Effects of artificial light at night on plant reproductive success

Master thesis

Faculty of Science, University of Bern

handed in by

Olivia Küchler

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Supervisor

PD Dr. Eva Knop

ABSTRACT

The influence of artificial light at night (ALAN) on plants and their interaction with insects is largely unknown. In this study, we investigated the impact of ALAN on plant reproductive success. Focusing on the plants' perspective provides insights into pollination success and helps to advance our understanding of plant-insect interactions. We used four study species (*Centaurea jacea*, *Cirsium oleraceum*, *Daucus carota*, *Silene vulgaris*) and four treatments (open-pollinated, day-pollinated, night-pollinated and permanently caged) to unravel differences in seed number and mean seed mass between plants on dark sites and plants on artificially lit sites. While results varied across the different species, the strongest association between light and seed set was found in open-pollinated plants. We found a positive effect of ALAN on seed number in *C. jacea* and a lower parasitism rate in *S. vulgaris* under illuminated conditions. Our results provide evidence for ALAN affecting direct and cascading mechanisms, including both trophic and non-trophic interactions. To our knowledge, this is the first study showing the effect of ALAN on plant-insect interactions by a top-down mechanism. We emphasize the importance of further examining the effects of light on diurnal pollinator communities and on plant reproductive success in order to arrive at a comprehensive understanding of plant-insect interactions experiencing ALAN.

Keywords: artificial light at night, light pollution, plant-pollinator interactions, plant reproductive success, seed set, pollinating seed parasites, top-down process

INTRODUCTION

Pollination is a key ecosystem service which is of high importance in maintaining biodiversity (Hooper *et al.* 2005, Potts *et al.* 2010). Nowadays, pollinators are undergoing a decline due to various threats, such as land-use change, alien species, climate change and pesticides (Memmott *et al.* 2007, Kearns *et al.* 1998). It has been shown that a decrease in pollinator diversity can lead to a parallel loss in wild plants diversity (Biesmeijer *et al.* 2006). As 80% of all wild plants directly depend on pollination by insects, it is likely that a pollinator decline may entail drastic ecological consequences (Potts *et al.* 2010).

So far, most studies dealing with the importance and endangerment of pollination interactions have focused on diurnal pollinators, disregarding that also nocturnal insects, particularly moths (Lepidoptera), can play a pivotal role for pollination provision in diverse ecosystems (Devoto *et al.* 2011, LeCroy *et al.* 2013). Pollination by moths has in several cases even been shown to be of higher quality and efficiency than diurnal pollination (e.g. Wolff *et al.* 2002, Young 2002). Moth populations are also declining, most likely suffering from similar threats as diurnal pollinators, among them land use change and climate change (Fox *et al.* 2014). In addition, nocturnal pollinators are particularly exposed to the threat of artificial light at night (henceforth: ALAN), also referred to as light pollution (Fox 2013, Macgregor *et al.* 2015). The increasing use of artificial night lighting leads to a fast expanding illumination of nightscapes by numerous light sources and by sky glow (Gaston *et al.* 2014, Hölker *et al.* 2010).

To date, studies have mainly investigated the impact of artificial light on moths (e.g. van Geffen *et al.* 2014, van Langevelde *et al.* 2011). However, only few studies also analyzed the cascading effects of ALAN on the interaction between plants and insects by top-down, bottom-up or non-trophic processes (Bennie *et al.* 2015). To our knowledge, there is no study showing ALAN to affect top-down processes, for example by modifying parasite or predator abundance. In turn, Bennie *et al.* (2015) found evidence for ALAN affecting bottom-up mechanisms: a shift in flower abundance due to light led to the resource-mediated control of aphids. Another study has examined the effects of ALAN on a non-trophic process, namely pollination, by assessing the

consequences of the altered behavior of light disturbed moths on plant-pollinator interactions, thereby finding a lower abundance of nocturnal flower visitors on *Cirsium oleraceum* and consequently a reduced seed mass in illuminated plants (Zoller 2016). Integrating plant reproductive success into the investigation of plant-pollinator interactions has two main benefits: First, it can provide insights into pollination success (Ne'eman *et al.* 2009); and second, it allows for a better understanding of plant-insect interactions by taking into account the plants' perspective.

