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Mikael Ohlson

Seed dispersal and phenology of the invasive plant species *Bunias orientalis* and *Lupinus polyphyllus* in South-East Norway

Cathrine Rask-Jensen
Master of Science in Natural Resource Management
Faculty of Environmental Sciences and Natural Resource Management

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Cathrine Rask-Jensen

Abstract

The alien, invasive species *Bunias orientalis* and *Lupinus polyphyllus* are in expansion in Norway and pose an ecological threat to native species. The species form large and dense populations on wastelands, previous agricultural land, and along linear, anthropogenic structures like railways and road sides. *L. polyphyllus* reproduce primarily by seeds, but also via vegetative propagation. One plant can produce hundreds of seeds, which can be viable after 50 years. *B. orientalis* produce 200-5000 seeds per individual, and reproduce by seeds only. The aim of this study was to improve knowledge on seed dispersal ability of *Bunias orientalis* and *Lupinus polyphyllus* and to document their flowering and seed production phenology, which are relevant for future control of the species.

The seed dispersal and phenology study were implemented at two sites of *L. polyphyllus* in Ås, and two sites of *B. orientalis* in Oslo. Three source populations of 3x3 m^2 were fixed randomly at each site. A total of eight seed traps were placed in a straight line in the cardinal directions north - south at each side of the source population in respectively 0.5, 1, 2 and 4 meters distance. The source population functioned as a source for seed dispersal, as every individual of the target species outside, were cut down. The seed traps were emptied throughout the assessment period. Estimates of total mean seed production per source population were calculated to evaluate how much seeds were caught in the traps.

The significance of cardinal direction regarding seed dispersal, and the species-specific differences in seed dispersal distances per species, were tested statistically. To obtain information on the distribution of seed dispersal throughout the season, when the predominance occurred and how long it transpired, fruits were counted on three individuals per source population each week. The dispersal of fruits was recorded through the decrease in fruits per individual. Simultaneously, the pods and siliquae were divided into the stages of flower, unripe, medium ripe and ripe to document the phenology of the target species.

The phenology study provides approximate estimates of when the life cycle events can be presumed to occur for populations of the target species in SE Norway, though it vary annually. Control and management of the species should take place during the inflorescence, which in this study ended around 15.07 for both species. The results indicated that the ripening process and dispersal of fruits of the target species were very reciprocal to climate and habitat factors, and will probably be expedited with future climate changes.

Despite extensive seed production in all source populations, there were few seeds caught in the traps, mostly at 0.5 and 1 meters distance. There was a significant difference in seed dispersal to the different trap distances for *L. polyphyllus*, however, not for *B. orientalis*. The occurrence of insect and rodent activity around the traps at the sites of *L. polyphyllus*, indicated that the species were dependent upon zoochory. Furthermore, compared to from the target species, there were more seeds of other species caught in the traps, at all sites. This was also, presumably due to that seeds of the target species were transported outside the traps, considered that *L. polyphyllus* and *B. orientalis* have a successful expansion, and mainly reproduce by seeds.

The results indicated that the seed dispersal ability of *L. polyphyllus* and *B. orientalis* not was very efficient. Dispersal are probably highly effectuated by slipstreams from e.g. vehicles or trains, and germplasm being transported by vehicles or humans contribute to spread. The target species would not have been so effectively dispersed and managed to pose a threat to endemic species, if it was not for human intervention, and is otherwise dependent upon zoochory for dispersal of seeds.

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1. Introduction

According to IUCN (2000), invasive species are defined as “taxa introduced outside of their natural range either intentionally or unintentionally by human agency”. Before humans started to trade and transport invasive species, biogeographic barriers such as oceans and mountains contributed to isolation of ecosystems (Mooney & Cleland, 2001). Today, the world is influenced by globalization and international commerce and trade have increased the speed of transport of species across borders (Mooney & Cleland, 2001). The invasion of habitat by alien species is an increasing problem, and they are considered one of the main threats for biodiversity in Norway (Primack, 2014).

A total of 3140 alien species have been registered in The Norwegian Alien Species List, where 1532 were risk assessed. Not all species are necessary unwanted, and the criteria set for a species to be risk assessed were that they were established in the country after 1800 (Artsdatabanken, 2018). These species can pose an ecological threat for endemic species (Gederaas et al., 2012), and at the same time be vectors for diseases and parasites. A combination of invasion potential and ecological effect are used in the risk assessment of alien species, and they are thereafter divided into five categories ranging from no known risk (PO) to severe risk (SE). Species in the high (HI) and severe (SE) risk categories consists of 242 species (Artsdatabanken, 2018). Examples of species in the severe risk category are the target species in this master thesis, i.e. *Lupinus polyphyllus* and *Bunias orientalis*.

Alien species are estimated to cost the Norwegian society 4 billion kroners per year, based on calculations of gross domestic product. In total, 80 million kroners per year is used on countermeasures against invasive species (Magnussen et al., 2015). E.g., control of *Lupinus sp.* had a total cost of 1.8 million, and *Elodea canadiensis* had one of the highest costs with 2.4 million kroners used on countermeasures in 2013 (Magnussen et al., 2015). The socioeconomic costs for different government agencies are extensive. The Ministry of agriculture of food, Norwegian Environmental agency, The County Governor, Norwegian nature inspectorate and the Norwegian Public Roads administration use the most resources on countermeasures (Magnussen et al., 2015).

L. polyphyllus is originally from western parts of North America. It was introduced to Europe in 1826 and has progressively spread because of human activities. Before knowledge on invasive alien species were established, *L. polyphyllus* was sown because of its alluring appearance and to stabilize road sides, and traffic has contributed to further spread (Statens vegvesen, 2017). The first discovery in Norway of *L. polyphyllus* was in 1913 (Statens vegvesen, 2017), and it is now to be found in all counties, although not as frequent in inland regions and northern Norway (Artsdatabanken, 2012).

The species is a 50-150 cm tall perennial herb. It reproduces primarily by seed dispersal, but also via vegetative propagation with disjointed rhizomes. It flowers between June – August (Mossberg et al., 2007), with seed ripening in July - August, depending on weather conditions. The flowers sit in dense wreaths in a long cluster along the main stem with up to 80 or more single flowers per individual. Hundreds of seeds can be produced by a single plant with each pod containing 4-12 seeds, which can be viable after 50 years (Artsdatabanken, 2012).

L. polyphyllus has nitrogen-fixing root nodules, which makes it able to thrive in nutrient-poor areas, like road sides and wasteland. The species change the nutrient conditions in the soil in advantage to more competitive and nutrient demanding species. This leads to change in biological diversity. Those endemic species with a preference in nitrogen poor soil, such as *Dracocephalum ruyschiana* (VU) and *Myricaria germanica* (NT), are displaced and will not reestablish after removal of lupines (Statens vegvesen, 2017). Although *L. polyphyllus* now has expanded to its fully propagation potential in Norway, there is still a possibility of densification (Artsdatabanken, 2012).

Another plant with a growing population is *Bunias orientalis*, originating from West-Asia and Eastern Europe. It was probably first introduced to Norway with the import of grass seeds and ballast around 1800. Subsequently, the species have expanded substantially after its introduction (Artsdatabanken, 2018). The plant is a 50-120 cm tall semi-rosette, polycarpic, perennial hemicryptophyte (Oliver, 2012). The robust tap root can bring forth vegetative offspring contributing to new individuals. It also has a vast seed production, with 200 – 5000 seeds produced per full-grown plant. Reproduction take place by seeds only, if not disturbed (Korsmo, 1954). *B. orientalis* flowers from the second year or later, in June – July with seed ripening in July –August. It can produce a solid seed bank with up to about 800 seeds per liter of soil, and the seeds can be viable after 3 years (Steinlein et al., 1996). In consequence, the expansion of *B. orientalis* is difficult to monitor and control (Oliver, 2012).

Human transportation is the main cause of long-distance dispersal of *B. orientalis*. The species forms dense populations on previous agricultural land, dry wastelands, along road sides and railways. It thrives on dry base-rich soil, where it compete with endemic endangered and vulnerable species (Artsdatabanken, 2018). By forming dense, tall-growing populations it can also displace numerous species. Despite limited import of *B. orientalis*, the species expands in its climatic potential range, with potential for densification especially in Eastern Norway (Artsdatabanken, 2018).

The linear characteristic of anthropogenic elements like railways, roads and canals enhance species mobility. Opportunistic species may benefit from these elements, which can contribute to gene flow between populations. At the same time they act as retreat pathways through less suitable habitats (Van Der Windt & Swart, 2008). In addition, the occurrence of convenient vectors such as transport vehicles contribute significantly to further spread (Hulme, 2009).

According to the so called "Tens rule", there are three transitions a species must overcome to become invasive, i.e. "escaping", "establishing" and "becoming a pest" (Williamson & Fitter, 1996). At each transition around 80-95% of the number of individuals of alien species are lost. Re-entering of the invasion cycle after failing multiple times increase its probability of prosperity (Kolar & Lodge, 2001). Only about 1% of the alien species manage to establish and pose a threat (Mooney & Cleland, 2001).

The risk assessments of alien invasive species are based on a combination of invasion potential and ecological effect (Artsdatabanken, 2018). Even though there is good knowledge on most of the assessed species, the expert group making these risk assessments still have various conjectures to state the degree of advancement of certain invasive alien species (Nygaard P. H. pers. comm. 2017). E.g. in the latest risk assessment of *B. orientalis* and *L. polyphyllus* in the Norwegian Alien Species List (2018), the expansion velocity (m/year) is for both species stated "with uncertainty" (Artsdatabanken, 2018).

1.1 Problem statement

There is an ongoing and continuous dispersal of *B. orientalis* and *L. polyphyllus* over large areas in Norway (Artsdatabanken, 2018). As there is to some degree conjectures in the risk assessment of these species, there is a need for basic knowledge about their biology, and in particular their phenology and dispersal potential. In consideration of this, the main aim of this study was to bring knowledge on seed production and seed dispersal ability of the target species *L. polyphyllus* and *B.orientalis.*

It has been showed that to control invasive plant species has been effective at the time in the life cycle called the compensation point, is effective. This is when there's a minimum of energy stored in the below ground plant parts. To eradicate at this time increases the probability of the plant dying back, as the plants regenerative capacity is at its lowest (Oliver, 2012). If *B. orientalis* was to be controlled after the compensation point, the plant would have had time to develop a powerful taproot, with increased probability of vegetative propagation from remaining rhizomes. The compensation was found to be in older individuals of *B. orientalis*, when the plants had started to elongate, with an average height of 26 cm and in inflorescence (Oliver, 2012).

A further aim of my study was therefore, to document the phenology of inflorescence, the ripening process of the fruits and seeds, and on the timing of seed dispersal, in populations of the target species in SE Norway. Additionally, how these processes are affected by climate and habitat factors. The results can provide implications for when controlling of the target species should occur (i.e. before the compensation point).

The results of my study will add to the knowledge-base for the progress of colonization. Furthermore, give a supplementary explanation for the fast spread the last decades, and how alien, invasive species in the severe (SE) Norwegian Alien Species List category manage to establish, reproduce and pose a threat to endemic species. Finally, the thesis may bring essential information for different public and private agencies who aim at monitor, manage and control the species.

2. Materials and methods

2.1 Field work locations and study system

The South-Eastern parts of Norway are the most heavily populated in the country. Regions in Oslo and Akershus which are not built down, are often cultivated. These circumstances made the counties a convenient study area for the target species of this thesis (Artsdatabanken, 2018). The field work consisted of a seed dispersal and phenology study at two sites of *L. polyphyllus* in Ås, in Akershus county (site 1: 59°39’ N, 10°44’ E, site 2: 59°39’ N, 10°44 E), and two sites of *B. orientalis* in Oslo (site 3: 59°56’N, 10°42’E, site 4: 59°56’N, 10°42’E). Site 1 and 2 of *L. polyphyllus* were close to the European route E6, and the sites of *B. orientalis* were situated in a wasteland area nearby the Oslo University Hospital.

The sites were situated in anthropogenic disturbed areas. Management in form of grass cutting occurred at the sites of *B. orientalis*, and runoff from traffic at the sites of *L. polyphyllus*. At site 1 and 2 in Ås, fertilizers from agriculture, and nitrogen-fixing plants such as *Trifolium pratense* and *L. polyphyllus*, allegedly contributed to nitrogen enrichment of the soil (Berg et al., 1987).

The climate in Oslo and Akershus is continental, and the winter cold in nearby areas of the Oslofjord often is delayed (Mamen, 2011). July in Akershus has the highest monthly average temperature found in Norway ranging from 15-17 °C (Askheim, 2016). The combination of productive soil and mild climate make the area around the Oslofjord the most eligible for agriculture in the country, contributing to suitable habitat for *L. polyphyllus* and *B. orientalis*. The vegetation in, and around the sites, consisted mainly of boreonemoral vegetation types (Askheim, 2016). The soil probably differed from being base-rich to more acidic. Dependent on these nutrient conditions, species community varied (UiO, 2011) (Appendix 8 - 12).

2.2 Seed dispersal and seed identification

The doormat approach was used in the seed dispersal study, which has been used in other studies for seed rain assessment (Birks & Bjune, 2010; Graae et al., 2011; Molau & Larsson, 2000). At each site, three source populations of 3x3 m^2 were fixed randomly; however, at locations with abundant occurrence of phototoxic *Heracleum mantegazzium* and very sparse occurrence of the target species, source populations were arranged restricted randomly due to pragmatic and safety considerations.

A total of 8 seed traps were placed per source population in a straight line in the cardinal directions north - south at each side in respectively 0.5, 1, 2 and 4 meters distance. The radius between the outermost trap and source population did not exceed 4 meters, as seed dispersal is likely to occur within this range (Ohlson, M. pers. comm. 2017). In sum, 24 seed traps were used per study site, and a total of 96 seed traps were used for the whole study. The traps were 2x1 dm^2, made from Astro turf^{TM} doormats attached to the ground with 7.5 cm long nails through each corner. These types of doormats have been used for seed rain assessments in the polar regions, within the International Tundra Experiments (Molau & Mølgaard, 1996), and have proved to be efficient for diaspores of variable sizes (Molau & Larsson, 2000).

The 12 source populations were comprehensively arranged according to the criteria that the average distance between each source population was >10 meter. In order to avoid seed dispersal in trap alignments from other than the intended corresponding source population, the distance between the ends of seed trap alignments in the North-South direction, belonging to different associated source populations, was > 5 meters or more.

Inside the source populations the target species were not cut down and functioned as a source for seed dispersal. The sites were prepared by cutting down every individual of the target species outside the source populations with hedge shears, deliberately avoiding other species so that the influence of background level of seed rain and microsite limitation were taken into consideration (Eriksson & Ehrlén, 1992) . The residue vegetation simulated natural resistance for seed dispersal to occur from the source populations. Since the sites were manipulated, the obtained information about seed dispersal ability was not comprehensively as it eventuates in nature, but it provide a good estimate.

The control period of the seed traps was customized until seed dispersal was expected to occur soon, through information obtained from the phenology study. This was when both assembled pods, and the pods in situ had begun to ripen, open and release seeds. Furthermore, when the decrease in siliquae and pods on the individuals of the target species progressed.

The seed dispersal study lasted from July 24th to November 6th of 2017 for both target species.

On Mondays from July 15th to September 25th the seed traps were examined and emptied into zip lock plastic bags marked with study site (1-4), source population (a-c), distance from source population in meters, cardinal direction (N-S) and date. The assembled pods and siliquae were brought to the lab at Ås, where to be cut open with a scalpel and number of seeds per fruit noted. From September 25th – November 6th when seed dispersal for *L. polyphyllus* was predominantly complete, although not entirely for *B. orientalis*, the seed traps remained in the field at all sites without weekly emptying for the remaining seed dispersal to occur. This was done due to considerable work with the phenology study and limited time for field work in this period.

On November 6st the seed dispersal for *B. orientalis* was generally complete, and all seed traps were collected and sealed in zip lock plastic bags marked with required information. They were further brought to the lab where to be flushed and all seeds extracted using a 250 μm strainer.

To substantiate the forthcoming species identification of seeds caught in the traps, and make it less demanding, all species in the source populations, as well as in the areas outside in proximity, were identified and noted. The height of the three random and three subjectively chosen individuals of the target species in the source population were measured. Additionally, approximate estimations of height of the vegetation outside the source populations, in case of significance for the final results, were noted.

Seed identification

For species identification of the seeds, they were arrayed in petri dishes using a macroscope. Berggren (1969) and The Digital Seeds Atlas of the Netherlands (The Groningen Institute of Archaeology, 2006) in conjunction with comparison to seeds of species identified during previous field work (Appendix 12) were used for the nomenclature.

