Variations in the Seed Production of
Pinus densiflora Trees

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Current data on reproductive characters of endemic and native species are essential to provide a strategy for the conservation of these species. Red pine (*Pinus densiflora* Sieb. & Zucc.) is one of the dominant, native tree species in Korea, but its reproductive ecology is not well-known. In 1997, the pattern of variation in cone and seed yields contributing to the conservation of declining populations of red pines was examined. Plant height and dbh were measured, and several new cones were collected from each tagged tree after counting the number of cones on each tree. For a subset of cones sampled, the number of fertile scales, the number of seeds at three development stages (early/late aborted, and filled seed), seed wing size, wing color, and individual filled seed mass were measured. The three sites which differed significantly in mean plant size also differed in mean cone and seed production per plant. However, further analyses showed that most variation in characters examined occurred among plants within sites, but not among sites. An average of 90% of the potential seeds on the cones aborted at an early developmental stage, demonstrating that early abortion is a major factor affecting the number of filled seeds per cone. Individual seed mass was the only character which exhibited significant variations among sites as well as among trees within sites. Individual seed mass was overall negatively correlated with both the percentage of late abortion and the number of old cones per plant, suggesting that both the past and current years' reproductive activities have caused variations in seed mass. The potential dispersal distance of red pine seeds is quite large. However, wing loading was correlated with seed mass and number in a complex pattern across the sites. Distribution of seeds with varied colored wings differed among sites and among trees within sites. These results suggest that red pines at different sites might possess different strategies to cope with selection pressures acting during the final phase of reproduction, from seed dispersal to establishment. Then the 'fitted' red pine trees at each site should be identified and managed to conserve or restore populations.

In order to provide a strategy for the conservation of endemic and native species, current data on the reproductive characters of concerned species are essential. It is because population maintenance and, furthermore, the continuation of a certain species is attained through reproduction (Primack and Kang, 1989). It is widely known that not all ovules in a flower or flowers of a plant produce seeds or fruits, respectively. Such abortions of reproductive structures are attributed to the genetic incompatibility between paternal and maternal parents, particularly in outcrossing plants (Denti and Schoen, 1988; Smith et al., 1988; El-Kassaby and Barclay, 1992). Environmental factors such as water and minerals in soil, light, and pollen limitation also

contribute to the final seed yield (Caron and Powell, 1989a, b; Owens et al., 1991; Cremer, 1992).

Most of these studies were conducted using flowering plants in which the cycle of reproduction occurs within one or at most two years. However, for gymnospermous pine species in general, unlike flowering plants, it takes three years to complete the cycle of reproduction (Singh, 1978): flower bud formation in the summer of the year[-1], pollination in the spring of the year[0], and seed maturation in the fall of the year[+1]. Then during the long period of one reproductive episode, each reproductive stage of pines is likely to be specifically subjected to its environmental conditions (Houle and Filion, 1993). Studies on pines or spruces in temperate and boreal forests showed a strong correlation between climatic conditions such as temperature and precipitation over these three years (from year[-1] to year[+1]) and seed yields (Lee,

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1979; Caron and Powell, 1989a; Owens et al., 1991; Houle and Filion, 1993; Despland and Houle, 1997). However, the patterns disclosed in several species of the Pinaceae are not necessarily concordant, suggesting the possibilities of diverse reproductive strategies within closely related species.

Plant size such as height and growth habit may also alter the pattern of seed production. Smith et al. (1988) claimed that short broad trees of Pinus contorta occurring in open sites possessed a relatively higher ratio of aborted seeds due to higher selfing than tall trees in dense stands. In Picea glauca, taller trees tended to bear cones with larger number of scales which is an important component of seed yield (Nienstaedt, 1985). Variations in seed yield characters such as seed size and number may also accompany variation in wing sizes when plants are constrained in the resources for reproduction. An evolutionary explanation is also possible. Wing loading, which is a measure of seed dispersal ability, is correlated with both seed mass and wing size (e.g., Augspurger, 1986; McGinley et al., 1990). Not only seed mass, seed number, and wing loading, but also seed wing color could contribute to the fitness of the plant species. Seed wing color variations in Pinus sylvestris and P. contorta have been adaptively explained to lower the risk of seed predation (Nystrand and Granstrom, 1997).

The variation of the reproductive characters of red pines (Pinus densiflora Sieb. & Zucc.) which are one of the dominant tree species in Korea was examined. The geographic distribution, socioecolgy, growth pattern, and litter decomposition of red pines have been reported (Yim, 1980; Chang and Leem, 1986; Lee and Kim, 1987; Kim, 1989; Lee and Lee, 1989; Mun and Choung, 1996). A few studies on red pines in Korea (e.g., Yim and Kwon, 1976; Yim et al., 1981) showed clinal variations of cone and seed characters. Thus, there is almost no other ecological information on the reproductive characters of our native red pines. Considering the rapid decline in red pine populations in Seoul metropolitan areas and suburbs, it is urgent to have comprehensive data on the variations of cone and seed production within and among the red pine populations.

In this study, the following questions were specifically addressed. First, I examined the pattern of variations in cone and seed production of red pines across three sites in Seoul. I also evaluated the pattern of seed abortions, and related it to variations in seed number and size among cones of red pines. Finally, differences in wing loading and color within and among sites were assessed. These data provide the basic information necessary for the conservation or restoration of declining red pine populations.

Materials and Methods

Red pine is a native gymnosperm present all over

Korea. Needle-shaped leaves are 8-9 cm long and two in a fascicle. This species blooms in April to May and is pollinated by wind. Red pine is monoecious with yellowish, oblong-linear microsporangiate strobili (male cones) at the bottom of branches and purplish, ovulate strobili (female cones) at the tip of new branches. When female cones mature in the fall one year after pollination, they dehisce and disperse seeds with varied colored wings.

