Zusammenfassung

Titel der Arbeit: *Über* die Auswirkung von *Gamma*-Strahlen auf die Chromosomen *somatischer* Zellen bei der Fichte.

Samen der gemeinen Fichte (Picea Abies KARST.) wurden mit Gamma-Strahlen von Co_{60} bestrahlt. Als Strahlungsdosen wurden verwandt: 100, 500, 1000, 3000, 5000, 7500 und 10000 r. Die Mitose-Beobachtungen sind an Wurzelspitzen-Zellen bestrahlter und unbestrahlter Samen durchgeführt worden.

Es wurde festgestellt, daß es bei den aus bestrahlten Samen stammenden Zellen zu Veränderungen der relativen Chromosomen-Längen gegenüber den Kontrollen gekommen war (Tab. 1). Bei allen Bestrahlungsdosen wurden Chromosomen-Längenveränderungen in der Weise bewirkt, daß die stärkeren Abweichungen immer bei den großen und kleinen Chromosomen vorkamen, während bei den mittelgroßen Chromosomen nur kleinere Veränderungen auftraten. Dagegen hatte sich die Gesamtlänge der Chromosomen der einzelnen Zellen — bei verschiedenen Dosen —, verglichen mit den Kontrollen, nicht verändert (Tab. 4).

Bei Anwendung der Dosen 100 r bis 1000 r ist es nur bei einzelnen Chromosomen zu Längenabänderungen gekommen. Bei den größeren Dosen, d. h. von 3000 r bis 10000 r, kam es zu Chromosomenfragmentierungen sowie zu anderen Anomalien der Mitose. Es wurden sowohl Zellen mit kleinerer Chromosomenzahl als auch Zellen mit doppelter Chromosomenzahl, die paarweise angeordnet waren, erhalten.

Bei den Dosen 5000 r, 7500 r und 10000 r zeigte eine größere Anzahl Zellen im Stadium der Anaphase Brücken-Bildungen. Ferner kamen noch weitere Anomalien in diesem Stadium und auch im Übergangsstadium Anaphase-Telophase vor.

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The Degree of Natural Selfing in Slash Pine as Estimated from Albino Frequencies[1]

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The extent of selfing in forest trees is of interest to tree improvement workers because inbreeding often results in depression of vigor and other economically important traits. Although the overall importance of selfing has not yet been evaluated, it is of special interest where clonal orchards are used as the means of mass producing seed of a superior strain. In such orchards the potential for selfing is magnified because selfs can not only be produced from selfing of a ramet but also from mating of ramets of the same clone. Reliable knowledge of the extent of selfing that occurs under natural conditions will help to show the extent of selfing that may occur in seed orchards.

Although most pines are generally considered to be largely crosspollinated, there have been few experiments designed to estimate the relative amount of selfing vs. crossing that occurs under natural conditions. The assumption of the predominance of crossing is largely based on studies of natural barriers to selfing, such as dichogamy, and evidences of reduced seed or seedling yield from isolated trees and from artificial selfing. Such evidence does not, of course, provide a reliable estimate of the actual degree of natural selfing.

Many studies have shown that most coniferous species can be successfully selfed under artificial conditions. Seed and seedling yields from selfing are usually low. However, there is considerable variation in self-fertility both between species and among individual trees within species. Serbian spruce (Picea omorika [PANČIČ] PURKYNE), for example, has been shown to be highly self-fertile as tested under artificial pollination (LANGNER, 1959). Most western white pines (Pinus monticola DOUGL.) show a depressed seed yield from artificial selfing, but some individuals will yield fully as many seed and seedlings under selfing as under outcrossing (BINGHAM and SQUILLACE, 1955).

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Seed and seedling yields may or may not provide a reliable measure of the extent of natural selfing. Where self-fertility is low under artificial conditions, one can, of course, presume that natural self-fertility is low. However, where self-fertility is high under artificial conditions, natural self-fertility may be high or low depending upon the presence or absence of selective fertilization. The presence of selective fertilization in western white pine was demonstrated by SQUILLACE and BINGHAM (1958) and BARNES *et al.* Through a series of artificial crosses involving mixtures of "self" and "outcross" pollens, these authors showed that some individual western white pines favored outcrossing over selfing, while the reverse was true for other individuals.