The seeds of target species and others were species identified, counted and noted for study site (1-4), source population (a-c), distance from source population in meters and cardinal direction (N-S) for the period September 25th – November 6th 2017. The siliquae were opened with a scalpel and number of seeds noted.

Due to particularly high resemblance among seeds in specific genera e.g. *Elymus*, *Cirsium* and *Epilobium* species, certain seeds were identified to genus.

2.3 Phenology

Seed production

A phenology study was implemented on the target species to obtain information on the distribution of, and when the predominance of seed dispersal occurred throughout the season, furthermore how long it transpired.

By counting all pods and siliquae on three subjectively chosen individuals per source population each week at all sites, the decrease in fruits per individual, and thereby dispersal of seeds, was recorded systematically throughout the season. The assessment lasted from July 15th to September 25th of 2017 for *L. polyphyllus* and from July 15th to November 6th for *B. orientalis*, until the end of the seed dispersal periods.

The subjectively chosen individuals were smaller and used for the phenology study due to considerable amount of fruits per individual, with up to 3761 siliquae on *B. orientalis* and 942 pods on *L. polyphyllus*, observed in this study. The individuals, 36 in total, were repeatedly counted each week alongside the study of seed dispersal ability and maturation process of pods and siliquae. All designated individuals were marked with ribbons of assorted color so they could be easily recognized and differentiated during the field work.

Ripening process

To document the ripening process, the entirety counted on the subjectively chosen individuals, were divided into stages of flower, unripe, medium ripe and ripe. The categorization was conducted once a week, from July 15th to September 25th for *L. polyphyllus* and from July 15th to August 14th for *B. orientalis*. Hence, information about the amount of the siliquae and pods ripened per week, and when the flowering ended for the target species at all sites, were obtained. The categorization persisted the whole seed dispersal period for *L. polyphyllus*, but ended sooner for *B. orientalis* due to predicament with separating the stages.

During the summer, the siliquae did not change explicitly in shape, size or color in transition from unripe to medium ripe while still on the plants. Furthermore, two processes of maturation were identified, which possibly were caused by variation in sun exposure and moisture in the soil. At site 3 and 4 of *B. orientalis*, the siliquae from individuals in source populations situated close to a creek with moist soil, and were simultaneously under the shadow of the canopy of *Alnus* sp., were found to swell considerably, essentially doubling in size. Additionally, before appearance of the characteristic colors of being ripe (yellow or brown), a color transition from green to white along with hardening was observed. The siliquae from continuously sun exposed source populations, situated uphill and away from the creek, remained the same size and went from green to yellow or brown directly.

In a germination experiment carried out by Oliver (2012), siliquae from *B. orientalis* were collected four times during the summer 2011 from a road side population in Oslo and exposed to cold stratification of different durations in order to find time of seed ripening. The results showed no germination after harvesting on July 6th, 23% germination after harvesting on July 20th, 11% germination after harvesting on August 3rd and no germination in seeds harvested on August 17th.

Considering these results, and due to the possibility of ripe siliquae being both white and swollen or brown with persistent size (Fløistad, I. pers. comm. 2017), the entirety on *B. orientalis* was classified as ripe from August 21st until November 6th. The decrease in siliquae on the individuals from August 21st progressed, which indicated that the siliquae were ripe. A germination experiment could be implemented to investigate sprouting ability further, however, since this thesis main goal was to investigate seed dispersal ability, this was not prioritized. The pods on *L. polyphyllus* were easier to differentiate; thus, the whole seed dispersal period was categorized.

On the subjectively chosen individuals, as an extension of the phenology study, there were collected three pods and three siliquae from July 15th to September 25th from *L. polyphyllus*, and to November 6th from *B. orientalis* weekly per site to study the ripening process and gather data of seeds per fruit. The resultants were sealed in zip lock plastic bags marked with study site (1-4), source population (a-c), individual (1 - 3), species and date. The harvested fruits were divided into the ripening stages unripe, medium ripe and ripe, and fruits opened to record the number of seeds. Each collected pod and siliquae were taken photos of, before and after opening. A total of 540 pods from *L. polyphyllus* and 831 siliquae from *B. orientalis* were collected from the target species during the study.

The harvesting continued until the seed dispersal period was determined to be predominantly complete. For *L. polyphyllus*, this was when all pods, including the harvested pods and the pods still remaining on the stem in the field, principally had zero remaining seeds. For *B. orientalis*, the collection of siliquae continued until November 6th, right after the first snowfall. There were still some siliquae left on the individuals after the phenology study was discontinued.

2.4 Total mean seed production per source population

To assess the proportion of the seed production per source population of the target species were caught in the seed traps, estimates of total mean seed production per source population were calculated. In July, right after inflorescence, and before the initiation of seed dispersal, the total number of pods and siliquae were counted on three random chosen individuals, in addition to the previously specified subjectively chosen per source population at all sites. In total, fruits were counted on 72 individuals.

Six estimates of total mean seed production per source population were made based on the random, subjectively and finally the randomly and subjectively chosen individuals combined, in compliance with 14 different estimates of average number of seeds per fruit. The reason for calculating different estimates was to utilize all of the collected data. This made it possible to further assess the standard deviation, and thereby the quality of the six final estimates of seed production per source population.

To evaluate if the data for the random and subjective individuals could be combined in calculations of the estimations of seed production, a Mann-Whitney-Wilcoxon nonparametric test was used on the total number of fruits counted on the random, versus the subjective individuals for *L. polyphyllus* and *B.orientalis*. The tested data for total number of fruits per individual, were from the first census at 15.07, before the initiation of seed and fruit dispersal. If significantly different, it would be statistically most correct to base the estimates of seed production on data obtained from the randomly selected individuals. Both the standard deviation and test results were used to determine which of the estimates of seed production could be assumed to be most accurate.

Essentially, the estimates of average number of seeds per pod and siliquae, obtained in the phenology study, were multiplied by an estimate of average number of fruits per individual. Furthermore, by the total number of individuals per source population to calculate the estimates of the total mean seed production per source population. The estimates of average number of fruits per individual were made based on first the three random, then the three subjectively and lastly the random and subjectively chosen individuals combined.

Furthermore, there were two methods of calculating estimates of average number of seeds per pod and siliquae. The first estimates were based on all plausible harvested observations of pods and siliquae, 108 and 831 respectively, from the subjective individuals from the phenology study. The ripening, opening and spread of seeds commenced concisely after the harvesting had begun, so that the complete number of seeds per pod not were intact. The ripened pods which from seed dispersal had commenced, were removed from the calculation of the estimate, reasoning why there were fewer observations for *L. polyphyllus*.

The other estimates of average number of seeds per pod and siliquae were based on observations of pods and siliquae from individuals from each source population respectively. The average number of plausible observations per source population used for this estimate were 18 pods from *L. polyphyllus* and 138.5 siliquae of *B. orientalis*. Due to that the complete number of seeds not were intact in all pods, there were few plausible observations of pods per source population.

The two methods of calculating the average number of seeds per pod, resulted in 14 estimates, one per species and one per 12 source populations. These were further multiplied with the three different estimates of total number of pods or siliquae per source population based on number of fruits on the random, subjective and lastly randomly and subjectively chosen individuals combined. The approach resulted in six estimates of total mean seed production per source population.

To evaluate the precision of the six estimates, the standard deviations were calculated for each estimate respectively. The formula used for the exact variance of the product of two random variables was (Goodman, 1960):

$$\sqrt{V\widehat{ar\bar{x}} * \bar{y}}$$

$$= \frac{\sigma^2 \bar{y} * \mu x^2 + \sigma^2 \bar{x} \mu^2 y + \sigma \bar{x}^2 \sigma^2 \bar{y}}{\sqrt{\frac{\hat{\sigma}\, n^2}{n_2} * \bar{x} + \frac{\hat{\sigma} x^2}{n_1} + \frac{\sigma^2 x \sigma y^2}{n_1\, n_2}}}$$

The product was the estimate of total mean seed production per source population and the two random variables were the estimate of average number of fruits per source population and the estimate of average number of seeds per pod and siliquae.

The formula assumed that the product of two random variables was independent, meaning that the seed production per pod or siliquae were independent from the production of pods or siliquae per individual. Biologically, however, there is a possibility of interaction between these two random variables (Ohlson, M. pers. comm. 2018), but due to the uncertainty, independency was assumed. Moreover, rather complex statistics would have arisen if the variables were assumed to be dependent.

2.5 Data management and statistical analysis

All data were managed and saved in Excel 2010. The software R (version 3.5.0) (R Core Team, 2013) was used for statistical analysis where analysis and figures were modelled in R-studio version 1.1.419 (2012). To help manipulate data the package Tidyverse 1.2.0 (Wickham, 2017) was used. Most analyses were done for each species separately, although some tests were done per site to assess differences between the target species.

Seed production

To test if there was a significant difference between the number of fruits estimated by the subjectively versus the randomly selected individuals, a Wilcoxon-Mann-Whitney test was used with number of fruits per individual as response variable and random or subjective individuals as predictor variables. This was done for all observations per species, meaning observations for site 1 and 2 with *L. polyphyllus* were consolidated and site 3 and 4 with *B. orientalis* were consolidated.

Shapiro-Wilk tests for normality was used on the random and subjective individuals separately per species, and rejected the null hypothesis assuming normality for all groups, with the four p-values < 0.05. Log transformation did not have a significant effect for the data to fulfil criteria of normal distribution. Furthermore, it would be difficult to interpret test results if i.e. square root transformation was to be used, thus the use of non-parametric Wilcoxon-Mann-Whitney test.

Seed dispersal

Shapiro-Wilk tests for normality were used on the seed dispersal data, per site and species, where all p-values < 0.05. QQ-plots showed a clear indication of outliers which twisted normality per site and species, and the data did not fulfill criteria of normal distribution after log transformation. Due to data being heavily left skewed, transformation would not have a significant effect on the data to fulfill the criteria of normal distribution (Rimal, R. pers. comm. 2018). Non-parametric tests were therefore used on the seed dispersal data.

To test the significance of cardinal direction regarding seed dispersal for the target species a Wilcoxon-Mann-Whitney test was used. The cardinal direction was used as predictor variable and the total amount of seeds caught in the traps for the season as response variable. The results were summarized for site 1 and 2 and site 3 and 4, i.e. per species, and tested the median value of seeds caught in the north versus the south.

Further a Wilcoxon-Mann-Whitney test was used to test if there was a significant difference between the target species' seed dispersal to the cardinal directions north and south. The results for north were first filtered out to test if there was a significant difference, then the same procedure was used for the south. In this way it was tested if the amounts of seeds caught in the different cardinal directions were affected by the species. The total count of seeds per trap was response variable, and cardinal direction was predictor variable.

A Kruskal-Wallis non parametric ANOVA test was used for each species separately to test if there was a difference in seed dispersal to the different seed trap distances. As response variables were the total count of seeds caught in the traps, and as predictor variables the four trap distances.

Furthermore, to confer the species-specific differences in seed dispersal distances per species a Dunn test for multiple comparisons with Bonferroni correction was used (Dinno, 2017). The Dunn test performs Kruskal-Wallis with pairwise comparisons of different groups, in this case seed trap distances. A Wilcoxon-Mann-Whitney test or Kruskal-Wallis test would not give the right p-value for multiple pair-wise comparison; thus the p-value was adjusted using Bonferroni correction.

3. Results

3.1 Phenology study

3.1.1 Ripening process

Site 1 (*L. polyphyllus*)

The flowering at site 1 had in general ceased at the first census on 15.07, and the pollinated flowers had transitioned to unripe pods. However, a few individuals other than the studied were still flowering. The number of unripe pods peaked in all source populations in the first census, for then to decline. The last unripe pods were observed during the third census at 31.07 in source population a and b (Figure 1 & 2).

The trend for all subjectively chosen individuals in the source populations at site 1, was a rather abrupt transition from unripe to medium ripe or ripe pods mainly between the second census at 24.07 and third census at 31.07. Even though site 1 was situated on flat ground, and site 2 on a hillside with smaller individuals, there was on average no evident difference in the ripening process between the sites of *L. polyphyllus*. However, there was a difference in the ripening process among the source populations within the sites.

In source population a, the last unripe pods were observed in the third census at 31.07 in individual a3 (Figure 1).

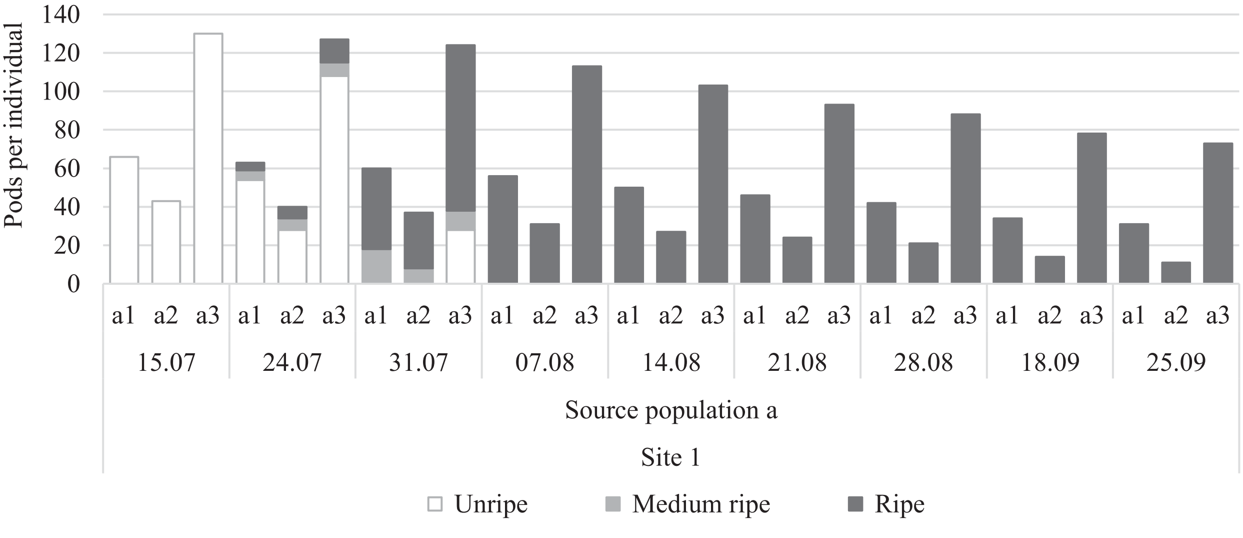

Figure 1: Number of unripe, medium ripe and ripe pods in one stacked column per plant, a1, a2 and a3, per census throughout the assessment period in source population a, at site 1 of *L. polyphyllus*.

Source population a had the latest transition from unripe to ripe pods in the third census at 31.07, one census later compared to source population b and c (Figure 1 - 3).

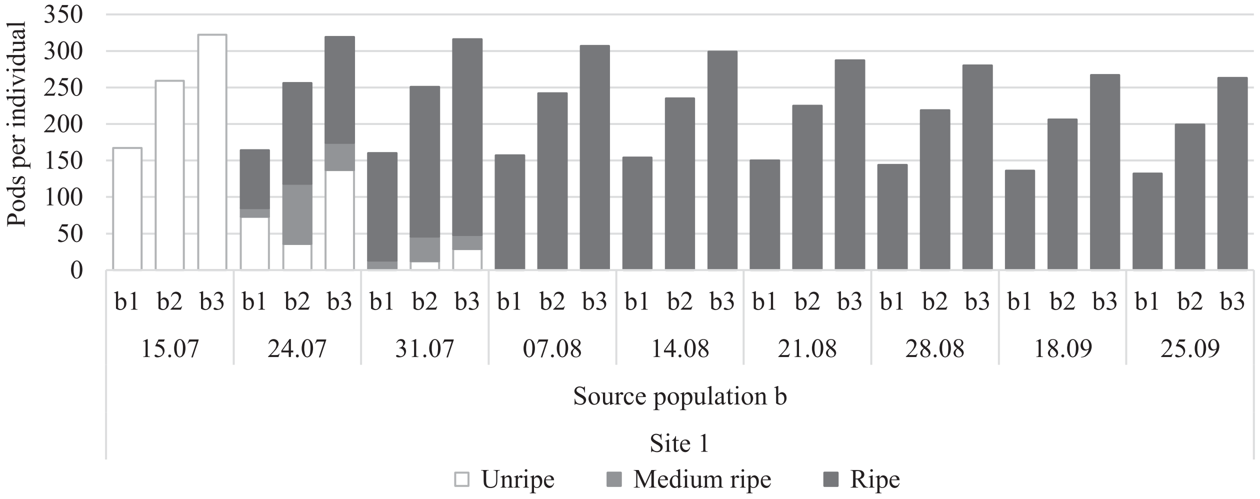

Figure 2: Numer of unripe, medium ripe and ripe pods in one stacked column per plant, b1, b2 and b3, per census throughout the assessment period in source population b, at site 1 of *L. polyphyllus*.

