sample ID	Treatment	Harvest	LA	LDW	LN	SL	SDW	FLW		Pod
								U	D	
141	CS	3	3185,80	5,432	93	100,1	6,837	24	4	4
90	CS	3	2723,70	4,642	58	93,4	7,013	2	0	0
116	CS	3	2972,30	5,071	82	88,1	5,097	18	11	7
115	CS	3	2199,70	3,608	61	98,1	5,440	8	4	4
123	CS	3	2675,60	4,975	68	102,5	7,755	3	0	0
54	NS	3	3355,50	7,605	103	106,7	12,578	2	7	0
100	NS	3	1323,30	4,265	76	105,2	5,516	26	8	6
103	NS	3	1974,30	4,039	59	112,5	8,699	0	0	0
52	NS	3	3356,30	6,297	94	99,2	8,422	51	17	26
143	NS	3	3174,30	6,365	112	95,1	8,580	51	17	48
66	NS	3	2575,60	6,355	67	97,1	7,185	5	2	0
78	NS	3	3236,40	6,372	100	105,6	9,507	29	9	7
127	NS	3	3074,10	6,073	118	95,3	7,326	45	14	7
92	NS	3	3280,80	6,893	89	106,0	12,164	2	0	0
85	NS	3	2501,40	5,703	64	110,9	10,477	3	0	0
118	NS	3	3002,80	5,743	85	107,5	8,759	29	14	27
81	NS	3	2013,20	3,851	71	117,0	9,704	0	0	0
108	NS	3	3237,10	6,872	119	82,4	7,960	29	16	27
94	NS	3	2961,50	5,355	90	97,4	9,178	18	4	5
102	NS	3	2404,30	4,780	74	103,2	9,634	7	4	2
77	C	3	1936,70	6,239	81	69,1	7,235	47	16	19
125	C	3	2271,20	8,293	106	68,8	6,692	36	5	10
101	C	3	1666,50	5,000	79	83,1	7,719	51	12	13
82	C	3	2106,00	7,119	92	66,3	7,250	26	2	1
73	C	3	1981,00	6,348	95	89,2	8,588	32	4	6
69	C	3	1706,10	5,453	81	73,5	6,934	22	3	5
113	C	3	2097,60	6,624	88	76,2	7,755	55	15	7
126	C	3	1975,80	5,872	109	100,8	11,959	24	8	6
80	C	3	2613,90	8,795	91	63,9	7,714	43	6	9
76	C	3	2603,00	9,587	93	105,4	13,473	6	0	0
142	C	3	2046,60	6,456	110	92,4	10,745	9	3	4
88	C	3	1506,50	6,820	77	82,9	7,568	6	2	1
133	C	3	3137,00	12,715	97	121,0	13,324	4	0	0
110	C	3	2444,60	9,237	110	73,3	8,226	13	5	12
114	C	3	2081,50	7,630	100	69,6	8,150	16	4	6

Appendix II.

Chlorophyll absorbance at different wavelengths.

Sample ID	Treatment	Harvest	Absorbance		
			750.0nm	664.0nm	647.0nm
1	CS	1	0,002	0,333	0,123
48	CS	1	0,003	0,33	0,123
50	CS	1	0,002	0,428	0,162
4	CS	1	0,003	0,509	0,193
8	CS	1	0,005	0,399	0,152
45	CS	1	0,001	0,371	0,141
20	CS	1	0,005	0,249	0,097
40	CS	1	0,013	0,363	0,146
27	CS	1	0,003	0,405	0,152
21	CS	1	0,01	0,373	0,145
3	CS	1	0,002	0,354	0,134
33	CS	1	0,004	0,337	0,123
25	CS	1	0,002	0,309	0,114
13	CS	1	0,003	0,404	0,15
30	CS	1	0,005	0,406	0,151
11	NS	1	0,002	0,395	0,147
10	NS	1	0,005	0,467	0,174
49	NS	1	0,002	0,389	0,146
41	NS	1	0,003	0,42	0,158
31	NS	1	0,003	0,515	0,193
19	NS	1	0,001	0,512	0,191
22	NS	1	0,002	0,452	0,168
34	NS	1	0,003	0,415	0,153
46	NS	1	-0,001	0,389	0,146
14	NS	1	0	0,373	0,138
7	NS	1	0,001	0,399	0,148
18	NS	1	0	0,45	0,168
44	NS	1	0,006	0,427	0,164
47	NS	1	0,016	0,393	0,164
5	NS	1	0,001	0,457	0,168
15	C	1	0,005	0,4	0,149
38	C	1	0,006	0,451	0,165
2	C	1	0	0,384	0,135
32	C	1	0,001	0,537	0,192
36	C	1	0,001	0,414	0,144
23	C	1	0,001	0,459	0,164