Objective estimates of the degree of natural selfing have been made in a few cases. CRAM (1960), utilizing albinism as a gene marker in an open pollinated progeny of a blue spruce tree (*Picea pungens* ENGELM.), estimated that 18 percent natural selfing occurred. Through an intricate and ingenious technique SARVAS (1962) estimated that in normal stands of Scotch pine (*Pinus sylvestris* L.) approximately 7 percent of full seed originates from self-fertilization. His study involved determinations of frequencies of aborted ovules in normal trees vs. those in "female" or in emasculated trees, embryo abortion after cross-fertilization and self-fertilization, and other factors.

Among hardwood species, green wattle (*Acacia decurrens* WILLD.) was estimated to be naturally cross-pollinated to the minimum extent of between 85 and 95 percent in plantations by use of recessive leaf characters as gene markers (PHILP and SHERRY, 1946). In a similar manner MOFFETT (1956) showed that minimum natural crossing in black wattle (*A. mollissima* WILLD.) ranged from 62 to 97 percent, with a mean of 84 percent. POSNETTE (1950) utilized the recessive character, albinism, and also a dominant character, "red pigmentation," to estimate that cross pollination varied from 18 to 43 percent over a 3-year period in a group of cacao (*Theobroma cacao* L.) trees.

This report describes a technique used in estimating the degree of natural selfing in slash pine (*Pinus elliottii* var. *elliottii* ENGELM.) through measurement of the frequency of albino seedlings originating from seed produced by open pollination in natural stands, and gives preliminary results. The results are not considered conclusive because the genetic constitution of most of the parent trees used in the study needs to be verified and also because the sampling intensity was weak in some instances.

Albinism and other Types of Chlorophyll Deficiency in Forest Trees

Albinism and other types of chlorophyll deficiency have been noted in seedlings of conifers including eastern white pine (*P. strobus* L.) (JOHNSON, 1945), Austrian pine (*P. nigra* var. *austriaca* [HOESS] ASHERS and GRAEBN.) (JOHNSON, 1948), Scotch pine (EICHE, 1955), Serbian spruce (LANGNER, 1959), blue spruce (CRAM, 1960), red pine (*P. resinosa* AIT.) (FOWLER, 1962) and western white pine (BARNES *et al.*). In the extreme case (albinism) the seedlings are apparently completely lacking in chlorophyll in the whole shoot. In other types the degree of the deficiency may not be as intense, the seedlings appearing yellow, yellow-green, or other colors. In some types certain plant parts only may be partially or wholly deficient. Finally, the deficiency may not appear in the newly germinated seedling but, rather, in certain plant parts developing at later stages (such as the deficiency in the primary needles of Austrian pine seedlings described by JOHNSON, 1948). True albinos usually die within a week or two after germination, while other types may live longer periods or indefinitely.

Chlorophyll deficiency has also been reported in tree species other than conifers including cacao (POSNETTE, 1950), Chinese chestnut (*Castanea mollissima* BL.) (MCKAY, 1956), Siberian pea-tree (*Caragana arborescens* LAMB.) (CRAM, 1958), quaking aspen (*Populus tremuloides* MICHX.) (LESTER, 1961), and sugar maple (*Acer saccharum* MARSH) (GABRIEL, 1962).

Apparently albinism and other types of chlorophyll deficiency in coniferous species are often due to a single recessive gene. Approximate 3 : 1 ratios of normal vs. albino seedlings in selfed progenies have been reported for Austrian pine (JOHNSON, 1948), blue spruce (CRAM, 1960), and western white pine (BARNES *et al*), altough in each case only a single parent tree was involved. The trait was also lethal in each case. JOHNSON (1945) reported a 3 : 1 ratio of normal vs. chlorophyll deficient seedlings in a selfed progeny of an eastern white pine. FOWLER (1962) reported a 5 : 1 ratio for a chlorophyll deficiency in a selfed red pine progeny, but suggested that the divergence from 3 : 1 may be due to lower survival of the deficient seeds and seedlings.

