Seed limitation restricts population growth in shaded populations of a perennial woodland orchid

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Abstract. Seed production and seedling recruitment are thought to be of minor importance in determining population dynamics and long-term viability in long-lived perennial plants. Seed addition experiments, on the other hand, have amply shown that supplemental addition of seeds almost always, irrespective of longevity, results in increased seedling recruitment. Any change in the environment that affects fruit and seed production can thus be expected to affect seedling recruitment, but the extent to which increased fruit and seed production affect overall population dynamics remains relatively unknown. In this paper, we present demographic data of six populations of the long-lived woodland orchid Orchis purpurea that were monitored for seven consecutive years (2002–2008) occurring in two contrasting light environments. We use a nested life table response experiment (LTRE) at the vital rate level to disentangle the relative contributions of each of six annual transitions, six sites, and two light environments on the population dynamics of this species and to determine vital rate variations that contributed most to variation in population growth rate. Population growth rates ($\lambda$) were significantly higher in the light environment than in the shaded environment (average $\lambda = 0.9930$ and $1.0492$ in the shaded and light environment, respectively). The LTRE analysis showed that variation in fecundity and, to a lesser extent, variation in growth made the largest total contributions to variation in $\lambda$, whereas the contributions of variation in survival were almost negligible. Fruit production was two times larger and the net reproductive rate ($R_0$) was approximately six times higher in the light environment than in shaded areas, suggesting that variables related to reproduction are the key drivers of population dynamics of this long-lived orchid species in different light environments. Our results indicate that light is an important factor affecting population dynamics of Orchis purpurea and illustrate that, even in long-lived species, flower and seed production can have important effects on the population dynamics.

Key words: Belgium; life table response experiment (LTRE); light environment; matrix population models; net reproductive rate; Orchis purpurea; vital rates; woodland herbs.

INTRODUCTION

In long-lived perennial plants, seed production and seedling recruitment are thought to be of minor importance in determining population dynamics and long-term viability (Franco and Silvertown 2004). A low level of reproduction suffices to balance low adult mortality rate of long-lived species, and the population growth rate is much more sensitive to changes in survival than in reproduction rates. However, recent meta-analyses of seed addition experiments (Clark et al. 2007, Poulsen et al. 2007) have shown that most plant populations are seed limited and that supplemental addition of seeds to populations almost always, irrespective of longevity, results in increased seedling recruitment. Even in species that produce huge amounts of seeds, increased seed production has been shown to translate into increased seed germination and seedling recruitment, as Ackerman et al. (1996) experimentally demonstrated for the tropical orchid Tolumnia variegata. Any change in the environment that affects fruit and seed production can thus be expected to affect seedling recruitment, but the extent to which increased fruit and seed production affect overall population dynamics remains relatively unknown (Clark et al. 2007).

In long-lived woodland herbs one of the important environmental factors that affect their population dynamics is light (Bierzychudek 1982, Whigham 2004). In general, most woodland herbs show a positive response to increased light penetrating to the soil (Cipollini et al. 1993, Whigham et al. 1993, Valverde and Silvertown 1998). The effect of light may be particularly important in determining the population demography of woodland orchids, as the dynamics of reproduction, growth, and survival are to some extent dependent on the amount of carbohydrates translocated.
to the belowground storage organs (Snow and Whigham 1989, Whigham and O’Neill 1991, Primack et al. 1994). Moreover, increased light penetration to the soil also results in a temporal increase in soil nutrients due to increased mineralization rates, which also has been shown to positively affect the fitness of orchid species (Whigham 1984). Jacquemyn et al. (2008), for example, demonstrated that in the perennial woodland orchid *Orchis mascula* populations in recently coppiced forests, where light availability was abundant, showed 2.5 times higher reproductive success compared to populations located in undisturbed habitats, where light penetration to the soil was very low. As a result of the increased flower and fruit production, total seed production, seed germination, and subsequent seedling recruitment may increase, particularly if populations are strongly seed limited.