The main transition from unripe to medium ripe and ripe pods occurred in the second census at 24.07 and in the third census at 31.07 in source population b. The last unripe pods were observed in individual b2 and b3 in the third census (Figure 2).

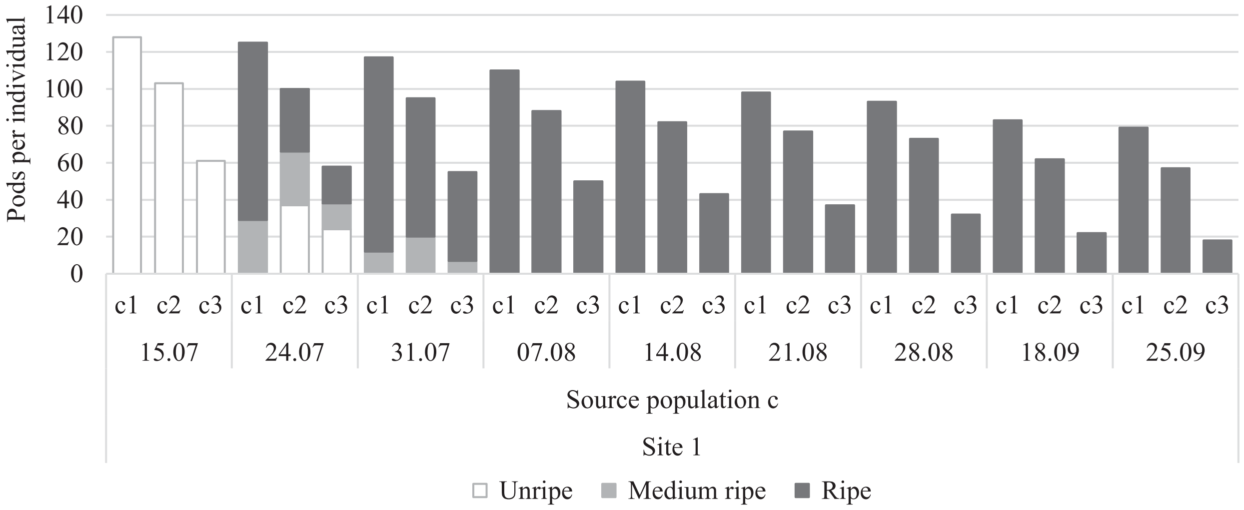

Figure 3: Number of unripe, medium ripe and ripe pods in one stacked column per plant, c1, c2 and c3, per census throughout the assessment period in source population c, at site 1 of *L. polyphyllus*.

In source population c, the last unripe pods as well as the predominance of transition from unripe to medium ripe or ripe pods, were observed in the second census at 24.07 (Figure 3), earlier than in a and b.

Site 2 (*L. polyphyllus*)

At site 2, the number of unripe pods peaked in the first census at 15.07. Generally, the ripening process was similar to site 1 with the main transition from unripe to medium ripe or ripe pods in the second and third census. There was however, a slightly greater divergence in the ripening process throughout the season at site 2.

E.g. in source population b, inflorescence was still in progress in individual b1, while the transition from unripe to medium ripe occurred in individual b2 in the first census at 15.07. There were distinctive differences between the source populations in the transition from unripe to ripe pods.

Furthermore, the ripening process had proceeded in source population b and c in the first census while in source population a, it occurred in the second census. This was also in contrast to site 1, where the transition from unripe to medium ripe or ripe first proceeded in the second census.

In source population b, the last unripe pods were observed in the fifth census at 21.08 in individual b1 (Figure 4). This was later than the other source populations at both site 1 and 2, where the last unripe pods were observed in the third census at 31.07. However, the late inflorescence and ripening process of pods occurred in only one study plant at site 2; and in general the inflorescence was at site 2 of *L. polyphyllus* complete by the first census at 15.07.

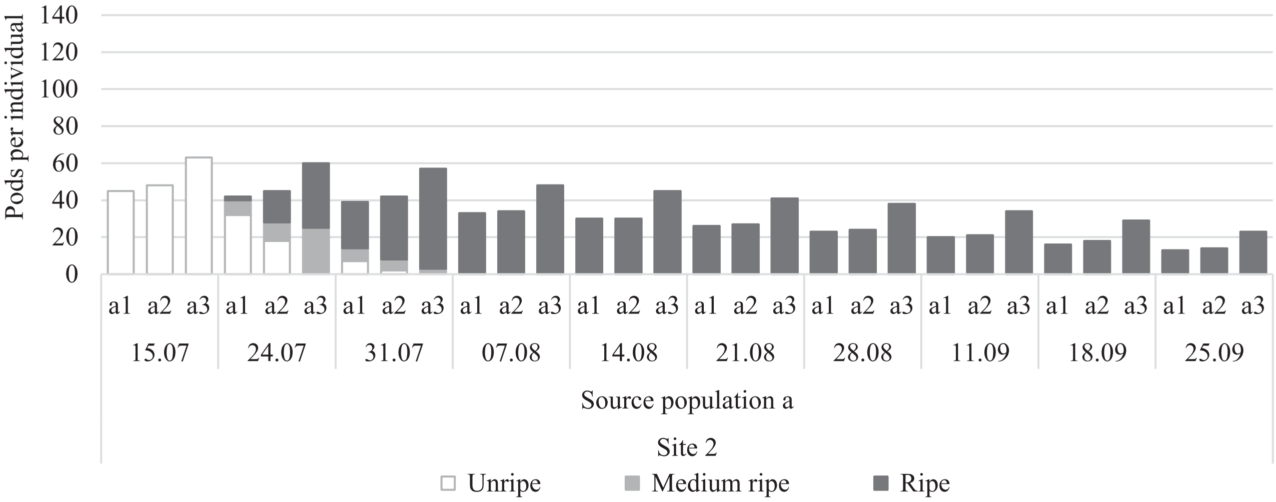

Figure 4: Number of unripe, medium ripe and ripe pods in one stacked column per plant, a1, a2 and a3, per census throughout the assessment period in source population b, at site 2 of *L. polyphyllus*.

In source population a, the transition from unripe to medium ripe and ripe pods occurred in the second and third census, similarly to the source populations at site 1. The last unripe pods were observed the third census at 31.07 in individual a1 and a2 (Figure 4). From the fourth census at 07.08 and onward, all pods were ripe, and decreased per individual due to fall. Source population a, had on average the penultimate ripening process of pods at the site 2.

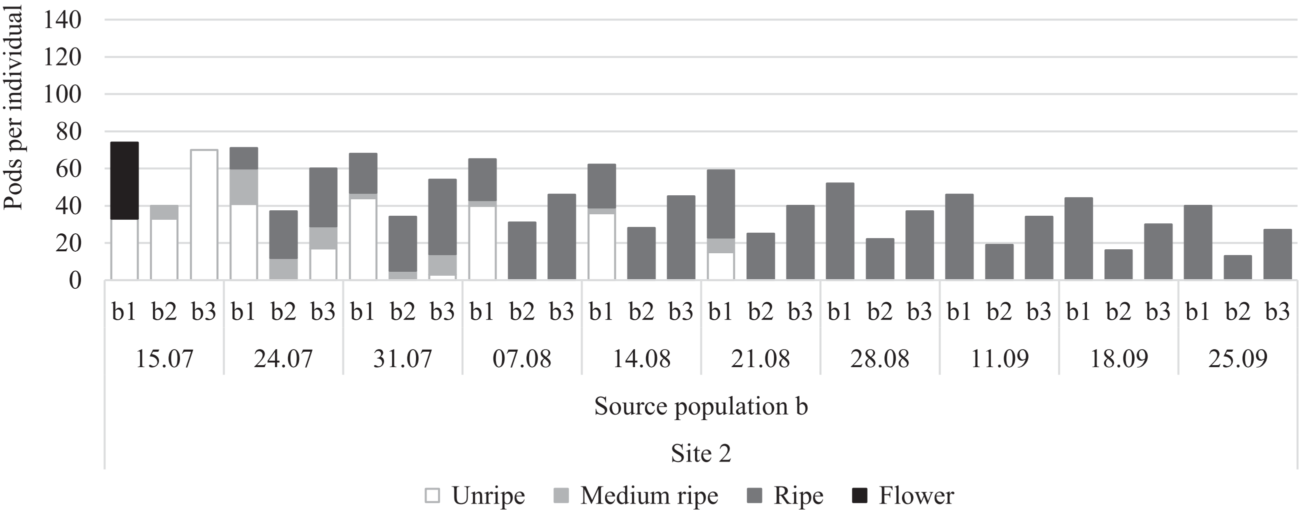

Figure 5: Number of unripe, medium ripe and ripe pods in one stacked column per plant, b1, b2 and b3, per census throughout the assessment period in source population a, at site 2 of *L. polyphyllus*.

In source population b, individual b1 was still in inflorescence in the first census at 15.07, whereas in individual b2 the ripening of pods had commenced (Figure 5). The main transition from unripe to ripe occurred in the second and third census for individual b2 and b3. For individual b1, the last unripe pods were observed in the sixth census at 21.08. In the next census at 28.08, all pods were ripe. All pods on individual b2 and b3 were ripe in the fourth census at 07.08, as for all subject individuals studied of *L. polyphyllus*. Individual b1 was a deviation from this trend, which still was in inflorescence in the first census with followed delayed ripening process.

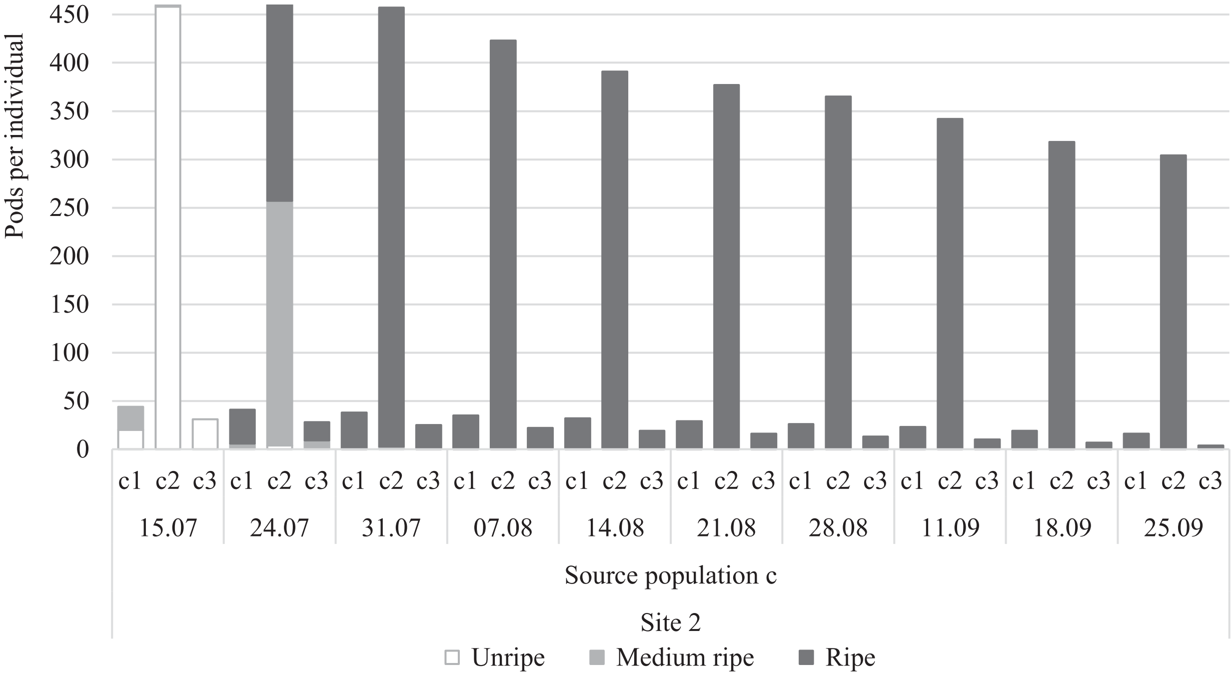

Figure 6: Number of unripe, medium ripe and ripe pods in one stacked column per plant, c1, c2 and c3, per census throughout the assessment period in source population c, at site 2 of *L. polyphyllus*.

In source population c, the pods on the three subject individuals went from predominantly unripe in the first census at 15.07, to mainly medium ripe and ripe in the second census at 24.07 (Figure 6). There was a quicker transition in the smaller individuals, where c2 still had 4 unripe and 253 medium ripe pods in contrast to c1 and c3 with mainly ripe pods in the second census (Figure 6). The last unripe pods were observed in the second census at 24.07, and most of the pods on the subject individuals were ripe in the third census at 31.07. This was the earliest transition from unripe to medium ripe and ripe pods on the studied subject individuals of *L. polyphyllus*.

Site 3 (*B. orientalis*)

Inflorescence was over on the subject individuals when the assessment period commenced in the first census at 15.07. Sporadically however, there were observed a few individuals still flowering at site 3. There were differences between the source populations in the amount of unripe, medium ripe and ripe siliquae in the first five censuses, and in the way the siliquae ripened in the respective.

There were mainly medium ripe and unripe siliquae on the subject individuals in all source populations in the first census. The last unripe siliquae were observed in the fifth census at 14.08 in individual a1- a3 in source population a, and individual c3 in source population c. The trend for site 3 was a gradual transition of the siliquae from unripe via medium ripe to ripe in the five first censuses. This was in contrast to the individuals at site 1 and 2 of *L. polyphyllys*, where there were a rather abrupt transition from unripe to ripe in the second and third census.

The siliquae on all subject individuals at site 3 and 4 were considered ripe from the sixth census at 21.08, partly due to predicament with separating medium ripe from ripe without a germination experiment. The fall of siliquae increased gradually from the fifth census at 14.08 and sixth census at 28.09, which indicated ripeness.

Observations of harvested siliquae from site 3 of showed two ways of ripening. Siliquae from source population a and c swelled considerably, remained green longer and turned fairly white, before speckled brown. In contrast, the siliquae collected from source population b at site 3, remained small in size and turned directly to more characteristic colors of being ripe, like yellow and brown (Figure 7).

Figure 7: Siliquae harvested from the three plants in source population a, b and c at site 3, in the fifth census at 14.08. Siliquae from source population a (left) and c (right) were still predominantly green and considerably larger and heavier than the siliquae harvested from source population b (middle), which already had turned yellow and brown.

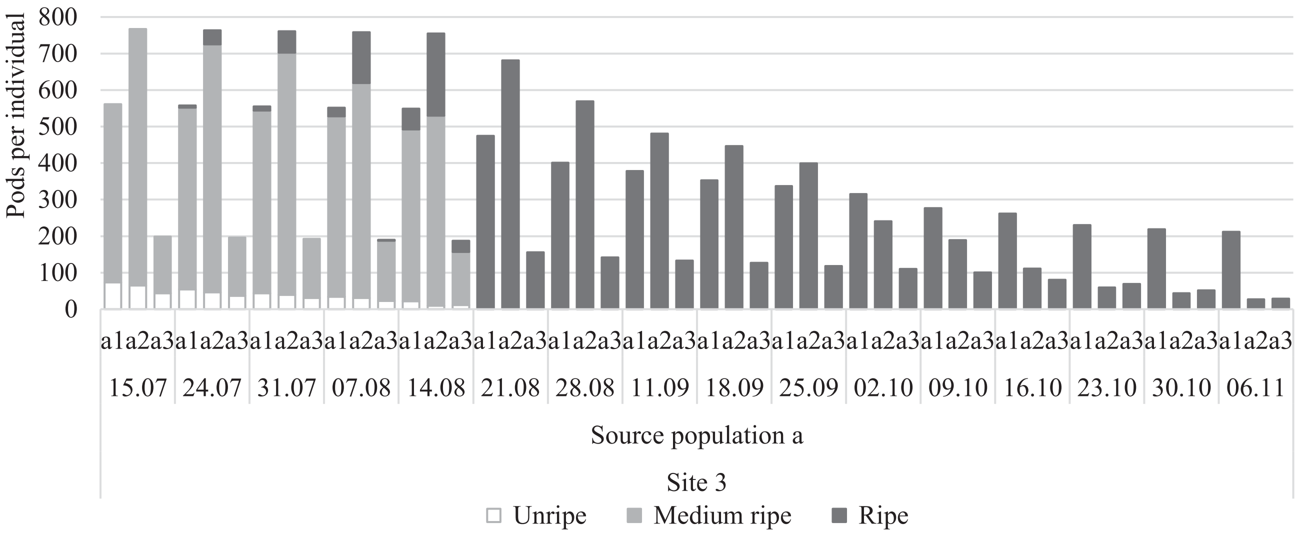

Figure 8: Number of unripe, medium ripe and ripe siliquae in one stacked column per plant, a1, a2 and a3, per census throughout the assessment period in source population b, at site 3 of *B. orientalis*.

