Cone abortion in *Pinus halepensis*: the role of pollen quantity, tree size and cone location

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This study describes the seasonal patterns of seed and cone abortion in natural *Pinus halepensis* trees and assesses the effects of pollen quantity, tree size and cone location on seed and cone abortion. The cone-set ratio was similar to the expected value, based on literature on woody perennials. The seed-ovule ratio, however, was almost twice as high as its expected value. The investment in protective cone elements was high and did not vary with the seed-ovule ratio of a cone. Pollination factors influenced cone abortion, as indicated by the high abortion rate at the end of the pollination period. Furthermore, abortive cones had lower pollination rates and lower pollen loads than well developed cones. Effects of resource availability were assessed as effects of tree size and cone position on twigs. Small trees aborted more cones than big trees and cone abortion was higher in apical cones than in basal cones. Abortion in *P. halepensis* is selective, mediated by both pollen quantity and resource availability. The relative importance of pollen and resources is suggested to be flexible, probably varying between trees and years. The high seed-ovule ratio of *P. halepensis* is the result of high pollination rate and selective abortion. The selective abortion might be due to the high allocation to protective cone elements relative to the allocation to seeds.

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Fruit and seed abortion occurs among angiosperms and gymnosperms as well as wind and insect pollinated species (Stephenson 1981). The rate of fruit and seed abortion varies between species depending on their breeding system. Self-incompatible outbreeders have lower fruit-flower and seed-ovule ratios than self-compatible inbreeders (Charlesworth 1989, Vaughton and Carthew 1993). Furthermore, wind-pollinated *Acacia* species had lower seed-ovule ratios than insect-pollinated *Acacia* species (Tybrik 1993). In general, annuals have higher fruit-flower (0.71) and seed-ovule ratios (0.85) than perennials (0.57 and 0.65 respectively), among which woody plants have the lowest fruit-flower (0.29) and seed-ovule ratios (0.33) (values from Wiens 1984, Charlesworth 1989).

Many studies have focused on factors affecting seed and fruit abortion (Sweet 1973, Owens et al. 1981, Herrera 1988, Zimmerman and Pyke 1988, Jong de and Klinkhamner 1989, Vaughton 1991, Mitchell 1997, Corbet 1998). These studies suggest that resource availability as well as pollen quantity and quality are the most important factors determining abortion rates. Three main trends in seed and fruit abortion can be distinguished. Ovules which receive low pollen quantity or quality are aborted more frequently (Schuster et al. 1993, Björkman 1995). Fruits with a high proportion of aborted ovules are more likely to be aborted (Sweet 1973, Owens et al. 1981). Flowers at basal positions are less frequently aborted than flowers at apical positions (Obeso 1993, Guitian 1994). Whether fruit abortion is

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mainly mediated by pollen factors, by resource availability, or equally by both factors is still a subject of discussion (Jong de and Klinkhamner 1989, Ackerman and Montalvo 1990, Medrano et al. 2000).

Despite the many studies on abortion in the last 30 years few have been on conifers (Stanley 1958). Among these only a few studies have assessed the effects of pollen quality (Burczyk et al. 1996) and quantity (Owens et al. 1981, 1991). Most studies on conifers were carried out in planted stands or seed-orchards from the point of view of forestry rather than ecology. These studies focused mainly on the influence of fertilizers (White et al. 1977, Fogal et al. 1999), hormones (Hare 1981, 1987, Fogal et al. 1999) and insects on seed and cone abortion (Yates and Ebel 1978, Chatelain and Goyer 1980, Goyer and Williams 1981, Rauf et al. 1984a, b, Schmid et al. 1986, Pasek and Dix 1988, Katovich et al. 1989, Connelly and Schowalter 1991). In this study, we assessed patterns of seed and cone abortion in *Pinus halepensis* Mill. *Pinus halepensis*, is a monoecious, wind-pollinated outbreeding tree and thus, according to general predictions in the literature, very high values of ovule and cone abortion would be expected. On the other hand, the cones produced by *P. halepensis* to protect the seeds seem like a costly investment (Poorter 1994). A high cone investment would favour a high seed-ovule ratio. Secondly, *P. halepensis* has a clear temporal separation between periods of pollination, fertilization and cone growth, which makes it possible to relate abortion to each developmental stage. Thirdly, each female cone contains over a hundred scales, each with two basal ovules, which store pollen in a pollen chamber. This offers a possibility to relate the variability in within-cone seed abortion to pollen quantity. Finally, the high variability in tree size and spatial variation in cone positions on twigs offers opportunities to assess the effects of differences in resource availability. In general, bigger trees and basal locations are associated with higher resource availability (Stephenson 1981).