Next to effects on flower and fruit production, increased light penetration can also be expected to affect probabilities of flowering and survival. Although most orchid species are capable of tolerating moderate levels of shade, recent shading and leaf removal experiments have indeed shown strong responses to light availability. In *Spiranthes spiralis*, for example, reducing daylight to 1% photosynthetic active radiation resulted in a dramatic decline (93%) in the number of plants surviving to the next year (Willems et al. 2001). In the woodland orchids *Cephalanthera rubra* and *Cypripedium calceolus*, defoliation did not affect survival, but it resulted in prolonged dormancy and thus decreased flowering (Shefferson et al. 2005). The number of flowers per inflorescence and height of the inflorescence also decreased when plants were shaded (Shefferson et al. 2006). High fruit set as a result of the increased light penetration may also induce some costs, for example by reducing the probability of flowering in the next year resulting in lower lifetime fecundity (Snow and Whigham 1989, Primack et al. 1994) and possibly lower overall growth rates. Furthermore, negative effects associated with too much canopy opening can also be expected for woodland herbs, for instance through desiccation or increased light competition with other low-stature plants.

Changes in the amount of light reaching the forest soil can therefore be expected to have pronounced effects on the demography of woodland orchids. However, most studies to date investigating the response of orchid species to different light conditions only focused on a limited part of the life cycle, most often flowering and survival (Willems et al. 2001, Shefferson et al. 2005, 2006). Because the dynamics of plant populations are essentially determined by their vital rates, i.e., birth, growth, and death rates (Schemske et al. 1994, Caswell 2001), studying variation in all vital rates across the entire life cycle of the species will obviously result in a better understanding of the demographic response of tuberous woodland orchids to varying light conditions and of life-history variation in plants more in general.

For the long-lived tuberous woodland orchid *Orchis purpurea* we investigated the manner in which differences in the amount of light penetrating to the soil affected each of its vital rates and the resulting population dynamics. Its demography was monitored for seven consecutive years in six populations. Three populations were located in undisturbed forest with light penetration to the soil generally being <1% (shaded environment), and three populations were located in bright conditions where >25% of the incoming radiation reached the forest soil (light environment). By explicitly incorporating fruit production, seed production, germination, and seedling establishment in our demographic models, we investigated to what extent differences in light conditions affected each of the vital rates. A nested life table response experiment (LTRE) was used to study how much these changes in vital rates, due to either the light environment or due to year or local site conditions, contributed to changes in projected population growth. A better understanding of the factors determining the population dynamics of this species will contribute to more detailed management prescriptions and ultimately to the conservation of this endangered species.

**Material and Methods**

**Study species**

*Orchis purpurea* Huds. (lady orchid; see Plate 1) is a diploid (2n = 42), tuberous, perennial orchid. Its distribution area extends from northern Spain through France, Austria, Switzerland, Germany, Hungary, Romania, and Bulgaria up the Crimea and into Turkey. It also occurs in Corsica and the mountains of central Italy, where it is one of the commonest woodland orchid species (Rose 1948). The species reaches the limits of its northwestern distribution in the United Kingdom, the northern part of Belgium (Flanders) and The Netherlands, and Denmark (Rose 1948). In Flanders and The Netherlands, the Lady Orchid is rare and threatened (van der Meijden 1990, Jacquemyn et al. 2005). The species occurs on chalk grasslands or in calcareous forests. In chalk grasslands, it usually occurs in the immediate vicinity of trees and shrubs, while in forest habitat it is mostly found in light gaps or along the forest edge.