Turning to hardwood species, we note that POSNETTE (1950) reported a 3 : 1 ratio for lethal albinism in a selfed progeny of a cacao tree. CRAM (1958) obtained the same ratio for a chlorophyll deficiency (yellow and lethal) in a selfed progeny of a Siberian pea-tree. MCKAY (1956) reported varying albino frequencies of up to 24 percent for crosses among 3 Chinese chestnut trees which had shown from less than 1 to 4 percent albinos upon open pollination. LESTER (1961) noted 301 normal to 80 chlorophyll deficient seedlings (which seems to suggest 3 : 1, but not conclusively) in a selfed progeny of an aspen tree. GABRIEL (1962) reported segregations of 31 : 4 and 25 : 4, normal vs. albino (lethal), for selfed progenies of two sugar maple trees, from which no definite conclusions could be drawn.

The occurrence and persistence of chlorophyll deficient genes in a population is believed to be, to some extent at least, the result of recurrent mutation. However, other factors such as selection against or for one or more of the possible genotypes may also operate to cause the frequencies of deficient genes to be maintained at a constant level.

Method

The present study was based upon albinos occurring in various groups of seedlings grown from seed sown in 1960, 1961, and 1962, as follows:

1960

(1) 31 lots of wind-pollinated seeds collected from individual mother trees during years 1957-59. Some of these were in a plantation of unknown (most likely north Florida) seed source while others were located in natural stands in north Florida and south Georgia.

1961

(1) 219 lots of wind-pollinated seeds collected in 1960 from individual mother trees growing in natural stands scattered throughout the entire range of typical slash pine plus 47 lots from trees within the range of South Florida slash pine (*Pinus elliottii* var. *densa* LITTLE and DORMAN).

Table 1. — Albino frequencies obtained in progenies of albino carriers[1]) and estimates of natural selfing

Carrier designation	Year seed sown								
	1960		1961[2])		1962		All years		Estimate of degree of natural selfing
	Total seedlings	Albino seedlings	Total seedlings	Albino seedlings	Total seedlings[3])	Albino seedlings	Total seedlings	Albino seedlings	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Percent*
3-E × wind	—	—	63	1,6	53	0,0	116	0,9	[4])0
4-A × wind	—	—	209	0,5	61	0,0	270	0,4	[4])0
6-A × wind	—	—	96	1,0	123	0,0	219	0,4	[4])0
7-B × wind	—	—	42	2,4	123	2,4	165	2,4	5
11-C × wind	—	—	106	0,9	270	0,7	376	0,8	[4])0
31-D × wind	—	—	240	6,7	—	—	240	6,7	23
35-A × wind	—	—	166	9,0	244	6,6	410	7,6	27
42-E × wind	—	—	79	5,1	175	0,0	254	1,6	2
G-27 × wind	117	0,8	12	,0	350	2,8	479	2,3	5
G-133 × wind	119	0,8	—	—	852	1,2	971	1,1	0
G-157 × wind	59	1,7	—	—	652	1,8	711	1,8	3

[1]) All wind pollinated progenies which produced one or more albinos.
[2]) Includes data from both of the two sowings made in 1961.
[3]) The counts of total seedlings shown here are approximate, being estimates made after the beds were inadvertently thinned
[4]) Actual value as computed by formula was negative, taken here to be 0.

Two sowings were made. In the first, approximately equal numbers of seed were sown for each lot. After germination, when progenies containing albinos could be identified, additional seed were sown for 4 of these to obtain better estimates of albino frequencies.

(2) A lot of artificially selfed seeds from a single tree in a natural stand in north Florida, which had produced albino seedlings by wind-pollination in the past.

(3) One bulk seed lot containing wind-pollinated seeds from about 30 trees located in a natural stand in north Florida.

1962

(1) Eight lots of wind-pollinated seeds from trees known to have produced albinos in the past. Four of these (3-E, 4-A, 6-A, and 7-B) were excess seed from the 1960 collections. The remaining 4 were re-collections, made in 1961.

(2) A mixture of wind-pollinated seeds grown in the Florida Forest Service's Baker Nursery. Approximately 1200 lineal feet of nursery beds, 4 feet wide, were examined.

Although the exact source of seed was not known in some cases, all lots, excepting the 47 South Florida slash pine progenies specifically mentioned, proved to be of the typical slash pine variety upon sowing.