The main goal of this study was to determine the level of seed and cone abortion in *P. halepensis* in relation to pollen quantity, tree size and cone location. We calculated the average cone-set ratio (the equivalent of the fruit-flower ratio) and seed-ovule ratio. The timing of abortion was determined and compared to the timing of pollination, fertilization and cone growth. Effects of pollen quantity were studied by measuring the proportion of pollinated ovules per cone as well as the number of pollen grains per ovule in well developed cones and abortive cones. Effects of tree size and cone location were assessed as effects of resource availability on cone abortion. A descriptive model for cone abortion patterns in *P. halepensis* is proposed based on the results.

Materials and methods

Site and trees

The study was carried out in a natural *P. halepensis* forest with trees of different ages in Carmel National Park, Mount Carmel, Israel. This area has a Mediterranean-type climate, which is typical for the natural distribution range of *P. halepensis*. Trees were selected within a size-range of 1–20 cm Diameter at Breast Height (DBH) of the trunk in several locations in the research area. This limited DBH range was chosen to exclude bigger trees that are too high (higher than 8 meters) for visual counts of cones.

Seed and cone abortion

Forty small trees, with DBH ranging from 1–10 cm, and 40 medium sized trees, with DBH ranging from 10–20 cm were randomly selected for the abortion measurements. To assess the timing of abortion, female cones on each tree were counted using binoculars. The counts started at the time of cone emergence (February 1998). Recounts took place 1 and 3 months after the end of the pollination period (March 1998), and continued every 4 months until the cones reached maturity 28 months later (June 2000). Cone-set ratio, the equivalent of the fruit-flower ratio, was calculated by dividing the number of mature cones (June 2000), by the number of young cones (February 1998). To determine the seed-ovule ratio, two mature cones were collected from each tree and dried in an oven at 60°C for 1 week to extract the seeds. We counted the number of full seeds and the number of scales (each representing two ovules) per cone. The seed-ovule ratio was calculated by dividing the number of seeds by the number of ovules per cone. The same cones were used to determine the dry weight of seeds and protective cone elements. The relative contribution of seeds and of protective cone elements to the total cone dry weight was calculated. The cone-set ratio, seed-ovule ratio and relative biomass investment in protective cone elements were determined for small and medium sized trees separately and for all trees combined. Comparisons between small and medium sized trees were performed by t-test. We also tested the relationship between the relative investment in protective cone elements and the seed-ovule ratio of the cone using linear regression. Percentages and ratios were arcsin-sqrt(x) transformed before submitting them to statistical analyses.

To determine the timing of cone growth, 10 other trees (with similar DBH range and locations) were selected and samples of 2 cones per tree were taken synchronously with the cone-counts mentioned above. The cones were dried at 60°C for 1 week and their dry weight was determined. To determine the number of

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well developed ovules between pollination and fertilization, we collected additional samples of 2 cones per tree in December 1998. All ovules on the cones were studied with a light microscope and divided in two groups: well developed ovules and shriveled ovules. The percentage of developed ovules prior to fertilization was calculated as the relative number of well developed ovules to the total number of ovules per cone.