Data on cone and seed production were obtained from the three sites of Seoul: Kwanak (KA) in a mixed forest of Mt. Kwanak, Dobong (DB) in the Mt. Puk'ansan National Park, and Hongneung (HN) within the Forestry Research Institute at Hongneung. In Oct. 1997, 16 - 31 trees were randomly selected and tagged, and their height (for KA and HN sites) and dbh (for all sites) were measured. The numbers of old (for all sites) and new cones (for KA and HN sites) on red pines were counted. Seeds disperse as soon as the cones turn brown and the scales open. Thus, several to more than 10 new, undehisced cones were collected from these sites, and each cone was kept in an envelope at room temperature for two months. Not all cones opened by this method, and the proportion of trees with serotinous cones was compared across the three sites. The numbers of filled and late aborted, empty seeds within dehisced cones were examined, and the filled seed mass was measured. Then, I calculated the total seed number per tree and mean individual seed mass per plant. The total seed number per tree was obtained by mulitiplying the mean number of seeds per cone by the number of nonserotinous cones. One-way ANOVAs with the site as a main factor were employed to examine the differences in plant size, cone, and seed characters among the sites.

In order to further examine the variation in percentages of seed development stages (early and late abortion, and filled seed) in details, five cones from each of the five trees at each site were randomly collected and the number of fertile scales was counted for each cone. As each scale bears two ovules on its upper surface, the total number of potential seeds per cone was estimated as twice the number of fertile scales per cone. Late aborted seeds were comparable to filled seeds in terms of seed and wing sizes. These seeds were empty, less than 5 mg in most cases, having only a shriveled female gametophyte and embryo. Early aborted seeds per cone were estimated by subtracting the sum of late aborted and filled seeds from the total potential seeds because they could not be easily separated from the scales. In many pine species, unpollinated ovules or ovules pollinated with inviable pollen usually result in very small, flattened "seeds" (Sarvas, 1962). Simply to avoid confusion in terminology, these unsuccessful ovules are termed as early aborted seeds. The percentages of early abortion, late abortion, and filled

Table 1. Means (±SD) and ranges (in parentheses) of plant size, cone, and seed characters of *Pinus densiflora* trees measured in 1997 at three sites, Kwanak, Dobong, and Hongneung, in Seoul

Character	Kwanak (N=21)	Dobong (N=16)	Hongneung (N=31)	Overall mean
Tree height (m)	4.7 ± 1.2 (2.5 - 7.0)	-	5.6 ± 1.4 (2.0 - 8.0)	5.3 ± 1.4 (2.0 - 8.0)
DBH (cm)	12.9 ± 4.0 (7.0 - 22.3)	14.3 ± 5.8 (4.8 - 24.1)	17.7 ± 4.1 (7.9 - 25.3)	15.5 ± 5.0 (7.0 - 22.3)
Old cones/plant	203.6 ± 2.8 (31 - 1607)	6.5 ± 2.1 (3 - 43)	139.6 ± 2.6 (18 - 1014)	78.2 ± 5.2 (3 - 1607)
New cones/plant	21.6 ± 3.1 (3 - 188)	-	52.1 ± 2.8 (14 - 331)	36.6 ± 2.7 (3 - 331)
Late aborted seeds/plant	115.6 ± 4.0 (5.0 - 1047.2)	-	160.6 ± 4.6 (0 - 1677.5)	141.2 ± 4.3 (0 - 1677.5)
Filled seeds/plant	67.9 ± 6.3 (0 - 2409.0)	-	281.8 ± 2.5 (16.2 - 1149.5)	158.9 ± 4.6 (0 - 2409.0)
Mean individual seed mass (mg)	9.81 ± 1.16 (7.85 - 13.36)	12.03 ± 1.42 (7.51 - 31.84)	13.68 ± 1.22 (9.14 - 20.79)	12.03 ± 1.30 (7.51 - 31.84)

Numbers of late aborted and filled seeds per plant were estimated by multiplying the mean numbers of these seeds per cone by new cone numbers on each plant. Tree height and new cone numbers were not measured at Dobong.

seed were obtained by dividing the number of seeds at each stage by the number of potential seeds per cone.

Seed wing length and width were measured for both late aborted and filled seeds. Each filled seed was weighed up to 0.1 mg, and the wing loading was obtained only for these seeds. Wing loading was defined as weight divided by wing area (millidynes · cm^{-2}) (Augspurger, 1986) and square-root of wing loading was used for the comparison across the sites. The expected mean dispersal distance of seeds was calculated following Cremer (1977). Concurrently, seed wing color was noted. Nested ANOVAs with the site and trees nested within the sites as two random factors were conducted to identify the relative importance of site and individual tree identity on seed characters such as the total potential seeds per cone, the proportions of early/late abortion and filled seed, individual seed mass, wing size and wing loading. When the effect of the site was not significant, one-way and two-way ANOVAs with tree identity and/or filled vs. empty seed category as factors were conducted separately for each site. Spearman rank correlation analyses were conducted to examine the relationship between the characters measured. The two-way contingency table analyses were employed to examine the distribution of seed wing colors across the sites and among the

trees within each site. I evaluated the adjusted standardized residuals to identify the categories which contributed significantly to the G-value. Statistical analyses were conducted using SAS (1985).

Results

Variations in cone and seed production among sites

Tree height and dbh of red pines showed a tendency to increase in the order of KA < DB < HN (Table 1). Thus, red pines at HN were significantly taller and larger than those at KA and DB (Table 2). The number of old cones borne on trees varied among plants within sites and among the three sites (Table 1). For example, red pine trees at KA possessed 31 - 1607 old cones while those at HN had 18 - 1014 old cones. Thus, the smaller trees at KA bore an average of 1.5 times higher number of old cones than the larger trees at HN, though statistically not being significant (Table 2). Red pines at DB had an extremely small number of old cones, for example, only 3.2% and 4.7% of those at KA and HN, respectively. Sixty eight percentage of variance in old cones borne on each red pine was explained by the site, and the difference in mean old cone number among the sites was highly significant (Table 2). On

Table 2. One-way ANOVA of the effect of site on cone and seed characters of *Pinus densiflora* trees at three sites, Kwanak (KA), Dobong (DB), and Hongneung (HN), in Seoul

Character	df	F	P	Note
Tree height (m)	1, 50	6.00	*	HN > KA
DBH (cm)	2, 64	7.68	***	HN > KA, DB
Old cones/plant	2, 65	68.07	***	KA, HN > DB
New cones/plant	1, 50	11.05	**	HN > KA
Late aborted seeds/plant	1, 49	0.60	ns	
Filled seeds/plant	1, 50	13.52	***	HN > KA
Mean individual seed mass (mg)	2, 64	10.53	***	HN > KA, HN = DB, DB = KA

Since new cone numbers were not measured at DB, model df was reduced to 1 for characters such as late aborted and filled seeds per plant
* P<0.05, ** P<0.01, *** P<0.001, ns = not significant.