Sample ID	Treatment	Harvest	Absorbance		
			750.0nm	664.0nm	647.0nm
39	C	1	0,004	0,405	0,147
24	C	1	0,001	0,426	0,15
43	C	1	0,002	0,419	0,151
12	C	1	0,001	0,63	0,234
37	C	1	0,002	0,351	0,126
9	C	1	0,005	0,351	0,13
26	C	1	0,002	0,461	0,166
35	C	1	0,003	0,477	0,173
42	C	1	0,002	0,377	0,134
56	CS	2	-0,002	0,594	0,236
53	CS	2	0,004	0,564	0,227
63	CS	2	-0,003	0,716	0,276
105	CS	2	-0,002	0,489	0,193
112	CS	2	0,001	0,647	0,251
98	CS	2	-0,001	0,52	0,203
61	CS	2	0,001	0,568	0,236
96	CS	2	-0,003	0,718	0,276
59	CS	2	-0,003	0,557	0,21
71	CS	2	0,005	0,566	0,231
119	CS	2	0	0,521	0,206
95	CS	2	0,001	0,618	0,248
131	CS	2	0,004	0,532	0,221
74	CS	2	0	0,568	0,232
99	CS	2	0	0,632	0,257
124	NS	2	0,001	0,632	0,255
60	NS	2	-0,001	0,752	0,291
75	NS	2	0	0,666	0,258
104	NS	2	0,002	0,594	0,236
72	NS	2	0	0,644	0,257
86	NS	2	0,031	0,626	0,278
84	NS	2	0,001	0,643	0,257
97	NS	2	0,003	0,738	0,294
62	NS	2	-0,001	0,644	0,255
87	NS	2	0,004	0,829	0,319
137	NS	2	0	1,006	0,394
134	NS	2	0	0,732	0,275
68	NS	2	-0,001	0,771	0,305
51	NS	2	-0,001	0,747	0,283
64	NS	2	-0,002	0,803	0,301

Sample ID	Treatment	Harvest	Absorbance		
			750.0nm	664.0nm	647.0nm
106	C	2	0,001	0,748	0,266
109	C	2	0,002	0,803	0,297
129	C	2	0,005	0,671	0,253
93	C	2	0,005	0,614	0,233
138	C	2	0,004	0,76	0,276
136	C	2	0	0,663	0,238
135	C	2	0,011	0,697	0,261
91	C	2	0,004	0,377	0,28
140	C	2	0,001	0,902	0,321
111	C	2	0,006	0,759	0,285
89	C	2	0,002	0,928	0,345
65	C	2	0,003	0,765	0,279
70	C	2	0,001	0,771	0,278
57	C	2	0,002	0,962	0,357
120	C	2	0,002	0,858	0,308
132	CS	3	0,05	0,616	0,278
117	CS	3	0,051	0,48	0,229
139	CS	3	0,053	0,669	0,307
128	CS	3	0,057	0,631	0,286
107	CS	3	0,05	0,578	0,254
67	CS	3	0,056	0,561	0,262
144	CS	3	0,053	0,643	0,303
83	CS	3	0,056	0,793	0,341
121	CS	3	0,05	0,603	0,279
130	CS	3	0,062	0,681	0,312
141	CS	3	0,052	0,679	0,305
90	CS	3	0,056	0,63	0,281
116	CS	3	0,051	0,713	0,307
115	CS	3	0,053	0,73	0,313
123	CS	3	0,05	0,681	0,298
54	NS	3	0,054	0,573	0,27
100	NS	3	0,055	0,562	0,256
103	NS	3	0,053	0,769	0,329
52	NS	3	0,059	0,647	0,298
143	NS	3	0,053	0,592	0,275
66	NS	3	0,054	0,658	0,293
78	NS	3	0,057	0,573	0,258
127	NS	3	0,052	0,655	0,286
92	NS	3	0,059	0,61	0,27

Sample ID	Treatment	Harvest	Absorbance		
			750.0nm	664.0nm	647.0nm
85	NS	3	0,056	0,947	0,395
118	NS	3	0,052	0,646	0,284
81	NS	3	0,06	0,899	0,387
108	NS	3	0,052	0,675	0,308
94	NS	3	0,055	0,642	0,286
102	NS	3	0,053	0,802	0,346
77	C	3	0,054	0,598	0,25
125	C	3	0,053	0,71	0,289
101	C	3	0,06	0,502	0,219
82	C	3	0,062	0,651	0,277
73	C	3	0,052	0,67	0,275
69	C	3	0,062	0,62	0,262
113	C	3	0,058	0,524	0,221
126	C	3	0,053	0,549	0,233
80	C	3	0,052	0,743	0,306
76	C	3	0,051	0,593	0,248
142	C	3	0,053	0,57	0,241
88	C	3	0,057	0,718	0,305
133	C	3	0,051	0,739	0,299
110	C	3	0,062	0,633	0,269
114	C	3	0,051	0,58	0,244

Appendix III.

Photosynthetic CO_2-uptake (µmol m^{-2} s^{-1}) at different levels of photon flux density (PFD) (µmol m^{-2} s^{-1}).

Sample ID	Treatment	Harvest		$C0_2$-uptake					
			PFD	0	50	100	250	500	1000
96	CS	2		-0,4	2,6	4,9	10	11,3	12,2
71	CS	2		-1	1,9	4,2	8,9	11	13
74	CS	2		-0,7	2,5	4,9	11	13,5	14,6
117	CS	3		-0,5	2,8	5,3	8,8	10,6	12,5
67	CS	3		-0,5	2,7	5	9,5	11,3	13,8
60	NS	2		-0,5	2,8	4,6	10,5	13,2	16,2
134	NS	2		-0,9	2,1	4,6	10,1	14,6	16,8
66	NS	3		-0,6	2,6	5,1	10,9	13,6	15,6
92	NS	3		-0,7	2,5	4,5	10,7	14,2	15,1
94	NS	3		-1	2	4,5	10,2	13,3	15,4
106	C	2		-1,5	1,8	4,2	10,9	19	25,3
140	C	2		-1,5	1,8	4,3	10,7	17,6	23,9
65	C	2		-1,1	2,5	5,6	11,8	19,2	25,3
69	C	3		-1,6	1,7	3,8	10,3	17,3	23,5
114	C	3		-1,6	1,7	4,2	10,5	17,3	23,9