Pollination and tree size

For the measurements of pollination rate and pollen load we selected 20 small and 20 medium sized trees, with the same DBH range as mentioned above. We defined two types of cones: well developed and abortive. Cones without any shriveled scales were defined as well developed. Cones with > 50% of shriveled scales, which would shrivel totally and be aborted later (personal observations), were defined as abortive cones. We collected randomly 1 well developed cone and 1 abortive cone from each tree and measured their length. Ten scales from the middle zone of each cone were cut off and examined with a light-microscope. The pollen grains located in the pollen chamber of each ovule (n = 20 per cone) were counted. Ovules with at least one pollen grain were defined as pollinated ovules. From these data we calculated the average percentage of pollinated ovules per cone (pollination rate) and the average number of pollen grains per ovule (pollen load). The ranges in pollination rate of well developed and abortive cones were calculated as well. The effect of cone status (well developed or abortive) and tree size (small or medium sized) on cone length, pollination rate and pollen load was tested by two-way ANOVA. The relationship between pollination rate and pollen load was tested using a linear regression test. Proportions

were arcsin-sqrt(x) transformed before submitting them to statistical analyses.

Pollination and cone position

To determine the effect of cone position on abortion, we used the same trees as described above in the pollination and tree size paragraph. We randomly collected, 40 cones located at the base of twigs (basal cones) and 40 located at the apex of twigs (apical cones). The distance between cones located on the base and the apex varied between 1 and 10 cm. Each cone was collected from a different twig and only twigs with one basal and one apical cone were sampled. This procedure avoids pairing of basal and apical cones and includes only cones that experienced the effects of the presence of another cone. Each cone was classified as well developed or abortive and the percentage of well developed and abortive cones was calculated for the basal and apical positions. From these cones we randomly selected 10 well developed and 10 abortive basal cones as well as 10 well developed and 10 abortive apical cones. For each cone, we determined the average length, pollination rate and pollen load, as described above. We also determined the range of pollination rate for well developed and abortive cones in basal and apical positions. The effects of cone position (basal or apical) and cone status (well developed or abortive) on cone length, pollen load and pollen rate was tested by two way ANOVA. Proportions were arcsin-sqrt(x) transformed before submitting them to the test.

Results

Seed and cone abortion

Cone abortion was highest just at the end of the pollination period (month 1 and 2 after cone emergence) and continued at medium rate for 4 more months. At this point, 74% of the total abortion already had taken place. The abortion of cones continued at a lower rate from 6 months after cone emergence. Rapid cone growth started 12 months after cone emergence, when 88% of the final total abortion had already occurred. Fast cone growth continued till 20 months after emergence and slowed down thereafter. Cone abortion rate was very low during and after the cone growth period until the final abortion percentage (77%) was reached at cone maturity, 28 months after pollination (Fig. 1).

The overall average ($\pm$ SE) cone-set ratio was 0.23 $\pm$ 0.02. The overall average proportion of developed ovules per cone prior to fertilization was 0.71 $\pm$ 0.01, and the overall average seed-ovule ratio was 0.60 $\pm$ 0.01. Separate measurements on small and medium
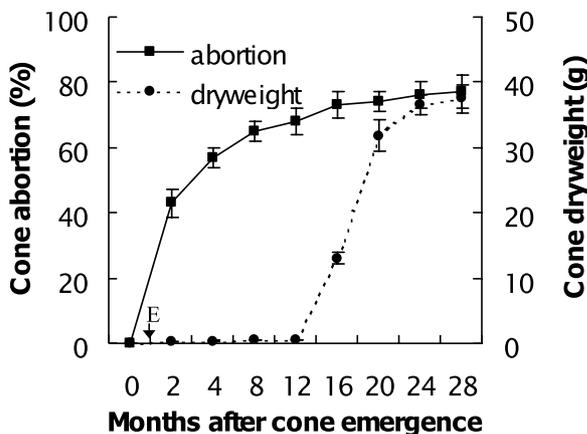

Fig. 1. The percentage of abortion of the total number of initiated cones and cone dry weight ($\pm$ SE) during a period of 28 months after cone emergence (February 1998). The end of the pollination period is marked with "E".

Table 1. Mean ($\pm$ SE) cone-set ratio, seed-ovule ratio and percentage of biomass (g dry weight) allocation to protective cone elements (%) in small and medium sized trees. Results of t-test are for the comparison between small and medium sized trees.