Table 3. Spearman rank correlation coefficients of plant size, cone, and seed characters among Pinus densiflora trees at three sites, Kwanak (KA), Dobong (DB), and Hongneung (HN), in Seoul

Character	Site	Plant height	DBH	Old cones	New cones	Late aborted seeds	Filled seeds
DBH	KA	0.59 *					
	DB	-					
	HN	0.43 *					
	Overall	0.64 ***					
Old cones/plant	KA	0.41	0.63 *				
	DB	-	-0.04				
	HN	0.30	0.47 **				
	Overall	0.28 *	0.29 *				
New cones/plant	KA	0.38	0.32	0.53 *			
	DB	-	-	-			
	HN	0.40 *	0.45 *	0.77 ***			
	Overall	0.47 ***	0.58 ***	0.53 ***			
Late aborted seeds/plant	KAI	0.18	0.23	0.45 *	0.96 ***		
	DB	-	-	-	-		
	HN	0.37 *	0.24	0.50 **	0.67 ***	0.28	
	Overall	0.34 *	0.32 *	0.42 **	0.73 ***		
Filled seeds/plant	KA	0.28	0.44 *	0.49 *	0.87 ***		
	DB	-	-	-	-		
	HN	0.43 *	0.35	0.43 *	0.58 **	0.39 *	
	Overall	0.47 ***	0.56 ***	0.33 *	0.77 ***	0.40 **	
Individual seed mass/plant	KA	-0.13	0.08	-0.32	0.46	0.06	0.09
	DB	-	0.58 *	-0.21	-	-	-
	HN	-0.27	0.13	-0.18	-0.20	-0.61 ***	-0.29
	Oerall	0.08	0.43 ***	-0.16	0.15	-0.23 *	0.22

Sample size is 21, 16, and 31 for KA, DB, and HN, respectively
* P<0.05, ** P<0.01, *** P<0.001.

the other hand, red pines at HN produced an average of 2.4-fold more new cones per plant than those at KA. Thus, although the total number of old and new cones per plant was relatively greater at KA than at HN, there was no statistically significant difference between the sites ($F_{1,50}=0.44$, P≫0.05; total number of cones per plant=234.9±2.6 and 198.0±2.4 at KA and HN, respectively).

At all sites, almost half of the trees produced cones all of which dehisced after drying, while the

remaining trees produced one to a few serotinous cones. Overall, 5.0% of new cones on red pines across the sites was serotinous. The median proportions of serotinous cones over new cones were 16.7%, 7.2%, and 0% at KA, DB, and HN, respectively, without exhibiting any significant differences (Kruskal-Wallis one-way ANOVA: $X^2=1.80$, df=2, P=0.407).

Red pines examined at these sites produced 0 to 2409 filled seeds per plant in 1997 (Table 1). Red pines at HN produced an average of 281.8±2.5 filled

Table 4. Mean (± SD) and ranges (in parentheses) of cone and seed characters among cones of five Pinus densiflora trees randomly selected from the tagged trees in 1997 at three sites, Kwanak (KA), Dobong (DB), and Hongneung (HA), in Seoul

Character	Kwanak	Dobong	Hongneung	Overall Mean
Total potential seeds/cone	143.9 ± 31.9 (88 - 204)	150.2 ± 23.0 (112 - 210)	166.8 ± 27.9 (114 - 224)	153.5 ± 29.0 (88 - 224)
Early aborted seeds/cone	127.8 ± 33.7 (81 - 198)	135.2 ± 25.5 (97 - 198)	151.0 ± 33.4 (88 - 212)	138.0 ± 31.1 (81 - 212)
Late aborted seeds/cone	4.7 ± 2.8 (0 - 13)	6.3 ± 5.0 (0 - 16)	4.1 ± 4.6 (0 - 13)	5.0 ± 4.3 (0 - 16)
Filled seeds/cone	11.4 ± 11.3 (0 - 35)	8.6 ± 9.2 (0 - 31)	11.5 ± 7.0 (2 - 30)	10.5 ± 9.3 (0 - 35)
Individual seed mass (mg)	9.85 ± 2.30 (5.00 - 16.30)	11.16 ± 3.87 (5.00 - 18.60)	12.52 ± 4.22 (5.00 - 20.60)	11.17 ± 3.69 (5.00 - 20.60)
Wing length (mm)	13.4 ± 2.9 (8.0 - 20.8)	14.1 ± 1.4 (10.5 - 17.3)	15.2 ± 1.9 (9.6 - 19.8)	14.2 ± 2.4 (8.0 - 20.8)
Wing width (mm)	4.9 ± 0.6 (3.1 - 6.7)	5.4 ± 0.7 (3.4 - 7.5)	5.2 ± 0.7 (2.5 - 7.0)	5.2 ± 0.7 (2.5 - 7.5)

Since three to five cones randomly selected from each tree were examined, sample size of cones was 21 at each site. Individual seed weight was measured only for filled seeds; N = 160, 107, and 156 for KA, DB, and HN, respectively. Wing size was measured for both late aborted and filled seeds; N = 258, 240, and 242 for KA, DB, and HN, respectively.

