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Generative development of scots pine (*Pinus silvestris* L.) grafts

The generative development of pine seedlings has often been described and this literature was reviewed in a separate paper (Giertych 1967). One could expect that the sexual development of a graft (a plant that arrose from the grafting of a scion from a mature tree onto a juvenile stock) will be somewhat different than that of a seedling, since from the very beginning the part of the graft that we are interested in is physiologically mature. Many of the studies on the physiology of reproduction in various species of pine have been conducted on grafts (Anonym 1963, Barnes and Bingham 1963, Chiba 1965, Faulkner 1966, Hermann 1951, Hirov 1964, Matthews 1963, Melchior 1962, Melchior and Heitmüller 1961, Nilsson 1955, Van Buijtenen and Brown 1962, Van Hoverbeke and Barber 1961) since this problem is of importance from the economic point of view. It is expected that in a short time forest seed production will be based primarily on seed orchards. For this reason the practical interest of man in the problem of pine flowering will center primarily on the strobile production by grafts. So far not many papers have been published dealing with the question of the development of generative potential of pine grafts (Wright 1964). This development will depend on the; 1° stage of physiological development of the mother tree and of the part of its crown from which scions have been collected, 2° the degree of scion rejuvenation as a result of the change of its position in the crown (from a lateral branch to the graft apex) and a change of the intensity and type of nutrition, 3° the effect of the juvenile root sytem of the stock on the physiologically mature crown of the graft, and 4° the health of the graft, which will depend on the quality of the union between scion and stock and on the physiological compatibility of the two.

It is generally assumed that the sexual development of a graft is quicker than that of a seedling, since the scion after grafting does not undergo complete rejuvenation. For example one does not observe in pine grafts a return to the stage of primary leaves development. On the other hand in pines where the natural sexual development is quick, as for example in *P. pinaster* Ait. the formation of male strobiles on the grafts

takes place later than on seedlings from seeds sown at the same time as the grafts were made (Illy 1967). This is because the grafting procedure inhibits for a certain time the development of a shoot. Conversly, when a juvenile seedling of *P. montana* Mill. is grafted onto a *Picea abies* (L.) Karst. stock this has led to a hastening of the male strobile formation, already in the 16th month from the germination of the seed (Hermann 1951). Seedlings of several pine species when grafted onto a mature *Pinus ponderosa* Laws. tree have promptly developed male strobiles (Mirov 1951). A similar phenomenon has been observed by Jablokov (1962) in the USSR where seedlings of *Pinus koraiensis* Sieb. et Zucc. grafted on six year old stocks of *Pinus silvestris* L. produced male strobiles after 3 years whereas eight year old seedlings were still barren. Thus an older stock or one that is of a different species can cause a hastening of the sexual development of the scion from a seedling in comparison with the seedlings growing freely.

Most commonly however we are dealing with a physiologicaly mature scion from a plus tree, grafted onto a young stock of the same species. Under such conditions we observe that the graft yields strobiles earlier than the seedling, though later than a shoot analogous to the scion but not severed off from the mature tree. In *Pinus resinosa* Ait., where seedlings reach reproductive maturity very late in life already after 10 years 97% of grafts have had female strobiles (Lester 1964). Similarily in *P. elliottii* Engelm. grafts produce strobiles earlier than seedlings (Goddard 1964). In *P. silvestris* L. where seedlings reach reproductive maturity relatively early (at 4 to 8 years) there are no major differences in this respect between seedlings and grafts however no information about sexual development of pine grafts has as yet been published. On the other hand it has been pointed out that mass strobile formation that could be considered as being of economic importance is to be observed on pine grafts about 25 years earlier than on seedling plantations. This observation is however confounded by the planting distance, since grafts are usually planted at a wide spacing that creates much more favourable conditions for strobile development than is the case in pine plantations (Wright 1964). A closer look at the progress of sexual development in pine grafts is also needed because of the often observed lack of pollen produced by seed orchards in sufficient quantites to pollinate all the available female strobiles (Lücke 1962, Lester 1964).

In the present study an attempt has been made to follow the sexual development of pine grafts from the point of view of the effects that the following factors might have on this development; 1° position in the crown of the mother tree from which scions have been collected, 2° position of the scion on the stock and 3° the fertilization of the grafts with ammonium nitrate.

In the crown of a mature tree some regions (fig. 1) and shoots of a certain type (fig. 2) bear male strobiles while others bear female ones. From the point of view of sexual development of a graft the physiological predisposition of a scion cannot be without consequence, for this

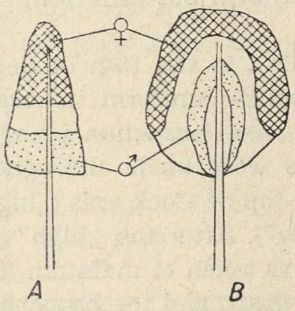

Fig. 1. Position of male and female strobiles in the crown of a pine tree growing in a stand *A* and growing free *B*. (after Mušketnik 1960)

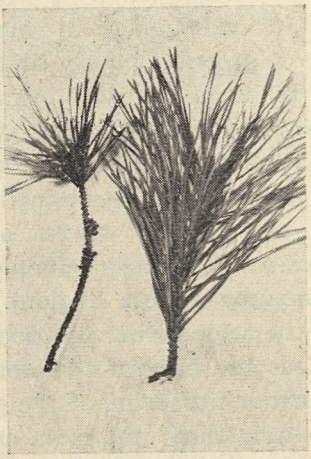

Fig. 2. Two types of scions. Left, a "male" scion from the "male" zone of the tree crown and right, a "female" scion from the "female" zone of the tree crown (see fig. 1)

reason it was considered of interest to compare the development of „male" and „female" shoots after grafting them onto juvenile stocks. As regards the sucess of grafting Bánó (1954) has already shown that shoots from the female part of the crown, even those with conelets, are the best ones to use as scions.

If the development of strobiles is dependent on the distribution of nutritive or hormonal substances within the crown of a tree this should also be reflected in the graft depending on the position that a scion will have on the stock. This is also connected with the change in growth intensity of the scion as a result of its transfer from a side branch onto the graft apex or from a leading shoot onto a lateral position on the graft. This aspect was also considered in the present study.

To what extent the process of sexual development is affected my mineral nutrition can be studied by treating with fertilizers. Nitrogen fertilization has been employed since the effect of this element on the sexuality of plants is best documented (Kamieńska 1967). It leads towards feminization, which was demonstrated also in pines (Giertych 1966, Giertych and Forward 1966, Holst 1961, Sweet and Will 1965).

