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Cover: To the left: one of the studied *Lathraea squamaria* patches. To the right: the parasitic plant *Lathraea squamaria*. Photos by Karin Kjellström.

Summary

Lathraea squamaria is a spring flowering root parasite that lacks chlorophyll and on which, to my knowledge, no recent ecological studies have been performed. Apart from studies on weeds and their part in crop damage, the number of ecological studies on parasitic plants is limited. I conducted an inventory of all *L. squamaria* patches in a 1.3 ha area where I studied the effect of several shoot and patch characteristics on seed set and what effect competition from other species has on different aspects of flowering. I also made a hand-pollination experiment to investigate if the studied *L. squamaria* population suffers from pollen limitation. Pollen limitation occurs when a plant has an inadequate pollen receipt and thus produces fewer fruits and/or seeds. My results showed that there were no correlations between the shoot and patch characteristics and seed set. However, the density of *L. squamaria* shoots in the patches was significantly decreasing when ground vegetation cover was increasing and is thus affected by competition from other species. The studied *L. squamaria* population was not suffering from pollen limitation in the spring of 2009.

Sammanfattning

Lathraea squamaria (vätteros) är en vårblomande rotparasit som saknar klorofyll. Så vitt jag vet har inga ekologiska studier utförts på denna art. Med undantag för ogräs och dess påverkan på skördar så är antalet ekologiska studier på parasiter få. Jag har genomfört en inventering av alla *L. squamaria*-patcher i ett 1,3 ha stort område där jag har undersökt om ett antal skott- och patchegenskaper påverkar fröproduktion och vilken effekt konkurrens från andra arter har på olika aspekter av *L. squamarias* blomning. Jag har även utfört ett handpollineringsförsök för att undersöka om denna population lider av pollenbegränsning. Pollenbegränsning förekommer när en växt inte får tillräckligt med pollen och därför producerar färre frukter och/eller frön. Mina resultat visade att det inte fanns några samband mellan fröproduktion och de skott- och patchegenskaper som jag studerat. Dock visade mina resultat att *L. squamaria* påverkas av konkurrens eftersom tätheten mellan dess skott minskade när marktäckningen av andra arter ökade. Den studerade *L. squamaria*-populationen led inte av pollenbegränsning våren 2009.

Introduction

In various plant species, only a limited part of all initiated ovules mature into seeds (Stephenson 1981; Ehrlén 1992; Boieiro et al. 2010). Among the processes responsible for this are predation or diseases; resource limitation; and pollen limitation. Pollen limitation occurs when the reproductive success of a plant is reduced due to insufficient pollen receipt (e.g. Ashman et al. 2004; Knight et al. 2005; Wesselingh 2007). Two aspects of pollen limitation occur: limitation of quantity or limitation of quality. This results in the plant producing fruits and/or seeds with lower quantity or quality than it would with adequate pollen receipt (Ashman et al. 2004; Aizen & Harder 2007). As a result of fewer pollinator visits or less pollen delivered per visit, pollen quantity may be reduced whereas reduced pollen quality may be the result of incompatible or aged pollen being delivered.

Ashman et al. (2004) present a number of reasons for pollen limitation. These include introduction of nonnative plants that are greatly attractive to pollinators; habitat fragmentation; decrease in population size; or loss of native pollinators. But pollen limitation may also be expected in non-disturbed systems (Burd 2008). Due to its effect on reproductive success, pollen limitation affects population viability and species abundance and may thus shift a plant community to be dominated by species less sensitive to pollen limitation. Plants may however evolve reproductive or life history characters to ensure its reproduction in response to pollen limitation (Burd 1994; Ashman et al. 2004). Given that the pollen receipt of a plant is affected by its floral phenotype, i.e. attraction and rewards for biotic pollination and aerodynamic morphology for abiotic pollination, pollen limitation may cause selection on floral traits. Other responses to pollen limitation may include the evolution of self-compatibility and/or selfing and wind pollination (Knight et al. 2005).

Burd (1994) conducted a survey of studies on 258 species and found that 62% of these had reported significant pollen limitation; Ashman et al. (2004) found that 73% of 85 studies had reported significant pollen limitation and Knight et al. (2005) found significant pollen limitation in 63% out of 482 studies. However, Knight et al. (2006) suggest that these figures may be at least in part due to biases in publication.