Table 5. Nested ANOVA of the effects of site and tree identity within sites on seed characters of five *Pinus densiflora* trees randomly selected from the tagged trees in 1997 at three sites, Kwanak, Dobong, and Hongneung, in Seoul

Cheracter	Site			Tree (Site)			Model		
	df	F	P	df	F	P	df	F	P
Total potential seeds/cone	2	1.43	ns	12	5.12	***	14, 48	5.36	***
% Early abortion	2	0.07	ns	12	5.11	***	14, 48	4.44	***
% Late abortion	2	0.77	ns	12	3.91	***	14, 48	3.78	***
% Filled seed	2	0.75	ns	12	5.22	***	14, 48	4.68	***
Filled seeds/cone	2	0.06	ns	12	4.18	***	14, 48	3.74	***
Individual seed mass (mg)	2	3.69	(*)	12	7.69	***	14, 408	10.45	***
Wing area (mm²)	2	2.76	ns	12	43.22	***	14, 725	44.18	***
Wing loading ²	2	0.39	ns	12	5.46	***	14, 408	4.88	***

The percentages of early, late, and filled seed were estimated by dividing the early aborted, late aborted, and filled seed numbers by total potential seeds per cone.
(*) P = 0.0510, *** P<0.001, ns = not signficant.

seeds per plant while those at KA had an average of 67.9 ± 6.3 filled seeds, demonstrating a 4.2-fold difference between the two sites. Thus, red pines at HN produced significantly higher number of filled seeds per plant than those at KA (Table 2). The number of late aborted seeds per plant did not differ significantly between the two sites (Table 2). Consequently, the mean proportion of filled seeds over the sum of filled and late aborted seeds was far higher at HN than at KA, i.e., 63.7% and 37.0%, respectively. Mean individual seed mass per plant varied among the three sites by a factor of 1.4 (Table 1). Mean individual seed mass differed among sites, with a significant difference only between HN and KA (Table 2).

Taller plants also had a larger dbh (Table 3), and these large red pines tended to bear more old as well as new cones per plant at both KA and HN. Thus, red pines with more old cones were producing more new cones. Plant size was also positively correlated with the number of late aborted and filled seeds per plant. In contrast, dbh and the cone number were independent of each other at DB. The patterns of correlation between mean individual seed mass per plant and other characters were quite dissimilar across the sites. For example, larger plants in dbh produced heavier seeds only at DB, while plants with a larger number of late aborted seeds yielded smaller seeds only at HN. Mean individual seed mass was consistently negatively, though insignificant, correlated only with old cone numbers per plant across the sites.

Variations in seed characters among trees within sites

The mean number of fertile scales per cone was in the range of 72.0, 75.1, and 83.3 at KA, DB, and HN, respectively. Across the three sites, only 7.1% of the average of 153.5 ovules on a cone matured to filled seeds (Table 4). The rest of ovules aborted early or late during seed development. About 90% of the ovules aborted at an early developmental stage at all sites, but the proportion of late aborted seeds ranged from 2.4 to 4.2%, slightly higher at DB than at HN.

Nested ANOVAs confirmed the source of variation in seed development stages. The potential seed numbers on a cone and the proportions of three developmental stages (early/late aborted and filled seed) differed significantly among the five maternal trees within each site, with no significant difference among sites (Table 5). In subsequent one-way ANOVAs with the tree identity as a main factor, the potential seed numbers on a cone differed significantly among trees at both KA and HN, but not at DB. Fig. 1 shows that cones on tree 3 at KA had 1.6 times larger number of potential seeds than those on trees 1 and 4, while cones on tree 3 at HN had 1.3 to 1.5 times larger number of potential seeds than those on trees 1, 2, and 4. The proportion of early abortion also differed significantly among trees at both KA and HN. Tree 4 at KA showed a far higher early abortion rate compared to tree 1, while tree 4 at HN experienced a lower early abortion rate than all the other trees (Fig. 1). However, a significant difference in the proportion of late abortion was detected only at HN. For example, tree 4 at HN exhibited a 65-fold higher probability of late abortion than tree 1. The percentage of filled seed differed significantly among trees at both KA and HN. At KA, about 15-16% of ovules in a cone matured into filled seeds in trees 1 and 5 in contrast to 1.6 - 0.7% in trees 3 and 4. At HN, 14% of ovules produced filled seeds in tree 4 compared to 4 - 6% in others.

Due to the high percentage of seed abortion during development, there were an average of 10.5 ±9.3 filled seeds per cone without a significant difference among sites (Tables 4, 5). The number of filled seeds per cone differed significantly among trees at both KA and HN (Fig. 1). At KA, tree 5 had 24 seeds per cone, about twice higher than the overall mean of filled seeds per cone. Tree 4 at HN also produced larger numbers of filled seeds per cone, particularly, than tree 3.

Overall, individual seed mass varied 4-fold, ranging from 5.0 to 20.6 mg. Unlike the other characters examined, individual seed mass was marginally significantly affected by the site while it was highly affected by the tree identity at each site (Table 5). That is,
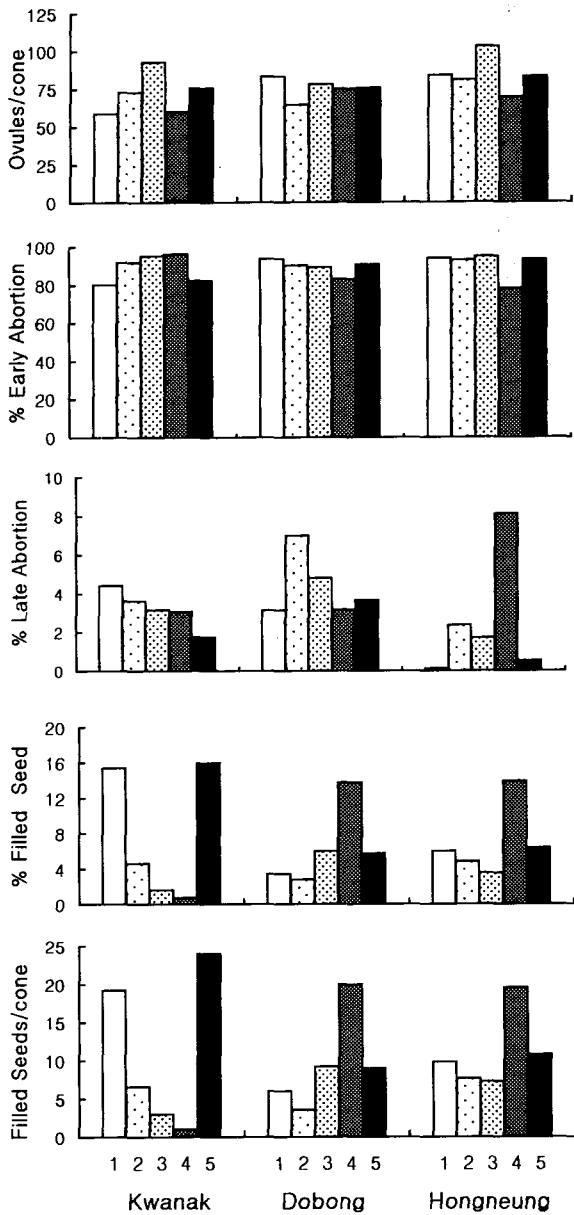
Fig. 1. Differences in mean seed characters among five red pine trees at each site, Kwanak (KA), Dobong (DB), and Hongneung (HN). One-way ANOVAs with the tree identity as a main factor on each character were separately conducted for each site. Ovules/Cone: KA F=6.24, P < 0.01, DB F=2.14, P > 0.05, and HN F=7.21, P < 0.01; % Early abortion: KA F=6.42, P < 0.01, DB F = 20.57, P < 0.001; % Late abortion: KA F=1.80, P > 0.05, DB F=0.91, P > 0.05, and HN F=34.62, P < 0.001; % Filled seed: KA F=7.89, P < 0.001, DB F=2.11, P > 0.05, and HN F=7.20, P < 0.01; Filled seeds/cone: KA F=7.47, P < 0.01, DB F=1.93, P > 0.05, and HN F=3.53, P < 0.05. Corrected total df is 20 for all ANOVAs.

Fig. 2. Differences in mean individual seed mass and wing loading among the five red pine trees at each site, Kwanak (KA), Dobong (DB), and Hongneung (HN). One-way ANOVAs with the tree identity as a main factor on individual seed mass and wing loading were separately conducted for each site. Individual seed mass: KA $F_{4,155}$= 17.67, P < 0.001, DB $F_{4,102}$=5.53, P < 0.001, and HN $F_{4,151}$=6.59, P < 0.001; Wing loading: KA $F_{4,155}$=7.63, P < 0.001, DB $F_{4,102}$ = 6.46, P < 0.001, and HN $F_{4,151}$=3.24, P < 0.05.

tree identity explained a greater proportion of variance in seed mass compared to the site (16.6% vs. 6.6%). Among the sites, red pines at HN produced the heaviest seeds, followed by those at DB and KA. Mean individual seed mass per cone also varied greatly among the trees at all sites. Thus, the significant difference among the trees was detected
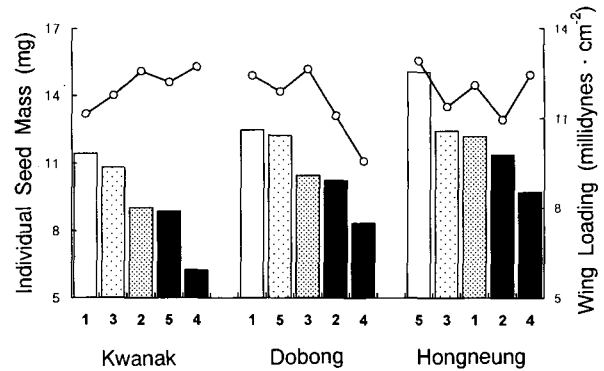
only in the individual seed mass at DB. Tree 1 at KA, trees 1 and 5 at DB, and tree 5 at HN yielded heavier seeds than other trees within the corresponding sites (Fig. 2).

The percentages of three seed development stages and the number of filled seeds per cone were quite consistently in correlation with each other (Table 6). Cones which aborted proportionally higher numbers of seeds at the early stage of seed development exhibited a lower rate of late abortion, and those cones produced lower number of filled seeds at all sites. Thus, the percentages of early and late abortion showed an inverse correlation with the potential seed number per cone. The filled seed number per cone was not particularly in correlation with the potential seed numbers per cone. The significantly negative correlation between the potential seed number per cone and the percentage of filled seed at HN reflects a significantly positive correlation between the potential seed number and the percentage of early abortion. Mean individual seed mass per cone was, overall, correlated negatively with the percentage of late abortion. However, the correlation coefficients of the individual seed mass with other characters, for example, the number of filled seeds per cone and the percentages of early and late abortion, appeared to differ across the sites. At KA, mean individual seed mass was negatively correlated with the percentage of early abortion, and positively correlated with the percentage of late abortion. The reversed pattern of correlation was observed among cones at HN. Also, the seed number was negatively correlated with seed mass among cones only at HN. Among these 10 trees randomly selected from KA and HN (5 trees from each site), the percentage of early abortion tended to decrease with an increase in plant height while that of late abortion tended to increase; correlation coefficients were not statistically

Table 6. Spearman rank correlation coefficients of seed characters among cones of five *Pinus densiflora* trees randomly selected at three sites, Kwanak (KA), Dobong (DB), and Hongneung (HN), in Seoul

