Provenance Study of Douglas-Fir in the Pacific Northwest Region[1])

II. Field Performance at Age Nine

By KENNETH E. ROWE and KIM K. CHING[2])

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Introduction

In 1954, a provenance study of Douglas-fir (Pseudotsuga menziesii [MIRB.] FRANCO var. menziesii) was begun in the Pacific Northwest Region. The original study provided for testing of seedlings grown from seed collected from 16 provenances to be outplanted at each of the plantations established at, or near, each seed collection site. Each cone collection was confined to a designated area with a radius of 25 miles, and the number of trees sampled in these collections ranged from 14 to 89.

A report of the first 2 years' growth in the nursery of seedlings from 14 seed sources was made in 1960 (CHING and BEVER, 1960). These groups of trees were outplanted in the spring of 1959, with the addition of two more sources (E and F) a year later. Early growth in the field of these provenance stocks was reported in 1965 (CHING, 1965). Between 1959 when plantations were established and 1965—1966 when assessments on growth at age nine were made, various disasters reduced the number of locations from 16 to 9. Seven locations are omitted from this report because of either total destruction or too limited a number of trees. Plantations had been damaged by animals at locations I, J, and N; by fire at location G; by frost at locations D and H; and by drought at location P.

In the present report, data from a northern California planting site, identified as Q, are reported. The extra location was not in the original study and no seed was collected there. This site, however, provides an excellent opportunity to see how far Douglas-fir can be moved. Table 1 shows the geographic descriptions and the cooperators for the 16 original seed sources.

Objectives of this study were to study the extent of the genetic variation of Douglas-fir in the Pacific Northwest; to search for a provenance, or provenances, whose seed would be expected to produce particularly productive forests in a given region; and to determine whether there is adaptation of seed sources to a particular planting-site climate as measured by elevation and latitude.

Procedure

A reciprocal design for planting 2-0 seedlings of the 16 provenances was adopted for this experiment, so that seedlings of the local provenance could be compared with stock from other provenances. Each of the outplanting areas (locations) has two plantations, except for location Q, in northern California, which has only one plantation. The plantations occupy 5.69 acres and are usually from ¼ to ½ mile apart. Each plantation has two blocks of 121 trees of each seed source spaced 8 by 8 feet. Only the innermost 49 trees of each seed source within each block were measured for height and survival.

Seedlings of seed sources E (Haney, B. C.) and F (Snoqualmie National Forest, Washington) were one year younger than the other 14 groups when measured at the end of the growing season in 1965. Heights at 4 years of age (1961) and at 8 years of age (1965) were plotted for each of these two sources in each block at each of the 10 loca-

Table 1. — Geographie Areas, Seed Sources, Plantation Sites, and Cooperators.

Seed source	Cooperator	Latitude	Elevation (ft)	Location
BRITISH COLUMBIA				
A	Canadian Forest Products, Ltd.	50° 30'	400-600	Nimpkish Forest, Vancouver Island
B	Crown Zellerbach Canada, Ltd.	49° 45'	1,300-1,700	Courtenay area, Vancouver Island
C	MacMillan and Bloedel, Ltd.	49° 10'	2,600-2,900	Sugar Loaf Mt., Vancouver Island
D	B. C. Forest Service	48° 50'	570-750	Mesachie Lake, Vancouver Island
E	Univ. British Columbia	49° 10'	500-700	Haney
WASHINGTON				
F	Weyerhaeuser Co.	47° 30'	3,900-4,100	Snoqualmie National Forest
G	Simpson Olympic Tree Farm	47° 15'	100-500	Shelton area
H	State Dept. of Natural Resources	46° 45'	1,850-2,000	Elbe area
OREGON				
I	State Board of Forestry	45° 30'	1,600-2,200	Tillamook area
J	Crown Zellerbach Corp.	45° 10'	1,600-2,000	Clackamas Tree Farm, Molalla
K	Crown Zellerbach Corp.	45° 10'	3,200-3,800	Clackamas Tree Farm, Molalla
L	Jack Stump & Kenneth McCrae	44° 50'	200	Willamette Valley, Salem
M	Oregon State University	44° 30'	1,800-2,000	McDonald Forest, Corvallis
N	U.S. Forest Service	43° 45'	1,800-2,000	Oakridge area
O	U.S. Forest Service	43° 45'	2,500-3,000	High Prairie, Oakridge
P	Medford Corporation	42° 20'	2,700-3,300	Butte Falls
CALIFORNIA				
Q	Simpson Timber Co.	41° 00'	2,250	Korbel

[1]) Paper 766, Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

[2]) Associate Professor, Department of Statistics, and Professor, School of Forestry, Oregon State University, respectively.

tions. Heights at 9 years of age (1966) then were estimated by graphical extrapolation, assuming accelerating growth. These estimates have been verified by actual height at 13 years as measured in 1970.