Following each sowing, albino seedlings were marked and recorded during several inspections within about 2 weeks after germination began, and after this period counts of normal seedlings were also obtained.

Usually little difficulty was encountered in identifying the albinos. The hypocotyls appeared reddish or reddish purple, and the cotyledons were at first white or pale yellow, then turning pale yellow to brown as the seedling approached death. Albinos died within about 2 weeks after germinating. Seedlings having other types of chlorophyll deficiencies, which were occasionally encountered, were not counted as albinos. Within progenies containing albinos, variation in the albino symptoms was not great. In the "bulk" seed lot and the commercial nursery beds, where other types of deficiency were noted, occasionally some difficulty was encountered in classifying albinos, but because of their relative infrequency the error caused here was probably not great.

Results

Of the 297 wind-pollinated progenies, 11 contained 1 or more albinos *(table 1)*. Albino frequencies in these progenies varied from 0.4 to 7.6 percent. All of the progenies containing one or more albinos came from parents located within the range of typical slash pine — none of the south Florida parents bore albinos.

The selfed lot (G-27 × G-27) produced 11 albinos out of a total of 34 seedlings, or 32.4 percent. This frequency is not significantly divergent from a 3 : 1 ratio as determined from a chi-square test (P = .35), and fits it better than other likely ratios, such as 9 : 7.

The "bulk" seed lot produced about .053 percent albinos, while in the commercial nursery a count of .045 percent was obtained *(table 2)*. In *table 2* all utilizable data were combined to obtain an average estimate of albino frequency, .052 percent, for wind-pollinated seeds from natural stands, to be used later in estimating carrier frequency.

Assumptions and steps followed in obtaining an estimate of the degree of natural selfing are outlined below. The trait is assumed to be affected by a single pair of genes for all carriers, even though this was verified for only one of them (G-27). The procedure is similar to that employed by Philp and Sherry (1946), Posnette (1950), and Cram (1960) with the exception that they did not attempt to account for abnormal seedlings resulting from crossing among heterozygotes. By "natural selfing" here we mean the production of viable seedlings by self-fertilization under na-

Table 2. — Data used in obtaining an estimate of average albino frequency in natural populations[1])

Seed lots	Year sown	Total seedlings	Albino seedlings
		Number	*Percent*
31 wind-pollinated lots	1960	3,759	0,0798
219 wind-pollinated lots	1961	17.366	,1036
„Bulk" - 30 mother trees	1961	15,170	,0527
Commercial nursery, 1200 lin. ft. of 4-foot beds	1962	142,600	,0449
All lots	—	178,895	,0520

[1]) All data excepting those from the second sowing of four wind-pollinated lots (carriers) made in 1961, the eight wind-pollinated lots (carriers) sown in 1962, and the single selfed progeny are included here. Use of the latter would have caused a bias in the estimate desired.

tural conditions and the number of such viable "selfs" is expressed as a percent of the total number of viable seedlings produced (selfed plus outcrossed seedlings). Since none of the South Florida slash pine progenies contained albinos, the data from typical slash pine only were used in the analysis, and hence the results are considered to apply strictly to the latter.

1. Albino seedlings (aa) can presumably be produced from either (1) selfing of albino gene carriers (Aa) or (2) mating of albino carriers. The result in either case is depicted below.

Aa × Aa ——→	AA	Aa	aa
Genotypic ratios	1	2	1
Phenotypic ratios	3 normal		1 albino

2. Among wind-pollinated seeds from an albino carrier, the frequency of albinos depends upon (1) the extent of selfing and (2) the extent of outcrossing to other albino carriers, which in turn depends upon the frequency of carriers in the stand.

3. The frequency of carriers was estimated by two methods: —

a. Of the 250 typical slash pine individual mother tree seed lots sown, 219 produced 50 or more seedlings (50 seedlings were arbitrarily considered to be a minimum number giving a reasonable chance for albinos to occur). Of these 219 progenies, 10 contained one or more albinos. The parents of these must be considered albino carriers since only they can produce albinos. The ratio $\frac{10}{219}$ = .046 or 4.6 percent is, then, an estimate of the frequency of carriers.

b. The estimate of average frequency of albinos from natural populations was .0520 percent *(table 2)*. This is the frequency of the "aa" genotype. Applying HARDY-WEINBERG formulae (FALCONER, 1960, p. 9), the frequency of the albino gene (q) is $\sqrt{\text{freq. aa}} = \sqrt{.000520} = .023$, where the total gene frequency is 1. Then p = frequency of the normal gene = 1-q = 1 -.023 = .977. Finally, the frequency of carriers = 2 pq = 2(.023) (.977) = .045 or 4.5 percent. This estimate is very close to the one obtained in "3a" above and will be used in the next step. The similarity of the two estimates, however, should not be taken to imply great accuracy or high uniformity among populations.

4. When an albino carrier mates with other trees under natural conditions, theoretically 4.5 percent of the time it will be mating with other carriers. Therefore, 4.5 percent of outcross seedlings will have resulted from matings of the type Aa × Aa. On the average, one-fourth of these outcross progenies should be albinos. We are assuming here that carriers are distributed randomly in the forests.

5. As noted earlier, when an albino carrier is selfed, one-fourth of its progenies will be albinos.

6. The two sources of albinos noted in "4" and "5" above comprise the total frequency of albinos produced by a given carrier under open pollination. This relation is expressed by the following equation:

$$R = .25\,(.045)\,(100\text{-}W) + .25W$$

in which R = the number of albinos expressed as a percent of all seedlings; W = the percent of selfing; and 100-W = the percent of outcrossing. This equation in effect states that the number of albinos a given carrier produces under open pollination is equal to one-fourth of its selfed progeny plus one-fourth of its progeny resulting from outcrossing to other carriers, all values expressed in relative terms. Since R, the percent of albinos, is known, W, the percent of selfing, can be computed. For this purpose the equation simplifies to:

$$W = \frac{R - 1.1}{.24}$$

The data for tree 31-D *(table 1)* will serve as an example. It produced 6.7 percent albinos under open pollination. Substituting this value for R in the above equation one obtains

$$W = \frac{6.7 - 1.1}{.24} = 23 \text{ percent,}$$

as an estimate of the degree of selfing for this particular tree.

Note that one could also obtain a rough estimate of the degree of selfing merely by multiplying the percent albinos times four. Such a procedure ignores the numbers of albinos resulting from outcrossing and results in estimates slightly larger than that given by the formula. If the frequency of carriers is much greater than that obtained in this experiment the discrepancy would, of course, be greater.

Estimates of the degree of selfing (using the above formula) for all 11 carriers are shown in *table 1*. They vary from as low as 0 percent for several trees to as high as 27 percent in one tree. A check of those trees showing rather high rates of selfing showed that they are not isolated trees, all having eight or more other flower-bearing trees within a 70-foot radius. This variation is in agreement with the high degree of variation in self-fertility found among individual western white pine trees by BINGHAM and SQUILLACE (1955).

It should be remembered that all of the estimates of natural selfing were made on albino carriers. Therefore, if one extrapolates the results to apply to slash pines in general he assumes that there is no appreciable difference in the degree of natural selfing between carriers and noncarriers.

Discussion

As noted earlier, the estimates of natural selfing obtained are based upon the assumption of single gene pair inheritance. If instead, inheritance of this trait is conditioned by more than one gene in some of the trees, the estimates of selfing obtained may be in error. Selfing of the untested carriers and also mating them with the proven genotype (G-27) will be required to check their genetic constitution. The proven genotypes, having a definite gene marker showing up early in life, would also be very useful for other genetics studies.

The geographic location of the carriers found in this study is of interest. Four of them are located in southeast Louisiana, one in the extreme western part of Florida, two in north central Florida, and one in southeast Georgia. The remainder were in a plantation for which the seeds likely came from north Florida or southeast Georgia. The clustering of four carriers in southeast Louisiana may be more than coincidence and is interesting in the light of EICHE's (1955) report that the parents of chlorophyll deficient progenies showed tendencies toward geographic patterns. Such clustering of carriers emphasizes the need for caution in interpreting results of this study.

The absence of albinos among the South Florida slash pine progenies grown is curious. However, further study would be needed to conclude that the albino gene does not exist in the South Florida variety.