*O. purpurea* perennates during the winter, and the leaves appear above the ground in February. Plants have one to four (sometimes up to seven) basal leaves of elliptic-ovate to lanceolate shape, 2–5 cm wide and 6–25 cm long (Rose 1948). Flowering takes place at the end of May. Under light conditions, plants may flower for two or more consecutive years, whereas under closed canopy flowering is mostly followed by one or several years when plants remain in a vegetative state. Dormancy, i.e., the failure of aboveground parts to appear in a growing season and the subsequent reappearance of full-sized photosynthetic plants in subsequent seasons, seldom occurs in this species (H. Jacquemyn and R. Brys,
personal observations). The height of the flowering stalks varies between 25 and 60 cm, reaching sometimes 80 cm (Jacquemyn et al. 2002). Flowering stalks carry 10–50 bright white to purple-brown flowers. The flowers are long-lived (21–28 days if unpollinated) and nectarless, but may produce a sweet odor. Like most other orchid species, O. purpurea is self-compatible (East 1940), and in our study area flowers are pollinated by generalist pollinators (most often bees and flies). Spontaneous autogamous pollination does not occur in this species (Jacquemyn et al. 2002). Seed capsules ripen by the end of June, followed by dehiscence and seed dispersal in August. From mid-August onward, all aboveground resources are reallocated to the tuber, and no living green parts are found above ground.

Study populations

This study was conducted in the east of Belgium (Voeren), where O. purpurea is locally abundant (Jacquemyn et al. 2007c). We studied six populations, all of which occurred in or along forests that were located on south-facing slopes and had similar soil and moisture conditions. Three populations were located in light environments (L1, L2, and L3), two of which consisted of a large canopy gap that was created in the winter of 2000–2001 in an attempt to restore the populations to their original state. The third was located in calcareous grassland immediately bordering a beech forest. The shaded sites (S1, S2, and S3) were all located in closed forest habitat and were largely overgrown by shrubs such as Sambucus nigra and Bryonia dioica. Light penetration to the soil in these sites was always <1%, whereas in the open sites >25% of the incoming radiation reached the forest floor (H. Jacquemyn, unpublished data).

Demographic data and construction of projection matrices

Because demographic monitoring of orchid populations is challenging and, particularly, seedlings may be overlooked, all populations were visited at least three times during the year. To facilitate demographic monitoring and to minimize the probability of overlooking individuals, each individual plant was mapped to the nearest centimeter. Additionally, each individual was tagged with plastic tags that were placed directly next to each individual. At the end of March, when all plants, including seedlings, had emerged but the vegetation was still very short, the whole population was meticulously screened for new individuals and survival of previously detected individuals. In early May, when plants were fully grown and flowering, each population was visited for a second time. At this time, the whole population was screened again, and occasionally new individuals were added to the data set and tagged. At that time, plant size was also determined by counting the number of leaves, and the flowering status of each individual was recorded. For each flowering individual we also counted the number of flowers. At the end of June or the beginning of July, all populations were visited for a third time, and for each flowering individual fruit set was determined by counting the number of fruits. All measurements were repeated annually between 2002 and 2008.

Although the life history of O. purpurea hasn’t been documented very well, most authors agree that seedlings exist belowground for more than one year, developing their first tuber during the second or third summer (Fuchs and Ziegenspeck 1927, Rasmussen 1995). This tuber grows into a short rhizome that sends out mycotrophic roots in autumn, and by the following year the first leaf may emerge (Fig. 1). Our own observations suggest that seedlings emerge the third year after seeds are dispersed (Jacquemyn et al. 2007b). Each O. purpurea individual was therefore classified into one of six classes: protocorms, tubers, seedlings, juveniles, nonflowering plants, and flowering plants (Fig. 1). A protocorm is the belowground stage, after seeds have germinated. Seedlings were defined as first-year vegetative plants. They have only one leaf, which is on average 10 cm long and 1.5 cm wide. Juveniles consisted of all vegetative plants older than one year, but with fewer than three leaves. Leaves were on average between 12 and 15 cm long and 2.5 cm wide. Nonreproductive adults had three or more leaves that vary in length between 15 and 25 cm and in width between 3 and 10 cm. Flowering individuals have similar leaf properties as nonflowering individuals.