Plant reproductive success does not only depend on its interaction with insects, but may also be influenced by the plants physiological characteristics (e.g. Ollerton & Lack 1998, Pires *et al.* 2013). Light serves the plant as source of information and energy and plays a role in a wide range of physiological processes, such as phenology and growth. Artificial light sources emit wavelengths that overlap with the absorption spectra of molecules regulating plant physiological responses, for example with chlorophyll (Gaston *et al.* 2013). It is therefore likely that artificial light can induce plant responses, thereby influencing plant physiology and reproductive success. Unfortunately, recent experimental approaches testing the real consequences of artificial light for plants are still scarce (Bennie *et al.* 2016).

The aim of this study was to examine the effects of ALAN on plant reproductive success in terms of seed set. Four plant species were used, among them both day- and night-pollinated plants, to get an idea of the influence of ALAN on diurnal as well as on nocturnal communities. Four treatments were applied: Plants which were always accessible for pollinators (henceforth: open-pollinated) experienced natural pollination conditions. The other treatments were chosen to unravel the underlying mechanisms: Plants which were accessible for pollinators only at day (henceforth: day-pollinated) or only at night (henceforth: night-pollinated) to disentangle diurnal and nocturnal pollination and plants which were never accessible (henceforth: permanently caged) to examine plant performance without any insect interaction, helping to distinguish effects of modified plant-pollinator interactions from effects of altered plant physiology.

MATERIALS AND METHODS

Study sites and experimental setup

Six ruderal areas in the Bernese Highlands (Switzerland) were used as study sites (Table 1). The different sites were comparable in terms of surroundings and vegetation. The flora was characterized by *Anthriscus sylvestris*, *Ranunculus sp.*, *Valeriana oficinalis* and the study species. Three sites were equipped with a LED street lamp (type AMPERA Midi 48 LED, 6800lm) at a height of 6 m (henceforth: lit sites). The three other sites were equipped with a fake lamp; an installation which is about the shape of the LED lamp but not emitting any light (henceforth: dark sites). Each site had a distance of at least 100 m to any small light source (e.g. houses or street lights) and at least 500 m to any big light source (e.g. sports fields).

Table 1. Coordinates and altitude of all six study sites.

Site name	Coordinates	Altitude (m.a.s.l.)
Lit site 1	46°39'48"N, 7°37'09"O	741
Lit site 2	46°39'07"N, 7°34'28"O	718
Lit site 3	46°37'22"N, 7°32'52"O	915
Dark site 1	46°40'06"N, 7°36'50"O	639
Dark site 2	46°38'37"N, 7°34'04"O	750
Dark site 3	46°36'32"N, 7°31'17"O	1037

The experiment was set up in a randomized block design, with two blocks on each site. Every block included all four treatments (open-pollinated, day-pollinated, night-pollinated, permanently caged). To implement the treatments, the plants were put in pollinator exclusion cages, which consisted of a wooden bottom (50*50 cm) and a wooden stick (1 m). To deny the pollinators access to the plants, a white net (mesh size: 1 mm) was laid over the cage. To that purpose, a plastic roof was fixed on the stick. The net was put over the roof and fastened on the bottom via elastic. When the plants should be accessible for pollinators, the net was removed and an umbrella was fixed on the stick, replacing the plastic roof in order to maintain comparable conditions in terms of rainfall and solar irradiation among the different treatments.

Study species

Four species naturally occurring in the study region were used: *Centaurea jacea* (Asteraceae), *Cirsium oleraceum* (Asteraceae), *Daucus carota* (Apiaceae) and *Silene vulgaris* (Caryophyllaceae). All species produced in previous experiments a higher seed set when pollinated than when relying on autogamy, due to low rates of self-compatibility or total self-incompatibility (Table 2).