MATERIALS AND METHODS

For the experiment scions have been used from one mature pine tree about 150 years old, felled on 11th of September 1963 in the experimental forest Zwierzyniec of the Institute of Dendrology and Kórnik Arboretum of the Polish Academy of Sciences. Two types of scions have been collected; 1° referred to in this paper as „male" from the inner part of the crown, growing poorly and with scars from old male strobiles, and 2° referred to as „female" from strong shoots at branch tips (fig. 2). Material collected in this way is genetically uniform but differs in the physiological predisposition of the scions.

The grafting was performed from the 12th to the 16th of September 1963 on two-year-old stocks, as far as possible uniform in size. These were grown from seeds obtained from the seed extraction plant in Nurzec (Białystok Forest Region). Side grafts were made throughout, but some of the scions were positioned near the top of stock axis („high") and others near the base of the stock axis („low"). After the „high" grafting in the further nursering of the graft note was taken to maintain the scion as the leading shoot and main crown of the graft, and the branches of the stock have been trimmed keeping them in the low part of the graft, but they were not removed altogether. After the „low" grafting the shoots of the stock have been trimmed only slightly in order to maintain the scion in the lower position smothered by the branches of the stock.

The third experimental variant was the fertilizer treatment. Half of the grafts have been supplied with an ammonium nitrate fertilizer (21% of nitrogen) at a rate of 200 g of the fertilizer per 1 m^2 of soil arround the grafts. The treatment was applied twice onto the same soil, on the 20th of September 1963 and on the 10th of June 1966. In figs. 5, 8, 11, 14, 17, and 21 this is indicated by black triangles. The fertilization in 1966 just preceded the period of strobile initiation.

The experiment was lied out in an orthogonal design with two replicates. It contains 8 experimental variants (2 types of scions × 2 grafting positions × 2 soil fertility levels) replicated twice which gave 16 blocks that have been distributed randomly in the nursery. In each block there were 50 scions grafted.

The results of the grafting under these experimental conditions have been reported upon in a paper on grafting methods (Giertych and Przybylski 1965). In May of the years 1964, 1965, 1966, 1967 and 1968 the number male and female strobiles and the number of live shoots on each ramet have been recorded. All the results have been subjected to an analysis of variance. Before the statistical analyses all the results that were in the form of binomial proportions have been transformed with the help of the Freeman-Tukey tables into agular values (Mosteller and Youtz 1961). Below only statistically significant results are reported.

RESULTS

SEEDLING MORTALITY

The percentage values presented in figs 3, 4 and 5 for the year 1964 inform about the grafting success which has been already reported upon (Giertych i Przybylski 1965). As can be seen from this data already from the onset of the experiment different numbers of grafts have been available in the individual experimental blocks, and therefore all other observations had to be referred to the number of living grafts present each year in the particular block.

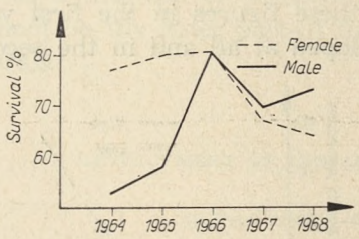

Fig. 3. Effect of scion type on the survival of ramets (as percentage of those alive the previous year)

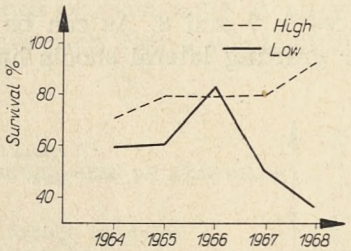

Fig. 4. Effect of grafting position on the survival of ramets (as percentage of those alive the previous year)

Comparing the ramets from various parts of the crown (fig. 3) it has been confirmed that „male" scions gave fewer successful unions than „female" ones (Bán ó 1954) and established that the former have a greater mortality in the first year. As soon however as scions establish a good union with the stocks the origin of the ramet from different parts of the ortet has no longer any effect on graft mortality.

On the other hand the position on the stock where the scion is located has a persitent effect on graft mortality (fig. 4). Among the scions

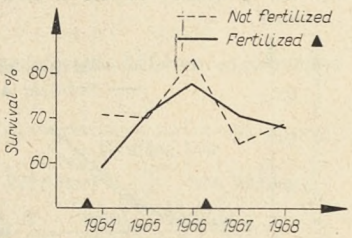

Fig. 5. Effect of fertilization with ammonium nitrate on the survival of ramets (as percentage of those alive the previous year)

grafted low not only a smaller percentage of takes was observed but also a sizable proportion of the scions was each year rejected by the stock. Except the year 1966 when generally graft mortality was very low, throughout the experiment each year it was observed that many of the

scions grafted low were gradually withering off, so that by 1968 the part of the experiment that concerned scions in the lower part of the stocks has practically ceased to exist.

The fertilizer treatment has had only a slight effect on the percentage of graft takes but in later years it did not have any significant effect on scion mortality (fig. 5).

VEGETATIVE DEVELOPMENT OF THE RAMETS

Each year the number of new shoots was counted on each ramet. The mean values for the individual experimental variants are presented in figures 6, 7 and 8. As can be seen from these figures in the first year after grafting lateral shoots have not developed at all and in the second

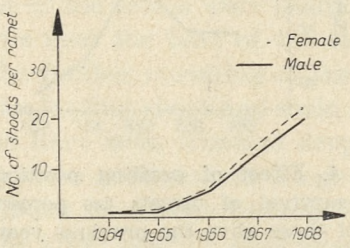

Fig. 6. Effect of scion type on the mean number of shoots on a ramet

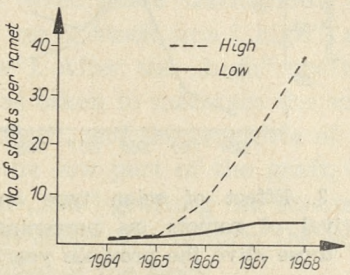

Fig. 7. Effect of grafting position on the mean number of shoots on a ramet

year the number was very slight. Only in later years the number of shoots per ramet begins to increase and does so with a geometric progression. In the year 1966, that is two vegetative seasons after grafting, the number of shoots on each scion is arround 5 - 6, that is it corresponds to the number of shoots that normally develop each year on a strong shoot of the previous year on a pine tree. Thus it can be said that the cutting off of a shoot from a mature tree and the grafting of it onto a young

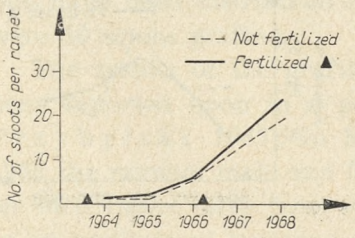

Fig. 8. The effect of fertilization with ammonium nitrate on the mean number of shoots on a ramet

stock inhibits its vegetative development by about two years. This inhibition of shoot development as a result of the grafting procedure will also have an effect on the rate of reproductive development of the ramets.