Variable	n	Small $\pm$ SE	Medium $\pm$ SE	t-test results
Cone-set ratio	80	0.15 $\pm$ 0.04	0.31 $\pm$ 0.03	$T_{1,78} = 3.527$, $p = 0.001$
Seed-ovule ratio	160	0.57 $\pm$ 0.01	0.63 $\pm$ 0.01	$T_{1,158} = 3.950$, $p < 0.001$
Cone biomass	160	93.3 $\pm$ 0.14	92.2 $\pm$ 0.20	$T_{1,158} = 4.297$, $p < 0.001$

sized trees showed that medium sized trees had significantly higher cone-set and seed-ovule ratios than smaller trees (Table 1). The overall average relative investment in biomass in protective cone elements was high: 92.8% $\pm$ 0.13. Medium sized trees invested slightly less in cone protection than small trees (Table 1). The seed-ovule ratio was positively correlated with the relative investment in protective cone elements ($F_{1,158} = 13.463$, $p < 0.001$), but this relation was very weak ($r^2 = 0.08$).

Pollination and tree size

Measurements of well developed and abortive cones showed a significant effect of cone status (Table 2): abortive cones were shorter (Fig. 2A), had a lower pollination rate (Fig. 2B) and a lower pollen load (Fig. 2C) than well developed cones. There was no significant effect of tree size on cone length, pollination rate and pollen load. We did not find a significant interaction between tree size and cone status (Table 2). Ovules from cones with high pollination rates also had larger pollen loads. This was evident in the positive relationship between the pollination rate and the pollen load ($F_{1,78} = 194.904$, $p < 0.001$ and $r^2 = 0.714$). The pollination rate of abortive cones ranged from 10 to 80% and of well developed cones from 40 to 100%.

Pollination and cone position

The percentage of well developed cones was higher in basal cones (70%) than in apical cones (40%). Both cone status and cone position had a significant effect on cone size (Table 3). Well developed basal cones were the biggest and abortive apical cones were the smallest, but there was no difference in cone size between abortive basal cones and well developed apical cones (Fig. 3). Pollination rate and pollen load were affected only by cone status, not by cone position (Table 3). Abortive cones had lower pollination rates and pollen loads than well developed cones (Table 4). There was no significant interaction between cone status and position (Table 3). Pollination rates of abortive cones ranged from 20 to 60% in basal cones and from 30 to 80% in apical cones. Well developed cones ranged in their pollination rate from 40 to 100% in basal cones and from 60 to 100% in apical cones.

Discussion

Seed and cone abortion

The generally accepted values for the fruit-flower and seed-ovule ratios for woody perennials are 0.29 and 0.33 respectively (values from Wiens 1984, Charlesworth 1989). Wind-pollinated outbreeding woody perennials such as *P. halepensis* are expected to have even lower values than insect-pollinated inbreeding ones, due to a lower efficiency of wind pollination (Owens et al. 1991, Tybrik 1993). The cone-set ratio of *P. halepensis* (0.23) corresponds quite well with the expected value, but the seed-ovule ratio (0.60) is almost twice as high. Medium sized trees have higher cone-set and seed-ovule ratios than small trees. The higher seed-ovule ratio is adaptive given the high biomass requirements for seed protection. High seed-ovule ratios were also found in other cone bearing pine trees, varying from 0.66 for *P. ponderosa* to 0.91 for *P. edulis* (Lanner 1998). The results show that 93% of the total biomass allocated to cones is invested in the protective cone elements. This investment is largely independent of the seed-ovule ratio of the cone. Thus, it is more economic in terms of biomass to develop cones with higher seed-ovule ratios. Moreover, selective abortion of fruits with less developing seeds may increase female reproductive success (Burd 1998).

Factors affecting abortion

To achieve a high seed-ovule ratio, first of all a high level of pollination is needed. Wind pollination is often

Table 2. The results of a two-way ANOVA for effects of cone status (well developed or abortive), tree size (small or medium) and their interaction on cone length (cm), pollination rate (%) and pollen load.