In source population a, the last unripe siliquae were observed in the fifth census at 14.08, and the respective source population was the only where all the subject individuals still had unripe siliquae in the fifth census (Figure 8). The siliquae were otherwise primarily medium ripe in the five first censuses, before a transition to ripe, and fall further increased from the sixth census at 21.08.

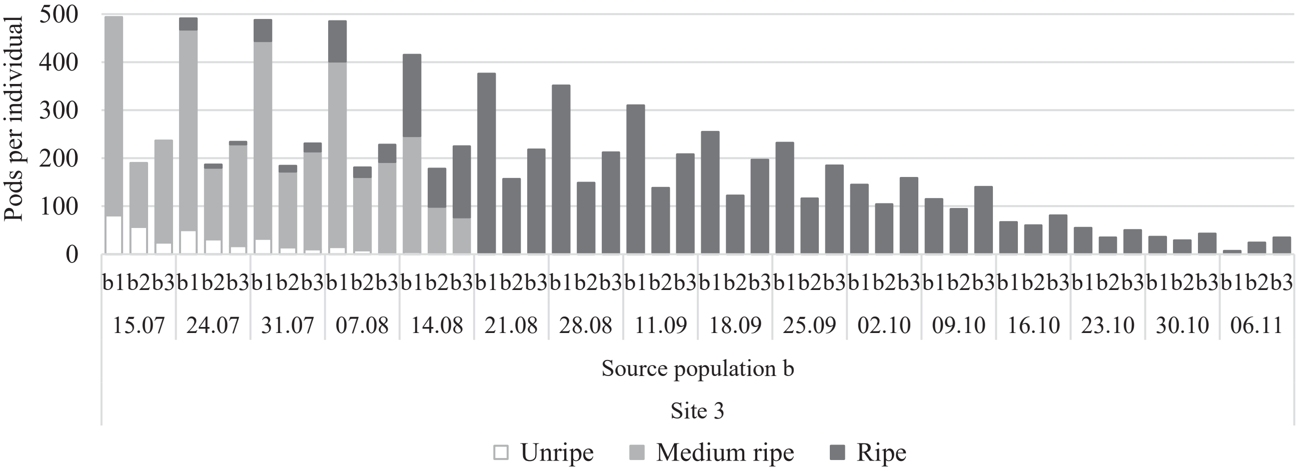

Figure 9: Number of unripe, medium ripe and ripe siliquae in one stacked column per plant, b1, b2 and b3, per census throughout the assessment period in source population a, at site 3 of *B. orientalis*.

The last unripe siliquae were observed in the fourth census at 07.08 in source population b (Figure 9), one census earlier than in a and c. The subject individuals also had a rather large proportion of ripe siliquae in the fifth census at 14.08, compared to in the other source populations.

The subject individuals in source population c had on average, the highest proportion of unripe siliquae in the five first censuses at site 3, with the last unripe siliquae observed in the fifth census at 14.08 in individual c3 (Figure 10).

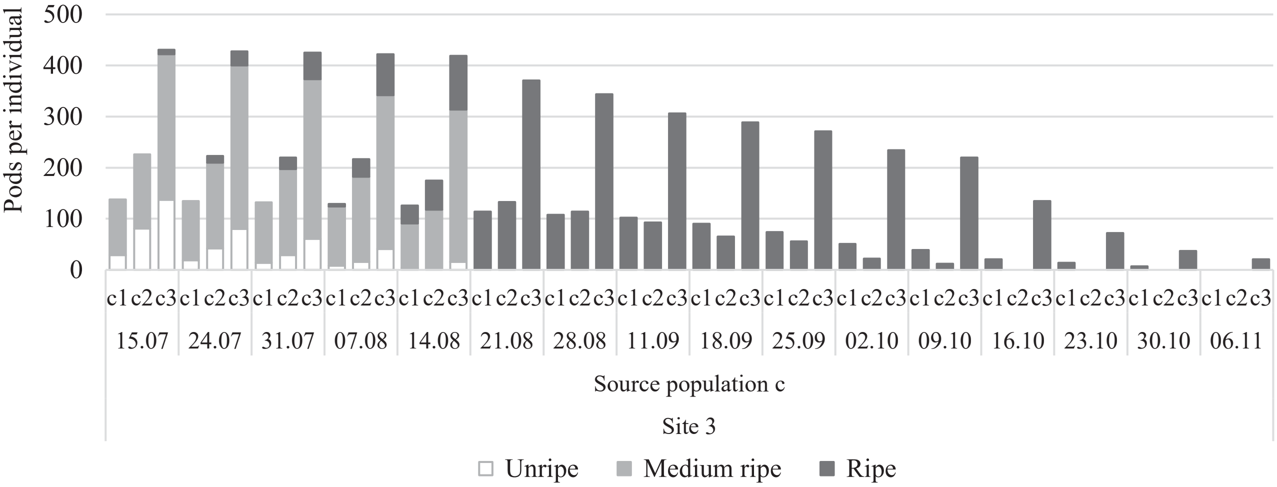

Figure 10: Number of unripe, medium ripe and ripe siliquae in one stacked column per plant, c1, c2 and c3, per census throughout the assessment period in source population c, at site 3 of *B. orientalis*.

Individual c2 had lost all siliquae in the 13th census at 16.10, and c1 all siliquae in the 19th census at 06.11, and were the only subject individuals to lose all siliquae at site 3.

Site 4 (*B. orientalis*)

Inflorescence was at site 4 predominantly over by the first census at 15.07, and the number of unripe siliquae peaked, for then to decline in the following censuses. There were mainly medium ripe siliquae on all plants in the five first censuses, with a gradual transition of the unripe and medium ripe siliquae to ripe. All siliquae were classified as ripe from the sixth census at 21.08, before fall increased.

The last unripe siliquae were observed in the fifth census at 14.08 in individual a2 in source population a, and in individual b1 in source population b. In comparison, there were at site 3, four plants left with unripe siliquae in the fifth census. Furthermore, individual a3 and c2 at site 4 had lost all the siliquae by the end of the assessment period in the 16th census at 06.11. This was in contrast to only one, c2, in source population c at site 3. There was an accelerated ripening process in form of quicker transition from unripe to ripe pods, and more individuals that lost all siliquae at site 4, compared to at site 3.

In source population a, the siliquae were mainly medium ripe and unripe when the assessment period commenced at 15.07 (Figure 11). The the last unripe siliquae were observed in individual a2 in the fifth census at 14.08.

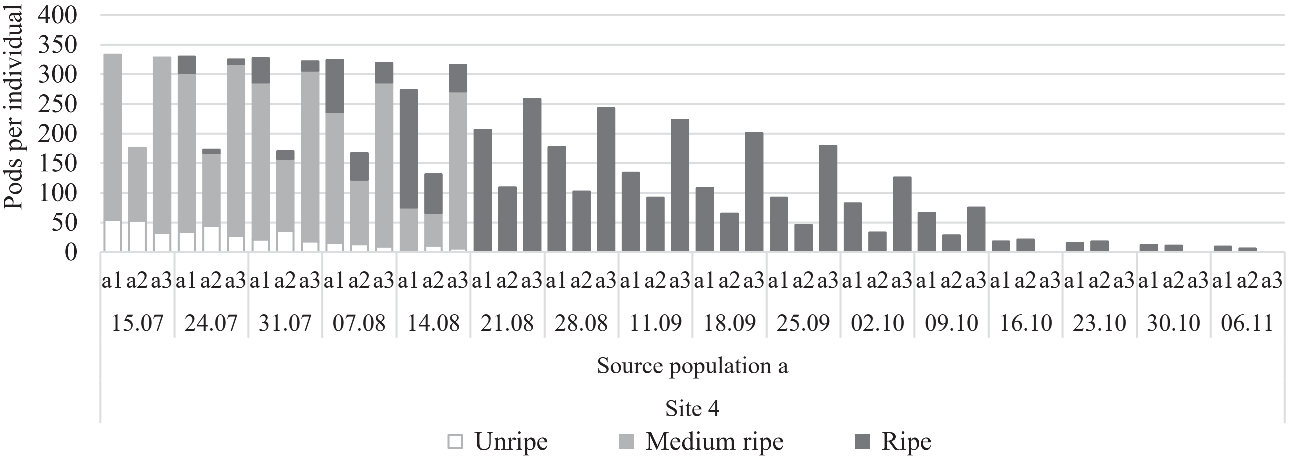

Figure 11: Number of unripe, medium ripe and ripe siliquae in one stacked column per plant, a1, a2 and a3, per census throughout the assessment period in source population a, at site 4 of *B. orientalis*.

Individual a1 had a rather abrupt transition from medium ripe, to mostly ripe siliquae, from the fourth census at 07.08 to the fifth census at 14.08. In the 13th census at 16.10, individual a3 had lost all siliquae. Loss of all siliquae in a3 were in contrast to the plants in source population b, where siliquae remained on all, in the last census at 06.11 (Figure 12).

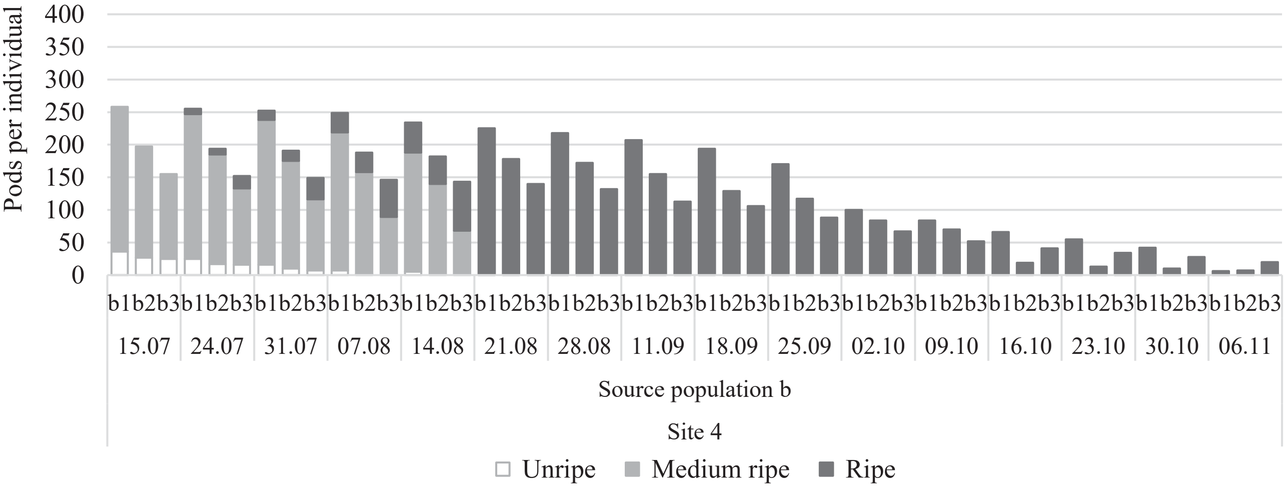

Figure 12: Number of unripe, medium ripe and ripe siliquae in one stacked column per plant, b1, b2 and b3, per census throughout the assessment period in source population b, at site 4 of *B. orientalis*.

There were on average a larger proportion of medium ripe siliquae in the fourth census at 07.08 and in the fifth census at 14.08 in source population b, compared to source population a and c, which in total had more ripe siliquae. The last unripe siliquae were observed in individual b1 in the fifth census at 14.08 (Figure 12).

There was a slower ripening process in source population b, than in a and c. Source population b was the only at site 4 where all plants still had siliquae left in the 16th census at 06.11.

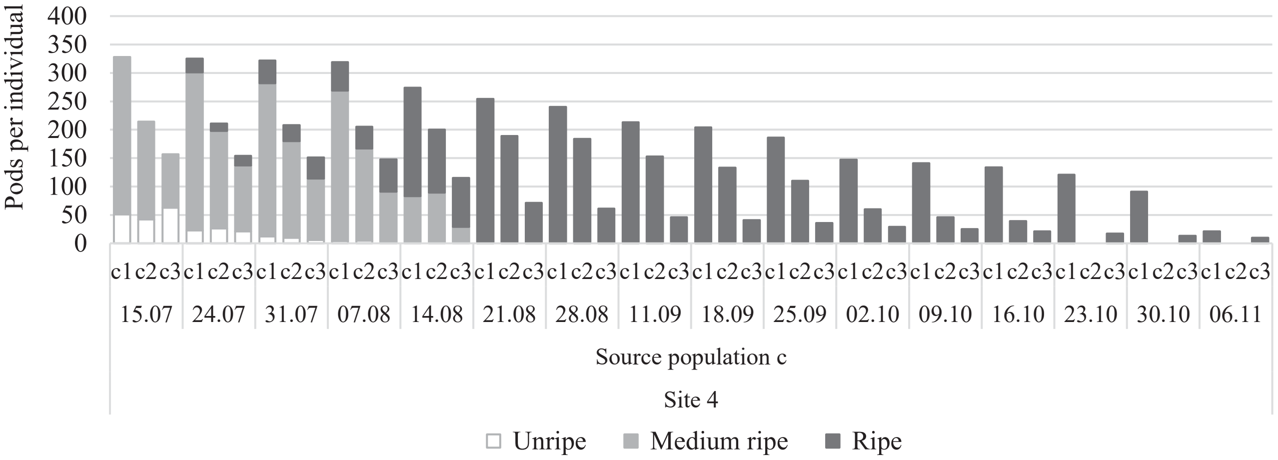

Figure 13: Number of unripe, medium ripe and ripe siliquae in one stacked column per plant, c1, c2 and c3, per census throughout the assessment period in source population c, at site 4 of *B. orientalis*.

In source population c, the last unripe siliquae were observed in the fourth census at 07.08, one census earlier than in source population a and b. Overall, there was a large proportion of ripe siliquae in the fifth census at 14.08 in the subject individuals (Figure 13). The plants in the other source populations at site 4, had comparably more unripe and medium ripe siliquae in the fifth census. Individual c2 had lost all siliquae in the 14th census at 23.10 (Figure 13).

3.1.2 Fruit ripening and seed production

The first census of the ripening process took place at 15.07 in the source populations at all sites, but the fall of siliquae and pods occurred later. At site 1 and 2 of *L. polyphyllus*, the fall of pods started in the third census at 31.07, and in the fourth census at 07.08. This was also approximately when the pods had begun to open and release seeds at both sites, i.e. in the third census at 31.07.

In general, the predominance of fall of pods occurred in the fourth census at 07.08 and in the fifth census at 14.08 at both sites of *L. polyphyllus*. No plants at site 1 or 2 had lost all pods by the tenth and last census at 25.09. However, the preponderance of harvested pods were empty at the last census, which indicated that the seed dispersal period was over by 25.09 at site 1 and 2.

Fall and spread of siliquae for *B. orientalis* at site 3 and 4 proceeded in the fifth census at 14.08 and in the sixth census at 21.08, on average two censuses later than for *L. polyphyllus*. The fall of siliquae at site 3 and 4 were distributed throughout the season, where most fall was registered in the sixth census at 21.08, seventh census at 28.08, 11th census at 02.10 and in the 13th census at 16.10. The seed dispersal was generally over in the 16th census at 06.11 at both sites of *B. orientalis*, approximately six weeks after it ended for *L. polyphyllus*.

Site 1 (*L. polyphyllus*)

The fall of pods begun in the fourth census at 07.08 in source population a, and in the third census at 31.07 in source population b and c at site 1 (Figure 14).