Population transition matrices of the form \( \mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t) \) were used to describe annual changes in population growth rates (\( \lambda \)). The transition matrix \( \mathbf{A} \) describes how individuals from each stage class in the vector \( \mathbf{n}(t) \) contribute to the stage classes in \( \mathbf{n}(t + 1) \). All possible transitions are depicted in Fig. 1. Because matrix elements are compounds of different vital rates, demographic comparisons between populations ideally should be made using vital rates (Franco and Silvertown 2004). Therefore, matrix elements were explicitly written as functions of several vital rates as shown in Eq. 1 (below)

\[
\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 \\
\sigma_1 & 0 & 0 & 0 & 0 & 0 \\
0 & \sigma_2 & 0 & 0 & 0 & 0 \\
0 & 0 & \sigma_3(1-\gamma_{53}) & \sigma_4(1-\gamma_{54}-\gamma_{64}) & 0 & 0 \\
0 & 0 & \sigma_5\gamma_{53} & \sigma_4\gamma_{54} & \sigma_5(1-\gamma_{65}) & \sigma_6\gamma_{56} \\
0 & 0 & 0 & \sigma_4\gamma_{64} & \sigma_5\gamma_{65} & \sigma_6(1-\gamma_{56})
\end{pmatrix}
\]
(Caswell 2001, Franco and Silvertown 2004, Jongejans et al. 2006), where \( u \) is the number of flowers per plant, \( v \) is the proportion of flowers that set seed, \( \pi \) is the proportion of seeds per fruit, and \( \varepsilon \) is the proportion of seeds that germinate to become belowground protocorms the next year; \( \sigma \) refers to survival and \( \gamma \) to growth (or, more generally, changing to another stage instead of staying within a stage class), conditional on survival. Based on counts of seeds, the numbers of seeds per fruit was set to 6000. \( \varepsilon \) was determined based on seed germination trials in the field. In each site, seed packages (90 per site) were buried in the soil along regular transects through the populations and retrieved one year later to determine the number of protocorms. Some orchid species have a persistent seed bank (Whigham et al. 2006). However, because we did not test the viability of the seeds after retrieving seed packages from the soil, a seed bank was not included in the model. Because the fate of protocorms and tubers is difficult to measure in the field, we calculated their annual survival rates by linking the numbers of seedlings to the numbers of protocorms produced two years before. Based on previous experiments (Jacquemyn et al. 2007b), we assumed that the survival rate of tubers is four times higher than that of protocorms, but this ratio did not affect the projected population growth rates nor any other matrix calculation. Since seed production was already monitored in 2001, we were not able to estimate tuber survival for the 2002–2003 transition and protocorm survival for the 2007–2008 transition. In these cases we used population-specific means instead.

For each population and for each year, the asymptotic growth rate (\( \lambda \)) was calculated as the dominant eigenvalue of the matrix \( \mathbf{A} \). To compare the overall growth rate between populations in the shaded environment and the light environment, we calculated the growth rates of the pooled matrices from each population. We used permutation tests (Caswell 2001:335) to test the null hypothesis of no effects of light (i.e., \( \theta = \hat{\lambda}_{\text{shaded}} - \hat{\lambda}_{\text{light}} = 0 \)). To do so, individuals were randomly assigned to one of the six populations so that the number of individuals for each matrix is exactly the

![Life cycle graph of *Orchis purpurea* (lady orchid). Arrows represent possible transitions between stages, and values are elasticity values of the mean matrix that was constructed with vital rates averaged over all years and sites. The study was conducted in Voeren in eastern Belgium.](image)