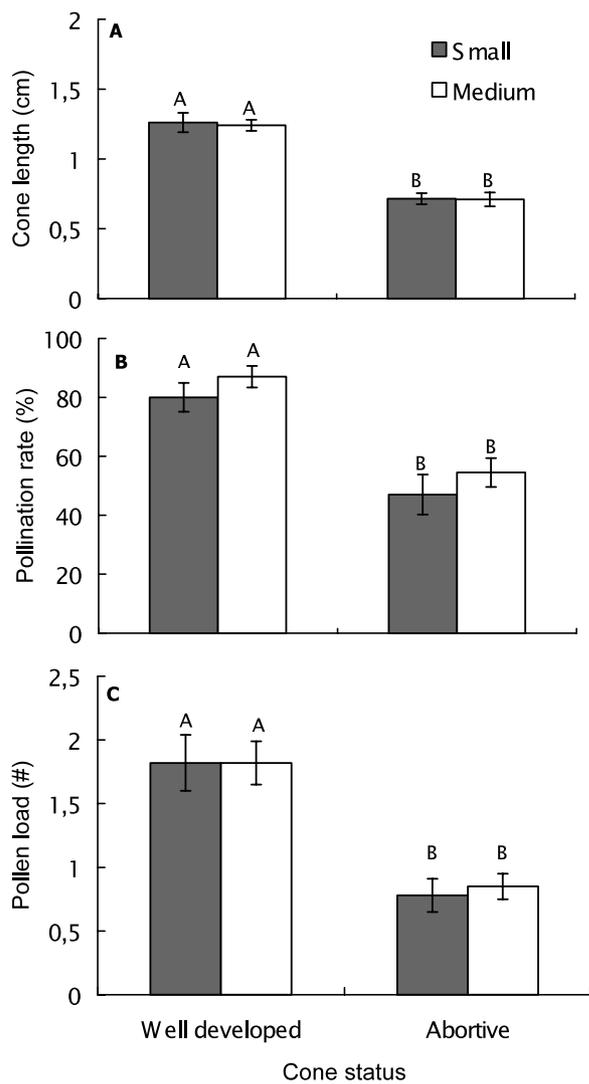| Variable	Factor	$F_{1,76}$-value	Probability
Cone length	Cone status	104.072	<0.001
	Tree size	0.056	0.813
	Status $\times$ size	0.020	0.887
Pollination rate	Cone status	40.491	<0.001
	Tree size	1.575	0.213
	Status $\times$ size	0.092	0.763
Pollen load	Cone status	39.099	<0.001
	Tree size	0.062	0.804
	Status $\times$ size	0.047	0.828

Fig. 2. The mean values of cone length (A); pollination rate (B); and pollen load (C) of well developed and abortive cones on small and medium sized trees. Error bars indicate SE. Result of a post-hoc Tukey test with $p < 0.05$ are shown by letters, different letters indicate significant differences between values.

high pollination rate, however, does not lead automatically to a high seed-ovule ratio, as we demonstrated with our results. The overall average pollination rate of well developed cones was 83.5%. However, the proportion of well developed ovules in a cone prior to fertilization was lower (0.71), and the post-fertilization proportion of developed ovules (or the seed-ovule ratio) finally was as low as 0.60. This amounts to a total abortion of ovules of 28% after pollination has taken place. Pre-fertilization reduction in the number of ovules is probably caused by problems during pollen germination or pollen-tube growth (Owens et al. 1981).

Table 3. Results of a two-way ANOVA for the effects of cone status (well developed or abortive), cone position (basal or apical) and their interaction on cone length, pollination rate and pollen load.

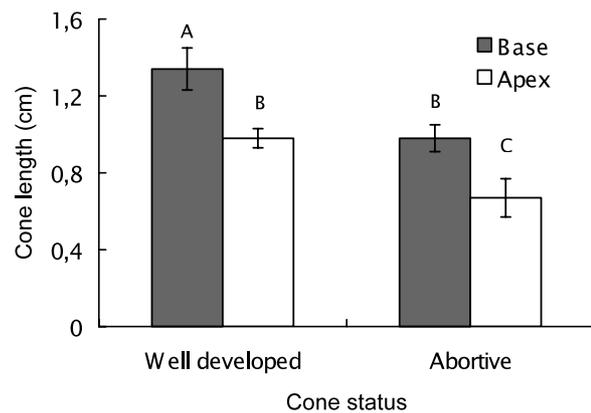| Variable	Factor	$F_{1,36}$-value	Probability
Cone length	Cone status	15.137	<0.001
	Cone position	16.068	<0.001
	Status × position	0.056	0.815
Pollination rate	Cone status	38.187	<0.001
	Cone position	0.119	0.733
	Status × position	1.548	0.221
Pollen load	Cone status	32.966	<0.001
	Cone position	0.391	0.536
	Status × position	0.934	0.340

Fig. 3. The mean length of well developed and abortive basal and apical cones. Error bars indicate SE. Result of a post-hoc Tukey test with $p < 0.05$ are shown by letters, different letters indicate significant differences between values.