A parasitic interaction is defined as an association between two organisms where one is benefiting to the detriment of the other (Musselman & Press 1995). Parasites are found among both prokaryotes and eukaryotes, e.g. the pathogenic prokaryotes which cause about half of all human diseases and *Plasmodium* among the protozoa, which cause malaria (Campbell & Reece 2002). Other examples are found among the fungi, with 30% of its species being parasites, many of which are serious agricultural pests. Parasitism is also found among plants

in a number of life forms, including trees, shrubs, vines and herbs that live in diverse habitats, from tropical forests to arctic islands (Musselman & Press 1995). About 1% of the angiosperms, approximately 3000 species, are parasitic.

Parasitic plants are, at least partially, using their hosts for supply of water, inorganic and organic solutes (Musselman & Press 1995). There is a great deal of variance in the degree of host dependency between species but parasites may be divided into two major groups depending on whether they are photosynthetic or not. Hemiparasites are photosynthetic but use the host for supplementation of their resources while holoparasites are not photosynthetic and draw all of their resources from other plants (Musselman & Press 1995; Campbell & Reece 2002). Numerically, 80% of the parasitic plant species are hemiparasites while 20% are holoparasites.

A structure called haustorium is used to gain access to the resources of the host (Musselman & Press 1995). The structure is a specialized projection that forms a close connection with the vascular system of the host. The haustorium is either attached to the host below or above ground which enables another classification of the parasitic plants: they are either root or shoot parasites. Numerically, 60% of the parasitic plants are root parasites while 40% are shoot parasites.

Parasitic plants occur in approximately 16 families (Musselman & Press 1995) where the Scrophulariaceae/Orobanchaceae family pair is the most diverse; it includes facultative hemiparasites, obligate hemiparasites, and holoparasites, as well as non-parasites (Young et al. 1999). *Lathraea* is the only European genus that is entirely holoparasitic (Bennett & Mathews 2006).

Lathraea squamaria is a parasitic, spring flowering herb that uses many of the species characterizing a broad-leaved deciduous forest as hosts. To my knowledge, no recent ecological studies have been conducted on this species.

The objectives of this study were:

- I. to assess the flowering phenology of *Lathraea squamaria*.
- II. to perform an inventory of the *Lathraea squamaria* patches in the southernmost part of the Näset peninsula, Tullgarn, Sweden.
- III. to examine what effect different shoot and patch characteristics have on seed set of *Lathraea squamaria*.
- IV. to study which aspects of *Lathraea squamaria* flowering that are affected by competition.
- V. to conduct a hand-pollination experiment to determine if *Lathraea squamaria* suffers from pollen limitation.

Material & Methods

Study system

This study was conducted in the southernmost part of the Näset peninsula, east of Tullgarn, 45 km SSW of Stockholm, in the province of Södermanland, Sweden (Fig. 1) where I studied *Lathraea squamaria* (Orobanchaceae). The area is characterized as a rich, mesic forest with a mixture of

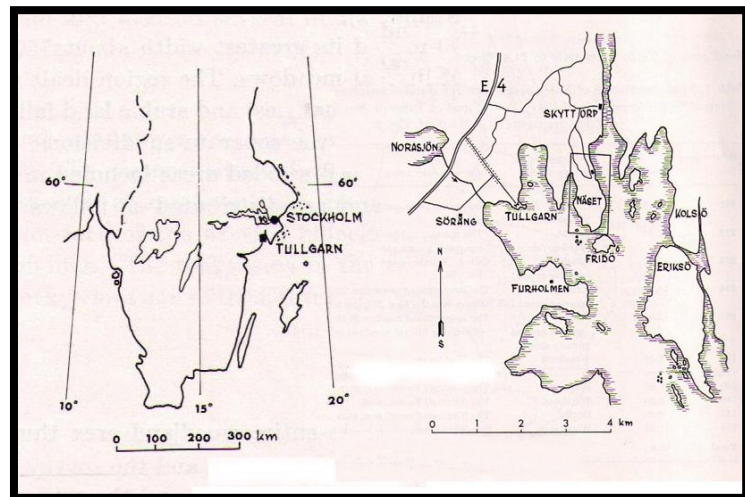


Figure 1. Map of the Tullgarn area. Edited map after Ryberg (1971).