Character	Site	Potential seeds	Filled seeds	Individual seed mass	% Early abortion	+% Late abortion
Filled seeds	KA	0.02				
	DB	0.37				
	HN	-0.19				
	Overall	0.07				
Individual seed mass	KA	0.13	0.29			
	DB	0.24	0.67			
	HN	0.16	-0.41			
	Overall	0.34 **	0.02			
% Early abortion	KA	0.15	-0.94 ***	-0.42		
	DB	0.21	-0.58 **	0.16		
	HN	0.52 *	-0.78 ***	0.33		
	Overall	0.28 *	-0.79 ***	0.14		
% Late abortion	KA	-0.27	0.16	0.44	-0.40	
	DB	-0.49 *	-0.13	-0.28	-0.66 **	
	HN	-0.46 *	0.34	-0.36	-0.47 ***	
	Overall	-0.48 ***	0.06	-0.27 *	-0.59 ***	
% Filled seed	KA	-0.10	0.98 ***	0.31	-0.96 ***	0.20
	DB	0.27	0.99 ***	0.07	-0.63 **	-0.07
	HN	-0.46 *	0.94 ***	-0.41	-0.81 ***	0.37
	Overall	-0.04	0.99 ***	0.00	-0.82 ***	0.11

Sample size is 19-21 for both KA and DB, and 21 for HN.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

significant (r=-0.48 and 0.46, respectively, P > 0.05 for both, N=10).

Variations in wing loading and wing color

The wing length and width of the 740 seeds examined were 8.0 - 20.8 mm and 2.5 - 7.5 mm, respectively (Table 4). Thus, wing size ranged from 24.0 to 122.3 mm^2 with an overall mean of 74.9 ± 18.6 mm^2. Like other seed characters, wing size variation occurred mainly among the trees within sites, not among the sites (Table 5). When a third variable, a filled vs. empty seed was incorporated into the Nested ANOVA, both the tree identity and filled vs. empty seed factors were significant (model $F_{15,724}=43.91$, $P < 0.0001$; site $F_{2,12.09}=2.89$, $P > 0.05$; tree (site) $F_{12,724}=39.78$, $P < 0.0001$; filled vs. empty seed $F_{1,724}=22.07$, $P < 0.0001$). In subsequent two-way ANOVAs with the tree identity and filled vs. empty seed as two factors, the effect of tree identity on wing size was consistently significant across the three sites, while the effect of filled vs. empty seed category on wing size varied among trees at both DB and HN (Table 7). Neglecting the effect of the tree identity, the filled seeds possessed significantly larger wings than the empty seeds ($X=78.5 \pm 19.4$ mm^2 and 70.1 ± 16.2 mm^2, N=423 and 317, respectively). Wing loading ranged

from 6.62 to 18.19 (millidynes · cm^{-2}) with an overall mean of 11.86 (millidynes · cm^{-2}). Wing loading differed significantly among trees within sites without a significant difference among sites (Table 5). The relationship between wing loading and seed mass appeared to differ among sites (Fig. 2). Correlation analyses further supported this result. The trees with smaller seeds in mass tended to have a higher wing loading at KA, while the seed mass was positively correlated with wing loading at the other sites (r= -0.90, 0.70, and 0.30 at KA, DB, and HN, respectively, P < 0.05 only at KA, N=5 for all pairs). Mean wing loading per plant was not significantly correlated with both the tree height and dbh (r=0.11 and 0.16, N=10 and 15, respectively, P > 0.05 for both). Strongly negative correlations between wing loading and both the old and new cone numbers per plant were observed at HN, but not at KA (HN: with old cones r=-0.80, P=0.10, with new cones r=-0.60, P=0.28; KA with old cones r=0.0, r=-0.10, P ≫ 0.05 for both, N=5 for all pairs).

The two-way contingency table analysis (site x wing color) showed a significant association between the site and wing color (Table 8). For example, at KA 78.3% of seeds had light brown colored wings, without any tree producing seeds with white wings.

Table 7. Two-way ANOVA of the effects of tree identity and filled vs. empty seed category on wing size of *Pinus densiflora* seeds at three sites, Kwanak, Dobong, and Hongneung, in Seoul

Source of variance	Kwanak			Dobong			Hongneung		
	df	F	P	df	F	P	df	F	P
Tree identity (Tree)	4	67.23	***	4	11.39	***	4	24.25	***
Filled vs. empty seed (Seed)	1	0.52	ns	1	9.74	**	1	2.95	ns
Tree * Seed	4	1.87	ns	4	2.85	*	4	2.40	(*)
Model	9, 248	39.04	***	9, 230	9.33	***	9, 232	17.51	***

(*) P = 0.0510, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

Table 8. Distribution of *Pinus densiflora* seeds with different colored wings at three sites, Kwanak, Dobong, and Hongneung, in Seoul

Wing color	Site			G
	Kwanak	Dobong	Hongeung	
White wing	0 -	62	170 +	
Light brown wing	202 +	144 +	21 -	448.35 ***
Dark brown wing	56	34 -	103 +	

Likelihood ratio Chi square is reported
***P<0.001. A +/- sign indicates where observed values were greater or less than the expected value at alpha = 0.05 level.

At DB, there were proportionally fewer dark brown winged seeds and more light brown winged seeds than expected. The HN site exhibited a bimodal pattern of seed wing colors in contrast to the other sites; the majority of seeds had either white wings or dark brown wings (57.8% and 35.0%, respectively). However, trees within sites were also characterized by a distinct seed wing color, supported by a significant association between the tree identity and wing color at all sites (Fig. 3). For example, at HN, trees 1 and 2 yielded seeds all having dark brown wings, while those of trees 3 and 4 produced only seeds with white wings.