Table 4. Mean ($\pm$ SE) pollination rate (%) and pollen load for well developed and abortive basal and apical cones (n = 20).

Variable	Cone status	Basal $\pm$ SE	Apical $\pm$ SE
Pollination rate	Well developed	85.0 ± 5.6	82.0 ± 6.6
Pollination rate	Abortive	46.7 ± 7.4	56.0 ± 7.4
Pollen load	Well developed	2.01 ± 0.26	1.73 ± 0.17
Pollen load	Abortive	0.80 ± 0.10	0.88 ± 0.12

associated with low pollination rates relative to insect pollination (Faegri and van der Pijl 1979). Our results, however, show that in individual cones of *P. halepensis* the pollination rate can reach 100%. This is a result of the specific pollination system of *P. halepensis*. As in other conifers, pollen (Benkman 1995, Runions et al. 1999) and cone morphology enable pollen to be distributed over most of the ovules in a cone (Niklas 1984, Owens et al. 1998) and several grains are allowed to enter the same micropyle. Our results show that this can lead to high pollination rates as well as high pollen loads. Thus, the pollination mechanism of *P. halepensis* is efficient despite the fact that it is wind mediated. A

Subsequent reduction in the number of ovules is caused by fertilization problems (Owens et al. 1991). Our results show that a high average level of seed-ovule ratio can be achieved in a population if only highly pollinated cones are selected for further development and the rest aborted.

The role of pollen quantity

Selective abortion is a common process in many species (Sweet 1973, Stephenson 1981, Stephenson and Winsor 1986, Niesenbaum 1999). Pollen quantity is one of the mediators of selective abortion, by causing ovule abortion within developing fruits (Lee and Bazzaz 1982, Bawa and Webb 1984). The first evidence in our study that pollen plays a role in cone abortion in *P. halepensis* is the timing of abortion, which occurs mainly at the end of the pollination period. Insufficiently pollinated ovules of *P. halepensis* abort before the late summer dormancy sets in (Sarvas 1962). This corresponds with a period till 7 months after the end of the pollination period in our study. During this period 84% of the total cone abortion takes place, indicating that a large part of the total cone abortion is a result of pollination-related factors. Pollen mediated selective abortion is expected to affect cones with low pollination rates and small pollen loads. This is supported by our other results, which clearly show that well developed cones have higher average pollination rates as well as larger average pollen loads than abortive cones. This effect was also found in other pine species (Sarvas 1962, Owens et al. 1981). It has been shown experimentally that higher pollen loads can lead to stronger offspring as a possible result of pollen competition (Schuster et al. 1993, Holm 1994, Björkman 1995, Niesenbaum 1999). Thus abortion of poorly pollinated ovules will avoid a waste of resources on poor quality offspring. Especially beacuse the loss of resources due to cone abortion is relatively low, as 88% of the total abortion takes place before the start of cone growth. Costs are also low, because the young female cones that are aborted do not invest in attractive elements for pollinators such as colored petals and nectar. Burd (1998) showed in a modeling study that excessive flower production is only advantageous if there is a variation in pollination rates between flowers, a low pre-abortion cost and effective selective abortion. As this seems to be the case for *P. halepensis*, the gain from selective abortion is assumed to be higher than its loss. Our data show that there is a pollination-threshold under which cones are always aborted. The lowest seed-ovule ratio of well developed cones in this study was 0.30, which would require a pollination rate of about 40%, taking into account pollen germination and fertilization failures as mentioned in the previous paragraph. This value corresponds well with the lower limit of the range

of pollination rates we found for well developed cones (40–100%) and can thus be seen as the threshold for abortion in *P. halepensis*. Although cones with pollination rates under 40% are always abortive and those over 80% are always well developed, there is a range between 40–80% in which cones can either be aborted or developed. This suggests that there are additional factors that influence cone abortion. This leads us to the second main mediator of fruit abortion: resource availability.