deciduous species in the tree layer and mainly hazel (*Corylus avellana*) in the understory (Ehrlén et al. 1992). Broad-leaved deciduous forests constituted by species such as ash (*Fraxinus excelsior*), wych elm (*Ulmus glabra*), small-leaved lime (*Tilia cordata*), hornbeam (*Carpinus betulus*), European beech (*Fagus sylvatica*), alder (*Alnus glutinosa*), Norway maple (*Acer platanoides*) and hazel are very rare (Mossberg & Stenberg 1999). Nevertheless, all of the above mentioned species can be found at the Näset peninsula (Ryberg 1971). Broad-leaved deciduous forests allow for a species-rich spring flora due to the additional nutrition provided by the annual leaf abscission; the access to a moist-rich soil due to the melting of snow and spring rains; and the generous entry of light before the canopy closes (Mossberg & Stenberg 1999). Tullgarn appears to be an ideal habitat for a species-rich spring flora. According to an inventory conducted in the province of Södermanland, the largest number of

naturally occurring wild species in the province is found at Tullgarn with over 700 species (Rydberg & Wanntorp 2001).

Lathraea squamaria is a spring flowering, protogynous, parasitic herb that is found in moist and rich soil, in deciduous forests and brushes (Mossberg & Stenberg 1999, 2005). It is distributed all over Europe, except for the northernmost parts, and also in western Asia as far east as Kashmir (Mossberg & Stenberg 1999). In Sweden, its distribution ranges from the province of Skåne in the south to its northernmost locality in the province of Gästrikland (Rydberg & Wanntorp 2001). *L. squamaria* is a non-photosynthetic root parasite (Rydberg & Wanntorp 2001), i.e. a holoparasite (Musselman & Press 1995). It uses several different species as hosts, e.g. bird cherry (*Prunus padus*), alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), midland hawthorn (*Crataegus laevigata*), and small-leaved lime (*Tilia cordata*) (Mossberg & Stenberg 1999). In the province of Södermanland, hazel (*Corylus avellana*) is the most common host (Rydberg & Wanntorp 2001).

L. squamaria has a white rhizome and a stout reddish stem with pale pink flowers (Mossberg & Stenberg 1999). The height range of the shoot is 7-25 cm. The flowers open sequentially (pers. obs.) and the shoot produces 10-25 flowers in a one-sided spray that is initially arching but is then erect. Flowering of *L. squamaria* takes place in April and May (Mossberg & Stenberg 2005) and it is pollinated mainly by bumble-bees (*Bombus* spp.) (Mossberg & Stenberg 1999) (Fig. 2). The fruit is an 8-11 mm long capsule (Mossberg & Stenberg 1999) that matures in early June (pers. obs.). The seeds have elaiosomes and are dispersed by ants (Den virtuella floran 2005).

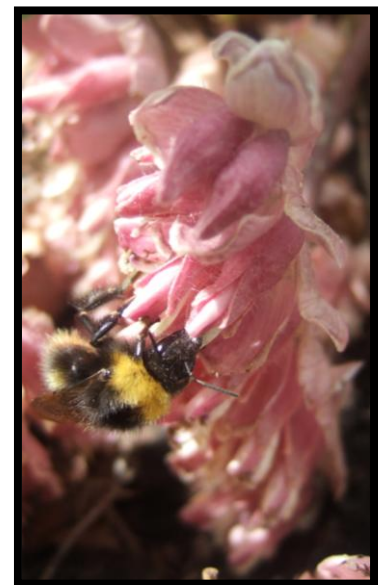


Figure 2. A bumble-bee pollinating *L. squamaria*.

Flowering phenology

I constructed an eight stages chart of the different phenologic stages of *L. squamaria* above ground (Fig. 3).



Figure 3. *L. squamaria* at its different phenologic stages above ground.

Stage 1: The shoot emerges above ground.

Stage 2: The shoot is arching; most of the flowers are still closed.