Discussion

About two thirds of the total variance in the number of old cones per red pine was explained by the site. For example, red pines at KA and HN bore an average of 203.5 and 139.7 cones per tree, respectively, whereas those at DB had an average of only 6.5 cones per tree. Since old cones reside persistently on red pines for up to five years (Yim, personal communication), it seems that red pines at KA and HN reproduced much more successfully than those at DB for the last five years. Plant size or climate factors such as precipitation and temperature are often believed to play a major role affecting reproduction in pines (Lee, 1979; Houle and Filion,

1993; Despland and Houle, 1997). However, red pines at KW and DB are similar in plant height. Furthermore, all three sites are in Seoul, likely to be under similar climate conditions. Site-specific factors such as disturbance by humans, soil quality, and genetic composition of trees may be responsible for the difference in the past reproductive activity of red pines among the three sites. Unlike the past cone production, new cone production in 1997 is significantly higher at HN than at KA. Yet the total number of cones per tree, combining old and new cones, does not differ significantly between KA and HN. In contrast, not only old cones, but also new cones are extremely rare at DB. Pines seem to be characterized by good and bad years of cone production. For example, *Pinus resinosa* and *P. banksiana* possess a reproductive cycle of ca. 2 and 4-6 yrs, respectively (Cremer, 1992; Houle and Filion, 1993). Since relevant information on the cycle of reproductive episode of red pines in Korea is not available at all, it is difficult to relate the differences in cone production among the three sites to the differences in the internal cycle of the reproductive period. However, the trade-off relationship between old and new cones at KA and HN suggests that the reproductive activities of red pines may also occur with a certain cycle. We are currently accumulating data on cone production in red pines in Korea.

The percentage of serotiny also varies widely from 0 to 100% among individual trees within sites, though almost half of the trees at all three sites bear only nonserotinous cones. The median percentage of serotinous cones of red pines is quite low, 5% in this study and 7% in Japan (Yim and Shidei, 1973). Serotiny of *Pinus banksiana* and *P. contorta* acts as an above-ground seed bank (McGinley et al., 1990; Houle and Filion, 1993). However, seeds within serotinous cones in red pines in Japan often fail to be released (Yim and Shidei, 1973). Although fire in
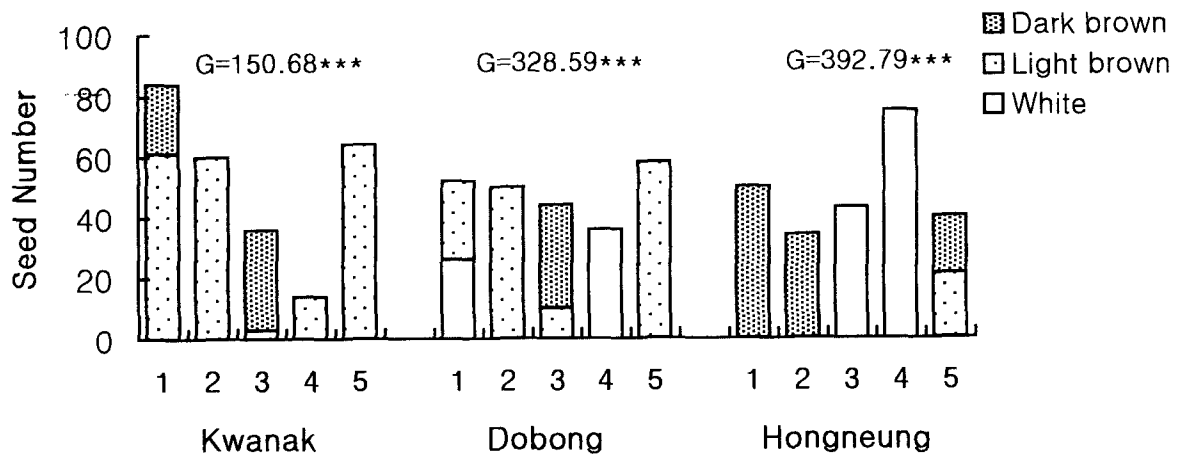

Fig. 3. The distribution of seeds with varied colored wings across the five red pine trees at each site (Kwanak, Dobong, and Hongneung). G-scores from the two-way contingency table analyses are reported for each site. ***P < 0.0001.

red pine forests occurs in the dry season in Korea (e.g., Kim, 1989; Mun and Choung, 1996), the fire cycle is not clear and even prescribed burning is not well established in Korea. In such habitats, serotiny is less likely to be an advantageous trait in terms of seed dispersal and establishment at the right time.

Overall, only 7.1% of the potential seeds on a cone mature to filled seeds in red pines, but potential seeds are not particularly associated with the final filled seeds. Similar results have been reported in several studies (e.g., Yim and Shidei, 1973; Caron and Powell, 1989a). This filled seed percentage in red pines is quite low compared to 70% in natural conditions of black spruce (Park and Fowler, 1984). The percentage of filled seeds varies according to years and environmental conditions. For example, the filled seed percentage ranges from 13 to 46% for three years in young plantations of *Picea mariana* (Caron and Powell, 1989a). *Pinus contorta* also shows a wide range of variation in the filled seed percentage with a degree of selfing, tree density, cone position, and wind direction (Smith et al., 1988), though always higher than 40%. They show that self-pollination brings about only 17% of filled seeds of cross-pollination: trees in open sites have a lower percentage of filled seeds than those in closed sites: cones on higher branches or cones on windward side of trees exhibit a higher percentage of filled seeds.

Early abortion rate amounts to about 90% at all sites in this study, which is much higher than 65%, the sum of early and late abortion, in red pines in Japan (Yim and Shidei, 1973). In pines in general, ovule abortion occurs mainly during the summer immediately following pollination, for example, before fertilization, resulting in the formation of an empty seed (Sarvas, 1962; Owens et al., 1981). Thus, as in many species of the Pinaceae (e.g., Owens et al., 1982; Allison 1990; Owens et al., 1991), early abortion of unpollinated ovules may be a major cause determining the number of filled seeds per cone in red pines. Three things should be considered to confirm the possibility of pollen limitation. First, we have to know whether such a great loss of reproductive potential is a typical pattern in red pines in Korea. Second, it is necessary to examine the presence of 'good' and 'bad' years in red pines. Third, we also have to obtain information on the male cone and pollen production at these sites. However, our results reveal unique trade-off relationships between reproductive characters of red pines: between early and late seed abortions, between early abortion and filled seed number, and between past and current reproduction in terms of cone production and individual seed mass. Thus, the effect of pollen limitation or inviable pollination on the percentage of filled seeds seems to interact with the resource level of the plants.

