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Appendix

Let (s,t) denote the greatest common divisor of arbitrary integers s and t, and let "|" denote the division without remainder property.

Theorem: The equation

$$i + xR + yC \equiv m \pmod n \qquad (1)$$

where i, R, C, m and n are fixed, has integer solutions for x, y if and only if ((R,C),n) | (m-i).

Proof. All equivalences will be modulo n, so the qualifier (mod n) will be omitted for convenience sake.

Case (a). Assume that R and C are relative prime, i.e. (R,C) = 1. From the Euclidean algorithm, e.g. NIVEN and ZUCKERMAN (1972), there are integers x_0, y_0 such that

$$x_0R + y_0C = 1$$

$$\therefore x_0(m-i)R + y_0(m-i)C = m-i$$

$$\therefore i + x_0(m-i)R + y_0(m-i)C = m$$

$$\therefore i + xR + yC \equiv m$$

where $x \equiv x_0(m-i)$ and $y \equiv y_0(m-i)$.

Now note that ((R,C), n) = (1,n) = 1 which always divides (m-i).

Case (b). Assume ((R,C),n) = d where $d > 1$.

Necessity: If there is a solution to equation (1) then

$$i + xR + yC = m + kn \text{ for some } x, y, k.$$

$$\therefore xR + yC - kn = m-i.$$

Since d divides the lefthand side, it must also divide the righthand side, i.e. d | (m-i).

Sufficiency: Assume d | (m-i).

Since ((R/d,C/d),n/d) = 1, the Euclidean algorithm can be invoked and there must be x_0, y_0 such that

$$x_0(R/d,C/d) + y_0(n/d) = (m-i)/d.$$

There also exists x_1, y_1 such that

$$x_1(R/d) + y_1(C/d) = (R/d,C/d)$$

$$\therefore (m-i)/d - y_0(n/d) = x_0(R/d,C/d)$$

$$= x_0x_1(R/d) + x_0y_1(C/d)$$

Multiplying throughout by d gives

$$m - i - y_0n = x_0x_1R + x_0y_1C$$

$$\therefore x_0x_1R + x_0y_1C \equiv m - i$$

as required.

Genetic Variation in the Phenology of Flowering in Black Pine

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Summary

The flowering phenology in black pine (*Pinus nigra* ARNOLD) was investigated in a clonal seed orchard for 2 successive years (1986 and 1987). The orchard was established in October 1978 in an area of 11 ha, at Koumani Peloponnesos, Greece and included 52 clones.

The results showed that significant genetic variation exists among clones in the commencement of the phenological stages of both, male and female flowers. Early and late flowering clones are not synchronized in receptivity and pollen shedding with the optimum time of the entire seed orchard and therefore the assumptions of panmictic equilibrium is violated. The date of commencement of flowering stages is under strong genetic control. The broad sense heritability values on individual tree basis were: 0.69 for the bud burst date in both years and 0.67 and 0.70 for the date of commencement of receptivity for the years 1986 and 1987, respectively. The H values on clone mean basis for the time of commencement of receptivity were 0.87 and 0.88 for the years 1986 and 1987, respectively.

The duration of flowering stages is under weak genetic control. The H values on individual tree basis of the duration of bud burst, were found 0.34 and 0.36 for the years 1986 and 1987 respectively. The corresponding H values for the duration of receptivity were 0.12 and 0.28. The date of commencement of pollen shedding is also weakly inherited characteristic (H=0.23), while the duration of pollen shedding is completely under environmental control. In all cases the year x clone interaction effect was insignificant indicating that the early flowering clones are maintained early in all years.

The duration of receptivity of individual flower was ranking from 2 days to 8 days, while the duration of the entire seed orchard was found 32 days and 27 days for the years 1986 and 1987 respectibely.

Key words: Black pine, seed orchard, genetic variation, genetic base, heritability, correlation, effective population size, flowering receptivity, panmixis.

FDC: 165.3; 165.53; 181.8; 181.521; 174.7 *Pinus nigra*; (495).

Zusammenfassung

In einer Klon-Samenplantage ist in den Jahren 1986 und 1987 die Blütenphänologie der Schwarzkiefer (*Pinus nigra*

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ARNOLD) untersucht worden. Die Plantage, die im Oktober 1978 begründet wurde, befindet sich in Kumani auf dem Peloponnes, Griechenland, nimmt eine 11 ha große Fläche ein und enthält 52 Klone.

Die Untersuchungsergebnisse zeigten, daß es zwischen den verschiedenen Klonen einen statistisch gesicherten Unterschied beim Datum der phänologischen Stadien von weiblichen und männlichen Blüten gibt. Die Flugzeit des Blütenstaubs und die Bestäubungszeit von Früh- und Spätblütlern fallen nicht zusammen mit den mittleren Flug- und Bestäubungszeiten der ganzen Plantage und demzufolge kommt die Voraussetzung des Mischungs-Gleichgewichts nicht zustande. Das Datum der phänologischen Stadien befindet sich unter starker genetischer Kontrolle. Die Werte der Heretabilität im weiteren Sinne, bezogen auf das Individuum, waren für das Datum des Erscheinens der Fruchtblätter in beiden Jahren 0,69, während sie für das Datum des Bestäubungsbeginns für die Jahre 1986 und 1987 jeweils 0,67 bzw. 0,70 betragen. Die H-Werte bezogen auf die Klon-Mittelwerte für das Datum des Bestäubungsbeginns, waren 0,87 und 0,88 für die Jahre 1986 bzw. 1987.