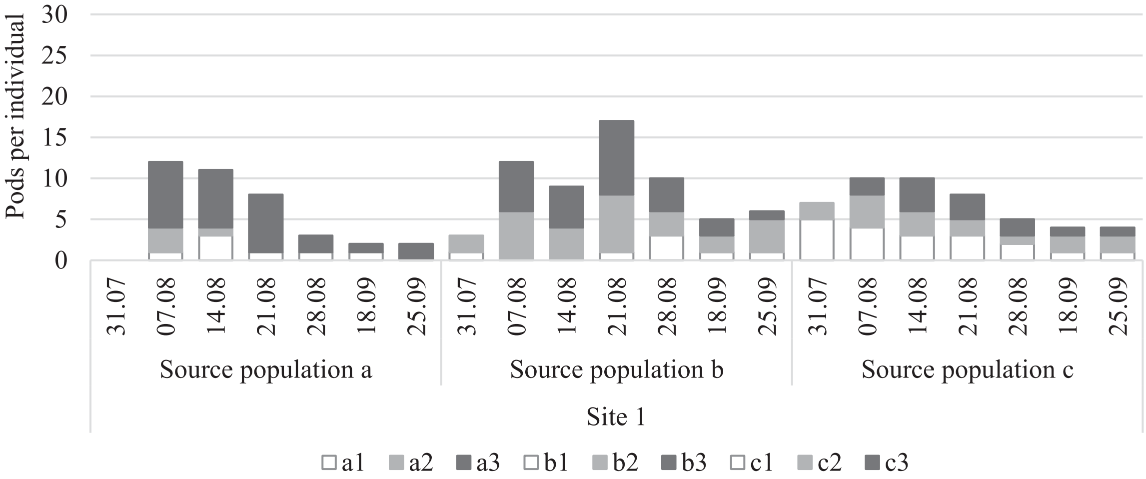

Figure 14: Fall of pods from the three plants, a1-a3, b1-b3 and c1-c3 combined in one stacked column, from each source population (a-c), per census throughout the assessment period at site 1 of *L. polyphyllus*. The first two censuses were removed due to no fall.

The fall peaked in the fourth census at 07.08 and in the fifth census at 14.08, in source population a and c. In source population b, most of the fall was distributed between the fourth census at 07.08 and the seventh census at 28.08, with a peak in the sixth census at 21.08, one to two censuses later than in source population a and c.

There was an abrupt transition from fall of zero pods in the third census at 31.07 to 17 pods in the fourth census at 07.08 in source population a. Compared to the study of ripening process, there was also a sudden transition from unripe to mostly ripe pods from the second census at 24.07 to the third at 31.07 in the same source population. Generally, the transition from unripe to ripe was rather abrupt, and the predominance of fall of pods occurred approximately one to two censuses after the pods were ripe. In source population b however, though there was a large proportion of fall in the fourth and fifth census, it peaked in the sixth, three censuses after most pods were ripe in the third census at 31.07. The seed dispersal period was at site 1 determined to be over in the last census at 25.09, due to that that the harvested pods were mostly empty in the last two censuses.

Site 2 (*L. polyphyllus*)

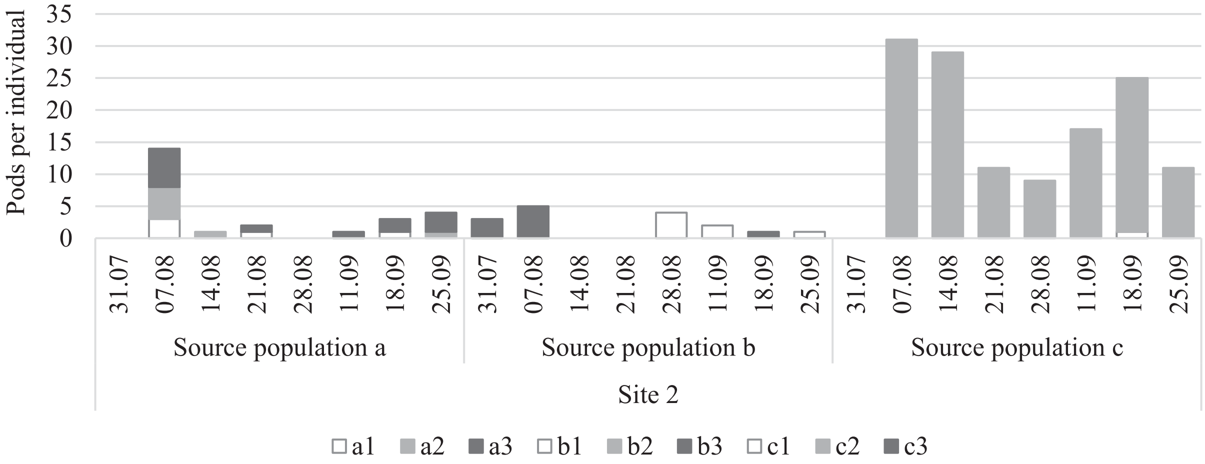

Figure 15: Fall of pods from the three plants, a1-a3, b1-b3 and c1-c3 combined in one stacked column, from each source population (a-c), per census throughout the assessment period at site 2 of *L. polyphyllus*. The first two censuses were removed due to no fall.

At site 2, the fall commenced in the fourth census at 07.08 in source population a and c, and in the third census at 31.07 in source population b (Figure 15). The plants in source population a and b were smaller than the plants in c, explaining the considerable differences in fall, which peaked in all source populations in the fourth census at 07.08.

Source population a and c had an abrupt transition from fall of zero pods in the third census at 31.07 to the top peak in the next census at 07.08, similar to in source population a at site 1. The peaks occurred in all of the source populations one census after the pods had transitioned to ripe, which were mainly in the third census at 31.07 at site 2. The seed dispersal was in general complete in the tenth census at 25.09 as at site 2.

Site 3 (*B. orientalis*)

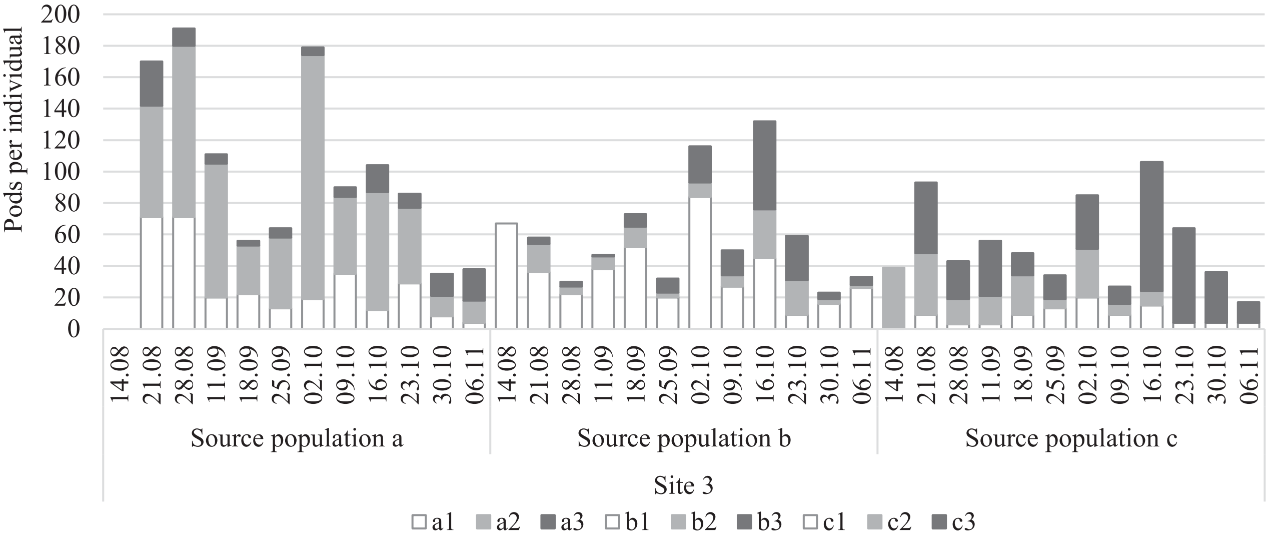

Figure 16: Fall of siliquae from the three plants a1-a3, b1-b3 and c1-c3 combined in one stacked column, from each source population (a-c), per census throughout the assessment period at site 3 of *B. orientalis*. The first four censuses were removed due to no fall.

At site 3 of *B. orientalis*, the dispersal of siliquae commenced in the sixth census at 21.08 in source population a, and one census earlier in source population b and c, in the fifth census at 14.08 (Figure 16).

Due to large individuals in source population a, there was on average more fall than in b and c. The fall peaked in the seventh census at 28.08 in source population a, and in the 13th census at 16.10 in source population b and c, considerably later than in a. The fall was distributed throughout the season, with significant increase in the 11th census at 02.10 and in the 13th census at 16.10 in all source populations. There was a rise in fall in the sixth census at 21.08, though it was less conspicuous in source population b (Figure 16).

The fall decreased gradually in the source populations in the three last censuses, and individual c1 and c2 in source population c had lost all siliquae in the 19th and last census at 06.11. Though there were individuals with a few siliquae left, the seed dispersal period was predominantly complete by the 16th census at 06.11 at site 3.

Site 4 (*B. orientalis*)

At site 4, the fall of siliquae begun in the fifth census at 14.08 in all source populations (Figure 17).

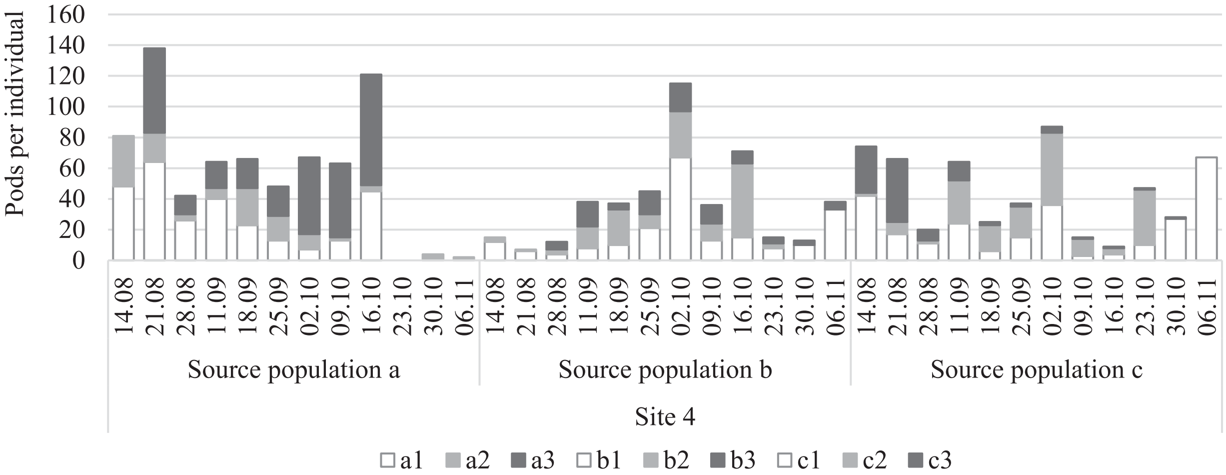

Figure 17: Fall of siliquae from the three subject plants a1-a3, b1-b3 and c1-c3 combined in one stacked column, from each source population (a-c), per census throughout the assessment period at site 4 of *B. orientalis*. The first four censuses were removed due to no fall.

The fall peaked in the sixth census at 21.08 in source population a, and in the 11th census at 02.10 in source population b and c. This was on average, one to two censuses earlier than in the source populations at site 3 (Figure 16). There was a sudden increase from fall of no siliquae in the fourth census at 07.08, to considerable fall in the fifth census at 14.08 and sixth census at 21.08 in source population a and c. In source population b however, there was little fall from the fifth census at 14.08 to the sixth census at 28.08 (Figure 17).

The dispersal of siliquae was generally distributed throughout the season. There were similar patterns regarding timing of when most of the fall occurred in the source populations, although a few deviations were observed. The peaks in fall were at site 4 generally in the fifth census at 14.08, sixth census at 21.08, 11th census at 02.10 and in the 13th census at 16.10. Source population b deviated with little fall in the fifth and sixth census, and c with little fall in the 13th census. Furthermore, there was an increase in fall in source population b and c in the 16th at 06.11. The plants a3 and c2 had lost all siliquae by the last census, whereas in source population b, no individual lost all siliquae. The seed dispersal was generally over by the 16th census at 06.11 at site 4.

3.3 Total mean seed production per source population

There were significant differences in number of fruits on the random versus the subjective individuals for both *L. polyphyllus* and *B. orientalis*. (Wilcoxon-Mann-Whitney-test; $p < 0.05$) (Figure 18). Due to this, the estimates of total mean seed production based on fruits counted on random individuals could be assumed to be statistically most correct, and counted fruits on the random and subjective individuals should not be combined in calculations of seed production. Nevertheless, the standard deviations were higher for the estimates of seed production based on the random than for the subjective individuals, and random and subjective individuals combined (Figure 19).

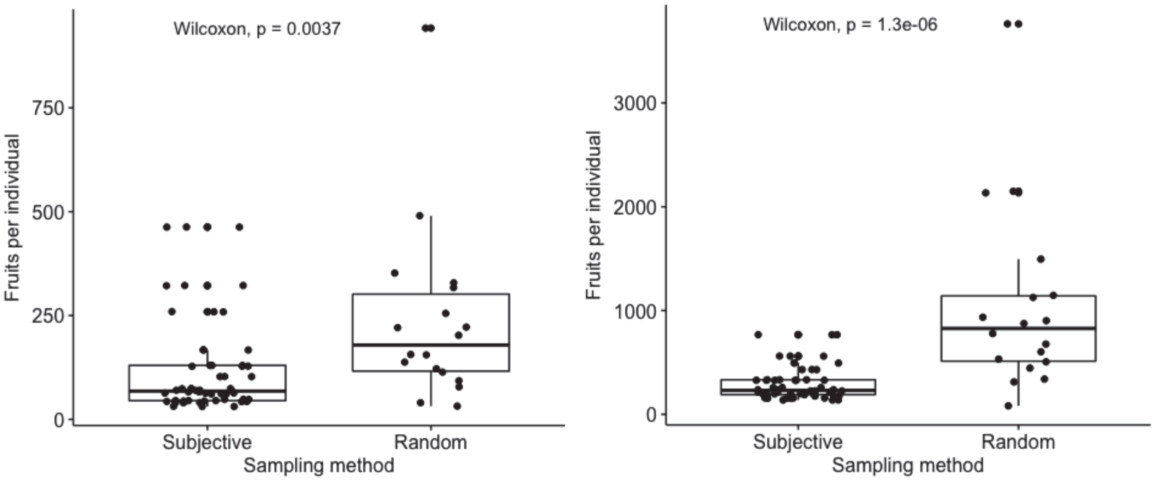

Figure 18: GG boxplot for the observations of fruits per plants of *L. polyphyllus* (left) and *B. orientalis* (right). The total count of fruits per individual are shown by the dot plot. There was a greater spread in number of fruits on the random individuals, than the subjective, for both species.

Furthermore, the standard deviation was on average lower, when the calculation of seed production per source population was based on estimates of seeds per fruit with observations from the specific source population, and not on all plausible observations of seeds per fruit collected for the species in total (Figure 19). To use estimates of seed per fruit with observations from the respective source population for calculation seed production per source population was also biologically correct (Ohlson, M. pers. comm. 2018).

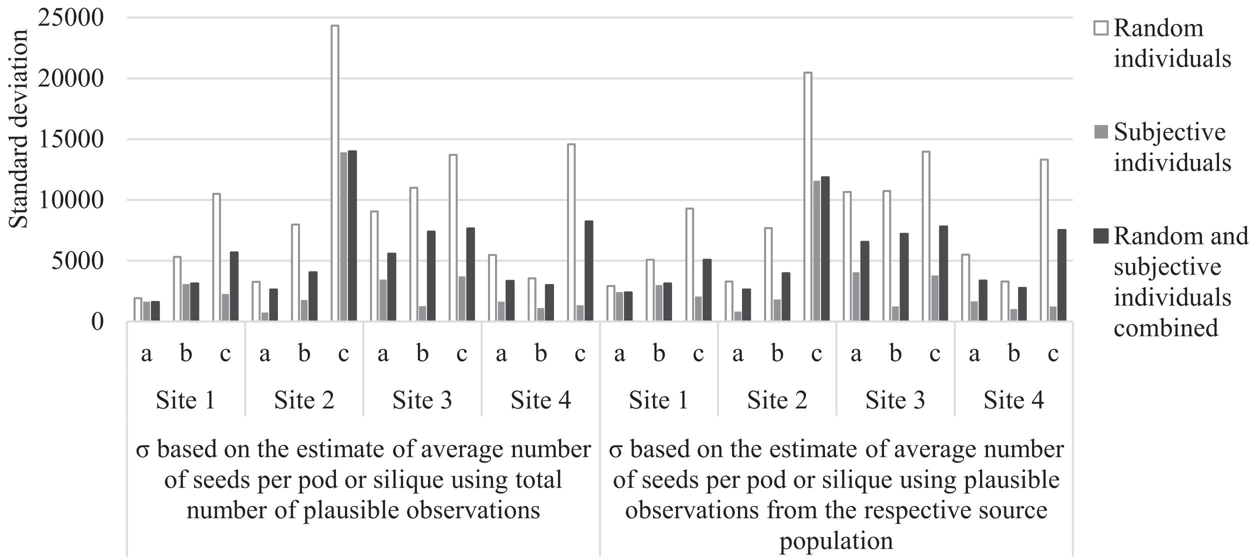

Figure 19: Standard deviations for the estimates of seed production per source population (a-c) for the different sites (1-4). The calculations were based on two estimates of average number of seeds per pod or silique (left and right), and the different estimates of fruit per individual, based on random, subjective and random and subjective individuals combined.