From figs. 6 and 8 it can be seen that origin of the scion from different parts of the mother tree crown and the fertilizer treatment have not had any major influence on the vegetative development of the ramets as measured by the number of shoots on them. In 1968 there was a slight increase in the number of shoots per ramet as a reaction to the fertilizer treatment in 1966 (fig. 8). This was observed only on the ramets from „male" scions and was not statistically significant. The position of the scion on the stock (fig. 7) is of paramount importance to the rate of ramet development. The scions in the high position grew much more profusely than those in the low position. This of course is analogous to the vegetative development observable within the crown of a pine tree, where shoots within the crown produce few laterals or even none at all while a shoot on the outer part of the crown yields each year a whorl of many laterals.

DEVELOPMENT OF THE ABILITY TO PRODUCE FEMALE STROBILES

a) Percentage of ramets with female strobiles

In the first year after grafting no female strobiles have been observed on any of the scions. If in the buds on the scions female strobiles were present at the time of grafting these were aborted during the 1963/64 winter. In the normal conditions a female strobile undergoes development throughout the winter (Duff and Nolan 1958). On the graft however, when the bud of the freshly grafted scion was in an unusual position and certainly had insufficient vascular links with the stock for normal nourishment of the female strobile, not a single one attained the stage of anthesis. In later years a gradual increase in the percentage of ramets with female strobiles is observable (table 1) with the exception that in 1968 there were fewer of them than in 1967.

The origin of scions from different parts of the mother tree crown

Table 1

Percentage of ramets with female strobiles in various years and for the different experimental variables

	Grafted high				Grafted low			
	Fertilized		Not fertilized		Fertilized		Not fertilized	
	female scions	male scions	female scions	male scions	female scions	male scions	female scions	male scions
1964	0	0	0	0	0	0	0	0
1965	1.6	0	4.7	0	0	0	0	0
1966	18.6	8.2	39.2	10.2	2.4	0	0	0
1967	26.9	35.1	26.6	3.9	4.5	12.5	0	0
1968	4.8	32.4	21.2	3.9	0	0	0	0

has had in 1966 a significant effect on the percentage of ramets with female strobiles (fig. 9). In that year the „female" scions have much more frequently had female strobiles than „male" scions. This concerns in particular the scions grafted high on the stock, which can be seen from table 1 and which proved to be of importance because the interaction between the type of scions and grafting position was statistically significant.

The small number of ramets that have had female strobiles already in 1965 were all from „female" scions grafted high (table 1). In the years 1967 and 1968 the type of scion has no longer had any significant effect on the percentage of ramets with female strobiles (fig. 9). To summarize it can be said that the „female" scions are quicker to attain the capacity for female strobile production but already after the 4th year after grafting the type of scion ceases to play any role in the initiation of female strobiles.

The location of the scion on the stock has from the very beginning a very serious influence on the percentage of ramets with female strobiles (fig. 10, table 1). It can almost be said that in the low position female strobiles do not develop at all.

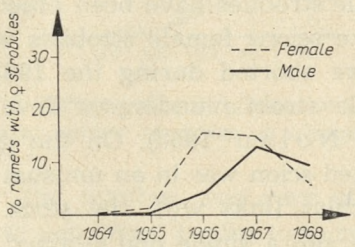

Fig. 9. The effect of scion type on the percentage of ramets with female strobiles

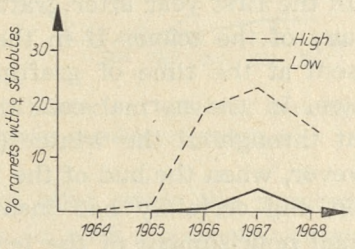

Fig. 10. The effect of grafting position on the percentage of ramets with female strobiles

The fertilization with ammonium nitrate done in 1963, that is at the time of grafting, practically did not have any influence on the percentage of grafts with female strobiles. The slightly significant interaction in 1966 between the grafting position and soil fertility indicates that the fertilization in 1963 has had a negative effect on the flowering of ramets in the high position and a positive one on the production of female strobiles in the low position (table 1).

After the fertilization performed in 1966 a distinctly positive effect of this treatment was observed on the percentage of ramets with female strobiles in the following year (fig. 11). Two years after the treatment this effect was still observable. Both in 1967 and 1968 the positive effect of this fertilization on the initiation of female strobiles was observable only on the „male" scions (table 1), that is on those that have had a lo-

wer disposition for strobile production. Thus the fertilization has helped in obliterating the differences between types of scions in their capacity for female strobile initiation (fig. 9).

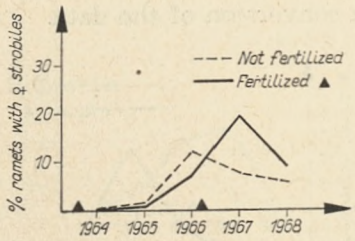

Fig. 11. The effect of fertilization with ammonium nitrate on the percentage of ramets with female strobiles

It should also be pointed out that starting from the year 1966 female strobiles begun to appear on the parts of the graft belonging to the stock, that is after 5 years from the sowing of seeds for the stocks. In 1968 this production of strobiles was massive in charcter while on scions it was relatively poor.

b) The mean number of female strobiles on a scion

In figures 12, 13 and 14 the mean number of female strobiles per scion is presented. Generally speaking the overall shapes of the graphs was the same as for the percentage of scions with female strobiles (figs. 9, 10 and 11). This indicates that the development of the intensity of female strobile production by the scions is correlated with the progress of their attainement of the capacity for female strobile production. The experimental variants affect the number of scions with female strobiles in the same way as they affect the intensity of this flowering.