Die Dauer der Blütezeit befindet sich unter schwacher genetischer Kontrolle. Die H-Werte, bezogen auf das Individuum, für das Ausschlagen der Blütenaugen waren 0,34 und 0,36 für die Jahre 1986 bzw. 1987. Die H-Werte für die Fruchtbarkeitsdauer waren 0,12 und 0,28. Das Datum des Flugzeitbeginns des Blütenstaubs ist unter schwacher genetischer Kontrolle (H=0,23), während die Flugzeitdauer des Blütenstaubs vollkommen von der Umwelt gesteuert wird. In allen Fällen war der Einfluß der Klone aufeinander statistisch unsicher. Dies zeigt, daß frühblühende Klone diese Eigenschaft für immer behalten. Die Fruchtbarkeitsdauer einer Blüte schwankt zwischen 2 und 10 Tagen, während diese für die ganze Plantage 32 und 27 Tage für die Jahre 1986 bzw. 1987 betrug.

Introduction

The phenology of the flowers of the gymnosperms has been investigated and described in details by many authors (SARVAS, 1962, 1968; CHAMBERLAIN, 1966; MIROV, 1967; DORMAN, 1976; LILL and SWEET, 1977). However, a brief summary is given here for clarification of the terms and processes.

In pines the female flower, also called conelet or megasporiangiate strobilus consists of an axis upon which the ovuliferous scales are arranged. On the upper face of each ovuliferous scale of the conelet are located 2 ovules. Each ovule consists of a mass of cells enclosed in a cover. The ovules are inverted so that the opening of the micropyle faces the axis of the conelet. Similar is also the structure of the male strobilus. It consists of an axis on which microsporophylls are borned. In the under side of each microsporophyll are found 2 pollen sacks, which at the maturity shedds pollen. At this time (time of pollination) the scales of the conelet are separated and form nearly right angle with the axis, so that the pollen grains can penetrate between them and reach the micropyles of the ovules. The ovules secrete a fluid that fills the opening of the micropyle and after the pollen grains are enclosed, the fluid is withdrown until the grains reach the nucellus (SARVAS, 1962; LILL and SWEET, 1976; DORMAN, 1976). Later on when the pollen grain germinates the pollen tube is formed which reach the female gametophyte and the haploid sperm nuclei is fused with the egg cell nuclei to form the diploid zygote that develops into embryo. The significance of adaptation (structure and function) of the flowers of gymnosperms is discussed in details by STERN and ROCHE (1974).

Flowering process in a seed orchard is of great importance, since it affects the gene exchange between the clones and consequently the genetic composition of the seed produced. WEIR and ZOBEL (1975) have pointed out that knowledge of flowering phenology is of great importance and fundamental need for the successful operation of any seed orchard. It is well known (EL-KASSABY et al., 1984, 1988) that failure in synchronization of female frower receptivity and pollen shedding has negative effect on the panmictic equilibrium, that is prerequisite in any idealized seed orchard.

Variation in receptivity and pollen shedding time has been studied in nany forest tree species (SARVAS, 1962, 1968; JONSSON et al., 1976) and treatments, such as supplimental mass pollination and water spray cooling have been proposed and in some cases implemented to overcome the differences in flowering time (DENISON and FRANKLING, 1975; EL-KASSABY et al., 1984).

In this paper the variation of different phenological stages of the female and male flowers development, as well as, the synchronization in receptivity and pollen shedding are investigated in a clonal seed orchard of black pine. Information of this nature are urgently needed for the successful management of the seeds orchards.

Materials and Methods

Plant Materials

The work reported here was carried out in an 11 ha clonal seed orchard of black pine (*Pinus nigra* ARNOLD), located in the western part of Peloponnesos, Greece, close to the place of ancient Olympia. The orchard was established in October 1978 and comprises 52 clones derived from intensively selected plus trees in the natural forest of Pelopennesos. Grafts were 2 years at the time of establishment and were planted at a spacing 6m x 6m. Clones (1 ramet per clone) were randomly assigned within replications with 1 only restriction. No grafts of the same clone were planted closer than 30m. The soil of the area developed from Tertiary deposits, is a clay loam, moderately acid with adequate supply of metalic cations and organic mater (NAKOS, 1979). Three replications were sampled and phenological observations of the different stages of the female flower development were made in 2 successive years (1986, 1987). The dates of pollen shedding was also studied in 1987. In each clone ramet the 4th whorl from the ground was sampled and 4 branches, each one with different orientation (east, west, north, south) were labelled. The labeling of the conelets was made in such a way, so that they were reprisentative with regards to growth, position and orientation within the crown. This was necessary, since earlier studies have shown that variation exists in flowering dates even within the same tree (VIDACOVIC, 1974; JONSSON et al., 1976). The stages of conelet development have been described by several researchers (BRANLETT and O'GWYNN, 1981). In this paper 4 stages of the female flower were recognized and studied: Stage 1. In this stage the female bud is increasing in size, becomes cylindrical, but is still completely covered within the bud scales. Stage 2. The apex of the enlarged cylindrical bud is opened and the first ovuliferous scales are appeared. At this stage the ovules are not receptive, but pollen grains may get inside the bud scales and if they survive they might be able to take part in fertilization. Such buds must not be isolated and included in control matings (JONSSON et al., 1976; BRAMLETT and O'GWYNN, 1980).