**Fig. 1.** Life cycle graph of *Orchis purpurea* (lady orchid). Arrows represent possible transitions between stages, and values are elasticity values of the mean matrix that was constructed with vital rates averaged over all years and sites. The study was conducted in Voeren in eastern Belgium.
same as the original numbers of observations. After permuting individuals, matrices were constructed and for each matrix the population growth rate was calculated. To test the hypothesis of no differences in population growth rates between populations in the shaded and light environment, we computed

$$\Pr[\theta \geq \theta_{\text{obs}} | H_0] = \frac{\#\{\theta^{(i)} \geq \theta_{\text{obs}}\} + 1}{N_p + 1}$$

(2)

where $N_p$ is the number of permutations, $\Pr$ is the probability that randomly generated values of $\theta$ are larger than the observed value of $\theta$, and $\#$ stands for the number of observations for which $\theta^{(i)} \geq \theta_{\text{obs}}$. If $\Pr$ is very small, we reject the null hypothesis of no differences in growth rates between the light and shaded environments.

These demographic data were also used to assess habitat-specific demographic variation in life expectancy and net reproductive rate. The life span, i.e., the expected age at death, conditional on passing through the seedling stage, was calculated using Eq. 6 in Cochran and Ellner (1992). The net reproductive rate ($R_0$), which is the average number of offspring produced by an individual over its entire life span, was calculated using Eq. 18 in Cochran and Ellner (1992). We used the pooled matrix rather than the individual matrices for these calculations. These analyses were conducted with the program STAGECOACH (Cochran and Ellner 1992).

**LTRE analysis**

Life table response experiment (LTRE) analyses were used to assess the relative importance of light environment, population, and year in explaining variation in $\lambda$ (Horvitz et al. 1997, Jongejans and de Kroon 2005). Because population was nested within the light environment, a nested term was included in the analysis (see also Elder and Doak 2006, Endels et al. 2007).

In order to investigate which demographic parameters contributed most to the observed variation in $\lambda$, the effects of light regime, population nested within light regime, year, and the residual effect were decomposed as follows:

$$\lambda \approx \lambda^{\text{kmn}} + \omega^{km} + \alpha(\lambda)^{kmn} + \beta^{mn} + \alpha(\alpha)^{kmn}$$

(3)

where $\lambda^{kmn}$ is the projected population growth rate of the mean matrix (i.e., the matrix constructed from the geometric means of the vital rates), $\omega^{km}$ is the main effect of the $k$th light level of the $m$th site within light environment, $\beta^{mn}$ is the effect of the $m$th year, $\alpha(\lambda)^{kmn}$ is the effect of the $m$th year, $\alpha(\alpha)^{kmn}$ is the residual effect. Estimation of the treatment effects and decomposition into contributions from each vital rate were done as follows:

$$\omega^{km} = \sum_{i,j} \sum_{p} (\lambda_{p}^{km} - \tau_{p}^{m} \frac{\partial \lambda_{i} \partial a_{ij}}{\partial \tau_{p}} \bigg|_{(1/2)(A^{m} + A^{-})}$$

(4)

The net reproductive rate ($R_0$), which is the average number of offspring produced by an individual over its entire life span, was calculated using a transition matrix constructed with the geometric averages of the means of all vital rates and the geometric means of the means of all vital rates and the vital rate values of the light environment, population, or interaction of interest. Accuracy of the first-order approximation was assessed by testing for concordance of observed and expected values of $\lambda$ (Cooch et al. 2001). All LTRE analyses were conducted using R (R Development Core Team 2008).

**Results**

**Flower and fruit production**

Mean flower and fruit production were significantly smaller in the shaded environment than in the light environment ($F_{1,4} = 9.89$ and 42.18; $P = 0.035$ and 0.003, respectively). Plants produced on average 34.5 flowers in the shaded environment, whereas in the light environment plants had 42.6 flowers (Appendix A). Plants produced on average 2.1 fruits per inflorescence in the shaded environment, whereas in the light environment fruit production was approximately twice as high (4.1 fruits per plant).