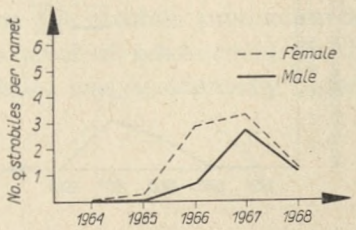

Fig. 12. The effect of scion type on the number of female strobiles per ramet

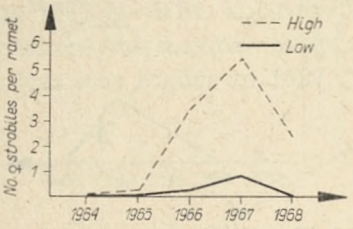

Fig. 13. The effect of grafting position on the number of female strobiles per ramet

c) The mean number of female strobiles on a shoot

The intensity of strobile production by scions has to be dependent on the number of available shoot apices on which they could become initiated. The number of these apices increases each year and is dependent on

the position on the stock in which the scion is located (fig. 7). Thus in order to be able to discuss the sexual development of ramets independently of their size it is necessary to speak about the mean number of strobiles per shoot. In figures 15, 16 and 17 results are presented of such a conversion of the data.

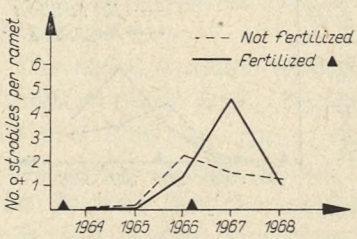

Fig. 14. The effect of fertilization with ammonium nitrate on the number of female strobiles per ramet

From these graphs it can be seen that „male" scions (fig. 15) and those grafted low on the stock (fig. 16) have started female strobile production a year later (in 1966 as against 1965) than the „female" scions grafted high. In 1966 difference between „female" and „male" strobiles is most distinct as well as between the high and low position on the stock. The „female" scions, even though they did not have any more shoots (fig. 6) had more female strobiles per shoot (fig. 15). In the years 1967 and 1968 in which the crop of strobiles was relatively small there were no differences in female strobile production between the different types of scions.

Ramets in the high position as distinct from those grafted low on the stock, have produced more shoots (fig. 7) as a result of which they have had more female strobiles (fig. 13). Furthermore in the years 1965 and

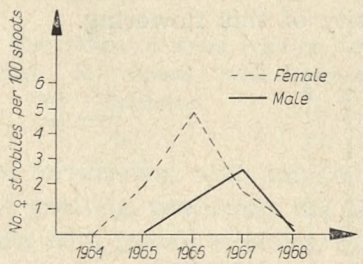

Fig. 15. The effect of scion type on the number of female strobiles per 100 shoots

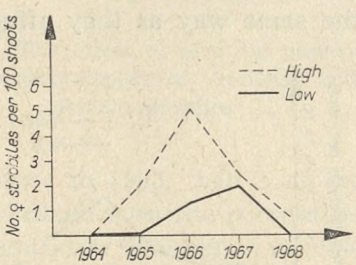

Fig. 16. The effect of grafting position on the number of female strobiles per 100 shoots

1966 they have had more strobiles per shoot (fig. 16). In the years 1967 and 1968 when the strobile crop was low the number of female strobiles was determined by the number of shoots and not by the position of the scion on the stock.

Fertilization with ammonium nitrate in June 1966 did not affect the number of shoots (fig. 8) but it has markedly increased the number of

female strobiles per shoot in 1967 (fig. 17) which explains the observed increase in the number of female strobiles per ramet and in the percentage of ramets with them. This fertilizer treatment did not affect the well

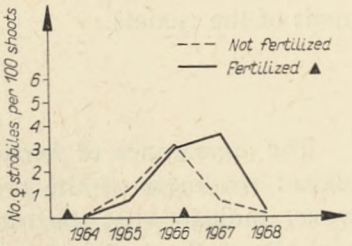

Fig. 17. The effect of fertilization with ammonium nitrate on the number of female strobiles per 100 shoots

flowering „female" scions positioned high on the stock but it has had an effect on ramets in the other variants of the experiment (table 1). In 1968 the effect of the fertilizer treatment in June 1966 was still positive on the number of female strobiles on „male" scions but it was negative on „female" scions (table 1).

d) A comparison of the female strobile production in 1966 and 1967

Comparing the number of female strobiles in the years 1966 and 1967 on the scions growing in the high position it was observed that in the individual experimental variants, the replicate in which the number of female strobiles per shoot was high in 1967 it was also high in 1966 compared with the other replicate. In order to capture this correlation numerically, each mean number of female strobiles per shoot for each experimental variant was given a value of 100 and the individual values for the replicates were expressed as a percentage of this mean. These values were then entered onto fig. 18. There is a distinct correlation between the strobile production in 1966 and in 1967 ($r=0.94$, significant at 99% level of confidence). In the replicates where the number of female strobiles was accidentally higher in 1966 it was also higher in 1967. The

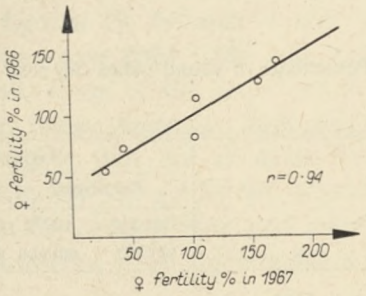

Fig. 18. A correlation between the female strobile production in 1966 and in 1967 (in units of the percentage of the mean for each experimental variable)

experimental variability was eliminated here by comparing all the values to the experimental means, the site variability was negligible because the variance between replicates was non existant ($F<1$), and genetically the

scions were identical since they all came from the same mother tree, thus it can be assumed that this correlation has been caused by differences between the stocks or in the quality of the union between the scion and stock. This is one further factor influencing the rate of sexual development of the ramets.

e) Cone mortality

The appearance of female strobiles on the ramet indicates the physiological readiness of the organism for sexual functions, it does not however indicate that the ramet is strong enough to nourish a developing cone. From horticultural practice as well as from the experience in tending young seed orchards it is known that the first flowers appearing on a scion are best removed in order to obtain a stronger vegetative development of the ramet. The development of cones was not covered by the present studies, however the percentage of healthy cones a year after anthesis was recorded (table 2). The dashes in table 2 indicate that there were no female strobiles the previous year (see table 1). „Female" scions not only produced more strobiles in the year 1966 but also they were able to rear some healthy cones from them, while on „male" scions there were fewer female strobiles and all of them aborted during the year (fig. 12, table 2). Also the strobiles of 1967 have had a lower survival to spring of 1968 on „male" scions than of „female" ones. Fertilization with ammonium nitrate in 1963 did not have any effect on the number of female strobiles that have emerged in 1966 (fig. 14) but the fertilization performed on the 10th of June 1966, that is immediately ofter pollination, has had a negative effect on the development of these strobiles with the result that more of them aborted before May 1967 (table 2). At the same time this fertilizer treatment in 1966 has increased the number of female strobiles in 1967 particularily on „male" scions (fig. 17, table 1). Of these strobiles more cones have survived till spring 1968 (table 2) than on the unfertilized grafts, though still less than on the „female" scions.

Table 2

Percentage of sound cones one year after strobile emergence for the various experimental variables

	Grafted high				Grafted low			
	Fertilized		Not fertilized		Fertilized		Not fertilized	
	female scions	male scions	female scions	male scions	female scions	male scions	female scions	male scions
1965	–	–	–	–	–	–	–	–
1966	0	–	0	–	–	–	–	–
1967	17	0	47	0	0	–	–	–
1968	24	16	22	0	0	0	–	–

The abortion of cones in the low position on the stock could have been caused by lower incidence of cone pollination, however considering the poor development of these ramets (fig. 7) it can be assumed that regardless of pollination, nutrition of the developing cones could have encountered difficulties.

f) Recapitulation

1° The origin of scions from various parts of the tree crown has an effect on the initiation of female strobiles only in the first few years, and already after 4 years from grafting these differences disappear.

2° The position of the scion on the stock has an effect on the development of female strobiles for three years after which this effect is only indirect, though very substancial, through the rate of vegetative development.

3° Fertilization with ammonium nitrate immediately before strobile initiation has a favourable influence on the number of female strobiles that will appear next year on „male" scions and on scions grafted in the low position, but at the same time it increases the abortion of young strobiles already on the tree at time of the treatment.

4° The union between the scion and the stock is not always of equal quality since it is dependent on the grafting procedure and on the physiological compatibility of the stock and scion, and this also has an effect on the development of female strobiles on the ramets.

DEVELOPMENT OF THE ABILITY TO PRODUCE MALE STROBILES

a) The occurence of male strobiles

The influence of the experimental variables on the percentage of ramets with male strobiles is presented in figures 19, 20 and 21 and in table 3. As can be seen from these data in the years 1965, 1966 and 1967 there were practically no male strobiles at all. None of the experimental variables had had a significant influence in these years on their occurance. Table 3 and figures 19, 20 and 21 suggest that the strobiles that did appear in these years occur more frequently on the grafts not treated with the ammonium nitrate fertilizer than on the treated ones and rather on „female" scions than on „male" ones. However these differences are not significant.

In the year 1964 male strobiles appeared relatively abundantly, this anthesis however concerns only the strobiles that have developed on shoots that were already in the bud on the scion at the time of grafting,

and therefore have formed already on the mother tree. Male strobiles do not develop during the winter (Duff and Nolan 1958) as a result of which the grafting procedure did not have such a deletirious effect on

Table 3

Percentage of ramets with male strobiles in various years and for the different experimental variables

	Grafted high				Grafted low			
	Fertilized		Not fertilized		Fertilized		Not fertilized	
	female scions	male scions	female scions	male scions	female scions	male scions	female scions	male scions
1964	2.7	50.2	0	64.2	1.5	37.2	0	58.4
1965	6.1	1.6	5.0	4.2	2.5	0	6.1	0
1966	0	0	2.4	1.6	0	0	9.6	0
1967	4.5	0	3.5	0	0	0	0	0
1968	17.5	6.3	27.9	5.8	0	0	0	0

these strobiles as it had on the female ones. Where male strobiles were present in a bud, there they have developed in the spring. This explains the great difference between the „male" and „female" scions in this respect (fig. 19). On the latter there simply were no male strobile initials in the buds at time the scions were cut from the ortet.

Presentation of separate data for the mean number of shoots with male strobiles per scion or the mean percentage of shoots with male strobiles would be pointless for the years 1964 - 1967 since on none of the ramets were there more than one shoot with male strobiles, and thus all conversions of the data would be only a change of units for the data

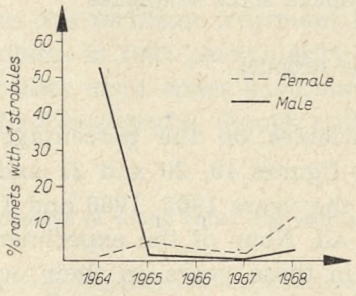

Fig. 19. The effect of scion type on the percentage of ramets with male strobiles

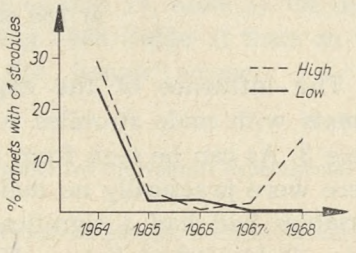

Fig. 20. The effect of grafting position on the percentage of ramets with male strobiles

already presented in table 3 and figures 19, 20 and 21, and would yield no further information.

In 1968 somewhat more male strobiles have appeared (table 3, figs. 19, 20 and 21). These strobiles were observed only in the high position

(fig. 20) on the stock. The fertilizer treatment in 1966 has slightly reduced the number of scions with male strobiles but not significantly. The type of scion however did have a significant effect. Namely „female" scions had more male strobiles than the „male" scions (table 3, fig. 19).

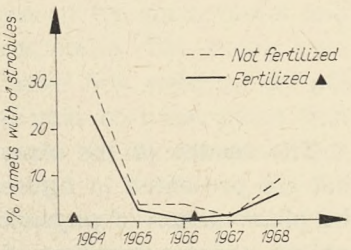

Fig. 21. The effect of fertilization with ammonium nitrate on the percentage of ramets with male strobiles

b) Size of the male inflorescence

In the year 1964, when a larger number of male strobiles appeared it was possible to subject the size of the male inflorescence to a closer scrutiny.

Generally speaking the number of male strobiles on an inflorescence (a shoot) was on the scions considerably smaller than is normal for pine in natural conditions. The tiers of strobiles on a shoot were counted. Their number varied from 1 to 9. Mean values are presented in table 4.

Table 4

Mean number of male strobile tiers on "male" scions as observed in 1964 in relation to the experimental variables

	Grafted high	Grafted low	Mean
Fertilized	3.2	4.8	4.0
Not fertilized	5.2	4.1	4.7
Mean	4.2	4.5	4.3

From a statistical analysis of the data it appears that there is a strongly significant interaction between the grafting position and the fertilizer treatment. This interaction is caused by the strong negative influence of the ammonium nitrate fertilization on the scions in the high position while at the same time in the low position no significant effect was observable. This implies that the fertilization done in 1963 at the time of grafting has had a negative influence on the development of strobiles in buds of scions grafted high.

In 1968 the size of the male inflorescences was also recorded. There were no differences in this respect between the „male" and „female" scions, but in the ramets that have been treated with the ammonium

nitrate fertilizer in 1966 the inflorescences had on an average less tiers of strobiles than in the unfertilized variant (3.8 vs. 5.2 respectively). Thus it can be concluded that treating with an ammonium nitrate fertilizer causes a reduction in the number of male strobiles developing on a shoot.

DISCUSSION

The results of the observations on vegetative development of ramets that are presented in figures 6, 7 and 8 suggest certain conclusions about the phenomenon of physiological differentiation of a tree crown. Grafting inhibits the development of shoots for a period of about two years, after which the vegetative development on a stock is no longer dependent on the type of scion that was used nor on the nitrogen fertilization, it is however very dependent on the position it has on the graft. Thus the development is possibly controlled by the insolation or shading of the growing points or by an internal nutritional regulation within the whole plant (or graft as in our case) but not by the external supply of nitrogen nor by topophysis (the non-genetic physiological predisposition of plant parts) of the apical meristem of the scion. If, as W a r e i n g (1958) suggests, the small number of side shoots on high order whorls well within the tree crown is caused by ageing of the meristem, then this ageing process is promptly reversed when the scion is grafted onto the top of a stock and conversely strong „female" shoots (juvenile?) when grafted low on the stock quickly age. Under ageing W a r e i n g (1958) includes such processes as reduction in growth and a reduction in the number of side shoots on a whorl and interprets it as the effect of malnutrition of the shoot by the main axis of the branch coupled with correlative inhibition of lateral buds by the main ones. In the light of the results presented here this interpretation seems likely, however I should hesitate to refer to such easily reversible processes as belonging to gerontological phenomena. In *Pinus radiata* it has been found that the vegetative growth of scions from 35 years old trees is very much poorer (by about 45%) than that of scions from young 10 years old trees (S w e e t 1964). If this were also applicable to *P. silvestris* than it must not be considered that „female" and „male" scions are physiologicaly young and old respectively, since their vegetative development is similar (fig. 6). In the process of physiological ageing one should only include ontogenetic progression and not the intensity of growth or vegetative development. In this sence the „male" scions appear to be somewhat younger physiologically than the „female" ones since after grafting (and not counting the strobiles that were already in the buds at time of grafting) they are slower to attain the capacity for female (figs. 9, 12 and 15) and even male (fig. 19) strobile production. This is in agreement with the theory that trees start

ageing from the apical meristems on branch tips (Schaffalitzky de Muckadell 1956).

On the basis of the foregoing discussion I should suggest that different parts of the tree crown should not be treated as „old" or „young" but as zones specialized for certain biological functions as for example growth in height, nutrition of trunk and roots, formation of female strobiles and nutrition of cones, and the formation of male strobiles. The shoots specialized for the production of male strobiles have few needles, do not develop side buds and grow poorly, however all this does not mean that they are physiologically older than other tree parts. In altered conditions they can assume different functions.

The question of crown specialization is closely connected with the phenomenon of apical dominance. One of the theories attempting to explain this phenomenon (Kuse 1961) is that the inhibition of lateral buds takes place through malnutrition since the terminal bud picks up bulk of the nutrients, among other ways also by a hormonal regulation of the transport (Booth et al. 1962). The observed effect of the interaction between the grafting position and the fertilizer treatment on the size of the male strobile clusters is in agreement with that theory and with the observable effect of the main shoots on the poor growth and vegetative development of laterals (Moorby and Wareing 1963) since the fertilizer had a marked influence only on the scions grafted high (table 4).

In this case the nitrogen fertilizer has had a negative effect on the development of the cluster of male strobiles, while in the year 1966 the nitrogen fertilizer has had a positive effect on the initiation of female strobiles and also a negative one on the size of male strobile clusters in 1968. Besides the percentage of scions with male strobiles was also reduced by this fertilizer treatment though this effect was not statistically significant. This confirms the results obtained on *Pinus resinosa* (Giertych and Forward 1966) and on *Pinus radiata* (Sweet and Will 1965), indicating that an external nitrogen supply stimulates the initiation of female strobiles and reduces the number of male, while lack of nitrogen has the opposite effect. The positive effect of nitrogen supply on female strobile initiation in 1967 (table 1) has been observed only in the lower part of the stock and on scions with a slower reproductive development („male"), which would suggest that in „female" scions grafted high the nitrogen supply in control conditions was not limiting for female strobile initiation. This is not surprising since the grafts grew on relatively fertile soil.

Since fertilization with ammonium nitrate has had a negative effect on the young developing strobiles already present on the shoots at the time of treatment (table 2) the net increase in female strobiles as a result of fertilizer application may be obtained only at a time when the

current crop of conelets is small. As Faulkner (1966) pointed out the best fertilizer effects on seed yields are obtained if the treatment happens to precede a naturally copious strobile initiation. Since in pine on the average every second year is a seed year, it may prove practical to apply the fertilizer in the spring of a seed year, that is at the time when there are many two year old cones, few young strobiles, and preceding an expected rich initiation of new strobiles.

When discussing the factors controlling strobile initiation it is necessary to comment on the question whether attainement by trees of a state of sexual maturity (first strobiles) is the same phenomenon as the initiation of strobiles on individual shoots. In other words, is the lack of strobiles on a young tree caused by a lack of conditions for their initiation on all the shoots, and the first strobiles indicate that such conditions have been attained at some of them or do the reproductive functions have two prerequisites, a sexual maturity of the whole tree and appropriate conditions within a given shoot? In the second interpretation the first prerequisit when met would be permenent and the second would depend on the year, position in the crown and many external conditions. On the basis of the results obtained in the present study one could assume that we are dealing with one and the same phenomenon since for scions grown in various conditions their entering into the state of physiological capacity for female strobile production (figs. 9, 10 and 11) and the intensity of that production (fig. 12, 13 and 14) have been affected in the same way by external conditions. Furthermore in the years 1967 and 1968 the number of female strobiles is dependent on the number of shoots and not on the position of the scions on the stock (fig. 16), in other words the strobile production was not determined by insolation or internal hormonal regulation but by the state of ramet development. The number of scions with female strobiles is also dependent on the quality of the grafting unions (fig. 18). Since the grafting success has also an influence on the vegetative development of the ramets (number of shoots) there does not appear to be any difference in the mechanism controlling the percentage of flowering scions and the intensity of that flowering.

This conclusion concerns scions and not seedlings. There is still the possibility that the material used in this experiment was already physiologically mature and did not undergo rejuvenation as a result of grafting onto young stocks, and that truly juvenile seedlings first require some conditions for the attainement of sexual maturity and then specific conditions for the initiation of strobiles.

The difference in the duration of sexual development of seedlings and of scions is not particularily large in *P. silvestris*. In seed orchards one can expect serious crops of cones after 15 years while in stands after 40 years, however it is not the age that is decisive here but the stocking (Wright 1964). In the experiment described here the scions grew with

small spaces between them which provided a shade for the lower branches on which male strobiles were expected. Female strobiles started to appear two years after grafting. On the same grafts but on shoots belonging to the stock female strobiles started to appear in 1966 that is five years after seed sowing. As is known even two year old seedlings happen at times to yield strobiles (Wright and Bull 1963), in other words there is in this respect a considerable individual variation. Thus it is not possible to treat a comparison of this one pine clone from the forest range Zwierzyniec (near Kórnik) with the seedlings from Nurzec (in the Białystok region) as being of particular significance. Generally first male strobiles occur sporadically on younger pines than first female strobiles (Wright 1964) but in greater numbers female strobiles occur first in about the 5th vegetative season and male ones much later. In the experiment described here until 1967 no male strobiles have been found on the part of the graft belonging to the stock although some of the 6 year old seedlings from the same sowing as those used for the grafting have sporadically had them. The scions have produced male strobiles sporadically until 1968 that is for 5 years. Thus no major differences were observed in the age at which male strobiles were developed on the scions and on seedlings.

Finally it must also be stressed that the results reported here concern only one, not particularily fruitful clone of pine. Generalization of these results may therefore be risky.

SUMMARY

Sexual development of pine grafts was followed for 5 years 1° on ramets growing in a dominant position on the stock and in a supressed position among the stock shoots, 2° on ramets coming from scions collected in the „male" and in the „female" zone of the crown (figs. 1 and 2), and 3° on grafts that have and have not been fertilized with ammonium nitrate. It has been established that in vegetative development and in survival the differences between ramets coming from different scions, and those due to fertilizer treatments, quickly disappear, while the position on the stock has a profound influence. In the lower part of the stock a ramet is not able to develop while in the upper position it grows well.

Generative development of both the female and male fertility is delayed by a year or two on ramets coming from „male" scions compared with those from „female" scions. Fertilization with ammonium nitrate increases the number of female strobiles in the year following treatment, decreases the size of the male strobile clusters, and lowers the survival of one year old conelets. The position on the stock has an effect on the generative development of ramets only, though very markedly, through its effect on vegetative development.

LITERATURE

1. Anonym — 1963. The effect of fertilization, spacing and cultivation on flower production. Circ. Tex. For. Ser. No. 79. For. Abs. 25 : 1964 no. 3438.
2. Bánó I. — 1954. Egy erdeifenyö anyafa vizgälata magtermö ültetvény létesitese szempontjából. Erdesz. Kutatas Budapest 3 : 73 - 82. For. Abs. 17 : 1956 no. 1348.
3. Barnes R. V., Bingham R. T. — 1963. Flower induction and stimulation in western white pine. U.S. For. Ser. Pap. Interm. For. Range. Exp. Sta. no. int. 2 : 1 - 10, For. Abs. 25 : 1964 no. 477.
4. Booth A., Moorby J., Davies C. R. Jones H., Wareing P. F. — 1962. Effects of indolyl-3-acetic acid on the movement of nutrients within plants. Nature 194 : 204 - 205.
5. Chiba S. — 1965. Experiments on the flower induction on grafts of *Pinus strobus* (Preliminary report). Oji Inst. For. Tree Impr., Hokkaido, Kuriyama. Tech. Note no. 39.
6. Duff G. H., Nolan N. J. — 1958. Growth and morphogenesis in the Canadian forest species. III. The time scale of morphogenesis at the stem apex on *Pinus resinosa* Ait. Can. J. Bot. 36 : 687 - 706.
7. Faulkner R. — 1966. A review of flower induction experiments and trials 1948 - 63. Rep. on For. Res. for. Yr. ended March 1965 For. Comm.: 207 - 218.
8. Giertych M. — 1966. Rozmieszczenie regulatorów wzrostu u *Pinus resinosa* Ait. w stosunku do jej rozwoju. Zesz. Nauk. Univ. M. Kopernika w Toruniu, Nauki Mat. Przyr. zeszyt 12 — Biologia (VIII): 35 - 42.
9. Giertych M. — 1967. Zarys fizjologii sosny zwyczajnej. Rozmnażanie generatywne. Red. S. Białobok i W. Żelawski, PWN Poznań: 269 - 294.
10. Giertych M., Forward D. F. — 1965. Growth regulator changes in relation to growth and development of *Pinus resinosa* Ait. Can. J. Bot. 44 : 717 - 738.
11. Giertych M., Przybylski T. — 1965. Badania nad metodami szczepienia sosny i świerka. Arboretum Kórnickie 10 : 183 - 192.
12. Goddard R. E. — 1964. The frequency and abundance of flowering in a young slash pine orchard. Silv. Genet. 13 : 184 - 186.
13. Hermann S. — 1951. In primärstadium blühende Kiefer. Naturwissenschaften 38 : 381 - 382.
14. Hirov A. A. — 1964. Stimulation of flowering in Scots pine seed orchards. Lesn. Z. Archangelsk 7(5): 36 - 38. For. Abs. 26 : 1965 no. 5044.
15. Holst M. J. — 1961. Experiment with flower promotion in *Picea glauca* (Moench) Voss. and *Pinus resinosa* Ait. Recent Advances in Botany Vol. II: 1964 - 1968. Univ. of Toronto Press.
16. Illy G. — 1967. Recherches sur l'amélioration génétique du pin maritime. Ann. Sci. For. 23(4) : 757 - 948.
17. Jablokov A. S. — 1962. Selekcja dreviesnyh porod. Selhozizdat, Moscow.
18. Kamieńska A. — 1967. Zagadnienie determinacji płci u roślin. Wiad. Bot. 11(4) : 269 - 280.
19. Kuse G. — 1961. Correlative growth of lateral bud in *Ipomoea batatas* shoot. Memoirs Coll. Sci. Univ. Kyoto. Ser. B. 28 (3) : 431 - 453.
20. Lester D. T. — 1964. Flowering on red pine grafts. J. For. 62(2) : 116 - 117.
21. Lücke H. — 1962. Wann kann Plantagensaatgut anerkannt werden? Silv. Genet. 11 : 66 - 68.
22. Matthews J. D. — 1963. Factors affecting the production of seed by forest trees. For. Abs. 24 : i-xiii.
23. Melchior G. H. — 1962. Weitere Untersuchungen zur Förderung der Blütenbildung der Kiefern durch Rückschnitt. Silv. Genet. 11 : 11 - 15.
24. Melchior G. H., Heitmuller H. H. — 1961. Erhöhung der Zahl der männ-

lichen Blüten an *Pinus silvestris*. Pfropflinge durch Rückschnitt. Silv. Genet. 10 : 180 - 186.
25. Mirov N. T. — 1951. Inducing early production of pine pollen. Calif. For. and Range Exp. Sta. Res. Note 80. For. Abs. 13 1952 no. 2913.
26. Moorby J., Wareing P. F. — 1963. Ageing in woody plants. Ann. Bot. 27 : 291 - 308.
27. Mosteller F., Youtz C. — 1961. Tables of the Freeman-Tukey transformation for the binomial and Poisson distribution. Biometrika 48 (3 and 4) : 433 - 440.
28. Mušketik L. M. — 1960. O polovom dimorfizmie sosny obyknoviennoj. Biul. Glav. Bot. Sada. Moskva 37 : 112 - 115.
29. Nilsson B. — 1955. Markbehandlingens iverkau på blomsätting och fröbeskaffenhet hos ympträd av tall. Svenska Skogsv. Fören. Tidskr. 53(3) : 305 - 310. For. Abs. 18 : 1957 no. 3942.
30. Schaffalitzky de Muckadell M. — 1956. Experiments on development in *Fagus silvatica* by means of herbaceous grafting. Physiol. Plant. 9 : 396 - - 400.
31. Sweet G. B. — 1964. The effect of physiological age of scion on growth of grafts in *Pinus radiata* N. Z. For. Res. Notes No. 37 : 1 - 8.
32. Sweet G. B., Will G. M. — 1965. Precocious male cone production associated with low nutrient status in clones of *Pinus radiata*. Nature Lond. 206 (4985) : 739.
33. Van Buijtenen J. P., Brown C. L. — 1962. The effect of crown pruning on strobili production of loblolly pine. Proc. For. Genet. Workshop, Macon, Ga., S. For. Tree Impr. Comm. publ. no. 22 : 88 - 93.
34. Van Haverbeke D. F., Barber J. C. — 1961. Less growth and no increased flowering from changing Slash pine branch angle. Res. Note Stheast. For. Exp. Sta. no. 167 : 1 - 2. For. Abs. 23 : 1962 no. 3477.
35. Wareing P. F. — 1958. Reproductive development in *Pinus silvestris* in The Physiology of Forest Trees. Ed. K. V. Thimann. Roland Press N. Y.: 643 - 654.
36. Wright J. W. — 1964. Flowering age of clonal and seedling trees as a factor in choice of breeding system. Silv. Genet. 13 : 21 - 27.
37. Wright J. W., Bull W. I. — 1963. Geographic variation in Scotch pine. Silv. Genet. 12(1) : 1 - 25.

MACIEJ GIERTYCH

Rozwój generatywny szczepów sosny pospolitej (Pinus silvestris L.)

Streszczenie

Przez pięć lat śledzono rozwój szczepów sosnowych — 1° na zrazach rozwijających się w pozycji dominującej i w pozycji przygłuszonej wśród pędów podkładki, 2° u zrazów z „męskiej" i „żeńskiej" części korony (ryc. 1 i ryc. 2), oraz 3° na szczepach nawiezionych i nienawiezionych saletrą amonową. Stwierdzono, że w rozwoju wegetatywnym i w przeżywalności różnice między jakością zrazów oraz wpływ nawożenia szybko zanikają, natomiast pozycja w koronie podkładki ma znaczenie kapitalne. W dolnej części korony podkładki zraz nie jest zdolny do rozwoju, podczas gdy w pozycji górnej rozrasta się dobrze.

Rozwój generatywny, czyli obradzanie kwiatów zarówno żeńskich jak i męskich, jest o rok lub dwa opóźniony na zrazach „męskich" w stosunków do zrazów „żeńskich". Nawożenie saletrą amonową zwiększa liczbę kwiatów żeńskich w rok po nawożeniu, zmniejsza rozmiar kwiatostanów męskich i ogranicza przeżywalność jednorocznych szyszeczek. Pozycja zrazu wśród pędów podkładki decyduje o rozwoju generatywnym zrazu tylko pośrednio (chociaż bardzo silnie) poprzez rozwój wegetatywny.

МАЦЕЙ ГЕРТЫХ

Генеративное развитие привитых растений Pinus silvestris L.

Резюме

В течение пяти лет проводились наблюдения над привитыми растениями сосны: 1) на привоях, развивающихся среди побегов подвоя в угнетённом состоянии, или наоборот, господствующих; 2) на привоях из „мужской" и „женской" частей крон (рис. 1 и 2); 3) на растениях, удобренных и не удобренных аммиачной селитрой. Установлено, что для вегетативного развития и для выживаемости привоев имеет существенное значение их расположение в кроне деревьев. В нижней части кроны подвоя привой не способен к развитию, а в верхней разрастается хорошо. В то же время различия, возникшие под влиянием удобрения или качества привоев, быстро исчезают.

Генеративное развитие, или образование как мужских, так и женских цветков, на „мужских" привоях задерживается на год или на два по сравнению с „женскими". Удобрение аммиачной селитрой приводит через год к увеличению числа женских цветков, одновременно уменьшается размер мужских соцветий, ограничивая выживаемость одногодичных шишек. Положение привоя среди побегов влияет на генеративное развитие хотя и сильно, однако не непосредственно, а через вегетативное развитие.