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Inheritance of leaf oil terpene patterns in selfed Progeny and some crosses of coastal Douglas-fir

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Summary

The leaf oil terpene composition of Douglas-fir parent trees or their clones and some of their S_1 and S_2 progeny propagated by ORR-EWING (4), as well as outcrosses within these families, and some narrow and wide coastal variety crosses was determined. Considerable variation in terpene percentages was recorded in all crosses except the dwarf form of the S_2 generation. In the latter uniform terpene patterns were found in members of the same family, but different families had different terpene patterns. It could be confirmed that the coastal variety pattern type B is the quantitative intermediate between types A and C. There was only minor evidence for female dominance in terpene inheritance.

Key words: *Pseudotsuga menziesii*, Coastal Douglas-fir crosses, selfed progeny, leaf oil terpene composition.

Zusammenfassung

Bei Douglasien-Mutterbäumen bzw. deren Klonen und einigen Abkömmlingen aus der von ORR-EWING durchgeführten Kreuzung dieser Klone, d.h. aus deren S_1 und S_2 Nachkommenschaft, sowohl aus Fremdung als zugleich innerhalb der Familien sowie bei einigen enger oder weiter entfernt verwandten Küstenvarietäten wurde die Zusammensetzung der Terpene im Öl der Nadeln untersucht. Dabei konnte in allen Kreuzungen eine beträchtliche Variation festgestellt werden, außer in Zwergformen der S_2 Generation. Letztere enthielten innerhalb der Familien einheitliche Terpenmuster. Bei der Vererbung der Terpen-Zusammensetzung war nur in geringem Maße weibliche Dominanz festzustellen.

Introduction

ORR-EWING (1977) was remarkably successful in inbreeding coastal Douglas-fir, *Pseudotsuga menziesii* var. *menziesii* (MIRB.) FRANCO., to the S_3 generation. A particular feature in some of the selfed progeny is a segregation into normal ("tall") and dwarf forms. Clones of the parent trees and many of the S_1 and S_2 inbreds propagated by ORR-EWING are still growing at the Cowican Lake Forest Experiment Station, Vancouver Island, and they presented a unique opportunity to explore further the mode of inheritance of the leaf oil terpene patterns in Douglas-fir. Previously, we have reported on inheritance of such patterns in four full-

sib families of F_1 intervarietal crosses (two coastal variety and four interior or Rocky Mountain variety, var. *glauca*, parents) as well as in wind-pollinated progeny (VON RUDLOFF and REHFELDT, 1980). Some pertinent conclusions especially regarding the natural intergrading of these two varieties could be drawn. Whereas the leaf oils of both varieties contain 21 major and at least 8 minor monoterpenes (VON RUDLOFF and REHFELDT, 1980) (VON RUDLOFF, 1972, 1973, 1975), as well as 9–12 sesquiterpenes (3,8), such geographic variation can be described by the relative amounts of β -pinene, the terpinene — sabinene group (α - and γ -terpinene, terpinolene, terpinen-4-ol, α -thujene, and sabinene), the camphene group (santene, tricyclene, camphene, borneol, and bornyl acetate), and limonene (VON RUDLOFF and REHFELDT, 1980). The various quantitative terpene patterns can be designated as coastal type A (> 50% β -pinene), coastal type C (> 50% terpinene group), Rocky Mountain or interior type (> 50% camphene group) and the various intermediates thereof (VON RUDLOFF, 1973). Furthermore, the relative amounts of the camphene group are apparently controlled by a single dominant gene, whereas the other terpenes showed quantitative inheritance (i.e. their relative amounts are under the control of several genes (VON RUDLOFF and REHFELDT, 1980). Earlier we had shown that the leaf oil terpene composition of conifers is under strong genetic control during the quiescent and dormant season (VON RUDLOFF, 1972, 1975).

In addition to the leaf oils of the selfed families, we also analyzed those of some narrow and wide crosses between coastal variety parent trees (HEAMAN, 1970). In inheritance studies, grafts rather than the parent trees are sometimes only available for sampling. To ensure that ramets are strictly comparable to the ortets, we analyzed two sets of clones and their parents, and also possible variation within the crown of older and younger trees of the coastal variety, as this had been done previously only with interior Douglas-fir and one younger coastal variety tree (VON RUDLOFF, 1972).