Stage 3: The shoot is still slightly arching; the flowers at the basal half have opened. Stage of all hand-pollination experiment shoots.

Stage 4: The shoot is erect; most stigmas have withered but the occasional stigma of the top flowers is still receptive.

Stage 5: The flowers have started to produce capsules. Stage of seed collection.

Stage 6: The top flowers have produced capsules. Stage of seed collection.

Stage 7: The seeds have matured.

Stage 8: After seed dispersal, the shoot withers. (No photo)

Stage x: The shoot has withered prematurely.

I made the first observation of *L. squamaria* in the area on April 26th, but given the size of the shoot (stage 2) it had emerged a few days earlier. The first observation of a shoot with matured seeds was done on June 3rd. These observations were not associated to the same shoot, so I cannot say anything about the flowering period of individual shoots but the observations enabled me to make an estimation of the period from emergence to seed dispersal in the studied *L. squamaria* population to approximately one month.

I made the last observation of a stage 3 shoot on May 14th, which suggests that the last emergence of a shoot took place a few days earlier. I can therefore estimate the period of emergence of new shoots for *L. squamaria* in my study area to approximately 2-3 weeks.

Data collection

I made an inventory of all *L. squamaria* patches in a 1.3 ha area (Fig. 4). A patch was defined as a group of shoots separated from another group by at least two meters. I located 76 patches in this area and randomly selected 30 of these for a more detailed survey of *L. squamaria* seed production and characteristics of its shoot and patch. The sole criterion for the selected patches was that at least two shoots of *L. squamaria* were at flowering stage 3 (Fig. 3).



Figure 4. The location of 76 *Lathraea squamaria* patches in a 1.3 ha area of the Näset peninsula, in the province of Södermanland, Sweden. Black squares: patches with conducted experiment, white squares: non-experimental patches. Edited map after Ryberg (1971).

Effect of shoot and patch characteristics on seed set

At each of the 30 experimental patches I took digital photos to estimate the ground vegetation cover. Vegetation cover was calculated using the Optipix Wide Histogram tool in Photoshop CS3 (Adobe 2007). By placing a circular frame (30 cm radius) around five randomly selected shoots and then counting the framed shoots I made an estimate of density of shoots in each patch. The density in each patch (dp) was calculated by using the following formula: $dp = (s_1+s_2+s_3+s_4+s_5)/5$ where s_1 - s_5 are the number of shoots in the five randomly placed frames.

I measured patch area (m^2) and total number of *L. squamaria* shoots in the 30 experimental patches but also in the 46 non-experimental patches. The patch characters were measured during four days between May 27th and June 2nd 2009.

Hand-pollination experiment

To study pollen limitation in *L. squamaria*, I performed a hand-pollination experiment. I randomly selected and marked 124 shoots in the 30 experimental patches; 62 shoots were hand-pollinated while 62 shoots were open-pollinated and used as a control group. Every hand-pollinated shoot was paired with an open-pollinated shoot in the same patch. All shoots included in the study were at the time of pollination treatment at their flowering stage 3 (Fig. 3 and 5). Five flowers with receptive stigmas were marked on each shoot and pollen from one donor flower, i.e. four dehiscing anthers, was brushed across each stigma (Fig. 5). Thus five donor flowers were used per one receiving hand-pollinated shoot. Due to the rhizome of *L.*



squamaria, pollen was collected outside a radius of 100 m from the focal plant but within a radius of 200 m. This was done to ensure cross-pollination. At the time of the experiment, I recorded the height of the 124 shoots and the distance to their most adjacent hazel. The hand-pollination experiment was conducted during nine days between April 29th and May 14th 2009.

Figure 5. A *L. squamaria* shoot at stage 3 when all hand-pollinations were conducted. The arrow points to a receptive stigma.

Seed collection and counting

All the capsules produced from the marked flowers were collected during four days between May 27th and June 2nd 2009. At the time of collection I estimated the shoot density by placing a circular frame (30 cm radius) around each experimental shoot and then counting the framed *L. squamaria* shoots. At seed maturation, the *L. squamaria* capsule springs open and flings the seeds (Den virtuella floran 2005) and due to lack of knowledge of the exact phenologic development of *L. squamaria*, I collected the seeds before maturation (Fig 6).