**Matrix analyses**

Elasticity analysis (de Kroon et al. 2000) of the mean matrix indicated that survival and growth transitions between the reproductive and vegetative adult stages contributed most (82%) to the projected population growth rate (Fig. 1). During the seven years of monitoring, $\lambda$ ranged from 0.9341 to 1.1240 (Fig. 2; Appendix B). When averaged over years, population growth rates varied between 0.9834 ± 0.0321 (mean ± SD) and 1.0052 ± 0.0427 in populations of the shaded environment and were significantly lower than those of the light environment, where they varied between 1.0082 ± 0.0430 and 1.0727 ± 0.0305. In almost all of the six transition years, projected rates of $\lambda$ were larger in populations of the light environment than in those of the shaded environment (Fig. 2).

Plants in the light environment had a higher life expectancy than plants in the shaded environment (average life expectancy 65.89 and 44.09 yr in the light
and shaded environments, respectively). Plants also produced a significantly larger number of offspring over their entire life span in the light environment ($R_0 = 5.81$) than in the shaded environment ($R_0 = 0.93$).

**LTRE analysis**

Overall, the LTRE models fitted the projected population growth rates of the separate matrix models reasonably well: the LTRE models deviated only 0.64% on average (Appendix C). The LTRE analyses showed that populations of the light environment contributed positively to the variation in $\lambda$ (Fig. 3A). We found relatively little variation in population growth rates between populations in the shaded environment, but considerable variation between populations in the light environment (Fig. 3B). The population L3 was performing particularly badly, compared to the other two populations of the light environment. There was also considerable year-to-year variation, with the 2003–2004 transition being an exceptionally good transition and 2007–2008 being the worst (Fig. 3C).

In all these effects, decomposition analysis showed that variation in fecundity and, to a lesser extent, variation in growth made the largest total contributions to variation in $\lambda$, whereas the contributions of survival were almost negligible (Appendix D). Despite considerably large positive contributions of germination of seeds, the generally lower population growth rates in populations of the shaded environment were primarily due to lower fecundity and less growth from nonflowering plants to flowering plants (Fig. 4). Year variation was primarily due to variation among recruitment among years and to a minor extent to survival of flowering plants and probability of flowering. The strong effect of site within light environment was also primarily due to differences in seedling recruitment, with a pronounced negative contribution of site L3, where very few recruits were observed compared to the other two sites.

**Discussion**

Using extensive demographic monitoring of several *O. purpurea* populations and LTRE analyses, we have shown that increased light penetration to the soil had a major, positive impact on the population dynamics of this long-lived orchid species. Population growth rates in the light environment were significantly larger than those in the shaded environment, indicating that populations increased in size under increased light availability, whereas in shaded forest, populations remained very stable or slightly decreased. Nonetheless, substantial variation was observed between sites within light environment and years, suggesting extensive spatiotemporal variation. In the following, we discuss the mechanisms most likely responsible for the differences in projected values of population growth rate and translate our findings to some practical implications for management.
Fig. 3. Results of the life table response experiment (LTRE) analysis with a nested design: contributions of main effect of (A) light environment, (B) light environment nested within site, and (C) year transition to variation in population growth rates of Orchis purpurea.

Fig. 4. Decomposition (fixed-effects life table response experiment [LTRE]) of the differences in population growth rate (λ) of the shaded and light treatments (compared to the λ of the mean matrix) into contributions by the differences in the lower vital rates. Abbreviations are: φ, the number of flowers per plant; υ, the proportion of flowers that set seed; π, the number of seeds per fruit; ε, the proportion of seed that germinate to become belowground protocorms the next year; σ, survival; and γ, growth (or, more generally, changing to another stage instead of staying within a stage class) conditional on survival.
Impact of light on flowering and fruiting