The role of resource availability

The influence of resource availability is indicated by the different cone abortion rate of small and medium sized trees. Small trees have a higher abortion percentage (lower cone-set ratio) than medium sized trees, although their pollination rates are the same. This implies that small trees are forced to abort a relatively higher proportion of well pollinated cones than medium sized trees, probably because small trees invest proportionally less in reproduction and more in growth. Abortion of a higher proportion of well pollinated cones explains the lower seed-ovule ratio of small trees. The influence of resource availability may also be indicated by the effect of position of cones on the twigs. The results show that apical cones are more often aborted than basal cones. This corresponds with studies on flowering plants (Obeso 1993, Guitian 1994, Corbet 1998). No difference in pollination efficiency between cones separated by 5 meters was found (Goubitz unpubl.). Therefore, it can be assumed that the pollination efficiency is similar in basal and apical cones, which are separated only by 1–10 cm. We do, however, expect a difference in resource availability between basal and apical cones. The flow of water and minerals from the root and assimilates from basal needles reaches the basal cones before the apical cones on its way to the apical buds (Stephenson 1981), leading to higher resource availability at the base. The larger size of basal cones corresponds to their expected higher resource availability. Moreover, well developed apical cones are the same size as basal abortive cones, although their pollination rate and pollen load is much higher. This shows that cone location is more important for their growth than pollination rate or pollen load. Thus, it is possible that well pollinated apical cones are aborted more often due to lack of resources than well pollinated basal cones. This is confirmed by our results, which show a higher average pollination rate for abortive apical cones than for abortive basal cones. Another possibility is that basal cones will develop despite a low pollination rate, which would predict a lower average pollination rate of well developed basal cones. The results, however, show the opposite: the pollination rate tends to be slightly higher for well developed apical cones. In conclusion, basal

Fig. 4. A model for flexible cone abortion. The x-axis represents time indicating important events such as cone initiation, pollination, fertilization and the start of cone growth. The y-axis represents the number of cones per tree, indicating a theoretical maximum number of cones in case of limited resources. The numbers 1, 2 indicate the difference in numbers of cones per tree between non-limiting and limited resource events, under different preceding pollination intensities.
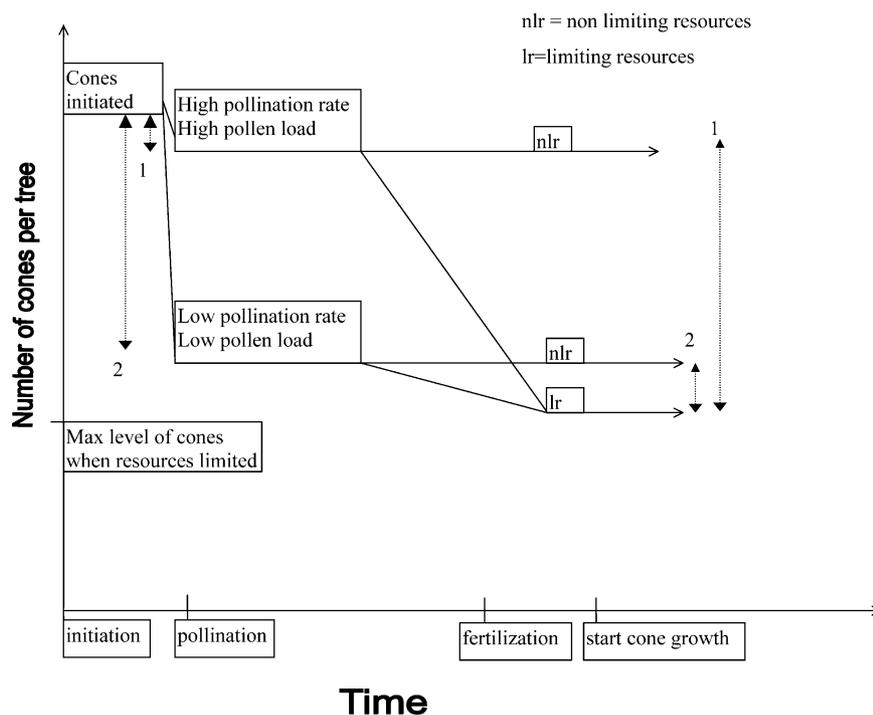
cones grow more than apical cones even under low pollination rates, but they are aborted when insufficiently pollinated (under 40%). In contrast apical cones can be aborted despite a high pollination rate. This is also reflected in the range of pollination rates. Abortive basal cones have an upper limit of pollination rates of 60%, whereas in apical cones this upper limit is 80%. Furthermore, well developed basal cones have a lower limit of 40%, whereas for apical cones this limit is 60%. In conclusion, resource mediated abortion affects apical cones more than basal cones, which explains the higher abortion rate of apical cones.