In pines, not only seeds but also cones them-

selves abort. In *Pinus radiata*, 4-50% of female cones have been reported to abort after pollination (Sweet and Thulin, 1969; Cremer, 1992). Cones abort when more than 20% of ovules abort in *Pinus sylvestris* (Sarvas, 1962). If cones of red pines also abort before and after pollination, red pines in Korea would experience a far greater loss of reproductive potential than other pines which were previously examined. Even if cones provide a relatively large proportion of resources for its own growth via photosynthesis, for example, 19.2% in *Pinus serotina* (Bazzaz et al., 1979), such a great loss is likely to cause a cost for red pines. It is necessary to examine the degree of cone abortion in red pines to understand the reproductive cost in red pines.

Seed number and mass are negatively, though not significant, correlated with cones only at HN where red pines reproduced most actively among the three sites in 1997. The percentage of late abortion is also negatively correlated with individual seed mass only at HN. Late abortion is believed to be more costly compared to early abortion (Bawa and Webb, 1984). In fact, late aborted seeds in red pines are comparable to filled seeds in external seed size, though they are lighter in mass and have smaller seed wings. These data suggest that the HN site is more constrained in terms of the resources available for reproduction than the other sites. The number of old cones is also a character which was consistently negatively correlated with individual seed mass across the sites. If cone biomass is an acceptable currency of reproductive cost as shown in *Pseudotsuga menziesii* (El-Kassaby and Barclay, 1992), a trade-off relationship between cone production and seed size is likely to occur. Thus, it is interpreted that both the profuse reproduction in the past, for example, for the past five years, and the relatively active reproduction in the current year have caused variations in individual seed size. Not only the seed set (e.g., Smith et al., 1988; Allison, 1990; Owens et al., 1991) but also seed size of red pines appears to be susceptible to lack of pollen and resources.

Although seeds or diaspores with large wing loading fall more rapidly than those with smaller wing loading, the rate of descent also varies with the morphology of diaspores. Wing loading ranges from 39-198 (millidynes · cm^{-2}) among 34 species of wind-dispersed tropical trees, and the relationship between the rate of descent and wing loading is not exactly concordant among the five aerodynamic groups defined by Augspurger (1986). Wing loading variations also occur among closely related species. For example, the seven temperate tree species with diaspores of samara showed a great range of variations in wing loading (37 to 262 [millidynes · cm^{-2}]) (Green, 1980). Mean wing loading of red pines, for example, 11.86 (millidynes · cm^{-2}), is small compared to that reported in those previous studies. Morphologically, red pine seeds

belong to the autogyro group (e.g., Augspurger, 1986). With small wing loading and having an autogyro type diaspore, seeds of red pines fall at a rate of 19.90 - 26.84 cm · sec^{-1} in still air, supporting that autogyro group falls most slowly at a given value of wing loading among the five groups as stated by Augspurger (1986). Red pines disperse their seeds mostly in mid October to early December. A mean wind speed during this period was of 2.35 m · sec^{-1} in 1997 (Korea Meteorological Administration, 1998). Consequently, the mean expected dispersal distance of red pines with an average height of 5.3 m is 105 m. This potential dispersal distance is quite large considering the seed mass of red pines. These results are directly related to the life history traits of red pines. Red pines demand light for successful growth and reproduction, being likely to be under strong selection for seed dispersal ability.

If selection for seed dispersal is strong, larger seeds should be equipped with larger wings to maintain wing loading at each site. Most variation in wing loading occurs among the red pine trees at all sites. Furthermore, the relationship between seed mass and wing loading among the trees was not concordant across the three sites. For example, the wing loading decreases as seed mass increases at KA while the opposite pattern exists at DB. Seed mass variation is also not independent of variation in seed number. These complex patterns of the relationship among seed mass, number, and wing loading across the sites suggest that red pines at different sites might possess different strategies to cope with selection pressures acting during the final phase of reproduction, from seed dispersal to establishment.

After seed dispersal, background matching in color might be important to lower the risk of seed predation by birds and small mammals such as squirrels and field mice. According to Yim and Shidei (1975) on red pines in Japan, 86 - 97% of the fallen seeds on the forest floor were eaten by birds and field mice. They even suggest that the seedling density is inversely related to the animal density. A recent study by Nystrand and Granstrom (1997) clearly demonstrates the selective advantage of background matching of seed color with substrate. Pinus contorta, which is a fire-adapted pine with serotinous cones, disperse their seeds primarily on freshly burnt surfaces, benefiting from producing uniformly black or dark brown seeds. In contrast, P. sylvestris which germinates over the years after a fire produces varied colored seeds. The conspicuous differences in seed wing color are observed in red pines. No seeds with white wings at KA, proportionately more seeds with light brown wings at DB, and excessively larger proportion of seeds with light brown wings at HN than expected. Furthermore, 11 out of the 15 trees examined across the sites yield seeds with uniformly colored wings. These results suggest the genetic control not only over the

seed mass and seedling growth of various tree species (e.g., Yim and Kwon 1976; Nienstaedt, 1985; El-Kassaby and Barclay, 1992; Kang et al., 1992), but also over seed wing color and potential selection for background matching in red pines. Yet it is difficult to conclude the adaptive meaning of wing color variation in red pines because predator species and their activities have not been examined at these sites. The HN site shows a particularly interesting pattern, for example, two trees each producing seeds with uniformly colored wings, either dark brown or white. If the wing color matching the substrate lowers the risk of predation at this site, and if directional selection is occuring, it is expected that the current bimodal distribution of wing color would disappear among the recruiting trees.

Considering the longevity of red pines, the percentage of filled seeds may not be a single important factor affecting the continuation of red pine populations. This study indicates that individual seed mass, wing loading, and even wing color can also exert influence over the fitness of red pines at each stage of life history. Within-site variation is overwhelmingly large in most characters examined, suggesting that there is enough genetic variation among individual trees within sites. As a consequence, in order to conserve or restore the declining red pine populations, red pine trees which produce 'fitted' seeds should be identified and properly managed at each site.

Acknowledgements

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