Figure 19 presents the standard deviations for the estimates of seed production. In general, the standard deviations were higher, when the estimates of fruits per individual were based on the random individuals, than when based on the subjective, or random and subjective individuals combined. However, due to the statistical significant difference in the number of fruits in the random versus the subjective individuals, the estimates of seed production were in conclusion, statistically and biologically most correct when based on estimates of number of fruits per individual with observations from random individuals, and on estimates of seeds per fruit with observations from the specific source population (Figure 20).

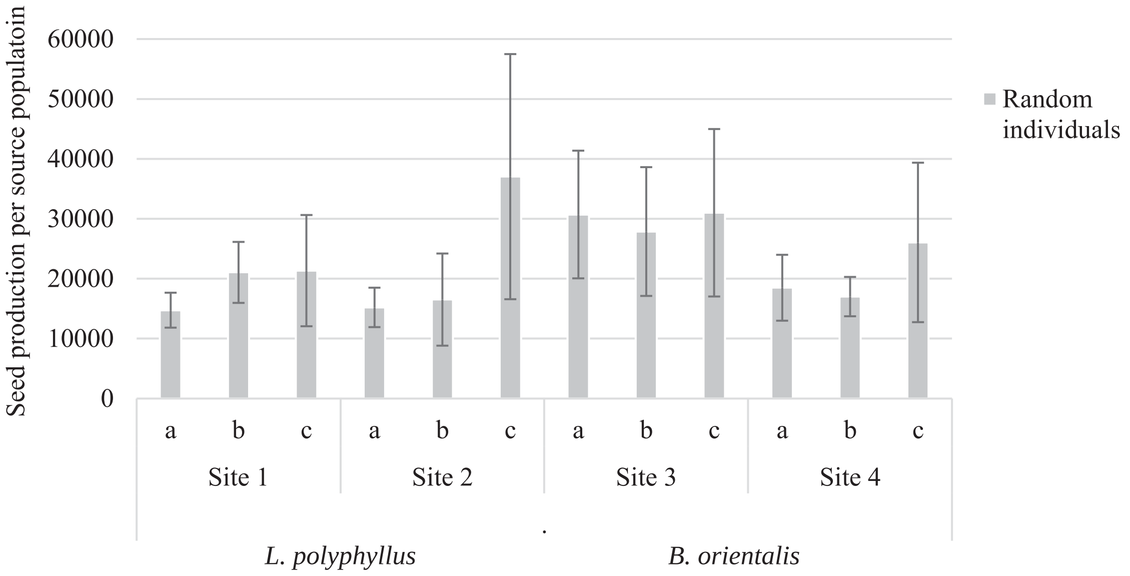

Figure 20: Estimate of total mean seed production for the source populations (a-c) per site (1-4) with standard deviation. Calculations were based on the random individuals, and the estimate of average number of seed per pod or silique using plausible observations from the respective source population.

The different estimates of seed production per source population and standard deviation were calculated to evaluate the quality of the estimates (Appendix 2 – 7).

1.4 Seed dispersal

For *L. polyphyllus*, a total of 26 seeds were caught in the north facing traps, and 42 seeds were caught in the south. *B. orientalis* had a lower number of caught seeds, only 8 and 21 in the north and south, respectively (Table 1). Even though there were more seeds caught in the south for both species, the trap direction was not statistically significant regarding seed dispersal within each target species (Wilcoxon-Mann-Whitney test; p = 0.6974 for *L. polyphyllus* and p = 0.6436 for *B. orientalis*.).

Though there was no significant difference between north and south regarding seed dispersal for the target species separately, there was a significant difference between the species' seed dispersal to the north (Wilcoxon-Mann-Whitney test; p = 0.0166), and no significant difference to the south (p = 0.1796). Based on this result, *B. orientalis* have significantly less seed dispersal to the north, with 8 seeds, compared to *L. polyphyllus*, with 26 seeds (Table 1). However, there were few observations, and the results may not be representative for the species.

Table 1: Average number of seeds caught per trap in the north and south direction for each species and site, with standard deviation and standard error. Total number of seeds caught in the traps are the seeds caught throughout the entire assessment period added together.

Cardinal direction, species and site	**Average number of seeds caught per trap**	**SD**	**Total number of seeds caught in the traps**
North			
Lupinus polyphyllus	1.1	± 1.4	26
Site 1	1.7	± 1.7	20
Site 2	0.5	± 0.7	6
Bunias orientalis	0.3	± 0.8	8
Site 3	0.3	± 0.9	4
Site 4	0.3	± 0.7	4
South			
Lupinus polyphyllus	1.8	± 4.5	42
Site 1	0.6	± 0.9	7
Site 2	2.9	± 6.2	35
Bunias orientalis	0.9	± 2.2	21
Site 3	1	± 1.8	12
Site 4	0.8	± 2.6	9

There was a significant difference in seed dispersal to the different trap distances for *L. polyphyllus* (Kruskal-Wallis test; $p = 0.02483$), and no significant difference between the trap distances for *B. orientalis* ($p = 0.2044$).

When the differences in seed dispersal between the trap distances were tested more thoroughly, there were no significant differences between the trap distances for *B. orientalis* (Dunn-test with Bonferroni correction; $p > 0.05$ for all 6 comparisons in total), or significant outliers. The predominance of seed dispersal landed in the seed traps at 0.5 and 1 meters distance, with a few deviations (Table 2). There were fewer seeds in the traps at 2 and 4 meters distance, compared to at the sites with *L. polyphyllus* (Table 2).

For *L. polyphyllus*, there were a significant differences between the traps at 0.5 and 2 meters (Dunn-test; $p = 0.0366$) and 0.5 and 4 meters (Dunn-test; $p = 0.0166$*). The difference was most prevalent between 0.5 and 4 meters.

The seed production in source population c, at site 2 of *L. polyphyllus*, was estimated to be 37036 (Appendix 3). Only 32 seeds in total were caught in the 8 traps around the respective source population, and had an outlier of 22 seeds caught in a trap at 4 meters distance in the south direction (Figure 21). The vast seed production per source population (Appendix 3), and on average few seeds caught in the traps in total (Table 2), occurred for all source populations at site 1-4. There were on average caught 1.5 seeds in the traps at the sites with *L. polyphyllus* and 0.8 seeds in the traps with *B. orientalis* (Table 2). This was few seeds, considering that the estimates of seed production varied from 14751 in source population a, at site 1, to 37036 at the most in source population c, at site 2 with *L. polyphyllus*. For *B. orientalis* the estimates of seed production ranged from 17017 in source population b at site 4, to 31010 in source population c, at site 3 (Appendix 3).

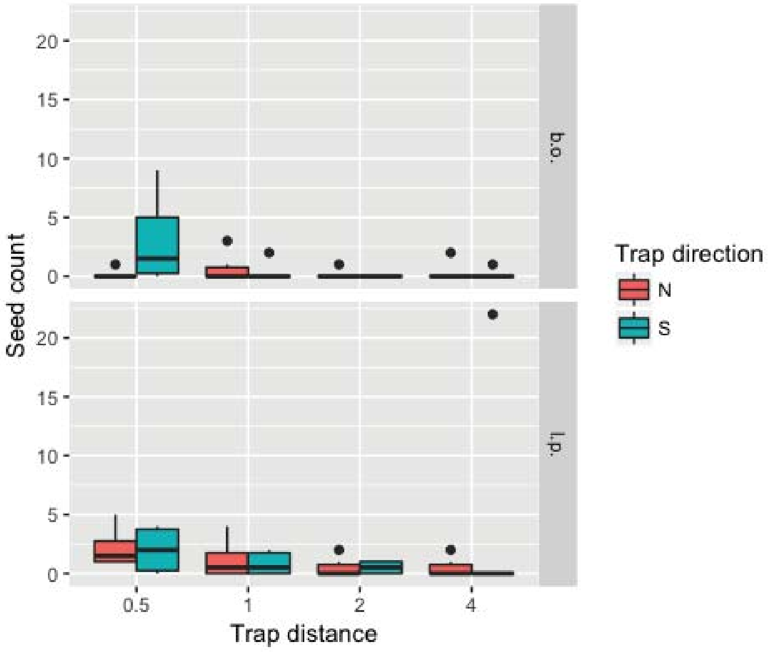

Figure 21: Boxplot over seed dispersal to seed traps at the different distances (0,5 – 4 meters) from the source populations for *B. orientalis* above, and *L. polyphyllus* under, showing median seed dispersal to the different trap distances and the variation, in addition to outliers.

After the final collection to empty the seed traps, there were in addition to the seeds from the target species, found numerous of seeds from other species, e.g. 241 seeds from *Circium* sp. in one seed trap at site 4 of *B. orientalis* (Appendix 11).

Table 2: Average number of seeds caught per trap per site, trap distance and per species for *L. polyphyllus* and *B. orientalis*, with standard deviation and standard error. Total number of seeds caught in the traps are the seeds caught throughout the entire assessment period added together.

Species, site and trap distance	**Average number of seeds caught per trap**	**SD**	**Total number of seeds caught in the traps**
Lupinus polyphyllus	1.5	± 3.4	73
Site 1	1.3	± 1.8	30
0.5	2.7	± 2.6	16
1	1.3	± 1.5	8
2	0.7	± 0.8	4
4	0.3	± 0.8	2
Site 2	1.8	± 4.5	43
0.5	2.3	± 1.9	14
1	0.7	± 1.0	4
2	0.3	± 0.5	2
4	3.8	± 8.9	23
Bunias orientalis	0.8	± 2.1	37
Site 3	0.9	± 2.0	22
0.5	2.5	± 3.4	15
1	1	± 1.5	6
2	0	± 0	0
4	0.2	± 0.4	1
Site 4	0.6	± 2.3	15
0.5	1.8	± 4.5	11
1	0.2	± 0.4	1
2	0.2	± 0.4	1
4	0.3	± 0.8	2

2. Discussion

4.1 Phenology

4.1.1 Ripening process

L. polyphyllus

There were principally, no evident differences in the ripening process between site 1 and 2 of *L. polyphyllus*. However, there were slight differences in the ripening process between the source populations within the sites. The ripening of pods were either expedited or delayed with approximately one to two censuses in certain source populations, probably correlated with variation in climate and habitat factors. The results for site 1 and 2 indicated that the ripening process was very susceptible to the amount of direct sun exposure and temperature (Khanduri et al., 2008).

In general, the transition from unripe to medium ripe pods occurred earlier in the source populations at site 2 (Figure 4 - 6) than at site 1 (Figure 1 - 3). The difference in ripening speed was may due to the smaller size of the individuals at site 2, and that site 1 was less sun exposed.

Site 1

At site 1, source population a received limited direct sun light due to the canopy of trees and being situated in immediate proximity to woods. Source population b was intermediately sun exposed, which presumably was the reason for an accelerated ripening process compared to in the less sun exposed source population a (Figure 1 & 2). Furthermore, source population c was the most sun exposed at site 1, and probably as a result had an earlier ripening process than in both a and b (Figure 3).

Site 2

Despite continuous sun exposure, source population b had the latest ripening process at site 2 (Figure 5), and was a deviation from the trend that the ripening process of the pods was very susceptible by the amount of sun exposure or shadow. Source population c was continuously sun exposed throughout the day, and presumably as a result, had the earliest transition from unripe to mainly medium ripe and ripe pods on the studied individuals of *L. polyphyllus*, in the second census at 24.07 (Figure 6). There was an accelerated ripening process in individual c1 and c3 compared to c2, maybe because the respective individuals were considerably smaller had fewer pods than c2 (Figure 6).

B. orientalis

The ripening process was similar for the siliquae in the plants at site 3 and 4 of *B. orientalis*. The proportion of siliquae in the different ripening categories varied to a small extent between the source populations in the specific censuses, which may was related to the variation in soil moisture, and amount of direct sun exposure.

Continuous shadow and proximity to a creek which provided moisture, could have been contributing factors in the swelling of siliquae and the delay in ripening process in source population a and c at site 3 (Figure 8 & 9). The siliquae from source population b remained small, and immediately turned yellow and brown, maybe due to the continuous sun exposure, and drier soil in the respective source population (Figure 7).

Individual c1 and c2 in source population c, which was less sun exposed, were the only individuals at site 3 that lost all siliquae (Figure 10). As sun exposure can lead to a faster ripening process, it was expected that fully sun exposed plants would lose all siliquae sooner than less sun exposed plants. However, in practice, partial or intermediate sun exposure caused a slow ripening process, which led to large and heavy siliquae, with maybe a higher probability of release. This could be an adaptive strategy of less sun exposed individuals of *B. orientalis*. Though the ripening of siliquae were slower, they would still be released by the end of the seed dispersal period due to being large and heavy. The plants may have morphologically or physiologically adapted to being situated in both less sun exposed and moist, or sun exposed and dry patches in the habitat (Bazzaz, 1991).

There was a quicker transition from unripe to ripe pods, and more individuals that lost all siliquae at site 4 compared to the individuals at site 3 (Figure 8 - 10 & 11 - 13), likely a result of that the source populations in general were more directly sun exposed, than at site 3.

Site 3

In addition to trees, the vegetation around source population a was high, resulting in shadow and intermediate sun exposure. This could be why the respective source population had a rather large proportion of unripe and medium ripe siliquae in the fifth census at 14.08 (Figure 8), compared to source population b and c, where the plants had more ripe siliquae (Figure 9 & 10).

Source population b was continuously sun exposed. Furthermore, it was situated uphill and away from a creek at the site, and therefore the soil was potentially dry due to this. The combination of habitat and climate factors likely contributed to a faster ripening process (Figure 9), than in source population a and c (Figure 8 & 10). Source population c had the slowest ripening process at site 3 (Figure 10), which probably was due the surrounding vegetation was a tall, dense monoculture of *Chamerion angustifolium*, which in addition to the nearby canopy of *Alnus* sp., provided shadow.

Site 4

Source population b was the least sun exposed at site 4. This was probably the reason for an on average larger proportion of medium ripe siliquae in the plants in the fifth census at 14.08, compared to in source population a and c, where there were more ripe siliquae in the same census (Figure 11 - 13). Furthermore, that source population b was the only at site 4 where all plants still had siliquae left in the 16th census at 06.11 (Figure).

The accelerated ripening process in source population c, compared to in source population a and b, and loss of all siliquae in individual c2 (Figure 13), was presumably due to the fact that source population c was the most sun exposed at site 4. The surrounding vegetation consisted mainly of low graminoids which enabled more sun exposure of the taller individuals of *B. orientalis* inside the source population.

4.1.2 Fruit ripening and seed production

L. polyphyllus

Weather factors i.e. amount of direct sun exposure probably affected the ripening process and thereby, when fall of pods commenced. In general, the fall peaked in the fourth census at 07.08 at site 1 and 2 (Figure 14 & 15), likely as a result of that the pods were predominantly ripe in the third census at 31.07 (Figure 1 - 6), and increased precipitation in the same time period.

Site 1 and 2 of *L. polyphyllus* were in proximity, and there was at site 1, a similar increase in fall from the third census at 31.07 to the fifth census at 14.08 (Figure 14 & 15), which further indicated that changes in weather factors affected the distribution of when most of the fall occurred in the season.

Site 1 (*L. polyphyllus*)

In source population b, the fall peaked three censuses after the pods had transitioned to ripe, in contrast to in source population a and c where it peaked in the fourth census at 07.08. Source population a and b were less sun exposed than c. Less extensive sun exposure may have caused seed dispersal and fall of pods in source population b to be more distributed throughout the season, instead of an early peak, as in a and c (Figure 14).