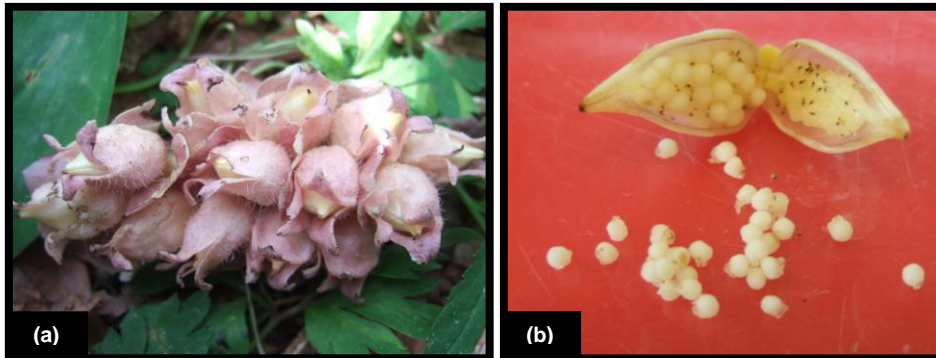


Figure 6. (a) A *L. squamaria* shoot at seed collection. (b) A not yet matured capsule at seed counting.

The seeds were counted in the laboratory. I eliminated a number of shoots and capsules from this study due to one or several of the following reasons: missing shoot marker, missing flower marker, withered shoot with no developed seeds, uprooted or damaged shoot or damaged or preyed capsule (Fig. 7).



Figure 7. Examples of possible *L. squamaria* predators.

Statistical analyses

Effect of shoot and patch characteristics on seed set

I used the open-pollinated shoots to examine the effect of shoot characteristics (shoot density, shoot distance to hazel and shoot height) and patch characteristics (ground vegetation cover, density of shoots in each patch, number of shoots and patch area (m²)) on seed production using a multi-way anova. Due to the elimination of experimental shoots and seed capsules (see Seed collection and counting), I used between 1-5 seed capsules per shoot to calculate the average number of produced seeds per shoot. I examined between 1-4 shoots per patch which were used to calculate the mean production of seeds for each of the 27 patches. I also used the characteristics of these shoots to calculate the means for the shoot characteristics.

Effects of ground vegetation on L. squamaria

Since *L. squamaria* is suggested to require the surrounding ground vegetation to not be fully covered (Rydberg & Wanntorp 2001), I tested the effect of ground vegetation cover on number of shoots, patch area (m²) and density of shoots in each patch in the 30 selected experimental patches in my study area using one-way anovas. To achieve normality, I log transformed ground vegetation cover, number of shoots, patch area and density of shoots in each patch.

Hand-pollination experiment

Due to the elimination of experimental shoots and seed capsules (see Seed collection and counting); between 2-5 seed capsules per shoot were used in the pollination treatment analysis. I used the number of seeds of these capsules to calculate the mean and SD of the produced seeds per shoot. I examined the effect of pollination treatment (open-pollination and hand-pollination) on the mean and SD of the produced seeds, using a paired t-test, with 44 pairs of open-pollinated and hand-pollinated shoots.

The statistical analyses were performed with the free software R version 2.10.1 (R Development Core Team 2009).

Results

My study area included 58 *L. squamaria* patches/ha; the average size of a patch was 1.88 m² (SD = 2.36, range 0.1-11.3). The average number of shoots in each patch was 27.5 (SD = 25.7, range 3-149). Six out of 30 patches contained prematurely withered shoots. The capsules in my study area contain on average 83.4 seeds (SD = 33, range 3-155).

Effect of shoot and patch characteristics on seed set

None of the shoot and patch characteristics that I examined had any significant effect on *L. squamaria* seed set (Table 1).

Table 1. The effect of ground vegetation cover, density of shoots in patches, patch shoot number, patch area, shoot density, shoot distance to hazel, and shoot height on the number of produced seeds in *L. squamaria* was tested with a multi-way anova (n = 27).