The rather high frequency of albinos found for natural populations (.052 percent) is interesting from the standpoint of population dynamics. If the two genotypes that survive, AA and Aa, have equal adaptive values and the selection coefficient against the homozygous recessive is 100 percent (as in the case of the completely lethal albino gene) the mutation rate is approximately equal to the frequency of the homozygous recessives (FALCONER, 1960, p. 37). Thus the implied mutation rate for our data would be .052, or roughly $\frac{1}{2000}$. This is much higher than mutation rates commonly found for other traits and organisms, which are frequently in the neighborhood of about $\frac{1}{100,000}$ (DOBZHANSKY, 1951, p. 58). Thus it is possible that the mutation rate for albinism in slash pine is actually much lower than $\frac{1}{2000}$ and that some other factor such as heterozygote preference (natural selection favoring heterozygotes over both the homozygotes) may be operating to maintain the gene at such a relatively high frequency. This interesting possibility should be investigated.

Summary

An estimate of the degree of natural selfing in 11 slash pine (typical) trees which apparently carry the albino gene ("carriers") was obtained through analysis of albino frequencies. One of the carriers was selfed and an approximate 3 : 1 ratio of normal vs. albino seedlings was obtained. Wind-pollinated progenies of all carriers contained varying proportions of albinos. The frequency of carriers was estimated to be about 4½ percent of all trees for the populations sampled. The above information was then utilized to estimate the degree of natural selfing, assuming one-factor inheritance for all carriers. The natural selfing estimates thus obtained for the 11 trees varied from 0 to 27 percent; nine of the trees showed 5 percent or less selfing while two of them showed 23 and 27 percent, respectively. Because of the assumption of one-factor inheritance and because of meagerness of data in some instances the results are considered preliminary.

Zusammenfassung

Titel der Arbeit: *Der Grad natürlicher Selbstung bei Pinus elliottii, geschätzt an Albino-Häufigkeiten.*

Über den Grad natürlicher Selbstung wurde bei 11 (typischen) Bäumen von *Pinus elliottii,* die offenbar für das Albino-Gen „Träger" waren, durch die Analyse von Albino-Häufigkeiten eine Schätzung erhalten. Einer dieser Träger wurde geselbstet und erbrachte eine annähernde 3 : 1-Verteilung von normalen und Albino-Sämlingen. Nachkommenschaften aus Windbestäubung aller Träger enthielten variierende Anteile an Albinos. Die Häufigkeit der Träger ließ sich auf etwa 4½% aller Bäume für die untersuchte Population schätzen. Die oben erwähnte Information wurde dann genutzt, um den Grad natürlicher Selbstung zu schätzen, wobei eine monofaktorielle Vererbung für alle Träger angenommen wurde. Die Schätzungen natürlicher Selbstung, die so für die 11 Bäume erhalten wurden, schwankten von 0 bis 27%; 9 Bäume zeigten 5% oder weniger Selbstung, während 2 von ihnen 23% und 27% aufwiesen. Wegen der Annahme einer monofaktoriellen Vererbungsweise und wegen der geringen Anzahl von Daten bei einigen Beispielen werden jedoch die Ergebnisse als vorläufig angesehen.

Résumé

Titre de l'article: *Evaluation du taux d'autofécondation naturelle chez Pinus elliottii d'après les fréquences des albinos.*

On a pu estimer le taux d'autofécondation naturelle chez 11 *Pinus elliottii* qui portaient apparemment le gène albinos («porteurs») grâce à l'analyse des fréquences des albinos. Un des porteurs a été autofécondé et l'on a obtenu une répartition des semis normaux par rapport aux semis albinos correspondant à peu près au rapport 3/1. Les descendances par fécondation libre de tous les porteurs contenaient des proportions variables d'albinos. La fréquence des porteurs dans la population étudiée a été estimée à environ 4,5%. Ce chiffre a été alors utilisé pour évaluer le degré d'autofécondation en supposant une hérédité monofactorielle pour tous les porteurs. Les estimations d'autofécondation naturelle ainsi obtenues variaient de 0 à 27% pour les 11 arbres; 9 d'entre eux avaient un taux inférieur à 5% alors que 2 autres présentaient un taux de 23 et 27% respectivement. En raison de l'hypothèse de l'hérédité mono-factorielle et de l'insuffisance de certaines données, il faut considérer ces résultats comme tout à fait provisoires.

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