The flexible abortion model

This study shows that both resource availability and pollen quantity play a role in cone abortion of *P. halepensis*. Some authors have proposed one factor to be more important than the other in flowering plants (Jong de and Klinkhamner 1989, Ackerman and Montalvo 1990, Medrano et al. 2000). Other studies have concluded that both factors play an equal role in selective abortion (Vaughton 1991, Corbet 1998, Arista et al. 1999, Trueman and Wallace 1999). In this study most abortion takes place after pollination, before cone growth and thus pollen quantity seems to be the most important factor in cone abortion. However, we expect that the role of pollen quantity and resource availability may differ between years and individual trees. We propose a model (Fig. 4) in which pollination rate and

resource availability play a flexible role in cone abortion. First, pollination rates determine how many ovules can develop into seeds, and when less than a critical percentage of the ovules is pollinated (in this study 40%), cones are aborted (Bertin 1982, Winsor et al. 1987). Remaining cones, subsequently can develop into mature seed cones only when there are sufficient resources. If the resource availability is limited, part of these well pollinated cones will be aborted as well (Stephenson 1981). Stephenson et al. (1988) suggested that mostly fruits with the few seeds will be the ones to be aborted in this case. The path followed in the model will vary between trees and years as it depends on the cone-, pollen- and resource-status of a tree, which depend on tree size, stand density, soil nutritional status and weather conditions (Owens and Molder 1977). Because cone development in *P. halepensis* is a two-year process, the final abortion rate depends on the tree status over two subsequent years. An individual tree may therefore experience several possibilities: a good year for pollination may be followed by a good year for cone development, a bad pollination year may be followed by a bad year for cone development, a good pollination year may be followed by a bad year for cone development and vice versa. Thus, resource availability may be the main limiting factor for cone-set in one case (no. 1, Fig. 4) and pollination may be the main limiting factor in another case (no. 2, Fig. 4). Quantification of this model can be done by artificially changing resource availability to trees and study abortion patterns over several years. We acknowledge that

selective abortion in pines may also be affected by other factors such as self-pollination (Karkkainen et al. 1996), genetic load and maternal genotype (Karkkainen et al. 1999), fertilization problems (Owens et al. 1991), predation and pathogens (Rauf et al. 1984a, b, De Groot and Fleming 1994). This kind of abortion can be included in the model as well. The idea that the role of pollen and resource availability in cone abortion is flexible rather than fixed, makes sense in the unpredictable Mediterranean-type climate in which *P. halepensis* naturally occurs. In this climate for example, rainfall is often a limiting resource but is highly variable among years (Mooney and Kummerow 1981).

Conclusions

In conclusion, the cone-set ratio of *P. halepensis* corresponds to the generally expected value for wind pollinated woody species. This relatively low cone-set ratio is the result of a high abortion level, mediated by pollen quantity and resource availability. The role of pollen quantity and resource availability is proposed to be flexible and is variable among trees and years. The selective abortion combined with effective pollination cause the relatively high seed-ovule ratio of *P. halepensis*. This high seed-ovule ratio is adaptive due to the high investment in protective cone elements in *P. halepensis*.

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