Analysis

Analyses of the actual measured height indicated a very high correlation ($r = 0.90$) between the average height and the error variances at each of the 10 locations. Such a strong relation indicates that better statistical analysis can be accomplished if the original observations are transformed ta free the error variances of their dependence upon the magnitude of the observations. Although all analyses and comparisons are made using the transformed data, tables of means (***Tables*** 2, *3 and* 6) have been backtransformed to the original units of measure, solely for the convenience of the reader. The comparisons of source and location means in ***Table*** 2 were made by the method of Hartley (SNEDECOR and COCHRAN, pages 273—274, 1965). Tests of significance were based upon the assumptions that source and location effects are fixed and that plantations, blocks within plantations, and other environmental effects are random.

Results and Discussion

The analysis in ***Table*** 4 indicates very highly significant ($P < 0.001$) differences between locations and between seed sources. Location Q is omitted from this analysis. Of course, one would expect differences in growth over such a wide range of elevations of planting lacations, and there are genetic differences between local races of Douglas-fir. The very highly significant ($P < 0.001$) interaction between locations and sources would not necessarily be expected, however, and will be considered in some detail.

Differences in growth at different planting locations are, to a large extent, the consequence of differences in elevation. About 83 percent of the variation can be accounted for by linear regression on elevation. Exceptions are often of more interest, however, and after accounting for elevation, trees grew much less at location B than expected on the basis of its low elevation.

Genetic differences sometimes are expressed to a greater or lesser degree in different environments. Elevation and latitude of planting site are coarse descriptions of environment. The separate analyses of seed sources at each location (***Table*** 5) indicate some differences in the amount of variation because of seed source. The magnitude of the differences in variation, however, as seen by the seed-source mean squares, show no identifiable evidence of association with elevation or latitude of planting site as descriptions af environmental conditions.

Statistical comparison of the average height of trees from the 16 seed sources in ***Table*** 2 does not, of itself, indicate that any sources are clearly superior or inferior. Joint consideration of ***Table*** 2 and ***Table 3,*** however, makes more definite conclusions almost unavoidable. For example, ***Table*** 2 indicates that trees from seed collected at location ***C*** are nearly 10 cm taller than those from the next best seed source, and ***Table 3*** shows that this source is among the top four sources at all locations except Q. Trees grown from seed collected at locations N and P are at least 8 cm shorter than those from the next lower source ***(Table 2),*** and ***Table 3*** shows the same trend. They are among the five sources with shortest trees at all locations, except that trees of source N have grown reasonably well at location C.

Evidence of interaction between seed sources and locations indicates that, in some manner, seedlings from a particular provenance have grown better at some locations than at others. There may be changes in the actual rank or the magnitude of difference between sources at different locations, or some of both. ***Table*** 6 presents approximations of the seed source by location interaction effects. They are only approximate, because they have been retransformed to be presented in metric units.

Regardless of the apparent nature of the interaction, it is more satisfying to be able to explain all or at least part of the differential growth. ABOU-EL-FITTOUH, RAWLINGS, and MILLER (1969) have used additional environmental variables to aid in the explanation of such genotype by environment interactions. Elevation and latitude of planting site have been treated here as quantitative descriptions of the environment of a location.

The interactions were analyzed by fitting the nine effects, for each of the 16 sources, to second-order response surfaces of planting-site elevation and latitude. These interactions are effects in addition to the average effects of locations and of sources. The fitting of these response surfaces accounted for 80% of the sum of squares for interaction. The F-value (1.02) for the interaction residual is most indicative of the apparent nearly complete accounting of the interaction.