Table 2. An overview of the four study species.

Species	Reproduction	Main pollinators	Inflorescences
C. jacea	stated to be self-incompatible (e.g. van Rossum 2010), but low rates of selfing have been observed (Steffan-Dewenter *et al.* 2001)	diurnal pollinators (van Rossum 2010)	flower heads
C. oleraceum	low rate of self-compatibility (Zoller 2016)	diurnal and nocturnal pollinators (personal observations)	flower heads
D. carota	self-incompatible on flower and umbel level, but not on plant level (Koul *et al.* 1989)	diurnal pollinators (Lamborn & Ollerton 2000)	umbels
S. vulgaris	low rate of self-compatibility (Young 2002)	nocturnal pollinators (Jürgens 2006)	single flowers

Experimental procedure

C. jacea, *D. carota* and *S. vulgaris* were raised in individual pots under common garden conditions. All *S. vulgari*s plants were cut once at the height of 5 cm because the flowers started to bloom too early in the season. This allowed the complete recovering and flowering of the plants a few weeks later. On *D. carota* and *S. vulgaris*, an insecticide (Perfekthion®, 40% Dimethoate) was applied twice because infestation by lice was reaching levels severely endangering plant or seed development (see Appendix 1).

Bud bearing plants were put on the field just before blooming. Every plant was randomly assigned to one treatment. For *C. oleraceum*, plants being already present at the study sites were used. They were not put into cages but the flower heads were bagged by white mesh (mesh size: 0.5 mm).

The experiment lasted for 40 days (16.07.2016 to 15.08.2016). During this period, every day at sunset and sunrise the pollinator exclusion cages were changed in order to maintain the treatments: At dawn, the nets were removed from the day-pollinated and installed on the night-pollinated plants, at dusk vice versa. Cages ensuring the permanently caged treatment were always covered by a net, whereas the open-pollinated ones were never covered. As the caging took approximately two hours, the routine was started one hour before sunset or sunrise. Day- and night-lengths were kept constant among all sites by always performing the routine in the same order. The handling of the nets was done with caution in order to avoid pollen removal by the net, shaking of the plants and plant damage. The plants were watered whenever the potting soil was dry.

Every plant remained on the field until all its inflorescences had withered, until it had to be taken inside to prevent seed loss or until the final day of the experiment. All inflorescences that were used for analyses were exposed to the treatment for at least five days. Removed plants were taken indoors for complete seed maturation. In *C. oleraceum*, withering flower heads build umbrellas, on which the seeds are attached for dispersal. To avoid seed loss, the flower heads were bagged as soon as they started to build umbrellas.

Data gathering

When the seeds of an inflorescence were matured, the inflorescence was removed from the plant and dried for 72h at 25°C. The seeds were then extracted, counted, weighted and stored in Eppendorf Tubes® in the dark. Both the number of seeds and seed mass are crucial determinants for the reproductive success of a plant: Seed number directly affects the number of seedlings, whereas seed mass can influence next generation fitness parameters, such as growth and

germination rate (Castro 1999, Du & Huang 2008). Therefore, seed set was assessed in terms of two variables: the total number of seeds per inflorescence (henceforth: SEED NUMBER) and the mean mass per seed per inflorescence (henceforth: MEAN SEED MASS). In *C. oleraceum*, each bag contained several flower heads building a dense group at the end of the stem. The number of flower heads per bag was counted to calculate mean SEED NUMBER and MEAN SEED MASS per flower head.

Beside seed measures, other variables were recorded, such as any observed case of parasitism. Parasitism could be observed in *D. carota* and *S. vulgaris*, but was only analyzed for *S. vulgaris*: The rate of parasitism was calculated given the number of parasitized flowers divided by the number of total flowers per plant (henceforth: PARASITISM RATE). In *D. carota*, parasitism was not analyzed because the parasites spread out after the plants were removed from the field. Finally, it was impossible to determine which caterpillars originated from the field and which afterwards migrated from an adjacent plant. Moreover, inflorescence weight was measured after extracting the seeds and drying the inflorescence for 72h at 80°C. Plant height was measured when the plant was removed from the field. Plant above ground biomass was weighted after drying the plant for 72h at 80°C. The number of field days every plant experienced was noted. The total number of inflorescences a plant produced was counted. The abundance of all study species was assessed for each site. Finally, light intensity and mean temperature were recorded for each cage. For *C. oleraceum*, light intensities were measured for each plant individually and the temperatures of the corresponding open-pollinated cages were used.

Data analysis

The effect of light and treatment differed among the species. In statistical models including all species, this resulted in significant species*light and species*treatment interactions. To simplify the model outputs, each species was analyzed separately. Three response variables were tested: SEED NUMBER, MEAN SEED MASS and, for *S. vulgaris*, PARASITISM RATE.

To test for the effect of light and treatment on SEED NUMBER, Generalized Linear Mixed Effects Models were run. An observation-level factor was included as random effect to account for overdispersion. Because for *C. oleraceum*, mean SEED NUMBER per flower head was analyzed, Linear Mixed Effects Models were used.

We performed Linear Mixed Effects Models to test for differences in MEAN SEED MASS of plants in dark versus lit sites within different treatments. The response variable was tested for normal distribution and square-root- or log-transformed in order to fit the model assumptions.

The influence of light and treatment on PARASITISM RATE in *S. vulgaris* was tested with Linear Mixed Effects Models. The response variable was tested for normal distribution.

In all models, the interaction between light (dark, lit) * treatment (open-pollinated, day-pollinated, night-pollinated, permanently caged) was included as fixed effect and plantID nested within cageID nested within siteID were included as random effects. We additionally tested the effect of height, total number of inflorescences, abundance, inflorescence weight and temperature on all three response variables. Parameters which significantly influenced a response variable were incorporated into the corresponding model.

All analyses were done using the lme4 package (Bates *et al.* 2015) in R v. 3.3.2 (R Core Team 2016). For Linear Mixed Effects Models, effects were tested based of F-statistics, using the anova command and the lmerTest package (Kuznetsova *et al.* 2014). To test for significant effects in Generalized Linear Mixed Effects Models, we stepwise deleted the explanatory variables or the interaction between them from the full model and compared the models with and without a respective variable or interaction by likelihood-ratio tests.

RESULTS

In total, 169 plants, 582 flowers and 9651 seeds have been analyzed (see Appendix 2 for detailed information about the data and Appendix 3-6 for detailed results).

C. jacea

The interaction effect between light and treatment on SEED NUMBER was not significant but showing a tendency ($\chi^2 = 6.594$, p = 0.0860). Within all treatments, plants on lit sites produced heavier seeds than plants on dark sites. This difference was significant in open-pollinated plants (z-value = 3.012, p = 0.0025, Figure 1a). None of the night-pollinated plants on dark sites produced any seeds. In turn, plants on lit sites produced seeds when pollinated only at night (Figure 1b).
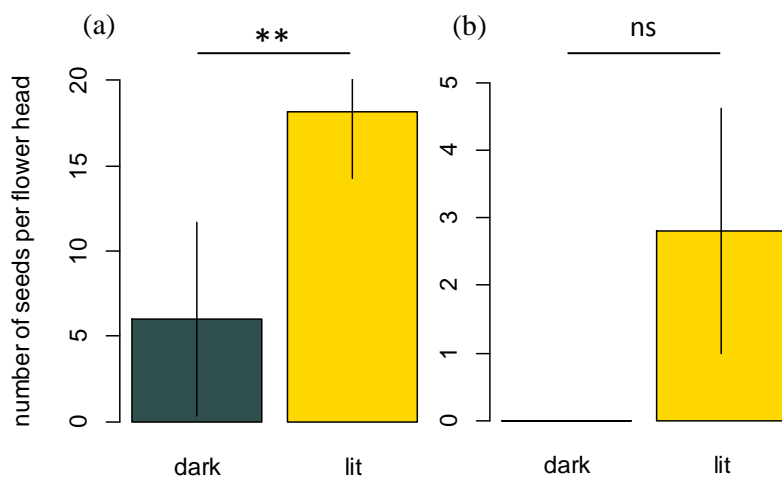
Figure 1. SEED NUMBER (mean ± SE) in open-pollinated (a) and night-pollinated (b) *C. jacea* plants on dark sites compared to plants on lit sites (** p = 0.0025).