Increased light penetration to the soil had a positive effect on population growth rates of this species. Results of the LTRE analysis showed that this was partly due to increased fecundity and increased probabilities of flowering. Plants in the light environment flowered more frequently and produced significantly more flowers than plants in the shaded environment. These results are in agreement with previous shading experiments that showed decreased flowering probabilities after shading in the woodland orchids *Cephalanthera rubra* and *Cypripedium calceolus* (Shefferson et al. 2006) and in the grassland orchid *Spiranthes spiralis* (Willems et al. 2001). In shaded sites, the average flowering frequency was 0.20, whereas in the light environment plants flowered on average five out of seven years. Besides, the probability of flowering again when a plant had flowered the previous year was virtually zero in shaded areas, whereas in the light environments plants were perfectly capable of flowering for several consecutive years.

Besides increased flowering probabilities, our results also showed that the increased light penetration to the soil was associated with higher levels of pollination and fruit set. Similar to the results presented here, Jacquemyn et al. (2008) showed that in the related *Orchis mascula* the mean number of fruits per plant varied between 1.75 and 12.1 (mean = 6.17 fruits per plant) among populations in recently coppiced woodland and was significantly higher than that for populations in undisturbed woodland (mean = 1.66, range = 1.36–2.06 fruits per plant). The percentage of flowers setting fruit varied between 20.5% and 55.5% in recently coppiced woodland and between 8.8% and 13.2% in undisturbed woodland. The open and sunny conditions in coppiced woodland probably attract more potential pollinators and therefore increased fruit set.

Seed limitation

As early as the 19th century, Darwin (1862) observed that of all life-history stages, successful germination and seedling establishment are the most critical in orchids. Although a single plant may produce thousands of seeds in one reproductive season, very few, if any, will survive to parenthood. Therefore, any increase in fruit and seed production can be expected to result in increased seed germination and seedling recruitment, provided local growth conditions allow for successful germination. There is indeed some evidence that experimental increase of fruit set through hand-pollination increased seed germination in the tropical epiphytic orchid *Tolumnia variegata* (Ackerman et al. 1996), but it remains unclear whether these results also hold for terrestrial orchids.

Here we have shown that average fruit production was twice as high in the open sites than in the shaded sites. At the same time, the net reproductive rate ($R_0$) was approximately five times larger in the open sites than in the shaded sites. Because germination rates were lower in the open sites, these results thus suggest that the increased seedling recruitment might be partly explained by increased fruit and seed production. Results from the LTRE analysis indeed showed that the higher population growth rates in light environments were contributed in large part by increased fruit production. These results are to some extent surprising, considering that for long-lived species, the importance of fruit and seed production and seedling recruitment to overall population dynamics is expected to be low (Franco and Silvertown 2004).

Seed germination and seedling establishment

Seed germination percentages varied substantially between sites, ranging from 0.1% to 2%, and were higher in the shaded environments than in the light environments. Although it is known that fungi are important to orchid germination and early development (Rasmussen 1995), we currently have no data that suggest that the availability of fungi has affected seed
germination patterns within these populations. Previous research (Jacquemyn et al. 2007b) has shown that seed germination can vary substantially between sites and that a thick humus layer may impede seed germination within sites. This might be particularly true for site L3 in the open conditions, where a germination percentage of only 0.1% was observed. Although plants flowered profusely and set seed abundantly, hardly any seedling recruitment was observed, and population growth rates quickly decreased from approximately 1.06 to 0.93, yielding an overall growth rate of 1.01. The observed low germination percentage thus explains the pronounced negative contribution of germination to the observed higher population growth rates in the open sites.