Seed number				
Explanatory variable	Sum Sq	Df	F-value	P-value
Ground veg. cover	218.4	1	0.2853	0.5994
Density of shoots in patches	61.4	1	0.0802	0.7801
Patch shoot number	471.3	1	0.6156	0.4424
Patch area	41.8	1	0.0546	0.8177
Shoot density	47.2	1	0.0616	0.8066
Shoot distance hazel	74.9	1	0.0979	0.7578
Shoot height	221.0	1	0.2886	0.5973
Residuals	14546.1	19		

Effects of ground vegetation on L. squamaria

The density of shoots in the *L. squamaria* patches was the only patch characteristic that was significantly correlated with ground vegetation cover (Fig. 9 & Table 2). The density of shoots decreased when ground vegetation increased and is thus affected by competition.

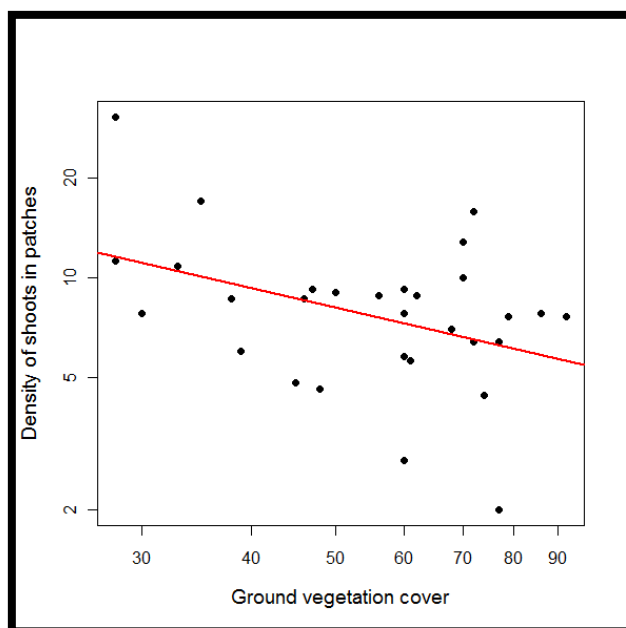


Figure 9. The effect of ground vegetation cover on the density of shoots in the *L. squamaria* patches. The explanatory and response variables were log transformed. The analyses were done with a one-way anova (f = 5.4, n = 30, p = 0.028).

Table 2. The effect of ground vegetation cover on density of shoots in each patch, patch shoot number and patch area in the *L. squamaria* patches in my study area. The explanatory and response variables were log transformed. The analyses were done with one-way anovas (n = 30).

Density of shoots in patches				
Explanatory variable	Sum Sq	Df	F-value	P-value
Ground veg. cover	1.2494	1	5.4041	0.02756*
Residuals	6.4735	28		

Patch shoot number				
Explanatory variable	Sum Sq	Df	F-value	P-value
Ground veg. cover	0.8455	1	1.8577	0.1837
Residuals	12.7439	28		

Patch area				
Explanatory variable	Sum Sq	Df	F-value	P-value
Ground veg. cover	0.7173	1	0.7207	0.4031
Residuals	27.8699	28		

Hand-pollination experiment

The average number of produced seeds in the open-pollinated shoots was 85.3 (SD = 32.2, range 3-155) and in the hand-pollinated shoots 81.3 (SD = 33.7, range 5-155). There was no significant difference between the number of produced seeds (Fig. 8 a). Neither was there a significant difference between the SD of the number of produced seeds between the two pollination treatments (Fig. 8 b).

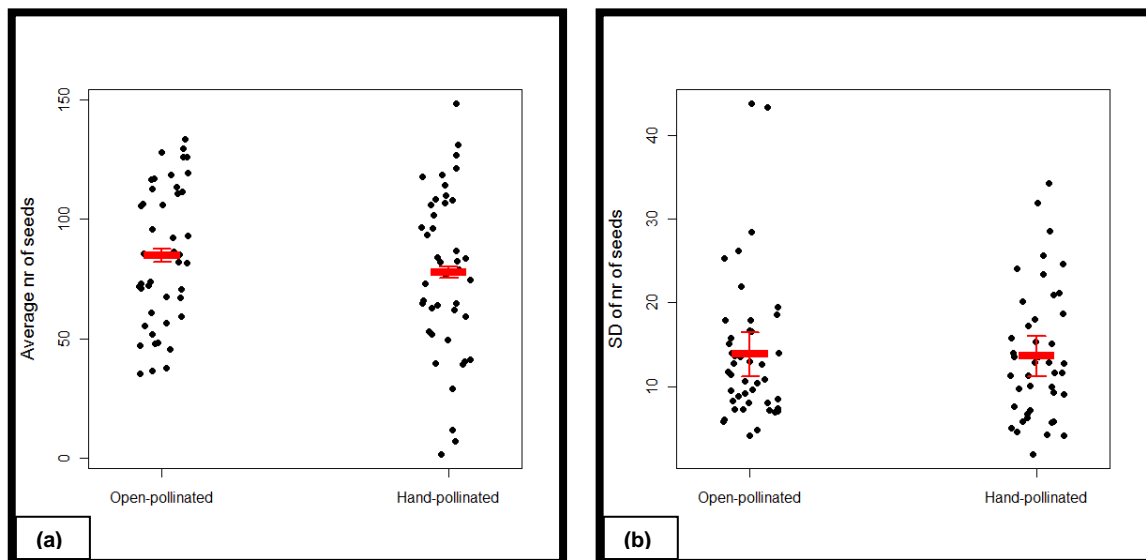


Figure 8. (a) The effect of open-pollination and hand-pollination on the average number of produced seeds (mean values \pm 95% CI indicated in red) in *L. squamaria*, analyzed with a paired t-test ($t = 1.5$, $n = 44$, $p = 0.15$). (b) The effect of open-pollination and hand-pollination on the SD of the produced number of seeds (mean values \pm 95% CI indicated in red) in *L. squamaria*, analyzed with a paired t-test ($t = 0.12$, $n = 44$, $p = 0.91$).

Discussion

According to Rydberg & Wanntorp (2001), to flourish, *L. squamaria* requires the ground vegetation not to be fully covered. *L. squamaria* is thus affected by competition from other species but which aspect of flowering that is affected is not stated. My results show that the density of shoots in the patches is affected by competition while no effect could be detected for patch area or number of shoots. Considering that the rhizome of *L. squamaria* is a large underground structure and that *L. squamaria* is a holoparasite and consequently do not compete with other herbs for its resources, the effect of competition on shoot density may imply that space is the limiting factor. When competition is high, the rhizome must adapt as to where to emerge above ground and grow larger distances to find suitable sites. Competition from other herbs did not affect the seed set of *L. squamaria*, neither did the size of the shoot, its distance to its host, the density around the shoot nor the size of the patch.

My results show that *L. squamaria* in the Tullgarn area did not suffer from pollen limitation. There was no difference in the mean or SD of the number of produced seeds between open-pollinated and hand-pollinated shoots. According to several surveys of publications on pollen limitation (Burd 1994; Ashman et al. 2004; Knight et al. 2005), it occurs in the majority of study systems. However, as Knight et al. (2006) suggest, these findings may be due to biases in publication. Thus, systems without pollen limitation may be more common than appeared. Haig & Westoby (1988) proposed that a plant living in an environment without stochastic events would in time evolve to allocate its resources optimally between attracting pollinators and producing seeds to ensure that enough pollen arrives while it still has resources to mature the fertilized ovules. It would evolve floral traits to increase pollinator visits until it reaches an equilibrium. At this equilibrium, the plant would not produce any additional seeds as a result of additional pollen due to lack of resources. However, there are often complex interactions between pollen limitation and resource limitation (Haig & Westoby 1988; Brookes et al. 2008). The sufficiency of pollination varies between flowers, plants and years (Burd 1994) and in any given year, different stochastic events could make either resource or pollen availability the limiting factor (Haig & Westoby 1988). The results of my study state that the Näset *L. squamaria* population in the spring of 2009 received an optimal amount of pollen for its available resources.

Burd (1995) proposed a theory that plants produce more ovules per flower than the average number of fertilizations. Such overproduction of ovules would allow the plant to capitalize on occasional large pollen loads if it could direct resources toward fertilized ovules. Zimmerman & Pyke (1988) argue that only hand-pollinating a fraction of the flowers of a plant in a

supplemental experiment may result in an incorrect significant result of pollen limitation because of the plant's ability to reallocate resources. The resource reallocation would in such case increase the seed production in the hand-pollinated flowers but not in the whole plant and therefore not be a true result for pollen limitation. Since I only hand-pollinated a fraction of the flowers on every *L. squamaria* shoot in my study, this is another indication that *L. squamaria* actually receives an adequate quantity of pollen to be able to fertilize its ovules with its available resources. If not, it is possible that reallocation of resources to the hand-pollinated shoots would have increased the number of seeds in these flowers or that these flowers would have produced a smaller variance of number of seeds.

According to incidental observations during my study, the top grazed shoots had produced what seemed to be larger capsules than the intact shoots, which could be a sign of *L. squamaria*, somehow being resource limited (Fig. 10). The remaining capsules appeared to have produced more and/or larger seeds than capsules on intact shoots. If this is the case, the intact shoots cannot produce seeds to its maximal potential, i.e they may be resource limited (Burd 1994).



Figure 10. A top grazed *L. squamaria* shoot.

The majority of studies on parasitic plants have been conducted in the laboratory concerning crop pests which has caused many basic aspects of the true ecology of parasitic plants to be unknown (Pennings & Callaway 2002). One example is host choice; what makes some hosts better than others is not fully understood (Press & Phoenix 2005) but parasites may prefer woody perennial hosts over herbaceous annuals because they are available as a resource for a longer period of time (Kelly et al. 1988). *L. squamaria* solely use woody perennials as hosts and is perhaps therefore neither resource nor pollen limited. Its life strategy where it obtains all of its resources from reliable hosts may have enabled it to evolve to avoid pollen limitation.

When it comes to host preference, most parasites are generalists, i.e. they can potentially parasitize on several different species (Pennings & Callaway 2002). Despite them being generalist, many parasites show a high degree of host preference and discriminate between hosts and increase their parasitism on hosts that enhance their growth and reproduction the

most (Press & Phoenix 2005). It has been suggested that the preferable host of *L. squamaria* is hazel (Rydberg & Wanntorp 2001). Without making an in-depth survey of the host choice of the *L. squamaria* shoots in my study area, the majority of the patches were in close proximity to hazel stands. Hazel may be the host that most greatly enhances the growth and reproduction of *L. squamaria*. Since the majority of the shoots in the population at Näset seem to parasitize on it, they might gain more resources compared to other populations that parasitize on other host species. Parasitizing on the optimal resource generating host might have enabled this population to focus resources towards pollinator attractors and/or rewards and thereby avoid pollen limitation which might not be the case in other populations. That different populations can evolve differently was demonstrated by Eriksen, Molau & Svensson (1993) who studied two populations of the parasitic plant *Pedicularis lapponica* which adapted differently to pollination frequency. One population was almost self-incompatible whereas the other population showed significantly higher levels of self-compatibility in response to lower levels of pollinators.

Several shoots in my study area withered prematurely (Fig. 3 x). Many of these shoots had produced capsules but aborted the seeds. Several environmental conditions may determine that only a fraction of the produced ovules develop into viable seeds (Stephenson 1981; Ehrlén 1992; Boieiro et al. 2010) and for a plant to be able to produce seeds, access to resources is an important aspect (Stephenson 1981). *L. squamaria* is completely dependent on the fitness of its host to obtain resources (Musselman & Press 1995). This was evident in the most numerous and the densest of the patches in my study area. It was concentrated around a large hazel stand that had been cut down and the stored resources of its roots could not support this large patch. This caused over 50% of the shoots in the patch to wither prematurely.

Conclusions

The density of shoots in the *L. squamaria* patches decreased as the competition from other species increased. A better understanding of the rhizome of *L. squamaria* has to be gained to fully explain this pattern. The studied population of *L. squamaria* was not suffering from pollen limitation in the spring of 2009. To obtain clarity in the complex patterns of pollen and resource limitation and also how a parasitic plant in particular is affected by them, further studies on both pollen and resource limitation would have to be conducted, preferably over several years and in several populations.

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