MEAN SEED MASS was significantly affected by plant height (F-value = 4.478, p = 0.0482). When height was included in the model, there was no significant influence of light, light*treatment or treatment on MEAN SEED MASS.

C. oleraceum

There was no significant effect of light or light*treatment on SEED NUMBER and MEAN SEED MASS. However, both response variables varied significantly among the different treatments

(F-values = 9.942 and 11.046, p < 0.001), with the permanently caged plants producing the fewest and the lightest seeds.

D. carota

Umbel weight did significantly affect SEED NUMBER (χ^2 = 17.857, p < 0.001) and was therefore incorporated into the model. There was no significant influence of light, light*treatment or treatment on SEED NUMBER and MEAN SEED MASS.

S. vulgaris

There was no significant effect of light, light*treatment or treatment on SEED NUMBER. Taller plants produced significantly heavier seeds (F-value = 11.134, p = 0.0093). When plant height was included in the model, there was no significant effect of light or light*treatment on MEAN SEED MASS. In turn, light significantly increased plant height (F-value = 13.543, p = 0.0212). Treatment explained a significant amount of variance in MEAN SEED MASS (F-value = 9.820, p = 0.0024). Surprisingly, seeds produced by selfing in permanently caged plants were the heaviest, whereas seeds produced by open-pollinated plants were the lightest. PARASITISM RATE was not significantly affected by the interaction between light and treatment. In turn, it was in tendency influenced by light (F-value = 3.552, p = 0.0884). Light was found to significantly reduce PARASITISM RATE in open-pollinated plants (t-value = -2.143, p = 0.0386, Figure 2). PARASITISM RATE significantly differed between the different treatments (F-value = 7.082, p < 0.001).
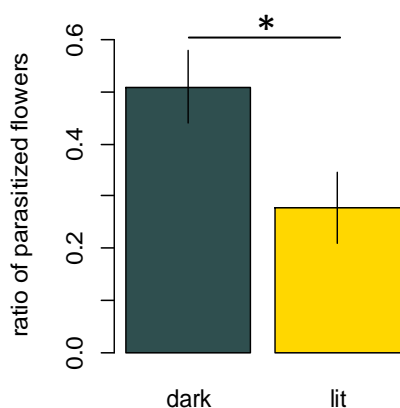
Figure 2. PARASITISM RATE (mean ± SE) in open-pollinated *S. vulgaris* plants on dark sites compared to plants on lit sites (* p = 0.0386).

DISCUSSION

The effects of ALAN were most distinct within open-pollinated plants. Those experience the impact of light to the full extent, whereas night- and day-pollinated plants undergo a reduced pollination regime and therefore a weaker effect of light. For example, night-pollinated plants will be less pollinated by moths than open-pollinated plants because they are inaccessible for pollinators occurring already at dusk or still at dawn. The impact of light on nocturnal pollination will therefore be strongest in open-pollinated plants.

C. jacea

We found a positive effect of light on reproductive success in *C. jacea* (Figure 1). None of the night-pollinated plants on dark sites produced any seeds. In contrast, plants on lit sites produced seeds when only pollinated at night (Figure 1b). This indicates the absence of diurnal pollinators at night on dark sites and the presence of diurnal pollinators at night on lit sites. Steffan-Dewenter *et al.* (2001) found a positive correlation between the number of seeds per flower head and the number of flower visits by bees in *C. jacea*. This suggests that the differences in SEED NUMBER arose from altered plant-pollinator interactions. Most likely, this alteration is a result of the greater abundance of diurnal insects at night close to light sources, as observed in a study conducted in parallel by Etter (2016) on the same sites.

Interestingly, studies about light pollution depict the importance of further studying the influence of ALAN on moths and plant-moth interactions (e.g. Fox 2013, Macgregor *et al.* 2015). However, our results indicate that also diurnal pollinators may play an important role in plant-pollinator interactions under illuminated conditions.

C. oleraceum

We could not find an effect of light on seed set in *C. olercaeum*, although reproductive success clearly differed between the treatments and was lowest for permanently caged plants, showing that pollination contributes a high portion to seed set. Unlike in our study, Zoller (2016) found a

significantly reduced seed mass in lit plants. Our results support Zoller's (2016) findings, because within all treatments, we found the same tendencies, with light reducing both SEED NUMBER and MEAN SEED MASS. Unfortunately, the resulting differences were too small to be statistical significant. However, it can be assumed that the number of replicates was too low to achieve significance rather than conclude that there was no effect of ALAN.

D. carota

As neither SEED NUMBER nor MEAN SEED MASS differed between the treatments, reproductive success in *D. carota* did not seem to depend on pollination. A reason for this may be that the numerous flowers produce a high amount of powder pollen that is easily distributed by wind or by any movement of the umbels. Despite the fact that umbels are self-incompatible within themselves, they are able to pollinate each other (Koul *et al.* 1989). As every *D. carota* plant in this study produced several umbels, it is to be assumed that cross-pollination between different umbels occurred and that the resulting reproductive success is comparable to the one resulting from insect pollination.

S. vulgaris

Previous studies found evidence for a disruptive effect of ALAN on moths, leading to reduced pollen transport and lower abundance of flower visitor moths on lit sites (Macgregor *et al.* 2016, Zoller 2016). As *S. vulgaris* is almost completely relying on pollination by moths, one would expect a lower seed set in plants on lit sites. This consequence could not be observed in this study for two possible reasons: First, pollination success and plant reproductive success do not necessarily correlate because seed set often depends on post-pollination processes (e.g. Cane & Schiffhauer 2003, Corbet 1998, reviewed in Ne'eman *et al.* 2009). Second, artificial light may cause changes in plant reproductive success that were not detected because they were outbalanced by processes counteracting the negative effects of light on seed set: The higher growth of plants in lit sites increased MEAN SEED MASS in lit plants, the higher PARASITISM RATE reduced SEED NUMBER in plants on dark sites.

The influence of ALAN on seed parasitism (Figure 2) showes that light does not only interfere with mutualistic interactions, such as pollination, but also with antagonistic interactions. *Hadena rivularis* was found to be the moth that was responsible for the observed parasitism in *S. vulgaris*. *H. rivularis* is a pollinating seed parasite: While laying eggs into a flower, it simultaneously acts as pollinator. Nevertheless, such an interaction ends up in an overall negative balance for the plant, because the harm from flower herbivory and seed predation is higher than the benefit from pollination (Petersson *et al.* 1991). Interestingly, this finding suggests the cascading effect of ALAN through a top-down process: the lower parasite activity or abundance on lit sites led to higher plant fitness in lit plants. To our knowledge, this is the first time that ALAN could be shown to affect a top-down mechanism. Considering the disruption effect found by Zoller (2016), the cascade seems to be induced by the disturbed behavior rather than the reduced abundance of pollinating parasite moths on lit sites.

CONCLUSION

We found evidence for ALAN affecting ecological communities by both direct and cascading mechanisms. Surprisingly, light was found to affect top-down mechanisms, most likely by altering parasite activity. It remains to be tested if shifts in resource availability (e.g. by increased plant growth in lit plants in *S. vulgaris* or by wider dispersal of *C. jacea* due to higher seed number in lit plants) also affect insect communities by bottom-up mechanisms.

Particular plants, including *C. jacea*, and insects, namely diurnal pollinators, seem to profit from the new niche provided by the illumination of nightscapes. A benefit for those species, which thus become stronger competitors, will most likely come along with drawbacks for other, presumably nocturnal, species. This might end up in a shift in plant and insect communities. The investigation of the impact of ALAN on diurnal insects could provide deeper insights into the effects of ALAN on plant-pollinator interactions.

ALAN was found to alter plant reproductive success by modifying plant-insect interactions as well as by changing plant physiology. Because plant responses were often complex, the

consideration of various variables was essential to distinguish those effects. By missing an underlying mechanism and exclusively looking at seed output, there is a risk of drawing wrong conclusions. It seems therefore crucial to experimentally examine plant reproductive success when studying plant-pollinator interactions instead of simply deriving it from pollination success.

This study finally highlights the complexity of the influence of ALAN on plant and insect communities and on their interactions. For a more comprehensive understanding, the direct effects of ALAN, as well as its effects on cascading mechanisms, including trophic and non-trophic interactions, need to be further investigated.

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APPENDICES

Appendix 1. Detailed information about plant raising and treatment.

	Sowing	Plant transplanting	Moving (green-house to garden)	Insecticide application	Cut
C. jacea	17.03.2016	08.04.2016	21.05.2016	-	-
C. oleraceum	plants being present on the study sites were used			-	-
D. carota	grown by the garden-center Hauenstein Rafz, delivered on 15.07.2016 when all buds were still closed			31.08.2016, 22.09.2016	-
S. vulgaris	17.03.2016	06.04.2016	21.05.2016	05.05.2016, 18.05.2016	13.05.2016

Appendix 2. An overview of the number of analyzed plants, inflorescences and seeds per plant species.

	Plants	Inflorescences	Seeds
C. jacea	32	53	651
C. oleraceum	41	71	3929
D. carota	48	128	4214
S. vulgaris	48	330	857
Total	169	582	9651

Appendix 3. Results of Generalized Linear Mixed Effects Models testing for the effect of light and treatment on SEED NUMBER in all four study species. ΔAIC represents the calculation $\text{AIC}_{\text{Model without respective variable or interaction}} - \text{AIC}_{\text{Model with respective variable or interaction}}$. Thus positive values indicate that the respective variable or interaction lowered the model AIC. Significant tests and tendencies are shown in bold.

	Response variables	ΔAIC	χ^2	P	Est.	SE
C. jacea	light	1.37	3.378	**0.0661**	2.560	1.463
	treatment	26.84	32.835	**< 0.001**	see Appendix 3a	
	light*treatment	0.6	6.594	**0.0860**	see Appendix 3b	
D. carota	umbel weight	15.86	17.857	**< 0.001**	0.0295	0.0073
	light	-1.98	0.020	0.8873		
	treatment	-3.87	2.126	0.5467		
	light*treatment	-4.21	1.793	0.6168		
S. vulgaris	light	-1.79	0.2142	0.6435		
	treatment	-3.22	2.781	0.4266		
	light*treatment	-59.59	0	1		

Appendix 3a. Model estimates (Est.) and standard errors (SE) for the effect of the different treatments on SEED NUMBER in *C. jacea*. Significant effects are shown in bold.

Treatment	Est.	SE	*P*
Intercept (open-pollinated)	-0.3605	0.7648	0.6374
permanently caged	-4.2686	1.4770	**0.0039**
night-pollinated	-3.3991	1.0808	**0.0017**
day-pollinated	2.3313	0.8613	**0.0068**

Appendix 3b. Model estimates (Est.) and standard errors (SE) for the interaction effect between light and the different treatments on SEED NUMBER in *C. jacea*. Significant effects are shown in bold.

Light*treatment	Est.	SE	*P*
Intercept (dark*open-pollinated)	-1.019	0.935	0.2758
lit*open-pollinated	3.783	1.193	**0.0025**
dark*permanently caged	-20.225	515.231	0.9687
dark*night-pollinated	-24.950	460.837	0.9568
dark*day-pollinated	4.022	1.190	**< 0.001**
lit*permanently caged	15.958	515.231	0.9753
lit*night-pollinated	21.408	460.836	0.9629
lit*day-pollinated	-3.468	1.596	**0.0297**

Appendix 4. Results of Linear Mixed Effects Models testing for the effect of light and treatment on SEED NUMBER in *C. oleraceum*. Significant effects are shown in bold.