Site 2 (*L. polyphyllus*)

A correlation between precipitation and fall of the pods was apparent and assumable at site 2 of *L. polyphyllus* (Friedman & Stein, 1980). The mean middle temperature and mean accumulated precipitation in mm were 16.76 °C and 1.11 mm in the period from the second census at 24.07 to the third census at 31.07, while from the third census to the fourth census at 07.08 the parameters were 15.09 °C and 4.21 mm in Ås. Furthermore, from the fourth census at 07.08 to the fifth at 14.08, they were 15,14 °C and 8,63 mm (Norwegian Meteorological Institute, 2018).

The differences between the mean middle temperatures were minor compared to the differences in mean accumulated precipitation, which was more than doubled between the three censuses. The fall of the pods and precipitation increased simultaneously from the third census at 31.07 to the fourth census at 07.08 in all of the source populations (Figure 15). This was most apparent in the largest individual c2, in source population c, where the trend with high precipitation accompanied with considerable fall of pods also continued to the next census at 14.08 (Figure 15).

The fall was generally at its lowest during the mid-part of the assessment period (Figure 15), in contrast to at site 1, where the fall of pods throughout the assessment period was similar to negative binomial distribution (Figure 14). The differences among the sites were maybe due to the fact that the individuals in source population a and b at site 2 were smaller, than the individuals at site 1. There were probably proportionally less fall of pods from the smaller plants compared to from the larger, and the seed dispersal occurred to a greater extent directly from the pods still attached to the small individuals. The seed dispersal was, therefore, less represented for the smaller plants in source population a and b at site 2 (Figure 15), than for the larger individuals at site 1 (Figure 14), which lost more pods. Though there was no fall of pods in the seventh census at 28.08 in source population a, and in the fifth census at 14.08 and sixth census at 21.08 in source population b at site 2 (Figure 15), the seed dispersal was still ongoing from the pods attached to the stems.

B. orientalis

There was a similar distribution of when the predominance of fall occurred in the source populations at site 3 and 4 (Figure 16 & 17), probably due to changes in certain weather factors, as the sites were in close proximity. A similar amount of sun exposure and temperature caused the siliquae to ripen in approximately the same censuses. Furthermore, precipitation and wind affected the plants mechanically, which may have led to the increase in fall in certain censuses, especially late in the assessment period, when the siliquae were already ripe. That the fall increased or peaked, in the sixth census at 21.08 in most source populations, could be related to that most siliquae had transitioned to ripe in the sixth census at 21.08.

Site 3 (*B. orientalis*)

The dispersal of siliquae commenced one census earlier in source population b, in the fifth census at 14.08, may due to more ripe siliquae in the plants, than in source population a, where the plants had more unripe and medium ripe siliquae in the same census (Figure 8 & 9 & Figure 16). In source population c, the fall of siliquae occurred one census earlier than in a, despite being the least sun exposed at site 3. It could have been due to enlarged, heavier siliquae, which thereby, probably were easier released (Figure 7).

In the study of ripening process, all siliquae were considered ripe from the sixth census at 21.08 in source populations a - c (Figure 8 - 10), which coincided with the rise in fall in the source populations at site 3, in the same census, except in source population b (Figure 16). The fact that the siliquae were ripe from the sixth census at 21.08, was may also the reason for the peak in fall in the seventh census at 28.08 in source population a (Figure 16). The sudden increase in fall in the fifth and sixth census, from fall of zero siliquae in the fourth census at 07.08 in all plants, and the fluctuations in fall throughout the season were also probably, due to changes in precipitation, wind and temperature.

Site 4 (*B. orientalis*)

Expedited commenced fall of siliquae and earlier peaks in source population a and c at site 4, than at site 3, could be explained by that site 4 was situated in a south faced hillside, and was more sun exposed than site 3 (Figure 17).

The increase from fall of no siliquae in the fourth census at 07.08, to considerable fall in the fifth census at 14.08 and sixth census at 21.08 in source population a and c (Figure 17), concurred with the transition to a larger proportion of ripe siliquae in the fifth census (Figure 11 & 13). In source population b, however, the least sun exposed at site 4, there was a greater proportion of medium ripe siliquae than in a and c in the fifth census (Figure 12), which was may why there were little fall from the fifth census at 14.08 to the sixth census at 28.08 (Figure 17). The increase in fall in source population b and c in the 16th census at 06.11, was maybe due to snow precipitation and decrease in temperature (Matlack, 1989) (Figure 17). Changes in weather factors most likely caused the similarities of when fall occurred in source population a – c at site 4.

4.2 Seed dispersal

Though the trap direction was not statistically significant regarding seed dispersal within each target species (Wilcoxon-Mann-Whitney test; p = 0.6974 for *L. polyphyllus* and p = 0.6436 for *B. orientalis*.), there were more seeds caught in the south direction for both target species (Table 1). It could be due to that there was lower vegetation around the seed traps in the south, which increased the probability of seeds landing in the traps.

Furthermore, it would have enabled sun exposure of the individuals of *B. orientalis* in the south of the source populations. The sun exposed siliquae ripened faster and remained small in size (Figure 7). In contrast, less sun exposed siliquae grew larger and may fell, to a greater extent directly to the ground, rather than being dispersed by wind outwards to the seed traps, than the smaller siliquae. This may explain why more than doubled amount of seeds were caught for *B. orientalis* in the south (21 seeds), than in the north (8 seeds), in the traps (Table 1).

It could also be why there was a significant difference between the species' seed dispersal to the north (Wilcoxon-Mann-Whitney test; p = 0.0166), and no significant difference to the south (Wilcoxon-Mann-Whitney test; p = 0.1796). Less seeds from *B. orientalis* landed in the north facing traps, perhaps due to the specific way of ripening (Figure 7). There is consequently, proportionally less difference between the number of seeds caught in total in the north, versus south facing traps for *L. polyphyllus*, than for *B. orientalis* (Table 1). When comparing 8 and 26 seeds caught in the north facing traps, for *B. orientalis* and *L. polyphyllus* respectively, there is a significant difference. Sun exposure of the individuals was possibly of less importance for the seed dispersal from north facing individuals of *L. polyphyllus*, than of *B. orientalis*.

The significant difference in seed dispersal to the different trap distances for *L. polyphyllus* (Kruskal-Wallis test; p = 0.02483), was maybe due the relatively large and heavy seeds. This was further indicated when there for *L. polyphyllus* was found a significant difference between the traps at 0.5 and 2 meters (Dunn-test; p = 0.0366), and 0.5 and 4 meters (Dunn-test; p = 0.0166*). The seeds of *L. polyphyllus* probably mostly fell straight downward, and were less affected by wind to be dispersed outwards to the traps at farther distance, resulting in a significant difference between the traps at 0.5 meters and 2 meters (Table 2).

Furthermore, at site 2, southwards of source population c, there was an outlier of 22 seeds caught in the trap at 4 meters distance (Figure 21) The outlier maybe caused that the significant difference become most prevalent between 0.5 and 4 meters. In the same trap, two seeds of *Crataegus intricata* were also found (Appendix 9), which were approximately the same size as the seeds of *L. polyphyllus*. Where the respective seed traps were situated, a large colony of *Formicidae* sp. was observed, which indicated that secondary seed dispersal, here zoochory, was the reason for the outlier (Culver & Beattie, 1978; Heinken et al., 2007). Further substantiating this, was the observation of 8 insect heads in a seed trap at site 1 of *L. polyphyllus*, indicating insect activities in, and around the seed traps (Seckbach & Dubinsky, 2010). Vertebrate-mediated dispersal by rodents of the seeds of *L. polyphyllus* was also likely, as there were observations of rats and nests at site 1 and 2 (Briggs et al., 2009; Forget & Milleron, 1991; Xiao et al., 2005)

For *B. orientalis*, there was no significant difference in seed dispersal to the different trap distances (Kruskal-Wallis test; $p = 0.2044$). Furthermore, no significant differences between the trap distances, or significant outliers were observed (Dunn-test with Bonferroni correction; $p > 0.05$ for all 6 comparisons in total). Despite the fact that there were no observations of insect activity or significant difference between the trap distances at the sites of *B. oritentalis*, zoochory was probably important for the movement of seeds for both target species, but to a greater extent for *L. polyphyllus*. The siliquae were in about the same size and weight as the seeds of *L. polyphyllus*, and the few siliquae in the traps at 2 and 4 meters distance (Table 2), could have been transported by insects or rodents. The siliquae were may also easier dispersed outwards by wind than the seeds of *L. polyphyllus*.

The vast seed production per source population (Appendix 3), and proportionally few seeds caught in the traps in total (Table 2), further indicated that zoochory was of importance for the target species. The seeds and siliquae of *B. orientalis* and *L. polyphyllus* probably fell straight downward, and were to a less extent affected by wind. This resulted in that few seeds were caught in the seed traps, even though there were extensive seed production in all of the source populations.

In addition to the seeds from the target species, numerous seeds from other species were found in the seed traps after the final collection (Appendix 8 – 11). This also indicated that *B.*

orientalis and *L. polyphyllus* were especially dependent upon zoochory, although some of the individuals of the species outside the source populations were in closer proximity to the seed traps. The seeds from individuals outside the source populations were may dispersed easier due to being lighter, and having morphology evolved for anemochory e.g *Alnus* sp. (Flint, 2015) and *Betula pendula* (Picard & Baltzinger, 2012), which were found in great numbers in several seed traps (Appendix 8 – 11). This may reason why there were more seeds from species other than *B. orientalis* and *L. polyphyllus* in the seed traps, whose seeds and siliquae rather to fell directly to the ground, were less affected by wind, and were probably, mainly dispersed by insects or rodents.

3. Conclusion

The results indicated that the phenology of the target species was very reciprocal to climate and habitat factors. Particularly, the amount of sun exposure affected the ripening of the pods and the siliquae, and thereby, in addition to precipitation, when the predominance of seed dispersal occurred throughout the season for the target species. The timing of the life cycle events varies annually, and will be probably expedited with future climate changes (Cleland et al., 2007; Post & Stenseth, 1999). This substantiate why it's challenging eradicate the species, as the time of when the species should be monitored, is important. The results from the phenology study provide approximate estimates of when the life cycle events can be expected to occur for populations of the target species in SE Norway.

Flowering at the sites of *B. orientalis* ended circa at 15.07, and the species should be managed and controlled (cut or eradicated) before this. Furthermore, preferably when the plants are on average 26 cm, with visible inflorescence and elongating, to increase the probability of eradication. This is when the compensation point is most likely to occur (Oliver, 2012). To control after inflorescence, when ripening of siliquae have progressed, from 15.07 to 14.08, is not optimal. Dispersal of siliquae commenced around 14.08.

To hinder dispersal of *L. polyphyllus* by limiting seed production, it is best to cut during flowering. However, not too early during the flowering because of the higher probability of that resprouted leaf stalks would produce new flowers and fruits (Brobäck, 2015). Based on this study, cutting should therefore, occur before 15.07, which was when the flowering ended at the sites of *L. polyphyllus*. It is not expedient to monitor from 15.07 to 31.07, as the transition from unripe to ripe siliquae had progressed, and the risk of that the plants are able to disperse is higher. Seed dispersal commenced approximately at 31.07. To get more information on the timing of *L. polyphyllus* cutting, and thus to optimize the chances of roots dying back and hinder vegetative propagation with disjointed rhizomes, a study of when the compensation point for the species occur, is needed.

Even though the target species reproduce primarily by seed dispersal, the dispersal ability of the species were apparently not very efficient. Few were were caught, despite extensive seed production in all source populations (Appendix 3). The seeds predominantly landed in the traps at 0,5 and 1 meters distance. The occurrence of insect and rodent activity in and around the traps at the sites of *L. polyphyllus*, indicated that dispersal was dependent upon zoochory by both invertebrates and vertebrates. Furthermore, the vast amount of seeds from other species in the traps at all sites, compared to from the target species (Appendix 8 – 11), also indicated that transport of seeds probably occurred outside the traps by zoochory.

The study substantiate why populations of *B. orientalis* and *L. polyphyllus* often are found along anthropogenic structures like railways and road sides. The target species reproduce primarily by seeds, but the dispersal ability was seemingly not very efficient. The progressive spread and successful reproduction are probably highly effectuated by slipstreams from e.g. vehicles or trains, and germplasm being transported by vehicles or humans (Zwaenepoel et al., 2006). *L. polyphyllus* and *B. orientalis* would not have been so effectively dispersed, established and manage to pose a threat to endemic species, if it was not for human intervention (Nathan et al., 2008), and is otherwise dependent upon zoochory for dispersal of seeds.

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5. Appendix

Appendix 1: Test results from R.

Wilcoxon-Mann-Whitney - Significant difference in fruits per individual between the random and subjective individuals:

L. polyphyllus:

```
> Utest.Lupin

     Wilcoxon rank sum test with continuity correction


data:  fruits.pr.indv by rndm_sbj
W = 709.5, p-value = 0.00371
alternative hypothesis: true location shift is not equal to 0
```

B. orientalis:

```
> Utest.Bunias

     Wilcoxon rank sum test with continuity correction


data:  fruits.pr.indv by rndm_sbj
W = 858, p-value = 1.331e-06
alternative hypothesis: true location shift is not equal to 0
```

Wilcoxon-Mann-Whitney – Difference between cardinal directions per species**:**

L. polyphyllus:

```
# Wilcoxon rank sum test with continuity correction
#
# data:  count.trap.tot by trap_direction
# W = 306, p-value = 0.6974
# alternative hypothesis: true location shift is not equal to
0
```

B. orientalis:

```
# Wilcoxon rank sum test with continuity correction
#
```

```
# data:  count.trap.tot by trap_direction
# W = 271, p-value = 0.6436
# alternative hypothesis: true location shift is not equal to
0
```

Wilcoxon-Mann-Whitney - Difference between species per trap direction:

North:

```
# Wilcoxon rank sum test with continuity correction
#
# data:  count.trap.tot by species
# W = 187, p-value = 0.0166
# alternative hypothesis: true location shift is not equal to
0
```

South:

```
# Wilcoxon rank sum test with continuity correction
#
# data:  count.trap.tot by species
# W = 232, p-value = 0.1796
# alternative hypothesis: true location shift is not equal to
0
```

Kruskal-Wallis - Difference in seed dispersal to the different seed trap distances:

L. polyphyllus:

```
# Kruskal-Wallis rank sum test
#
# data:  count.trap.tot by trap_dist
# Kruskal-Wallis chi-squared = 9.3638, df = 3, p-value =
0.02483
```

B. orientalis:

```
# Kruskal-Wallis rank sum test
#
# data:  count.trap.tot by trap_dist
# Kruskal-Wallis chi-squared = 4.5896, df = 3, p-value =
0.2044
```

Dunn-test - species-specific differences in seed dispersal distances per species:

B. orientalis:

```
> dunn.test(bo_data$count.trap.tot, bo_data$trap_dist, method
= "bonferroni")
```

```
  Kruskal-Wallis rank sum test

data: x and group
Kruskal-Wallis chi-squared = 4.5896, df = 3, p-value = 0.2


                           Comparison of x by group
                                 (Bonferroni)
Col Mean-|
Row Mean |        0.5          1          2
---------+---------------------------------
       1 |   1.011140
         |     0.9358
         |
       2 |   2.042107   1.030967
         |     0.1234     0.9077
         |
       4 |   1.546450   0.535309  -0.495657
         |     0.3660     1.0000     1.0000

alpha = 0.05
Reject Ho if p <= alpha/2
```

L. polyphyllus:

```
> dunn.test(lp_data$count.trap.tot, lp_data$trap_dist, method
= "bonferroni")
  Kruskal-Wallis rank sum test

data: x and group
Kruskal-Wallis chi-squared = 9.3638, df = 3, p-value = 0.02


                           Comparison of x by group
                                 (Bonferroni)
Col Mean-|
Row Mean |        0.5          1          2
---------+---------------------------------
       1 |   1.728401
         |     0.2517
         |
       2 |   2.506182   0.777780
         |     0.0366     1.0000
         |
       4 |   2.773298   1.044897   0.267116
         |    0.0166*     0.8882     1.0000

alpha = 0.05
Reject Ho if p <= alpha/2
```

Appendix 2: Estimates of total mean seed production based on random individuals per source population, and the estimate of average seeds per fruits based on all observations per species, with standard deviation.

Site	Species	Source population	Estimate of total mean seed production	SD
1	*L. polyphyllus*	A	9905	1933
1		B	22956	5324
1		C	24426	10488
2		A	16021	3250
2		B	17396	7967
2		C	45158	24339
3	*B. orientalis*	A	26173	9050
3		B	28615	10998
3		C	30477	13699
4		A	18446	5461
4		B	18553	3555
4		C	28588	14578

Appendix 3: Estimates of total mean seed production based on random individuals per source population, and the estimate of average seeds per fruits based on observations of fruits for the respective source population, with standard deviation.