Materials and Methods

Leaf samples (30–150 g. each) were collected during late fall and winter 1981 and 1982 from trees at the Cowican Lake Forest Experiment Station as listed in Table 1. Other

Table 1. — Trees growing at the Cowichan Lake Forest Experiment Station from which foliage samples were taken. The parent tree samples were from grafts.

Parent tree No. and origin; S ₀	Selfed Progeny:		
	S ₁	S ₂	S ₃
U.B.C. ¹⁾ No. 1	-	-	-
U.B.C. ¹⁾ No. 2	2.13 (Dwarf)	-	-
	2.21 (Tall)	2.21 (10 Tall & 10 Dwarf)	-
	-	2.26 (trees No. 3, 4 & 5)	2.26.5 (10 trees bulked)
Robertson Valley ²⁾			
No. 11	11.12 (Tall)	-	-
	11.17 (Dwarf)	11.17 (10 non-segregated)	-
	11.23 (Tall)	11.23 (10 Tall & 10 Dwarf)	-
	11.25 (Tall)	11.25 (10 Tall & 10 Dwarf)	-
	11.32 (Tall)	11.32 (bulked & tree No. 6)	11.32.6 (4 trees bulked)
	11.97 (Dwarf)	11.97 (10 Tall & 10 Dwarf)	-
<u>Outcrosses:</u>			
	S ₁	S ₂	
	2.21 X 11.40 (8 trees)	2.26.4 X 11.32.6 (10 bulked)	
	2.26 X 11.17 (10 trees)	2.26.5 X 11.32.6 (10 bulked)	
	2.26 X 2.21 (10 trees)		
	2.13 X 11.25 (10 trees)	S ₂ X S ₁	
	2.13 X 11.32 (7 trees)	2.26.5 X 11.32 (10 bulked)	
	11.12 X 11.32 (7 trees)		
<u>Intervarietal Crosses:</u>			
	F ₁		
No. 28, Ladysmith ²⁾	28 X 36 (3 trees)		
No. 36, Duncan ²⁾	36 X 28 (3 trees)		
No. 72, Koksilah Ridge ²⁾	72 X 598		
No. 83, Haney, B.C.	83 X 517; 83 X 598		
No. 102, Cowichan-Skutz ²⁾	102 X 28; 102 X 36 (3 trees each)		
No. 109, Cowichan-Skutz	109 X 28; 109 X 36 (3 trees each)		
No. 517, Bella Coola, B.C.	-		
No. 598, California	-		

1) University of British Columbia, Vancouver, B. C.

2) Vancouver Island

Table 2. — Within-crown variation of, and parent ortet-clonal ramet leaf oil terpene composition in coastal Douglas-fir.

Age of tree	Millstream Road trees			Tree No. 108	6 ramets
	10-12 yr.	90-95 yr.	90-95 yr	73-75	
<u>Terpene:</u>	%	%	%	%	%
α-Pinene	7.4 ± 0.3	14.4 ± 0.4	15.9 ± 0.8	14.7	15.7 ± 0.5
β-Pinene	23.7 ± 0.4	41.0 ± 0.9	44.2 ± 6.0	51.5	48.9 ± 1.5
Terpinene group ¹⁾	50.0 ± 1.5	25.1 ± 0.9	2.4 ± 0.3	6.3	6.8 ± 0.6
Limonene	2.3 ± 0.2	1.0 ± 0.1	2.1 ± 0.3	1.5	1.4 ± 0.2
Camphene group ²⁾	0.3 ± 0.1	0.9 ± 0.2	6.7 ± 1.5	1.1	1.6 ± 0.3
Citronellol group ³⁾	4.8 ± 0.3	10.0 ± 0.4	2.3 ± 0.4	4.2	4.6 ± 0.6
Other monoterpenes ⁴⁾	11.0 ± 0.5	6.7 ± 0.5	15.5 ± 2.0	9.1	10.2 ± 1.1
Sesquiterpenes ⁵⁾	0.5 ± 0.1	0.9 ± 0.3	9.7 ± 1.7	11.6	9.8 ± 2.3

1) α-Thujene, sabinene, α- and γ-terpinene, terpinolene and terpinen-4-ol

2) Santene, tricyclene, camphene, borneol and bornyl acetate.