	Response variables	*F*	df	*P*	Est.	SE
C. oleraceum	light	0.486	3.686	0.5270		
	treatment	9.942	25.816	**< 0.001**	see Appendix 4a	
	light*treatment	0.395	25.816	0.7578		

Appendix 4a. Model estimates (Est.) and standard errors (SE) for the effect of the different treatments on SEED NUMBER in *C. oleraceum*. Significant effects and tendencies are shown in bold.

Treatment	Est.	SE	*P*
Intercept (open-pollinated)	9.2327	0.7398	**< 0.001**
permanently caged	-5.3159	1.0338	**< 0.001**
night-pollinated	-2.0027	1.0332	**0.0544**
day-pollinated	-1.7417	1.0332	**0.0920**

Appendix 5. Results of Linear Mixed Effects Models testing for the effect of light and treatment on MEAN SEED MASS in all four study species. Significant effects are shown in bold.

	Response variables	*F*	df	*P*	Est.	SE
C. jacea	light	0.381	6.698	0.5574		
	treatment	3.557	5.119	0.1007		
	height	4.478	5.402	**0.0482**	0.0161	0.0076
	light*treatment	3.357	6.022	0.1165		
C. oleraceum	light	1.872	10.259	0.2005		
	treatment	11.046	26.172	**< 0.001**	see Appendix 5a	
	light*treatment	0.856	26.172	0.4764		
D. carota	light	0.600	3.837	0.4835		
	treatment	0.550	40.153	0.6511		
	light*treatment	1.183	40.153	0.3283		
S.vulgaris	light	4.059	2.902	0.1404		
	treatment	9.820	10.178	**0.0024**	see Appendix 5b	
	height	11.134	8.593	**0.0093**	0.0118	0.0039
	light*treatment	0.858	10.289	0.4933		

Appendix 5a. Model estimates (Est.) and standard errors (SE) for the effect of the different treatments on MEAN SEED MASS in *C. oleraceum*. Significant effects are shown in bold.

Treatment	Est.	SE	*P*
Intercept (open-pollinated)	2.2197	0.1818	**< 0.001**
permanently caged	-1.4427	0.2682	**< 0.001**
night-pollinated	-0.3227	0.2599	0.225
day-pollinated	-0.0874	0.2599	0.739

Appendix 5b. Model estimates (Est.) and standard errors (SE) for the effect of the different treatments on MEAN SEED MASS in *S. vulgaris*. Significant effects are shown in bold.

Treatment	Est.	SE	*P*
Intercept (open-pollinated)	0.5714	0.0953	**0.0012**
permanently caged	0.3054	0.1353	**0.0367**
night-pollinated	0.0658	0.0803	0.4281
day-pollinated	0.3545	0.0962	**0.0028**

Appendix 6. Results of Linear Mixed Effects Models testing for the effect of light and treatment on PARASITISM RATE in *S. vulgaris*. Significant effects and tendencies are shown in bold.

	Response variables	*F*	df	*P*	Est.	SE
S. vulgaris	light	3.5519	10	**0.0884**	-0.1516	0.0805
	treatment	7.0818	30	**< 0.001**	see Appendix 6a	
	light*treatment	0.8582	30	0.4734		

Appendix 6a. Model estimates (Est.) and standard errors (SE) for the effect of the different treatments on PARASITISM RATE in *S. vulgaris.* Significant effects are shown in bold.

Treatment	Est.	SE	*P*
Intercept (open-pollinated)	-0.4569	0.1898	**0.0237**
permanently caged	-1.0462	0.1989	**< 0.001**
night-pollinated	-0.0408	0.1989	0.8387
day-pollinated	-0.4891	0.1989	**0.0193**