Stage 3. The scales of the female conelet are gradually separated and form nearly right angle with the axis of the conelet. At this stage the pollen grains can easily penetrate between the scales and reach the pollen chamber of the ovules. This is the stage of maximum receptivity. Stage 4. At this stage the ovuliferous scales increase in size and thickness so that no pollen grains can anymore penetrate between them to reach the ovules (receptivity passed). In the same (4th whorl), 4 clusters of male catkings with different orientations were also labelled and the dates of pollen shedding were recorted. The observations were made every second day during the flowering seasons and the different stages were recognized using hand lens.

Statistical Evaluation

The earliness of flowering i.e., the dates at which the female flowers were first recorded at stages 2, 3 and 4 were expressed in days required from May first to reach these stages and the resulted data were subjected to analyses of variance. The same was also applied for the dates at which the male flowers started shedding pollen. The duration of the stages 2 and 3 of the female flower, as well as, the duration of pollen shedding were also analyzed. The assumption underlying the analyses are outlined by BECKER (1967). The data of all variables, before the analyses, were checked for normality using probability plots constructed as is suggested by GNANADESIKAN (1977). Analyses of variance and calculation of variance components were conducted for each year separately and the two years combined. The form of analysis is shown in *table 1* (ANDERSEN, 1960; COCKERHAM, 1963). Estimates of broad sense heritability (H) were obtained on individual tree and clone mean basis, each with different phenotypic variance as follows:

$$H = \frac{\sigma_c^2}{\sigma_c^2+\sigma^2} \text{ (individual tree basis)}$$

$$H = \frac{\sigma_c^2}{\sigma_c^2+\sigma^2/n} \text{ (clone mean basis)}$$

The (H) values on clone mean basis are applicable for estimating genetic gain by selecting clones from the specific population, i. e. the seed orchard and establishing new clonal seed orchards or for roguing the existed. Because the data come from only one environment, the estimates of the genetic variances (σ_c^2) include the effect of clone x environment interaction component of variance. However, despite this restriction the variances and heritability estimates are valid and applicable to the specific environmental conditions under which the material are grown. Cloning effect variance may bias the (H) values obtained, but as it has been discussed in another paper (MATZIRIS, 1993), its magnitude is negligible and can be ignored.

Product moment and Spearman rank correlations among all combinations of the characteristics were estimated following appropriate procedures (SNEDECOR and COHRAN, 1968, page 193).

Design summary: Randomized complete block; 52 clones, one tree per clone per replication; 3 replications sampled.

Results and Discussion

The overall means of the characteristics studied are shown in *table 2*. It can be seen that 1986 was an early flowering year in comparison to 1987. There was a 10 day shift in the receptive period between the 2 years. In 1986 the receptive period extented from May 5 to May 31 (*Figure 1*). On May 19, 80% of the total flowers in the seed orchard were receptive and on May 13 the first female flower entered into stage 4,i.e., at this time the scales of the conelet increased in thickness and no pollen grains could be able to reach the ovary. In the late year 1987, the first receptive flower was recorded on May 15 and the last on June 15. In this year the maximum number of the receptive flowers (90% of the total) was found on May 30. The

Table 1. — Separate and combined over years analyses of variance.

Source	D.F.	Expected Mean Squares
Separate Analyses		
Replications	r-1	
Clones	c-1	$\sigma^2 + r\sigma^2_c$
Error	(r-1)(c-1)	σ^2
Combined Analysis		
Years	y-1	
Replications	y(r-1)	
Clones	c-1	$\sigma^2 + r\sigma^2_{yc} + yr\sigma^2_c$
Clones x years	(c-1)(y-1)	$\sigma^2 + r\sigma^2_{yc}$
Error	y(r-1)(c-1)	σ^2

c = number of clones = 52
r = number of replications = 3
σ^2 = variance due to error
σ^2_{cy} = variance due to interaction of clones x years
σ^2_c = variance due to differences among clones which is interpreted as the total genetic variance

Table 2. — Mean number of days from May 1st required for the commencement of bud burst (stage 2), receptivity (stage 3), termination of receptivity (stage 4) and duration in days of stages 2 and 3, for the years 1986 and 1987.

Characteristic	1986				1987			
	X̄	MIN.	MAX.	S.D.	X̄	MIN.	MAX.	S.D.
Bud burst (stage 2)	8.29	- 5	19	4.88	21.91	10	30	3.34
Receptivity (stage 3)	12.56	5	21	3.07	23.54	14	34	3.42
Termination of receptivity (stage 4)	22.08	13	30	3.27	33.78	16	42	3.29
Duration in days of stage 2	5.77	2	14	2.66	4.38	1	11	2.21
Duration in days of stage 3	10.72	4	16	2.77	14.55	7	21	2.90

receptive period in the entire seed orchard was 32 and 27 days for the years 1986 and 1987 respectively, while the receptive period for individual flowers varied from 2 days to 10 days. Receptive periods as long as, 31 days for Scots pine (JONSSON et al., 1976), 35 days for *Pinus radiata* (LILL and SWEET, 1977) 30 days for Douglas fir (EL-KASSABY et al., 1984), and 33 days for sitka spruce (EL-KASSABY and REYNOLDS, 1990) have been reported. The duration of receptivity of individual flowers (2 days to 10 days) found here is longer from that reported by VIDACOVIC (1974) in the same species (1 day to 3 days) and little shorter from the receptive period (2 days to 13 days) found by LILL and SWEET (1977) in *Pinus radiata*, grown in New Zealand. It seems that environment factors such as, temperature, humidity and winds are responsible, not only for the duration of the receptive period of individual flowers but also for the length of receptivity in the entire seed orchard.

The large variation among clones in the phenological stages of flowering and their duration time is evident from the analyses of variance (*Table 3*). The differences are very large and statistically significant for all characteristics in both years, with an exception only the duration of stage 3 in year 1986 which was found insignificant. The scales of the conelets of the earliest clone 51 started emerging from the top of the conelet on March 25, while the latest clone 52 reached this stage on May 12. i. e., 17 days later. For the year 1987 the dates of commencement of

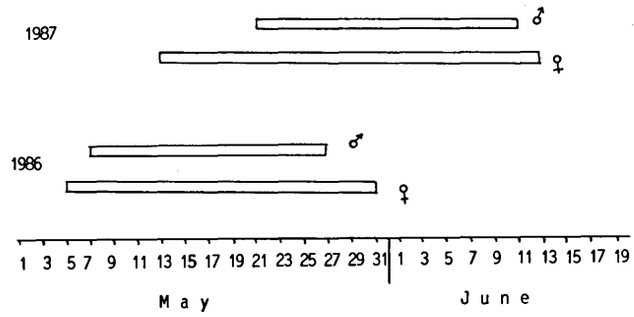

Figure 1. — Range of receptivity and pollen shedding in the clonal seed orchard of black pine.

this stage were 12 and 29 of May for the 51 and 52 clone respectively. Considering receptivity, the variation among clones was highly significant in both years. The early flowering clone 51 reached receptivity, on the average, 7.66 days after May first, while the latest clone 52 reached this stage on May 19. The percentage of flowers containing receptive ovules for these two clones (earliest and latest), as well as, the overall mean of the 52 clones inculded in the seed orchard is grafically shown in *figure 2* for the year 1986 and in *figure 3* for the year 1987. It is obvious from these figures that there are only few days at which overlapping of the receptive periods of the clones 51 and 52

Table 3. — Analysis of variance (A) and variance components, and heritability estimates (B) for earliness of flowering and duration of flowering stages.

A. Analysis of variance

		Mean squares[1] 1986					Mean squares 1987				
		Commencement of stages			Duration of stages		Commencement of stages			Duration of stages	
Source of variation	D.F.	(2)	(3)	(4)	(2)	(3)	(2)	(3)	(4)	(2)	(3)
Replications	2	8.795	2.333	2.776	8.910	5.718	18.564**	13.462 *	0.795	35.179**	6.641
Clones	51	57.433**	22.687**	22.743**	12.062**	9.351	26.041**	28.263**	20.064**	6.819**	13.266 **
Error	102	7.331	2.908	4.906	4.659	6.816	3.584	3.475	6.390	3.336	6.066

B. Variance components and heritability estimates

	Estimated values for 1986					Estimated values for 1987				
	Commencement of stages			Duration of stages		Commencement of stages			Duration of stages	
Parameter[2]	(2)	(3)	(4)	(2)	(3)	(2)	(3)	(4)	(2)	(3)
σ^2_c	16.701	6.593	5.946	2.468	0.967	7.660	8.263	4.558	1.161	2.400
σ^2	7.331	2.908	4.906	4.659	6.816	3.584	3.475	6.390	3.336	6.066
H_1	0.67	0.69	0.57	0.34	0.12	0.67	0.70	0.42	0.36	0.28
H_2	0.92	0.87	0.78	0.61	0.30	0.86	0.88	0.68	0.51	0.54

1) *,**, statistically significant at the 0.05 and 0.01 probability level, respectively.
2) σ^2_c, variance between clones which is interpreted as the total genetic variance.
σ^2, error variance.
H_1, H_2, broad sense heritability on individual tree and clone mean basis respectively.

occur, although both of them are coming from the same area. Only 20 % o fthe flowers of these clones are receptive at the same time. The whole phenology of the flowering stages in the seed orchards is shown in *figures 4* and *5*.

Two characteristics of the male flower were studied, namely the date at which the catkings start shedding pollen and the pollen shedding period. The analyses of variance (*Table 4)* showed that the differences among clones for the earliness of shedding pollen are statistically significant, while for the duration of shedding are not. This indicates that the duration of pollen shedding is affected, much more, than the conelet receptivity, from the weather conditions. These results are in agreement with those reported by Sarvas (1962) and Jonsson et al.,

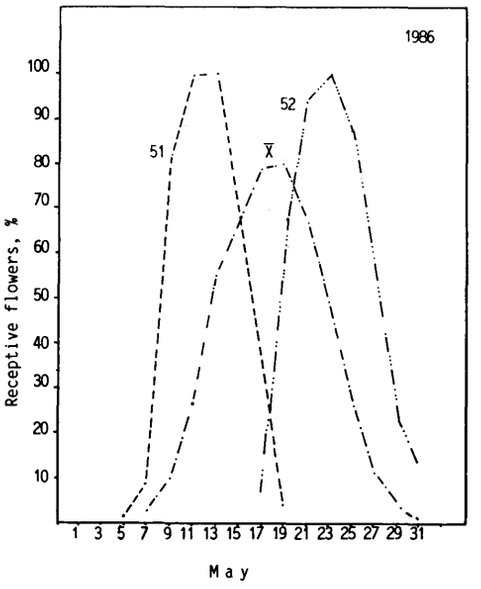

Figure 2. — The percentage of flowers containing receptive ovules in May 1986 for the earliest (51) and latest (52) clone as well as for the mean values of all (52) clones.

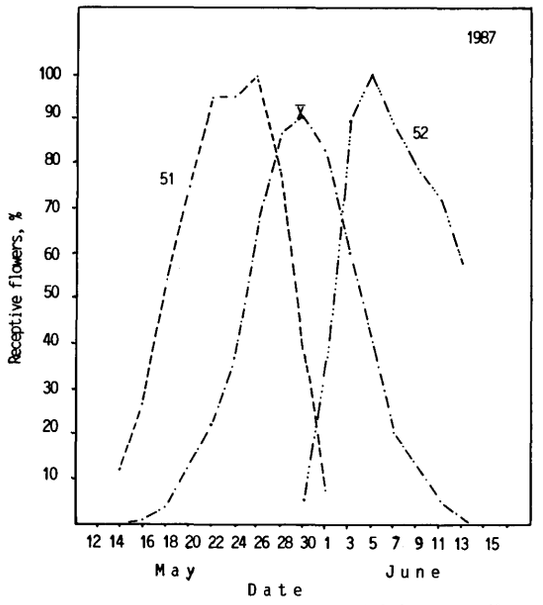

Figure 3. — The percentage of flowers containing receptive ovules in May and June, 1987 from the earliest (51) and latest (52) clone as well as for the mean values for all (52) clones.

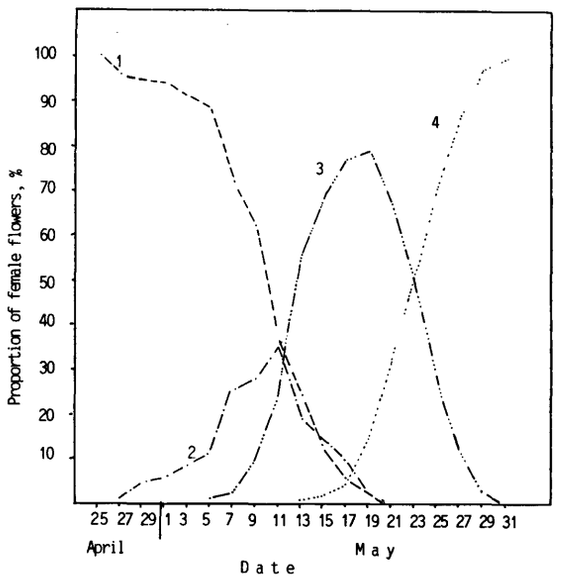

Figure 4. — Flowering stages of 52 clones in year 1986 (1 pregnan flowering bud; 2 ovuliferous scales are emerging from the top of the conelet; 3 flowers are receptive, 4 receptivity passed.

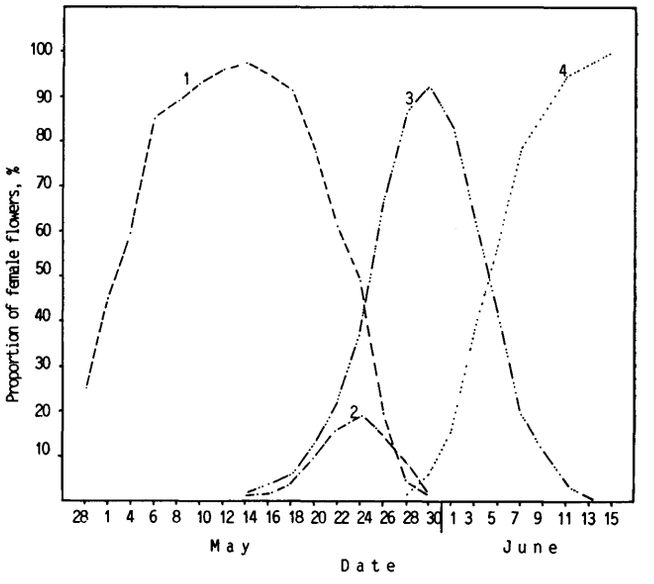

Figure 5. — Flowering stages of 52 clones in year 1987 (1 pregnan flowering bud; 2 ovuliferous scales, are emerging from the top of the conelet; flowers are receptive; 4 receptivity passed).

(1976) in Scots pine. They also found significant differences among clones for the time of commencement of pollen shedding and insignificant differences for the duration of pollen shedding. The strong influence of the weather conditions on the duration of pollen shedding has been stressed by Sarvas (1962) and Gullberg et al. (1982).

Pollen dispersal began on May 1 in 1986 and May 21 in 1987 i. e., 2 days and 8 days after the commencement of the conelet receptivity (*Figures 6* and *7*). It is apparent from the examination of the figures, that clones which have receptive flowers when maximum quantities of pollen are available are more heavily pollinated, than those with flowers that become receptive prior or later that time. Lill and Sweet (1977) have reported that 7 pollen grains are cought in the vicinity of each ovule and that this point was not reached until the time when 70% of the clones

Table 4. — Analysis of variance (A) and variance components and heritability estimates (B) for the date of commencement of pollen shedding and the duration of shedding in 1987.

A. Analysis of variance

Source of variation	D.F.	Mean squares 1/	
		Commencement	Duration
Replications	2	8.788	42.429
Clones	51	19.606*	11.020
Replications x clones	102	10.370	11.057

B. Variance components and heritability estimates

Parameter 2/	Estimated values	
	Commencement	Duration
σ^2_c	3.078	0.0
σ^2	10.370	11.057
H_1	0.23	0.0
H_2	0.47	0.0

1) *, statistically significant at the 0.05 probability level.
2) H_1, H_2, broad sense heritability estimates on individual tree and clone mean basis respectively.
σ^2_c, variance between clones which is interpreted as the total genetic variance.
σ^2, error variance.

were shedding pollen. The *figures* (*6* and *7*) also show that the pollen is released later from the commencement of the receptive time and last for shorter period of time. This suggests that the dates of maximum pollen shedding and female receptivity are not completely synchronized, as it is desired, and thus late receptive clones cannot be pollinated by early pollen shedding clones and vise versa. A characteristic consequence of this abnormality was observed in the late frowering clone 52. Because of the lack of sufficient pollen when the female flowers were receptive, the number of cones produced by this clone was small and furthermore the number of seed per cone is much below the average of the whole seed orchard. Therefore clone 52 should be maintained in the seed orchard as pollen donor, only if the progeny test results indicate that it is superior in economically important characteristics.

Variation among clones in synchronization of flowering and in cone and seed production is found to occur in nearly all first generation seed orchards (SARVAS, 1962, 1968; SWEET, 1975; JONSSON et al., 1976; BHUMIBHAMON, 1978; EL-KASSABY et al., 1984; EL-KASSABY and REYNOLDS, 1990; MATZIRIS, 1993). Thus the ideal population model, which implies that effective population number is equal to actual number of clones in the seed orchard is not valid. Although that in natural stands a constant number of progeny per parent is not necessary for the ideal situation but a randomly varying number (CROW and KIMURA, 1970, page 110), in the seed orchard studied, because the variation is not random but genetically controled (MATZIRIS, 1993), the assumptions of the equal contribution of all clones and panmixis are voilated. Treatments, such as, irrigation mist to delay bud development and increase panmixis, use of hormones to stimulate clones of low fecundity to produce more flowers, supplimental mass pollination to maximize the seed orchard crosses and mixing seed for several years to take advantages of the clone x year interaction in cone and seed production and enlarge the genetic base have been recommended (DENISON and FRANKLING, 1975; KOSKI, 1980; BRIDGEWATER and TREW, 1981; SCHMIDTLING, 1982; EL-KASSABY et al., 1983, 1989; SCHOEN et al., 1986; EL-KASSABY and REYNOLDS, 1990; REYNOLDS and EL-KASSABY, 1990).

Year x Clone Interaction

In general, clonal variation in the commencement and duration of flowering stages followed the yearly trend, i e., all clones flowered earlier in year 1986 and later in 1987. Of interest is the fact that clones which are early in one year usually maintain this attitude and the same holds true for the late clones. The lack of clone x year interaction effects were verified in the combined analyses of variance carried over the 2 years (*Table 5*). It can be seen from the table that the clone x year interaction effects were insignificant for all characteristics. When the clones were ranked according to the number of days required from May first to reach receptivity, there was a high degree of parallelism in rankings of the 2 years, indicating the lack of interaction. Clone 51 was in the top in both years, while clone 52 was in the bottom.

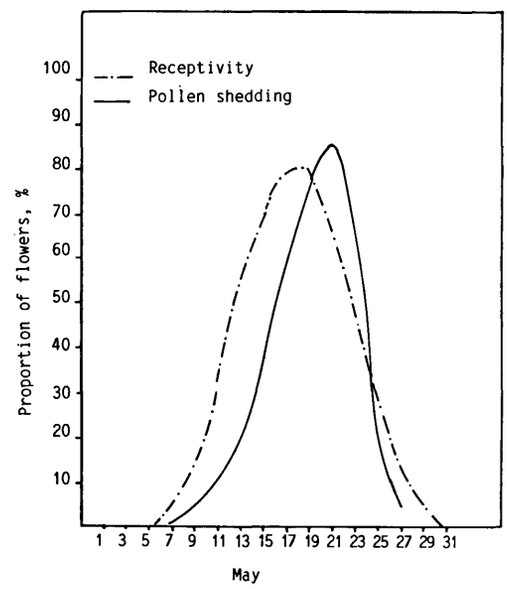

Figure 6. — Receptivity and pollen shedding time for the 1986 flower season in the clonal seed orchard of black pine.

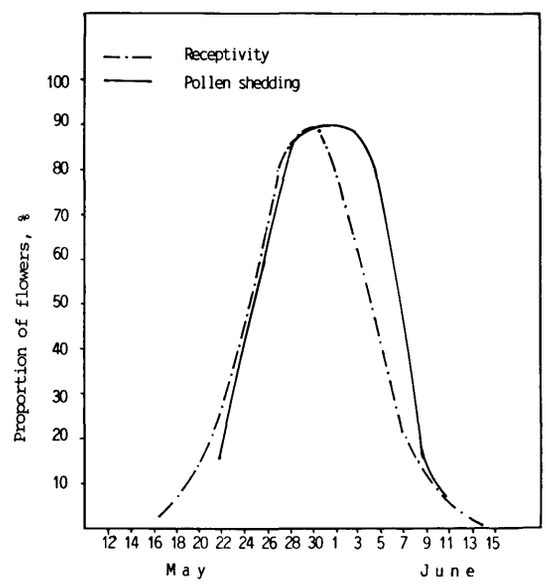

Figure 7. — Receptivity and pollen shedding time for the 1987 flowering season.

Table 5. — Combined analyses of variance over years for the dates of commencement of stages 2,3 and 4 as well as for the duration of stages 2 and 3.

Source of variation	D.F.	Mean Squares [1]				
		Commencement of stage			Duration of stage	
		2	3	4	2	3
Years	1	7140.820**	9430.322**	8708.421**	51.212**	382.043**
Replications	4	13.679	7.895	1.785	20.257	6.179
Clones	51	27.176**	15.416**	12.119**	4.713*	4.656
Years X clones	51	4.159	1.599	2.150	1.577	2.881
Error	204	5.457	3.191	5.648	3.997	6.445

1) *, ** statistically significant at the 0.05 and 0.01 probability level.

Between and Within Years Correlations

The relationship between the characteristics studied is shown in *table 6,* in which the product moment and SPEARMAN rank correlations are listed. The year to year correlation coefficients for the bud burst date is positive, quite high and statistically significant ($r = 0.72$, $p < 0.01$, $n = 156$). The corresponding correlation for the date of onset of receptivity was also significant ($r=0.68$). SPEARMAN rank correlations had similar values; $r=0.71$ for the bud burst date and $r=0.67$ for the date of onset of receptivity. These correlations indicate that the ranking of clones is highly significant or expressing it another way, that there are no significant chages in the ranking of clones for the date of commencement of the phenological stages in the years examined. This verifies the lack of clone x year interaction effect found in the analysis of variance and indicates the high degree of genetic control of these characteristics. Significant year to year correlations for flowering stages have been also reported in Scots pine (JONSSON et al., 1976) and in Douglas fir (EL-KASSABY et al., 1984). The values in Scots pine were from 0.70 to 0.87, which are very close with the values found in the present study.

The year to year correlation for the duration time of stage 2 (from bud burst date up to the date of receptivity) was found positive and quite low ($r=0.24$) and for the duration of stage 3 (period of receptivity) the correlation was even smaller ($r=0.12$). The results indicate that the duration of flowering stages of the clones is not consistent from year to year and that is strongly affected by environmental fluctuations.

The correlations in flowering stages within the years are, in all cases, positive and statistically significant, ranking from 0.72 to 0.85 for the year 1986 and from 0.62 to 0.86 for 1987 (*Table 6*). It is of interest that the correlations between flowering stages and their duration time are all negative. This means that the earliest flowering clones are maintained receptive for longer period of time. It seems that the lower temperatures that dominate in the earlier days of flowering are responsible for the longer receptive period observed. The correlation between the dates of commencement of receptivity and pollen shedding, although is positite and statistically significant, its magnitude is quite low ($r=0.35$), indicating that only a small portion (10%) of the variation in the date of pollen shedding is attributed to the date of female receptivity. Although that, on the average ,the time of pollen shedding commences few days later than the time of receptivity, there are found clones shedding pollen earlier from the receptive time of their conelets.

Table 6. — Product moment (above diagonal line) and Spearman rank (below diagonal line) coefficients for flowering characteristics in a clonal seed orchard of black pine.

Characteristic [1]		(X_1)	(X_2)	(X_3)	(X_4)	(X_5)	(X_6)	(X_7)	(X_8)	(X_9)	(X_{10})	(X_{11})	(X_{12})
1 9 8 6													
Commencement of stage 2	(X_1)		0.85	0.72	-0.69	-0.04	0.72	0.73	0.49	-0.33	-0.24	0.27	-0.02
Commencement of stage 3	(X_2)	0.86		0.72	-0.43	-0.18	0.70	0.68	0.45	-0.26	-0.22	0.24	-0.02
Commencement of stage 4	(X_3)	0.71	0.71		-0.40	0.18	0.57	0.61	0.50	-0.69	-0.04	0.26	0.04
Duration of stage 2	(X_4)	-0.60	-0.39	-0.32		0.21	-0.35	-0.36	-0.16	0.24	0.20	-0.04	-0.15
Duration of stage 3	(X_5)	-0.04	-0.17	0.17	0.26		0.02	0.10	0.20	-0.05	0.12	0.15	-0.05
1 9 8 7													
Commencement stage 2	(X_6)	0.71	0.69	0.52	-0.26	0.00		0.86	0.62	-0.53	-0.34	0.27	-0.05
Commencement stage 3	(X_7)	0.72	0.67	0.59	-0.27	0.09	0.84		0.64	-0.45	-0.41	0.35	-0.10
Commencement stage 4	(X_8)	0.60	0.54	0.61	-0.16	0.23	0.70	0.72		-0.30	-0.18	0.32	-0.12
Duration stage 2	(X_9)	-0.33	-0.26	-0.16	0.18	-0.05	-0.52	-0.43	-0.32		0.45	-0.05	0.01
Duration stage 3	(X_{10})	-0.26	-0.23	-0.02	0.20	0.16	-0.34	-0.40	-0.16	0.44		0.00	0.01
Commencement of pollen shedding	(X_{11})	0.34	0.34	0.30	-0.01	0.15	0.30	0.42	0.38	-0.10	-0.05		-0.78
Duration of pollen shedding	(X_{12})	0.00	-0.05	0.06	-0.18	0.01	-0.06	-0.11	-0.08	0.06	0.11	-0.63	

1) Stage 2, flowering scales are emerging from the top of the female strobilus;
Stage 3, commencement of receptivity;
Stage 4, receptivity is terminated.

Heritability estimates

It is evident from the analyses of variance that a high degree of variation in the flowering stages exists among clones. The broad sense heritability estimates (H) on individual tree had as follows, for the years 1986 and 1987; 0.69 and 0.67 for the bud burst date, 0.69 and 0.70 for the date of receptivity. For the duration of flowering stages the H values were much lower (*Table 3*), indicating that environmental factors are predominant for the expression of these characteristics. The duration of pollen shedding is completely under environmental control, while that of receptivity is weakly inherited.

The H values on clone mean basis were, as expected, much higher. In 1986 the values were 0.92 for the bud burst date, 0.87 for the date of receptivity and 0.78 for the date of termination of receptivity. Similar were also and the H values estimated in 1987 (*Table 3*). The results clearly shows that the phenological stages of flowering in black pine are under strong genetic control. Therefore great attention must be paid to these characteristics when management of existed or establishment of new seed orchards are made.

Conclusions

From the study of the phenological stages of flowering in a black pine clonal seed orchard for two successive years the following conclusions can be drown:

1. A high degree of genetic variation in phenological stages of both male and female flowering exist in black pine. The genetic component of the earliness of flowering in all cases is very strong, while the year x clone interaction is very low and statistically insignificant.

2. The assumptions for an idealized seed orchard, as far as, synchronization in flowering and panmictic equilibrium are concerned, are not valid. This abnormality (lack of complete synchronization in flowering of the clones) reduces the random gene exchange among clones and consequently reduces the effective population size of the seed orchard and the genetic base of the seed produced.

3. The duration of receptive times is a weakly inherited characteristic, while that of pollen shedding is completely under the control of environmental parameters.

4. Year to year correlations for the dates of commencement of bud burst and receptivity are positive and very high indicating the strong genetic control of these characteristics. The variation and high heritability values found, indicate that selecting for flowering synchronization in black pine is going to result in rapid genetic gain in these characters.

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