Because mortality rates of seedlings were very low once they were observed above ground, our data also suggest that strong selection occurs in the earlier stages of seedling establishment. Although germination rates are in general low (~1% of the seeds germinated), the vast number of seeds produced each year indicates that the proportion of protocorms that successfully grows into a seedling is very low. In an attempt to incorporate the underground phase in our demographic analyses, growth from seeds to protocorms and subsequent growth of protocorms and tubers was included in the analysis. The LTRE analysis showed a positive contribution of protocorm and tuber growth in the open sites to the observed variation in population growth rates. The reason for this remains unclear: it might be that nutrient conditions in the soil in the shaded sites are sufficient to promote germination, but do not suffice to support further growth. An important suggestion from this research would therefore be to include more detailed investigations of protocorm and tuber survival under different light conditions in further demographic modeling of orchid population dynamics. To the best of our knowledge, very few studies have attempted this, yet it might lead to better insights into the importance of the belowground growth phases in determining overall population dynamics of orchid species under different ecological conditions.

Spatiotemporal variation

Despite the clear effects of light environment on population dynamics of *O. purpurea*, there was still considerable variation between populations within sites and between years, which corresponds to previous studies that have investigated spatial and temporal variation in population dynamics of plant species (Horvitz and Schemske 1995, Fréville et al. 2004, Jongejans and de Kroon 2005). These results also agree with long-term studies that have been conducted on other orchids and that have documented considerable year fluctuations in population dynamics, probably resulting from variation in climatic conditions. For example, in a long-term (26 years) study of the population dynamics of *Himantoglossum hircinum* using matrix models, Pfeifer et al. (2006) showed variation in population growth rates varying between 0.8 and 1.4. In this case, population growth rates were negatively influenced by low temperatures in winter. Similarly, in a 30-year study of *Spiranthes spiralis*, Jacquemyn et al. (2007a) found population growth rates varying between 0.82 and 1.53. In our study, the large, positive effect of the 2002–2003 and especially the 2003–2004 transitions can most likely be traced back to the change in management in 2001, when the forest canopy was opened. The positive effect was mainly due to the swift response of nonflowering plants becoming flowering shortly after the location was opened. Such a response has been observed in other orchid species as well. In the related *O. mascula*, >50% of all adult plants in populations occurring in sites that were recently coppiced were flowering, whereas in undisturbed forest only a minor fraction of 14% were flowering (Jacquemyn et al. 2008). Opening of the canopy thus immediately results in increased flowering probabilities.

Besides this temporal variation, we also found extensive spatial variation between populations, indicating that local site conditions may have a large impact on population dynamics of orchid species. Interestingly, in the shaded environment, very little spatial variation was observed, suggesting very stable populations and very little effect of local site conditions. On the other hand, we observed very large spatial variation between populations in the light environment. Inspection of the LTRE shows that this was mostly due to differences in seed germination. Hence, the availability of suitable fungi to promote seed germination may be an important factor determining the response of orchid populations to changing light conditions.

Implications

These results have important implications for the management of these forests. Traditionally, these forests were managed in a coppice regime, implying that once every 10 or 20 years, all aboveground biomass was removed and plants were allowed to regrow. However, due to societal changes and altered demands for forest products, coppicing went into rapid decline during the 20th century. As a result, many populations have declined in size or even went extinct (Jacquemyn et al. 2007c). Restoration of the traditional coppice management therefore is expected to result in rapid increase in size of the few *O. purpurea* remaining populations, provided conditions for germination and establishment are suitable (Eichhorn and Eichhorn 2007).

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LITERATURE CITED


APPENDIX A

Flower and fruit production in *Orchis purpurea* during eight consecutive years in six locations (*Ecological Archives* E091-011-A1).

APPENDIX B

Vital rates used to construct matrix models of six *Orchis purpurea* populations collected during seven consecutive years (2002–2008) (*Ecological Archives* E091-011-A2).

APPENDIX C

Projected population growth rates ($\lambda$) and life table response experiment (LTRE) model effects of six *Orchis purpurea* populations collected during seven consecutive years (2002–2008) (*Ecological Archives* E091-011-A3).

APPENDIX D

Decomposition of life table response experiment (LTRE) effects (Appendix C) into contributions by vital rate differences (*Ecological Archives* E091-011-A4).