Figure 2 shows response contours of the six sources for which the second-order response surface was significant ($P < 0.05$). They represent a wide variety of types of contour surfaces and nearly the entire range of possible optimums in elevation and latitude. Source D ***(Fig. 2)*** prefers the southerly latitudes near 43° and, to some extent, the lower elevations. This is one example that also can be seen readily in ***Table*** 6. Source E has a very distinct preference

Table **2. — Average 9-Year Heights of Seedlings by Location for Sixteen Seed Sources and by Seed Source at Nine (Q omitted) Locations.**

Planting location	Height[1] (cm.)	Seed source	Height (cm.)
L	${}^{a}268.9^{a}$	C	${}^{a}151.0^{a}$
E	${}^{a}261.6^{a}$	D	${}^{a,b}141.5^{a,b}$
A	${}^{b}178.7^{b}$	B	${}^{b,c}137.8^{a,b,c}$
Avg (-Q)	129.7	G	${}^{b,c}137.6^{a,b,c}$
O	${}^{c}111.9^{c}$	E	${}^{b,c,d}136.6^{a,b,c}$
B	${}^{c}110.7^{c}$	I	${}^{b,c,d}135.8^{a,b,c}$
M	${}^{c}108.7^{c}$	K	${}^{b,c,d}135.4^{a,b,c}$
C	${}^{c}103.0^{c}$	H	${}^{b,c,d}131.7^{b,c}$
K	${}^{d}72.7^{c,d}$	Avg	${}^{b,c,d}129.7^{b,c}$
F	${}^{d}66.4^{d}$	M	${}^{b,c,d,e}129.4^{b,c}$
		J	${}^{b,c,d,e}128.3^{b,c}$
Q[2]	134.3	O	${}^{c,d,e}125.5^{b,c,d}$
		L	${}^{d,e,f}122.7^{c,d}$
		F	${}^{e,f}121.8^{c,d}$
		A	${}^{e,f}121.0^{c,d}$
		P	${}^{f}112.3^{d}$
		N	${}^{f}111.8^{d}$

[1] Pre-superscripts that are alike indicate that means are not significantly different at $P < 0.05$. Post-superscripts are for $P < 0.01$.

[2] There was only one plantation at this location. The only statistically significant diffemnces were that there was less growth than at locations E and L.

Table 3. — Height (cm) and Survival (%) of Trees of Each Source Grown at Ten Locations. Sources at Each Location are Arranged by Decreasing Height from Left to Right.

Location	Seed source, height, and survival																
	Source	G	C	O	B	H	K	J	M	L	A*	D	P	F	I	E	N
A	Height (cm)	240	204	199	195	194	187	186	184	181	181	174	167	157	150	143	140
	Survival (%)	98	99	98	98	95	96	98	97	98	97	97	98	95	97	90	99
	Source	C	K	J	I	G	H	L	E	M	B*	F	D	O	A	P	N
B	Height (cm)	126	122	121	120	119	118	111	111	110	109	106	104	103	102	98	96
	Survival (%)	99	98	99	99	97	95	97	97	97	95	97	100	97	93	97	97
	Source	I	J	K	C*	L	E	N	H	A	B	G	D	M	P	O	F
C	Height (cm)	119	118	116	115	109	108	106	103	101	100	100	97	96	92	86	86
	Survival (%)	89	93	95	93	84	89	81	85	85	95	82	95	86	89	88	91
	Source	G	C	E*	H	I	K	B	D	A	M	J	L	F	O	P	N
E	Height (cm)	301	300	295	274	273	269	268	260	255	254	248	248	246	237	236	231
	Survival (%)	96	96	94	98	95	94	88	98	85	93	96	93	92	86	91	92
	Source	F*	E	C	I	D	M	B	J	K	H	G	O	L	P	N	A
F	Height (cm)	94	90	81	75	72	70	66	66	66	62	61	58	58	56	53	48
	Survival (%)	84	72	76	92	89	82	60	84	84	58	60	74	74	84	70	39
	Source	C	I	D	B	H	K*	A	G	J	M	O	E	N	F	L	P
K	Height (cm)	86	85	84	77	76	75	75	74	74	73	72	70	65	63	61	55
	Survival (%)	88	81	87	85	85	88	77	77	90	87	83	67	80	74	81	77
	Source	D	E	C	B	M	G	O	I	H	K	F	P	L*	J	A	N
L	Height (cm)	332	326	308	301	294	281	279	276	261	260	257	250	238	235	226	206
	Survival (%)	80	55	70	75	67	71	68	82	56	76	68	68	60	64	33	66
	Source	C	D	B	E	I	H	K	G	O	F	A	L	N	M*	J	P
M	Height (cm)	151	144	127	126	118	115	108	106	105	103	102	96	95	94	92	76
	Survival (%)	60	56	54	58	69	48	76	34	57	55	61	58	62	36	62	40
	Source	D	B	K	C	G	M	O*	L	J	I	A	P	H	E	N	F
O	Height (cm)	138	130	125	117	117	117	116	113	110	109	109	105	104	102	99	88
	Survival (%)	80	77	68	64	67	75	77	61	74	77	48	64	62	55	70	49
	Source	E	F	M	L	O	G	J	I	D	B	C	K	A	P	N	H
Q	Height (cm)	206	183	148	143	143	139	137	132	127	126	126	124	116	115	106	102
	Survival (%)	69	80	62	74	78	79	71	67	89	76	71	60	54	77	71	50

* Local seed source

Table 4. — Analysis of Variance of Transformed 9-Year Height at Nine Locations.

Source of variation	Degrees of freedom	Mean square	F-value
Location	8	1,592.15	34.24***
Regression	5	2,263.52	48.69***
Elevation alone	1	10,603.34	228.07***
Other	4	178.56	3.84*
Residual	3	4,731.21	10.18**
Plantation/Location	9	46.49	3.22*
Block/Plantation	18	14.46	6.76***
Seed source	15	22.80	10.66***
Source x Location	120	4.13	1.93***
Regression	75	5.31	2.50***
Residual	45	2.17	1.02
Error	405	2.14	

*P < 0.05
**P < 0.01
***P < 0.001

Table 5. — Between and Within Seed Source Mean Squares from Analyses of Variance at Each Location and F-tests of Seed Source Variation.

Location	Between seed sources	Within seed sources	F-value[1]
A	8.54	2.14	4.00***
B	2.46	1.68	1.15
C	3.67	1.49	1.72*
E	3.48	2.46	1.63
F	9.69	1.40	4.55***
K	4.20	2.78	1.97*
L	8.84	1.82	4.15***
M	10.75	1.76	5.04***
O	4.21	3.58	1.97*
Q	6.44	2.42	3.02***

[1] F-tests are for 15 and 405 degrees of freedom using the pooled error mean square (2.14) from Table 4.

*P < 0.05
***P < 0.001

Table 6. — Seed Source by Location Interaction Effects. Back-transformed to Original Units of Measure (Cm).

Planting			Seed source															
Location	Elevation (ft)	Latitude	A	B	C	D	E	F	G	H	I	J.	K	L	M	N	O	P
A	350	50°30'	11	3	-2	-15	-33**	-10	38**	9	-28**	6	0	9	4	-14	20	9
B	1350	49°45'	-2	-10	-4	-19*	-7	2	1	5	4	14	7	7	-1	1	-5	2
C	2750	49°10'	7	-12	-7	-18	-2	-14	-12	-2	12	20*	10	15	-8	24*	-17	4
E	550	49°10'	5	-5	0	-12	11	-1	13	5	0	-7	-2	-1	-4	0	-10	3
F	4000	47°30'	-24**	-9	3	-3	31**	55**	-17	-9	8	0	-7	-9	5	-6	-10	-2
K	3500	45°10'	13	-1	-1	6	-11	-8	-6	3	12	3	-2	-12	0	7	3	-11
L	200	44°50'	-16	9	0	22*	23*	1	-2	-7	-2	-18	-11	-11	14	-19*	9	8
M	1850	44°30'	1	11	24*	27*	12	1	-11	4	3	-18	-7	-8	-17	3	0	-23*
O	2750	43°45'	5	11	-14	16	-18	-20*	-3	-12	-9	-1	8	9	5	4	9	10

* Transformed effect significantly different from zero (P < 0.05).
** Transformed effect significantly different from zero (P < 0.01):

for intermediate latitudes about 46—47° and additional preference for low-elevation sites. Source F also has a preference for intermediate latitudes of about 47—48° at all elevations and a particular preference for very low or very high elevations. Its optimum is very close to the native site (47° 30' and 4,000 feet). Source G indicates a

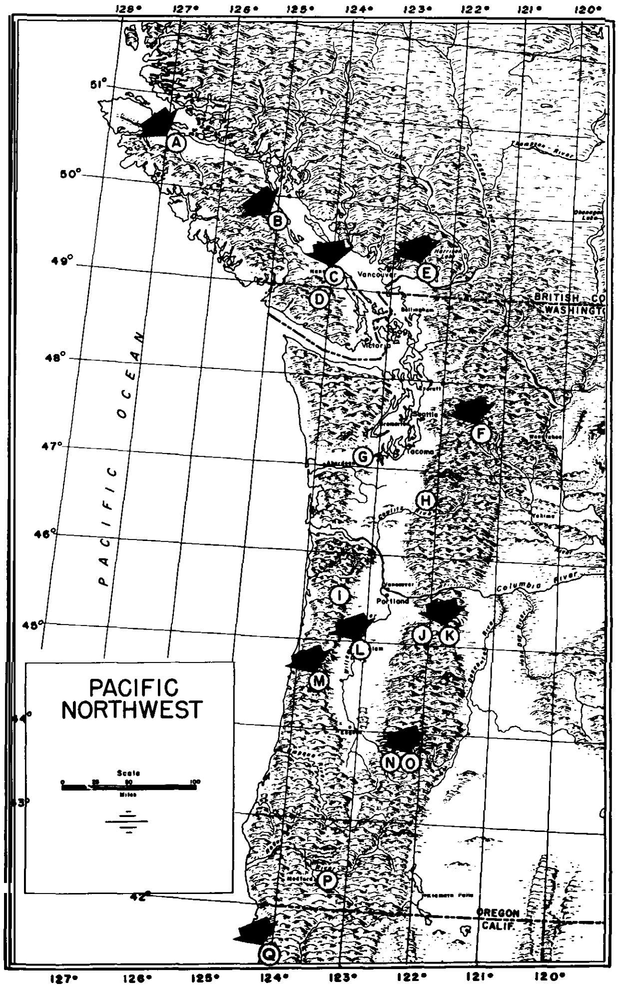

Figure 1. — Locations of plantations in provenance study of Douglas-fir. Arrows indicate those reported here. A, Nimpkish Forest; B, Courtenay area; C, Sugarloaf Mountain; E, Haney area; F, Snoqualmie National Forest; K, Molalla area; L, Salem area; M, McDonald Forest; O, High Prairie, Oakridge; Q, Korbell.

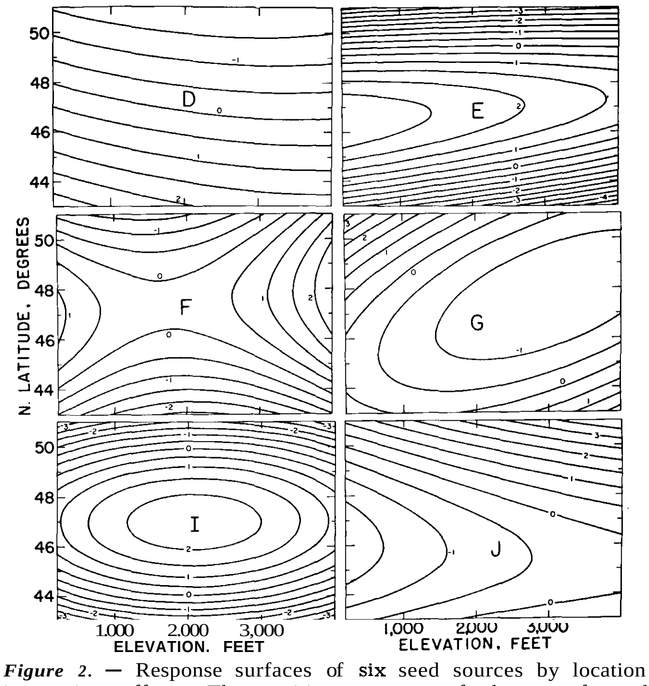

Figure 2. — Response surfaces of six seed sources by location interaction effects. The positive contours of the transformed interaction effects indicate the relative preference of the seed source.

preference for either low-elevation northerly sites or high-elevation southerly sites. Source I has an indicated optimum at 47° and 2,100 feet. Source J has a distinct preference for high northerly sites, particularly in contrast to low-elevation sites at latitudes near 46°. Other sources showed less interaction (Table *6)* and less indication of a preference for any particular site as typified by latitude and elevation.

Conclusion

The analyses shown in Tables 4 *and* 5 clearly indicate that there is wide genetic variation in Douglas-fir and affirm the possibility of selecting for improved growth rate at juvenile age. Most of the provenance lots are approaching the age of producing both male and female flowers at several locations, so one could now make crosses for further selection. NILSSON (1963), in his work on Picea abies, has already demonstrated the advisability of producing hybrids from widely separated provenance stocks.

Tables 2 and 3 show that trees from seed sources N and P were consistently poor in height growth. Trees from seed source C were generally superior in total growth, particularly if its poor performance at location Q is ignored. There is considerable consistency with results concerning growth at age three presented previously (CHING, 1965). Six common locations are included in this report, and for these locations the same four seed sources (B, C, D, and G) produced the tallest trees, and trees from seed sources L, A, N, and P are still four of the five shortest at age nine. Furthermore, most seed sources maintained their relative ranking at a given location. There are notable exceptions, of course. Sources D at location B, G at location K, and H at location O rank considerably lower at age nine than they did at age three. In all of these three examples, their growth at the particular location is now unusually low with respect to their growth at other locations. Source K at location O has improved its relative position and now ranks near what might be expected from its growth at all locations. There is ample evidence (IRGENS-MOLLER, 1967; MUNGER and MORRIS, 1936; SILEN, 1964) that a long-rotation species, such as Douglas-fir, no doubt will be subjected to a great variety of climatic changes as well as biological disturbances that will alter the growth pattern. Surprisingly little change has occurred in the relative ranking of the seed sources of this provenance study.

The fitting of second-order response surfaces of planting-site elevation and latitude appears to account almost completely for the interaction between seed sources and locations. Six sources showed statistically significant preferences for sites of particular latitude and/or elevation. A wide variety of contours and optimums are represented among the six sources. Other sources showed less interaction and less indication of a preference for a particular site as typified by elevation and latitude.

One must bear in mind that height growth at any age is only one of the many criteria in the total evaluation of any provenance study. The assessment of height at an early age is necessary for the consideration of juvenile-mature correlations.

Key words: Douglas-fir, provenance, genotype-environment interaction, response surface.

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Variation in Rooting of Pinus strobus L. and P. griffithii McClelland × P. strobus L. Trees*)

By L. ZSUFFA

Ontario Ministry of Natural Resources
Forest Research Branch
Maple, Ontario

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White pine vegetative propagation trials were initiated to preserve the genetic gain achieved in the selection of blister rust resistant trees. The trials aimed at detecting easily-rootable trees of P. strobus and P. *griffithii* X *strobus*. The latter is a vigorously growing, blister-rust resistant hybrid.

Published Data

According to NIENSTAEDT et al. (1958), genotypic variation in rooting is common. Species within a genus vary in this respect, as do individuals within a species. ZUFA (1972) observed variation in rooting between and within populations of P. strobus and P. griffithii X strobus. Clonal variation in rooting of P. strobus was reported by SNOW (1940), DORAN (1957), and PATTON and RIKER (1958). However, a fluctuation in rooting of the same clones in different years was also noticed. In fact, THOMAS and RIKER (1950) observed more variation in rooting of cuttings between years, than between clones.

ZUFA (1972) evaluated the various propagation techniques used in his trials and concluded that, (i) coarse sand was a good rooting media, (ii) December, January and March cutting collection and planting dates showed similar rooting, (iii) rooting decreased with age, but no significant difference was noted with propagules taken from trees up to 10 years of age, (iv) cuttings placed in rooting beds rooted as well as cuttings in polystyrene tubes, and (v) needle fascicles rooted as well as cuttings.

Materials and Methods

The rooting trials were established in the period of 1968 to 1971 with stem cuttings of P. strobus and P. griffithii X

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