3) Citronellol, citronellyl acetate, and geranyl acetate.

4) Mainly myrcene, car-3-ene, α- and β-phellandrene, ocimene, fenchone, linalool, sabinene hydrate, α-terpineol.

5) Mainly cadinene-murolene and their corresponding alcohols.

Table 3. — The leaf oil terpene composition of the coastal Douglas-fir parent No. 11 (Robertson valley) and some of its S_1 progeny.

	S_0 No. 11	S_1 11.12 tall	11.17 dwarf	11.23 tall	11.25 tall	11.32 tall	11.97 dwarf
Terpenes ¹⁾							
α -Pinene	9.9	13.7	6.5	13.4	5.7	10.6	4.3
β -Pinene	36.7	44.3	19.2	50.2	13.8	21.9	9.3
Terpinene group	25.1	9.0	56.4	9.9	61.9	39.5	67.1
Limonene	2.0	3.0	1.5	1.9	1.4	2.4	1.5
Camphene group	1.1	1.1	0.4	1.6	0.3	3.9	0.4
Citronellol group	5.2	7.4	3.2	6.2	1.0	5.7	4.1
Other monoterpenes	9.0	10.4	9.9	9.9	10.5	10.4	9.5
Sesquiterpenes	11.0	11.1	2.9	6.9	5.4	5.6	3.8
Terpene pattern type ²⁾	B	A/B	C/B	A	C	B/C	C

1) same terpene groups as listed in Table 1
2) cf. Ref. 5—7

collections were made from the parent trees No. 10—18 at Robertson Valley, No. 108 at Cowichan-Skutz, and wild trees along the upper Millstream Road, Greater Victoria. The latter trees were sampled at 4—6 different heights to determine within-crown variation; two 90—95 year-old trees were sample just after felling.

The leaves were separated from the twigs by dipping into liquid nitrogen, steam-distilled for 5 hr., and the recovered volatile oil was analyzed by gas-liquid chromatography as described earlier (2,5). The relative percentage of the individual terpenes were determined by digital integration and summation of the gas chromatographic peak areas with a Hewlett-Packard model 3340A data system. The experimental error was 0.1—0.3% for well-resolved peaks and 0.3—0.8% for overlapping ones.

Results and Discussion

The variation of the relative amounts of the leaf oil terpenes in the crown of a 10—12 year-old and two 90—95 year-old coastal Douglas-fir trees is shown in Table 2. The variation in four other young trees was within the same low limits as the first one. In such young trees, and some older ones, the within-crown variation is almost within the experimental error of the method and this is in good agreement with our earlier results (VON RUDLOFF, 1972). However, in one of the 90—95 year-old trees considerable variation from one level to the next was found (Table 2), the largest deviation from the means occurring in the lower branches of the crown. Thus, when comparing parents ortets with their ramets it is advisable to sample

Table 4. — The leaf oil terpene composition of the coastal Douglas-fir parent No. 2 (University of British Columbia), S_1 2.21 and some of its S_2 progeny.

	S_0 No. 2	S_1 2.21	S_2 2.21 Dwarf	2.21 Dwarf	2.21 Dwarf	2.21 Dwarf	2.21 Dwarf	S_2 2.21 10 tall
Terpene ¹⁾								
α -Pinene	9.8	9.0	16.2	15.3	13.9	14.0	15.1	8.9
β -Pinene	34.1	26.5	52.0	54.0	49.2	47.7	50.2	26.7
Terpinene group	27.1	44.2	4.4	4.2	5.5	1.5	4.5	29.9
Limonene	1.6	1.7	1.9	1.1	2.3	2.4	2.1	1.6
Camphene group	2.1	0.8	1.6	1.3	1.3	1.1	1.2	0.7
Citronellol group	9.3	4.1	8.1	6.8	5.4	10.5	6.8	7.0
Other monoterpenes	8.5	9.2	11.0	12.3	15.5	13.5	14.4	11.8
Sesquiterpenes	7.5	4.5	4.8	5.0	6.6	9.2	5.3	3.1
Terpene pattern type ²⁾	B	B/C	A	A	A	A	A	A/B to ³⁾ C

1) same terpene groups as listed in Table 1
2) of Ref. 5—7
3) see text.

Table 5. — The leaf oil terpene composition of the coastal Douglas-fir parent tree No. 11 (Robertson valley) and some of its S₂ progeny (means of 6–10 trees each).

	S ₀	S ₂		S ₂		S ₂	
	No. 11	11.23	11.23	11.25	11.25	11.97	11.97
		Dwarves	Talls	Dwarves	Talls	Dwarves	Talls
Terpenes¹⁾							
α-Pinene	9.9	8.5	12.7	6.2	8.1	2.8	7.9
β-Pinene	36.7	28.0	45.0	15.7	25.1	3.1	24.0
Terpinene group	25.1	32.4	16.7	56.1	49.9	77.3	47.8
Limonene	2.0	2.1	1.7	2.1	1.6	1.1	1.9
Camphene group	1.1	0.8	0.8	0.6	0.6	0.2	0.6
Citronellol group	5.2	7.4	8.9	9.4	4.7	2.4	5.8
Other monoterpenes	9.0	13.6	11.5	12.2	9.0	11.1	10.6
Sesquiterpenes	11.0	7.2	2.7	1.7	1.0	2.0	1.4
Terpene pattern type²⁾							
	B	B	A/B	C/B	C/B	C	C/B

1) same terpene groups as listed in Table 1
2) cf. Ref. 5–7

only the branches from that part of older parents trees from which scions were taken. When this precaution was taken, clonal ramets had virtually the same leaf oil terpene composition as the ortet (e.g. tree No. 108, Table 2).

Parent tree No. 11 of the selfing experiments by ORR- EWING was found to have the intermediate coastal terpene pattern type B (Table 3, 1st, column), but the percentages of the sesquiterpenes were unusually high. This was also found in tree 12 of the S₁ family, but not in other members of this family (Table 3). The terpene patterns of these S₁ offsprings varied from type A (S₁ 11.23) to type C (S₁ 11.25 and S₁ 11.97), which indicates that the coastal type B pattern is simply the intermediate of types A and C. In S₁ 11.32 the camphene group percentage was 3.9%, which comes close to the lower limit we set for coastal-interior intermediates (VON RUDLOFF, 1972, 1973, 1975) (VON RUDLOFF and REHFELDT, 1980).

Both tall and dwarf forms of the S₂ generation of trees S₁ 2.21, S₁ 11.25, S₁ 11.32 and S₁ 11.97 were available for sampling. In each set of the selfed progeny the terpene patterns of the tall forms were fairly variable, but those of the dwarf forms were uniform, indicating a trend towards homozygosity. Whereas all the dwarves of the S₂ 2.21 family had the type A leaf oil terpene pattern (Table 4), the dwarves derived from parent 11 had either type B/C, type C/B, or type C patterns (Table 5). Thus the terpene pattern *per se* is not linked with the dwarf form, but rather the uniformity of the terpene percentages. It may be significant that when the parent tree has the intermediate coastal type B pattern, its selfed progeny can segregate into the more extreme types A and C, but when the parents have either the type A or C patterns the selfed progeny segregates less extensively. This confirms that the

Table 6. — The leaf oil terpene compositions of the outcrosses of S₁ and S₂ selfed progeny (10 crosses each, bulked).

	S ₁ 2.26	S ₁ 2.26	S ₁ 2.13	S ₁ 2.13	S ₁ 11.12	S ₁ 2.21	S ₂ 2.26.5	S ₂ 2.26.4	S ₂ 2.26.5
	x	x	x	x	x	x	x	x	x
	S ₁ 11.17	S ₁ 2.21	S ₁ 11.32	S ₁ 11.25	S ₁ 11.32	S ₁ 11.40	S ₂ 11.32.6	S ₂ 11.32.6	S ₁ 11.32
Terpenes¹⁾									
α-Pinene	10.7	11.8	7.9	6.1	7.8	6.6	12.3	11.1	11.5
β-Pinene	38.8	38.8	21.5	13.6	20.4	16.1	42.8	37.6	36.8
Terpinene group	30.8	30.5	47.5	63.6	47.6	61.4	18.7	21.7	27.2
Limonene	1.9	2.0	1.1	1.2	1.4	1.5	1.8	2.1	1.8
Camphene group	0.7	0.8	0.6	0.5	0.9	0.5	0.9	1.0	0.8
Citronellol group	5.2	4.7	9.2	4.8	7.3	3.3	10.3	12.0	8.9
Other monoterpenes	9.4	8.8	10.2	7.9	11.8	8.6	9.6	11.3	10.7
Sesquiterpenes	2.5	2.6	2.0	2.3	2.8	2.0	3.6	3.2	2.3
Terpene pattern type²⁾									
	B/A	B/A	C/B	C/B	C/B	C/B	A/B	B/A	B/A

1) same terpene as listed in Table 1
2) cf. Ref. 5–7

Table 7. — The leaf oil terpene composition of some wide coastal Douglas-fir crosses and their parents.

	Clone 72 Vanc. Is.	Clone 598 Calif.	72 x 598	Clone 83 Haney	83 x 598	Clone 517 Bella Coola	83 x 517
Terpenes ¹⁾							
α -Pinene	12.6	12.4	10.9	19.6	14.4	15.2	12.9
β -Pinene	39.8	43.8	38.4	55.2	49.9	46.4	49.5
Terpinene group	15.5	9.1	3.0	2.4	6.2	11.6	2.9
Limonene	2.8	1.5	2.7	2.0	1.7	3.4	2.5
Camphene group	1.2	1.7	2.9	5.8	1.1	6.0	2.8
Citronellol group	9.7	5.3	22.5	1.3	7.0	2.2	6.7
Minor monoterp.	9.7	13.4	14.1	9.6	14.1	9.6	11.1
Sesquiterpenes	8.1	11.6	4.0	4.0	5.5	4.1	10.7
Terpene pattern type ²⁾							
	A/B	A/B	A/B	A- coastal intermediate	A	A/B- coastal intermediate	A

1) Same terpene groups as listed in Table 1

2) cf. Ref. 5—7

type B patterns is indeed simply the quantitative intermediate of types A and C, and that in pure coastal populations variations from A through B to C and *vice versa* can be expected. The reasons for a preponderance of type A in coastal populations from northern British Columbia and of type C in the Pemberton — D'Arcy area of British Columbia and in southern Oregon are obscure, no direct relationship between terpene patterns and local ecology *per se* being evident from the data obtained previously. In selfed progeny that did not segregate into the "tall" and "dwarf"

forms, fairly variable leaf oil terpene patterns were found in all trees (e.g. S₂ 2.17 from type A to type B).

The leaf oil composition of some of the outcrosses of the selfed progeny is shown in Table 6. Whereas some dominance of the female parent is evident in the outcrosses with S₂ 2.26 trees 3, 4 and 5 (all type A/B), this was not found in the others (e.g. S₁ 11 progeny). The results from the analysis of the wide coastal crosses (Table 7) also show little female dominance. Most of the terpene percentages were intermediate between those of the parents (as expected).

Table 8. — The leaf oil terpene compositions of some narrow coastal Douglas-fir crosses and their parents.

	Parent No. 28 Ladysmith	Parent No. 36 Duncan	28 x 36	36 x 28	Parent No. 102 Cowichan- Skutz	102 x 28	102 x 36	Parent No. 109 Cowichan- Skutz	109 x 28	109 x 36
Terpenes ¹⁾										
α -Pinene	15.8	13.9	14.4	13.6	15.6	15.6	14.4	18.3	15.8	15.9
β -Pinene	53.8	42.8	47.0	43.3	41.8	50.5	44.0	48.5	49.9	50.1
Terpinene group	5.6	26.3	13.3	16.3	18.7	10.0	21.4	4.7	6.9	9.9
Limonene	2.3	1.5	1.6	1.7	2.1	1.6	1.7	2.8	2.2	1.9
Camphene group	1.6	1.1	1.0	0.9	5.0	0.9	0.7	8.1	0.8	0.9
Citronellol group	3.5	2.4	11.9	12.2	1.6	9.6	9.0	3.5	12.3	11.8
α -Terpineol	5.0	3.9	2.8	3.5	4.7	2.9	2.3	3.3	3.1	2.2
Other monoterpenes	7.3	5.0	7.3	7.8	7.3	8.1	5.8	7.1	8.3	6.7
Sesquiterpenes	5.1	3.1	0.7	0.7	3.2	0.8	0.7	3.7	0.7	0.6
Terpene pattern type ²⁾										
	A	A/B	A/B	A/B	A/B- coastal intermediate	A	A/B	A- coastal intermediate	A	A

1) Same terpene groups as listed in Table 1

2) cf. Ref. 5—7

ted in quantitative inheritance), but several transgressions are evident. Most noteworthy are higher percentages of the citronellol group and car-3-ene, and lower ones of α -terpineol and the sesquiterpenes. These terpenes did not appear to have any significance in describing geographic variation of natural populations (VON RUDLOFF, 1972, 1973, 1973, 1975) (VON RUDLOFF and REHFELDT, 1980). Similar conclusions could be drawn from the leaf oil compositions of the narrow crosses (parent trees 28, 36, 102, and 109). When one of the parents has a small amount of interior intermediacy (e.g. trees 83, 102, 109, and 517 with 5–6% camphene group), this feature is lost in the crosses. We have reported earlier on the abrupt reduction of the camphene group percentages (dominant in the Rocky Mountain variety) in the zones of overlap of the two varieties when sampling the more westerly stands (VON RUDLOFF and REHFELDT, 1980).

Conclusion

In coastal Douglas-fir there is a high degree of variability in the leaf oil terpene patterns, which indicates a high degree of heterozygosity. Only in the dwarf form of the S_2 generation is a trend towards homozygosity evident. Female dominance does not appear to be a major factor in leaf oil terpene inheritance. Hence, in chemosystematic studies utilizing leaf oil terpene compositions, variable patterns from type A through B to C (VON RUDLOFF, 1973) can be expected in coastal populations. The small degree

of intermediacy with the interior variety found in some coastal locations may be lost in the next generation.

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Number of Offspring and Plot Sizes Required for Progeny Testing

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Summary

The accuracy of progeny testing is examined in relation to numbers of offspring tested and plot size used in the field design. Two mathematical solutions are presented, together with results of subsampling studies employing data for *Pinus radiata* in New Zealand and Australia. The mathematical solutions determine either the size of the differences between families in a progeny test which should be detected as statistically significant, or the probability that the family having the best true mean will also have the best observed mean in a progeny test. The general recommendation from both the mathematical and subsampling studies is that 10 to 20 individuals per family, growing in single-tree plots or two-tree non-contiguous plots, are sufficient to reliably evaluate each family.

Key words: Progeny testing, family means, plot size, field design.

Zusammenfassung

Die Genauigkeit einer Nachkommenschaftsprüfung wird in bezug auf die Anzahl der getesteten Nachkommen und die Anzahl der Bäume je Parzelle, die im Freilandversuch notwendig sind, untersucht. Hierzu werden zwei algebraische Lösungen vorgeschlagen, zusammen mit den Ergebnissen aus den Stichprobenentnahmestudien unter Ver-

wendung der Daten für *Pinus radiata* in Neuseeland und Australien. Es wird allgemein empfohlen, daß 10–20 Nachkommen pro Familie, die in Einzelbaumparzellen oder in Parzellen mit je zwei Bäumen, aufwachsen, für eine zuverlässige Auswertung jeder Familie genügen.

Résumé

La précision du test de la descendance est examinée par rapport aux nombres de descendants testés et au nombre d'arbres sur une parcelle usée pour les essais sur le terrain. L'auteur propose deux solutions algébriques et énonce à la fois les résultats des études du sous-échantillonnage, en employant les données pour les pins (*Pinus radiata*) en Nouvelle-Zélande et en Australie. Il préconise généralement que 10 à 20 descendants par famille, qui croissent sur les parcelles supportant une ou deux arbres, suffisent pour évaluer d'une manière digne de confiance chaque famille.

Introduction

A major problem in progeny testing is "How many individuals are required to adequately evaluate each family?" One solution is given by ROBERTSON (1957) with particular reference to animal breeding. This author provides estimates of genetic gain from progeny testing where a limit exists on the total number of offspring that can be tested, and the breeder has the opportunity to compromise between number of families tested (which determines the intensity of subsequent selection among families) and number

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