Site	Species	Source population	Estimate of total mean seed production	SD
1	*L. polyphyllus*	A	14751	2915
1		B	21056	5089
1		C	21351	9280
2		A	15214	3290
2		B	16520	7689
2		C	37036	20455
3	*B. orientalis*	A	30715	10655
3		B	27875	10745
3		C	31010	13974
4		A	18495	5500
4		B	17017	3280
4		C	26058	13305

Appendix 4: Estimates of total mean seed production based on the subjective chosen individuals per source population, and the estimate of average seeds per fruits based on all observations per species, with standard deviation.

Site	Species	Source population	Estimate of total mean seed production	SD
1	*L. polyphyllus*	A	4922	1620
1		B	16687	3078
1		C	11024	2253
2		A	6425	729
2		B	9788	1752
2		C	17541	13903
3	*B. orientalis*	A	10548	3443
3		B	4117	1268
3		C	11306	3706
4		A	8843	1637
4		B	7436	1097
4		C	6249	1350

Appendix 5: Estimates of total mean seed production based on the subjective chosen individuals per source population, and the estimate of average seeds per fruits based on observations of fruits for the respective source population, with standard deviation.

Site	Species	Source population	Estimate of total mean seed production	SD
1	*L. polyphyllus*	A	7329	2423
1		B	15306	3006
1		C	9636	2062
2		A	6101	826
2		B	9295	1810
2		C	14387	11568
3	*B. orientalis*	A	12379	4055
3		B	4010	1240
3		C	11504	3788
4		A	8866	1658
4		B	6820	1017
4		C	5696	1238

Appendix 6: Estimates of total mean seed production based on the random and subjective chosen individuals combined per source population, and the estimate of average seeds per fruits based on all observations per species, with standard deviation.

Site	Species	Source population	Estimate of total mean seed production	SD
1	*L. polyphyllus*	A	7413	1599
1		B	19821	3139
1		C	17725	5679
2		A	11223	2631
2		B	13592	4044
2		C	31350	14002
3	*B. orientalis*	A	18361	5567
3		B	16366	7385
3		C	20892	7661
4		A	13644	3336
4		B	12995	2994
4		C	17418	8237

Appendix 7: Estimates of total mean seed production based on the random and subjective chosen individuals combined per source population, and the estimate of average seeds per fruits based on observations of fruits for the respective source population, with standard deviation.

Site	Species	Source population	Estimate of total mean seed production	Standard deviation
1	*L. polyphyllus*	A	11040	2407
1		B	18181	3128
1		C	15494	5065
2		A	10658	2625
2		B	12907	3972
2		C	25711	11866
3	*B. orientalis*	A	21547	6559
3		B	15943	7210
3		C	21257	7823
4		A	13680	3366
4		B	11918	2758
4		C	15877	7519

Appendix 8-11: Total number of seeds from the target species caught in the seed traps the whole assessment period 15.07.18 – 18.11.17. Furthermore, seeds > 250 µm from other species caught in the time period 25.09.17 – 18.11.17, when the seed traps remained in the field without weekly emptying, were identified and noted for the respective site (1-4), source population (a-c), cardinal direction (N-S) and trap distance (0,5-4 meter).

Appendix 8: N: North, S: South. Species specification: *L. p.*: *Lupinus polyphyllus*, *A. n.*: *Anthriscus sylvestris*, *A. v.*: *Artemisia vulgaris*, *B. p.*: *Betula pendula*, *C.* sp: *Cirsium* sp., *D.g.*: *Dactylis glomerata*, *E.* sp.: *Elymus* sp., *G.* sp.: *Galeopsis* sp., *P.m.*: *Plantago major*, *R.l.*: *Rumex longifolius*, *R.r*: *Ranunculus repens*, *R.* sp.: *Ranunculus* sp., *T.* sp.: *Trifolium* sp., *T. i.*: *Tripleurospermum inodorum*, *U.* sp.: *Urtica* sp.

Site 1	**Source population a**								**Source population b**								**Source population c**							
Trap distanc	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S
Cardin al	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4
Specie																								
L. p.	1	1		2					3	4	2		1		1		5	2			3	1	1	
A. n.																	19	12	19	12				
A. v.	<20	<20	<20	<20	3	5			<20	<20	<20	15	<20	12	5	5	<20	14	10	10	<20	<20	<20	<20
B. p.	16	6	17	3	38	12	47	14	12	10	9	8	15	7	22	20	4	10	13		23	17	18	27
C. sp.					3	1			3	1	12		2		3			1		1		1		
D. g.					7	2	4		2				7	5	2		11	4		2	1			2
E. sp.	1					4	1				1	1	2			9				4				
G. sp.						2														4			1	
P. m.				4	1																			
R. l.	18	1	3	13	18	35	11		5	1	27	10	2	1		1				18	1	1		1
R. r.						4					3							2						
R. sp.	1		2				1																	
T. sp.	3	12	30	21		1					1	6	7	7	9						1		21	
T. i.												<100												
U. sp.					1										1						4	3		1
Unidentified		6			1		2	11								2			2			2		

Appendix 9: N: North, S: South. Species specification: *L. p.*: *Lupinus polyphyllus*, *A. v.*: *Artemisia vulgaris*, *B. p.*: *Betula pendula*, *C. j.*: *Centaurea jacea*, *C.* sp.: *Cirsium* sp., *C. i.*: *Crataegus intricata*, *E.* sp.: *Epilobium* sp., *G.* sp: *Galeopsis* sp., *G. v.*: *Gallium vernum*, *G. u.*: *Geum urbanum*, *L. v.*: *Leucanthemum vulgare*, *U. u.*: *Urtica urens*, *P. p.*: *Poa palustris.*

Site 2	**Source population a**								**Source population b**								**Source population c**							
Trap distan	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S
Cardinal	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4
Species																								
L. p.	1								1			1	4	2			2		1		4	2	1	22
A. v.		3				1				<20	<10	<10			1									2
B. p.	2	1			1					3	3		1	1	2		1	8	1	3	10	15	5	8
C. j.																							1	
C. sp.								16								4		1					1	1
C. i.																	1							2
E. sp.			1																					
G. sp.				1					18	14	21	16	18	7	17	7							1	
G. v.																					4			
G. u.																	1						1	
L. v.																	2	1				1		
U. u.			1										22	3		7								
P. p.															1									
Unidentified																		1						

Appendix 10: N: North, S: South. Species specification: *B. o.*: *Bunias orientalis*, *A. p.*: *Acer platanoides*, *A.* sp.: *Alnus* sp., *A. s.*: *Anthriscus sylvestris*, *A. t.*: *Arctium tomentosum*, *B. p.*: *Betula pendula*, *C. a.*: *Chamerion angustifolium*, *C.* sp: *Cirsium* sp., *G.* sp.: *Galeopsis* sp., *G.* sp.: *Galium* sp., *R. i.*: *Rubus idaeus*, *R. l.*: *Rumex longifolius*, *U.* sp.: *Urtica* sp.

Site 3	**Source population a**								**Source population b**								**Source population c**							
Trap distanc	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S
Cardinal	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4
Species																								
B. o.					6	2		1		3			2				1				1			
A. p.						1																		
A. sp.	6	4	4	4	8	9	11	5	5	3	2	8	2	1	4	4	17	8	15	25	12	6	9	3
A. s.	5	44	2	7	4	11	4	12	27	25	29	16	27	28	18	3	53	26	5	10	14	1		
A. t.																		34	1	7				
B. p.	1	4	3	4	1	4	2	1	17	10	7	3	19	28	18	6	13	9	15	7	8	4	9	2
C. a.									2								10		6	7	4			
C. sp.					11	58	1		1		1			2	1	1								
G. sp.				3																				
G. sp.										2	2						1							
R. i.																					1			
R. l.								1	12	4	7		2		1						1			
U. sp.		11	31	8	4	4		2	28	11	32	15		1			38	64	140	44	9	15	10	21
Unidentified											2	1												

Appendix 11: N: North, S: South. Species specification: *B. o.*: *Bunias orientalis*, *A. p.*: *Acer pseudoplatanus*, *A.* sp.: *Alnus* sp., *A.* s.: *Anthriscus sylvestris*, *A. t.*: *Arctium tomentosum*, *B. p.*: *Betula pendula*, *C. a.*: *Chamerion angustifolium*, *C.* sp.: *Cirsium* sp., *D. g.*: *Dactylis glomerata*, *G.* sp.: *Galium* sp., *G. v.*: *Galium vernum*, *P.* sp.: *Persicaria* sp., *R. i.*: *Rubus idaeus*, *R. l.*: *Rumex longifolius*, *S. l.*: *Solidago canadiensis*, *U.* sp.: *Urtica* sp.

Site 4	**Source population a**								**Source population b**								**Source population c**							
Trap distanc	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S	N	N	N	N	S	S	S	S
Cardinal	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4	0,5	1	2	4
Species																								
B. o.				2						1	1		9											
A. p.															1									
A. sp.	10	4	5	17			8		5	13	8	12	7	6	3	2	7	12	8	4	8	8	9	2
A. s.	9	7	1	1	3	9	5	4		1	1		1	2	15	9	1	1	2		1		1	4
A. t.	1	4	13		5					4				3	27	5			2					
B. p.	26	26	10	6	4	1	6	1	9	22	9	10	16	26	21	12	19	31	33	31	18	18	8	6
C. a.	3						1		1															
C. sp.					1							1		1		1		1		1			241	10
D. g.													3		1								5	
G. sp.		1	1		5		1			1				10	6		48	6	12	1	46	10	3	
G. v.						3																		
P. sp.										1						5								
R. i.	1	1																						
R. l.	11	7	43	1	1	1	1		10	4	1		1	1	9	1		2					2	4
S. l.		2																						
U. sp.	39	74	124	159	99	13	34	73	3	3	7	8	12	20	6	2		1						
Unidentified			2																					

Appendix 12: Species identified during field work after removal of the target species at the different sites (1-4). They were found either inside (I), in the area in the north (N) or south (S) of the source populations (a-c). Approximate coverage of the respective species was estimated (%).

Species	**Site 1 (*L. polyphyllus*)**	**Site 2 (*L. polyphyllus*)**	**Site 3 (*B. orientalis*)**	**Site 4 (*B. orientalis*)**
Achiella millefolium	b: I, N, S	c: I (5%), N, S (5%)		c: S
Aegopodim podagraria	b: N, S c: N	c: S	a: I (15%), N, S (10%)	c: N (5%), S
Alchemilla sp.	a: S			c: S
Alchiella millefolium				
Anthriscus sylvestris	a: I, S b: N, S c: I (7%), N (5%)	a: N, S c: N	a: I, N (5-10%), S (10%) b: I (7%), N (7%), S (10%) c: I (3%), N (10%),S (5%)	a: I, N, S (5%) b: S c: I, N, S
Arctium tomentosum (SE)			a: N c: N (20%)	a: I, N (10%), S b: I (5%), N (5%), S (10%) c: N, S
Artemisia vulgaris	a: I, N (30%), S (15%) b: interior (10%), north (20%) south (20%) c: interior (7%), north, south (5%)	a: interior (10%), north, south (5%) b: interior, north (15%)	a: north	a: north, south c: interior (5%), north, south (5%)
Avenella flexuosa	a: north (5%) b: interior, south	a: interior (30%), south (20%) b: interior (10%), north (20%), south (20%) c: interior (bunndekker 30-40%), north (20%), south (20-30%)	a: interior b: interior (10%), north	
Betula pendula		c: north		
Bunias orientalis (SE)			a: north (40% leaves), south (30%) b: north (15%), south (5%) c: south (5%)	a: north (20%), south (20%) b: north (5%), south (10%) c: north (5%), south
Calystegia sepium spectabilis (SE)	a: north b: south			b: south
Carduus crispus multiflorus	a: north			
Centurea jacea		c: north		b: south c: interior, north
Centaurea sp.	b: south			

Chamerion angustifolium	c: interior		b: south c: north (20%), south (80%)	a: interior (40%) north (20%), south (20%) b: interior (30%) north (90%), south (10%) c: north
Cirsium arvense	a: interior, south b: interior, north (5%) c: interior (5%) north, south (5%)	a: interior, north, south b: interior (5%), north, south (20%) c: north, south	a: interior, north, south (10%) b: interior, north, south	a: interior, north, south b: north, south c: interior (25%), north, south (20%)
Corylus avellana		c: north		
Crataegus intricata		c: interior, north, south		
Dactylis glomerata	a, interior, south (15%) b: interior, north (10%) south (20%) c: interior (10%) north (60%)	a: north, south (5%)	b: interior	c: north (10%), south
Deschampsia cespitosa cespitosa	b: south (dominating)			
Dryopteris filix-mas		a: north		
Elymus caninus	a: interior, north (5%) c: south (5%)		c: interior, south (10%) b: north, south c: interior, north	a: north, b: interior (5%), south
Elymus sp.	a: south (20%) b: interior (5%) north (10%) south (20%) c: interior (7%), north (10%)			x
Epilobium lactiflorum				b: south
Equisetum arvense		c: north	a: interior, north b: south	
Festuca rubra		c: north		
Filipendula ulmaria	c: interior, north, south (2%)			
Galeopsis sp.		a: north (10%), south (10%), b: north (10%), south (5%)		
Galeopsis tetrahit		a: interior (15%) b: interior (5%)	b: south	
Galium mollugo (LO)			b: interior, north c: interior (4%), north	a: interior, north, south (10%) b: interior (5%), south c: interior (10%), north

				(5%), south (10%)
Galium verum		c: interior (5%), south (10%)	a: south (20%)	
Geranium sp.	c: north, south			
Geranium sylvaticum	a: north			
Geum rivale		c: north		x
Geum sp.		c: south		b: south c: north, south
Glechoma hederacea				b: south c: north, south
Graminides			b: south (70%) c: north (20%)	c: interior (15%), south (10-15%)
Heracleum mantegazzium (SE)		c: north (10%)		
Hieracium umbellatum		b: north, c: north		
Hypericum perforatum	a: north, south			c: interior
Laburnum sp. (PH/SE)			a: north b: south	
Lathyrus pratensis	a: interior, north (5%), south b: south c: south (5%)	a: north		a: south b: south
Leucanthemum vulgare	a: interior b: interior c: south	c: interior (15%), north, south (15%)		
Linaria vulgaris			b: south	b: south c: interior
Lupinus polyphyllus (SE)	a: south (5% regrowth) b: north (5% regrowth) b: south (10%) c: north, south (5%)	a: north (10%), south (10%), b: north (20%), south (20%) c: interior (40%)		
Malva moschata (LO)	a: north			
Onagraceae sp.		a: north, south b: north		
Parthenocissus sp. (NK)	a: north (5%)			
Persicaria maculosa			b: south c: interior	a: north c: north, south
Phleum pratense	a, interior, north, south b: south c: south (5%)			
Plantago major	a: interior, north b: south			
Poa palustris		b: interior, north, south		

Poa sp.	a, interior b: south (5%) c: south		a: interior, north (30%) b: interior c: interior	a: south b: interior
Populus tremula	c: south			
Ranunculus repens	a: interior, north (5%), south b: north, south c: interior	b: north		
Rhytidiadelphus squarrosus		b: interior (20%bunndekker), north, south (20%) c: interior (20-30% bunndekker), south (20-30% bunndekker)		
Rubus idaeus	c: north	a: north, south	c: north	
Rubus odoratus (PH)	c: interior, north (15%)			
Rumex longifolius	a: interior, north b: north		b: north	a: north b: south c: interior
Solidago canadiensis (SE)	b: south			c: interior (5%), north, south
Taraxacum sp.	a: north, south	a: south c: north		
Trifolium pratense	a: south b: north, south			
Trifolium sp.	a: north c: south			
Tripleurospermum inodorum	b: interior, north c: south			b: south
Tussilago farfara	a: south b: interior, north	c: interior (5%), south		b: south c: interior (5%) c: north, south
Urtica dioca			a: interior, north b: interior, north, south, c: interior (2%), north (20%), south (10%)	a: interior (10%), north (10%) b: interior (10%), south c: north, south
Urtica urens (VU)	a: north b: interior, north, south c: interior, north	a: north (10%), south (10%) b: interior (10%), north (25%), south (20%)		
Verbascum nigrum			b: interior	c: north
Vicia cracca	a: north, south	c: interior, south		
Vicia hirsuta				c: interior
Vicia sepium	a: north			

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway